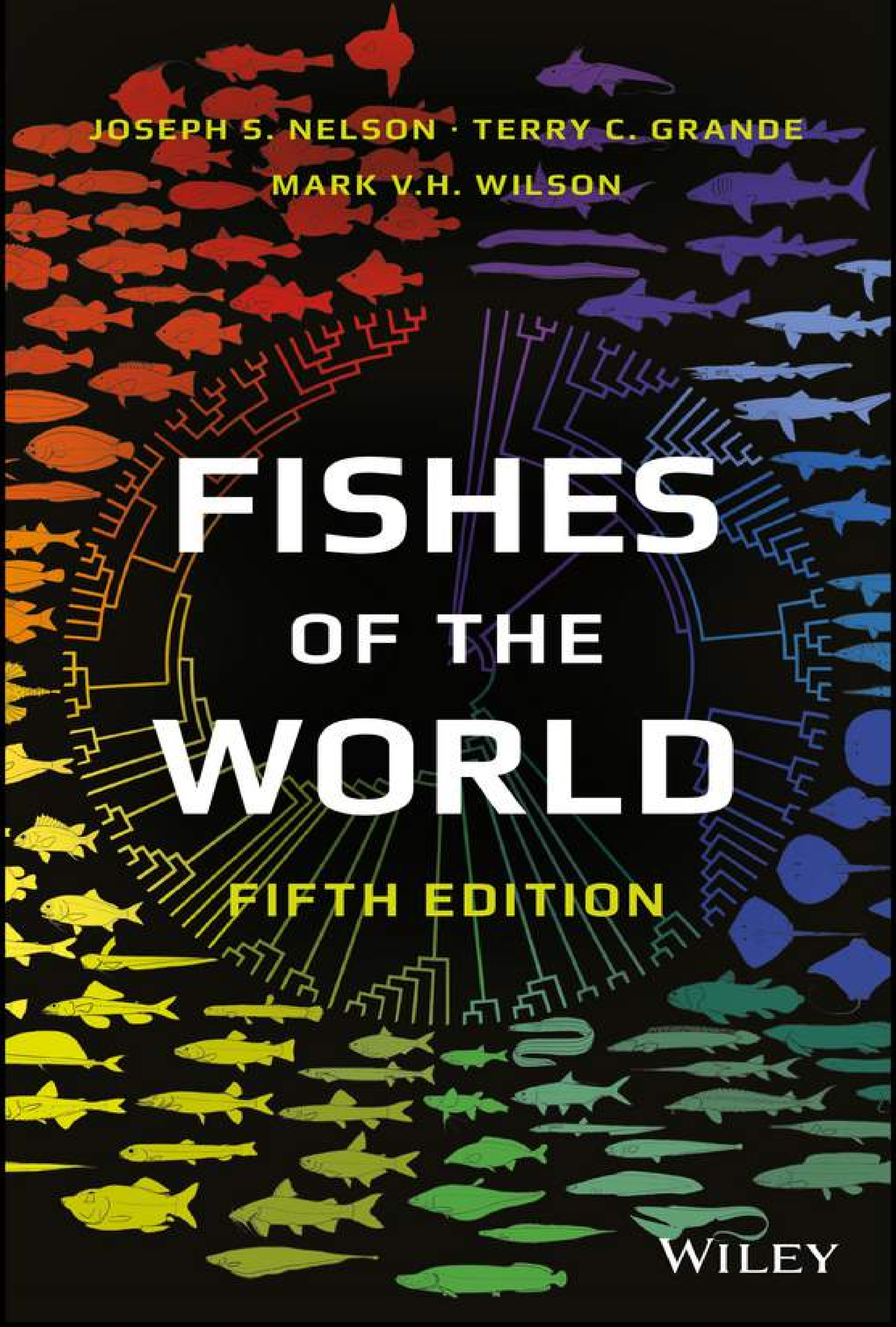

JOSEPH S. NELSON · TERRY C. GRANDE

MARK V.H. WILSON

FISHES OF THE WORLD

FIFTH EDITION

WILEY

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Fifth Edition

Joseph S. Nelson
Terry C. Grande
Mark V. H. Wilson

WILEY

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Contents

MEMORIES OF JOE NELSON **xxix**
FOREWORD **xxxiii**
PREFACE **xxxvii**
ACKNOWLEDGMENTS **xxxix**

INTRODUCTION **1**
  Taxonomic Diversity **3**
  Importance to People **4**
  Systematics and Classification **4**
  Anatomical Terminology **7**
  Distribution and Biogeography **8**
  Human Impacts **11**

PHYLUM CHORDATA **13**
  SUBPHYLUM UROCHORDATA (Tunicata: the tunicates) **15**
    Class ASCIDIACEA (ascidians), 15
    Class THALIACEA (salps), 15
      Order PYROSOMIDA, 15
      Order DOLIOLIDA, 15
      Order SALPIDA, 15
    Class APPENDICULARIA, 15
  SUBPHYLUM CEPHALOCHORDATA (Acrania, in part) **16**
      Order AMPHIOXIFORMES (lancelets), 16
        Family BRANCHIOSTOMATIDAE, 16
        Family EPIGONICHTHYIDAE, 16

†SUBPHYLUM CONODONTOPHORIDA (conodonts) 17
  †Class CONODONTA, 17
SUBPHYLUM CRANIATA 18
INFRAPHYLUM MYXINOMORPHI 19
  Class MYXINI, 20
    Order MYXINIFORMES (1)—hagfishes, 20
      Family MYXINIDAE (1)—hagfishes, 20
INFRAPHYLUM VERTEBRATA (vertebrates) 22
SUPERCLASS PETROMYZONTOMORPHI 23
  Class PETROMYZONTIDA, 23
    Order PETROMYZONTIFORMES (2)—lampreys, 23
      †Family MAYOMYZONTIDAE, 24
      Family PETROMYZONTIDAE (2)—northern lampreys, 24
      Family GEOTRIIDAE (3)—southern lampreys, 25
      Family MORDACIIDAE (4)—southern topeyed lampreys, 26
†SUPERCLASS PTERASPIDOMORPHI 26
  †Class PTERASPIDOMORPHA, 26
  †Subclass ASTRASPIDA, 27
    †Order ASTRASPIDIFORMES, 27
  †Subclass ARANDASPIDA, 27
    †Order ARANDASPIDIFORMES, 27
  †Subclass HETEROSTRACI, 28
    †CARDIPELTIDA, 28
    †CORVASPIDIDA, 28
    †LEPIDASPIDIDA, 28
    †TESSERASPIDIDA, 28
    †TRAQUAIRASPIDIFORMES, 28
    †TOLYPELEPIDIDA, 28
    †Order CYATHASPIDIFORMES, 28
      †Family AMPHIASPIDIDAE, 28
      †Family CYATHASPIDIDAE, 29
    †Order PTERASPIDIFORMES, 29
      †Family ANCHIPTERASPIDIDAE, 29
      †Family PROTASPIDIDAE, 29
      †Family PROTOPTERASPIDIDAE, 29
      †Family PSAMMOSTEIDAE, 29
      †Family PTERASPIDIDAE, 29
†SUPERCLASS ANASPIDOMORPHI 29
  †Class ANASPIDA, 29
    †Order ANASPIDIFORMES, 29
†SUPERCLASS THELODONTOMORPHI 30
  †Class THELODONTI, 30
    †Order ARCHIPELEPIDIFORMES, 31
    †Order FURCACAUDIFORMES (fork-tailed thelodonts), 31
    †Order THELODONTIFORMES, 31

†SUPERCLASS OSTEOSTRACOMORPHI 32
- †Class CEPHALASPIDOMORPHI, 33
  - †Order CEPHALASPIDIFORMES, 33
  - †Order GALEASPIDIFORMES, 34
  - †Order PITURIASPIDIFORMES, 34

SUPERCLASS GNATHOSTOMATA (jawed vertebrates) 34

†Grade PLACODERMIOMORPHI 36
- †Class PLACODERMI, 36
  - †Order PSEUDOPETALICHTHYIFORMES, 37
  - †Order ACANTHOTHORACIFORMES, 37
  - †Order RHENANIFORMES, 37
  - †Order ANTIARCHIFORMES (antiarchs), 37
    - †Family CHUCHINOLEPIDIDAE, 38
    - †Family YUNNANOLEPIDIDAE, 38
    - †Family SINOLEPIDAE, 38
    - †Family MICROBRACHIIDAE, 38
    - †Family BOTHRIOLEPIDIDAE, 38
    - †Family ASTEROLEPIDIDAE, 38
    - †Family GERDALEPIDIDAE, 39
  - †Order PETALICHTHYIFORMES, 39
  - †Order PTYCTODONTIFORMES, 39
  - †Order ARTHRODIRIFORMES (arthrodires), 39
- EUGNATHOSTOMATA, 40

GRADE CHONDRICHTHYOMORPHI 40
- Class CHONDRICHTHYES—cartilaginous fishes, 40
    - †Family PROTODONTIDAE, 43
    - †Family KATHEMACANTHIDAE, 43
  - †Order POLYMEROLEPIDIFORMES, 44
  - †Order OMALODONTIFORMES, 44
  - †Order ANTARCTILAMNIFORMES, 44
    - †Family BANDRINGIDAE, 45
  - †Order PHOEBODONTIFORMES, 45
    - †Family PHOEBODONTIDAE, 45
    - †Family JALODONTIDAE, 45
- †Superorder CLADOSELACHIMORPHA, 46
  - †Order CLADOSELACHIFORMES, 46
    - †Family CLADOSELACHIDAE, 46
  - †Order SYMMORIIFORMES, 46
    - †Family SYMMORIIDAE, 46
    - †Family FALCATIDAE, 46
- †Superorder CTENACANTHIMORPHA, 46
  - †Order CTENACANTHIFORMES, 46
    - †Family CTENACANTHIDAE, 47
  - †Order SQUATINACTIFORMES, 47
    - †Family SQUATINACTIDAE, 47
- †Superorder XENACANTHIMORPHA, 47
  - †Order BRANSONELLIFORMES, 47

- †Order XENACANTHIFORMES, 47
  - †Family DIPLODOSELACHIDAE, 47
  - †Family XENACANTHIDAE, 47

Subclass HOLOCEPHALI, 48
- †Order INIOPTERYGIFORMES, 49
- †Order ORODONTIFORMES, 49
- †Order EUGENEODONTIFORMES, 50
- †Order PETALODONTIFORMES, 50
- †Order DEBEERIIFORMES, 50
- †Order HELODONTIFORMES, 50

Superorder HOLOCEPHALIMORPHA, 50
- †Order PSAMMODONTIFORMES, 50
- †Order COPODONTIFORMES, 50
- †Order SQUALORAJIFORMES, 51
- †Order CHONDRENCHELYIFORMES, 51
- †Order MENASPIFORMES, 51
- †Order COCHLIODONTIFORMES, 51
- Order CHIMAERIFORMES (3)—chimaeras, 51
  - Family CALLORHINCHIDAE (5)—plownose chimaeras, 52
  - Family RHINOCHIMAERIDAE (6)—longnose chimaeras, 52
  - Family CHIMAERIDAE (7)—shortnose chimaeras or ratfishes, 53

Subclass EUSELACHII (sharks, rays, and related fossils), 53
- †Order PROTACRODONTIFORMES, 55

†Infraclass HYBODONTA, 55
- †Order HYBODONTIFORMES, 55
  - †Family HYBODONTIDAE, 56
  - †Family TRISTYCHIIDAE, 56
  - †Family DISTOBATIDAE, 56
  - †Family ACRODONTIDAE, 56
  - †Family POLYACRODONTIDAE, 56
  - †Family LONCHIDIIDAE, 56
  - †Family STEINBACHODONTIDAE, 56
  - †Family PSEUDODALATIIDAE, 56
  - †Family PTYCHODONTIDAE, 56
  - †Family HOMALODONTIDAE, 56

Infraclass ELASMOBRANCHII, 56

Division SELACHII—sharks, 58

Superorder GALEOMORPHI, 58
- †Order SYNECHODONTIFORMES, 59
  - †Family PALAEOSPINACIDAE, 59
- Order HETERODONTIFORMES (4)—bullhead sharks, 59
  - Family HETERODONTIDAE (8)—bullhead sharks, 59
- Order ORECTOLOBIFORMES (5)—carpet sharks, 59
  - Family PARASCYLLIIDAE (9)—collared carpet sharks, 60
  - Family BRACHAELURIDAE (10)—blind sharks, 60
  - Family ORECTOLOBIDAE (11)—wobbegongs, 61

        Family HEMISCYLLIIDAE (12)—bamboo sharks, 61
        Family GINGLYMOSTOMATIDAE (13)—nurse sharks, 62
        Family STEGOSTOMATIDAE (14)—zebra sharks, 62
        Family RHINCODONTIDAE (15)—whale sharks, 63
    Order LAMNIFORMES (6)—mackerel sharks, 63
        †Family OTODONTIDAE, 64
        †Family XIPHODOLAMIIDAE, 64
        †Family CARDABIODONTIDAE, 64
        †Family CRETOXYRHINIDAE, 64
        †Family ARCHAEOLAMNIDAE, 64
        †Family PSEUDOSCAPANORHYNCHIDAE, 64
        †Family ANACORACIDAE, 64
        †Family PSEUDOCORACIDAE, 64
        Family MITSUKURINIDAE (16)—goblin sharks, 64
        Family ODONTASPIDIDAE (17)—sand tiger sharks, 65
        Family PSEUDOCARCHARIIDAE (18)—crocodile sharks, 65
        Family ALOPIIDAE (19)—thresher sharks, 66
        Family MEGACHASMIDAE (20)—megamouth sharks, 66
        Family CETORHINIDAE (21)—basking sharks, 67
        Family LAMNIDAE (22)—mackerel sharks, 67
    Order CARCHARHINIFORMES (7)—ground sharks, 68
        Family SCYLIORHINIDAE (23)—cat sharks, 69
        Family PROSCYLLIIDAE (24)—finback cat sharks, 70
        Family PSEUDOTRIAKIDAE (25)—false cat sharks, 70
        Family LEPTOCHARIIDAE (26)—barbeled hound sharks, 70
        Family TRIAKIDAE (27)—hound sharks, 70
        Family HEMIGALEIDAE (28)—weasel sharks, 71
        Family CARCHARHINIDAE (29)—requiem sharks, 71
        Family SPHYRNIDAE (30)—hammerhead sharks, 72
Superorder SQUALOMORPHI, 73
    Series HEXANCHIDA, 73
    Order HEXANCHIFORMES (8)—six-gill sharks, 73
        Family CHLAMYDOSELACHIDAE (31)—frilled sharks, 74
        Family HEXANCHIDAE (32)—cow sharks, 74
    Series SQUALIDA, 75
    Order SQUALIFORMES (9)—dogfish sharks, 75
        Family CENTROPHORIDAE (33)—gulper sharks, 75
        Family ETMOPTERIDAE (34)—lantern sharks, 75
        Family SOMNIOSIDAE (35)—sleeper sharks, 76
        Family OXYNOTIDAE (36)—rough sharks, 76
        Family DALATIIDAE (37)—kitefin sharks, 77
        Family SQUALIDAE (38)—dogfish sharks, 77
    Series SQUATINIDA, 78
    †Order PROTOSPINACIFORMES, 78
    Order ECHINORHINIFORMES (10)—bramble sharks, 78
        Family ECHINORHINIDAE (39)—bramble sharks, 78

Order SQUATINIFORMES (11)—angel sharks, 79
  Family SQUATINIDAE (40)—angel sharks, 79
Order PRISTIOPHORIFORMES (12)—saw sharks, 80
  Family PRISTIOPHORIDAE (41)—saw sharks, 80
Division BATOMORPHI—rays, 80
Order TORPEDINIFORMES (13)—electric rays, 82
  †Family ARCHAEOBATIDAE, 82
  Family TORPEDINIDAE (42)—torpedo electric rays, 82
  Family NARCINIDAE (43)—numbfishes, 83
Order RAJIFORMES (14)—skates, 84
  †Family Cyclobatidae, 84
  Family RAJIDAE (44)—skates, 84
Order PRISTIFORMES (15)—guitarfishes and sawfishes, 85
  †Family Sclerorhynchidae, 85
  †Family Ptychotrygonidae, 85
  Family "RHINOBATIDAE" (45)—guitarfishes, 85
  Family RHINIDAE (46)—bowmouth guitarfishes, 86
  Family RHYNCHOBATIDAE (47)—wedgefishes, 87
  Family PRISTIDAE (48)—sawfishes, 87
Order MYLIOBATIFORMES (16)—stingrays, 87
  Family PLATYRHINIDAE (49)—thornbacks, 87
  Family ZANOBATIDAE (50)—panrays, 88
  Family PLESIOBATIDAE (51)—deepwater stingrays, 88
  Family UROLOPHIDAE (52)—round stingrays, 89
  Family HEXATRYGONIDAE (53)—sixgill stingrays, 89
  Family DASYATIDAE (Trygonidae) (54)—whiptail stingrays, 90
  Family POTAMOTRYGONIDAE (55)—river stingrays, 91
  Family GYMNURIDAE (56)—butterfly rays, 92
  Family UROTRYGONIDAE (57)—American round stingrays, 92
  Family MYLIOBATIDAE (58)—eagle rays, 93
Grade TELEOSTOMI **95**
†Class ACANTHODII—acanthodians, 96
†Order CLIMATIIFORMES, 98
  †Family BROCHOADMONIDAE, 99
  †Family CLIMATIIDAE, 99
  †Family GYRACANTHIDAE, 99
  †Family EUTHACANTHIDAE, 99
†Order DIPLACANTHIFORMES, 99
  †Family CULMACANTHIDAE, 100
  †Family DIPLACANTHIDAE, 100
  †Family GLADIOBRANCHIDAE, 100
†Order ISCHNACANTHIFORMES, 100
  †Family ISCHNACANTHIDAE, 100
  †Family PORACANTHODIDAE, 100
†Order ACANTHODIFORMES, 100
  †Family MESACANTHIDAE, 100

    †Family CHEIRACANTHIDAE, 100
    †Family ACANTHODIDAE, 101
- Class OSTEICHTHYES—bony fishes and tetrapods, 101
  - †Order DIALIPINIFORMES, 101
- Subclass SARCOPTERYGII—lobe-finned fishes and tetrapods, 102
- Infraclass ACTINISTIA—coelacanths, 103
  - Order COELACANTHIFORMES (17)—coelacanths, 104
    - †Family MIGUASHAIIDAE, 104
    - †Family DIPLOCERCIDAE, 104
    - †Family HADRONECTORIDAE, 104
    - †Family RHABDODERMATIDAE, 104
    - †Family LAUGIIDAE, 104
    - †Family WHITEIIDAE, 104
    - †Family REBELLATRICIDAE, 104
    - †Family COELACANTHIDAE, 105
    - †Family MAWSONIIDAE, 105
    - Family LATIMERIIDAE (59)—gombessas or coelacanths, 105
- Infraclass ONYCHODONTIDA, 106
  - †Order ONYCHODONTIFORMES, 106
    - †Family ONYCHODONTIDAE, 106
- Infraclass DIPNOMORPHA, 106
- †Superorder POROLEPIMORPHA, 106
  - †Order POROLEPIFORMES, 106
    - †Family POROLEPIDAE, 107
    - †Family HOLOPTYCHIIDAE, 107
- Superorder DIPNOI, 107
  - †Order DIABOLEPIDIFORMES, 107
    - †Family DIABOLEPIDIDAE, 107
  - †Order DIPNORHYNCHIFORMES, 107
    - †Family URANOLOPHIDAE, 107
    - †Family DIPNORHYNCHIDAE, 107
    - †Family CHIRODIPTERIDAE, 107
  - †Order Dipteriformes, 107
    - †Family STOMIAHYKIDAE, 108
    - †Family DIPTERIDAE, 108
    - †Family CHIRODIPTERIDAE, 108
    - †Family RHYNCHODIPTERIDAE, 108
    - †Family PHANEROPLEURIDAE, 108
    - †Family FLEURANTIIDAE, 108
  - †Order CTENODONTIFORMES, 108
    - †Family URONEMIDAE, 108
    - †Family CTENODONTIDAE, 108
  - Order CERATODONTIFORMES (18)—living lungfishes and their fossil relatives, 108
    - †Family ARGANODONTIDAE, 109
    - †Family CERATODONTIDAE, 109

        †Family ASIATOCERATODONTIDAE, 109
        Family NEOCERATODONTIDAE (60)—Australian lungfishes, 109
        Family LEPIDOSIRENIDAE (61)—South American lungfishes, 109
        Family PROTOPTERIDAE (62)—African lungfishes, 109
†Infraclass RHIZODONTIDA, 110
    †Order RHIZODONTIFORMES, 110
        †Family RHIZODONTIDAE, 110
†Infraclass OSTEOLEPIDIDA, 110
    †Order OSTEOLEPIDIFORMES, 110
        †Family CANOWINDRIDAE, 110
        †Family MEGALICHTHYIDAE, 110
        †Family OSTEOLEPIDIDAE, 110
        †Family TRISTICHOPTERIDAE, 110
        †Family RHIZODOPSIDAE, 110
†Infraclass ELPISTOSTEGALIA, 110
    †Order ELPISTOSTEGALIFORMES, 110
        †Family ELPISTOSTEGALIDAE, 110
Infraclass TETRAPODA—tetrapods, 111
Subclass ACTINOPTERYGII—ray-finned fishes, 111
        †Family HAPLOLEPIDAE, 113
    †Order CHEIROLEPIDIFORMES, 113
    †Order PALAEONISCIFORMES, 113
    †Order DORYPTERIFORMES, 114
        †Family DORYPTERIDAE, 114
    †Order PLATYSOMIFORMES, 114
        †Family PLATYSOMIDAE, 114
        †Family BOBASATRANIIDAE, 114
    †Order TARRASIIFORMES, 115
        †Family TARRASIIDAE, 115
    †Order GUILDAYICHTHYIFORMES, 115
        †Family GUILDAYICHTHYIDAE, 115
    †Order PHANERORHYNCHIFORMES, 115
        †Family PHANERORHYNCHIDAE, 115
    †Order SAURICHTHYIFORMES, 115
        †Family SAURICHTHYIDAE, 115
    †Order REDFIELDIIFORMES, 115
        †Family REDFIELDIIDAE, 115
    †Order PTYCHOLEPIDIFORMES, 115
        †Family PTYCHOLEPIDIDAE, 115
    †Order PHOLIDOPLEURIFORMES, 116
        †Family PHOLIDOPLEURIDAE, 116
    †Order PERLEIDIFORMES, 116
        †Family CEPHALOXENIDAE, 116
        †Family CLEITHROLEPIDIDAE, 116
        †Family COLOBODONTIDAE, 116
        †Family PERLEIDIDAE, 116

    †Family PLATYSIAGIDAE, 116
  †Order LUGANOIFORMES, 116
    †Family LUGANOIDAE, 116
  †Order PERLEIDIFORMES, 116
Infraclass CLADISTIA, 116
  Order POLYPTERIFORMES (19)—bichirs, 116
    Family POLYPTERIDAE (63)—bichirs, 117
Infraclass CHONDROSTEI, 118
  †Order CHONDROSTEIFORMES, 118
    †Family CHONDROSTEIDAE, 118
  Order ACIPENSERIFORMES (20)—paddlefishes and sturgeons, 118
    †Family PEIPIAOSTEIDAE, 118
    Family POLYODONTIDAE (64)—paddlefishes, 118
    Family ACIPENSERIDAE (65)—sturgeons, 119
NEOPTERYGII, 121
  †Order PYCNODONTIFORMES, 121
Infraclass HOLOSTEI (gars, bowfins, and relatives), 121
Division GINGLYMODI, 122
  †Order DAPEDIIFORMES, 122
    †Family DAPEDIIDAE, 122
  Order LEPISOSTEIFORMES (21)—gars, 122
    †Family OBAICHTHYIDAE, 123
    Family LEPISOSTEIDAE (66)—gars, 123
  †Order SEMIONOTIFORMES, 123
    †Family SEMIONOTIDAE (Lepidotidae), 124
    †Family CALLIPURBECKIDAE, 124
  †Order MACROSEMIIFORMES, 124
    †Family MACROSEMIIDAE, 124
Division HALECOMORPHI, 124
  †Order PARASEMIONOTIFORMES, 125
  †Order IONOSCOPIFORMES, 125
  Order AMIIFORMES (22)—bowfins, 125
    †Family CATURIDAE, 125
    †Family LIODESMIDAE, 125
    †Family SINAMIIDAE, 125
    Family AMIIDAE (67)—bowfins, 126
Division TELEOSTEOMORPHA, 126
†Subdivision ASPIDORHYNCHEI, 127
  †Order ASPIDORHYNCHIFORMES, 127
    †Family ASPIDORHYNCHIDAE, 127
  †Order PACHYCORMIFORMES, 127
    †Family PACHYCORMIDAE, 127
Subdivision TELEOSTEI, 128
  †Order PHOLIDOPHORIFORMES, 129
    †Family PHOLIDOPHORIDAE, 129
  †Order DORSETICHTHYIFORMES, 130

†Family DORSETICHTHYIDAE, 130
†Order LEPTOLEPIDIFORMES, 130
†Family LEPTOLEPIDIDAE, 130
†Order CROSSOGNATHIFORMES, 130
†Family VARASICHTHYIDAE, 130
†Family CROSSOGNATHIDAE, 130
†Family NOTELOPIDAE, 130
†Family PACHYRHIZODONTIDAE, 130
†Order ICHTHYODECTIFORMES, 131
†Family ALLOTHRISSOPIDAE, 131
†Family CLADOCYCLIDAE, 131
†Family SAURODONTIDAE, 131
†Family ICHTHYODECTIDAE, 131
†Order TSELFATIIFORMES, 131
†Family Plethodidae (= Bananogmiidae), 132
†Family Protobramidae, 132
†Family Tselfatiidae, 132
†Order ARARIPICHTHYIFORMES, 132
†Family ARARIPICHTHYIDAE, 132
Supercohort TELEOCEPHALA—crown-group Teleostei, 132
Cohort ELOPOMORPHA, 133
Order ELOPIFORMES (23)—tenpounders, 135
Family ELOPIDAE (68)—tenpounders (ladyfishes), 135
Family MEGALOPIDAE (69)—tarpons, 135
Order ALBULIFORMES (24)—bonefishes, 136
Family ALBULIDAE (70)—bonefishes, 136
Order NOTACANTHIFORMES (25)—halosaurs and deep-sea spiny eels, 137
Family HALOSAURIDAE (71)—halosaurs, 137
Family NOTACANTHIDAE (72)—deep-sea spiny eels, 138
Order ANGUILLIFORMES (26)—eels, 139
Family PROTANGUILLIDAE (73)—primitive cave eels, 140
Family SYNAPHOBRANCHIDAE (74)—cutthroat eels, 141
Family HETERENCHELYIDAE (75)—mud eels, 142
Family MYROCONGRIDAE (76)—myroconger eels, 143
Family MURAENIDAE (77)—moray eels, 143
Family CHLOPSIDAE (78)—false morays, 144
Family DERICHTHYIDAE (79)—longneck or narrowneck and shorttail eels, 145
Family OPHICHTHIDAE (80)—snake eels and worm eels, 145
Family MURAENESOCIDAE (81)—pike congers, 147
Family NETTASTOMATIDAE (82)—duckbill eels, 147
Family CONGRIDAE (83)—conger eels, 147
Family MORINGUIDAE (84)—spaghetti eels, 149
Family CYEMATIDAE (85)—bobtail snipe eels, 149
Family MONOGNATHIDAE (86)—onejaw gulpers, 150

    - Family SACCOPHARYNGIDAE (87)—swallowers, 150
    - Family EURYPHARYNGIDAE (88)—gulpers or pelican eels, 150
    - Family NEMICHTHYIDAE (89)—snipe eels, 151
    - Family SERRIVOMERIDAE (90)—sawtooth eels, 151
    - Family ANGUILLIDAE (91)—freshwater eels, 152
- OSTEOGLOSSOCEPHALA, 153
- Cohort OSTEOGLOSSOMORPHA, 153
  - †Order LYCOPTERIFORMES, 154
    - †Family LYCOPTERIDAE, 154
  - Order HIODONTIFORMES (27)—mooneyes, 155
    - Family HIODONTIDAE (92)—mooneyes, 155
  - Order OSTEOGLOSSIFORMES (28)—bonytongues, 155
    - Family PANTODONTIDAE (93)—butterflyfishes, 156
    - Family OSTEOGLOSSIDAE (94)—osteoglossids or bonytongues, 156
    - Family NOTOPTERIDAE (95), 158
    - Family MORMYRIDAE (96)—elephantfishes, 159
    - Family GYMNARCHIDAE (97)—abas, 160
- CLUPEOCEPHALA, 160
- Cohort OTOCEPHALA, 161
- Superorder CLUPEOMORPHA, 162
  - †Order ELLIMMICHTHYIFORMES, 163
    - †Family ARMIGATIDAE, 163
    - †Family SORBINICHTHYIDAE, 163
    - †Family PARACLUPEIDAE (= Ellimmichthyidae), 164
  - Order CLUPEIFORMES (29)—herrings, 164
    - Family DENTICIPITIDAE (98)—denticle herrings, 165
    - Family PRISTIGASTERIDAE (99)—longfin herrings, 166
    - Family ENGRAULIDAE (100)—anchovies, 167
    - Family CHIROCENTRIDAE (101)—wolf herrings, 169
    - Family CLUPEIDAE (102)—herrings (shads, sprats, sardines, pilchards, and menhadens), 169
- Superorder ALEPOCEPHALI, 172
  - Order ALEPOCEPHALIFORMES (30)—slickheads and tubeshoulders, 172
    - Family PLATYTROCTIDAE (103)—tubeshoulders, 172
    - Family BATHYLACONIDAE (104)—bathylaconids, 173
    - Family ALEPOCEPHALIDAE (105)—slickheads, 173
- Superorder OSTARIOPHYSI, 174
  - Series ANOTOPHYSI, 175
  - Order GONORYNCHIFORMES (31)—milkfishes, 175
    - Family CHANIDAE (106)—milkfishes, 176
    - Family GONORYNCHIDAE (107)—beaked sandfishes, 177
    - Family KNERIIDAE (108)—knerias and snake mudheads, 178
  - Series OTOPHYSI, 179
  - Subseries Cypriniphysi, 180

Order CYPRINIFORMES (32)—carps, loaches, minnows, and relatives, 180
- Family CYPRINIDAE (109)—minnows, carps, and loaches, 181
- Family PSILORHYNCHIDAE (110)—mountain carps, 186
- †Family JIANGHANICHTHYIDAE, 186
- Family GYRINOCHEILIDAE (111)—algae eaters, 187
- Family CATOSTOMIDAE (112)—suckers, 187
- Family BOTIIDAE (113)—botiid loaches, 189
- Family VAILLANTELLIDAE (114)—long-fin loaches, 190
- Family COBITIDAE (115)—loaches, 190
- Family BALITORIDAE (116)—hillstream or river loaches, 191
- Family GASTROMYZONTIDAE (117)—gastromyzontid or sucker loaches, 191
- Family NEMACHEILIDAE (118)—stone loaches, 192
- Family BARBUCCIDAE (119)—fire-eyed loaches, 192
- Family ELLOPOSTOMATIDAE (120)—sturgeon-mouthed loaches, 192
- Family SERPENTICOBITIDAE (121)—serpent loaches, 193

Subseries Characiphysi, 193

Order CHARACIFORMES (33)—characins, 193
- Family DISTICHODONTIDAE (122)—distichodontids, 194
- Family CITHARINIDAE (123)—citharinids, 195
- Family CRENUCHIDAE (124)—South American darters, 195
- Family ALESTIDAE (125)—African tetras, 196
- Family HEPSETIDAE (126)—African pikes, 196
- Family ERYTHRINIDAE (127)—trahiras, 197
- Family PARODONTIDAE (128)—parodontids, 197
- Family CYNODONTIDAE (129)—cynodontids, 198
- Family SERRASALMIDAE (130)—pacus, silver dollars, and piranhas, 198
- Family HEMIODONTIDAE (131)—hemiodontids, 199
- Family ANOSTOMIDAE (132)—toothed headstanders, 200
- Family CHILODONTIDAE (133)—headstanders, 200
- Family CURIMATIDAE (134)—toothless characiforms, 201
- Family PROCHILODONTIDAE (135)—flannel-mouth characiforms, 201
- Family LEBIASINIDAE (136)—pencil fishes, 202
- Family CTENOLUCIIDAE (137)—pike-characids, 203
- Family ACESTRORHYNCHIDAE (138)—acestrorhynchids, 203
- Family CHARACIDAE (139)—characins, 203
- Family GASTEROPELECIDAE (140)—freshwater hatchetfishes, 206

Subseries Siluriphysi, 207

Order SILURIFORMES (34)—catfishes, 207
- †Family ANDINICHTHYIDAE, 210
- †Family BACHMANNIIDAE, 210
- Family DIPLOMYSTIDAE (141)—velvet catfishes, 210

†Family HYPSIDORIDAE, 211
Family CETOPSIDAE (142)—whale catfishes, 211
Family TRICHOMYCTERIDAE (143)—pencil catfishes or parasitic catfishes, 212
Family NEMATOGENYIDAE (144)—mountain catfishes, 214
Family CALLICHTHYIDAE (145)—callichthyid armored catfishes, 214
Family SCOLOPLACIDAE (146)—spiny dwarf catfishes, 215
Family ASTROBLEPIDAE (147)—climbing catfishes, 216
Family LORICARIIDAE (148)—suckermouth armored catfishes, 216
Family SILURIDAE (149)—sheatfishes, 218
Family AUSTROGLANIDIDAE (150)—rock catfishes, 219
Family PANGASIIDAE (151)—shark catfishes, 219
Family CHACIDAE (152)—squarehead, angler, or frogmouth catfishes, 220
Family PLOTOSIDAE (153)—eeltail catfishes, 220
Family RITIDAE (154)—ritas and nanobagrids, 221
Family AILIIDAE (155)—Asian “schilbeids”, 221
Family HORABAGRIDAE (156)—imperial or sun catfishes, 222
Family BAGRIDAE (157)—bagrid catfishes, 222
Family AKYSIDAE (158)—stream catfishes, 223
Family AMBLYCIPITIDAE (159)—torrent catfishes, 224
Family SISORIDAE (160)—sisorid catfishes, 224
Family ERETHISTIDAE (161)—erethistid catfishes, 225
Family AMPHILIIDAE (162)—loach catfishes, 226
Family MALAPTERURIDAE (163)—electric catfishes, 227
Family MOCHOKIDAE (164)—squeakers or upside-down catfishes, 227
Family SCHILBEIDAE (165)—schilbeid or butter catfishes, 228
Family AUCHENOGLANIDIDAE (166)—auchenoglanidids, 228
Family CLAROTEIDAE (167)—claroteids, 229
Family LACANTUNIIDAE (168)—Chiapas catfishes, 229
Family CLARIIDAE (169)—airbreathing catfishes, 230
Family HETEROPNEUSTIDAE (170)—airsac catfishes, 231
Family ANCHARIIDAE (171)—Malagasy catfishes, 231
Family ARIIDAE (172)—sea catfishes, 231
Family ASPREDINIDAE (173)—banjo catfishes, 232
Family DORADIDAE (174)—thorny catfishes, 233
Family AUCHENIPTERIDAE (175)—driftwood catfishes, 234
Family CRANOGLANIDIDAE (176)—armorhead catfishes, 235
Family ICTALURIDAE (177)—North American catfishes, 235
Family HEPTAPTERIDAE (178)—heptapterids, 236
Family PIMELODIDAE (179)—long-whiskered catfishes, 236
Family PSEUDOPIMELODIDAE (180)—bumblebee catfishes, 238
Order GYMNOTIFORMES (35)—Neotropical knifefishes, 238
Family GYMNOTIDAE (181)—nakedback knifefishes, 238

Family RHAMPHICHTHYIDAE (182)—sand knifefishes, 239
Family HYPOPOMIDAE (183)—bluntnose knifefishes, 240
Family STERNOPYGIDAE (184)—glass knifefishes, 240
Family APTERONOTIDAE (185)—ghost knifefishes, 241
Cohort EUTELEOSTEI, 241
Order LEPIDOGALAXIIFORMES (36)—salamanderfishes, 242
Family LEPIDOGALAXIIDAE (186)—salamanderfishes, 242
Superorder PROTACANTHOPTERYGII, 243
Order SALMONIFORMES (37)—trout, salmon, and whitefish, 244
Family SALMONIDAE (187)—trout, salmon, and whitefish, 244
Order ESOCIFORMES (38)—pikes and mudminnows, 248
†Family PALAEOESOCIDAE, 249
Family ESOCIDAE (188)—pikes, 249
Family UMBRIDAE (189)—mudminnows, 251
Superorder OSMEROMORPHA, 252
Order ARGENTINIFORMES (39)—marine smelts, 252
Family ARGENTINIDAE (190)—argentines or herring smelts, 253
Family OPISTHOPROCTIDAE (191)—barreleyes or spookfishes, 253
Family MICROSTOMATIDAE (192)—pencilsmelts, 253
Family BATHYLAGIDAE (193)—deepsea smelts, 254
Order GALAXIIFORMES (40)—galaxiiforms, 254
Family GALAXIIDAE (194)—galaxiids, 254
Order OSMERIFORMES (41)—freshwater smelts, 256
Family OSMERIDAE (195)—Northern Hemisphere smelts, 257
Family PLECOGLOSSIDAE (196)—Ayu or sweetfish, 257
Family SALANGIDAE (197)—icefishes or noodlefishes, 258
Family PROTOTROCTIDAE (198)—southern graylings, 258
Family RETROPINNIDAE (199)—southern smelts, 258
Order STOMIIFORMES (42)—dragonfishes, 259
Family GONOSTOMATIDAE (200)—bristlemouths, 259
Family STERNOPTYCHIDAE (201)—marine hatchetfishes, 260
Family PHOSICHTHYIDAE (Photichthyidae) (202)—lightfishes, 261
Family STOMIIDAE (203)—barbeled dragonfishes, 261
Superorder ATELEOPODOMORPHA, 265
Order ATELEOPODIFORMES (43)—jellynose fishes, 265
Family ATELEOPODIDAE (204)—jellynose fishes, 265
Superorder CYCLOSQUAMATA, 266
Order AULOPIFORMES (44)—lizardfishes, 266
†Family ICHTHYOTRINGIDAE, 267
†Family DERCETIDAE, 267
†Family PRIONOLEPIDIDAE, 267
†Family HALECIDAE, 267
Family SYNODONTIDAE (205)—lizardfishes, 268
Family AULOPIDAE (206)—flagfins, 268
Family PSEUDOTRICHONOTIDAE (207)—sand-diving lizardfishes, 269

    Family PARAULOPIDAE (208)—cucumber fishes, 269
    Family IPNOPIDAE (209)—deepsea tripod fishes, 270
    Family GIGANTURIDAE (210)—telescopefishes, 271
    Family BATHYSAUROIDIDAE (211)—largescale deep-sea lizardfish, 271
    Family BATHYSAURIDAE (212)—deepsea lizardfishes, 272
    Family CHLOROPHTHALMIDAE (213)—greeneyes, 272
    Family NOTOSUDIDAE (214)—waryfishes, 273
    Family SCOPELARCHIDAE (215)—pearleyes, 273
    Family EVERMANNELLIDAE (216)—sabertooth fishes, 274
    Family SUDIDAE (217)—sudid barracudinas, 274
    Family PARALEPIDIDAE (218)—barracudinas, 274
    †Family ENCHODONTIDAE, 275
    Family ALEPISAURIDAE (219)—lancetfishes, 275
    Family LESTIDIIDAE (220)—naked barracudinas, 276
Superorder SCOPELOMORPHA, 276
  Order MYCTOPHIFORMES (45)—lanternfishes, 276
    Family NEOSCOPELIDAE (221)—blackchins, 277
    Family MYCTOPHIDAE (222)—lanternfishes, 277
  †Order CTENOTHRISSIFORMES, 280
Superorder LAMPRIMORPHA, 280
  Order LAMPRIFORMES (46)—opahs, 280
    Family VELIFERIDAE (223)—velifers, 281
    Family LAMPRIDAE (224)—opahs, 282
    Family LOPHOTIDAE (225)—crestfishes, 283
    Family RADIICEPHALIDAE (226)—tapertails, 283
    Family TRACHIPTERIDAE (227)—ribbonfishes, 283
    Family REGALECIDAE (228)—oarfishes, 284
Superorder PARACANTHOPTERYGII, 284
  Order POLYMIXIIFORMES (47)—beardfishes, 285
    Family POLYMIXIIDAE (229)—beardfishes, 286
  †Order SPHENOCEPHALIFORMES, 286
    †Family SPHENOCEPHALIDAE, 287
  Order PERCOPSIFORMES (48)—trout-perches, 287
    Family PERCOPSIDAE (230)—trout-perches, 287
    †Family MCCONICHTHYIDAE, 288
    Family APHREDODERIDAE (231)—pirate perches, 288
    Family AMBLYOPSIDAE (232)—cavefishes, 289
  Order ZEIFORMES (49)—dories, 289
    Family CYTTIDAE (233)—lookdown dories, 290
    Family OREOSOMATIDAE (234)—oreos, 290
    Family PARAZENIDAE (235)—smooth dories, 291
    Family ZENIONTIDAE (236)—armoreye dories, 291
    Family GRAMMICOLEPIDIDAE (237)—tinselfishes, 292
    Family ZEIDAE (238)—dories, 292
  Order STYLEPHORIFORMES (50)—tube-eyes or thread-tails, 293

    Family STYLEPHORIDAE (239)—tube-eyes or thread-tails, 293
  Order GADIFORMES (51)—cods and hakes, 293
    Family MELANONIDAE (240)—pelagic cods, 295
    Family STEINDACHNERIIDAE (241)—luminous and southern hakes, 295
    Family BATHYGADIDAE (242)—rattails, 296
    Family MACROURIDAE (243)—grenadiers (rattails), 296
    Family TRACHYRINCIDAE (244)—whiptails and trachyrincines, 296
    Family EUCLICHTHYIDAE (245)—eucla cod, 297
    Family MORIDAE (246)—deepsea cods, codlings, hakelings, 298
    Family MACRURONIDAE (247)—southern hakes, 298
    Family MERLUCCIIDAE (248)—merlucciid hakes, 298
    Family RANICIPITIDAE (249)—tadpole cods, 299
    Family BREGMACEROTIDAE (250)—codlets, 300
    Family MURAENOLEPIDIDAE (251)—eel cods and moray cods, 300
    Family GADIDAE (252)—cods, 300
Superorder ACANTHOPTERYGII, 302
  Series BERYCIDA, 303
  Order HOLOCENTRIFORMES (52)—squirrelfishes, 304
    Family HOLOCENTRIDAE (253)—squirrelfishes, 304
  Order TRACHICHTHYIFORMES (53)—roughies, 305
    Family ANOPLOGASTRIDAE (254)—fangtooths, 305
    Family DIRETMIDAE (255)—spinyfins, 306
    Family ANOMALOPIDAE (256)—flashlight or lanterneye fishes, 306
    †Family PSEUDOMONOCENTRIDAE, 307
    Family MONOCENTRIDAE (257)—pinecone fishes, 307
    Family TRACHICHTHYIDAE (258)—roughies, 308
  Order BERYCIFORMES (54)—beryciforms, 308
    Family GIBBERICHTHYIDAE (259)—gibberfishes, 310
    Family STEPHANOBERYCIDAE (260)—pricklefishes, 310
    Family HISPIDOBERYCIDAE (261)—hispidoberycids, 310
    Family RONDELETIIDAE (262)—redmouth whalefishes, 311
    Family BARBOURISIIDAE (263)—red (redvelvet) whalefishes, 311
    Family CETOMIMIDAE (264)—flabby whalefishes, 312
    Family MELAMPHAIDAE (265)—bigscale fishes, 313
    Family BERYCIDAE (266)—alfonsinos, 314
  Series PERCOMORPHA, 314
  Subseries Ophidiida, 315
  Order OPHIDIIFORMES (55)—cusk-eels, 315
    Family CARAPIDAE (267)—pearlfishes, 316
    Family OPHIDIIDAE (268)—cusk-eels, 317
    Family BYTHITIDAE (269)—viviparous brotulas, 318
    Family APHYONIDAE (270)—aphyonids, blind cusk-eels, 319
    Family PARABROTULIDAE (271)—false brotulas, 320
  Subseries Batrachoidida, 320
  Order BATRACHOIDIFORMES (56)—toadfishes, 320

    Family BATRACHOIDIDAE (272)—toadfishes, 321
Subseries Gobiida, 323
Order KURTIFORMES (57)—nurseryfishes and cardinalfishes, 324
    Family KURTIDAE (273)—nurseryfishes, 324
    Family APOGONIDAE (274)—cardinalfishes, 324
Order GOBIIFORMES (58)—gobies, 326
    Family RHYACICHTHYIDAE (275)—loach gobies, 327
    Family ODONTOBUTIDAE (276)—freshwater sleepers, 327
    Family MILYERINGIDAE (277)—blind cave gobies, 328
    Family ELEOTRIDAE (278)—spinycheek sleepers, 328
    Family BUTIDAE (279)—butid sleepers, 329
    Family THALASSELEOTRIDIDAE (280)—ocean sleepers, 329
    Family OXUDERCIDAE (281)—*Gobionellus*-like and mudskipper gobies, 329
    Family GOBIIDAE (282)—gobies, 331
Subseries Ovalentaria, 333
    Family AMBASSIDAE (Chandidae) (283)—Asiatic glassfishes, 334
    Family EMBIOTOCIDAE (284)—surfperches, 335
    Family GRAMMATIDAE (Grammidae) (285)—basslets, 336
    Family PLESIOPIDAE (286)—roundheads, 336
    Family POLYCENTRIDAE (287)—South American leaffishes, 337
    Family POMACENTRIDAE (288)—damselfishes, 337
    Family PSEUDOCHROMIDAE (289)—dottybacks, 339
    Family OPISTOGNATHIDAE (290)—jawfishes, 341
Order MUGILIFORMES (59)—mullets, 341
    Family MUGILIDAE (291)—mullets, 342
Order CICHLIFORMES (60)—cichlids and convict blennies, 342
    Family CICHLIDAE (292)—cichlids, 342
    Family PHOLIDICHTHYIDAE (293)—convict blenny, 345
Order BLENNIIFORMES (61)—Blennies, 346
    Family TRIPTERYGIIDAE (294)—triplefin blennies, 346
    Family DACTYLOSCOPIDAE (295)—sand stargazers, 347
    Family BLENNIIDAE (296)—combtooth blennies, 348
    Family CLINIDAE (297)—kelp blennies, 349
    Family LABRISOMIDAE (298)—labrisomid blennies, 350
    Family CHAENOPSIDAE (299)—tube blennies, 351
Order GOBIESOCIFORMES (62)—clingfishes, 351
    Family GOBIESOCIDAE (300)—clingfishes, 352
Order ATHERINIFORMES (63)—silversides, 354
    Family ATHERINOPSIDAE (301)—New World silversides, 355
    Family NOTOCHEIRIDAE (302)—surf silversides, 357
    Family ISONIDAE (303)—surf sardines, 357
    Family MELANOTAENIIDAE (304)—rainbowfishes and blue eyes, 358
    Family ATHERIONIDAE (305)—pricklenose silversides, 360
    Family DENTATHERINIDAE (306)—Mercer’s tusked silverside, 360

- Family PHALLOSTETHIDAE (307)—priapiumfishes, 361
- Family ATHERINIDAE (308)—Old World silversides, 362

Order BELONIFORMES (64)—needlefishes, 363
- Family ADRIANICHTHYIDAE (309)—adrianichthyids, 364
- Family EXOCOETIDAE (310)—flyingfishes, 365
- Family HEMIRAMPHIDAE (311)—halfbeaks, 366
- Family ZENARCHOPTERIDAE (312)—viviparous halfbeaks, 367
- Family BELONIDAE (313)—needlefishes, 368
- Family SCOMBERESOCIDAE (314)—sauries, 369

Order CYPRINODONTIFORMES (65)—killifishes, 369
- Family APLOCHEILIDAE (315)—Asian rivulines, 371
- Family NOTHOBRANCHIIDAE (316)—African rivulines, 371
- Family RIVULIDAE (317)—New World rivulines, 371
- Family PROFUNDULIDAE (318)—Middle American killifishes, 372
- Family GOODEIDAE (319)—goodeids, 372
- Family FUNDULIDAE (320)—topminnows, 374
- Family VALENCIIDAE (321)—Valencia toothcarps, 374
- Family CYPRINODONTIDAE (322)—pupfishes, 375
- Family ANABLEPIDAE (323)—four-eyed fishes, 376
- Family POECILIIDAE (324)—livebearers, 378

Order SYNBRANCHIFORMES (66)—swamp eels, 380
- Family SYNBRANCHIDAE (325)—swamp eels, 381
- Family CHAUDHURIIDAE (326)—earthworm eels, 382
- Family MASTACEMBELIDAE (327)—freshwater spiny eels, 382

Order CARANGIFORMES (67)—jacks, 383
- Family NEMATISTIIDAE (328)—roosterfishes, 383
- Family CORYPHAENIDAE (329)—dolphinfishes, 384
- Family RACHYCENTRIDAE (330)—cobias, 384
- Family ECHENEIDAE (331)—remoras (sharksuckers), 384
- Family CARANGIDAE (332)—jacks and pompanos, 385
- Family MENIDAE (333)—moonfishes, 387

Order ISTIOPHORIFORMES (68)—barracudas and billfishes, 387
- Family SPHYRAENIDAE (334)—barracudas, 388
- Family XIPHIIDAE (335)—swordfishes, 389
- Family ISTIOPHORIDAE (336)—billfishes, 389

Order ANABANTIFORMES (69)—labyrinth fishes, 390
- Family ANABANTIDAE (337)—climbing gouramies, 391
- Family HELOSTOMATIDAE (338)—kissing gouramies, 391
- Family OSPHRONEMIDAE (339)—gouramies and fighting fishes, 392
- Family CHANNIDAE (340)—snakeheads, 394
- Family NANDIDAE (341)—Asian leaffishes, 394
- Family BADIDAE (342)—chameleonfishes, 395
- Family PRISTOLEPIDIDAE (343)—(Malayan) leaffishes, 395

Order PLEURONECTIFORMES (70)—flatfishes, 395
- Family PSETTODIDAE (344)—spiny turbots, 397

Family CITHARIDAE (345)—largescale flounders, 397
Family SCOPHTHALMIDAE (346)—turbots, 398
Family PARALICHTHYIDAE (347)—sand flounders, 398
Family PLEURONECTIDAE (348)—righteye flounders, 399
Family BOTHIDAE (349)—lefteye flounders, 400
Family PARALICHTHODIDAE (350)—measles or peppered flounders, 401
Family POECILOPSETTIDAE (351)—bigeye flounders, 401
Family RHOMBOSOLEIDAE (352)—rhombosoleids, 401
Family ACHIROPSETTIDAE (353)—southern flounders, 402
Family SAMARIDAE (354)—crested flounders, 402
Family ACHIRIDAE (355)—American soles, 402
Family SOLEIDAE (356)—soles, 403
Family CYNOGLOSSIDAE (357)—tonguefishes, 404
Order SYNGNATHIFORMES (71)—pipefishes and seahorses, 405
Family PEGASIDAE (358)—seamoths, 406
Family SOLENOSTOMIDAE (359)—ghost pipefishes, 407
Family SYNGNATHIDAE (360)—pipefishes and seahorses, 407
Family AULOSTOMIDAE (361)—trumpetfishes, 409
Family FISTULARIIDAE (362)—cornetfishes, 409
Family MACRORAMPHOSIDAE (363)—snipefishes, 410
Family CENTRISCIDAE (364)—shrimpfishes, 410
Family DACTYLOPTERIDAE (365)—flying gurnards, 411
Order ICOSTEIFORMES (72)—ragfishes, 412
Family ICOSTEIDAE (366)—ragfishes, 412
Order CALLIONYMIFORMES (73), 412
Family CALLIONYMIDAE (367)—dragonets, 412
Family DRACONETTIDAE (368)—slope dragonets, 413
Order SCOMBROLABRACIFORMES (74)—longfin escolars, 413
Family SCOMBROLABRACIDAE (369)—longfin escolars, 413
Order SCOMBRIFORMES (75)—mackerels, 414
Family GEMPYLIDAE (370)—snake mackerels, 415
Family TRICHIURIDAE (371)—cutlassfishes, 415
Family SCOMBRIDAE (372)—mackerels and tunas, 416
Family AMARSIPIDAE (373)—amarsipas, 418
Family CENTROLOPHIDAE (374)—medusafishes, 418
Family NOMEIDAE (375)—driftfishes, 419
Family ARIOMMATIDAE (376)—ariommatids, 419
Family TETRAGONURIDAE (377)—squaretails, 420
Family STROMATEIDAE (378)—butterfishes, 420
Order TRACHINIFORMES (76), 421
Family CHIASMODONTIDAE (379)—swallowers, 421
Family CHAMPSODONTIDAE (380)—gapers, 422
Family PINGUIPEDIDAE (381)—sandperches, 422
Family CHEIMARRHICHTHYIDAE (382)—New Zealand torrentfishes, 422

Family TRICHONOTIDAE (383)—sanddivers, 423
Family CREEDIIDAE (384)—sandburrowers, 423
Family PERCOPHIDAE (385)—duckbills, 424
Family LEPTOSCOPIDAE (386)—southern sandfishes, 425
Family AMMODYTIDAE (387)—sand lances, 425
Family TRACHINIDAE (388)—weeverfishes, 426
Family URANOSCOPIDAE (389)—stargazers, 426
Order LABRIFORMES (77)—wrasses and relatives, 427
Family LABRIDAE (390)—wrasses, 428
Family ODACIDAE (391)—cales, 429
Family SCARIDAE (392)—parrotfishes, 429
Order PERCIFORMES (78)—perches, 430
Family CENTROPOMIDAE (393)—snooks, 431
Family LATIDAE (394)—lates perches, 432
Family GERREIDAE (395)—mojarras, 433
Family CENTROGENYIDAE (396)—false scorpionfishes, 433
Family PERCILIIDAE (397)—southern basses, 433
Family HOWELLIDAE (398)—oceanic basslets, 434
Family ACROPOMATIDAE (399)—lanternbellies, 434
Family EPIGONIDAE (400)—deepwater cardinalfishes, 434
Family POLYPRIONIDAE (401)—wreckfishes, 435
Family LATEOLABRACIDAE (402)—Asian seaperches, 435
Family MULLIDAE (403)—goatfishes, 436
Family GLAUCOSOMATIDAE (404)—pearl perches, 436
Family PEMPHERIDAE (405)—sweepers, 437
Family OPLEGNATHIDAE (406)—knifejaws, 437
Family KUHLIIDAE (407)—flagtails, 438
Family BATHYCLUPEIDAE (408)—bathyclupeids, 438
Family TOXOTIDAE (409)—archerfishes, 438
Family ARRIPIDAE (410)—Australasian salmon (kahawai), 439
Family DICHISTIIDAE (411)—galjoen fishes, 439
Family KYPHOSIDAE (412)—sea chubs, 440
Family TERAPONTIDAE (413)—grunters or tigerperches, 441
Family PERCICHTHYIDAE (414)—temperate perches, 442
Family SINIPERCIDAE (415)—Chinese perches, 442
Family ENOPLOSIDAE (416)—oldwives, 442
Family PENTACEROTIDAE (417)—armorheads, 443
Family DINOPERCIDAE (418)—cavebasses, 443
Family BANJOSIDAE (419)—banjofishes, 444
Family CENTRARCHIDAE (420)—sunfishes, 444
Family SERRANIDAE (421)—sea basses, 446
Family PERCIDAE (422)—perches, 448
Family LACTARIIDAE (423)—false trevallies, 450
Family DINOLESTIDAE (424)—long-finned pikes, 450
Family SCOMBROPIDAE (425)—gnomefishes, 450
Family POMATOMIDAE (426)—bluefishes, 451

Family BRAMIDAE (427)—pomfrets, 451
Family CARISTIIDAE (428)—manefishes, 452
Family MONODACTYLIDAE (429)—moonfishes (fingerfishes), 452
Family PRIACANTHIDAE (430)—bigeyes (catalufas), 453
Family LEIOGNATHIDAE (431)—ponyfishes, slimys, or slipmouths, 453
Family CHAETODONTIDAE (432)—butterflyfishes, 454
Family POMACANTHIDAE (433)—angelfishes, 455
Family MALACANTHIDAE (434)—tilefishes, 456
Family HAEMULIDAE (435)—grunts, 457
Family HAPALOGENIIDAE (436)—barbeled grunters, 457
Family LUTJANIDAE (437)—snappers, 457
Family CAESIONIDAE (438)—fusiliers, 458
Family CIRRHITIDAE (439)—hawkfishes, 459
Family CHIRONEMIDAE (440)—kelpfishes, 459
Family APLODACTYLIDAE (441)—marblefishes, 460
Family CHEILODACTYLIDAE (442)—morwongs, 460
Family LATRIDAE (443)—trumpeters, 460
Family CEPOLIDAE (444)—bandfishes, 461
Family SCATOPHAGIDAE (445)—scats, 462
Family SIGANIDAE (446)—rabbitfishes, 463
Family BOVICHTIDAE (447)—temperate icefishes, 464
Family PSEUDAPHRITIDAE (448)—catadromous icefishes, 464
Family ELEGINOPSIDAE (449)—Patagonian blennies, 465
Family NOTOTHENIIDAE (450)—cod icefishes, 465
Family HARPAGIFERIDAE (451)—spiny plunderfishes, 466
Family ARTEDIDRACONIDAE (452)—barbeled plunderfishes, 466
Family BATHYDRACONIDAE (453)—Antarctic dragonfishes, 466
Family CHANNICHTHYIDAE (454)—crocodile icefishes, 467
Order SCORPAENIFORMES (79)—mail-cheeked fishes, 467
Family SCORPAENIDAE (455)—scorpionfishes (rockfishes), 468
Family APLOACTINIDAE (456)—velvetfishes, 473
Family ESCHMEYERIDAE (457)—cofishes, 473
Family PATAECIDAE (458)—Australian prowfishes, 474
Family GNATHANACANTHIDAE (459)—red velvetfishes, 474
Family CONGIOPODIDAE (460)—racehorses (pigfishes or horsefishes), 475
Family TRIGLIDAE (461)—searobins (gurnards), 475
Family PERISTEDIIDAE (462)—armored searobins, 476
Family BEMBRIDAE (463)—deepwater flatheads, 476
Family PLATYCEPHALIDAE (464)—flatheads, 477
Family HOPLICHTHYIDAE (465)—ghost flatheads, 477
Family NORMANICHTHYIDAE (466)—barehead scorpionfishes or mote sculpins, 478
Family BATHYMASTERIDAE (467)—ronquils, 478
Family EULOPHIIDAE (468)—eulophiids, 478

- Family ZOARCIDAE (469)—eelpouts, 479
- Family STICHAEIDAE (470)—pricklebacks, 480
- Family CRYPTACANTHODIDAE (471)—wrymouths, 480
- Family PHOLIDAE (472)—gunnels, 480
- Family ANARHICHADIDAE (473)—wolffishes, 481
- Family PTILICHTHYIDAE (474)—quillfishes, 481
- Family ZAPRORIDAE (475)—prowfishes, 481
- Family SCYTALINIDAE (476)—graveldivers, 482
- Family HYPOPTYCHIDAE (477)—sand eel, 482
- Family AULORHYNCHIDAE (478)—tubesnouts, 483
- Family GASTEROSTEIDAE (479)—sticklebacks, 483
- Family INDOSTOMIDAE (480)—armored sticklebacks, 484
- Family ANOPLOPOMATIDAE (481)—sablefishes, 485
- Family ZANIOLEPIDIDAE (482)—combfishes, 486
- Family HEXAGRAMMIDAE (483)—greenlings, 487
- Family TRICHODONTIDAE (484)—sandfishes, 488
- Family JORDANIIDAE (485)—longfin sculpin, 488
- Family RHAMPHOCOTTIDAE (EREUNIIDAE) (486)—grunt sculpins, 489
- Family SCORPAENICHTHYIDAE (487)—Cabezon, 489
- Family AGONIDAE (HEMITRIPTERIDAE) (488)—poachers and searavens, 490
- Family COTTIDAE (489)—sculpins, 491
- Family PSYCHROLUTIDAE (490)—fathead sculpins, 493
- Family BATHYLUTICHTHYIDAE (491)—Antarctic sculpins, 494
- Family CYCLOPTERIDAE (492)—lumpfishes (lumpsuckers), 494
- Family LIPARIDAE (493)—snailfishes, 495

Order MORONIFORMES (80)—temperate basses, 495
- Family MORONIDAE (494)—temperate basses, 496
- Family DREPANEIDAE (495)—sicklefishes, 496
- Family EPHIPPIDAE (496)—spadefishes, 497

Order ACANTHURIFORMES—(81) surgeonfishes and relatives, 497
- Family EMMELICHTHYIDAE (497)—rovers, 498
- Family SCIAENIDAE (498)—drums (croakers), 498
- Family LUVARIDAE (499)—louvar, 500
- Family ZANCLIDAE (500)—Moorish Idols, 500
- †Family MASSALONGIIDAE, 501
- Family ACANTHURIDAE (501)—surgeonfishes, 501

Order SPARIFORMES (82)—breams and porgies, 502
- Family CALLANTHIIDAE (502)—splendid perches or groppos, 503
- Family SILLAGINIDAE (503)—sillagos (whitings, smelt-whitings), 503
- Family LOBOTIDAE (504)—tripletails, 503
- Family NEMIPTERIDAE (505)—threadfin breams, 504
- Family LETHRINIDAE (506)—emperors or emperor breams, 505
- Family SPARIDAE (507)—porgies, 505

Order CAPROIFORMES (83)—boarfishes, 506
  Family CAPROIDAE (508)—boarfishes, 507
Order LOPHIIFORMES (84)—anglerfishes, 508
  Family LOPHIIDAE (509)—goosefishes, 508
  Family ANTENNARIIDAE (510)—frogfishes, 509
  Family TETRABRACHIIDAE (511)—tetrabrachiid frogfishes, 510
  Family LOPHICHTHYIDAE (512)—lophichthyid frogfishes, 510
  Family BRACHIONICHTHYIDAE (513)—handfishes (warty anglers), 510
  Family CHAUNACIDAE (514)—coffinfishes or sea toads, 511
  Family OGCOCEPHALIDAE (515)—batfishes, 511
  Family CAULOPHRYNIDAE (516)—fanfins, 513
  Family NEOCERATIIDAE (517)—spiny seadevils, 513
  Family MELANOCETIDAE (518)—black seadevils, 514
  Family HIMANTOLOPHIDAE (519)—footballfishes, 514
  Family DICERATIIDAE (520)—double anglers, 515
  Family ONEIRODIDAE (521)—dreamers, 515
  Family THAUMATICHTHYIDAE (522)—wolftrap anglers, 516
  Family CENTROPHRYNIDAE (523)—prickly seadevils, 516
  Family CERATIIDAE (524)—warty seadevils, 516
  Family GIGANTACTINIDAE (525)—whipnose anglers, 517
  Family LINOPHRYNIDAE (526)—leftvents, 517
Order TETRAODONTIFORMES (85)—plectognaths, 518
  Family TRIODONTIDAE (527)—threetooth puffers, 519
  Family TRIACANTHODIDAE (528)—spikefishes, 520
  Family TRIACANTHIDAE (529)—triplespines, 520
  Family ARACANIDAE (530)—deepwater boxfishes, 521
  Family OSTRACIIDAE (531)—boxfishes (cowfishes and trunkfishes), 521
  Family BALISTIDAE (532)—triggerfishes, 522
  Family MONACANTHIDAE (533)—filefishes, 523
  Family MOLIDAE (534)—molas (ocean sunfishes), 524
  Family TETRAODONTIDAE (535)—puffers, 524
  Family DIODONTIDAE (536)—porcupinefishes (burrfishes), 526

BIBLIOGRAPHY **527**
INDEX **651**

Memories of Joe Nelson

Terry Grande and Mark Wilson asked if I could write a short essay involving my own personal memories of Joe, and I willingly agreed to do so. It should be noted that the paragraphs below are not an in-depth summary of Joe's life, but rather personal recollections. A more complete summary of his most interesting life and highly productive scientific career, written by David G. Smith for the continuing series entitled "Historical Perspectives," appeared recently on pages 169–176 of *Copeia,* 2011, no. 4.

In 1976, Joseph S. Nelson published the first edition of his book, *Fishes of the World,* involving all living and extinct groups of fishes. The work was widely recognized as the definitive source of information on fish classification, and a "must have" reference in the library of any person seriously involved in work with this group of animals. The success of this book, coupled with ongoing changes in knowledge and understanding of fish classification, brought the realization that periodic updates to this book would be necessary. This resulted in new editions during each succeeding decade (1984, 1994, and 2006), and it was Joe's intention that these would be followed by another edition during the succeeding decade. However, Joe's illness and subsequent passing made it impossible for him to finish the project alone, and led him to invite Terry Grande and Mark Wilson to assist him, and then, when his illness became terminal, to complete the project without him.

I first met Joe Nelson, during the 1970s, at one of the annual meetings of our primary professional society, the American Society of Ichthyologists and Herpetologists (ASIH). I was already aware of his work on salmonid fishes, nine-spine sticklebacks, and New Zealand marine fishes through the exchange of reprints of publications, and particularly his landmark 1976 work, the first edition of *Fishes of the World*, which had been accepted by ichthyologists (and scientists in general) as the most important published modern summary on classification of the world's living and fossil fishes. This publication had already propelled Joe, at the relatively young age of 39, to the forefront among world ichthyologists.

Although I knew Joe only casually in those early days, we nevertheless had frequent opportunities to discuss matters of mutual interest, especially those involving taxonomic and distributional problems involving North American marine and freshwater fishes. He immediately struck me as a friendly and soft-spoken person, and certainly not one to make a big deal of his already impressive professional accomplishments. This impression was one I never had any reason to change and, it can be said without fear of contradiction, one that has always been shared by all his colleagues and friends.

An incident occurred at a social gathering at one of these meetings when a young student, upon seeing the name on his name tag, approached Joe and rather tentatively asked, "Are you *the* Joe Nelson?" His positive response elicited an expression of awe, and in subsequent years this incident led to our referring to Joe as "*The* Joe Nelson."

As noted, Joe and I were regular attendees at the annual ASIH meetings. We were sometimes accompanied by our respective spouses, Claudine and Nancy, both of whom were more interested in the attractions and activities associated with the local meeting site than sitting in a room listening to presentations on fishes. The 1988 ASIH meeting in Ann Arbor, Michigan, was one such occasion, and that meeting can be pinpointed as the beginning of a long and enduring friendship. In subsequent years, when the question arose whether Nancy might choose to accompany me to the meetings, the deciding factor was whether Joe and Claudine would be there. This friendship resulted in trips together to rather exotic meeting sites such as La Paz, Baja California (Mexico), in 2000, and Manaus, Brazil, in 2003.

In 1991, Joe was asked to serve as chair of the joint AFS (American Fisheries Society)–ASIH committee on common and scientific names of fishes (often abbreviated to "c & sn of fishes"). This committee, which had been in existence since the late 1940s, is charged with maintaining and publishing, at approximate ten-year intervals, an updated checklist, with broad indications of distributions, of all species of United States and Canadian freshwater fishes and of marine species occurring within the 200-meter depth limit. The geographical scope of the list was expanded in the sixth edition, in 2004, to include Mexico as well. This list serves as an important authoritative reference for taxonomists, fisheries biologists, aquarists, and those involved in matters of conservation. Equally important are the accompanying appendices, which include explanations and justifications for changes or additions to the list. Throughout the preceding years, I had regularly provided pertinent information to the committee as it came to my attention. Shortly after assuming the chair, Joe invited me to join the committee on a formal basis.

Joe's years of productive ichthyological research had resulted, by the turn of the century, in well over one hundred papers in professional journals, together with books such as the definitive regional work co-authored with Martin Paetz, *The Fishes of Alberta,* first published in 1970 and then revised in 1992, and especially the aforementioned four editions of *Fishes of the World.* His distinguished record of publications throughout the years resulted in Joe being selected, at the 2002 ASIH meetings in Kansas City, Missouri, as the recipient of the prestigious Robert H. Gibbs Award, presented by the society "for an outstanding body of published work in systematic ichthyology."

Although the introduction of computers had by now greatly facilitated exchanges of information, the volume and complexity of new information made it necessary for the committee to meet, either yearly or every other year, for four-day work sessions, at which time ongoing issues and new information could be discussed and resolved on a face-to-face basis. Such meetings were normally held during the winter or early spring, and this, plus the fact that two of the committee members happened to reside in Gainesville, Florida, were factors in that city usually being selected as the meeting site. Claudine often used that opportunity to accompany Joe and escape the wintry weather of northern Canada for a few days.

Breaking with the usual pattern, the bi-yearly meeting of the c & sn of fishes committee was held in Mexico City in March 2009. At the meeting, Joe made a comment about feeling more fatigued than usual, although this was not immediately apparent to us and did not seem especially alarming, considering the somewhat thinner air associated with the higher elevation of Mexico City. At the ASIH meetings in Portland, Oregon, the following July, his fatigue had not abated, although it was not enough to prevent Joe from enjoying the meetings, which were highlighted by his election as ASIH President for the coming year.

Tests done shortly thereafter, however, showed the ongoing fatigue to be symptomatic of a serious medical problem, in which his bone marrow was not producing sufficient numbers of normal red and white blood cells. The condition, termed "Myelodysplastic Syndrome," could progress to acute leukemia. This led to a regimen of blood transfusions and several experimental drugs, of which one seemed to hold the most promise for a prolonged and undiminished quality of life.

At the 2010 ASIH meetings in Providence, Rhode Island, Joe received the Robert K. Johnson Award for long-term distinguished service to the society. Although he was unable to attend the meetings, an arrangement was made by which members could communicate visually with Joe via the Internet. This allowed a large number of us to express our best wishes and hopes for improvement to his health.

In the meantime, it became evident that Joe's health would not allow him to fulfill his obligations as ASIH President-Elect, forcing him to resign this position, as he did also chairmanship of the committee on common and scientific names of fishes.

Despite this, the positive effects of his treatment during the subsequent year were sufficiently encouraging that Joe and Claudine were making plans to attend the 2011 ASIH meetings in Minneapolis, Minnesota, in July. A few weeks before the meeting, however, came the devastating news that the experimental drug was no longer working, and blood transfusions were the only option. From this point on, Joe's health underwent a precipitous decline, ending in his passing on August 9, 2011. In 2013, Joe's importance to ichthyology was recognized when ASIH established the Joseph S. Nelson Lifetime Achievement Award for an outstanding body of work in ichthyology.

At the 2012 ASIH meetings in Vancouver, British Columbia, Claudine presented a touching tribute to Joe during the plenary session. Her presentation brought home to us once again the realization that a wonderful friend and colleague was no longer with us. We will always miss you, Joe!

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November 2015

Foreword

In 1976, Joseph S. Nelson published a modest volume with a bold title: *Fishes of the World*. Nelson was not the first to publish a book so named, but he was to become—for the next four decades—the only modern author associated with that title. This book, and the three editions that followed, are known simply by his last name: *Nelson* became the standard secondary reference for fish systematics.

To write *Fishes of the World* was a complex task. The first edition came 10 years after Greenwood et al.'s (1966) wholesale reorganization of fish classification, seven years after Gareth Nelson's (1969) classification of vertebrates based on the cladistic principles of Hennig (1966), and just three years after the audacious *Interrelationships of Fishes* of Greenwood, Miles, and Patterson (1973). For many, Nelson (1976) supplanted all of these because of its accessibility as a textbook and its philosophical aim: an eclectic mix of traditional and cladistic taxa diagnosed by both primitive and derived characters. A typical family account included the taxon, its common name, an outline sketch, a brief distribution, some maps (in the first two editions), a synopsis of characters (both primitive and derived), an estimate of the number of species, and some other comments that Joe considered to be of interest. Treatments could be uneven, yet this formula was repeated in all following editions. Nelson was cautious, especially about new taxa. His compromise was to discuss what he considered to be a radical proposal, such as that of the Neoteleostei by Rosen (1973), but not incorporate it into his classification.

After critical reviews of the first edition (e.g., Winterbottom, 1977, *Journal of the Fisheries Research Board of Canada*, 34:2431-2432), Joe published an expanded second edition in 1984. At 523 pages, the second Nelson (1984) was 107 pages longer than the first. Popularity of the first edition transferred to the second, and by the mid-1980s, before the age of the Internet, Joe Nelson and his book became a central clearing house for fish classification. Fish systematists enjoyed debating the latest classifications, and the largely morphological characters that supported them, with Joe at the annual meetings of the American Society of Ichthyologists and Herpetologists. Joe was kind and dignified as he engaged junior and senior ichthyologists with equal interest and respect. The newly published, monographic dissertations of an emerging generation—for example, Vari (1978) on terapontid perches, Johnson (1980) on lutjanids, Parenti (1981) on cyprinodontiforms, Stiassny (1981) on cichlids, and L. Grande (1982) on clupeomorphs—were cited and their classifications incorporated, in part, into Nelson (1984). This was validation of our place in the field of systematic ichthyology.

A decade passed between the second and third editions. Cladistic analysis and classification, once considered rogue, were now mainstream in systematic ichthyology. The pace of publication of revisionary studies of fishes increased, as did the third edition: Nelson (1994), at 600 pages, was the largest of the volumes to date. The distribution maps of the first two editions were eliminated due to space considerations. The third edition exposed more of Joe's unique views of characters and classification (Parenti, 1995, *Copeia,* 1: 262-264). He alone combined the billfish families Xiphiidae and Istiophoridae into the Xiphiidae. Further, he admitted to omitting characters that he found difficult to describe briefly, even if diagnostic. Many of the characters he listed are "field" or "key characters," useful to identify specimens, but not necessarily to infer phylogenetic relationships. Joe absorbed criticism readily and alone. Despite the benefits a collaborator may have brought to the project, he never took on a co-author until asking Terry Grande and Mark Wilson to join him in writing the current edition, a job they would complete without him.

The fourth edition was published a decade ago. Dominance of the Internet meant that Nelson (2006) was no longer the sole, ready source of information on fish classification. *The Catalog of Fishes*, the spectacular achievement of Bill Eschmeyer, was available online (www.calacademy.org) and included fishes in a classification. Nonetheless, Nelson (2006) had become firmly established as the leading source of information on taxon diagnoses, summaries of species composition, and classification of fish taxa. Countless numbers of publications on fish systematics begin with a summary of number of species and other relevant data, citing the source as "Nelson (2006)." It stands alone as "the single most important book for fish classification" (Britz, 2006, *Journal of Fish Biology,* 69:1901).

The last edition of *Fishes of the World* that Joe wrote alone just hinted at the molecular phylogenetic revolution that was soon to come. These molecular studies and their proposed classificatory changes are summarized ably in this fifth edition by Grande and Wilson. Like Joe, they too use restraint in revising classifications and incorporate a judicious mix of the old and the new. There is a tension between using molecular versus morphological variation as phylogenetic data, and in what proportion, analogous to the tension that once existed between adopting a traditional versus a cladistic classification. Resolution of this tension is likely not imminent, and we may not wish it so, as it enlivens discussion and debate and moves systematic ichthyology onwards.

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Preface

Many years ago, when preparing to enter the American Museum of Natural History/CUNY doctoral program, I (TCG) was handed the first edition of Nelson's *Fishes of the World* by my Masters advisor who said, "Memorize it." I spent that summer memorizing the contents of the book. My first day in Donn Rosen's ichthyology class, with book in hand, I was prepared—or at least I thought I was—and thus began my love of *Fishes of the World.* Little did I know that years later, I would receive a call from my friend and colleague Joe Nelson, to help him finish the fifth edition of the book. Life had come full circle and I was honored and ecstatic to work with Joe on this project. Sadly, my friend died soon after I agreed to help with the book, and my enthusiasm quickly turned to panic.

Mark Wilson (Joe's long-time colleague at the University of Alberta), had also agreed to help. We began sifting through Joe's library, files, and correspondence, trying to assemble the information needed to revise the book. We quickly realized that Joe had been unable to make much progress apart from gathering some scientific papers and accumulating comments and corrections from colleagues about the previous edition. We enlisted two amazing colleagues, W. Cal Borden (who was a postdoc in the Grande lab, and is now an Assistant Professor at Saginaw Valley State University) and John C. Bruner, research assistant in the Wilson lab at University of Alberta, to help search through the enormous volume of systematic and taxonomic publications that had appeared since 2005. We also later solicited the help of colleagues with expertise in specific fish groups to read and critique sections of the book (see Acknowledgments). However, any errors or omissions remain the responsibility of the authors.

Since the last edition of "*Fishes*" was published, the field of ichthyology has seen an explosion of published research, molecular systematics has become mainstream, new species descriptions have flourished, and large collaborative projects such as the NSF-funded Best Fish Phylogeny Project, the All Catfish Species Inventory Project, and the Cypriniform, Euteleost and Chondrichthyan Tree of Life projects have expanded our knowledge, challenged traditional paradigms, and stimulated new efforts. Transformative technologies in both morphology (e.g., 3-D scanning and imaging) and molecular systematics (e.g., Next-Gen Sequencing) are yielding their first results and promise to advance the field even further. In the paleontological and morphological realm, there have been international collaborations, meetings, and publications generated by the Early/Lower Vertebrates and the Mesozoic Fishes communities, as well as advanced anatomical, biomechanical, physiological, and ecological studies of extant fishes. This edition of *Fishes of the World* is written to reflect the present state of knowledge in the field, which is dynamic and constantly changing. This book shows how far we have come, and reflects current thinking, but by no means should it be taken as the final answer. There is much work still to do and there are many exciting discoveries ahead.

In the fifth edition of *Fishes of the World*, we have tried to preserve key features of the previous editions such as the iconic little fishes and the pithy and sometimes eccentric style of presentation that have been a hallmark of this much loved book. We also retain the style of scientific presentation for continuity with previous editions.

The fifth edition, however, differs in many respects from previous editions. We have tried to eliminate redundancy in the descriptions. To update diversity data such as numbers of species and genera, including synonymies, we used a combination of original literature and web-based resources. The systematic relationships and classifications of all fish groups were evaluated and updated in light of current, strongly supported research findings. In cases where there was conflict among studies and no convincing evidence for change, we retained the traditional placement of the group and discussed the conflict and alternative hypotheses. Systematic relationships are now represented by a greater number of simple cladograms. We have also added a significant number of new references and brought back important references dropped from previous editions.

Numerous additional fossil taxa, many of them discovered in recent years, have now been included. However, as in previous editions, space does not permit a comprehensive treatment of the diverse and remarkable fossil record of fishes.

Working on this edition has given us a renewed appreciation for the enormity of the task that Joe Nelson completed for each of the previous editions and a deeper understanding of the innovative and important work of our many ichthyological colleagues. It is our sincere hope that you, the reader, will find this edition of *Fishes of the World* to be worthy of the memory of Joe Nelson.

Acknowledgments

We wish to first thank the many people who have helped Joe throughout the years in the preparation of the first four editions of *Fishes of the World*. This edition builds on their efforts, and their help is greatly appreciated. Please see the complete list of acknowledgements in edition four, including the following: James Albert, M. Eric Anderson, Maria Elisabeth de Araújo, Gloria Arratia, William E. Bemis, Tim M. Berra, Jack C. Briggs, John C. Bruner, George H. Burgess, Kent E. Carpenter, Jeff C. Carrier, Marcelo de Carvalho, François Chapleau, Bruce C. Collette, Sara Collette, Leonard J. V. Compagno, Wilson J.E.M. Costa, Ed J. Crossman, Mrinal K. Das, Mario C. C. de Pinna, Dominique A. Didier, Brian S. Dyer, William N. Eschmeyer, Rainer Froese, Carter R. Gilbert, Nancy Gilbert, Lance Grande, Eileen D. Grogan, William C. Hamlett, David W. Greenfield, Harry J. Grier, Gavin F. Hanke, Carl L. Hubbs, Sir Ronald A. Javitch, Zerina Johanson, G. David Johnson, Maurice Kottelat, Dick Lund, John G. Lundberg, John G. Maisey, Keiichi Matsuura, Richard L. Mayden, John E. McCosker, Bob M. McDowall, John D. McEachran, Michal Miksik, Michael M. Mincarone, Masaki Miya, John F. Morrissey, Jack A. Musick, Heok Hee Ng, J. Ralph Nursall, Larry M. Page, Lynne R. Parenti, Nick V. Parin, Colin Patterson, Daniel Pauly, John R. Paxton, Ted W. Pietsch, E. Phil Pister, Francisco J. Poyato-Ariza, Jack E. Randall, Claude B. Renaud, Tyson R. Roberts, Ierecê L. Rosa, Richard H. Rosenblatt, Hans-Peter Schultze, Kwang-Tsao Shao, Stephen H. Shih, Gerald R. Smith, William F. Smith-Vaniz, Kenneth L. Soehn, Victor G. Springer, Melanie L. J. Stiassny, Hsi-Jen Tao, Bruce A. Thompson, Andrea Tintori, James C. Tyler, Edward O. Wiley.

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We wish to extend our deepest thanks to colleagues who have taken the time to offer suggestions for improvement and/or to read and critique specific sections of the book manuscript. Their expertise and extraordinary knowledge of fishes has greatly improved the published version: Gloria Arratia (Actinopterygii), Cal Borden (Lampriformes, Paracanthopterygii), John Bruner (Perciformes), Kerin Cleason (Batomorphi), Bruce Collette (Beloniformes, Istiophoriformes, Scombriformes), Kevin Conway (Cypriniformes and Gobiesociformes), Todd Cook (Elasmobranchii), Matt Davis (primitive Neoteleostei: Ateleopodomorpha, Cyclosquamata, Scopelomorpha), Dominique Didier (Holocephali), Christopher Fielitz (Aulopiformes), Katia Gonzalez-Rodriguez (primitive Actinopterygii), Lance Grande (basal crown Actinopterygii), Zeehan Jaafar (Gobiiformes), G. David Johnson (Elopomorpha, Ovalentaria), John Lundberg (Siluriphysi), John Maisey (Chondrichthyes), Jon Moore (Berycida), Lynne Parenti (Ovalentaria), Ted Pietsch (Lophiiformes), Leo Smith (Scorpaeniformes), James Tyler (Acanthuriformes and Tetradontiformes), Mark Westneat (Trachinoidei, Labroidei). Your advice was very important to us.

Special thanks go to Cal Borden, John Bruner and Todd Cook for the many hours they spent researching the literature, and for all of the fish discussion and debate that ensued.

We sincerely thank Carter Gilbert for contributing his remembrances of Joe, and Lynne Parenti for contributing the Foreword of the book and for all of her support throughout this process, especially during the last months.

I (TCG) wish to thank my EToL collaborators for five wonderful years of intense fish discussions, debate and learning together. My special thanks go to: Rich Broughton, Andrés Lópes, Guillermo Ortí, Leo Smith and Ed Wiley. If ever there was an academic guardian angel, it was Gloria Arratia. I wish to thank her for the many years of fish conversations, collaborations and friendship. Many thanks go also to John Maisey and Maria da Gloria P. de Carvalho for sharing their scientific expertise mixed with friendship, laughter and encouragement.

To all of our Mesozoic Fishes friends and colleagues we warmly thank you for the wonderful years of camaraderie, great fish discussions and insightful discovery. It is an honor to know you all. Ping pong, hiking in the woods (thanks H.-P.), and Mexican hot chocolate will always have special memories for us. Similarly, the many colleagues and friends who shared their expertise and congenial company during the meetings and field trips of the Early/Lower Vertebrates symposia and the Circum-Arctic Paleozoic Vertebrates project deserve special mention. I (MVHW) learned so much

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Finally and most importantly, we wish to thank Joe Nelson for entrusting his book to us, and Claudine Nelson for giving us access to Joe's files and correspondence and for all of her support throughout the years. We are deeply grateful.

-T.C.G. & M.V.H.W.

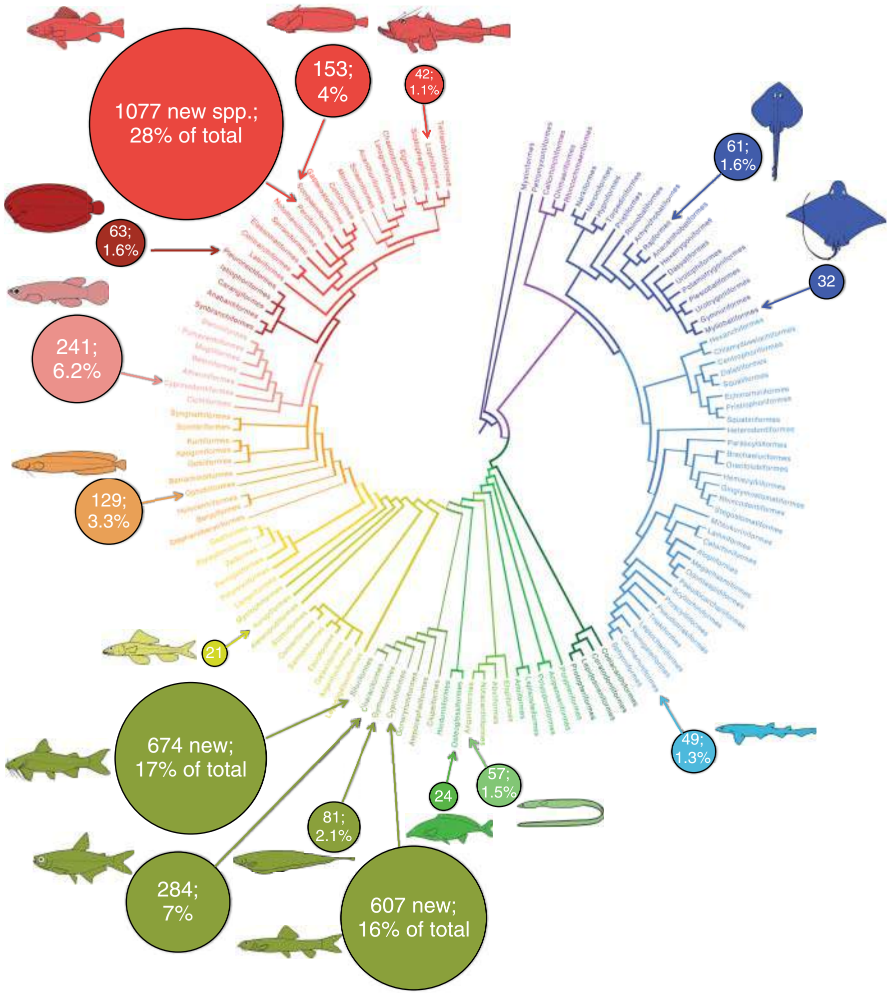
Introduction

Over one-half—32,000 species and counting—of the world's living vertebrates—more than 60,000 species—are fishes. They arose and began to radiate more than 500 million years ago and both now and in the past exhibit incomparable diversity in their morphology, in the habitats they occupy, in their physiology, and in their behavior. This diversity is, in part, what makes understanding their evolutionary history and establishing a classification so challenging and yet fascinating. From hagfishes and lampreys to sharks, lungfishes and flatfishes, fishes include a vast array of amazing adaptations to almost all aquatic environments on earth.

Since the last edition of *Fishes of the World* (2006), a great many (thousands) of important studies on fish diversity, biology, morphology, and phylogenetic relationships have been published. We now have a much better understanding of their evolutionary relationships than we had even a decade ago. Science is a continually forward-moving search for knowledge, and this book reflects scientific knowledge about fishes as it exists today. As is normal in science, future researchers will build upon and improve upon what we know now.

The body of information known about fishes is vast and includes all aspects of biology. Fishes are fascinating to researchers because of the wealth of information and diversity to be found, both in fossil and living (extant) taxa. Since the 2006 version of this book, exciting new discoveries about fish morphology and evolution have been published. These include studies about the evolution of jaws, teeth, paired fins, internal fertilization, mimicry, hearing, and the biomechanics of feeding and locomotion. There have also been revolutionary findings concerning phylogenetic relationships, such as the hypotheses that extinct placoderms may be paraphyletic, that the Holostei are again monophyletic, that elopomorphs rather than osteoglossomorphs are the basal lineage of crown teleosts, that *Lepidogalaxias* is the most basal living euteleost, and that paracanthopterygians are once again united, though with revised membership.

The toolbox of the fish systematist has expanded to include molecular sequence analysis, evolutionary (including molecular) developmental biology, and technological advances such as 3D imaging to visualize complex internal morphology of both fossil and extant species. The new tools are being applied to many of what were the most intractable problems in fish systematics, including the relationships of rays, catfishes and percomorphs. There has also been an explosion in the number and variety of web-based databases



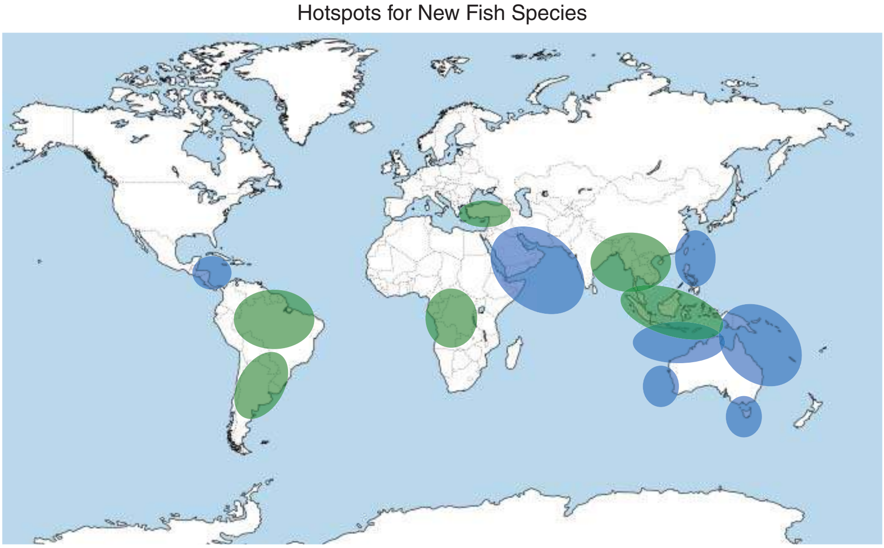
Groups of fishes in which at least 20 new species were described in the decade 2005–2014. The area of each circle is approximately proportional to the number of new species in the group. The total number of new species described was about 3900, raising the total of known valid species to more than 32,000 (Eschmeyer and Fong, 2015).

and interactive tools, including Encyclopedia of Life, Phenoscape, Fishbase, Catalog of Fishes, Index to Organism Names, World Registry of Marine Species (WORMS), online academic libraries, journal publishers' web sites, the Paleobiology Database, and Fossilworks, all of which are available to almost any researcher, and all of which have been consulted by us. We also compiled and consulted thousands of original journal articles to better understand the current state of ichthyological knowledge.

Taxonomic Diversity

Since the 2006 version, more than 3890 species have been named. The species numbers of fishes given in the text, as in previous editions, are intended to be conservative estimates of valid described species, not of all named species nor of what might be undescribed. They are based, as far as possible, on the latest taxonomic revisions of families and genera and the opinions of the specialists.

There are 85 orders and 536 families of fishes recognized in this edition. Interestingly, about two-thirds of all species in the largest families are freshwater fishes, whereas only about 43% of all fishes are predominantly freshwater species. Freshwater habitats comprise only a small proportion of the earth's surface water, but contain a disproportionately large number of the world's fish species. The known diversity of both freshwater and marine fishes continues to increase rapidly, and the regions of the world where the greatest number of new discoveries are being made are indicated in the following figure.



Geographic regions of the world in which discoveries of new fish species have been most numerous. Newly discovered marine fishes have been found most often in the SW Caribbean, NW Indian Ocean, southern China Sea, and off the corners of Australia. Newly discovered freshwater fishes have been found most often in the Amazon Basin and the Parana Basin of South America, western Equatorial Africa, and southeastern Europe, especially near Turkey, as well as in Southeast Asia.

Importance to People

Fishes, like many other forms of life, are of immense value to humans. They have long been a staple item in the diet of many peoples, unfortunately leading to the downfall of many species (e.g., Atlantic Cod, *Gadus morhua*, fished to the brink of commercial extinction in the Western North Atlantic). Today fishes form an important element in the economy of many nations while giving incalculable recreational and psychological value to the naturalist, sports enthusiast, and home aquarist. They are also the subject of international and domestic agreements (Great Lakes Fishery Commission, a cross-border cooperation between the United States and Canada in the control of lamprey) and disagreements (suspension of albacore tuna fishing by Canadian fisherman in US waters in 2012). Many government institutions are devoted to the study of fish biology and propagation (e.g., propagation of *Esox lucius* and *E. masquinongy* for stocking by the Jake Wolfe Fish Hatchery, Illinois). Particular aspects of various species lend themselves to studies in behavior, ecology, evolution, genetics, and physiology. They are used as general indicators of pollution, partly to the direct benefit of humans and partly to protect what people consider a valuable and necessary part of their heritage and life.

Systematics and Classification

Systematics is the study of biological diversity, including reconstructing the phylogenetic (genealogical) relationships of organisms. Taxonomy is that part of systematics dealing with the theory and practice of describing diversity and erecting classifications. Classification is the practice of arranging items into groups or categories, and the resulting arrangement is called a classification. Taxa (singular taxon) are groups of organisms recognized in a classification and given biological names (e.g., Salmoniformes, Salmonidae, *Oncorhynchus*, *Oncorhynchus nerka*). A category is the level or rank at which the taxon is placed (e.g., order, family, genus, species). Generally, the objective in constructing a classification of a group of organisms is to reflect what are thought to be the evolutionary relationships of the various taxa in a hierarchical system of named groups.

We give examples of recognized generic names for each family; if the number is relatively small, we usually list them all. In choosing listed examples of generic names for large families, we have tried to choose: (1) genera with many species; (2) the type genus of the family, a subfamily, or a nominal family no longer recognized; (3) genera whose species exhibit some extreme biological diversity or unusual features, especially if mentioned in text; and (4) genera whose species are commonly encountered or are important in commercial fishery, sports fishery, or aquarium use. Generic synonyms are usually given only for genera recognized as valid in earlier editions of this book but that are now considered junior synonyms, or for cases when a family-group taxon is made synonymous because its type genus has been synonymized.

We consider fossils to be critical in understanding evolutionary relationships. Unfortunately, the fossil record in fishes is incomplete (more so in some than in other groups), and many decisions must be made with little or no evidence from fossils. However, we can answer many critical questions of interrelationships of higher taxa only with the assistance of the fossil record and not, conclusively at least, from extant material only. Many important fossil taxa are ranked along with extant taxa in the classification of this book, and many others are mentioned where appropriate.

A framework of formally named and ranked taxa is an important aid to understanding and communicating the implied relationships among groups of organisms. Completely unranked classifications are popular in some circles but are not used here because they communicate little information to those without specialized knowledge.

As in previous editions, we recognize a large number of named taxa in a formal hierarchy of taxonomic categories. The taxa are always intended to be monophyletic (i.e., clades), but in many cases future research may show that they are not, and the classification must be modified accordingly.

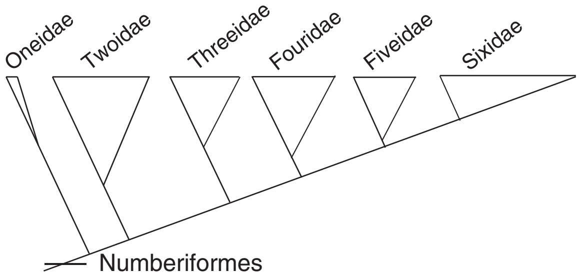
The categories used, and their endings in parentheses when consistent, are as follows: phylum, subphylum, superclass, grade, class, subclass, infraclass, division, subdivision, superorder (these 10 categories are centered in the text; the following categories are aligned left), series, subseries, infraseries, order (-iformes), suborder (-oidei), infraorder, superfamily (-oidea), family (-idae), subfamily (-inae), tribe (-ini), genus, subgenus, and species. Not all categories are employed within any one particular taxon. A dagger (†) denotes those taxa containing only fossil species.

Although there is a framework of named and ranked taxa, not all recognized (named) taxa are assigned a rank (i.e., placed in a named category). The following are examples of major taxa that are part of the classification but for which no formal rank is assigned: Vertebrata, Neoteleostei, and Acanthomorpha.

This edition, like earlier editions, adopts a simplified classification scheme, although even the simplified scheme can appear daunting. The number of categories and of named taxa are minimized by employing the "sequencing convention" for multiple named taxa at the same rank. For example, in a sequenced list of families within an order, the first family is the sister group of all others in the list, the second family is the sister of all except the first two, and so on. The last two families in the list are interchangeably each other's sisters. Consider this example classification of a hypothetical order with six families:

Order Numberiformes
Family Oneidae
Family Twoidae
Family Threeidae
Family Fouridae
Family Fiveidae
Family Sixidae

The sequence of the listed families tells us the phylogeny, using the sequencing convention. For example, Family Oneidae is the sister group of the clade of all five other families, and the Family Threeidae is the sister group of the clade of families Fouridae through Sixidae. The last two families could have been listed in either order, since they are each other's sisters. The tree that reflects these relationships is as follows:

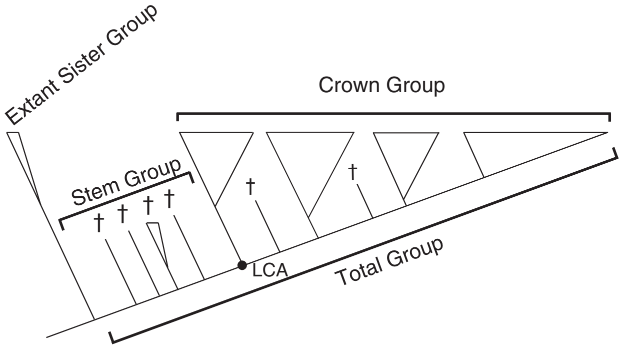


In some larger taxa, we use the term "basal" or "most basal" when referring to the lineage, usually of low diversity, that is sister to all others in the group. Some call these more basal lineages "early-branching lineages." Less often used but sometimes useful is the term "apical" or "more apical" to refer to a taxon that is high in the branching of the group's tree. A basal group is, of course, of equal age to its sister group and is not necessarily more primitive. In the tree shown above, the Family Oneidae would be considered basal while the families Fiveidae and Sixidae would be considered apical.

We report for many extant taxa the geologic age of the oldest reliably identified fossil members to give the reader an appreciation for the known fossil record. Such fossils give the minimum ages of lineages based on concrete data from the fossil record, even though in many cases the group in question must be considerably older than its first fossils because older fossils belonging to its sister-group are known. The difference between these two ages implies, for the lineage with the younger first fossil, a "ghost lineage": a period of time during which it is inferred to have existed but is not recorded by fossils found to date.

It has become popular in phylogenetic literature to include estimates of past divergence times of lineages based on rates and amounts of molecular evolution. We do not list them or use them here.

In discussing fossil relationships, we make use of the concept of stem and crown groups. For any given taxon with extant members, the crown group is all those species descended from the last common ancestor (LCA) of all the extant members (see figure). Note that certain fossil taxa can be members of the crown group.



Tree diagram illustrating stem-group and crown-group concepts.

The stem group or stem-group taxa are all those extinct taxa known by fossils that are more closely related to this particular crown group than they are to any other extant clade. The Total Group is the sum of the stem group and the crown group. Using a real example, the Teleosteomorpha are the Total Group for teleostean fishes. The Teleocephala are the Crown Group teleosts.

A friendly word on the terms "fishes" and "fish" and on capitalizing their common names: The term "fishes" is properly used when referring to individuals of more than one species. However, when referring to one or more individuals of one species, the term "fish" is appropriate. Hence, it is correct to refer to 100 Rainbow Trout as fish, but to two different trouts, such as one Brook Trout and one Brown Trout, as fishes (the plural form Rainbow Trouts is discouraged). The common names of the three species given in this example (which happen to be in three different genera) were capitalized. The principles of common names in fishes established in 1960 by a joint committee of the American Fisheries Society and the American Society of Ichthyologists and Herpetologists, and explained in Nelson et al. (2004) are followed, except that the official common name of a species is treated as if it were a proper noun (see Nelson, Starnes, and Warren, 2002), as is common for some other groups of vertebrates (such as birds).

Anatomical Terminology

When given, the numbers of abdominal and caudal vertebrae are placed in parentheses after the total vertebral number—for example, 25 (10 + 15). When possible, the length is qualified by giving standard length (SL), fork length (FL), or total length (TL). Also included are estimated numbers of recognized (valid) genera and species (in some cases the number of species in each genus is also given). These figures are always for living forms, even if fossils are known for the taxon; selected fossil taxa are mentioned separately. The degree of agreement with these figures by specialists will vary from group to group (in part due to the subjective matter of lumping and splitting). For example, nearly everyone would agree that there are but two valid species of described percopsids, but one can easily find disagreement on the number of valid species of cichlids and gobiids that should be recognized.

Proposals to change the names of some bones from those used in previous editions to conform better with probable homologies have not been adopted unless otherwise indicated. For example, as noted in Janvier (1996) and Schultze (2008), what are commonly termed the frontals and parietals in actinopterygians, terms originally taken from human anatomy, are now known to be homologous with the parietals and postparietals, respectively, of early tetrapods.

Distribution and Biogeography

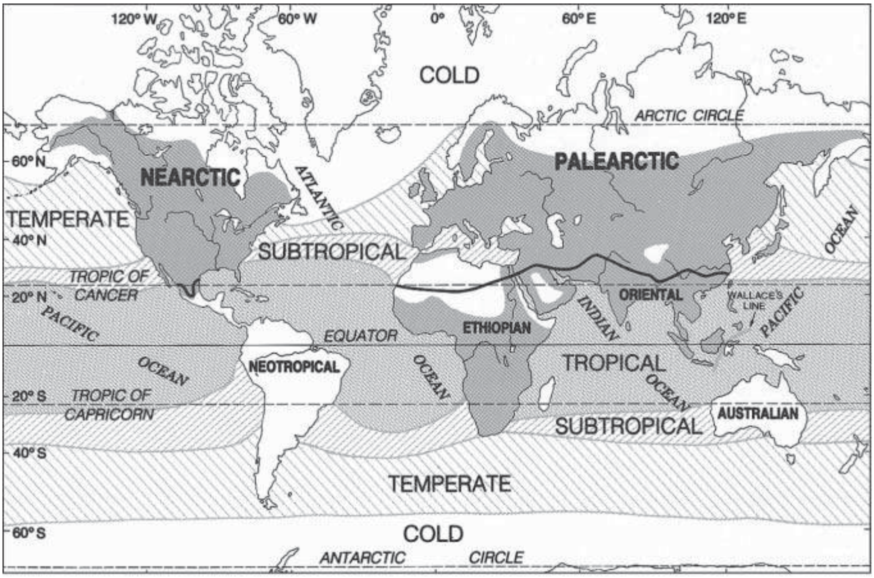
Fishes occur in lakes, streams, estuaries, and oceans throughout the world. In most species of fishes, all individuals live entirely either in fresh or in marine waters. Over 225 species are diadromous, regularly living part of their lives in lakes and rivers and part in the oceans. Among these, most are anadromous, spawning in fresh water but spending much of their time in the sea. A few are catadromous, spawning in the oceans but returning to fresh water. Classification of some species as marine, diadromous, estuarine, or freshwater is impossible, except as a generalization. Just as in an otherwise marine family there may be one species confined to fresh water, so in some species there are populations that occur in an environment opposite that of most others. Individuals of some otherwise marine species ascend rivers for short distances in part of their range, and those of some species that are usually freshwater are anadromous in some areas. Many freshwater and marine species are also common in brackish-water estuaries. About one-third of the 555 families have at least one species with individuals that spend at least part of their life in fresh water. Berra (2001) gives much information and distribution maps for the freshwater fish families.

Many environmental factors influence just where a certain species will predominate. Competition and other biological interactions may exert a strong influence along with physicochemical factors. In freshwater environments, species may show a preference for lakes or streams. Variations in preferences may exist over the range of a species. Among lakes they may show a preference for deep, cold, oligotrophic lakes or for shallower, warmer, and more productive mesotrophic and eutrophic lakes. In lake waters they may show a preference (horizontal and vertical) for the open-water limnetic zone, the benthic area, or shallow littoral areas. Fishes may even be restricted to certain types of bottom or do best under certain physicochemical conditions. Stream fishes may prefer riffle or quiet areas, and a zonation of species is usually found from the headwaters to the mouth. In the oceans, the vast majority of fishes are coastal or littoral. Most of those living beyond the 200-m-deep continental shelf (oceanic species) are deep-sea (mesopelagic, bathypelagic, abyssopelagic, or benthic at various depths); only a small minority regularly live close to the surface in the well-lighted upper 200-m zone (epipelagic), a region much larger in volume than the coastal waters. The epipelagic and mesopelagic fishes, which consist of both large predators and small plankton feeders, are varied, whereas most of the bathypelagic and abyssal fishes are relatively small.

Many species, both geologically young and old, have small ranges; the smallest is perhaps that of the Devils Hole Pupfish, *Cyprinodon diabolis*, found only in one spring in Ash Meadows, Nye County, Nevada. Many areas have a high degree of endemism. Marine fishes face the obvious land barriers (notably the New and Old World land masses) and mid-ocean barriers as well as many ecological and physiological barriers; freshwater species are limited by marine and land barriers. Some species have remarkably large ranges, and it would be interesting to know why some of their relatives have small ranges.

Over 130 marine species are known to extend around the world in tropical or subtropical waters. Many genera are represented in both the Pacific and Atlantic, but, almost always, different species are involved. Representatives of many marine genera and of some species occur in the temperate and polar faunas of both hemispheres. Individuals of some of these bipolar or antitropical taxa are surface-bound; others are deepwater. The vast majority of species, however, are tropical; most of the rest occur only in the Northern or only in the Southern Hemisphere. We know little of the abyssal depths and their species composition. Many abyssal species have been found at widely separated localities, which suggests that some may be virtually worldwide. No freshwater species is circumtropical, but two species, *Esox lucius* and *Lota lota*, are circumpolar and several others are almost so. No genus of freshwater fish has an antitropical distribution. Many freshwater fishes have shown a remarkable ability to disperse across newly exposed land areas following glaciation. In addition, they may occur in isolated waters in deserts as a result of a reduction of waters from times when drainage systems were connected.

In both fresh and marine waters, the largest number of species occurs in the tropics. There is a reduction toward the polar areas, although numbers of individuals in certain northern species are large. A great many species of freshwater fishes occur in tropical Africa, southeastern Asia, and the Amazon River—by far the world's largest river. For a tropical region, Central America has relatively few freshwater species because of the physiography and geological history of the area. Most oceanic islands lack indigenous fishes confined to fresh water, and continental areas recently exposed from the last ice age— for example, northern regions of North America, Europe (especially western Europe), and Asia—tend to have a relatively sparse fish fauna. In tropical areas, Africa exhibits the greatest diversity of nonostariophysan freshwater fishes; South America exhibits surprisingly little. In temperate areas, eastern North America shows the greatest diversity in nonostariophysan fishes. In marine waters, the Indo-West Pacific (Red Sea and Indian Ocean to northern Australia and Polynesia) is the richest, with the most species occurring in the New Guinea to Queensland area. In terms of diversity, southeastern Africa and Queensland appear to have the largest number of families of marine shorefishes. The West Indian or Caribbean fauna (southern Florida to northern Brazil) is also a rich one. The western African fauna, however, is relatively poor. Arctic and Antarctic faunas are depauperate. In all, the greatest number of fish species in the world inhabit the southeastern Asian region.



Broad surface thermal zones of the ocean, biogeographic regions of the continents, and native distribution of the family Cyprinidae, the most species-rich family of vertebrates. The biogeographical regions express degrees of endemism and are useful indicators of numbers and proportion of endemic organisms. We rarely use the continental regions in the text, and ichthyologists do not use them as much as in former times; the Nearctic and Palearctic are frequently combined into one region, the Holarctic. The thermal divisions of the sea denote tropical (or warm), subtropical, temperate, and cold (or polar) waters; warm temperate is sometimes used for all or part of the subtropical and warmer parts of the temperate (versus cool temperate) waters. Surface isotherms, used to define thermal regions, are subject to seasonal and annual changes. Major biogeographic regions recognized in the oceans include the Indo-West Pacific, tropical western Atlantic, tropical eastern Atlantic, North Pacific, North Atlantic, and Mediterranean-East Atlantic. Marine oceans share different similarities with one another; for example, for many families the tropical eastern Pacific shows a greater resemblance to the western Atlantic than to the Indo-West Pacific because of the mid-Pacific barrier and the relatively recent marine connection across the Isthmus of Panama. Information on the generalized thermal zones is based partly on Briggs (1974) and modified by numerous other sources. Distribution of the family Cyprinidae, shown by the shaded land area, is based on Berra (2001) and papers in Winfield and Nelson (1991).

Various methodological and philosophical approaches are used to explain the origin of distributional patterns of fishes, including areas of endemism. Both dispersal and vicariant events are important. Dispersal is regarded here as the movement, active or passive, of individuals to areas new to the existing population. Barriers of varying effectiveness may be involved as well as varying degrees of chance of reaching particular sites. It is of greatest biogeographic significance if the breeding range of the species is increased. Vicariance is the fragmentation of a former continuous distribution of the ancestral group into geographically separated units through the appearance of a barrier—for example, through plate tectonics. Both dispersal and vicariant approaches are used to explain disjunct distributions (the occurrence of a taxon in different areas with a marked geographical gap between them).

Examples of disjunct distributions include the following: occurrence of *Prosopium coulteri* in western North America and in Lake Superior; *Geotria australis* and *Galaxias maculatus* in Australia, New Zealand, and South America; cottids and agonids in cool temperate waters of the Northern and Southern Hemispheres; characiforms, aplocheiloids, and cichlids in Africa and South America. Plate tectonics had a profound effect on the distribution of many freshwater and marine fishes (e.g., it could well explain the occurrence of characiforms in South America and Africa), but not all disjunct distributions have a likely plate-tectonic explanation.

Human Impacts

We consider it desirable to maintain the fish diversity that systematists study, and systematists can play a leading role in protecting this diversity. We recognize the value of and our dependency upon fishes and other organisms, but our threats to the integrity of the environment also pose a serious threat to our fishes. As examples, according to the Great Barrier Reef Marine Park Authority, rising sea surface temperatures, ocean acidification, and rising sea level will negatively affect over 1600 species of fishes that live on the reef. Increased temperatures associated with lower dissolved oxygen levels in estuaries are affecting distribution patterns and abundance of Menhaden along the Atlantic and Gulf Coasts. The reduction of Menhaden, an important food source for larger fishes such as Bluefin (*Pomatomus saltatix*) and Bluefin Tuna (*Thunnus thynnus*), may likely have devastating effects on these fisheries.

Changing distribution patterns of many species and the extinction of native fishes has been directly linked to the human intervention. One recent and familiar example is the inadvertent introduction of the Round Goby (*Neogobius melanostomus*) native to central Eurasia, into the Great Lakes system via the ballast water of commercial tankers. In Lake Michigan, the Round Goby has outcompeted the native Mottled Sculpin (*Cottus bairdi*), causing its extirpation. The sheer mention of the famous Asian carp (actually the collective name for four species of carp that were imported in the 1970s to clean catfish ponds in the southern United States, but which then escaped and headed north) causes alarm. These carps are spreading widely in North American waterways, leading to habitat destruction and provoking sometimes unwise and expensive containment measures. Systematists have unique roles as experts on natural geographic distributions and as witnesses recording changes in biodiversity, whether natural or human-induced.

Phylum Chordata

Chordates are part of the superphylum Deuterostomia. The possible relationships of the chordates and deuterostomes to other metazoans were discussed by Halanych (2004). He restricted the deuterostomes to the chordates and their immediate sister group, comprising the hemichordates, echinoderms, and the wormlike *Xenoturbella*. Holland et al. (2015) reviewed the most popular theories about the origin of chordates.

The phylum Chordata has been used by most modern workers to encompass members of the subphyla Urochordata (tunicates or sea-squirts), Cephalochordata (lancelets), and Craniata (fishes, amphibians, reptiles, birds, and mammals). A fourth, fossil-only subphylum (†Conodontophorida, or conodonts) is also included here, although some authorities place it within the Craniata. Among extant taxa, the Cephalochordata and Craniata form a monophyletic group according to most authors (e.g., Cameron et al., 2000; Halanych, 2004) but some (e.g., Lowe et al., 2015) place Urochordata closest to Craniata.

Many exciting fossil finds in recent years reveal what the first fishes may have looked like, and these finds push the fossil record of fishes back into the early Cambrian, farther back than previously known. There is still much difference of opinion on the phylogenetic position of these new Cambrian species, and many new discoveries and changes in early fish systematics may be expected over the next decade. Some of the discoveries and controversies include the following.

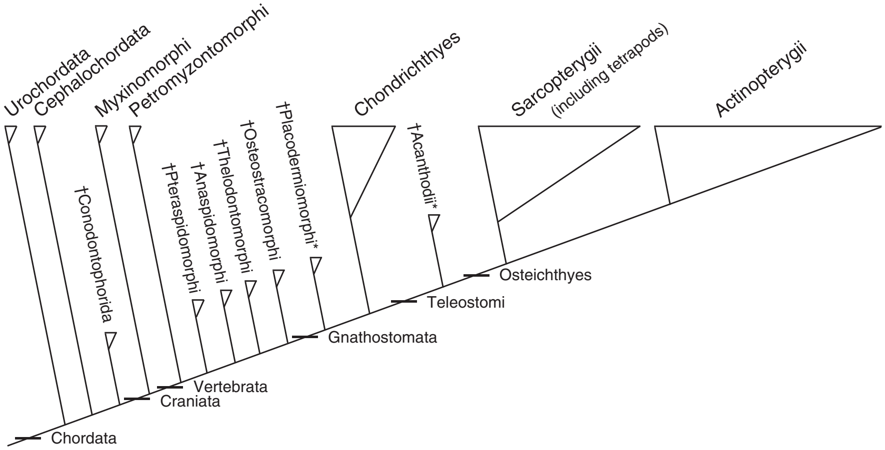
As noted by Halanych (2004), Shu and collaborators have discovered fossil ascidian urochordates (e.g., †*Cheungkongella*), cephalochordate-like yunnanozoans (†*Haikouella* and †*Yunnanozoon*), and possible jawless craniates (†*Myllokunmingia*; its possible junior synonym is †*Haikouichthys*) over the last two decades, thus pushing the origins of these three major taxa at least back to the Early Cambrian (approximately 530–540 million years ago). These Early Cambrian fossils from Yunnan, China, lacked bone, but some of their soft anatomy was fossilized (Janvier, 1999; Shu et al., 1999).

Concerning †*Myllokunmingia* and †*Haikouichthys*, Shu et al. (1999) presented a phylogeny with †*Myllokunmingia* as sister to the remaining vertebrates and †*Haikouichthys* as sister to a clade with lampreys. Hou et al. (2002) described details of a new specimen co-occurring with the nominal †*Myllokunmingia fengjiaoa* and †*Haikouichthys ercaicunensis* and concluded that all are conspecific, favoring use of the oldest name †*Myllokunmingia fengjiaoa.* Characters include filamentous gills, V-shaped myomeres, and a distinct dorsal fin (the latter indicating a more derived condition than in the hagfish). Their phylogenetic analysis suggested that (the combined) †*Myllokunmingia* is either the sister group to the lampreys or the sister group to the vertebrates. However, not all authorities have agreed about the synonymy. Shu et al. (2003a) continued to argue that the taxa were distinct, placing †*Haikouichthys* either in a trichotomy with hagfishes and all vertebrates (i.e., including possibly as a stem craniate) or as the sister group to all vertebrates (i.e., in a position similar to that of †*Myllokunmingia*).

Concerning the yunnozoans, Shu et al. (2003b) and Shu and Morris (2003) proposed that the Early Cambrian †*Haikouella* and †*Yunnanozoon* are stem-group deuterostomes, and questionably placed them in the phylum †Vetulicolia, class †Yunnanozoa, family †Yunnanozoidae (= †Yunnanozoonidae). However, Mallatt et al. (2003) disagreed, interpreting †*Haikouella* not as a non-chordate stem-group deuterostome but rather as a chordate that is the immediate sister group of all craniates. The details of the relationships of these highly interesting fossils remain to be settled.

Other debates concern extant taxa, including a disagreement about the correct classification of the hagfishes (Myxiniformes) and the lampreys (Petromyzontiformes). This debate is discussed below under subphylum Craniata.

The following tree diagram illustrates the arrangement of the main chordate taxa adopted here and treated in the pages that follow. The diagram and the



Phylogeny of the main groups of Chordata. Explanation of symbols: †: taxon is extinct; *: taxon is paraphyletic according to some authorities.

following pages include a selection of key fossil groups, each indicated by a shorter branch and by a dagger preceding its name.

SUBPHYLUM UROCHORDATA (Tunicata: the tunicates)

The tadpole larvae of tunicates possess gill slits, dorsal hollow nerve cord, notochord, and a muscular, unsegmented tail; the adults are usually sessile filter feeders and usually lack the preceding features. Feeding is by means of a mucous trap (i.e., endostyle) inside the pharynx as in cephalochordates and ammocoete larvae.

About 1,600 extant species are known, in three classes. Fossils include †*Shankouclavis* and possibly †*Cheungkongella* from the Early Cambrian Chengjiang biota of China (Shu et al., 2001; Chen et al., 2003). Although ascidian-like, their relationships to a particular class of Urochordata are unclear (Chen et al., 2003).

Class ASCIDIACEA (ascidians)

Larvae of ascidians free-swimming, tadpole-like (short-lived and nonfeeding); adults sessile benthic, solitary or colonial, and without a tail.

Ascidians are marine and distributed worldwide, extending from the intertidal well into the abyssal-benthic regions of the oceans.

Class THALIACEA (salps)

Larvae and adults of salps transparent, pelagic; adults may be solitary or colonial. They tend to be planktonic but are generally capable of weak movements. Remarkable life cycles are characteristic of this group, with sexual and asexual reproductive stages occurring.

Order PYROSOMIDA. Marine, worldwide except the Arctic Ocean. They can emit a strong phosphorescent light. Colonies tubular with a common atrial chamber and varying in length from about 3 cm to 1 m.

Order DOLIOLIDA (Cyclomyaria). Marine; primarily tropical to temperate. Generally barrel-shaped with eight or nine muscle bands around the body.

Order SALPIDA (Hemimyaria). Marine, all oceans. Cylindrical or prism-shaped.

Class APPENDICULARIA (Larvacea)

Pelagic, marine, all oceans from Arctic to Antarctic. Larval characteristics (such as tail) retained in adult.

SUBPHYLUM CEPHALOCHORDATA (Acrania, in part)

The notochord of cephalochordates extends to the anterior end of the body, anterior to the brain. Cranium absent; vertebrae absent; no cartilage or bone; heart consisting of a contractile vessel; red blood corpuscles absent; liver as a gut diverticulum; musculature segmented; epidermis as a single layer of cells; excretion by protonephridia with solenocytes; endostyle specialized (with iodine-fixing cells); true brain absent, but two pairs of cerebral lobes and nerves present; sexes separate.

About 30 species. Fossils likely include †*Pikaia* from the Middle Cambrian Burgess Shale of Canada, and †*Cathaymyrus* from the Early Cambrian Chengjiang fossil site in China (Shu et al., 1996; Conway Morris and Caron, 2012; Donoghue and Keating, 2014).

Cephalochordates and craniates share the following attributes (some also are present in the urochordates): notochord present (at least in embryo), a dorsal tubular central nervous system, paired lateral gill slits (at least in embryo), post-anal tail, hepatic portal system, and endostyle (homologous with the thyroid).

Order AMPHIOXIFORMES (lancelets). The lancelets (or amphioxus) are small (up to 8 cm long), slender, fishlike animals, probably close to the ancestral vertebrate lineage. They spend most of their time buried in sand or coarse shell gravel and occur primarily in shallow-water tropical and subtropical seas with some species extending into temperate waters as far north as Norway and as far south as New Zealand; they are particularly common off China. Feeding occurs by straining minute organisms from the water that is constantly drawn in through the mouth. A good coverage of lancelets was given in Poss and Boschung (1996) and other articles in the same issue.

Family BRANCHIOSTOMATIDAE. Marine; Atlantic, Indian, and Pacific.

Double row of gonads; metapleural folds symmetrical, located laterally along ventral side and ending near the atriopore, neither fold connected with the median ventral fin.

One genus, *Branchiostoma*, with about 23 species.

Family EPIGONICHTHYIDAE (Asymmetrontidae). Marine; Atlantic, Indian, and Pacific.

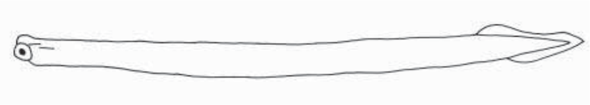
Gonads present along right side only; metapleural folds symmetrical, right fold continuous with ventral fin, which passes to the right of the anus, and left fold ending behind atriopore.

One genus, *Epigonichthys* (synonyms *Asymmetron*, *Heteropleuron*), with about seven species, occurring primarily in the Indo-West Pacific.

† SUBPHYLUM CONODONTOPHORIDA (conodonts)

†Class CONODONTA

Conodonts were diminutive, eel-like animals with a dental apparatus of many distinctively shaped, phosphatic, tooth-like structures arranged in an intricate pattern of paired and unpaired elements. Their lifestyle is often supposed to have been one of scavenging dead and dying animals, with the dental apparatus being used to tear and slice flesh from carcasses and then process it for ingestion. The tooth-like elements themselves are often called conodonts, are usually found as isolated fossils, and can often be identified to the species level; the diversity, rapid evolution, and wide geographic distribution of conodont species has made them useful as biostratigraphic indicators for much of their Late Cambrian to Late Triassic geologic range. Conodonts were reviewed by Aldridge and Donoghue (1998), with additional information in Purnell et al. (2000).



Although known in the fossil record for over a century and a half since their initial discovery by Pander (1856), their phylogenetic position has long been the subject of debate. Some earlier workers thought that these interesting eel-like animals might be related to early fishes (and therefore they were included in the Chordata by Nelson, 1976). It has only been since the early 1990s, with the discovery of articulated, soft-body fossils, that their chordate affinities were confirmed; inclusion within Chordata has not been seriously challenged since then; however, their precise relationships within Chordata are still a matter of much discussion. For example, Krejsa and Slavkin (1987) argued that they have a relationship to hagfishes. Nelson (1994) placed conodonts between the cephalochordates and the craniates, in the subphylum †Conodontophorida, as done here. Donoghue et al. (2000), among others, placed them within vertebrates or even as stem gnathostomes ("crownward" of both hagfishes and lampreys); Nelson (2006) followed this approach. However, Kemp (2002) gave evidence that conodont "teeth" do not contain hard tissues homologous with bones and teeth of vertebrates, as agreed by Donoghue and Keating (2014). Recently, Turner et al. (2010) evaluated much old and new evidence and concluded that conodonts were neither vertebrates nor craniates, though this was disputed by Donoghue and Keating (2014). In the present edition, we follow Turner et al. (2010), and once again classify conodonts, as in Nelson (1994), as subphylum †Conodontophorida, closely related to but not within the subphylum Craniata.

SUBPHYLUM CRANIATA

Notochord never extending in front of brain; cranium present; vertebrae usually present; cartilage or bone or both present; heart chambered; red blood corpuscles usually present; brain well developed; 10 to 12 pairs of cranial nerves; dorsal and ventral nerve roots usually united; nephridia absent; epidermis with several cell layers; endostyle only in larval lampreys (ammocoetes) and transformed into thyroid tissue in all others; sensory capsules (e.g., nasal, optic, otic) present; neural crest forms in the embryo and induces the development of many important tissues and organs. The neural crest is a vertebrate novelty from which the first vertebrate bony tissues may have arisen (e.g., probably dermal bones, teeth, anterior neurocranium, and visceral arches). Maisey (2001a) reviewed the structure and function of the craniate inner ear and identified 33 apomorphic characters of the membranous labyrinth and associated structures in craniates, gnathostomes, and elasmobranchs.

The classification followed here, except for the relationships of conodonts and †*Eriptychius*, is based on the cladogram and classification of Donoghue et al. (2000). Their classification was sequenced (each taxon in the sequence at the same rank being sister to all following taxa at that rank) as follows: Cephalochordata, Myxinomorphi, Petromyzontomorphi, †Conodonta, †Pteraspidomorphi (with †*Astraspis*, †Arandaspida, and †Heterostraci sequenced in that order), †Anaspidomorphi, †Thelodontomorphi (represented in their study only by †*Loganellia*), †Osteostracomorphi (including †Osteostraci, †Pituriaspida, and †Galeaspida), and finally a clade of the poorly known †*Eriptychius* plus gnathostomes. An excellent introduction to the lower vertebrates known from the fossil record is that of Long (2011).

Although vertebrates or craniates without jaws are often called agnathans, derived from an earlier taxonomic name Agnatha, meaning “lacking jaws,” this is no longer considered a valid taxon because the various members represent separate and successive branches from the vertebrate stem (see earlier phylogeny diagram); thus, agnathans are paraphyletic. However, the term agnathan is a useful one that is still often used to refer collectively to these primitive fishes. Similarly, the ostracoderms, formerly used for fossil, armored jawless fishes, are also now agreed to be a paraphyletic assemblage. Forey (1995) reviewed past theories of character evolution and relationships of agnathans and gnathostomes.

The (paraphyletic) jawless fishes (agnathans) share the following mostly primitive features: lack of jaws that are derived from gill arches (a biting apparatus, not derived from gill arches, is present in some fossil forms and in hagfishes); one or two (vertical) semicircular canals (one canal but two ampullae reported in myxiniforms, two canals in petromyzontiforms, at least two in pteraspidiforms, two and not three in osteostracans) but no agnathan has been shown to have the third, horizontal canal that is present in all gnathostomes; vertebral centra never present (only the notochord); gills covered with endoderm and directed internally; gill arch skeleton fused with neurocranium, external to gill lamellae; gills opening to surface through pores or a single pore rather than through slits; bony exoskeleton present in most.

The term cyclostome is sometimes used for the living jawless fishes (hagfishes and lampreys); this group is considered by most paleontologists and others using morphological evidence to be paraphyletic (i.e., not a clade). The corresponding hypothesis, called the "vertebrate hypothesis," holds that lampreys are more closely related to gnathostomes than to hagfishes, and is followed here. According to this view, hagfishes are craniates but not vertebrates. Their sister group is the vertebrates, of which the lampreys are the earliest branch still extant.

However, there is an alternative hypothesis, termed the "cyclostome hypothesis," which holds that lampreys and hagfishes are monophyletic together and sister groups to each other. The latter grouping is an old idea that was discarded by morphologists as not explaining the morphological data well, including evidence from fossils, but it is supported by molecular evidence from Mallatt and Sullivan (1998), Mallatt et al. (2001), Kuraku et al. (1999), Delarbre et al. (2002), and Takezaki et al. (2003), to name some early proponents. Under this hypothesis, the many morphological differences between lampreys and hagfishes evolved after their ancestral lineage split. Recently, developmental data for hagfishes has been interpreted as supporting the cyclostome hypothesis (e.g., Oisi et al. 2013; but see Miyashita and Coates 2015).

Unfortunately, there are very few fossil representatives for either hagfishes or lampreys (Janvier and Sansom 2015), and molecular evidence is only available from extant species. Moreover, available outgroups such as cephalochordates and conodonts do not show homologs of the key debated features seen in hagfishes, lampreys, and gnathostomes, leaving most morphological and developmental observations equally consistent with the cyclostome and paraphyletic hypotheses (Miyashita and Coates 2015). To help resolve this issue, Meyer and Zardoya (2003) suggested using larger data sets with greater taxon sampling, but the discovery of more primitive outgroups, or perhaps intermediate fossils linking two of the three groups would probably help settle the controversy.

There are about 16 genera and 118 species of extant jawless fishes in four families, although there are many more orders, families, genera, and species of fossil agnathans known than of extant agnathans (e.g., Long, 2011). The three major clades of craniates that have living species—hagfishes, lampreys, and gnathostomes—have a total of about 60,000 species (including tetrapods).

INFRAPHYLUM MYXINOMORPHI

This taxon is thought to be the sister group of vertebrates and to be the most primitive known craniate taxon. Extant hagfishes are excluded from the Vertebrata primarily because they lack arcualia (embryonic or rudimentary vertebral elements).

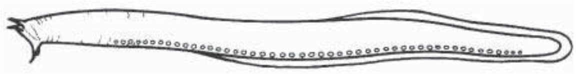
Class MYXINI

Order MYXINIFORMES (Hyperotreti) (1)—hagfishes. One semicircular canal (and one macula); single olfactory capsule with few folds in sensory epithelium, and olfactory nerves with separate bundles; no bone; lens and extrinsic eye muscles absent; 1–16 pairs of external gill openings; adenohypophysis with undifferentiated cellular elements, not divided into distinct regions (unlike in vertebrates); hypoglossal nerve absent (represented by separate, segmentally arranged, anterior spinal nerves); body naked, eel-like; no paired fins; no trace of lateral-line system in adults, neuromasts absent.

Hagfishes are unique among craniates in having only one semicircular canal, which is orientated so that it projects onto all three planes of rotation (lampreys and fossil agnathans, where known, have two and gnathostomes have three) (Jørgensen, 1998; McVean, 1998).

One family with 78 species. The three subfamilies recognized here are based on Fernholm et al. (2013). A probable fossil hagfish, †*Myxinikela siroka*, of Pennsylvanian age (about 300,000,000 years ago), described in 1991, is known from a single specimen from Illinois (Bardack, 1998). Janvier (1996) speculated that the fossil †*Gilpichthys*, of Mississippian age, might have affinities with the myxiniforms (see also later under †Mayomyzontidae).

Family MYXINIDAE (1)—hagfishes. Marine, temperate zones of the world (and Gulfs of Mexico and Panama).



Dorsal fin absent (caudal fin extends onto part of dorsal surface); eyes degenerate; barbels present around biting mouth; teeth only on tongue, plus one on “palate”; dorsal and ventral nerve roots united; nasohypophyseal sac not blind, opening into pharynx; no spiral valve or cilia in intestinal tract; numerous mucous pores along body (shown in sketch); no cerebellum; ovaries and testes in same individual but only one gonad functional; eggs large, yolky, up to 30 per individual; no metamorphosis; low blood pressure. In stating that their eyes are degenerate, it is assumed that hagfishes evolved from an ancestor with eyes, and this is supported by the possible hagfish fossil †*Myxinikela*, which is thought to have had relatively well-developed eyes (Bardack, 1998). There is some variation in the structure of their eyes. In *Eptatretus*, generally in shallower water than *Myxine*, the eye has a vitreous body and well-differentiated retina and lies beneath unpigmented skin (presumably the more primitive state), whereas the deepwater *Myxine glutinosa* lacks a vitreous body, has a poorly differentiated retina, and is buried beneath muscle (Locket and Jørgensen, 1998). The external nasohypophyseal opening is terminal, and it is through this opening that respiratory water passes backward to the gills (unlike lampreys).

Hagfishes are scavenger feeders, emerging from burrows and mostly eating the insides of dying or dead invertebrates and vertebrates. They are the only craniate in which the body fluids are isosmotic with seawater. The mucous pores occur in two ventrolateral lines, each with about 70–200 slime glands that contain mucous cells and thread cells. The thread from the discharged thread cell of hagfishes probably gives tensile strength to the slime. The thread cell itself is not known from any other animals. The secreted slime may be important for defense, where it may clog the gills of other fishes and cause suffocation. Hagfishes can go through knotting movements to free themselves from entanglement, escape capture, or tear off food. Extensive information on hagfishes is found in Jørgensen et al. (1998). Maximum length is up to about 1.1 m, attained in *Eptatretus carlhubbsi.*

Six genera with about 78 species. The following classification is based on Fernholm et al. (2013).

SUBFAMILY RUBICUNDINAE. Elongated tubular nostril; reddish or pinkish body color.

One genus, *Rubicundus* with up to four species. This recently named subfamily is thought to be the sister group of other hagfishes (Fernholm et al., 2013).

SUBFAMILY EPTATRETINAE. Efferent branchial ducts open separately to the exterior with 5–16 external gill openings.

One genus (Fernhom and Quattrini 2008; Fernholm et al., 2013), *Eptatretus* (synonyms *Bdellostoma* and *Polistotrema*, *Paramyxine,* and *Quadratus*) with about 51 species (McMillan, 1999; McMillan and Wisner, 2004). Fernholm (1998) treated *Paramyxine* (with species from Japan and Taiwan) as a synonym of *Eptatretus*; however, it continued to be recognized by workers such as Mok (2001) and Mok et al. (2001). *Quadratus* had been established for species of *Paramyxine* with nonlinear and crowded gill apertures by Wisner (1999), who recognized it in its own subfamily, Quadratinae. Wisner (1999) also placed *Paramyxine* (with gill apertures linear or near linear) in its own subfamily, Paramyxininae. The two new subfamilies were distinguished from the Eptatretinae by having the first efferent branchial duct much longer than the last (versus all being about equal in length). However, Fernholm (1998) regarded *Paramyxine* as synonymous with *Eptatretus.* A recent molecular phylogeny and revised taxonomy by Fernholm et al. (2013) separated the subfamily Rubicundinae from the Eptatretinae and confirmed the four generic synonymies listed above with *Eptatretus.* Additional new species were described recently by Mincarone (2000), Mincarone and McCosker (2004), Mok et al. (2001), Mincarone and Stewart (2006), and by Fernholm and Quattrini (2008). Oisi et al. (2015) studied the adult form and development of homologs of the hypobranchial muscles and their innervation.

SUBFAMILY MYXININAE. Efferent branchial ducts opening by a common external aperture on each side (i.e., only one pair of branchial openings). The pharyngocutaneous duct, which exits the pharynx behind the gills, is present only on the left side and probably functions to permit the pharynx to be flushed, thus clearing particles too large for the afferent branchial ducts. Four genera and about 27 species.

Myxine. Anal fin ending posterior to branchial aperture; 5 to 7 pairs of gill pouches. Atlantic and Pacific; about 22 species. Wisner and McMillan (1995) and Fernholm (1998) recognized 19 species. *Myxine limnosa* is not recognized here for reasons given in Nelson et al. (2004). New species have been named recently by Mincarone (2001a), Mok and Kuo (2001), Mok (2002), and Møller et al. (2005).

Notomyxine tridentiger. The pharyngocutaneous duct opens separately to the exterior, leaving two apertures on the left side instead of one as in all other Myxininae (in which it opens into the left common branchial aperture). Buenos Aires to Tierra del Fuego.

Neomyxine biniplicata. A pair of short ventrolateral finfolds behind the branchial region (lateral finfolds are absent in other hagfishes). Cook Strait, New Zealand.

Nemamyxine. Anal fin extending anterior to branchial apertures. Two species, one from New Zealand and the other from southern Brazil, Uruguay, and northern Argentina (Mincarone, 2001b).

INFRAPHYLUM VERTEBRATA (vertebrates)

The following taxa, placed within six superclasses, are recognized here in the Vertebrata following Donoghue et al. (2000). This monophyletic group contains members possessing or inferred to be derived from ancestors with features such as a dermal skeleton and embryonic neural crest.

Many of the earliest vertebrate remains are known from isolated microfossils (microvertebrates, ichthyoliths) such as scales and teeth. Their use in providing information on such things as evolutionary origin, geologic age, and geographic distribution of taxa and for providing phylogenetic characters were reviewed by Turner (2004), particularly for microfossils of thelodonts, chondrichthyans, and acanthodians. Such microfossils can usually very precisely be identified to order, family, genus, and species, and their positions on the body can often be reconstructed with confidence, but it can be challenging to allocate them to the correct higher taxonomic groups.

†*Anatolepis heintzi.* known from the Late Cambrian to Early Ordovician in Spitsbergen and Greenland, was originally described as heterostracan agnathan, but its placement as a vertebrate was later questioned. Smith and

Sansom (1995), however, showed that dentine is present in the tubercles, and it is placed in the Vertebrata, although in an uncertain position.

SUPERCLASS PETROMYZONTOMORPHI

Class PETROMYZONTIDA

Order PETROMYZONTIFORMES (Hyperoartii) (2)—lampreys. Two semicircular canals; seven pairs of external lateral gill openings; eyes well developed in adult, lateral (except in *Mordacia*); single median nostril (nasohypophyseal) opening between eyes with pineal eye behind; body naked, eel-like; no bone; no paired fins; one or two dorsal fins present; tail diphycercal (isocercal) in adults, hypocercal in ammocoete larvae; barbels absent; teeth on oral disc and tongue (except in fossil form); dorsal and ventral nerve roots separated; nasohypophyseal sac with external opening only; spiral valve and cilia in intestinal tract; small cerebellum; sexes separate; eggs small, not yolky, occurring in the hundreds (*Mordacia praecox*) to thousands; larval stage (ammocoete) undergoes radical metamorphosis in freshwater. All lampreys die shortly after spawning.

Lampreys are either parasitic or nonparasitic, and both life-history types characterize individuals of closely related species. It is believed that nonparasitic species have been independently derived from a parasitic species. The parasitic phase, after metamorphosis from the ammocoete larvae but before reproducing, goes through a period of feeding on blood from other fishes (very rarely on other animals) by rasping through their skin. The nonparasitic phase reproduces, without feeding, after metamorphosis. It is always confined to fresh water, whereas the parasitic form may be freshwater or anadromous. No parasitic freshwater lampreys are known from the Southern Hemisphere. Maximum length of larvae about 22 cm and parasitic adult about 1.2 m.

The sister group of the petromyzontiforms was previously thought to be, by different authorities, myxinids (see preceding discussion), †*Jamoytius kerwoodi*, or anaspidiforms. They were placed in the Class Cephalaspidomorphi in Nelson (1994). Their sister group is now postulated to be the large clade of all other vertebrates, following Donoghue et al. (2000).

The phylogenetic study of Gill et al. (2003) found a trichotomy among the monophyletic Northern Hemisphere family Petromyzontidae and the two Southern Hemisphere families Geotriidae and Mordaciidae, and recommended that all three be treated as separate families. This recommendation is followed here. In the previous edition, all four lineages were recognized as subfamilies within the one family, Petromyzontidae.

There are 10 genera with 40 extant species (Renaud, 1997, 2011; Gill et al., 2003; Kullander and Fernholm, 2003). The order was recently reviewed by

Renaud (2011), who recognized 40 species in three extant families. Three additional species have since been described. One family is known only from fossils. About 29 species are confined to fresh water, and 18 feed parasitically as adults.

†Family MAYOMYZONTIDAE. Pennsylvanian. Teeth absent. The only species assigned to this family, †*Mayomyzon pieckoensis*, described in 1968, is known from Illinois from the same geological horizon as the fossil hagfish †*Myxinikela* (Bardack, 1998). The specimens are all small in size but have adult characteristics. They are known from marine beds but need not have been marine themselves. Their known character states were compared to other lampreys in Gill et al. (2003).

A second species of fossil lamprey, †*Hardistiella montanensis*, from the Mississippian Period (about 320,000,000 years ago) in Montana, is of uncertain relationship to †*Mayomyzon*. This species retains a distinct hypocercal tail, has rays in the anal fin, and appears to lack an oral sucker. The number of gill openings cannot be determined. Other fossil agnathans include †*Gilpichthys* and †*Pipiscius*, but Bardack (1998) argued that they cannot be placed with any known family lineage.

Family PETROMYZONTIDAE (2)—northern lampreys. Anadromous and freshwater; cool zones of the Northern Hemisphere, generally north of 30°N.

Three or four lateral circumoral teeth on each side of oral aperture (five or more in other lampreys); dorsal fins continuous or contiguous in mature adults (separate in other lampreys); small or no gular pouch in adult males; cloaca located under anterior half of second dorsal fin or anterior half of posterior lobe of the single dorsal fin in adults (Gill et al., 2003).

The following recognition of subfamilies is based on the cladogram of Gill et al. (2003). The subgenera recognized in *Lampetra* by Nelson (1994), with the exception of *Okkelbergia*, are recognized as genera following Renaud (1997, 2011) and Gill et al. (2003). The numbers of species follow Renaud (1997, 2011).

Eight genera with 42 species.

SUBFAMILY PETROMYZONTINAE. Median velar tentacles absent (one or two in other lampreys). Two genera with seven species as follows.

Ichthyomyzon. Freshwater; eastern North America; three pairs of species (i.e., six species), each pair with an ancestral parasitic species and a nonparasitic derivative.

Petromyzon marinus. Anadromous (landlocked in Great Lakes region); Atlantic drainages of Canada, United States, Iceland, and Europe (including the Mediterranean); parasitic.

SUBFAMILY LAMPETRINAE. Tuberculated or papillose velar tentacles in most (smooth in other lampreys); 60 to 70 trunk myomeres in most (usually fewer than 60 or more than 70 in other lampreys).

Six genera as follows. According to the cladogram of Gill et al. (2003), *Caspiomyzon* is sister to the other five genera and *Tetrapleurodon* is sister to a clade comprising the remaining four genera, in which several nominal species exist that are of uncertain status and are not recognized here; these could be recognized in three sequenced tribes.

Caspiomyzon wagneri. Caspian Sea basin; probably parasitic.

Tetrapleurodon. Freshwater; Rio Lerma system of southern Mexico; nonparasitic and parasitic; two species, *T. geminis* and *T. spadiceus.*

Entosphenus. Anadromous and freshwater; coastal regions of North Pacific in North America and Asia; parasitic and nonparasitic; seven species.

Eudontomyzon. Freshwater; Black Sea drainage (primarily Danube basin), China, and Korea; parasitic and nonparasitic, five species.

Lampetra. Anadromous and freshwater; coastal regions of Europe and North America; parasitic and nonparasitic; ten species (this includes the nonparasitic *L. aepyptera,* southeastern United States, recognized in the subgenus *Okkelbergia* in Nelson (1994).

Lethenteron. Anadromous and freshwater; circumarctic drainage basins, western Pacific coast south to Japan, coastal regions of western Alaska, eastern North America, and Adriatic Sea basin; parasitic and nonparasitic; seven species.

Family GEOTRIIDAE (3)—southern lampreys. Anadromous; Southern Hemisphere, southern Australia, Tasmania, New Zealand, Chile, Argentina, and the Falkland and South Georgia islands.

Teeth on oral disc are spatulate-shaped (pointed or rounded in other lampreys); supraoral lamina (= supraoral plate) with two large centrally located teeth flanked by two lateral flanges; transverse lingual lamina strongly trident, bident at maturity; velar tentacles 23–32; the two median velar tentacles are fused for at least a third of their length; two of the oral papillae are enlarged; presence of two types of cone and one rod in the retina; two simple diverticula in midgut of ammocoetes; caudal and second dorsal fins well separated in the immature (continuous or contiguous in other lampreys); dorsal fins separate from each other in mature adults; approximately 180 mainly acrocentric chromosomes; prominent longitudinal dorsolateral blue-green stripe on either side of adult body during the marine phase and early part of the upstream migration (Gill et al., 2003). Parasitic.

One species, *Geotria australis* (e.g., Hubbs and Potter, 1971; Kullander and Fernholm, 2003).

Family MORDACIIDAE (4)—southern topeyed lampreys. Anadromous and freshwater; Southern Hemisphere, southeastern Australia, Tasmania, and southern Chile.

Velar tentacles fewer than 5; dorsal fins separate from each other in mature adults; two discrete supraoral laminae (= supraoral plate); transverse lingual lamina with enlarged median cusp flanked by small cusps and a larger subterminal cusp; lateral circumorbitals elongated, extending throughout much of the lateral field of the oral disc; no fimbriae around oral disc; oral papillae absent in the apical region of the oral disc; eyes dorsolateral in immature and dorsal in mature adults (lateral to dorsolateral in other lampreys); retina with a large rod photoreceptor and no cone receptor; cloaca located under posterior half of second dorsal fin; 76 metacentric and submetacentric chromosomes; ammocoetes with single intestinal diverticulum in which the internal walls are folded (Gill et al., 2003). Parasitic and nonparasitic.

One genus, *Mordacia*, with three species (e.g., Hubbs and Potter, 1971; Kullander and Fernholm, 2003).

THE FOLLOWING FOUR SUPERCLASSES, the so-called ostracoderms (†Pteraspidomorphi, †Anaspidomorphi, †Thelodontomorphi, and †Osteostracomorphi) represent clades of craniates with bony dermal armor or scale covering; their status as monophyletic groups is generally agreed, but the precise sequence of their branching is still in doubt; some authorities (e.g., Donoghue et al., 2000) have placed †Pteraspidomorphi as the first branch, while others (e.g., Janvier, 2015) have placed †Anaspidomorphi as first in the sequence. All four are known only from the Devonian and earlier periods. Among the gnathostome (jawed vertebrate) features that appear in one or more of these clades are paired (pectoral and pelvic) fins. Coates (2003) discussed the possible evolutionary origin of paired fins, and reevaluated classic theories of limb evolution, including Gegenbaur's transformational hypothesis of gill arches to limb girdles and the more widely accepted lateral fin-fold theory credited to both Balfour (1876) and Thacher (1876). Wilson et al. (2007) reviewed the occurrence and morphology of paired fins in various agnathans and primitive gnathostomes, concluding that homologous but sometimes rudimentary precursors of both pectoral and pelvic fins of gnathostomes occurred in †Anaspidomorphi, †Thelodontomorphi, and †Osteostracomorphi. Paired fins are unknown in the †Pteraspidomorphi.

†SUPERCLASS PTERASPIDOMORPHI

†Class PTERASPIDOMORPHA (Diplorhina)

Shield made of a large dorsal and ventral median plates; oak leaf–shaped tubercles on dermal bone; true bone cells absent (the acellular nature of the bone may be a primitive rather than a secondary condition, unlike "acellular" bone in higher fishes, which is derived from cellular bone); at least two semicircular canals.

Monophyly of this group was recognized by Blieck et al. (1991) and Gagnier (1993). This has been supported by Janvier (1996) and Donoghue et al. (2000), but they express differing views on the sister-group relations of the Astraspida, Arandaspida, and Heterostraci, here ranked as subclasses. The cladistic results of Donoghue et al. (2000), in finding †*Astraspis* to be sister to the Arandaspida and Heterostraci, are followed here.

As with many fossil groups, especially the agnathans, it must be remembered that many character states are poorly known or only inferred (e.g., see descriptions in Janvier, 1996).

†Subclass ASTRASPIDA

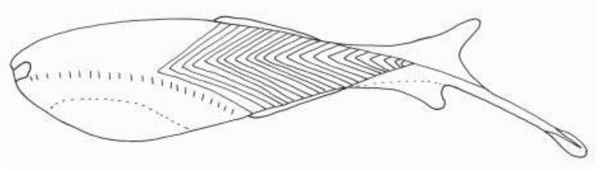
Thick, glassy enameloid caps on the tubercles of the ornamentation; eyes small and laterally placed; gill openings at least eight, relatively large and with no cover; paired fins absent (Janvier, 1996).

†Order ASTRASPIDIFORMES. Marine, North America and Siberia, Late Ordovician to Early Silurian, jawless vertebrates, comprising at least †*Astraspis* (including †*Pycnaspis*). The poorly known Ordovician †*Eriptychius* (placed in the Eriptychiida) (e.g., Gagnier, 1993; Janvier, 1996) is placed here by some; however, Donoghue et al. (2000) raised the possibility, despite incomplete information, that it may be the sister group to the jawed vertebrates (gnathostomes).

†Subclass ARANDASPIDA

Eyes in extreme anterior position, facing anteriorly at front of head; paired depressions on top of head interpreted as paired pineal and parapineal organs (if so, the only vertebrate with this condition); at least 10 external branchial openings present (with individual bony covers); paired fins absent (Janvier, 1996).

†Order ARANDASPIDIFORMES. Ordovician, marine, so far known from the Southern Hemisphere (Australia and South America).



This group contains perhaps four genera as follows: (i) from South America, †*Sacabambaspis* and possibly †*Andinaspis*, and (ii) from the Northern Territories, Australia, †*Arandaspis* and possibly †*Porophoraspis* (e.g., Ritchie and

Gilbert-Tomlinson, 1977; Gagnier, 1993, 1995; Sansom et al., 2005; Pradel et al., 2007).

†Subclass HETEROSTRACI

Pair of external lateral gill openings, emptying from several gill pouches; exoskeleton consisting of head covered in dermal armor consisting of plates of dentine and aspidine, generally with a honeycomb-like structure, covering the branchiocephalic region and body with large scales covering the trunk and tail; eyes lateral, extremely small; sclerotic ring absent; movable paired fins absent; anal fin absent; tail internally hypocercal, externally often symmetrical; perhaps two olfactory capsules (diplorhinal condition) with only an internal opening into the mouth area. Species with interlocking tesserae in the dermal armor are known as the tessellated pteraspidiforms or heterostracans. Keating et al. (2015) made a detailed, comparative histological study of the dermal skeleton of heterostracans. Maximum length is 1.5 m, usually much smaller. Pteraspidiforms are well known from the Early Silurian to the Late Devonian.

Taxa of uncertain affinities, of which some are not definitely known to be heterostracans, include the following (names with endings from Janvier, 1996):

†CARDIPELTIDA (e.g., †*Cardipeltis*).

†CORVASPIDIDA (e.g., †*Corvaspis*).

†LEPIDASPIDIDA (e.g., †*Lepidaspis*).

†TESSERASPIDIDA (e.g., †*Tesseraspis*).

†TRAQUAIRASPIDIFORMES (e.g., †*Phialaspis,* †*Toombsaspis,* and †*Traquairaspis*).

†TOLYPELEPIDIDA (e.g., †*Athenaegis* and †*Tolypelepis*).

Some of these are known as "tessellate heterostracans," known only from fragments and indeed not necessarily heterostracans. Other possible heterostracans include †*Aserotaspis* and †*Astraspis.*

Karatajute-Talimaa and Smith (2004) established a new order of tesselate pteraspidomorph agnathans, the Tesakoviaspidida, with one family, the †Tesakoviaspididae for the Early Silurian †*Tesakoviaspis concentrica* of unique histology (but most closely related to that of the †Mongolepidida). Its affinity with such groups as the astraspids is unknown.

†Order CYATHASPIDIFORMES. Ornamentation of longitudinal, dentine ridges (separated by grooves lacking dentine); dorsal shield a single plate. Two major clades are recognized by Janvier (1996), given here as families.

†Family AMPHIASPIDIDAE (e.g., with the genera †*Eglonaspis,* †*Kureykaspis,* and †*Prosarctaspis*).

†Family CYATHASPIDIDAE (e.g., with the genera †*Anglaspis*, †*Dinaspidella*, †*Irregulareaspis*, †*Nahanniaspis*, †*Poraspis*, and †*Torpedaspis*). †*Nahanniaspis* was regarded as the sister group of the †Cyathaspididae by Janvier (1996). The pattern of skeletal growth is known for both †*Dinaspidella* and †*Nahanniaspis* and was very similar; small dorsal and ventral shields and midline scales formed first, then grew outwards to meet laterally (Greeniaus and Wilson, 2003).

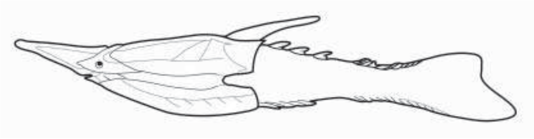
†Order PTERASPIDIFORMES. Dorsal shield composed of several plates, ornamented, except in psammosteids, with concentric dentine ridges, and usually able to grow radially. Five major taxa are given in Janvier (1996), given family rank here, as follows.

†Family ANCHIPTERASPIDIDAE (e.g., †*Rhachiaspis* and †*Ulutitaspis*).

†Family PROTASPIDIDAE (e.g., †*Cyrtaspidichthys*).

†Family PROTOPTERASPIDIDAE (e.g., †*Protopteraspis*).

†Family PSAMMOSTEIDAE (e.g., †*Drepanaspis*, †*Psammolepis*, and †*Pycnosteus*).

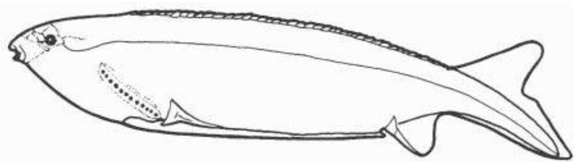


†Family PTERASPIDIDAE (e.g., †*Errivaspis*, †*Pteraspis*, †*Rhinopteraspis*, and †*Unarkaspis*).

†SUPERCLASS ANASPIDOMORPHI

†Class ANASPIDA

†Order ANASPIDIFORMES (Birkeniae, Birkeniida). Six to 15 or more pairs of external lateral gill openings; branchial region posteriorly placed with first gill pouch well behind eye (as in lampreys); eyes large and lateral; tail hypocercal with large epichordal lobe (perhaps in part or entirely corresponding to the posterior dorsal fin); anterior dorsal fin absent, but a series of dorsomedian scutes present; unique pectoral spines or rods present; anal fin reduced or absent; body usually covered with dorsoventrally elongated ornamented scales (which are virtually absent in †*Lasanius*); body fusiform and somewhat compressed; mouth terminal; complex dermal head armor present in some; bone cells absent. Maximum length about 15 cm. Silurian (primarily Late Silurian, although some Late Devonian taxa, e.g., †*Endeiolepis* of Quebec, may be anaspidiform), predominantly freshwater.



Genera include †*Birkenia*, †*Lasanius*, †*Pharyngolepis*, and †*Rhyncholepis* (e.g., Arsenault and Janvier, 1991; Janvier, 1996). †*Jamoytius* and †*Euphanerops* are regarded as sister taxa to the †Anaspida (Donoghue et al., 2000).

†SUPERCLASS THELODONTOMORPHI

†Class THELODONTI

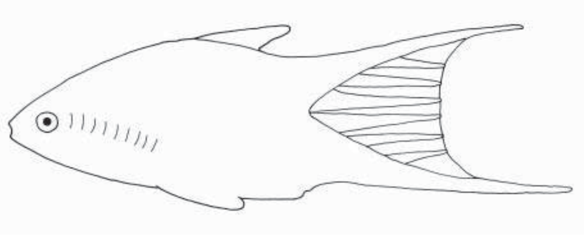
Thelodonts are known primarily from isolated micromeric scales, important for stratigraphic correlations (e.g., Soehn et al., 2001; Turner, 2004; Zigaite, 2013; and discussion above under "VERTEBRATES"), although many near-complete body fossils are known. Most thelodonts have a depressed body form, with horizontal mouth, asymmetrical tails, one dorsal fin and paired pectoral fin flaps, but species of †Furcacaudiformes are compressed, have near circular mouths, and have a nearly symmetrical tail. Late Ordovician to Late Devonian (Turner, 1992). Ordovician genera include †*Sandivia* (Karatajute-Talimaa, 1997) and †*Stroinolepis* (Märss and Karatajute-Talimaa, 2002).

There are questions on the monophyly of thelodonts and their interrelationships. For example, Wilson and Caldwell (1998) placed thelodonts (less the †Furcacaudiformes) in a polytomy with gnathostomes, and the †Furcacaudiformes were regarded as a sister group to all. Turner (1991) and others suggested that thelodonts and gnathostomes are closely related. Both taxa share features such as lateral line continuing on body, lining of buccal cavity, pharynx and branchial skeleton with denticles and complex platelets; and Märss and Ritchie (1998) noted that †*Shielia taiti* and †*Lanarkia* species have pelvic fin flaps and epicercal tails, respectively, two additional gnathostome characters. Donoghue and Smith (2001) found †*Turinia pagei* and the †Galeaspida to be sister taxa, and the sister group to the †Osteostraci plus jawed vertebrates. In their phylogenetic analysis, Donoghue and Smith (2001) also regarded the thelodonts with a depressed body as a monophyletic group, of which †*Turinia pagei* was the least derived member. The furcacaudiforms were resolved as an unnatural group, one taxon being the sister taxon to the "conventional" thelodont clade, and the other, the sister taxon to this clade plus galeaspids, osteostracans, and jawed vertebrates. However, Donoghue and Smith (2001) had few relevant characters and few species in their analysis, whereas Wilson and Märss (2004, 2009) studied all relevant thelodont genera and found that the †Thelodonti as a whole and the thelodont clade †Furcacaudiformes (and others) are monophyletic. The definitive work on thelodonts in recent years is the *Handbook of Paleoichthyology* volume by Märss, Turner, and Karatajute-Talimaa (2007).

We here follow Donoghue et al. (2000) on the higher classification of craniates and thus place the thelodonts as sister to †Osteostracomorphi + Gnathostomata, recognizing that their position is somewhat uncertain, as those authors only used one thelodont taxon, †*Loganellia*, in their analysis. The classification below is also provisional and follows, as does the orthography, Wilson and Märss (2009).

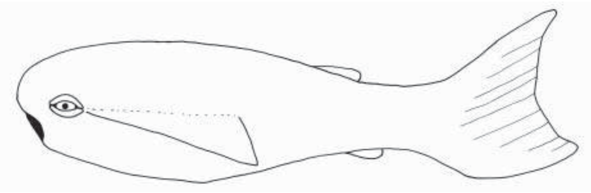
†Order ARCHIPELEPIDIFORMES. These are primitive, Silurian thelodonts that somewhat resemble heterostracans, though they lack the solid, bony head shields of the latter; they also lack derived features of other thelodont clades. Two families, †Archipelepididae (†*Archipelepis*) and †Boothialepididae (†*Boothialepis*).

†Order FURCACAUDIFORMES (fork-tailed thelodonts). Body compressed, eyes lateral and large, branchial openings in an oblique row; stomach present (barrel-shaped); dorsal and ventrolateral fin flaps present in some; caudal fin with large dorsal and ventral lobes and scale-covered, tapered fin supports. The lateral line branches to both lobes of the tail.



Wilson and Caldwell (1993) discovered a group of thelodonts in northwestern Canada that had compressed bodies and large, fork-like tails, rather than the depressed bodies common in other thelodonts. They named two families: the Silurian †Pezopallichthyidae (†*Pezopallichthys*) and the Early Devonian †Furcacaudidae (†*Canonia,* †*Furcacauda,* †*Cometicercus,* and †*Sphenonectris*). According to Wilson and Märss (2009), the group could include as many as five other families (seven in all): †Nikoliviidae (e.g., †*Chattertonodus,* †*Nikolivia*), †Lanarkiidae (e.g., †*Lanarkia,* †*Phillipsilepis*), †Drepanolepididae (e.g., †*Drepanolepis*), †Barlowodidae (e.g., †*Barlowodus,* †*Sophialepis*), and †Apalolepididae (e.g., †*Apalolepis*) (Wilson and Caldwell, 1998; Märss et al., 2002, 2007, 2009; Wilson and Märss, 2004, 2009). Märss and Ritchie (1998) suggested that †*Lanarkia horrida* had an epicercal, heterocercal tail, and that its tail fins had scale-covered ray-like supports (as with fork-tailed thelodonts).

†Order THELODONTIFORMES (= †Coelolepidiformes). This group contains most of the thelodonts with depressed (somewhat ray-like) body form. Well-preserved examples are known from Scotland and Estonia.



Perhaps ten families: †Turiniidae (e.g., †*Turinia*), †Coelolepidae (e.g., †*Thelodus*), †Katoporodidae (†*Goniporus,* †*Katoporodus,* †*Overia,* and †*Zuegelepis*), †Loganelliidae (e.g., †*Loganellia,* †*Stroinolepis*), †Longodidae (e.g., †*Longodus*), †Helenolepididae (e.g., †*Helenolepis*), †Phlebolepididae (e.g., †*Erepsilepis,* †*Phlebolepis*), †Shieliidae (e.g., †*Trimerolepis,* †*Eestilepis,* †*Valiukia,* †*Paralogania,* and †*Shielia*), †Eestilepididae (e.g., †*Eestilepis,* and †Talivaliidae (†*Glacialepis* and †*Talivalia*).

†*Turinia* had a near-global distribution if its entire temporal range is considered (Jiang, 1992). The internal anatomy of †*Turinia pagei,* with eight pairs of gills and a stomach, is especially well known (Donoghue and Smith, 2001). †*Shielia taiti* has ventral abdominal paired fin flaps that are interpreted as pelvic fins, in addition to its more anterior pectoral paired fins (Märss and Ritchie, 1998; Wilson et al., 2007).

†SUPERCLASS OSTEOSTRACOMORPHI

The Osteostracomorphi (comprising the cephalaspidiforms or osteostracans, the galeaspidiforms, and provisionally the less well-known pituriaspidiforms) are now considered to be the sister group to the jawed vertebrates (gnathostomes) by many researchers. Janvier (2001), in finding that ostracoderms in general are more closely related to gnathostomes than to either hagfishes or lampreys, and that cephalaspidiforms and galeaspidiforms are the closest well-known relatives of the gnathostomes, reconstructed the characters of hypothetical ancestors of various clades. Although they are regarded as the closest relatives of gnathostomes, there is no convincing evidence of gnathostome-like gill arches in osteostracomorphs. More systematic work is also required before a consensus is reached concerning which if any gill arch is homologous with gnathostome jaws and which agnathan clade shared the most recent common ancestry with the jawed vertebrates. Cephalaspidomorphs are the only non-gnathostome clade with an undoubtedly heterocercal (epicercal: upwardly turned) axis in the tail, like that of gnathostomes.

Osteostracomorphi present interesting biogeographic patterns (e.g., Sansom (2009): †Cephalaspidiformes are known from western Asia, Europe, Arctic islands, and North America; †Galeaspidiformes are known from southeastern China and Vietnam; †Pituriaspidiformes are known so far only from Australia. It thus appears that the closest known relatives of the Gnathostomata (which are the vast majority of vertebrates) became isolated in at least three different regions of the Paleozoic world and radiated independently in those regions.

†Class CEPHALASPIDOMORPHI (Monorhina)

Only two semicircular canals; some bony regions in cephalaspidiforms may have true bone cells; single dorsomedian nostril (nasohypophyseal) opening between eyes but divided internally, with median pineal eye behind, except in galeaspidiforms.

†Order CEPHALASPIDIFORMES (Osteostraci). Dorsal and lateral areas of cephalic shield with depressed areas in exoskeleton and canals connecting them to the otic region (this may have been a sensory organ, perhaps detecting sound waves or electric fields); usually 10 pairs of gill chambers and 10 pairs of external ventral gill openings; branchial region anteriorly placed (first gill opening at least level with eye); long rostral process present in some (e.g., †*Boreaspis*); eyes dorsal, closely spaced; sclerotic ring present; endolymphatic ducts and sand-sized granular filling present in otic region; head with complex, ornamented, polygonal interlocking plates capable of independent growth, becoming fused in many; mouth ventral; head depressed anteriorly, triangular posteriorly; body triangular in cross section and flattened ventrally; scales of body ornamented and dorsoventrally elongated; anal fin absent; pectoral fins, probably homologous to gnathostome pectoral fins, known in most (e.g., the basal †*Ateleaspis*, †*Superciliaspis*, †*Waengsjoeaspis*) but absent in tremataspids; tail heterocercal, epicercal (notochordal axis upwardly bent), with small, ventral, horizontal paired extensions. Maximum length about 60 cm, though most are much smaller. Late Silurian to Late Devonian, freshwater or marine, of western Asia, Europe, and North America. These are the best known of the fossil agnathans because of excellent external and internal skeletal preservation. This group is usually known as the Osteostraci and sometimes as cephalaspids by paleontologists.

Hawthorn et al. (2008) learned from a growth series of the cornuate species †*Superciliaspis gabrielsei* that individual elements (head tesserae, body scales) of the exoskeleton could grow in a variety of ways and fuse together to form larger units. Sahney and Wilson (2001) studied granular labyrinth infillings in such osteostracans as †*Waengsjoeaspis* and †*Superciliaspis*, as well as in early gnathostomes. They suggested that the endolymphatic pore openings in osteostracans functioned in a way similar to that in many living chondrichthyans: exogenous sand-sized grains enter the labyrinth of the inner ear through the endolymphatic pores and thus contribute to the mass of exogenous and internally made grains that stimulate the sensory macula. These sand-like grains are functional precursors to the internally made otoliths (ear stones) of higher ray-finned fishes.

Sansom (2009) presented a revised phylogeny and a morphological character analysis, building on the work of Janvier (1985). Taxa are recognized as non-cornuate (e.g., †*Ateleaspis,* †*Hirella,* and †*Hemicyclaspis*) when they lack posterolateral, extended points on their head armor. Those with cornua are part of a large, monophyletic clade, the †Cornuata, with at least nine families: †Benneviaspidae, †Cephalaspidae, †Dartmuthiidae, †Kiaeraspidae, †Sclerodidae (=†Sclerodontidae), †Superciliaspididae, †Thyestiidae, †Tremataspidae, and †Zenaspidae (e.g., Berg, 1940; Janvier, 1985, 1996; Sansom, 2009; Scott and Wilson, 2015). Afanassieva (1995) discussed the taxonomy of the †*Tremataspis*-like forms and recognized five suborders. Marss et al. (2015) found that even small fragments of dermal armor can be identified to genus and species because of distinctive characteristics of their ornament and histology.

†Order GALEASPIDIFORMES. The cephalic shield, though variable in shape, resembles that of the cephalaspidiforms. Instead of having a minute dorsal nasohypophyseal opening like that of cephalaspidiforms, galeaspidiforms have a large median dorsal opening in front of the eyes that connects with the paired nasal cavities and with the pharynx. The function of this unusual structure remains poorly understood. Galeaspidiforms possessed up to 45 pairs of gill compartments, the greatest number among vertebrates (Janvier, 2004); they possessed acellular perichondral bone associated with globular calcified cartilage (Zhu and Janvier, 1998), lacked a dorsal and paired fins, and may have had a hypocercal tail. Early Silurian (†*Komoceraspis*) to Late Devonian of China and northern Vietnam (Jiang, 1992).

Wang (1991, 1995) reviewed a number of taxa. Jiang (1992) recognized 10 families during a revision of the group. Many genera have been described (e.g., †*Duyunolepis,* †*Eugaleaspis,* †*Hanyangaspis,* †*Huananaspis,* †*Macrothyraspis,* †*Pentathyraspis,* and †*Polybranchiaspis*).

†Order PITURIASPIDIFORMES (Pituriaspida). This enigmatic group has unusual morphological features including an anteriorly projecting rostrum, and an elongate bony armor covering the head and trunk, but no dorsal nasohypophyseal opening. Beneath the orbits there is one pair of large openings of unknown function. Another pair of more ventral openings probably housed the pectoral fins. Two genera: †*Pituriaspis* and †*Neeyambaspis* (Young, 1991; Long, 2011).

SUPERCLASS GNATHOSTOMATA (jawed vertebrates)

Jaws present, derived from modified gill arches; endochondral bone present (see Smith and Hall, 1990); paired fins present primitively, paired fins or paired limbs usually present except where secondarily lost; three semicircular canals (and two or more maculae) always present, including in early fossil gnathostomes such as placoderms; gills covered with ectoderm and directed externally; gill arches not fused with neurocranium, internal to gill lamellae; gills opening to surface in fishes through slits (opercular opening, when present, may be pore-like); nerve fibers myelinated. There are many characters that carry over in the transition from jawless fishes to jawed vertebrates that were subsequently modified. For example, the notochord continues to be present in the various lineages of early gnathostomes but in some it is later replaced with vertebral centra, and a bony exoskeleton is present in early gnathostome fossils but absent in higher lineages.

There are many exciting questions on the origin and evolution of characters in the transition from jawless to jawed vertebrates (thought to be from osteostacans to placoderms). One such question concerns the phylogenetic origin of teeth (dentine based versus the horny teeth of lampreys). Smith and Johanson (2003) and Johanson and Smith (2003) suggested that teeth have originated at least twice, in derived placoderms, the arthrodires, and in the placoderm sister clade. However, Young (2003) reviewed past conclusions that placoderms have a primitively jawless mouth and concludes that no placoderm had typical teeth, but rather the tooth-like structures are made up of a special dentine unique to placoderms, called semidentine.

In the fossil record, placoderms appear in at least the mid-Silurian (Jiang and Dineley, 1988; Gardiner, 1993; Zhu et al., 2013) and acanthodians appear in the Early Silurian (e.g., Zidek, 1993), but in both cases the oldest fossils are fragmentary remains; scales and denticles attributed to chondrichthyans are doubtfully reported from the late Ordovician (see the section on Chondrichthyes).

Classically, all jawed vertebrates were recognized in two groups, the jawed fishes and the tetrapods. This was the arrangement in Nelson (1984) with all gnathostomes in either the Grade Pisces or the Grade Tetrapoda. It was well recognized many years earlier that although tetrapods form a monophyletic group, the jawed fishes did not. To better reflect the accepted phylogenetic relationships, Nelson (1994) did not recognize Pisces as a taxon and placed all jawed vertebrates in three taxa, the grades †Placodermiomorphi, Chondrichthiomorphi, and Teleostomi (comprising the acanthodians, sarcopterygians, which contains some fishes but mostly tetrapods, and the actinopterygians). While the former taxon Pisces is not monophyletic and no longer recognized in classification, the term "jawed fishes" is still a useful one, even though referring to a paraphyletic assemblage of lineages.

The jawed fishes comprise the first two grades of the Gnathostomata plus more than half of the extant species of the third grade (Teleostomi). In all, there are about 32,000 species of extant jawed fishes (Eschmeyer and Fong, 2015) and about 62,500 species of extant jawed vertebrates (gnathostomes) in total. This represents a disproportionate increase in the number of jawed fishes over that of tetrapods since the third edition of this book (Nelson, 1994), at which time the totals for fishes and tetrapods were more similar (an estimated 24,535 species of extant jawed fishes and about 48,100 species of gnathostomes in total).

†Grade PLACODERMIOMORPHI

The Grade rank is used here between the ranks of Superclass and Class. The sister group of the †Placodermiomorphi is the (unranked) clade Eugnathostomata (see below).

†Class PLACODERMI

Head and shoulder girdle with dermal bony plates (with bone cells); endochondral bone known in some taxa; head shield usually articulated (movable or not) with the trunk shield, with a double cervical joint; gill chamber extending anteriorly under neurocranium and may be covered laterally by dermal bone; probably five gill arches, no good evidence for spiracles; notochord unconstricted with vertebrae consisting only of neural and haemal arches and spines; tail diphycercal or heterocercal; anal fin probably absent. Although many features carry over from the osteostracans and other ostracoderms such as the notochord and head being mostly encased in bone, there are many features that are unique to placoderms. A few Silurian records are known with greatest abundance in the Devonian; there is no clear evidence of placoderms surviving a major extinction event at the end of the Devonian (see also Carr, 1995; Maisey, 1996).

Most primitive and many advanced groups of placoderms were marine. At least some arthrodiriforms, most antiarchiforms, and all phyllolepidiforms are inferred to have been freshwater (e.g., but see Schultze and Cloutier, 1996). Except for the arthrodires, most were bottom-living fish with depressed bodies; only two families had species with compressed bodies. Although placoderms have been found almost worldwide, very few Devonian ones are known from South America (Maisey, 1996). A rapid replacement of placoderms by the chondrichthyans occurred at the end of the Devonian. Maximum length 6 m, but most are much shorter.

There had until recently been a consensus that placoderms are monophyletic, and five features were given in Goujet and Young (2004) supporting this conclusion. Two other hypotheses as discussed by Janvier (1996) and Goujet and Young (2004) are i) placoderms and chondrichthyans are sister taxa, and ii) placoderms and osteichthyans (euteleostomes herein) are sister taxa. More recently several authors have suggested that placoderms are paraphyletic side branches from the eugnathostome stem lineage (e.g., Brazeau, 1999; Zhu et al., 2013; Brazeau and Friedman, 2015); however there is no consensus about how many such side branches there might be. The earlier hypothesis that placoderms are the monophyletic sister group to all higher gnathostomes (the Eugnathostomata, including Chondrichthyes, †Acanthodii, and the Osteichthyes), as suggested by Schaeffer (1975) and favored by Goujet and Young (2004), Carr et al. (2009), and implied by complex shared characters such as unique claspers (Long et al., 2015) is retained here.

The classification of this group is based primarily on Goujet and Young (2004). Problematic taxa such as the †Stensioelliformes from the Early Devonian (marine) of Germany are not placed in the present classification. Some placoderms have not been assigned to one of the known orders (Zhu et al., 2013), while at least one (†*Entelognathus*) is more closely related to Osteichthyes in some phylogenetic results (e.g., Long et al., 2015).

†Order PSEUDOPETALICHTHYIFORMES. One family, †Paraplesiobatidae, from the Early Devonian (marine) in Europe, with perhaps two genera, †*Pseudopetalichthys* and †*Paraplesiobatis.* In some recent phylogenetic analyses (e.g., Long et al., 2015) these are among the most primitive branches of †Placodermi.

†Order ACANTHOTHORACIFORMES. Primitive placoderms represented by several genera (e.g., †*Brindabellaspis,* †*Murrindalaspis,* †*Palaeacanthaspis,* †*Radotina,* and †*Romundina*) from the Early Devonian (marine) in Europe, Asia, and Arctic Canada.

Goujet and Young (2004) hypothesized that this taxon, with some of the oldest placoderm fossils, is the basal placoderm group. They proposed that one pectoral fin element (as opposed to three as in the traditional tribasal theory), an anterior insertion for the internal rectus extra ocular muscle, and two abducens-innervated eye muscles may be primitive for placoderms, and hence for all jawed vertebrates. †*Romundina* is among the best known of the acanthoraciforms and has been highlighted for illustrating steps in the evolution of the vertebrate face (Dupret et al., 2014). Regardless of its exact phylogenetic position, this order reveals much about the first known jawed vertebrates.

†Order RHENANIFORMES. One family, †Asterosteidae (including †*Gemuendina* and †*Jagorina*), with a ray-like body, and several genera from the Early to Late Devonian (marine) in the United States, Bolivia, and Germany. At least some rhenaniforms have a synarcual, like that of Holocephali and some Batomorphi (Johanson et al. 2015).

†Order ANTIARCHIFORMES (antiarchs). Pectoral fin a slender appendage covered by small dermal plates, articulating with the head by a ball-and-socket joint, and with a proximal/distal joint in some; bottom feeders with mouth subterminal, and eyes dorsal and closely placed; pineal organ between eyes; sockets of the head-body joint are on the head shield (opposite to the relationship in arthrodires). Maximum length about 1.2 m.

Carr et al. (2009) placed †Antiarchiformes in a primitive position within a monophyletic †Placodermi. Zhu et al. (2013) and Long et al. (2015) placed antiarchs in a near-basal position within a paraphyletic †Placodermi. Long et al. (2015) reported evidence for internal fertilization using paired dermal claspers of males and specialized dermal plates in females, but these claspers are not associated with pelvic fins as are those of chondrichthyans.

About seven families are recognized; at least Early Devonian (but see †*Shimenolepis* below) to end of Devonian (perhaps primarily freshwater to brackish) on, as a group, all major land masses. Classification based primarily on the phylogeny of Zhu (1996) and Zhu and Janvier (1996) with other details from Burrow and Turner (1999), Johanson (1997a,b), and Young and Zhang (1996). The names that Goujet and Young (2004) gave to the two major clades are †Yunnanolepida and †Euantiarchi. The names used for certain taxa above family level and their ranks are provisional.

Unassigned genera include †*Heteroyunnanolepis,* †*Zhanjilepis,* and †*Shimenolepis* (late Early Silurian from China, one of the oldest placoderms, likely an antiarch, but poorly known; Zhu, 1996:296), and †*Silurolepis,* from the early Late Silurian (Zhang et al., 2010), thought by Zhang et al. (2010) to be the most primitive, well-preserved antiarch.

†***Suborder Yunnanolepidoidei.*** At least two families.

†Family CHUCHINOLEPIDIDAE (†*Chuchinolepis* synonym †*Quijinolepis*).

†Family YUNNANOLEPIDIDAE (e.g., †*Phymolepis,* †*Yunnanolepis*).

†***Suborder Bothriolepidoidei.*** Two infraorders and a number of unassigned genera: e.g., †*Dianolepis,* †*Minicrania* (sister to the other members of the suborder), and †*Pterichthyodes.*

†*Infraorder Sinolepidida.* One family.

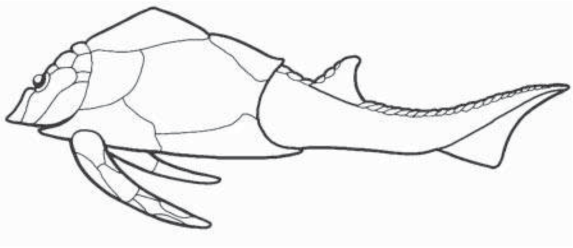
†Family SINOLEPIDAE (e.g., †*Grenfellaspis* and †*Sinolepis*).

†***Infraorder Euantiarcha.*** These are antiarchs with an articulated pectoral fin. Four families.

†Family MICROBRACHIIDAE (e.g., †*Microbrachius*).

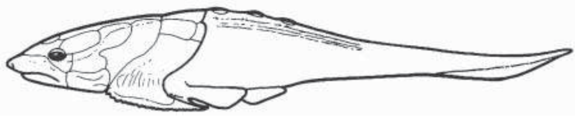
†Family BOTHRIOLEPIDIDAE (e.g., †*Bothriolepis*).

†ASTEROLEPIDIDAE (=†Pterichthyidae) (in figure) (e.g., †*Asterolepis,* †*Remigolepis,* †*Stegolepis*).



†Family GERDALEPIDIDAE (e.g., †*Gerdalepis*).

†Order PETALICHTHYIFORMES. A group of several genera (e.g., †*Eurycaraspis*, †*Lunaspis*, and †*Macropetalichthys*, Janvier, 1996) from Early to Late Devonian (marine) in North America, Europe, Morocco, Asia, and Australia.



†Order PTYCTODONTIFORMES. Large, sexually dimorphic pelvic fins with claspers in males (fertilization and early development were internal; Long et al., 2008, 2009). There are many, probably convergent resemblances with living holocephalans, including a sinarcual (fused anterior vertebrae; Johanson et al. 2015). One family, †Ptyctodontidae (e.g., †*Ctenurella* and †*Rhamphodopsis*), from Early Devonian to the end of the Devonian, in North America, Europe, Asia, Libya, Algeria, and Australia (e.g., Forey and Gardiner, 1986; Janvier, 1996).

†Order ARTHRODIRIFORMES (arthrodires). Most arthrodires were probably nektonic predators. This diverse group, the largest in number of genera and best known of the placoderms, is known from the Early Devonian to the end of the Devonian and is found on all major land masses. Some are reported to have a synarcual (Johanson et al. 2015). Several major groups are recognized (e.g., see Goujet and Young, 2004; Janvier, 1996).

†***Suborder Actinolepidoidei.*** Includes †Actinolepididae, the most primitive arthrodires, with, e.g., †*Actinolepis*, †*Aethaspis*, †*Bollandaspis*, †*Eskimaspis*, †*Heightingtonaspis*, and †*Kujdanowiaspis* (Johnson et al., 2000).

†***Suborder Phyllolepidoidei.*** One Middle and Late Devonian (freshwater) family, †Phyllolepididae, with three genera, †*Austrophyllolepis*, †*Placolepis*, and †*Phyllolepis*, known from Antarctica, Australia, Europe, and Greenland (Long, 1984; Ritchie, 1984). The †Antarctaspididae may be related to this group.

†***Suborder Phlyctaenioidei.*** E.g., †Phlyctaeniidae (e.g., †*Arctolepis*, in figure) and †Groenlandaspididae.

†*Suborder Brachythoracoidei.* Includes the †Eubrachythoraci with, based on information in Carr (2004), two major subgroups, the pachyosteomorphs and the coccosteomorphs. The brachythoracoids of the late Devonian were the first large marine vertebrate predators, with †*Dunkleosteus* having large, blade-like inferognathals (lower jawbones) and growing to be at least 6 m in length (e.g., Young, 2003). Another form that reached body sizes at least as large was †*Gorgonichthys.* Bite strength, jaw shape, and resulting jaw stresses in †*Dunkleosteus* and †*Gorgonichthys* were studied by Snively et al. (2010), who found †*Dunkleosteus* to have lower stress levels in its inferognathal bones. †*Dunkleosteus* has one of the strongest bite forces of any vertebrate (Anderson and Westneat, 2009). These huge fishes were the largest predators known from the Paleozoic Era.

Important coccosteomorph taxa include the following: †Buchanosteidae (a basal brachythoracid group; Carr, 2003), †Camuropiscidae (e.g., †*Camuropiscis*), †Coccosteidae (e.g., †*Coccosteus,* in figure), †Dinichthyidae (Carr and Hlavin, 1995, 2010, removed several genera from this family), †Dunkleosteidae (e.g., †*Dunkleosteus,* †*Eastmanosteus*), †*Gorgonichthys,* †*Hadrosteus,* †Mylostomatidae, †Panxiosteidae, †Selenosteidae, †Titanichthyidae, and †Wuttagoonaspididae.

EUGNATHOSTOMATA

The Eugnathostomata, unranked here, include the Chondrichthyes (sharks and rays), the †Acanthodii, and the Osteichthyes (bony fishes, including all tetrapods). The †Acanthodii as previously understood (e.g., Nelson, 2006) are likely paraphyletic, with some of them being related to Osteichthyes, some to Chondrichthyes, and some perhaps being stem-group Eugnathostomata (see the following discussion under †Acanthodii), but exactly which ones belong where is a subject of much discussion.

GRADE CHONDRICHTHYOMORPHI

Within the Eugnathostomata, the Chondrichthyomorphi are the sister group of the Grade Teleostomi and contain one class, Chondrichthyes.

Class CHONDRICHTHYES—cartilaginous fishes

Prismatic endoskeletal calcification; dermal skeleton consisting of denticles (placoid scales); skull lacking sutures in living forms; teeth replaced serially and usually not fused to jaws; fin rays soft, unsegmented (termed ceratotrichia); nasal openings on each side usually single (imperfectly divided by a flap into incurrent and excurrent openings) and more or less ventral; biting edge of upper jaw formed by palatoquadrate (and lower jaw by Meckel's cartilage); endolymphatic duct present; swimbladder and lung absent; intestinal spiral valve present; internal fertilization in almost all known taxa, fossil and extant, by means of pelvic claspers (of males, derived from the pelvic fin axis and termed myxopterygia) that are inserted in the female cloaca and oviduct(s); gestation periods of two years are known, the longest of any vertebrate; blood concentration of urea and trimethylamine oxide (converted from toxic ammonia) usually high, allowing water to be drawn freely into the body. Characters supporting a monophyletic Chondrichthyes (holocephalans and elasmobranchs) are given in Maisey (2001b), Didier (1995), Janvier (1996), and Grogan and Lund (2004), and unique shared characters of the spermatozoa are given in Jamieson (1991). The two key synapomorphies are the prismatic endoskeletal calcification and the pelvic claspers (Grogan and Lund, 2004).

The various means of jaw suspension of chondrichthyans are of much interest. Grogan et al. (1999) argued that autodiastyly is the ancestral condition from which holostyly and hyostyly (and from it, two types of amphistyly) were derived. However, Maisey (2001b) and Maisey and Anderson (2001) found that †*Pucapampella* (discussed below), considered a basal chondrichthyan, has a suspensory hyomandibula; therefore, autodiastyly may be the primitive pattern only for holocephalans. Chimaeroids exhibit holostyly (which has evolved several times in gnathostomes) in which the upper jaw (palatoquadrate) is completely fused to the cranium. However, elasmobranchs with hyostyly or amphistyly have an upper jaw that is suspended from the cranium by muscles and ligaments and variously braced to the cranium by processes of the palatoquadrate, cranium, and/or modified pharyngeal arches.

Although chondrichthyans have internal fertilization, there is much diversity both in where the last stages of embryonic development occur (viviparity and oviparity) and in the source of fetal nutrition (lecithotrophy and matrotrophy). The various modes are described in Hamlett (1999, 2005) and Carrier et al. (2004), and there is some gradation between them. Unfortunately, there are also differences as well as confusion in the literature about the appropriate terms to be used for the various modes. The terminology followed here is as clarified by Hamlett (2005) and Musick and Ellis (2005); the latter authors gave a phylogenetic analysis of the occurrence of the many reproductive modes. For reasons explained by Musick and Ellis (2005), it has been argued that viviparity is the primitive mode of reproduction in chondrichthyans (Grogan and Lund, 2004, originally proposed this idea on the balance of Paleozoic evidence including that from their Montana fossil site).

Based on Musick and Ellis (2005), in embryonic development, chondrichthyans exhibit both i) viviparity, in which developing eggs are retained in the female and free-swimming young are born, and ii) oviparity, in which fertilized eggs (in leather-like egg cases sometimes colloquially called "mermaid purses") are deposited on the sediment or attached to an object, with hatching being external to the female. The various ways of obtaining nutrition are as follows:

A. All nutrition from the yolk sac—Most chondrichthyan embryos, like those of actinopterygians, are lecithotrophic, obtaining all nutrition from the yolk sac. In this category, there can be either:

i) yolk sac viviparity or lecithotrophic viviparity (formerly known as ovoviviparity)—the most common state in Chondrichthyes (occurring in at least some members of all living orders of elasmobranchs except Heterodontiformes, Lamniformes, and Rajiformes).

ii) yolk sac oviparity or lecithotrophic oviparity—occurring in all living holocephalans, some selachians (e.g., all Heterodontiformes), and all Rajidae. All members exhibiting oviparity are lecithotrophic.

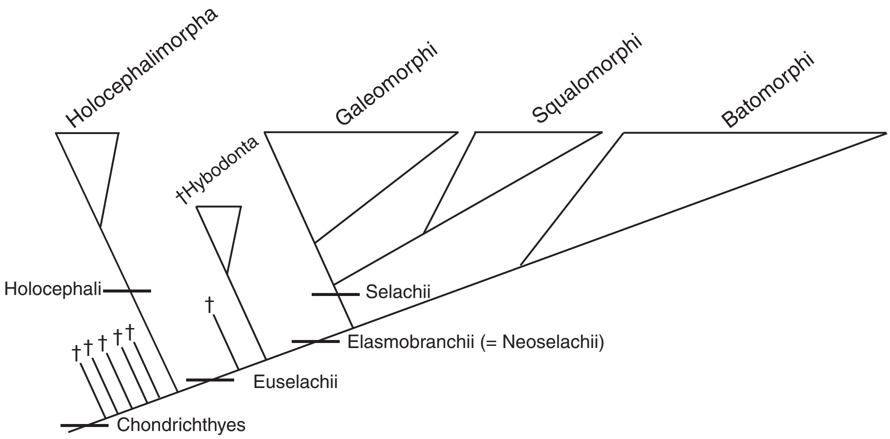
B. Some nutrition from the female (directly or indirectly)—In contrast to the above, some chondrichthyan embryos, where there is viviparity, obtain at least some nutrition from the female, either from uterine secretions, ova, siblings, or a placenta in what is termed:

iii) matrotrophy—There are several versions of this, including:

a) Nutrition from eating unfertilized eggs (oophagy)—all Lamniformes and some Carcharhiniformes. In *Carcharias taurus*, the largest embryo eats all smaller embryos and then feeds on unfertilized eggs.

b) Nutrition from uterine secretions (histotrophy)—there is either limited histotrophy, which occurs in many squaliform and carcharhiniform sharks, or lipid histotrophy in the myliobatiforms. Carcharhiniformes with placentas (see below) may pass through a histotrophic stage during development, after yolk stores are depleted, with the larva enveloped in a fold of the uterus (Hamlett, 1989), and prior to the placental phase of development.

c) Nutrition from a hematrophic yolk sac placenta (placentotrophy)—in many Carcharhiniformes (López et al., 2006). As yolk stores are depleted, the yolk sac is modified into a functional placenta, connected to the embryo by an umbilical cord (modified from the yolk stalk) through which the embryo receives nutrition and disposes of metabolic waste products (Hamlett, 1989).



Relationships of the major groups of Chondrichthyes.

Two main extant evolutionary lines of Chondrichthyes are recognized and ranked as subclasses: the holocephalans (see below under Holocephali for use of this name) and the elasmobranchs. Together, the two groups are considered monophyletic (e.g., Inoue, Miya, Lam et al., 2010). Within the elasmobranchs, there are two divisions, the Selachii (sharks) and the Batomorphi (rays) (see discussion below under Euselachii). The sharks are in turn divided between the Galeomorphi and the Squalomorphi.

There are several multiauthored sources reviewing our knowledge of chondrichthyan biology. Last and Stevens (2009) is an excellent book on Indo-Pacific taxa. Hamlett (1999) presents a systems approach to the anatomy and physiology of sharks and rays, in which Compagno (1999) discusses neoselachian phylogeny and body form and gives a checklist of living species of elasmobranchs. Carrier et al. (2004, 2012) review what we know of chondrichthyan phylogeny, zoogeography, and overall biology. Hamlett (2005) emphasizes reproductive biology, corrects many past errors in the literature, and reviews phylogeny. In addition, the FAO series such as Compagno (2001) and the various "Species identification guides" describe the biology and distribution of the species and give keys to species identification.

Important general works on chondrichthyan fossils include the five relevant volumes of the *Handbook of Paleoichthyology*, edited by H.-P. Schultze and authored by Zangerl (1981), Cappetta (1987, 2012), Stahl (1999), and Ginter et al. (2010). In our treatment below of fossil chondrichthyans, expanded significantly since Nelson (2006) and with the assistance to T. D. Cook and advice from J. G. Maisey, we have drawn extensively from all of these volumes, but especially from Ginter et al. (2010) and Cappetta (2012), the two most recent volumes.

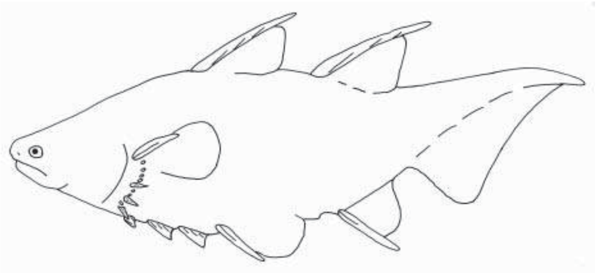
A good fossil record is known from the Early Devonian onwards (e.g., Ginter, 2004). However, the oldest chondrichthyan fossil remains are, somewhat controversially, said to be scales or dermal denticles of late Ordovician age (about 455 million years ago); the fossil record of chondrichthyan teeth does not begin until much later, the oldest known examples being earliest Devonian (about 415 million years ago). There thus remains some doubt about the relationships of the Ordovician forms.

THE FOLLOWING FOSSIL-ONLY TAXA are likely to be stem-group Chondrichthyes.

†*Obtusacanthus.* This Early Devonian genus from Canada had median and paired fin spines, monodontode scales of unique type, lacked teeth (although it had pointed lip scales oriented toward the mouth cleft), but nevertheless consumed vertebrate prey. Originally classified *incertae sedis* as to class and order (Hanke and Wilson, 2004) it has since been considered a stem chondrichthyan (e.g., Long et al., 2015) and by others as an acanthodian (e.g., Dupret et al., 2014).

†Family PROTODONTIDAE. E.g., †*Dendrodus*, †*Protodus*, †*Stigmodus*.

†Family KATHEMACANTHIDAE. Early Devonian; marine. Laterally growing polyodontode scales; globular calcified cartilage; teeth absent; all paired and median fins (except for caudal) with strong, leading-edge spines; paired fin spines in distinct pre-pectoral (arranged as "necklace") and pre-pelvic (along belly) series.



Well-preserved Early Devonian fossils of †*K. rosulentus* and †*S. elegans* from northern Canada display several chondrichthyan-like characters, along with other features usually associated with acanthodians (Gagnier and Wilson, 1996; Hanke and Wilson, 2010). †*Kathemacanthus* itself does not have teeth, although some other chondrichthyan-like fossils of the same age possess teeth.

Kathemacanthids are probably an early clade of stem-group chondrichthyans that retain some of the features of the common ancestor of chondrichthyans, acanthodians, and bony fishes (see below under Grade Teleostomi). Several recent broad scale phylogenies have included †*Kathemacanthus* and concluded that it is a stem chondrichthyan (e.g., Brazeau, 2009; Zhu et al., 2013; Long et al., 2015) although Dupret et al. (2014) placed it as the earliest branching acanthodian lineage.

Two genera, †*Kathemacanthus* and †*Seretolepis*.

†Order POLYMEROLEPIDIFORMES. Laterally growing polyodontode scales of distinctive form; caudal fin heterocercal; anal fin with small, leading-edge spine (Karatajute-Talimaa, 1968; Hanke et al., 2013).

†Order OMALODONTIFORMES. Two families, †Aztecodontidae (e.g., †*Aztecodus*, †*Manberodus*) and †Omalodontidae (e.g., †*Omalodus* and the very important †*Doliodus*). The oldest, undoubted chondrichthyan body fossil is said to be almost 409 million years old (early Devonian), a small specimen of †*Doliodus problematicus*, exhibiting large, paired pectoral fin spines and an intact dentition (Miller et al., 2003). Turner (2004) placed †*D. problematicus* in the family †Protodontidae but placed that family within the †Omalodontiformes; she noted similarities in the teeth of †*Doliodus* with teeth of †*Antarctilamna*.

†Order ANTARCTILAMNIFORMES. Two families are recognized by Ginter et al. (2010), †Antarctilamnidae (e.g., †*Antarctilamna*) and †Coronodontidae (e.g., †*Coronodus*). †*Antarcilamna* also has paired (pectoral) fin spines (like those of †*Doliodus* and kathemacanthids discussed above) with laterally growing polyodontode scales of a distinctive type, as also seen in some undescribed

Early Devonian chondrichthyan taxa. †*Antarctilamna* was originally described as a xenacanthiform because of its diplodont teeth, but diplodont teeth are now known in other groups (e.g., †*Doliodus,* above), and the likely paired pectoral fin spines rule out xenacanthiform relationships.

Groups thought to be related to the chondrichthyans but not otherwise treated here include the †Mongolepidida, with the genera †*Mongolepis,* †*Teslepis,* †*Sodolepis,* and †*Udalepis,* known from scales found from the Early Silurian in central Asia (Karatajute-Talimaa, 1995), and †Kannathalepididae (†*Kannathalepis* and †*Frigorilepis*) and †Wellingtonellidae (Märss et al., 2002). Additional early and poorly known fossil remains (e.g., †*Emsolepis*) were discussed by Turner (2004).

The Middle Devonian †*Pucapampella* from Bolivia, the earliest chondrichthyan in which the braincase can be studied in detail, may also be a primitive stem chondrichthyan whose phylogenetic position lies before the divergence of holocephalans and elasmobranchs (Maisey, 2001b). The primitive gnathostome features of †*Pucapampella,* e.g., ventral otic fissure present, prominent dorsal sellae, and endolymphatic ducts enclosed by the dorsal posterior fontanelle (endolymphatic fossa absent), are discussed by Maisey (2001b, 2004a). The ventral braincase of another Early Devonian †*Pucapampella*-like taxon from South Africa was described by Maisey and Anderson (2001). The South African form is much older than †*Pucapampella* and appears to be even older than †*Doliodus* (see above).

THE FOLLOWING CHONDRICHTHYAN TAXA have often been treated as stem elasmobranchs rather than, as here, stem chondrichthyans, but Maisey (2012) advocated limiting stem elasmobranchs to just a few taxa for which membership can be demonstrated.

†*Plesioselachus.* A Late Devonian fossil genus with amphistylic jaw suspension and thought to have a single dorsal fin and no anal fin (Anderson et al., 1999).

†*Gogoselachus.* This Late Devonian genus from the Gogo Formation of Australia had cladodont-type teeth, ctenacanth-type scales, two articulation facets for pectoral-fin basals on the pectoral girdle, and an endoskeleton of one- or two-layered calcified cartilage formed of polygonal tesserae (Long et al., 2015).

†Family BANDRINGIDAE. Pennsylvanian. Primarily freshwater. Snout elongated; caudal fin externally heterocercal, e.g., †*Bandringa*. Sallan and Coates (2014) classify this genus as *incertae sedis* within Elasmobranchii.

†Order PHOEBODONTIFORMES. Middle Devonian to Late Triassic. Two families are recognized by Ginter et al. (2010).

†Family PHOEBODONTIDAE. E.g., †*Phoebodus*, †*Diademodus*.

†Family JALODONTIDAE. E.g., †*Jalodus*.

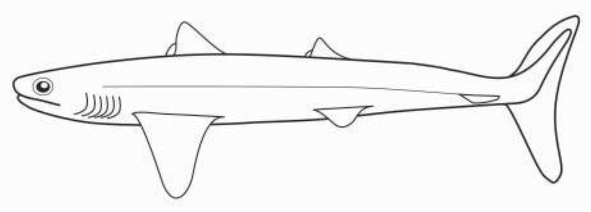
†Superorder CLADOSELACHIMORPHA

Cladodont-type tooth (tall central cusp and one or more pairs of lateral cusps on a broad base); claspers usually absent or unknown; no anal fin; paired fins in shape of triangular flaps; radials of fins unsegmented and extending almost to the edge of the fin.

The Devonian genus †*Coronodus* is sometimes placed here in its own family, †Coronodontidae.

†Order CLADOSELACHIFORMES. Two dorsal fins, at least a spine associated with the first. One family.

†Family CLADOSELACHIDAE. Late Devonian to Mississippian.



Maximum length about 2 m. Includes the well-known †*Cladoselache.* As yet there is no evidence for pelvic claspers in †*Cladoselache.*

†Order SYMMORIIFORMES. Carboniferous; two families (Ginter et al., 2010).

†Family SYMMORIIDAE. E.g., †*Cobelodus*, †*Denaea,* and †*Symmorium*. Additional genera sometimes classified separately in †Stethacanthidae, but included in †Symmoriidae by Ginter et al. (2010), include †*Orestiacanthus*, described by Lund (1984), and †*Stethacanthus*, redescribed by Coates and Sequeira (2001).

†Family FALCATIDAE. E.g., †*Damocles*, †*Falcatus*. Although most Paleozoic shark taxa became extinct at the Permian/Triassic boundary, Guinot et al. (2013) argued that Early Cretaceous teeth from France prove that some †Falcatidae and †Ctenacanthiformes survived until the Cretacous.

†Superorder CTENACANTHIMORPHA

Two orders, †Ctenacanthiformes and †Squatinactiformes.

†Order CTENACANTHIFORMES. Two dorsal fins, each with a spine; anal fin near caudal fin; cladodont-type teeth. Maximum length about 2.5 m. One family is recognized in this order by Ginter et al. (2010). Unassigned genera include †*Goodrichthys* and †*Carinacanthus.*

Middle Devonian to Triassic (Zangerl, 1981; Cappetta, 1987; Cappetta et al., 1993; Ginter et al., 2010; Cappetta, 2012).

†Family CTENACANTHIDAE. Late Devonian and Mississippian, e.g., †*Cladodoides*, †*Ctenacanthus*, †*Goodrichthys*.

†Order SQUATINACTIFORMES. One family.

†Family SQUATINACTIDAE. The Mississippian †*Squatinactis* from Montana resembles the extant *Squatina* in some body form features (e.g., Zangerl, 1981). It was placed in the †Cladodontiformes by Lund (1990).

†Superorder XENACANTHIMORPHA (Pleuracanthodii)

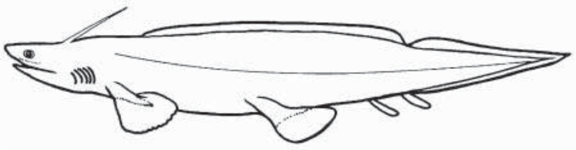
Two orders, †Bransonelliformes and †Xenacanthiformes.

†Order BRANSONELLIFORMES. E.g., †*Bransonella*. Ginter (2004) discussed the origin of the xenacanthimorphs including †*Bransonella* and the †Xenacanthiformes.

†Order XENACANTHIFORMES. Pleuracanth-type tooth (three cusps of variable size, usually two prominent lateral cusps and a smaller median one). Claspers in male; elongate dorsal fin base; diphycercal or heterocercal tail; two anal fins; posterior cephalic spine; radials of pectorals jointed and ending well before fin margin.

Two families are recognized in †Xenacanthiformes by Ginter et al. (2010).

†Family DIPLODOSELACHIDAE. These are primitive xenacanthiforms according to Soler-Gijón (2004).



Genera include †*Diplodoselache*, †*Lebacacanthus*, and †*Orthacanthus*.

†Family XENACANTHIDAE. Freshwater; Early Devonian to Triassic.

Genera include, †*Pleuracanthus*, †*Plicatodus*, †*Triodus*, †*Wardigneria*, †*Mooredontus*, and †*Xenacanthus*.

The remaining chondrichthyan taxa are thought to be within crown-group Chondrichthyes, which are divided between the Holocephali and the Euselachii, and include many extinct taxa. Extant crown-group taxa are arranged in 14 orders, 54 families, 192 genera, and about 1,200 species (Cappetta, 2012; Eschmeyer and Fong, 2015).

Subclass HOLOCEPHALI

Gill cover over the four gill openings, leaving one opening on each side; palatoquadrate fused to cranium (holostylic) in living forms (see above under Chondrichthyes for more detail); complete hyoid arch (with pharyngohyal present), followed by five gill arches; no hyomandibula in suspensorium; branchial basket mostly beneath the neurocranium; no spiracle opening; teeth as a few grinding plates in extant and a few fossil forms (e.g., †eugeneodontiforms, †*Helodus*, †petalodonts, †orodonts, †debeeriids, †gregoriids); no cloaca, separate anal and urogenital openings; skin in adult of extant forms naked except denticles on pelvic claspers (Chimaeridae and Rhinochimaeridae), and on frontal tenaculum and pre-pelvic tenacula in all males (specialized denticles and scales in many fossil forms); no stomach; no ribs; males of at least extant species with tenaculum (clasping organ) on head and anterior to pelvic fins (in addition to the pelvic claspers). It is recognized that this description is very incomplete for the vast diversity of fossil taxa. Late Devonian to present (with a major reduction in diversity after the Permian).

The higher classification of the Holocephali (= Euchondrocephali) is based in part on the phylogenetic works of Grogan and Lund (2000, 2004), but much detail of the composition of various taxa is based on Stahl (1999), who presents a different view of relationships (de Carvalho, 2004a gave valuable criticisms of the latter work). Didier (1995, 2004) also presented new insights into the phylogeny of this group and reviewed past works. *The Handbook of Paleoichthyology* volume by Ginter et al. (2010) reviews and organizes the many older fossil taxa known primarily from fossil teeth.

Users must be aware of the unfortunate use of different terms to describe the various groups of non-elasmobranch chondrichthyans. An example is the use of the name Holocephali for a more restricted clade of close relatives of the extant chimaeriforms (e.g., Lund and Grogan, 1997a), whereas it is here

Stahl (1999)	Lund and Grogan (1997); Grogan and Lund (2000, 2004)	Nelson (2006)	Nelson, Grande, and Wilson (2016)
Subclass Subterbranchialia	Subclass Euchondrocephali	Subclass Holocephali	Subclass Holocephali
Iniopterygia	Infraclass Paraselachii (included Iniopterygii; Paraselachii later seen as paraphyletic; e.g., Lund et al., 2014)	†Superorder Paraselachimorpha †Orodontiformes †Petalodontiformes †Helodontiformes †Iniopterygiformes †Debeeriiformes †Eugeneodontiformes	†Iniopterygiformes †Orodontiformes †Eugeneodontiformes †Petalodontiformes †Debeeriiformes †Helodontiformes
Holocephali (all others)	Holocephali (differs from Stahl)	Superorder Holocephalimorpha (all others)	Superorder Holocephalimorpha (all others)

used more traditionally to include the total group of chimaeriforms including all fossils more closely related to them than to the elasmobranchs, a group for which Grogan and Lund (1997) gave the name Euchondrocephali and Stahl (1999) used Zangerl's (1979) name Subterbranchialia.

The arrangement of Stahl (1999:45), as seen in the above table, separated the subclass Subterbranchialia into two clades, the †Iniopterygia and the Holocephali (different usage than given herein), with the following sequenced in the latter clade: †Chondrenchelyidae, †Helodontidae, †Psammodontidae, †Copodontidae, †Cochliodontiformes, †Menaspiformes, and Chimaeriformes. Grogan and Lund (2004) commented on their differences with Stahl (1999). In their †Paraselachii they placed †*Orodus*, petalodonts, helodonts, and other basal euchondrocephalans, debeeriids, iniopterygians, and edestids, while in their (more restricted) Holocephali they placed chimaeriforms, chondrenchelyids, †*Squaloraja,* cochliodonts, and †*Menaspis.* Ginter et al. (2010) suggested that †Paraselachii are a wastebasket grouping of poorly known taxa. More recently Lund et al. (2014) agreed that the †Paraselachii are paraphyletic. In this edition, we no longer recognize the †Superorder Paraselachimorpha. Instead, we list the various fossil orders in approximate phylogenetic sequence, recognizing that detailed relationships among them are subject to change.

Other taxa belonging to the Holocephali that are not otherwise mentioned include the autodiastylic †Harpacanthidae (Lund and Grogan, 2004a) and †Gregoriidae (with †*Bealbonn,* †*Gregorius,* and †*Strianta*; Lund and Grogan, 2004b). Cladistic analysis suggested that the †Gregoriidae have a basal position relative to the †*Orodus* + †*Helodus*–petalodontiform clade (Lund and Grogan, 2004a,b). The previously recognized fossil †*Desmiodus,* order †Desmiodontiformes (e.g., Cappetta et al., 1993; Nelson, 1994), is now considered a *nomen dubium* (Lund and Grogan, 2004b:520).

THE FOLLOWING FOSSIL-BASED TAXA of Holocephali are suggested to be early branches from the stem leading to Holocephalimorpha.

†Order INIOPTERYGIFORMES. Two families, †Iniopterygidae (including †*Iniopteryx* and †*Promyxele*) and †Sibyrhynchidae (Cappetta et al., 1993; Stahl, 1999). This taxon was considered to be sister to all other members of Holocephali as herein defined by Stahl (1999), who used the term Holocephali for that sister group and the Zangerl term Subterbranchialia for the entire group, but Lund and Grogan (2004a) considered it to be sister to †Debeeriidae. The iniopterygiforms were first described in 1973 and are known only from the Pennsylvanian Period in North America (Stahl, 1980; Zangerl, 1981). Although represented by poorly preserved body fossils, their teeth are very different from those of the other fossil holocephalan taxa, most of which are known mainly from teeth, thus making iniopterygians difficult to classify (Ginter et al., 2010).

†Order ORODONTIFORMES. Two families, †Orodontidae (e.g., †*Hercynolepis* and †*Orodus*) and †Leiodontidae (e.g., †*Leiodus*) (Cappetta et al., 1993; Ginter et al., 2010).

†Order EUGENEODONTIFORMES. Four families, †Agassizodontidae (including †Helicoprionidae), †Caseodontidae (e.g., †*Caseodus,* †*Fadenia,* †*Ornithoprion,* and †*Romerodus*), †Edestidae (e.g., †*Edestus,* †*Lestrodus*), and †Eugeneodontidae (e.g., †*Bobbodus,* †*Eugeneodus,* and †*Gilliodus*) (Cappetta et al., 1993; Ginter et al., 2010).

†Order PETALODONTIFORMES. Four families: †Janassidae (e.g., †*Janassa,* †*Fissodus*), †Pristodontidae (e.g., †*Davodus,* †*Pristodus*), †Belantseidae (e.g., †*Belantsea,* †*Ctenoptychius*), and †Petalodontidae (e.g., †*Polyrhizodus*) (Lund, 1989). Cappetta et al. (1993) gave reasons for recognizing only two families, but Ginter et al. (2010) recognized four. Some members, such as †*Janassa,* are ray-like in body form. The phylogenetic position of this group is particularly uncertain.

†Order DEBEERIIFORMES. Late Mississippian. One family, †Debeeriidae, with two genera, †*Debeerius* and †*Heteropetalus* (Grogan and Lund, 2000). In appearing intermediate in morphology to chimaeroid and selachian body plans, the cranial and postcranial morphology of †*Debeerius* suggests affinity with the cochliodonts and chimaeriforms, the heterodont dentition is similar to that of selachians, and yet this order was suggested to have the fundamental jaw suspension of gnathostomes (Grogan and Lund, 2000).

†Order HELODONTIFORMES. Late Devonian to Early Permian. Known primarily from teeth and tooth plates. One family, †Helodontidae, with one genus, †*Helodus* (synonym †*Pleurodus*) (Stahl, 1999).

Superorder HOLOCEPHALIMORPHA

Dentition consisting of a few large, permanent grinding tooth plates (selachianlike anterior teeth may also be present); palatoquadrate fused to neurocranium (holostyly); dorsal fin spine usually present. This diagnosis is very imperfect; some assumed members are known only from isolated tooth plates. The Superorder Holocephalimorpha = Subclass Holocephali of some.

†Order PSAMMODONTIFORMES. Late Devonian to Early Carboniferous. Position uncertain; known only from isolated tooth plates. One family, †Psammodontidae (e.g., †*Archaeobatis,* †*Lagarodus,* and †*Psammodus*) (Stahl, 1999; Elliott et al., 2004).

†Order COPODONTIFORMES. Carboniferous. Position uncertain; known only from tooth plates. One family, Copodontidae (e.g., †*Copodus*) (Stahl, 1999).

Of the following taxa, Grogan and Lund (2004) suggested that chondrenchelyiforms and menaspiforms are sister taxa as are cochliodontiforms and chimaeriforms, with all four being sister to the squalorajiforms, and all five taxa being placed in the †Cochliodontomorpha.

†Order SQUALORAJIFORMES. Early Jurassic. Body depressed. Stahl (1999) recognized this taxon as one of four suborders of Chimaeriformes and sequenced it between the †Echinochimaeroidei and †Myriacanthoidei. One family, †Squalorajidae, and one genus, †*Squaloraja* (Stahl, 1999).

†Order CHONDRENCHELYIFORMES. Early Carboniferous. Body elongate, pectoral fin biserial, and lower jaw long. One family, †Chondrenchelyidae (e.g., †*Chondrenchelys,* †*Harpagofututor,* and †*Platyxystrodus*) (Stahl, 1999).

†Order MENASPIFORMES. Early Carboniferous (Mississippian) to Late Permian. Three families, †Deltoptychiidae with †*Deltoptychius,* †Menaspidae with †*Menaspis,* and †Traquairiidae with †*Traquairius* (Stahl, 1999).

†Order COCHLIODONTIFORMES. Late Devonian to Permian. Known primarily from teeth and tooth plates. Two families, †Cochliodontidae (e.g., †*Cochliodus,* †*Deltodus,* †*Poecilodus,* and †*Sandalodus*) and †Psephodontidae (with †*Psephodus*) (Stahl, 1999).

Order CHIMAERIFORMES (3)—chimaeras. Stahl (1999) recognized four suborders of chimaeriforms; her †Squalorajoidei are recognized here as more basal following Grogan and Lund (2004). Three families, six genera, and 48 species.

†Suborder Echinochimaeroidei. Mississippian. Position uncertain. Differs from chimaeroids in having a dermal cranial armor of denticles, placoid squamation, a tuberculated first dorsal spine, and no frontal clasper in males (Lund, 1986; Stahl, 1999). One family, †Echinochimaeridae, with one genus, †*Echinochimaera.*

†Suborder Myriacanthoidei. Late Triassic to Jurassic. Two families, †Chimaeropsidae with one genus, †*Chimaeropsis,* and †Myriacanthidae (e.g., †*Acanthorhina,* †*Agkistracanthus,* †*Halonodon,* and †*Myriacanthus*) (Stahl, 1999).

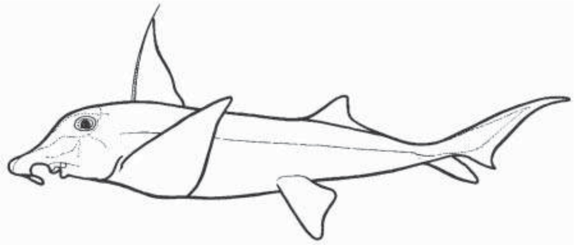
Suborder Chimaeroidei (chimaeras). Early Jurassic to present. Two dorsal fins, the first erectile, with short base, and preceded by an erectile spine, the second nonerectile, low, and with long base; mouth inferior. In living forms, at least, fertilization is internal; the deposited egg is encased in a brown horny capsule. Water for breathing is chiefly taken in through the nostrils. Maximum length about 1.5 m.

Six extant genera with about 48 species (Compagno, 2005; Didier, 2004; Didier et al., 2012). Fossil taxa, all in extant families, are given with the families.

Didier (1995), in a phylogenetic analysis of living taxa based on morphological characters, gave synapomorphic characters for the higher taxa and reviewed ideas on the origin of the Holocephali. More recently, both morphological (Didier et al., 2012) and mtDNA (Inoue, Miya, Lam et al., 2010) studies suggest that Callorhinchidae are the sister group of the other extant chimaeriforms.

Superfamily Callorhinchoidea (Callorhynchoidea). One family.

Family CALLORHINCHIDAE (Callorhynchidae) (5)—plownose chimaeras. Marine, continental and insular shelves and uppermost slopes; Southern Hemisphere (e.g., off southern South America, New Zealand, southern Australia, southern Africa).



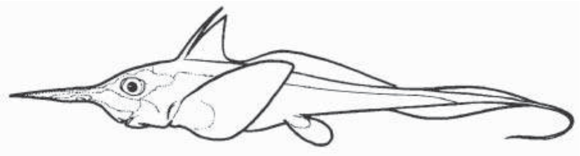
Snout with elongate, flexible, hoe-shaped process; lateral line canals closed; eyes small; tail heterocercal. Egg capsule large, ovoid (typically 27 cm × 13 cm), with wide, ribbed lateral web.

Fossil Callorhinchidae (earliest are Jurassic) include: †*Brachymylus,* †*Ischyodus,* and †*Pachymylus,* with †*Edaphodon* placed in its own subfamily, †Edaphodontinae, by Stahl (1999), and the Jurassic †*Eomanodon* and †*Ganodus* possibly also in this family. A very large, Late Cretaceous species of †*Edaphodon* was recently described from Antarctica (Gouiric-Cavalli et al., 2015). In addition, fossils of the extant genus *Callorhinchus* are known from the Eocene of Antarctica (Kriwet and Gázdzicki, 2003).

One genus, *Callorhinchus,* with three species (Didier, 1995, 1998, 2004). The orthography of the family name is changed to conform to the generic name (Eschmeyer, 1998; Didier et al., 2012).

Superfamily Chimaeroidea. Two families.

Family RHINOCHIMAERIDAE (6)—longnose chimaeras. Marine, deep oceanic, continental and insular slopes; Atlantic, Indian, and Pacific.

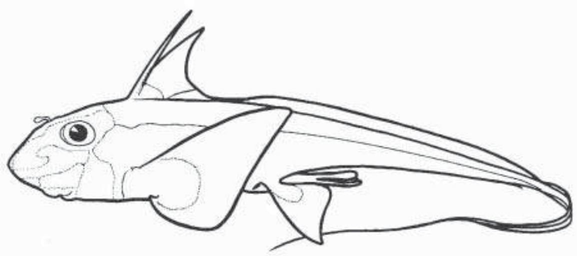


Snout long, fleshy, and pointed, not hook-like; lateral-line canals are open grooves; tail diphycercal; anal fin separated from caudal in *Neoharriotta* and joined with it in the other genera. Egg capsule ovoid (pear-like) (typically 15 cm × 6 cm), with ribbed lateral web.

Fossil Rhinochimaeridae (earliest in Jurassic) include †*Amylodon* and †*Elasmodus.*

Three genera, *Harriotta* (2), *Neoharriotta* (3), and *Rhinochimaera* (3), with about eight species (Compagno et al., 1990; Didier, 1995, 2004; Didier and Stehmann, 1996; Didier and Nakaya, 1999). Didier (1995, 2004) placed *Harriotta* and *Neoharriotta,* with thick tooth plates, in the subfamily Harriottinae, and *Rhinochimaera,* with smooth, thin tooth plates in the subfamily Rhinochimaerinae.

Family CHIMAERIDAE (7)—shortnose chimaeras or ratfishes. Marine; Atlantic and Pacific.



Snout (rostrum) short, fleshy, and rounded; lateral line canals are open grooves with those on snout widened; tail diphycercal. Egg capsule relatively small (typically 17 cm × 2.5 cm), spindle-shaped with distinct dorsal keel and little or no lateral web. A poison gland is associated with the dorsal spine, and the venom is painful to humans. Maximum total length about 1.4 m, attained in *Chimaera lignaria,* probably the largest extant chimaeroid.

Fossil Chimaeridae (earliest in Cretaceous), include †*Belgorodon.* In addition, fossils of the genus *Chimaera* are known from the Late Cretaceous and Eocene of Antarctica (Stahl, 1999; Stahl and Chatterjee, 1999).

Two genera, *Chimaera* (15) (with a notch separating the anal fin from the caudal fin) and *Hydrolagus* (22) (with anal fin joined to caudal fin), and about 37 species. Many new species have been discovered and named in the last decade (Didier et al., 2012; Kemper et al., 2014). Species of *Chimaera* occur in the northern Atlantic, off South Africa, Japan and northern China, Australia, and New Zealand, whereas species of *Hydrolagus* occur primarily in the northern and southwestern Atlantic, off South Africa, and in many areas in the Pacific (e.g., southern Alaska to southern California, Japan, Australia, and New Zealand) (Didier, 1995, 1998, 2002, 2004; Soto and Vooren, 2004; Didier et al., 2012). Most species are in the western Pacific off Japan and New Zealand. The allocation of some species to the above genera on the basis of the anal fin character is subject to change (Hardy and Stehmann, 1990; Didier, 2004).

Subclass EUSELACHII (sharks, rays, and related fossils)

Euselachians are typically predaceous fishes that use both smell and sight for obtaining their food.

There are currently two conflicting hypotheses regarding the phylogenetic relationships of crown euselachians, one based on morphological evidence and one based on molecular evidence (interestingly, older non-cladistic morphological studies showed the same conflict, some placing rays within sharks and others not). This type of conflict is common in fish systematics. In the present example, following Compagno's (1973, 1977) work, there was growing acceptance that while sharks and rays form a monophyletic group, sharks were a paraphyletic group without the inclusion of rays. Compagno (2001), Shirai (1992a, 1996), and de Carvalho (1996) agreed that rays (batoids or rajiforms) and pristiophoriforms are sister taxa and that both belong in the squalomorph clade.

However, while the studies of de Carvalho (1996) and Shirai (1996) presented sound morphological studies and analyses, there is evidence against some of their major conclusions. The cytogenetic data reviewed by Schwartz and Maddock (2002) and the molecular studies of Arnason et al. (2001) and Douady et al. (2003) presented preliminary evidence supporting the monophyly of sharks (without rays). Evidence for a similar conclusion was given by Maisey et al. (2004) based on fossil and molecular data and by Naylor et al. (2005, 2012) based on mitochondrial DNA sequences. This conclusion (sharks and rays as sisters) was accepted by McEachran and Aschliman (2004), Musick et al. (2004), and Musick and Ellis (2005). With fossils of both rays and neoselachian sharks dating to at least the Early Jurassic (Maisey et al., 2004; e.g., diverse Middle Jurassic euselachians are described by Underwood and Ward, 2004), we accept here that the paleontological evidence is more consistent with the hypothesis that sharks and rays are sister groups and of equal antiquity.

To summarize, there are two main hypotheses expressing the relationships of sharks and rays:

(i) the hypnosqualean hypothesis—the batomorphs (rays) are sister to the Pristiophoriformes and that clade (dubbed the Pristiorajea by de Carvalho, 1996) is sister to the Squatiniformes (the resulting clade being the Hypnosqualea), all of them sharing a common ancestry with the Squaliformes.

(ii) the selachian/batomorph (shark/ray) hypothesis—the sharks, as conventionally defined, are monophyletic without the inclusion of rays. The two groups are sisters and of equal antiquity. If correct, the morphological features used to argue for a monophyletic Hypnosqualea would have to be the result of convergence. This is the hypothesis adopted here.

Teeth are especially important in the fossil record of sharks and exhibit much variation between taxa. Many publications describe the teeth of living and fossil taxa, for example, works by S. P. Applegate, R. Lund, and J. G. Maisey have worked extensively on the taxonomy and systematics of fossil elasmobranchs. A general review of some aspects of shark behavior and acoustical biology may be found in Myrberg and Nelson (1990) and Myrberg (2001). Schwartz and Maddock (2002) review the cytogenetic data of euselachians.

The current classification of euselachians is very split compared to that of other fishes. The mean number of species per family is 18 and the median number is 5.3. About half of the species of sharks and rays are in four of the 51 families (Rajidae, Scyliorhinidae, Dasyatidae, and Carcharhinidae) whereas 11 families (about one-fifth of the total) are monotypic, having only one species in each.

Thirteen orders, 51 families, 189 genera, and about 1,150 species of extant elasmobranchs or euselachians. Some 513 species are sharks and 636 are skates and rays, including more than 150 named since the last edition of this book. There are many species of both sharks and rays yet to be described, with ray species still outnumbering the sharks. At least 28 species of sharks and rays are known primarily from fresh water.

The recent handbook volumes by Ginter et al. (2010) and Cappetta (2012) are especially valuable resources for the fossil taxa, as is the review by Thies and Leidner (2011) of the remarkable Late Jurassic record in Europe.

STEM-GROUP FOSSIL TAXA (by definition, all extinct) of Euselachii are listed first, followed by the crown-group taxa (extant clades and their close fossil relatives).

†*Acronemus.* This Middle Triassic shark, named by Rieppel (1982), is classified *incertae sedis* within Euselachii as suggested by Maisey (2011).

†Order PROTACRODONTIFORMES. This small group with the single recognized family †Protacrodontidae shows some similarity to the †Orodontidae and †Ctenacanthiformes (e.g., Zangerl, 1981), but was placed within Euselachii by Ginter et al. (2010).

†Infraclass HYBODONTA (hybodonts)

†Order HYBODONTIFORMES. Hybodontiforms have the features given above for the ctenacanthiforms. They differ, among other features, in their internal fin structure. Males have hooked cephalic spines above the eye that may have functioned as claspers during copulation. Hybodonts might have been as diverse in feeding and related behavioral strategies as are living sharks and rays (Maisey and de Carvalho, 1997). Some were several meters long, others only about 15 cm. Mississippian to Cretaceous.

Hybodontiforms are probably the closest extinct sister group to the elasmobranchs (Maisey et al., 2004), and this has been expressed here by giving the two groups equal rank, though it remains possible that they are paraphyletic. As noted by Maisey et al. (2004), of all euselachians, only these two lineages, the hybodonts and elasmobranchs, are known to have survived well into the Mesozoic (the other lineages becoming extinct in the Paleozoic, many in the Permo-Triassic mass extinction and the others during the Triassic) (but see Guinot et al., 2013, mentioned above). Only the elasmobranchs survived into the Cenozoic. Important references on hybodontiforms include those of Maisey (1982, 1989, 1991).

Hybodontiforms were the dominant selachians of the Triassic and Jurassic, and remained important until the Late Cretacous, including freshwater forms that lived in large river systems. Sometimes grouped in a single family (Hybodontidae), Cappetta (1987) and Cappetta et al. (1993) recognized several families. The most recent treatments by Ginter et al. (2010) and Cappetta (2012) divide hybodontiforms among up to ten families, listed with examples of genera as follows:

†Family HYBODONTIDAE (e.g., †*Egertonodus*, †*Hybodus*, †*Meristodondoides*, †*Pororhiza*, †*Priohybodus*, †*Thaiodus*).

†Family TRISTYCHIIDAE (e.g., †*Tristychius*).

†Family DISTOBATIDAE (e.g., †*Aegyptobatus*, †*Distobatus*, †*Glickmanodus*, †*Reticulodus*, †*Tribodus*).

†Family ACRODONTIDAE (e.g., †*Acrodus*, †*Acrorhizodus*, †*Asteracanthus*, †*Bdellodus*).

†Family POLYACRODONTIDAE (e.g., †*Palaeobates*, †*Polyacrodus*).

†Family LONCHIDIIDAE (e.g., †*Bahariyodon*, †*Diplolonchidion*, †*Hylaeobatis*, †*Isanodus*, †*Lissodus*, †*Lonchidion*, †*Parvodus*, †*Vectiselachos*).

†Family STEINBACHODONTIDAE (e.g., †*Steinbachodus*).

†Family PSEUDODALATIIDAE (e.g., †*Pseudodalatias*).

THE FOLLOWING TWO FAMILIES may belong either in †Division Hybodonta or in Division Neoselachii (Cappetta, 2012).

†Family PTYCHODONTIDAE (e.g., †*Heteroptychodus*, †*Ptychodus*).

†Family HOMALODONTIDAE (e.g., †*Homalodontus*).

Infraclass ELASMOBRANCHII (= NEOSELACHII)

This infraclass includes all extant sharks and rays. Following Maisey (2012), the Neoselachii of Compagno (1977) are considered synonymous with the Elasmobranchii of Bonaparte (1838). Two clades of elasmobranchs are recognized, the division Selachii (sharks) and the division Batomorphi (the rays and skates, often called the Batoidea, an orthography that has a superfamily ending and was more appropriate when they were classified at a much lower rank). The recognition of the rays as sister group to the Selachii is discussed above under Euselachii. The Selachii are in turn divided into two large clades, the superorder Galeomorphi and the superorder Squalomorphi. There are thus three main clades ((Galeomorphi, Squalomorphi), Batomorphi).

As noted in Maisey (2001b), in elasmobranchs the anterior and posterior semicircular canals are separated dorsally (they are variously united dorsally in chimaeroids, sarcopterygians, and actinopterygians).

The arrangement of these clades used here treats the galeomorphs first and the rays last, as has been conventional in past classifications. This has the ancillary advantage of placing the rays immediately after (but not as the closest relatives of) the most ray-like of the squalomorph sharks (the squatiniforms and the pristiophoriforms). In older classifications rays were thought to be close relatives of those ray-like sharks, but the resemblances are now considered to be a result of strong convergence. The arrangement used here makes it easier for the reader to compare them.

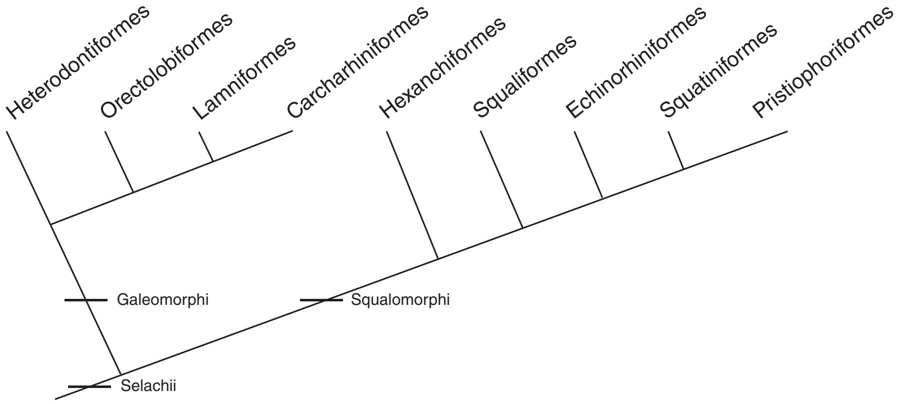
The elasmobranch fossil record begins in the Early Jurassic, and Maisey et al. (2004) gave a list of the earliest records of their modern taxa. All of the extinct orders of Elasmobranchii considered up to now are stem-group elasmobranchs, but the two extinct neoselachian orders listed below (†Synechodontiformes and †Protospinaciformes) are part of the crown-group Neoselachii (despite being extinct).

An overview of the higher categories of elasmobranchs adopted here is as follows:

- Infraclass Elasmobranchii
  - Division Selachii (sharks)
    - Superorder Galeomorphi
      - †Order Synechodontiformes (one family)
      - Order Heterodontiformes (one family)
      - Order Orectolobiformes (seven families)
        - Suborder Parascyllioidei (one family
        - Suborder Orectoloboidei (six families)
      - Order Lamniformes (seven families)
      - Order Carcharhiniformes (eight families)
    - Superorder Squalomorphi
      - Series Hexanchida (two families)
        - Order Hexanchiformes (two families)
      - Series Squalida
        - Order Squaliformes (six families)
      - Series Squatinida
        - †Order Protospinaciformes (one family
        - Order Echinorhiniformes (one family)
        - Order Squatiniformes (one family)
        - Order Pristiophoriformes (one family)
  - Division Batomorphi (rays)
    - Order Torpediniformes (two families)
    - Order Rajiformes (one family)
    - Order Pristiformes (five families)
    - Order Myliobatiformes (nine families)
      - Suborder Platyrhinoidei (one family)
      - Suborder Myliobatoidei (eight families)

Division SELACHII—sharks

Gill openings mainly lateral; anterior edge of pectoral fin not attached to side of head; anal fin present or absent; pectoral girdle halves not joined dorsally (but scapulocoracoids fused ventrally in both sharks and rays). These features, while not representing shared derived features of the clade, do serve to distinguish sharks from rays. See above under Infraclass Euselachii for reasons why the sharks and rays, unlike in the 1994 edition, are placed in separate taxa of equal rank.



The Selachii (= Selachimorpha, Pleurotremata) contain two superorders, the Galeomorphi, with four orders, and the Squalomorphi with five orders, and a total of 34 families, 106 genera, and at least 513 species.

Superorder GALEOMORPHI

Anal fin present (members of the other superorder with living species, the Squalomorphi, lack an anal fin, except for the Hexanchiformes). The recognition of galeomorphs as a monophyletic group follows Compagno (1988, 2001) and de Carvalho (1996) and discussed by Cappetta (2012). Synapomorphies include closed lateral line canal; ethmoidal region of neurocranium downcurved; hyomandibular fossa located anteriorly in the otic region; suborbitalis muscle originating on upper preorbital wall; suborbitalis muscle inserting directly on mandible anterior to adductor mandibulae; nasoral groove present; and pharyngobranchial blade present.

The composition is the same as the division Galeomorphii of de Carvalho (1996), superorder Galea of Shirai (1996), and superorder Galeomorphi of Compagno (2001); all have the same four orders as here. The sequencing of the orders is based on de Carvalho (1996), Goto (2001), and Musick and Ellis (2005), where the Heterodontiformes (the most primitive galeomorphs) are sister to the other three orders and the Orectolobiformes are sister to the Lamniformes and Carcharhiniformes. The classification, information on distribution, and much of the other information are based on Compagno (1999, 2001, 2005).

Four orders, 23 families, 76 genera, and about 352 species. One fossil order with one family is also recognized (Cappetta, 1987, 2012).

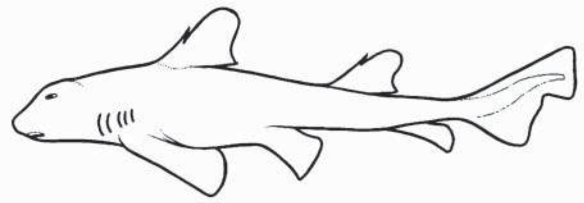
†Order SYNECHODONTIFORMES. One family. These were classified in Galeomorphi by Cappetta (2012).

†Family PALAEOSPINACIDAE. Permian or Early Triassic to Paleocene or perhaps Eocene. E.g., †*Palidiplospinax,* †*Synechodus*.

Order HETERODONTIFORMES (4)—bullhead sharks. Two dorsal fins, each with a spine (other galeomorphs lack dorsal fin spines); anal fin present; head elevated with crests above eyes; five gill slits, first the largest and posteriormost two or three behind pectoral fin origin; spiracle present but small; eyes dorsolateral, without nictitating fold; nostrils connected with mouth by deep groove. Vertebrae 103–123. Oviparous, screw-shaped egg cases.

One family (Compagno, 2001).

Family HETERODONTIDAE (8)—bullhead sharks. Marine, tropical to warm temperate, continental and insular shelves (primarily continental versus oceanic islands) and uppermost slopes (0–275 m, most shallower than 100 m); western Indian (Arabian Peninsula to South Africa) and Pacific (western Pacific from Japan to Tasmania and New Zealand, eastern Pacific from California to Galapagos Islands and Peru). See order for family characters. Maximum length 1.6 m, attained in *Heterodontus portusjacksoni*, most under 1 m. Also known as horn sharks or Port Jackson sharks.



One genus, *Heterodontus*, with nine species (Compagno, 2001; Baldwin, 2005). Cappetta (2012) included also two extinct genera (†*Paracestracion* and †*Proheterodontus*), with at least 15 extinct species.

Order ORECTOLOBIFORMES (5)—carpet sharks. Two dorsal fins, without spines; anal fin present; five gill slits, broad, last two to four above or behind pectoral fin origin; spiracles present, small to large, and close behind and about level with eyes; eyes usually dorsolateral on head (lateral in *Nebrius, Stegostoma,* and *Rhincodon*); eyes without nictitating membrane; mouth small to large, well in front of the eyes; nostrils longitudinal on snout, with prominent nasoral grooves and barbels in most.

Seven families, 14 genera, and 44 species (Compagno, 2001, 2005). Goto (2001), who gave a cladistic analysis of this order, gave keys to the families and the genera, placed the families Stegostomatidae and Ginglymostomatidae in synonymy with Rhincodontidae, and thus recognized only five families. The recognition of the two suborders follows Goto (2001) and is supported by molecular results of Naylor et al. (2012). Cappetta (2012) listed the following genera as Orectolobiformes but of uncertain familial placement: †*Annea*, †*Dorsetoscyllium*, †*Folipistrix*, †*Heterophorcynus*, †*Ornatoscyllium*, and †*Phorcynis*.

Suborder Parascyllioidei. Spiracles minute, without gill filaments; fifth (and last) gill opening large; origin of anal fin well in front of origin of second dorsal fin.

Family PARASCYLLIIDAE (9)—collared carpet sharks. Marine, tropical to temperate continental to slopes (1–435 m); western Pacific (Australia to Japan). The oldest fossils are Albian (late Early Cretaceous).

Vertebrae 159–199. Maximum length 3.3 m, in *Cirrhoscyllium expolitum*, most under 0.9 m.

Two genera, *Cirrhoscyllium* (3, South China Sea to Japan) and *Parascyllium* (5, Australia), with eight species (Compagno, 2001, 2005; Last and Stevens, 2008). According to Cappetta (2012) there is one extinct genus, the Albian to Eocene †*Pararhincodon*, with four species.

Suborder Orectoloboidei. Spiracles moderate to large, with gill filaments; fifth (and last) gill opening moderate in size; origin of anal fin behind origin of second dorsal fin.

Two superfamilies are recognized in this suborder.

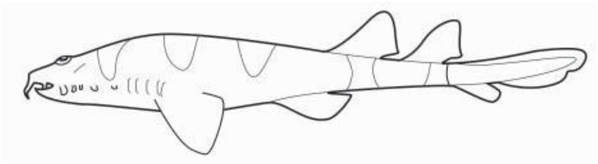
Superfamily Orectoloboidea. Naylor et al. (2012) found mtDNA-sequence support for a clade, recognized here as a superfamily, comprising Brachaeluridae and Orectolobidae.

Family BRACHAELURIDAE (10)—blind sharks. Marine, tropical to temperate continental shelf, primarily coastal (0–137 m); western South Pacific (off east coast of Australia). The oldest fossils are from the Middle Jurassic.

Spiracles large; nasal barbels very long; eyes dorsolateral. The common name comes from the habit of one of the species of closing its eyelids when removed from the water. Vertebrae 117–142. Maximum length about 1.2 m, attained in *Brachaelurus waddi*.

Two monotypic genera, *Brachaelurus* and *Heteroscyllium* (Compagno, 2001, 2005), though both species are placed in *Brachaelurus* by Goto (2001). The extant genus *Brachaelurus* is recorded first from the Early Cretaceous. Cappetta (2012) includes three extinct genera (†*Eostegostoma*, †*Palaeobrachaelurus*, and †*Paraginglymostoma*).

Family ORECTOLOBIDAE (11)—wobbegongs. Marine, tropical to warm temperate continental shelf (0–110 m); western Pacific (Japan to southern Australia). The oldest fossil orectolobids are Late Jurassic.



Head and body depressed; mouth nearly terminal; skin flaps along side of head and long barbels; spiracles large; enlarged fang-like teeth at symphysis of upper and lower jaws. Vertebrae 149–158. Maximum length about 3.2 m, attained in *Orectolobus maculatus.*

Three genera, *Eucrossorhinus* (1), *Orectolobus* (synonym *Crossorhinus*) (10), and *Sutorectus* (1), with 12 species (Compagno, 2001, 2005; Goto, 2008; Last et al., 2010). Fossils of the genus *Orectolobus* are as old as middle Eocene. Cappetta (2012) listed also five extinct genera in this family (†*Cederstroemia*, †*Cretorectolobus*, †*Eometlaouia*, †*Orectoloboides*, and †*Squatiscyllium*).

A recent phylogenetic analysis based on mtDNA (Corrigan and Beheregaray, 2009) did not support recognition of *Eucrossorhinus* and *Sutorectus* as distinct genera (the latter was suggested also by Vélez-Zuazo and Agnarsson, 2011), unless other lineages of *Orectolobus* are also recognized as distinct genera. We reserve judgement pending further study of morphology and additional molecular markers in this interesting group of sharks.

Superfamily Hemiscyllioidea. Naylor et al. (2012) found some mtDNA-sequence support for a clade including Hemiscylliidae, Ginglymostomatidae, Stegostomatidae, and Rhincodontidae, recognized here as a superfamily. Ginglymostomatidae were not included in the clade found by Vélez-Zuazo and Agnarsson (2011), but the exclusion was only weakly supported.

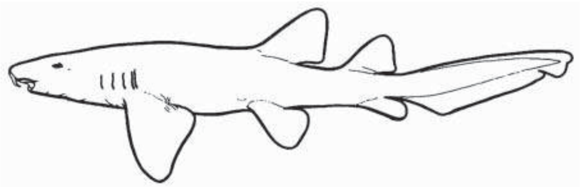
Family HEMISCYLLIIDAE (12)—bamboo sharks. Marine, tropical and subtropical, continental shelves (usually close inshore, up to about 100 m); Indo-West Pacific (Madagascar to Japan and Australia). The oldest fossils are from the Early Cretaceous.

Nasal barbels short; spiracles large; anal fin low and rounded, origin well behind origin of second dorsal fin. Vertebrae 151–192. Maximum length about 1.0 m, attained in *Chiloscyllium punctatum* and *Hemiscyllium ocellatum,* most under 70 cm.

Two genera, *Chiloscyllium* (8) and *Hemiscyllium* (9, primarily western Pacific, the long-tailed carpet sharks), with 17 species (Compagno, 2001, 2005). Naylor et al. (2012) presented preliminary results suggesting that *Chiloscyllium* might be paraphyletic with respect to *Hemiscyllium,* but they also noted that additional species, especially of *Hemiscyllium,* must be sampled to test this.

There are five extinct species of *Chiloscyllium,* the oldest from the Early Cretaceous, and four of *Hemiscyllium,* the oldest being latest Cretaceous. Cappetta (2012) included also three extinct genera (†*Acanthoscyllium,* †*Almascyllium,* †*Mesiteia*) in the family.

Family GINGLYMOSTOMATIDAE (13)—nurse sharks. Marine, tropical and subtropical inshore over continental and insular shelves (0 to about 100 m); western Atlantic (northern USA to southern Brazil), eastern Atlantic primarily off Africa, Indo-West and central Pacific (Africa to southern Japan, northern Australia, and Tahiti), and eastern Pacific (Mexico to Peru). The oldest fossils are Early Cretaceous.



Spiracles small (smaller than the eyes), behind the eyes; eyes lateral on head in *Nebrius*; nostrils with short to moderately long barbels; no lobe and groove around outer edges of nostrils; fourth and fifth gill slits almost overlapping. Vertebrae 135–195.

Maximum length about 3 m, attained in *Ginglymostoma cirratum* and *Nebrius ferrugineus.*

Two monotypic genera, *Ginglymostoma* and *Nebrius* (Compagno, 2001, 2005). However, there were many more species in the past. Cappetta (2012) listed 14 extinct species for *Ginglymostoma,* the oldest being late Late Cretaceous, and a further six extinct genera in the family (†*Cantioscyllium,* †*Delpitoscyllium,* †*Ganntouria,* †*Hologinglymostoma,* †*Plicatoscyllium,* and †*Protoginglymostoma*).

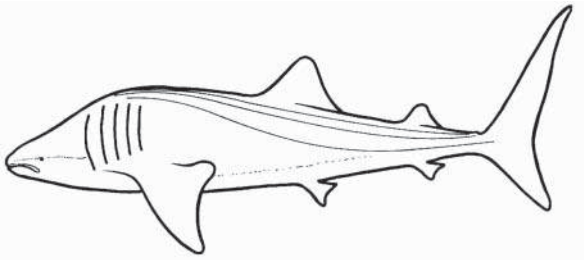
The extant genus *Pseudoginglymostoma,* formerly included in this family, belongs, based on mtDNA sequence phylogenetics, in a group with *Rhincodon* and *Stegostoma* (see below) according to Naylor et al. (2012).

Family STEGOSTOMATIDAE (14)—zebra sharks. Marine, primarily tropical inshore over continental and insular shelves (0–62 m); Indo-West Pacific (from Red Sea and off eastern Africa to southern Japan, northern Australia, and New Caledonia). The oldest fossils are Eocene.

Spiracles moderate in size and behind the eye; eyes lateral on head; caudal fin unusually long, almost as long as rest of shark. Vertebrae 207–243. Maximum length possibly 3.5 m, usually under 2.5 m.

Two genera, *Stegostoma fasciatum,* Zebra Shark (Compagno, 2001, 2005) and *Pseudoginglymostoma brevicaudatum,* Short-tail Nurse Shark; the latter belongs here rather than in Ginglymostomatidae, according to Naylor et al. (2012). The oldest fossils of *Stegostoma* are Eocene.

Family RHINCODONTIDAE (Rhiniodontidae) (15)—whale sharks. Marine, tropical to warm temperate coastal and oceanic (0–700 m); circumglobal Atlantic, Indian, and Pacific. The oldest fossils are late Paleocene.



Mouth exceptionally large and virtually terminal; gill openings exceptionally large, fifth well separated from fourth; eyes lateral; gill rakers elongate, plankton feeders; teeth reduced but numerous tooth rows; spiracles relatively small. Vertebrae 174. Maximum length at least 12 m, probably over 14 m, and perhaps up to 18 m (Colman, 1997). Even at "only" 12 m, this is the world's largest fish.

One species *Rhincodon typus*, Whale Shark (Compagno, 2001, 2005). Generic synonym: *Rhiniodon*. The oldest fossils of *Rhincodon* are late Oligocene according to Cappetta (2012), who also recognized one extinct genus, †*Palaeorhincodon*.

Order LAMNIFORMES (6)—mackerel sharks. Two dorsal fins, without spines; anal fin present; five gill slits, broad, last two may be above pectoral fin origin; spiracles usually present, small and behind eyes; eyes usually lateral (dorsolateral in *Carcharias*); eyes without nictitating membrane; barbels absent; mouth large and extending well behind eyes; spiral intestinal valve of ring type (appearing as a stack of rings), with 19–55 turns.

Many lamniforms are known to practice oophagy, in which an embryo eats the eggs representing its presumptive siblings or half-siblings in the womb prior to birth, and in some cases a form of cannibalism called embryophagy, in which the larger embryos eat smaller ones until the mother is left to give birth to only one large embryo (Gilmore, 1993).

Seven extant families with 10 genera and 15 species (Compagno, 2001). Naylor et al. (2012) and Vélez-Agnarsson (2011) have made a start at checking assignment of genera to families, but there is enough disagreement between those studies to prevent us making sweeping changes at this time.

Eight extinct families belong in the Lamniformes according to Cappetta (2012); they are listed first, followed by the extant families.

Fossil lamniforms that cannot readily be classified to family include some well-known forms, such as †*Cretodus*, †*Dwardius*, †*Eostriatolamia*, †*Palaeocarcharias*, †*Palaeocarcharodon*, †*Paranomotodon*, †*Priscusurus*, and †*Trigonotodus* (Cappetta, 2012).

†Family OTODONTIDAE. Paleocene to Pliocene. Extinct genera include †*Otodus* (see below) and †*Parotodus* (with four species). The well-known fossil genus †*Cretalamna* is likely a synonym of the genus †*Otodus* (Cappetta, 2012).

The extinct genus †*Otodus* contains three subgenera: †*Otodus* (†*Otodus*), with four species including †*Otodus obliquus*; †*Otodus* (†*Carcharocles*), with seven species and subspecies; and †*Otodus* (†*Megaselachus*), with two species: †*Otodus* (†*Megaselachus*) *chubutensis* and †*Otodus* (†*Megaselachus*) *megalodon*.

Thus, the famous, giant Megatooth Shark or Megalodon, which had huge teeth, grew to at least 11 and perhaps 20 m in length, and was formerly classified by various authorities in the genus *Carcharodon* or *Isurus* (see below, family Lamnidae) or †*Carcharocles* (the current family but in a different subgenus), is now usually considered to be a member of †Family Otodontidae, genus †*Otodus*, subgenus †*Megaselachus*.

†Family XIPHODOLAMIIDAE. Eocene. Two species in †*Xiphodolamia*.

†Family CARDABIODONTIDAE. Late Early Cretaceous (Albian) to early Late Cretaceous (Turonian). There are two species in the genus †*Cardabiodon*, including †*C. ricki*, which may have had an antitropical distribution in the Turonian (Cook et al., 2010).

†Family CRETOXYRHINIDAE. Late Early Cretaceous (Albian) to mid Late Cretacous (Campanian). There are three genera (†*Acrolamna,* †*Cretoxyrhina*, †*Dallasiella*). Cappetta included †*Archaeolamna* with this family, but it is here classified in the separate family †Archaeolamnidae (below).

†Family ARCHAEOLAMNIDAE. Late Early Cretaceous (Albian) to late Late Cretaceous (Maastrichtian). One species, †*Archaeolamnidae kopingensis*, and several less well-known and unnamed forms. Underwood and Cumbaa (2010) established the †Archaeolamnidae based on isolated but associated teeth. Cook et al. (2011) described a partial articulated skeleton with mostly intact dentition that clarified this shark's tooth replacement pattern and relationships.

†Family PSEUDOSCAPANORHYNCHIDAE. Early Cretaceous to late Late Cretaceous (Maastrichtian). Three genera (†*Leptostyrax*, †*Protolamna*, and †*Pseudoscapanorhynchus*).

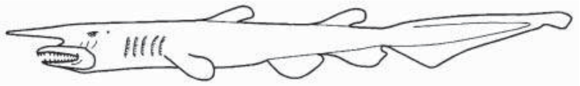
†Family ANACORACIDAE. Late Early Cretaceous (Albian) to late Late Cretaceous (Maastrichtian). Three genera (†*Nanocorax*, †*Ptychocorax*, and †*Squalicorax*).

†Family PSEUDOCORACIDAE. Late Cretaceous. There are two genera (†*Galeocorax* and †*Pseudocorax*).

THE REMAINING FAMILIES are extant, but most are well represented also by fossils.

Family MITSUKURINIDAE (16)—goblin sharks. Marine, outer continental and upper slopes and seamounts (100–1300 m, usually 270–960 m); scattered in eastern Atlantic (France to South Africa), western Atlantic (Gulf of Mexico and Guiana to French Guyana), western Indian (primarily South Africa), western Pacific (Japan, Australia, and

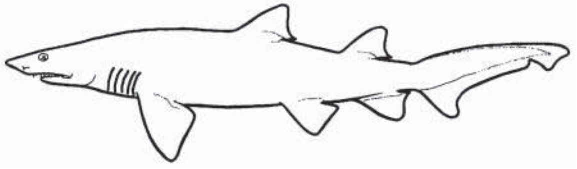
New Zealand), and eastern Pacific (southern California). The oldest fossils are Early Cretaceous.



Snout with a greatly elongated and flattened blade-like projection; jaws very protrusible; precaudal pit absent; eyes small; caudal fin long but ventral lobe not developed. Vertebrae 122–125. Maximum length 3.8 m.

One species, *Mitsukurina owstoni*, Goblin Shark (Compagno, 2001, 2005). Naylor et al. (2012), on evidence from mtDNA, suggest that *Mitsukurina* is sister to other extant lamniforms, but not with strong support. The oldest fossils of *Mitsukurina* are early Eocene in age, and two extinct species are recognized in the genus. Cappetta (2012) also listed the following extinct genera in this family: †*Anomotodon*, †*Scapanorhynchus*, †*Striatolamia*, and †*Woellsteinia*.

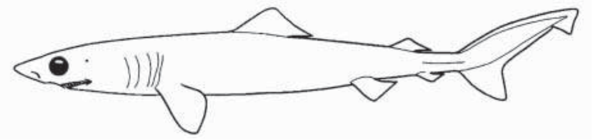
Family ODONTASPIDIDAE (17)—sand tiger sharks. Marine, tropical to temperate continental and insular shelves to deep slopes (1 to about 1600 m) with one species oceanic; Atlantic, Indian, and Pacific. The oldest fossils are Early Cretaceous.



Gill openings all in front of pectoral fin, relatively large but not extending onto dorsal surface of head; eyes relatively small; caudal peduncle without a lateral keel; caudal fin asymmetrical with relatively short ventral lobe. Vertebrae 156–183. Maximum length 4.1 m, attained in *Odontaspis ferox* (the other two species reach over 3 m). *Carcharias taurus*, the Sand Tiger, is the only shark so far shown to practise embryophagy (Gilmore, 1993).

Two genera, *Carcharias* (synonym *Eugomphodus*) (1: *C. taurus*, Sand Tiger, including *C. tricuspidatus* as a junior synonym) and *Odontaspis* (2: *O. ferox*, Smalltooth Sand Tiger, and *O. noronhai*, Bigeye Sand Tiger), with three species (Compagno, 2001, 2005). *Carcharias* and *Odontaspis* have been separate since the Cretaceous, their oldest fossils both being of Late Cretaceous age. Cappetta (2012) and Shimada et al. (2015) discussed extinct genera (e.g., †*Brachycarcharias*, †*Cenocarcharias*, †*Hypotodus*, †*Jaekelotodus*, †*Johnlongia*, †*Orpodon*, †*Pseudomegachasma*, †*Roulletia*, †*Sylvestrilamia*, and †*Turania*). The fossil genus †*Synodontaspis* is considered a synonym of *Carcharias*.

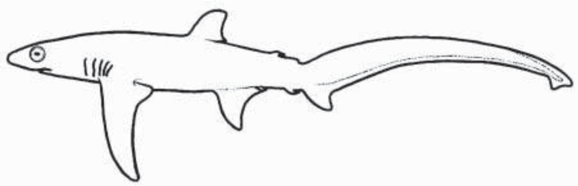
Family PSEUDOCARCHARIIDAE (18)—crocodile sharks. Marine, tropical to subtropical, inshore (rarely) to oceanic and circumglobal (surface to at least 590 m); scattered localities, western Atlantic (Brazil), eastern Atlantic (Cape Verde Islands to South Africa), western Indian (primarily southern Africa), parts of eastern Indian, western Pacific (southern Japan to northern Australia, North Island of New Zealand, and Hawaii), much of open Pacific (Hawaii to North and South America), and eastern Pacific (Baja California to Peru). The oldest fossils are early Eocene in age.



Eyes exceptionally large; gill openings extending onto dorsal surface of head; caudal peduncle with upper and lower precaudal pits and with low lateral keel; caudal fin asymmetrical with moderate lower lobe. Vertebrae 146–158. Maximum length 1.1 m.

One species, *Pseudocarcharias kamoharai*, Crocodile Shark (Compagno, 2001, 2005).

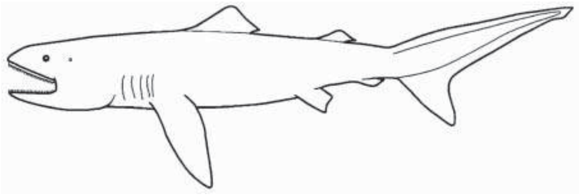
Family ALOPIIDAE (19)—thresher sharks. Marine, tropical to cold temperate, coastal and oceanic (surface–at least 500 m); scattered across Atlantic, Indian, and Pacific. The oldest fossils are early Eocene.



Upper lobe of caudal fin long and curving, about as long as rest of shark; last two gill openings above pectoral fin base; gill openings short; mouth small; pectoral fins long and narrow; eyes large; precaudal pits present. Vertebrae 282–477 (most variation is in the number of caudal vertebrae; *Alopias vulpinus* has the greatest number, 453–477). Maximum length at least 5.7 m, attained in *Alopias vulpinus*, the Pelagic Thresher, the species with the largest range.

One genus, *Alopias*, with three species (Compagno, 2001, 2005). *Alopias* is known from fossils are early as the early Eocene and has about seven extinct species. Extinct genera listed by Cappetta (2012) include †*Anotodus* and †*Usakias*.

Family MEGACHASMIDAE (20)—megamouth sharks. Marine, tropical to warm temperate, coastal (as shallow as 5 m) and oceanic (epipelagic from 8–166 m depth), probably circumtropical; Atlantic (Brazil and Senegal), Indian (western Australia), and Pacific (Japan, Philippines, Indonesia, Hawaiian Islands, and southern California). The oldest megachasmid fossils are late Oligocene.

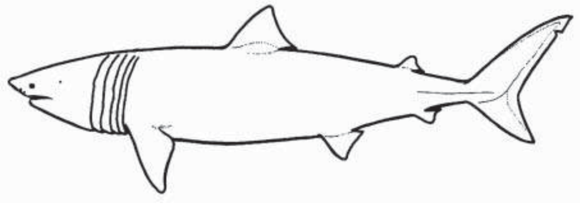


Head elongated, about length of trunk; mouth exceptionally large, terminal; snout short and broadly rounded; gill openings moderately long but not extending onto dorsal surface of head and with last two over pectoral fin base; teeth small, in numerous rows; gill rakers unique, of finger-like dermal papillae; precaudal pits present. Vertebrae 151. Maximum length 5.5 m.

This is one of the three species of gigantic filter-feeding sharks. First found in 1976 and described in 1983, the single extant species was known up to 2013 from only 63 confirmed sightings (see http://www.flmnh.ufl.edu/fish/ under "shark" for updates). It is the only shark thought to be subject to attacks from the semi-parasitic shark *Isistius brasiliensis.*

One species, *Megachasma pelagios*, Megamouth Shark (Compagno, 2001, 2005).

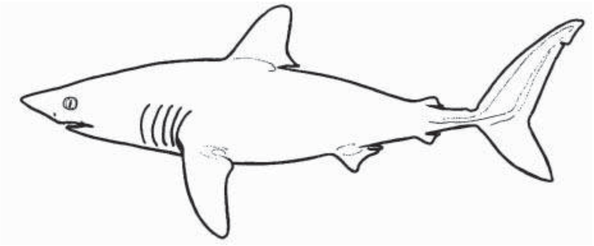
Family CETORHINIDAE (21)—basking sharks. Marine, warm temperate (rarely subtropical) to cool temperate, continental and insular shelves, possibly oceanic (usually in shallow water); Atlantic (including the Mediterranean and western Barents Sea), Indian (only off western Australia), and Pacific. The oldest fossils are from the middle Eocene.



Gill openings exceptionally large, extending almost to the top of the head; teeth small and numerous; mouth large; eyes small; gill rakers elongate (hair-like), modified dermal denticles (occasionally shed in this plankton feeder); caudal fin nearly symmetrical and caudal peduncle with strong lateral keel. Vertebrae 109–116. Maximum length perhaps up to 15.2 m, at least 10 m. One of the three species of gigantic filter-feeding sharks, this is the world's second largest fish species.

One species, *Cetorhinus maximus*, Basking Shark (Compagno, 2001, 2005).

Family LAMNIDAE (22)—mackerel sharks. Marine, tropical to cool temperate, continental and insular waters (to about 1,200 m) and oceanic; Atlantic, Indian, and Pacific. The oldest fossil record is from the early Paleocene.



Gill openings large, barely extending onto dorsal surface of head; teeth relatively few and enlarged; gill rakers absent; caudal fin nearly symmetrical and caudal peduncle with strong lateral keel and precaudal pits. Vertebrae 153–197. Maximum length at least 6.0 m, attained in *Carcharodon carcharias* (White Shark, also known as the Great White Shark, e.g., in FAO publications) (Compagno, 2001).

The distinctive rostral cartilages of various lamnid species were studied by Mollen et al. (2012). Lamnids are among the few sharks known to maintain internal body temperatures (in swimming muscles) well above external water temperatures through a counter-current heat-exchange system.

The White Shark is responsible for the majority of attacks on humans in many areas (e.g., for this and other information see Myrberg and Nelson, 1990; Ellis and McCosker, 1991; Klimley and Ainsley, 1996; Compagno, 2001; see also the International Shark Attack File [ISAF] at http://www.flmnh.ufl.edu/fish/). It also has one of the widest distributions of all elasmobranchs, being found around the world mostly in northern and southern temperate seas, while being rare in equatorial or tropical seas (a so-called antitropical distribution). Long-distance migration has been recorded from the western coast of North America to the Hawaiian Islands and back. One radio-tagged female Great White famously traveled from South Africa to Australia within 99 days, cruising mostly at shallow depths but diving frequently into much deeper waters of the Indian Ocean. Six months later the same shark was identified again off South Africa (Bonfil et al., 2005).

Three genera with five species (Compagno, 2001, 2005): *Carcharodon* (1, *C. carcharias*, White Shark), *Isurus* (2, *I. oxyrinchus*, Shortfin Mako, and *I. paucus*, Longfin Mako), and *Lamna* (2, *L. nasus*, Porbeagle, and *L. ditropis,* Salmon Shark, one of the fastest swimming sharks, believed able to achieve 80 km/h). *Carcharodon* is known from early Pliocene fossils, *Lamna* from the early Pliocene, and *Isurus* as early as early Oligocene, with one extinct species, *Isurus desori.* There are seven extinct genera listed by Cappetta (2012): †*Carchariolamna*, †*Carcharoides*, †*Cosmopolitodus*, †*Isurolamna*, †*Karaisurus*, †*Lethenia*, and †*Macrorhizodus.*

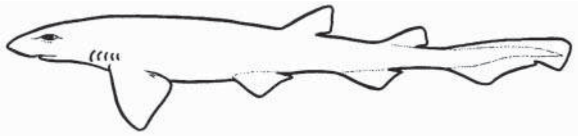
The giant fossil shark known as the Megatooth Shark or Megalodon had formerly been classified here by some but is now included in the extinct family †Otodontidae (see above) by most authorities (e.g., Cappetta, 2012).

Order CARCHARHINIFORMES (7)—ground sharks. Two dorsal fins (one dorsal fin in the scyliorhinid *Pentanchus profundicolus*, the Onefin Cat Shark, from the

Philippines), without spines; anal fin present; five gill slits, with the last one to three over the pectoral fin; gill rakers absent; mouth extending behind eyes; eyes with nictitating fold or membrane (lower eyelid, described in detail in Compagno, 1988); spiracles usually absent; intestinal valve of spiral or scroll type (described in Compagno, 1988:79–80). Development may be oviparous, ovoviparous, or viviparous.

Eight families, 51 genera, and at least 284 species (Compagno, 1999; FishBase). The classification of this order is based on Compagno (1999). Iglésias et al. (2005) presented molecular evidence that some of the genera and families are not monophyletic, but their phylogeny still was not fully resolved. Another molecular study with more complete taxon sampling but using a shorter segment of mtDNA (Naylor et al., 2012) suggested that the Scyliorhinidae, especially, might not be monophyletic.

Family SCYLIORHINIDAE (23)—cat sharks. Marine, temperate to tropical; continental and insular shelves and slopes; circumglobal, Atlantic, Indian, and Pacific. The oldest fossils are Middle Jurassic (Cappetta, 2012).



First dorsal fin base opposite or behind pelvic-fin base (in front of pelvic-fin base in all others); nictitating eyelids rudimentary; spiracles present; intestine with spiral valve. Maximum length at least 1.6 m, attained in *Scyliorhinus stellaris.*

Seventeen genera and about 150 species: *Apristurus* (37), *Asymbolus* (9), *Atelomycterus* (5), *Aulohalaelurus* (2), *Bythaelurus* (9), *Cephaloscyllium* (20), *Cephalurus* (1), *Figaro* (2), *Galeus* (17), *Halaelurus* (7), *Haploblepharus* (4), *Holohalaelurus* (5), *Parmaturus* (9), *Pentanchus* (1), *Poroderma* (2), *Schroederichthys* (5), and *Scyliorhinus* (15). Many new species have been recently named (Iglésias et al., 2004a,b, 2012; White et al., 2005, 2007, 2008; Human, 2006a,b, 2007; Human and Compagno, 2006; Gledhill et al., 2008; Jacobson and Bennett, 2007; Séret and Last, 2007, 2008a,b; Last and Stevens, 2008; Last and White 2008; Last et al., 2008a,b; Nakaya, Sato, and Iglésias, 2008; Nakaya, Sato, and Iglesias et al., 2008; Sasahara et al., 2008; Sato et al., 2008; Schaaf-Da Silva and Ebert, 2008; White and Ebert, 2008; McCosker et al., 2012; Nakaya and Kawauchi, 2013; Nakaya et al., 2013). Compagno (2005) provided diversity data, augmented in this edition by data from FishBase and others.

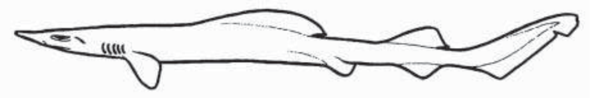
Human et al. (2006) presented molecular evidence from mtDNA concerning relationships of Scyliorhinidae. The mitochondrial molecular results of Naylor et al. (2012) suggest that Scyliorhinidae might be paraphyletic with respect to other carcharhiniforms. The proposed separation (Compagno, 1988, but not, e.g., 2005; Iglésias et al., 2005) of Pentanchidae (*Apristurus, Asymbolus, Cephalurus, Galeus, Lalaelurus, Haploblepharus, Holohalaelurus, Parmaturus, Pentanchus*) from the remaining Scyliorhinidae has gained some support but remains premature pending more extensive genetic and taxon sampling and morphological evaluation in relevant studies.

Family PROSCYLLIIDAE (24)—finback cat sharks. Marine, warm temperate to tropical, continental shelves and slopes; western North Atlantic (between Florida and Cuba) and Indo-West Pacific. The oldest fossil record is Middle Jurassic (Cappetta, 2012).

Nictitating eyelids rudimentary; spiracles present; posterior teeth comb-like; labial furrows (at corner of mouth) short or absent.

Three genera: *Ctenacis* (1), *Eridacnis* (3), and *Proscyllium* (3), with seven species (Compagno, 1999, 2005). An extinct genus from the Middle Jurassic, †*Praeproscyllium*, was named by Underwood and Ward (2004).

Family PSEUDOTRIAKIDAE (25)—false cat sharks. Marine, continental and insular slopes; part of North Atlantic, western Indian, and western and central Pacific (including to New Zealand).



First dorsal fin low, elongate, and keel-like; nictitating eyelids rudimentary; spiracles large; tooth rows exceptionally numerous, posterior teeth comb-like; intestine with spiral valve. Maximum length 2.9 m.

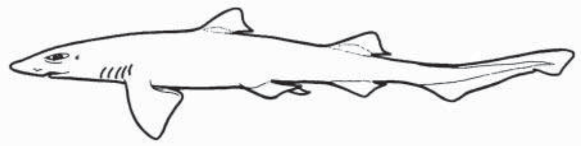
Three genera and four species: *Gollum* (2) (e.g., Last and Gaudiano 2011); *Planonasus* Weigmann et al., 2013 (1); *Pseudotriakis* (1) (e.g., Compagno, 1999, 2005).

Family LEPTOCHARIIDAE (26)—barbeled hound sharks. Marine, continental shelf; eastern Atlantic off Africa.

Labial furrows (at corner of mouth) very long; anterior nasal flaps formed into slender barbels; nictitating eyelids internal; spiracles small; intestine with spiral valve. Maximum length 8.2 m. The one species was not included in the study by Iglésias et al. (2005) but was suggested by Naylor et al. (2012) to be distantly related to Carcharhinidae. Based on that, we retain it in a separate family.

One species, *Leptocharias smithii*, Barbeled Hound Shark (Compagno, 1999, 2005).

Family TRIAKIDAE (27)—hound sharks. Marine, rarely in freshwater, tropical to cool temperate, continental and insular shelves and slopes; circumglobal, Atlantic, Indian, and Pacific. The oldest fossils are Early Cretaceous.



Labial furrows moderately long; anterior nasal flaps usually not slender or barbel-like; spiracles present; intestine with spiral valve. Maximum length 2.4 m, attained in *Triakis maculata.*

Compagno (1988) and Nelson (2006) recognized two subfamilies, Triakinae and Galeorhininae, but they are not recognized here because DNA sequence studies (López et al., 2006; Naylor et al., 2012) suggest that the type species of *Triakis* may be more closely related to members of Galeorhininae than to Triakinae as previously understood, and that both subfamilies recognized earlier are paraphyletic.

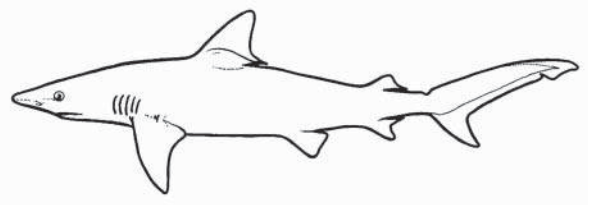
Nine genera include *Furgaleus* (1), *Galeorhinus* (1), *Gogolia* (1), *Hemitriakis* (6), *Hypogaleus* (1), *Iago* (2), *Mustelus* (28, smoothhounds), *Scylliogaleus* (1), and *Triakis* (5, leopard sharks, including *Cazon*), with 46 species. *Mustelus canis* enters fresh water for short periods in the western Atlantic (Compagno, 1999, 2005; Pietsch et al., 2012; White et al., 2009). Fossils of *Galeorhinus* date to the Late Cretaceous (Cenomanian), *Mustelus* to the late Paleocene, *Triakis* to the early Paleocene, and *Iago* to the early Eocene. Cappetta (2012) also recognized six extinct genera: †*Khouribgaleus,* †*Pachygaleus,* †*Paleogaleus,* †*Paratriakis,* †*Squatigaleus,* and †*Xystrogaleus.*

Family HEMIGALEIDAE (28)—weasel sharks. Marine, continental shelves; eastern tropical Atlantic (and possibly New England) and Indo-West Pacific. Oldest fossils are Eocene.

Dorsal fin margin undulated; precaudal pit present; nictitating membrane internal; spiracles small; labial furrows moderately long; intestine with spiral valve. Maximum length 2.4 m, attained in *Hemipristis elongata.*

Four genera, *Chaenogaleus* (1), *Hemigaleus* (2), *Hemipristis* (1), and *Paragaleus* (4), with eight species (Compagno, 1999, 2005; White et al., 2005; White and Harris, 2013). Fossils of *Chaenogaleus* are recognized as early as the early Miocene, *Hemipristis* in the Eocene, and *Paragaleus* in the middle Miocene.

Family CARCHARHINIDAE (29)—requiem sharks. Marine, occasionally in freshwater rivers and lakes, tropical to warm temperate, continental and insular shelves and slopes and oceanic; circumglobal, Atlantic, Indian, and Pacific. The oldest fossils are of early Paleocene age.



Dorsal fin margin undulated; precaudal pit present; spiracles usually absent; nictitating eyelids internal; intestine with scroll valve, lacking spiral valve. Maximum length at least 7.4 m, attained in *Galeocerdo cuvier.*

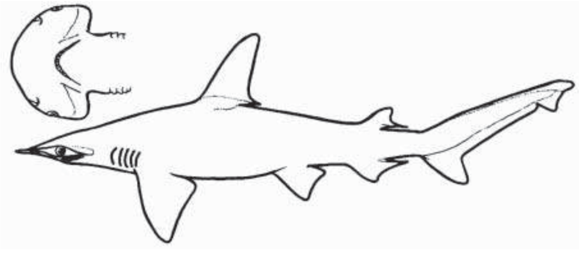
Seven species enter fresh water, with extended movements by *Carcharhinus leucas* (Bull Shark) and *Glyphis gangeticus* (Ganges Shark) (the latter, long thought to be confined to fresh and brackish water, may be conspecific with populations in Pakistan and Borneo based on mtDNA evidence; Li et al. 2015).

In the 1994 edition, sphryrnids (hammerhead sharks) were placed in this family because independent evidence based on morphological and molecular data suggested that the Carcharhinidae were not monophyletic unless sphryrnids were included in the family (Compagno, 1988:403; Naylor, 1992). Naylor (1992) did not, however, have data from *Scoliodon*, the taxon Compagno (1988) thought to be the sister group of sphryrnids. Musick and Ellis (2005) also placed sphryrnids within carcharinids. López et al. (2006), in a study focused on Triakidae, suggested similarly that sphyrnids might belong within Carcharhinidae. Molecular studies by Naylor et al. (2012) suggested that the Tiger Shark *Galeocerdo* could be the sister group of Carcharhinidae plus Sphyrnidae. In a study focused on Sphyrnidae, Lim et al. (2010) did not help settle this question because their study included only one species of *Carcharhinus.*

Carcharinids and sphryrnids are here recognized in separate families as in Compagno (1999, 2005) until better evidence of their interrelationships is found.

Twelve genera, *Carcharhinus* (34), *Galeocerdo* (1, Tiger Shark), *Glyphis* (5, river sharks), *Isogomphodon* (1), *Lamiopsis* (2), *Loxodon* (1), *Nasolamia* (1), *Negaprion* (2, lemon sharks), *Prionace* (1, Blue Shark), *Rhizoprionodon* (7), *Scoliodon* (2), and *Triaenodon* (1), with at least 58 species (Compagno, 1999, 2005, White, 2012; Li et al., 2015). The oldest fossils (with numbers of extinct species) are: *Carcharhinus* (4) middle Eocene, *Galeocerdo* (4) and *Glyphis* early Eocene, *Isogomphodon* (3) early Miocene, *Nasolamia* Pliocene, *Negaprion* early Miocene, *Prionace* early Pliocene, *Rhizoprionodon* (2) early Eocene, and *Scoliodon* Miocene. At least seven other fossil genera are included in this family (Cappetta, 2012).

Family SPHYRNIDAE (30)—hammerhead sharks. Marine (occasionally brackish), tropical to warm temperate, primarily continental shelf; Atlantic, Indian, and Pacific.



Lateral, blade-like extensions to the head (with eyes and nasal openings farther apart than in other sharks, perhaps conferring an advantage in homing in on food); spiracles absent. The head extensions, termed cephalofoils, range from being narrow and wing-like in the Indo-West Pacific *Eusphyra blochii* to being evenly rounded and spade-like in the New World *Sphyrna tiburo* (shown in the preceding figure). Surprisingly, narrower, spade-like shapes might have evolved from wider, more wing-like forms (Lim et al., 2010). Large individuals are very dangerous and there are many records of fatal attacks on humans. Maximum length 6.1 m, attained in *S. mokarran*.

Two genera, *Eusphyra* (1) and *Sphyrna* (9), with ten species (Compagno, 1999, 2005; Lim et al., 2010; Quattro et al., 2013). The oldest fossils, of early Oligocene age, are of *Sphyrna*, which has one extinct species (Cappetta, 2012).

Superorder SQUALOMORPHI

The composition of this superorder differs from the division Squalea of de Carvalho (1996) and the superorder Squalea of Shirai (1996). The greatest difference is that Batoidea (Batomorphi herein) are not recognized in this superorder (see above discusion under Euselachii).

Maisey (1980) recognized this group by its unique form of jaw articulation, the orbitostylic jaw articulation; hence, the group can be referred to as the orbitostylic sharks. According to Shirai (1996) and discussed by Cappetta (2012), monophyly is supported also by the following: anal fin absent; neurocranium basal angle; mesonasal flap absent; hyoid arch with arcuate extrabranchial cartilages dorsally and ventrally; pectoral supported by one or a few radials. Molecular phylogenetic studies include those of Vélez-Zuazo and Agnarsson (2011) and Naylor et al. (2012). These studies do not agree on all points.

Five orders, 11 families, 30 genera, and 161 species.

Three clades, ranked as series, are listed in phylogenetic sequence: Hexanchida, Squalida, and Squatinida.

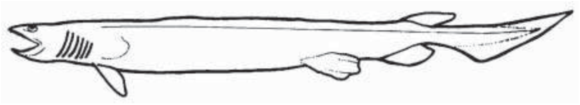
Series HEXANCHIDA. Chlamydoselachids (frilled sharks) and hexanchids (six-gill sharks) have long been considered among the most primitive living squalomorphs but whether they were successive sister groups to other squalomorphs or sister to each other in a monophyletic group has been less certain. Shirai (1992a, 1996) considered chlamydoselachids to be sister to all remaining euselachians, and he thus placed it in a separate order from the Hexanchiformes. We accept the evidence of de Carvalho (1996) that it and the Hexanchidae are sister taxa; this is supported also by the mtDNA and nuclear sequence phylogeny of Vélez-Zuazo and Agnarsson (2011) and the mtDNA-only results of Naylor et al. (2012), both of which place the resulting clade (Series Hexanchida herein) as the sister group of all other squalomorphs.

Order HEXANCHIFORMES (Notidanoidei) (8)—six-gill sharks. One dorsal fin, without spine; anal fin present; six or seven gill slits; eyes without nictitating fold; spiracle present but small, well behind eye. The homology of the extra arches is discussed by Shirai (1992b).

Two families with four genera and six species.

The following extinct families within Hexanchiformes are recognized by Cappetta (2012): †Orthacodontidae, Early Jurassic to Paleocene (Cappetta, 1987; e.g., *Sphenodus* = *Orthacodus*), †Paraorthacodontidae, and †Pseudonotidanidae.

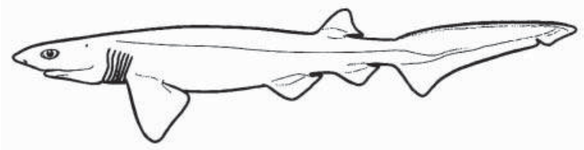
Family CHLAMYDOSELACHIDAE (31)—frilled sharks. Marine, continental and insular slopes, occasionally on shelves; scattered in western North Atlantic, eastern Atlantic (Norway to around South Africa), southwestern Indian, western Pacific (Japan to New Zealand), and eastern Pacific (California and Chile). The oldest fossils are Late Cretaceous (Santonian).



Six gill openings, margin of first gill continuous across throat; mouth terminal; teeth alike on upper and lower jaws, with three elongate cusps; lateral-line canal open; body very elongate. Maximum length about 1.9 m.

Two species, *Chlamydoselachus anguineus,* Frilled Shark, and the recently described *C. africana,* Southern Frilled Shark, found off southern Africa (Compagno, 1999, 2005; Ebert and Compagno, 2009). *Chlamydoselachus* is known by fossils as old as Late Cretaceous (Santonian). There is one extinct genus (not recognized as distinct by all authorities), called †*Proteothrinax* (its original name *Thrinax* replaced because it was a junior homonym; Pfeil, 2012) and recorded from the Paleocene onwards (Consoli, 2008).

Family HEXANCHIDAE (32)—cow sharks. Marine, temperate to tropical, continental and insular shelves and slopes; circumglobal, Atlantic, Indian, and Pacific. The oldest hexanchids are Early Jurassic.



Six or seven gill openings, margin of first gill not continuous across throat; mouth ventral; teeth in upper jaw different from those in lower jaw; lateral-line canal open in *Notorynchus.* Maximum length about 4.7 m, attained in *Hexanchus griseus.*

The braincase of *Notorynchus* is described by Maisey (2004b), based on high-resolution scanning and digital imaging. This study also gives new phylogenetic information on the elasmobranch braincase in fossils.

Three genera and four species (Compagno, 1999, 2005): *Hexanchus* (2) *H. griseus* and *H. nakamurai* with six gill openings (the latter recently redescribed by Ebert et al., 2013), along with *Heptranchias perlo* (sometimes placed in its own family Heptranchiidae) and *Notorynchus cepedianus* (sometimes placed in its own family Notorynchidae) with seven gill openings. The oldest records of the extant genera (with numbers of extinct species) are *Hexanchus* (5), Early Jurassic; *Heptranchias*, Late Cretaceous; *Notorynchus* (3), Early Cretaceous. There are perhaps 6 extinct genera (Cione, 1996; Cappetta, 2012), including †*Notidanodon*, Late Cretaceous to Eocene; †*Notidanoides*, Jurassic (the formerly generic name *Notidanus* is invalid; Maisey, 1986a); †*Pachyhexanchus*; and †*Weltonia*). The extinct genus †*Paraheptranchias* is sometimes grouped with *Heptranchias* in a separate family.

Series SQUALIDA. This taxon is sister to the Series Squatinida (see, e.g., Naylor et al., 2012) treated below. One order.

Order SQUALIFORMES (9)—dogfish sharks. Two dorsal fins, with or without spines; anal fin absent; five gill slits; spiracles present; nictitating lower eyelid absent; lateral-line canal closed (as it is in most euselachians).

The Echinorhinidae, placed in this order in Nelson (1994), are now placed in their own order following de Carvalho (1996), sister to Pristiophoriformes and Squatiniformes, as in the phylogeny of Naylor et al. (2012). Three of the families now recognized were regarded as subfamilies of Dalatiidae in Nelson (1994) (see Dalatiidae).

Six families, 22 genera, and at least 123 species. The families are listed approximately in phylogenetic sequence, mostly consistent with Naylor et al. (2012); this arrangement differs in important ways from that in Vélex-Zuazo and Agnarsson (2011).

Family CENTROPHORIDAE (33)—gulper sharks. Marine, warm temperate to tropical, continental and insular outer shelves and slopes; Atlantic, Indian, and Pacific (absent in eastern Pacific). The oldest fossils are of early Late Cretaceous age.

Both dorsal fins with spines and both spines grooved; teeth on lower jaw larger than those on upper jaw; precaudal pits and lateral keels absent on caudal peduncle.

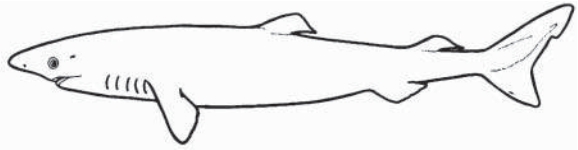
Two genera, *Centrophorus* (12) and *Deania* (4), with 16 species (Compagno, 1999, 2005, White et al., 2008). White et al. (2013) have redescribed the type species of *Centrophorus*, *C. granulosus*, a common, widely distributed, deep-water species. The oldest fossils of *Centrophorus* are late Late Cretaceous; those of *Deania* are early Paleocene (Cappetta, 2012).

Family ETMOPTERIDAE (34)—lantern sharks. Marine, tropical to temperate, continental and insular slopes (rarely on shelves), a few oceanic; parts of the Atlantic (extending north to Iceland), Indian, and Pacific.

Both dorsal fins with spines and both spines grooved; caudal fin with subterminal notch; luminous organs usually present on body. These are small sharks: the maximum length is under 90 cm in most species. Straub et al. (2010) provided a molecular phylogeny for the family and estimated its geologic age at about 60 Ma. They further suggested that *Miroscyllium* is not valid, being nested among species of *Etmopterus*. The other named genera represent distinct groups.

Five genera, *Aculeola* (1), *Centroscyllium* (7), *Etmopterus* (38 including *Miroscyllium*), and *Trigonognathus* (1), with 47 species (Shirai, 1992a; Shirai and Okamura, 1992; Compagno, 1999, 2005; Straub et al., 2010). Extant genera with extinct species are *Etmopterus* (2 extinct species) middle Eocene, *Miroscyllium* (1) middle Miocene, and *Trigonognathus* (1) middle Eocene. Extinct genera include †*Eoetmopterus*, †*Microetmopterus*, †*Paraetmopterus*, and †*Proetmopterus* (Cappetta, 2012).

Family SOMNIOSIDAE (35)—sleeper sharks. Marine, Arctic to sub-Antarctic, continental and insular slopes (on shelves in Arctic and sub-Antarctic), some oceanic; Atlantic, Indian, and Pacific. Oldest fossils are Late Cretaceous.

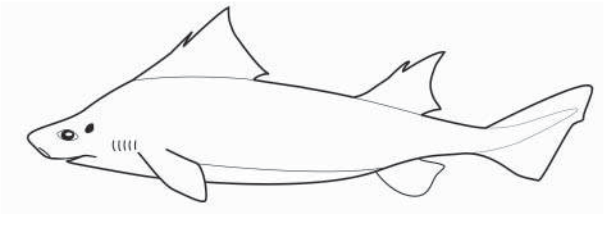


Dorsal fins usually without spines (present in a few species but small and in both fins); lateral ridge present on abdomen between pectoral and pelvic fins; luminous organs present in most.

Yano et al. (2004) reviewed the genus *Somniosus*. There is molecular support for restricting the family Somniosidae to the type genus and placing others in Oxynotidae (Naylor et al., 2012), although not all relevant genera have been examined up to now.

Five genera, *Centroscymnus* (5 including *Centroselachus* and *Proscymnodon*), *Scymnodalatias* (4), *Scymnodon* (1), *Somniosus* (5 including *Rhinoscymnus*), and *Zameus* (2), with 17 species (Compagno, 2005). *Somniosus* is in both the Arctic and sub-Antarctic and extends onto inner shelves. The oldest fossils of each genus (Cappetta, 2012) are: *Somniosus* (middle Eocene), *Centroscymnus* (Late Cretaceous), *Scymnodalatias* (middle Eocene), *Scymnodon* (middle Eocene), *Zameus* (Pliocene). There is one extinct genus, †*Cretascymnus* (Late Cretaceous).

Family OXYNOTIDAE (36)—rough sharks. Marine, continental and insular shelves and slopes; eastern Atlantic (including Mediterranean), western Atlantic, and western Pacific. Oldest fossils are Late Cretaceous.



Body very high and compressed, triangular in cross section; dorsal fins very high, each with a large spine that may be concealed by the fin; origin of first dorsal fin may extend far forward over gill openings; lateral ridge present on abdomen between pectoral and pelvic fins; skin very rough; luminous organs present.

One genus, *Oxynotus*, with five species (Compagno, 2005). *Oxynotus* has two extinct species and its oldest fossils are Miocene. There is one extinct genus (†*Protoxynotus*) of Late Cretaceous age.

Family DALATIIDAE (37)—kitefin sharks. Marine, tropical to temperate, continental and insular shelves and slopes and oceanic; Atlantic, Indian, and Pacific. The oldest fossils are Late Cretaceous.

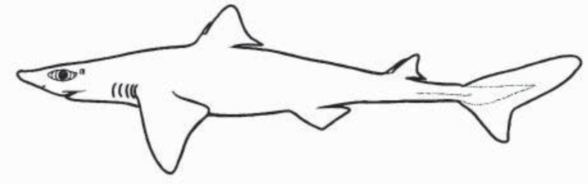
Dorsal fins without spines, except species of *Squaliolus* have a spine in the first dorsal fin; luminous organs present, appearing as black dots mainly on ventral surface (Shirai, 1992a).

One of the species of this group, *Squaliolus laticaudus*, and the proscylliid *Eridacnis radcliffei* are the smallest known sharks, reaching only about 25 cm in total length (Compagno, 1984a, b). Another small dalatiid shark is the Pocket Shark *Mollisquama parini*, which has a pocket-like recess just above its pectoral fin in which there is a gland possibly with a luminescence function (Dolganov, 1984). The small and pelagic cookiecutter sharks of the genus *Isistius*, with modifications to their feeding apparatus, cause crater-like wounds in other fishes and cetaceans (Shirai and Nakaya, 1992).

In Nelson (1994), the Etmopteridae, Somniosidae, and Oxynotidae were recognized as subfamilies of the Dalatiidae.

Seven genera, *Dalatias* (1), *Euprotomicroides* (1), *Euprotomicrus* (1), *Heteroscymnoides* (1), *Isistius* (2, cookiecutter sharks), *Mollisquama* (1), and *Squaliolus* (2), with 9 species (Compagno, 2005). Extant genera with known earliest fossil records are: *Dalatias* (early Paleocene), *Isistius* (late Paleocene), *Squaliodus* (middle Eocene). There are six extinct genera (Cappetta, 2012): †*Acrosqualiodus*, †*Angoumeius*, †*Eosqualiolus*, †*Euprotomicroides*, †*Paraphorosoides*, and †*Squaliodalatias*.

Family SQUALIDAE (38)—dogfish sharks. Marine, cool temperate to tropical, circumglobal on continental and insular shelves and slopes and on sea mounts; Atlantic, Indian, and Pacific. Oldest fossils are Early Cretaceous.



Both dorsal fins with spines and spines not grooved; teeth on lower jaw not much larger than those on upper jaw; upper precaudal pit usually present; caudal peduncle with a pair of lateral keels.

The Spiny Dogfish, *Squalus acanthias*, familiar to many comparative anatomy students, is one of the most cosmopolitan fish species, being widespread in the Northern and Southern Hemispheres, yet virtually absent in tropical waters and the Indian Ocean. This family was placed in its own order, Squaliformes, by Shirai (1992, 1996) and regarded as the sister group to all remaining euselachians, a relationship not followed here.

Members are also known as spurdogs and dogfishes. Newly discovered species are still often being described (e.g., Last et al., 2007).

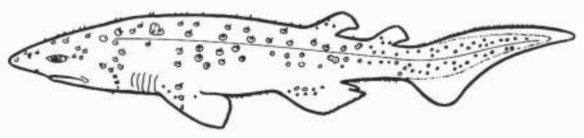
Two genera, *Cirrhigaleus* (3) and *Squalus* (26) for a total of 29 species (Compagno, 2005; Last et al., 2007). *Squalus*, with five extinct species, is known from the Late Cretaceous. There are four extinct genera: †*Centrophorides*, †*Centrosqualus*, †*Megasqualus*, and †*Protosqualus* (Cappetta, 2012).

Series SQUATINIDA. Sister-group relationships between Squatiniformes and Pristiophoriformes and between the latter two orders and the Echinorhiniformes are weakly supported by molecular results of Naylor et al. (2012). A different arrangement (Squatinidae (Echinorhinidae, Pristiophoridae) was suggested by Vélez-Zuao and Agnarsson (2011). Three extant orders and one fossil-only order.

†Order PROTOSPINACIFORMES. Late Jurassic, Bavaria. One family, †Protospinacidae, with one genus, †*Protospinax*. The position of this unusual fossil was resolved by de Carvalho and Maisey (1996) based on new material and cladistic analysis using a revised data matrix, largely from Shirai (1992a), with some differing interpretations of Shirai's characters. Their results supported Shirai's hypnosqualean group and they formally recognized the group as the Superorder Hypnosqualea, with †*Protospinax* as sister to the living hypnosqualeans (i.e., all remaing neoselachians in the present classification). Although that phylogeny is not followed here, †*Protospinax* is still regarded as sister to the remaining squalomorphs, the squatinids and pristiophorids.

Order ECHINORHINIFORMES (10)—bramble sharks. Bramble sharks were placed in their own order by de Carvalho (1996) based on several characters that he felt suggest that this taxon is sister to all remaining sharks (Squaliformes, Squatiniformes, and Pristiophoriformes) and to the rays (then called batoids). The only family was recognized in the Squaliformes in the last edition and in Compagno (1999). In the present work they are treated in their own order, and their postulated relationship has changed: they are classified as squalomorphs close to Pristiophoridae and Squatinidae on results from Vélez-Zuazo and Agnarsson (2011) and from Naylor et al. (2012), although with weak support.

Family ECHINORHINIDAE (39)—bramble sharks. Marine, cool to warm temperate, continental and insular shelves and slopes and some sea mounts; Atlantic, western Indian, and Pacific. The oldest fossils are of late Early Cretaceous age.

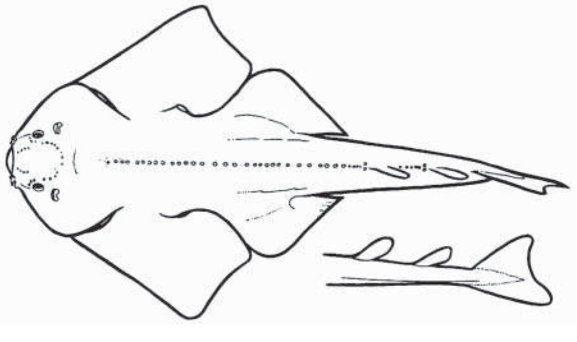


Both dorsal fins small and spineless, first dorsal fin originating over or behind pelvic fin origin (some other sharks such as the dalatiid *Isistius* have posteriorly placed dorsal fins, but they are not as far back); pelvic fins larger than second dorsal fin; body with coarse denticles; teeth alike in both jaws, rows linearly arranged; last gill slit distinctly larger than others; spiracles minute and well behind eyes; lateral-line canal open; caudal fin without a subterminal notch. Maximum length up to 2 m.

One genus, *Echinorhinus*, with two species (Compagno, 1999, 2005), *E. brucus* (shown in figure) in parts of the Atlantic (commonest in eastern Atlantic), Indian, and western Pacific with denticles relatively few and large, and *E. cookei* in parts of the Pacific with denticles relatively numerous and small. Cappetta (2012) recognized nine extinct species of *Echinorhinus*, as well as four extinct genera (†*Gibbechinorhinus*, †*Orthechinorhinus*, †*Paraechinorhinus*, and †*Pseudechinorhinus*).

Order SQUATINIFORMES (11)—angel sharks.

Family SQUATINIDAE (40)—angel sharks. Marine, temperate to tropical, continental shelves and upper slopes; Atlantic, southwestern Indian, and Pacific.



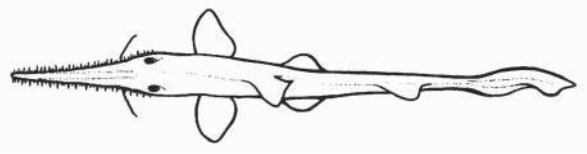
Body ray-like; eyes dorsal; two spineless dorsal fins; no anal fin; five gill openings; spiracle large; mouth almost terminal; nostrils terminal with barbels on anterior margin. Maximum length up to 2 m.

Squatina and the remaining euselachians (the pristiophorids and the batoids), termed the Hypnosqualean group, were regarded as a clade by Shirai (1992c, 1996) and by de Carvalho (1996) but not in the present work. Klug and Kriwet (2013) reviewed the fossil record of squatiniforms and concluded that the group originated in the Jurassic. The genus *Squatina* itself dates to the Early Cretaceous.

One genus, *Squatina*, with 22 species (Compagno, 1984a, 1999, 2005; Shirai, 1992c; Walsh and Ebert, 2007; Walsh et al., 2010; Vaz and De Carvalho, 2013).

Order PRISTIOPHORIFORMES (12)—saw sharks.

Family PRISTIOPHORIDAE (41)—saw sharks. Marine (rarely in estuaries), temperate to tropical, continental and insular shelves and slopes; western Atlantic in region of Bahamas, Florida, and Cuba, southwestern Indian off South Africa, and western Pacific from southern Australia to Japan.



Body shark-like; snout produced in a long flat blade with teeth on each side (teeth unequal in size, usually alternating large and small, and weakly embedded); one pair of long barbels; no dorsal fin spines (sometimes present as internal rudiments); anal fin absent; spiracles large. Maximum length 1.4 m.

Two genera, *Pliotrema* (1, six gill openings) and *Pristiophorus* (7, five gill openings), with eight species (Compagno, 1984a, 1999, 2005; Yearsley et al., 2008; Ebert and Wilms, 2013).

Division BATOMORPHI—rays

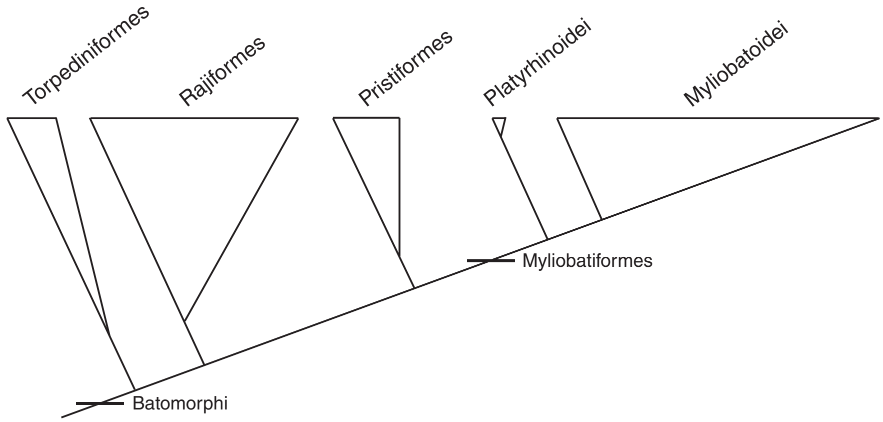
Gill openings ventral; anterior edge of the greatly enlarged pectoral fin attached to side of head via antorbital cartilage, anterior to the gill openings; anal fin absent; eyes and spiracles on dorsal surface; anterior vertebrae fused to form a synarcual; suprascapulae of pectoral girdles joined dorsally over vertebral column and articulating with column or synarcual or fused with synarcual; nictitating membrane absent, cornea attached directly to skin around the eyes; body generally strongly depressed; jaws protrusible in most because palatoquadrate does not articullate with neurocranium directly; in most, water for breathing taken in chiefly through the spiracle rather than the mouth (except for those living off the bottom); most rays give birth to live young (however, the skates are oviparous, i.e., egg layers, and have eggs encased in a horny capsule); the snout may function as an electroreceptive organ (as in all elasmobranchs).

Taxonomic names applied in older literature to rays as a whole include Batoidea, Batidoidimorpha, Hypotremata, Rajiformes, and Rajimorphi.

The common terms skate and ray are sometimes used as either/or (where a fish is either one or the other, but cannot be both). However, we prefer to use the term ray as a collective name for all members of the four orders of batomorphs. Thus, skates, in the strictest sense, are members of one particular order of rays, the Rajiformes. In this usage, both names refer to monophyletic groups, but skates are a subset of the rays, just as are sawfishes and stingrays. Skates differ from the other rays in many features of morphology and biology.

As discussed above under Euselachii, the separation of Batomorphi (rays) from Selachii (modern sharks), as followed here, rather than rays being nested within derived, ray-like shark groups such as Squatiniformes and Pristiophoriformes, has been advocated on molecular, fossil, and some morphological evidence by Douady et al. (2003), Maisey et al. (2004), McEachran and Aschliman (2004), Naylor et al. (2012), and Aschliman et al. (2012a,b).

Monophyly of the Batomorphi seems well established, but their internal interrelationships remain very uncertain. Although McEachran and Aschliman (2004) regarded their classification as a working hypothesis, it was an advance over the largely phenetic classification presented by Compagno (1999) and that of earlier authors. McEachran and Aschliman (2004) examined more morphological characters in more representatives of genera than previously done. They also used basal taxa as outgroups as a result of other recent studies.



Relationships of the major groups of Batomorphi.

Many different views have been proposed on batomorph interrelationships, with various taxa seen as the basal group (these ideas are briefly reviewed in McEachran and Aschliman, 2004). The higher classification given here is based on McEachran and Aschliman (2004), with modifications influenced by Naylor et al. (2012) and Aschliman et al. (2012).

Although most batomorphs have a strongly depressed body, some are relatively shark-like. McEachran and Aschliman (2004) showed that the depressed, disc-like body characteristic of most higher rays was probably independently achieved in two lineages. The depressed body of rajids was probably derived from a more robust-bodied rhinobatid-like ancestor, while the depressed body of higher myliobatiforms was probably derived from a robust-bodied platyrhinid-like ancestor.

McEachran and Aschliman (2004) comment on the diversity of pelvic claspers in batomorphs and suggest that they offer potential in resolving interrelationships. Two basic shapes are apparent in external form: Rajiformes have claspers that are long, slender, and depressed distally while the other batomorphs, as far as studied, have claspers that are short, stout, and cylindrical to moderately depressed.

Fossil batomorphs are known from as long ago as the Jurassic in Europe and Argentina and include taxa such as the rhinobatid genera †*Asterodermus*, †*Belemnobatis*, and †*Spathobatis* (Cappetta, 1987; Cione, 1999); the latter two genera may be sister taxa and were found by Brito and Seret (1996) to be basal batomorphs, supporting an earlier view of J. G. Maisey.

Dean et al. (2007) studied evolution of head and feeding mechanisms, while Ekstrom and Kajiura (2014) studied pelvic girdle shape relative to locomotion and phylogeny in batomorphs.

Four orders, 17 families, 83 genera, and at least 636 species.

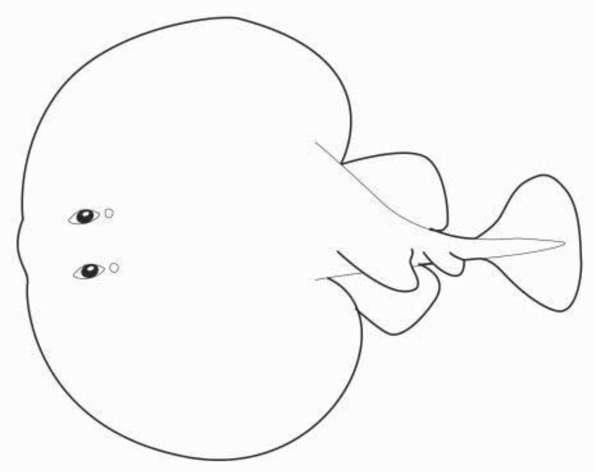
Order TORPEDINIFORMES (13)—electric rays. Powerful electric organs, derived from branchial muscles in head region (strongest discharges in the Torpedinidae); skin soft and loose; eyes small to obsolete; caudal fin well developed; dorsal fins 0–2. Electrical production is largely for feeding and defense.

Torpediniforms are regarded as the basal batomorph group and sister to the remaining members of this order in morphological studies (McEachran and Aschliman, 2004; Aschliman et al., 2012)., but some molecular studies (e.g., Aschliman et al., 2012b) place other groups such as skates in that position. Several species are blind.

Two families, 12 genera with about 65 species. McEachran and Aschliman (2004) recognized the monophyly of the extant taxa as shown. There is one extinct family.

†Family ARCHAEOBATIDAE. This extinct family, related to Torpediniformes by Cappetta (2012), dates from the Early Jurassic. Three genera are known: †*Cristabatis*, †*Doliobatis*, †*Toarcibatis* (Delsate and Candoni, 2001).

Family TORPEDINIDAE (42)—torpedo electric rays. Marine, continental and insular shelves and slopes; Atlantic (including Mediterranean Sea), Indian, and Pacific.



Disc truncate or emarginate anteriorly; jaws extremely slender; no labial cartilages; rostrum reduced.

In *Torpedo* (electric rays), the tail and dorsal and caudal fins are well developed. This genus is ranked as a separate Family by some workers (e.g., Compagno, 2005). *Torpedo* (including *Tetronarce*) has about 22 species (Compagno, 1999, 2005; de Carvalho et al., 2002; FishBase).

The second genus, *Hypnos*, or Coffin Ray, has only one species, *Hypnos monopterygius*. It has a very small tail and dorsal and caudal fins (Compagno, 1999, 2005). It lives on the continental shelf and uppermost slope, off Australia.

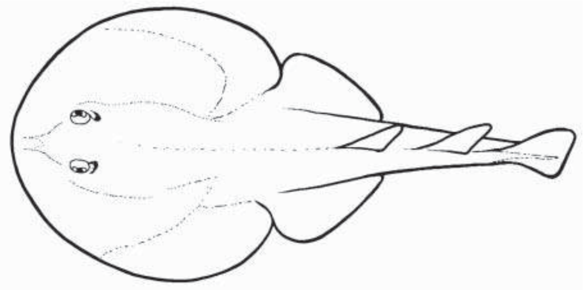
Two genera with 23 species. The oldest fossils are of the extinct genus †*Eotorpedo*, of early Paleocene age. The oldest fossil in *Torpedo* is of late Paleocene age; there are three extinct species (Cappetta, 2012).

Family NARCINIDAE (43)—numbfishes. Marine, tropical to warm temperate, continental and insular shelves and uppermost slopes; Atlantic, Indian, and Pacific.

Disc rounded anteriorly; jaws stout; strong labial cartilages; rostrum present.

Ten genera with at least 42 species. Several undescribed species are known to exist. The oldest fossils in the family are of late Paleocene age; there is one extinct species recognized (Cappetta, 2012).

SUBFAMILY NARCININAE (NUMBFISHES). Deep groove around mouth and lips; jaws long and strongly protractile; rostrum broad; usually two dorsal fins. This taxon is ranked as a separate family by some workers (e.g., Compagno, 2005).



Four genera, *Benthobatis* (4), *Diplobatis* (4), *Discopyge* (2), and *Narcine* (20), with 30 species (de Carvalho, 1999; de Carvalho et al., 2002, 2003; de Carvalho and Randall, 2003; Compagno, 1999, 2005). Four species of *Diplobatis* are recognized based on McEachran and de Carvalho's (2003:518–20) recognition of two subspecies of *Diplobatis pictus* (Compagno, 2005) as species. The oldest fossil in *Narcine* is late Paleocene; there is one extinct species in the genus.

SUBFAMILY NARKINAE (SLEEPER RAYS). Shallow groove around mouth; jaws short and weakly protractile; rostrum narrow; usually a single dorsal fin. Indo-West Pacific. This taxon is ranked as a separate family by some workers (e.g., Compagno, 2005).

Six genera, *Crassinarke* (1), *Electrolux* (1), *Heteronarce* (4), *Narke* (3), *Temera* (1), and *Typhlonarke* (2), with 12 species (Compagno, 1999, 2005).

Order RAJIFORMES (14)—skates. Caudal fin moderately well developed, reduced, or absent; tail extremely slender; dorsal fins 0–2; most with prickles or thorns (derived from placoid scales) on skin, often with a row along midline of back; claspers long, slender, and depressed distally. Oviparous, with eggs encased in horny capsule with four long tips.

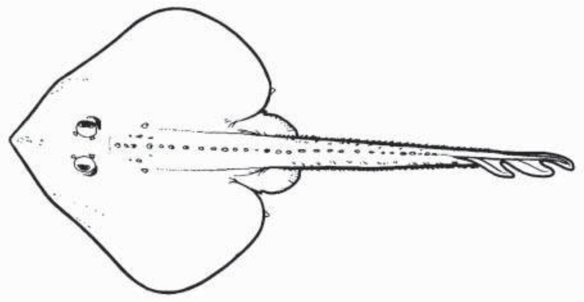
Members of this order were placed in the suborder Rajoidei with the same three families in the 1994 edition, but arranged differently in the 2006 edition. McEachran and Aschliman (2004) recognized only two families, the Rhinobatidae and Rajidae, with the two rhinid genera being listed as *incertae sedis* because of their uncertain relationships (see below under Rhinidae). Aschliman et al. (2012b) found weak molecular support for Rajiformes being sister to all other rays. McEachran and Konstantinou (1996) discussed the taxonomic occurrence and variation of alar and malar thorns in skates.

For a discussion of the terms “skates and rays” see above under Division Batomorphi.

One family, 32 genera, and 287 species. One extinct genus, †*Mafdetia,* is not assignable to a Family (Cappetta, 2012). There is one extinct family.

†Family Cyclobatidae. This extinct family with one genus is known from the early Late Cretaceous of Lebanon. According to Forey et al. (2003), Underwood (2006), and Cappetta (2012), †*Cyclobatis* is a rajiform. There are three extinct species (Cappetta, 2012).

Family RAJIDAE (44)—skates. Marine, tropical to polar seas, shallow to deep-water; Atlantic, Indian, and Pacific.



Caudal fin moderately well developed, reduced, or absent; tail extremely slender; weak electric organs derived from caudal muscles; dorsal fins 0–2; most with prickles on skin, often with a row along midline of back. Eggs encased in horny capsule with four long tips. Maximum total length about 2.5 m.

The Arhynchobatinae (softnose skates) and the rajines *Anacanthobatis* and *Cruriraja* were recognized as separate families from Rajidae by Compagno (1999, 2005), the Arhynchobatidae (softnose skates) and Anacanthobatidae (legskates), respectively. They are classified here following McEachran and Aschliman (2004), in whose cladogram *Anacanthobatis* and *Cruriraja* form a monophyletic group but one that is nested within the Rajinae. McEachran and Dunn (1998) give a detailed analysis of rajid interrelationships.

Thirty-two genera and about 287 species. The oldest fossil rajid is from the early Late Cretaceous (Cappetta, 2012). Fossil-only rajid genera include †*Rajorhina.*

SUBFAMILY RAJINAE (HARDNOSE SKATES). Nineteen genera, *Amblyraja* (10), *Anacanthobatis* (8), *Breviraja* (6), *Cruriraja* (8), *Dactylobatus* (2), *Dentiraja* (1), *Dipturus* (48), *Fenestraja* (8), *Gurgesiella* (3), *Hongeo* (1), *Leucoraja* (15), *Malacoraja* (4), *Neoraja* (5), *Okamejei* (15), *Raja* (29), *Rajella* (16), *Rostroraja* (1), *Sinobatis* (5), and *Zearaja* (3) with at least 188 species (Compagno, 1999, 2005; McEachran and Last, 1994; Aschliman et al., 2010). The oldest fossil of *Raja* is of mid Late Cretaceous age; there are at least 10 extinct species in the genus (Cappetta, 2012).

SUBFAMILY ARHYNCHOBATINAE (SOFTNOSE SKATES). Thirteen genera, *Arhynchobatis* (1), *Atlantoraja* (3), *Bathyraja* (53), *Brochiraja* (8), *Insentiraja* (2), *Irolita* (2), *Notoraja* (7), *Pavoraja* (6), *Psammobatis* (8), *Pseudoraja* (1), *Rhinoraja* (3), *Rioraja* (1), and *Sympterygia* (4), with at least 99 species (Compagno, 1999, 2005; Stevenson et al., 2004; Díaz de Astarloa et al., 2004; Aschliman et al., 2010; Iglésias and Lévy-Hartmann, 2012; Last and Séret, 2012).

Order PRISTIFORMES (15)—guitarfishes and sawfishes. Two extinct families with 24 genera; four extant families with 10 genera and 63 species.

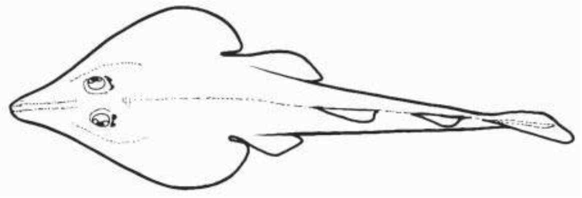
†Family Sclerorhynchidae. These rays known from the mid Early Cretaceous to the end of the Cretaceous resemble pristids and are represented primarily by their enlarged rostral teeth. Kriwet (2004a) provided insight into possible relationships of this group.

There are 21 extinct genera listed by Cappetta (2012), including †*Ankistrorhynchus*, †*Borodinopristis,* †*Ganopristis*, †*Ischyrhiza*, †*Onchopristis*, and †*Sclerorhynchus.*

†Family Ptychotrygonidae. This family is known from the late Early Cretacous to the end of the Cretaceous (Cappetta, 2012), and contains three genera: †*Ptychotrygon,* †*Ptychotrygonoides*, and †*Texatrygon*.

Family "RHINOBATIDAE" (45)—guitarfishes. Marine (rarely entering estuaries and freshwater), tropical to temperate, continental shelves and uppermost slopes; Atlantic, Indian, and Pacific.

Body intermediate between shark-like and skate-like; tail stout, not definitely marked off from body; two distinct dorsal fins and a caudal fin, the latter not bilobed; origin of first dorsal behind pelvics; denticles over body form a row on midline of back; tail without spine.



Compagno (1999) recognized this family in the order Rhinobatiformes, along with two others (herein placed in the Myliobatiformes). McEachran and Aschliman (2004) are followed here. Monophyly of this family is unlikely based on recent phylogenies (e.g., Aschliman et al., 2012a,b; Claeson et al., 2013), but there is not yet a consensus about detailed relationships of most of its members, many of which are unresolved in relevant studies.

Six genera, *Aptychotrema* (3), *Rhinobatos* (including *Acroteriobatus*, 36), *Glaucostegus* (3), *Tarsistes* (1), *Trygonorrhina* (2), and *Zapteryx* (3), with 48 species (Compagno, 1999, 2005; Last, 2004; Last et al., 2004, 2006).

The oldest fossil rhinobatid is from the Early Jurassic, making it one of the earliest known fossil rays. The extant genus *Rhinobatos* is known from the Early Cretaceous and later; there are at least 13 extinct species. Eight extinct genera are also known: †*Asterodermus,* †*Belemnobatis,* †*Doliobatis,* †*Euryarthra,* †*Isidobatus,* †*Paratrygonorrhina,* †*Rhombopterygia,* and †*Spathobatis* (Cappetta, 2012). The Early Cretaceous fossil †*Iansan* from Brazil may belong here but is of uncertain relationships (Brito and Seret, 1996).

Family RHINIDAE (46)—bowmouth guitarfishes. Marine, continental shelves; Indo-West Pacific.

Body intermediate between shark-like and skate-like (family called sharkrays in Compagno, 2005); caudal fin large, bilobed; origin of first dorsal over or in front of pelvics; snout and anterior part of head broadly rounded, with deep indentation separating it from the pectoral fin origin. Maximum total length at least 270 cm.

Rhina and *Rhynchobatus* (see next family) were placed together in family Rhinidae by Nelson (1994) and Compagno (1999), but the latter recognized the family in its own order, Rhiniformes. The evidence that the two genera formed a monophyletic group was considered to be weak. McEachran and Aschliman (2004) suggested that *Rhina* and *Rhynchobatus* might be successive sister groups of the remaining rajiforms, classifying them as *incertae sedis* until more evidence became available. The present treatment in placing them in separate families follows Compagno (2005), who placed them in separate suborders, and is largely consistent with the view of McEachran and Aschliman (2004). They are sometimes treated as subfamilies of Rhinobatidae.

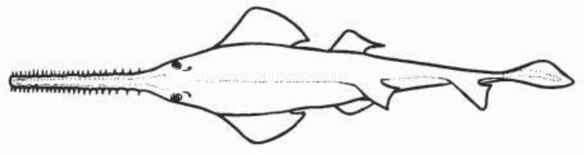
One extant species, *Rhina ancylostoma* (e.g., Compagno, 2005; Compagno and Last, 1999). Fossils of the same species first appear in the Miocene; there are no known extinct species.

Family RHYNCHOBATIDAE (47)—wedgefishes. Marine, continental shelves; eastern Atlantic (off Africa) and Indo-West Pacific.

Body intermediate between shark-like and skate-like; caudal fin large, bilobed; origin of first dorsal over or in front of pelvics; snout and anterior part of head broadly angular and wedge-shaped, with shallow indentation separating it from pectoral fin origin. Maximum total length at least 300 cm. See Family Rhinidae above for systematic notes.

One genus, *Rhynchobatus*, with seven species (Compagno, 2005; Compagno and Last, 1999; Last et al., 2013). Fossil rhynchobatids appear first in the early Eocene; there are two extinct species (Cappetta, 2012).

Family PRISTIDAE (48)—sawfishes. Marine (rarely occurring in freshwater and ascending rivers), circumtropical, continental shelves; Atlantic, Indian, and Pacific.



Snout produced in a long flat blade with teeth on each side (teeth of equal size and embedded in deep sockets); barbels absent; body somewhat shark-like, although the head is depressed; two distinct dorsal fins and a caudal fin. Maximum length over 6 m.

Two genera, *Anoxypristis* (1) and *Pristis* (6), with about seven species (de Carvalho and McEachran, 2003; Compagno, 1999, 2005). The oldest fossil pristids are from the early Eocene; there are at least eight extinct species in *Pristis*, and at least one extinct genus, †*Propristis* (Cappetta, 2012).

Order MYLIOBATIFORMES (16)—stingrays. Monophyly of this taxon is recognized after McEachran and Aschliman (2004). There has been strong support for monophyly of this order, including in the earlier works of Nishida (1990), Lovejoy (1996), and McEachran et al. (1996). Platyrhinids and *Zanobatus* were thought to form successive sister taxa to the myliobatoids by McEachran and Aschliman (2004) and Aschliman et al. (2012a), although Platyrhinoidei are sometimes grouped, albeit weakly, with Torpediniformes in molecular studies (Aschliman et al., 2012a, b; Naylor et al., 2012). Most members have enlarged brain development.

Ten families with 29 genera and 221 species.

Suborder Platyrhinoidei. This clade has both morphological (Aschliman et al., 2012a) and molecular (e.g., Aschliman et al., 2012b) support, but its relationships remain somewhat doubtful.

Family PLATYRHINIDAE (49)—thornbacks. Marine, continental shelves; tropical to cool-temperate, North Pacific (off Asia and North America, in Mexico and California).

Round or heart-shaped pectoral disc; long, stout shark-like tails with two large dorsal fins well anterior on the tail; strong thorns (derived from placoid scales) on dorsal surface of the disc and tail.

The family was redefined by de Carvalho (2004b). Molecular studies (Aschliman et al., 2012; Naylor et al., 2012) weakly suggest that Platyrhinidae might be primitive torpediniforms.

Two genera, *Platyrhina* (3, the fanrays, reviewed recently by Iwatsuki et al., 2011) and *Platyrhinoidis* (1), with a total of four species (Compagno, 1999, 2005; Compagno and Last, 1999).

Fossil platyrhinids appear in the Late Cretaceous. Extinct genera include †*Tethybatis* (de Carvalho, 2004b), †*Britobatis*, and †*Tingitanius* (Claeson et al., 2013). *Platyrhina* itself appears in the early Eocene (Cappetta, 2012).

Suborder Myliobatoidei. Monophyly of this clade was supported by de Carvalho et al. (2004), who recognized this group, at the ordinal level (Myliobatiformes) following Compagno (1973), as having numerous synapomorphies such as a serrated caudal spine and lacking thoracic ribs. They presented a revised classification but agreed with many past conclusions, e.g., Hexatrygonidae as sister to the remaining taxa and the families Gymnuridae and Myliobatidae (the pelagic stingrays) as sister groups; for an example of differences, see below under Dasyatidae.

The families are in approximate phylogenetic sequence as suggested by recent morphological and molecular results (e.g., Aschliman et al., 2012a,b; the superfamily structure of Nelson (2006) is no longer used here because it is not consistent with molecular phylogenies.

Family ZANOBATIDAE (50)—panrays. Marine; tropical, eastern Atlantic (off Africa) and possibly Indian.

Similar in appearance to the Platyrhinidae, *Zanobatus* was often included in the same family, but more recently it has been separated. It has also been said to be sister to all other rhiniforms (Naylor et al., 2012) or to the Myliobatiformes (Aschliman et al., 2012a,b).

One genus, *Zanobatus,* with one or possibly two species (Compagno, 1999, 2005).

Family PLESIOBATIDAE (51)—deepwater stingrays. Marine; continental and insular slopes, Indo-West Pacific (South Africa to Hawaii).

Nasal curtain incompletely united, not reaching the mouth (true also for *Hexatrygon,* which has six gill arches). Maximum length 2.7 m (Smith and Heemstra, 1986).

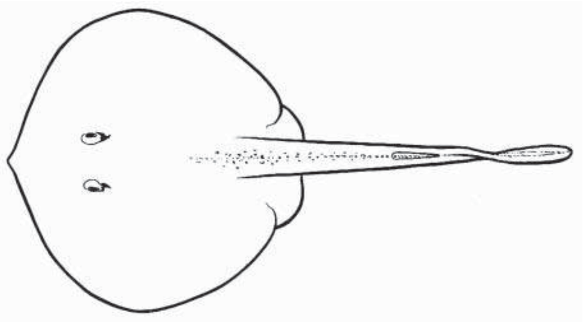
This family (as Plesiobatididae) was established by Nishida (1990) for the species *Plesiobatis daviesi,* recognized prior to that in the genus *Urotrygon.*

For alternate family placement see Hexatrygonidae above and Urolophidae below. The family is recognized here as done in the 1994 edition until analysis involving more species better clarifies relationships of the one included species.

The common name for the family in Compagno (1999, 2005) is giant stingarees.

One species, *Plesiobatis daviesi* (Compagno, 1999, 2005). The oldest fossils of the family are of Late Paleocene age (Cappetta, 2012).

Family UROLOPHIDAE (52)—round stingrays. Marine, continental shelves and upper slopes; western Pacific.

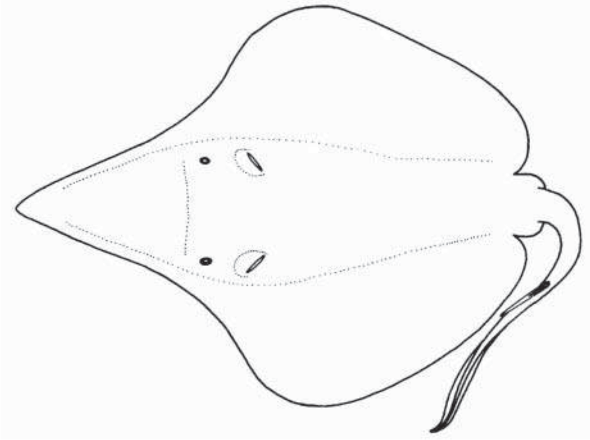


Disc less than 1.3 times as broad as long; caudal fin small but well-developed; dorsal fin present in some species (e.g., *Trygonoptera*, of Australia); tail moderately long with a barbed spine.

The family Urolophidae was formerly recognized as also including *Urobatis* and *Urotrygon* (e.g., by Nelson, 1994, although *Urobatis* was not listed but was regarded as a synonym of *Urolophus*, by Nelson et al., 2004, and by Compagno, 1999). McEachran et al. (1996) placed *Urobatis* and *Urotrygon* of North, Central, and South America and species of *Urolophus* from the same area, in their own family, the Urotrygonidae, and this is followed here. However, McEachran et al. (1996) regarded Indo-Pacific *Urolophus* as *incertae sedis* in the Hexatrygonidae and did not recognize the family Urolophidae. Subsequently, McEachran and Aschliman (2004) recognized the family but, unlike here, as also including the species *Plesiobatis daviesi*; de Carvalho et al. (2004) included only the following two genera. Family members are also known as stingarees.

Two genera, *Trygonoptera* (5) and *Urolophus* (24), with at least 29 species (Compagno, 2005; Séret and Last, 2003). The oldest fossils of the family and of *Urolophus* are from the early Eocene; there is at least one extinct species (Cappetta, 2012).

Family HEXATRYGONIDAE (53)—sixgill stingrays. Marine, continental and insular slopes; Indo-West Pacific (South Africa to Hawaii).

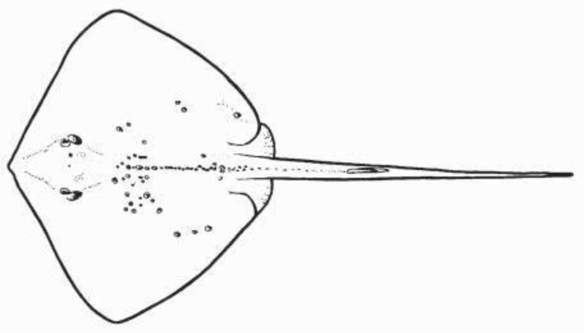


Six gill openings and six gill arches; snout elongate, thin (depressed), translucent; no supraorbital crests on cranium; spiracles large, well behind eyes, with external flaplike valve (the spiracle of other rays is closed by an internal valve); brain very small, posteriorly placed in large cranial cavity; tail with one or two serrate spines; disc longer than broad; nostrils wide apart, anterior nasal flaps short, not joined to form a broad nasal curtain that reaches the mouth.

McEachran et al. (1996) had earlier placed *Plesiobatis* and *Urolophus* (they included *Trygonoptera* as a synonym) in this family as *incertae sedis*.

Probably only one valid species, *Hexatrygon bickelli*, described in 1980 (Smith and Heemstra, 1986; Compagno, 1999, 2005). The oldest fossils of the family and of the genus *Hexatrygon* are from the middle Eocene; there is at least one extinct species (Cappetta, 2012).

Family DASYATIDAE (Trygonidae) (54)—whiptail stingrays. Marine (continental and insular shelves and uppermost slopes, one species oceanic), brackish, and freshwater, tropical to warm temperate; Atlantic (including the Mediterranean Sea), Indian, and Pacific.



Disc not more than 1.3 times as broad as long; no caudal fin; tail long (distance from cloaca to tip much longer than breadth of disc), very slender to whip-like, without dorsal fin but tail with one or more long, poisonous spines; caudal fin absent.

A few species of *Dasyatis* and *Himantura* and *Pastinachus sephen* occur in tropical to warm-temperate rivers and lakes. *Pteroplatytrygon violacea,* often placed in *Dasyatis,* is oceanic. McEachran and Aschliman (2004) provisionally recognized only three genera in the family, placing *Pastinachus* and *Urogymnus,* as well as *Dasyatis kuhlii* as *incertae sedis* in a superfamily Dasyatoidea, as were the Indo-West Pacific species of *Himantura* as *incertae sedis* (the two amphi-American species of *Himantura* were placed within the Potamotrygonidae). The study of de Carvalho et al. (2004) placed the dasyatid genera *Dasyatis, Himantura, Pastinachus* (but not included in their analysis), *Pteroplatytrygon, and Taeniura* as *incertae sedis* at a node sister to the clade comprising Gymnuridae and Myliobatidae; the family Dasyatidae was thus not recognized. Compagno (2005) anticipated that species of *Taeniura* and the two Western Hemisphere species of *Himantura* may belong in the Potamotrygonidae (see also Potamotrygonidae below).

Eight genera, *Dasyatis* (at least 41, synonyms include *Trygon* and *Urolophoides*), *Himantura* (at least 31, but see above note), *Makararaja* (1), *Neotrygon* (5), *Pastinachus* (5, synonym *Hypolophus*), *Pteroplatytrygon* (1), *Taeniura* (3), and *Urogymnus* (1), with at least 88 species (Compagno, 1999, 2005; Last and White, 2008, 2013).

Fossil dasyatids are appear first in the Early Cretaceous; *Dasyatis* appears in the early Late Cretaceous, with *Himantura, Pastinachus,* and *Taeniurops* not appearing until the Miocene; three extinct genera are †*Asterotrygon,* †*Heliobatis,* and †*Hypolophites.*

Family POTAMOTRYGONIDAE (55)—river stingrays. Freshwater; South America (Atlantic, including Caribbean, drainage).

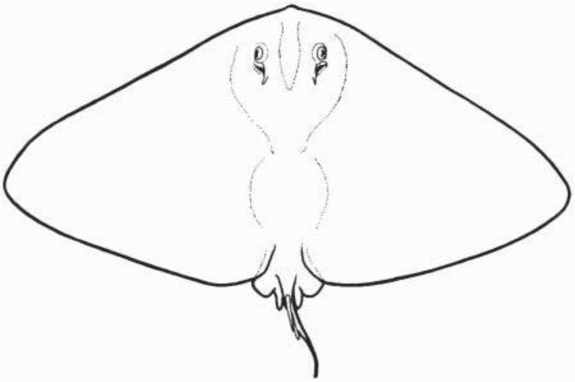
Long, median, anteriorly directed process from the pelvic girdle; angular cartilages present (except *Paratrygon*), within hyomandibular-Meckelian ligament; adaptation to fresh water as evidenced by rectal gland (used for salt secretion) reduced and low urea concentration in body fluids. Most species are quite colorful on the dorsal surface. A detailed study was given by de Carvalho et al. (2004). Maximum length over 100 cm.

Additional species may belong in this family that are here retained in the Dasyatidae pending further research to clarify their relationships. The species in question are the three marine species of *Taeniura,* occurring in the eastern Atlantic (and Mediterranean) and Indo-West Pacific, and two marine species of the large genus *Himantura, H. pacificus* (Pacific off Central America and northern South America) and *H. schmardae* (Atlantic off southern North America and northern South America) which were placed in the Potamotrygonidae by Lovejoy (1996) and followed by McEachran et al. (1996). However, McEachran and Aschliman (2004) retained *Taeniura* in the Dasyatidae (see also above under Dasyatidae). The taxon Potamotrygonidae was regarded as a subfamily of Dasyatidae in Nelson (1994). Eocene fossils of this family are known, and de Carvalho et al. (2004) and Brito and Deynat (2004) hypothesized that the family arose in the Late Cretaceaous or Early Tertiary.

Four genera, *Heliotrygon* (2), *Paratrygon* (1), *Plesiotrygon* (2), *Potamotrygon* (at least 21), with 26 species (Rosa, 1991; de Carvalho et al., 2003; Compagno, 1999, 2005; de Carvalho and Lovejoy, 2011). Both the family and the genus

Potamotrygon appear in the fossil record in the Miocene; there are four extinct species known (Cappetta, 2012).

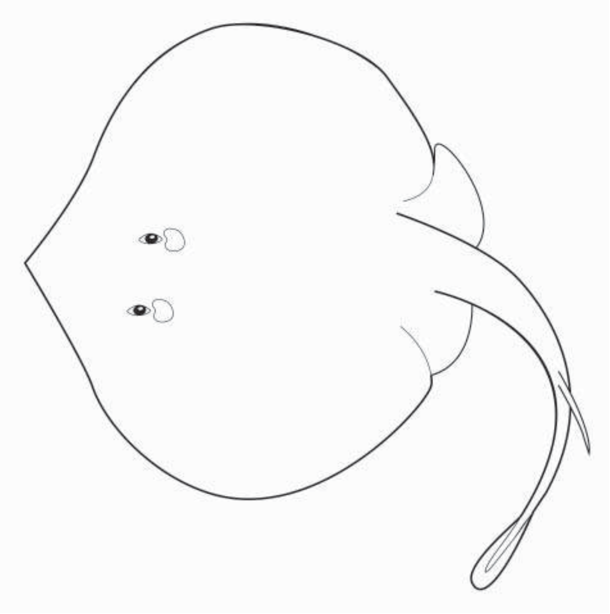
Family GYMNURIDAE (56)—butterfly rays. Marine; tropical to temperate, continental shelves, Atlantic, Indian, and Pacific.



Disc extremely broad (more than 1.5 times as broad as long); dorsal fin and tail spines present (and poisonous) or absent; tail short (distance from cloaca to tip much shorter than breadth of disc); no caudal fin.

One genus, *Gymnura*, with 14 species (Compagno, 1999, 2005). The oldest fossils of the family and of *Gymnura* are of late Paleocene age; the genus has three extinct species (Cappetta, 2012). Extinct genera include †*Jackquhermania* and †*Ouledia*.

Family UROTRYGONIDAE (57)—American round stingrays. Marine, tropical to warm temperate, continental shelves; western Atlantic and eastern Pacific.



Disc not more than 1.3 times as broad as long; tail slender and about as long as disc length, without dorsal fin but with one or more long, poisonous spines; caudal fin distinct.

This family, as noted above, was included in the Urolophidae in Nelson (1994).

Two genera, *Urobatis* (4) and *Urotrygon* (13), with 17 species (Compagno, 2005).

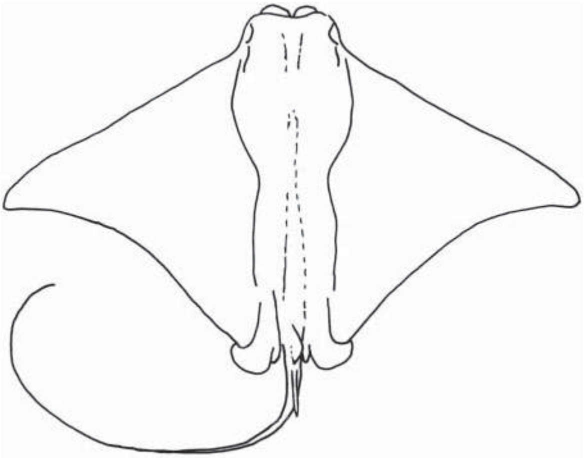
Family MYLIOBATIDAE (58)—eagle rays. Marine; tropical to warm temperate, continental and insular shelves to offshore but not oceanic, Atlantic, Indian, and Pacific.

Distinct but small dorsal fin present; most species with one or more long poisonous spines on tail; no caudal fin; head elevated above disc; eyes and spiracles lateral on head; gill openings about length of eye to much longer; six-sided, pavement-like teeth in horizontal arrangement; anterior propterygia of pectoral fin ventral to eye, meeting near midline to form median or paired subrostral lobes; whip-like tail much longer than disc. Some are famous for their ability to leap high into the air from the water.

Monophyly of this family was recognized by McEachran et al. (1996), although as a subfamily of Dasyatidae, and by de Carvalho et al. (2004), McEachran and Aschliman (2004), Naylor et al. (2012), Aschliman et al. (2012a, b), and Aschliman (2014). Although there is some evidence to suggest that the Myliobatinae as given below are paraphyletic, the three subfamilies (accorded Family status in Compagno, 1999, 2005) are retained as in Nelson (1994, 2006) because of their distinctive morphologies and their monophyly in the phylogenies of Aschliman et al. (2012a, b) and Naylor et al. (2012).

Three subfamilies, seven genera, and 40 species.

SUBFAMILY MYLIOBATINAE (EAGLE RAYS). Anterior face of cranium nearly straight; subrostral fin not incised.



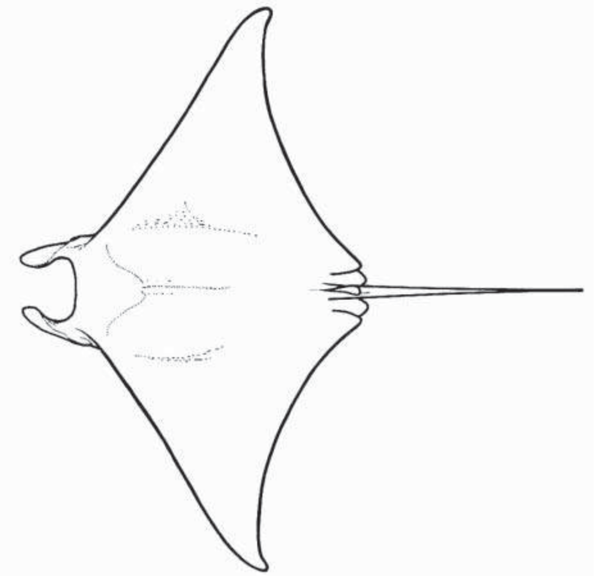
Four genera, *Aetobatus* (4), *Aetomylaeus* (4), *Myliobatis* (11), and *Pteromylaeus* (2), with 21 species (Compagno, 1999).

Fossils of the subfamily appear in the Late Cretaceous. The oldest fossils of extant genera (with numbers of extinct species) according to Cappetta (2012) are: *Aetobatus* (3), late Paleocene; *Aetomylaeus* (2), middle Miocene; *Myliobatis* (5), early Paleocene; *Pteromylaeus*, middle Miocene. Eight extinct genera are known, including †*Aktaua*, †*Brachyrhizodus*, †*Igdabatis*, and †*Leidybatis* (Cappetta, 2012).

SUBFAMILY RHINOPTERINAE (COWNOSE RAYS). Marine; tropical to warm temperate, continental shelves, Atlantic, Indian, and Pacific. Anterior face of cranium concave; subrostral fin incised (bilobed).

One genus, *Rhinoptera*, with eight species (Compagno, 1999, 2005). Rhinopterinae and *Rhinoptera* appear in the fossil record in the late Paleocene; there are four extinct species according to Cappetta (2012).

SUBFAMILY MOBULINAE (DEVIL RAYS). Marine; tropical to warm temperate, inshore and oceanic, Atlantic, Indian, and Pacific. Members of this family are the only living vertebrates with three pairs of functional limbs. The cephalic pair assist in feeding and are the anterior subdivision of the pectorals.



Some mantas grow to a width of about 6.1 m and a weight of more than 1,360 kg; largest members of the superorder (and, like the Whale Shark and Basking Shark, are zooplanktophagous, straining their food out of the water).

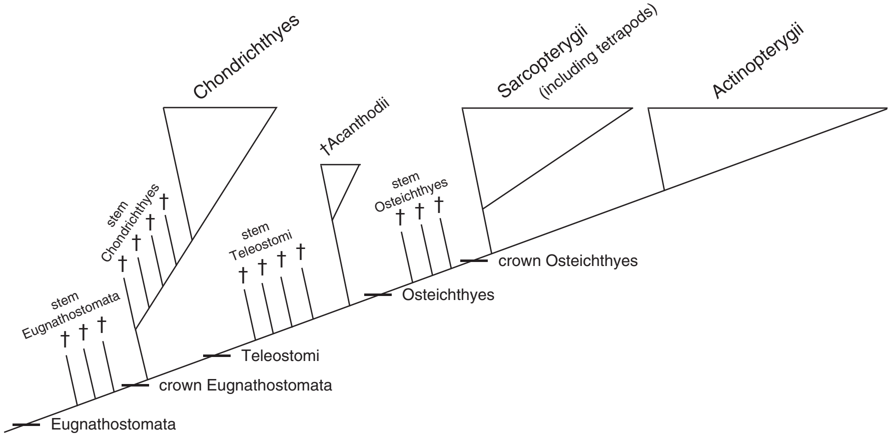
Two genera, *Manta* (2, Manta) and *Mobula* (9, devil rays), with about 11 species (Compagno, 1999, 2005). The two species of *Manta* (Marshall et al., 2009) seem to have speciated within the last half million years but are genetically and morphologically distinct even though their ranges overlap (Kashiwagi et al., 2012).

The relationships of the numerous fossil devil rays to living members were reviewed by Adnet et al. (2012). The oldest fossils of the extant genus *Mobula* (with six extinct species) are early Oligocene, and of *Manta* (one extinct species), late Miocene. According to Cappetta (2012), the oldest Mobulinae are of early Late Cretaceous age. There are six extinct genera (†*Archaeomanta*, †*Burnhamia*, †*Cretomanta*, †*Eomobula*, †*Eoplinthicus*, and †*Plinthicus*).

Grade TELEOSTOMI

The following two classes, the †Acanthodii and Osteichthyes (sister groups to each other, unless acanthodians are paraphyletic), account for the remaining vertebrates and have often been thought to form a monophyletic group termed the Teleostomi (and used previously in Nelson, 1994, 2006). The alignment of acanthodians with the others is based on their sharing three pairs of otoliths with the Actinopterygii, although their otoliths do differ in appearance and composition (a distinction must be made between the sandy statoconia of early fossil taxa and solid otoliths). As typically found in actinopterygians, there is, on each side, one otolith presumably in each of the three membranous sacs of the labyrinth of the inner ear; the three otoliths are the sagitta, usually the largest, in the sacculus; the asteriscus, in the lagena; and the lapillus, in the utriculus. In sarcopterygians there are two pairs of otoliths in dipnoans, one pair in *Latimeria,* and in tetrapods, secondarily derived statoconia (minute calcareous crystals = otoliths of some authors) similar to the statoconia in agnathans and most chondrichthyans. Arratia and Schultze (1991) discussed homologies of the palatoquadrate and associated dermal bones, along with evolutionary trends within the teleostomes. Arratia et al. (2001) gave further details, emphasizing features of the vertebral column and associated elements in these three groups.

Recent molecular studies (an example is Inoue, Miya, Lam, et al., 2010) are basically in agreement (for extant groups only) with the arrangement of the main subgroups of Gnathostomata adopted here, that is ((Holocephali (Selachii, Batomorphi))(Sarcopterygii, Actinopterygii)). Recently there has been controversy over the relationships of the rays (termed the Batomorphi in this edition; see the discussion under Euselachii, above), and uncertainty about the monophyly and relationships of the fossil-only †Acanthodii (discussed below).



Phylogeny of the main groups of Teleostomi.

The names †Acanthodii and Actinopterygii (originating with E. D. Cope in 1871) have each changed little in meaning over time, although monophyly of the †Acanthodii is considered doubtful. However, the terms Teleostomi (originating with C. L. Bonaparte in 1836), Osteichthyes (originating with T. H. Huxley in 1880), and Sarcopterygii have each been used for different combinations of taxa over time (the dates given are from the unpublished manuscript of the late D. E. McAllister, 1989, "A working list of fishes of the world"). The name Osteichthyes was earlier used only for bony fishes, without tetrapods, but now includes both and denotes a monophyletic group. Similarly, the name Sarcopterygii had earlier been used by A. S. Romer for a paraphyletic assemblage that included only fishes conventionally called crossopterygians and dipnoans (the lobe-finned fishes), but no tetrapods; however, as used here formally, the taxon Sarcopterygii is also monophyletic (following Wiley, 1979, and Rosen et al., 1981) since it now includes not only all lobe-finned fishes but also all tetrapods, which are in a real sense just modified lobe-finned fishes (as recently highlighted by Shubin, 2008).

The taxon Teleostomi contains about 61,000 extant valid species (there are no extant acanthodians, but there are about 30,500 extant actinopterygians, and about 30,500 extant sarcopterygians including tetrapods). Because one of the two classes (†Acanthodii) in Teleostomi is extinct, there are also about 61,000 extant valid species of Osteichthyes (also including tetrapods).

†Class ACANTHODII—acanthodians

Dermal and perichondral bone present, endochondral bone absent; jaws formed by palatoquadrate and Meckel's cartilage, both uncalcified, calcified, or with perichondral ossification; mandibular arch (palatoquadrate) probably closely associated with hyoid arch, with the spiracular gill cleft (homologous with spiracle of other fishes and eustachian tube of tetrapods) virtually closed; ornamented plate-like dermal cover over gill chamber (associated with hyoid arch) in most species; five gill arches; notochord persistent; neural and haemal arches present but vertebral centra lacking; rhombic to teardrop-shaped dermal scales present on body and fins; body scales usually grew by addition of concentric layers; stout spines present before the dorsal, anal, and paired fins; up to six paired spines present between the pectorals and pelvics in many, with small spines in a prepectoral series present in some species; caudal fin epicercal heterocercal. Burrow (2004) reviewed the acanthodians with dentigerous jaw bones and gave references to the recent acanthodian literature. Species of climatiiforms and acanthodiforms have a double mandibular joint. Perhaps Late Ordovician (as microfossils) to Early Permian (Zidek, 1993; Janvier, 1966; Hanke and Wilson, 2004). Articulated remains are known from Late Silurian to Early Permian.

The acanthodians, with their large eyes, terminal or near terminal mouth, and small nasal capsules, mostly were mid- and surface-water feeders. Many were microphagous while others, especially the ischnacanthiforms, ate fishes and invertebrates. Acanthodians are known from both freshwater and marine environments; the Mississippian to Permian †*Acanthodes* is known from both. They are the earliest well-known true jawed fishes, but the oldest species are poorly known because they are represented by isolated microremains. Maximum length is estimated at about 2.5 m; most are less than 20 cm.

Various views have existed on acanthodian relationships. Authors have variously proposed that they are i) the monophyletic sister group to all other gnathostomes (chondrichthyans, placoderms, and osteichthyans); ii) paraphyletic stem relatives of Eugnathostomata (gnathostomes excluding placoderms); iii) the monophyletic sister group to Chondrichthyes; iv) paraphyletic stem relatives of Chondrichthyes; v) the monophyletic sister group to the Osteichthyes (Sarcopterygii plus Actinopterygii); or vi) paraphyletic stem relatives of the Osteichthyes.

Some of these ideas have existed for many years. Watson (1937) felt that acanthodians were the most primitive known gnathostomes. He placed them in the Aphetohyoidea, along with several other groups, a taxon with equal rank to the Pisces. In many classifications of the 1930s to 1950s, they were placed in the class †Placodermi. Berg (1940) recognized acanthodians in their own class and placed them immediately before his class Elasmobranchii. Romer, in his classic 1966 "Vertebrate Paleontology," provisionally considered them to be the most primitive subclass of the osteichthyans because of certain resemblances to the actinopterygians. Important contributors to acanthodian classification in the 1970s and earlier included R. H. Denison, E. Jarvik, and R. S. Miles. There have also been many more modern studies on acanthodian systematics (e.g., Long, 1986, 1989; Warren et al., 2000; Zajíc, 1995).

As shown in phylogenetic analyses by Hanke and Wilson (2004), Brazeau (2009), Davis et al. (2012), Giles et al. (2015), and others, acanthodians are more diverse than previously appreciated, and the older three-Order classification (†Climatiiformes, †Ischnacanthiformes, and †Acanthodiformes) has been shown to be inadequate. For example, Hanke and Wilson (2004) described two new taxa (†*Obtusacanthus* and †*Lupopsyroides*) with some primitive gnathostome features, other characters similar to those of acanthodians, and others suggesting relationship to chondrichthyans. Brazeau (2009) suggested that another genus, †*Ptomacanthus*, was among forms that are related to chondrichthyans, whereas other acanthodian genera were thought to be related to bony fishes.

Several, more recent phylogenetic studies that included some acanthodian taxa placed them in different phylogenetic positions. For example, Brazeau (2012) found at least some acanthodians to be stem Eugnathostomata (the group including chondrichthyans plus teleostomes). Davis et al. (2012) found some but not all acanthodians to be stem members of the chondrichthyan radiation, others to be stem osteichthyans, and others stem eugnathostomes. Zhu et al. (2013) found all of the acanthodians considered in their analysis to be paraphyletic branches from the stem of the chondrichthyans. Dupret et al. (2014) found evidence for a monophyletic †Acanthodii, sister to chondrichthyans. Giles, Friedman, and Brazeau (2015) and Brazeau and Friedman (2015) suggested that all or most acanthodians are stem-group chondrichthyans, though after removal of a few genera that they suggest are separate stem-group chondrichthyan lineages, there remains a monophyletic †Acanthodii in their results. In most of these recent studies the character support for the various positions was weak. As a consensus has yet to emerge, we have chosen to retain acanthodians provisionally in the †class Acanthodii until a new arrangement is more widely agreed upon.

We recognize four orders. Some genera not assigned to orders may be very early offshoots of the acanthodian stem, such as:

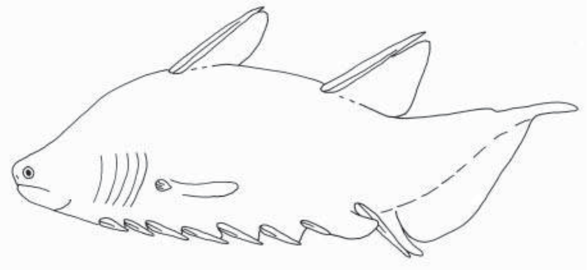
†*Lupopsyroides.* Early Devonian, possibly a stem acanthodian according to Hanke and Wilson (2004).

†*Lupopsyrus.* Early Devonian. Hanke and Davis (2012) restudied the only species, †*L. pygmaeus.* Giles, Friedman, and Brazeau (2015) agreed that it is a stem chondrichthyan.

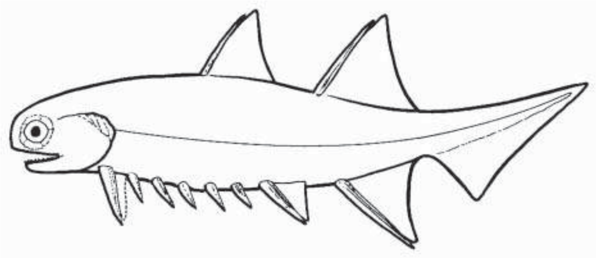
†Order CLIMATIIFORMES. Mid-Silurian to Pennsylvanian (North and South America, Greenland, Europe, Asia, Australia, and Antarctica). Most with ornamented dermal bones in ventral portion of shoulder girdle (other acanthodians possess only endoskeletal elements); two dorsal fins, each with a spine; intermediate (prepelvic) paired spines between the pectoral and pelvic fins in most taxa, up to six pairs in climatiids and perhaps absent in some †*Culmacanthus* and †*Acritolepis* (the latter might better be placed in the †Ischnacanthiformes, Burrow, 2004); teeth absent or, if present, not fused to jaws.

†Climatiiformes are very likely paraphyletic, constituting separate early branches of spiny fishes. There are four provisionally recognized families, as well as genera not assigned to families such as †*Paucicanthus*, which lacks paired fin spines (Hanke, 2002), †*Ptomacanthus*, which Brazeau (2009, 2012) has argued is a stem-group gnathostome, stem chondrichthyan, or stem teleostome, and †*Nostolepis*, which is known mainly by scales.

†Family BROCHOADMONIDAE. Early Devonian. Pectoral fins slender and delicate, elevated on flank, with one pair of very small fin spines; pelvic fin preceded by a long series of stout, paired fin spines each one followed by a flap of scale-covered skin. Anal fin very slender and very close to caudal fin. One genus, †*Brochoadmones*, originally described as an acanthodian, as agreed also by Hanke and Wilson (2004). Hanke and Wilson (2006) made a detailed study of the only named species †*B. milesi*, though additional species are known but unnamed as yet. Dupret et al. (2014) produced a phylogeny with a paraphyletic climatiiforms and †*Brochoadmones* as a very primitive, early acanthodian lineage, although Davis et al. (2012), Brazeau and Friedman (2015), and Giles, Friedman, and Brazeau (2015) have placed it as a stem chondrichthyan.



†Family CLIMATIIDAE. E.g., †*Brachyacanthus*, †*Climatius* (usually reached only 7.5 cm, shown in figure), †*Parexus* (with exceptionally long first dorsal spines), and †*Vernicomacanthus*.



Burrow et al. (2015) redescribed †*Climatius reticulatus* based on the best available fossils. Climatiids have sometimes been placed as stem Eugnathostomata (e.g., Davis et al., 2012) or as stem chondrichthyans (e.g., Giles, Friedman, and Brazeau, 2015).

†Family GYRACANTHIDAE. E.g., †*Gyracanthides*, with chondrichthyan-like scales

†Family EUTHACANTHIDAE. E.g., †*Euthacanthus*.

†Order DIPLACANTHIFORMES. Devonian. These acanthodians had long median fin spines and a single pair of prepelvic (previously called intermediate) spines between the pelvic and pectoral fins, or lacked such spines altogether. Formerly they were a suborder of †Climatiiformes.

†Family CULMACANTHIDAE. Devonian. One genus, †*Culmacanthus*.

†Family DIPLACANTHIDAE. Devonian; e.g., †*Diplacanthus*. The genus †*Tetanopsyrus*, revised by Hanke et al. (2001), is provisionally retained in this family.

†Family GLADIOBRANCHIDAE. Devonian. These apparently toothless acanthodians had smoothly ossified plates on the gnathal surface of the lower jaws, and very long fin spines (Hanke and Davis, 2008); e.g., †*Uraniacanthus* and its possible junior synonym †*Gladiobranchus* (Newman et al., 2012).

†Order ISCHNACANTHIFORMES. Late Silurian to Pennsylvanian of North and South America, Europe, Australia, Antarctica, and Asia. Two dorsal fins, each with a spine; teeth fixed to strong dermal jaw bones that attach to the oral border of the meckelian and palatoquadrate cartilages (Burrow, 2004; Blais et al., 2015); no prepelvic spines between the pectoral and pelvic fin spines. Two families.

†Family ISCHNACANTHIDAE. Many ischnacanthids had a complex array of teeth along their jawbones. Some also had separate tooth whorls, and tooth-like scales externally, near their lips and on their cheeks (Blais et al., 2011). Though many well preserved articulated specimens have been described (e.g., Blais et al., 2011, 2015), many others are known only from isolated jaws and fin spines, which are nevertheless usually diagnostic to genus and often to species (e.g., Hanke et al., 2001). In some cases, isolated elements have been combined to infer composite species based on faunal associations in the absence of articulated remains. Genera include †*Atopacanthus*, †*Erymnacanthus*, †*Euryacanthus*, †*Ischnacanthus*, †*Marsdenius*, †*Tricuspicanthus*, and †*Xylacanthus* (e.g., Hanke et al., 2001; Blais et al., 2011, 2015).

†Family PORACANTHODIDAE. One genus, †*Poracanthodes*.

†Order ACANTHODIFORMES. One posterior dorsal fin with spine; teeth absent; gill rakers well developed in later members of the clade (probably adapted for filter feeding); prepelvic spines absent or limited to one pair in the †Mesacanthidae. Early Devonian to Early Permian (North America, Europe, Asia, South Africa, Australia, and Antarctica). Three families.

Davis et al. (2011) redescribed the braincase of †*Acanthodes* and found phylogenetic evidence for osteichthyan affinities of acanthodiforms.

†Family MESACANTHIDAE. E.g., †*Mesacanthus,* †*Melanoacanthus*, and †*Promesacanthus* (e.g., Hanke, 2008).

†Family CHEIRACANTHIDAE. E.g., †*Carycinacanthus*, †*Cheiracanthus*, and †*Homalacanthus*.

†Family ACANTHODIDAE. Pelvic fins when present closer to pectoral fins than to anal fin, e.g., †*Acanthodes*, †*Acanthodopsis* (e.g., Burrow, 2004), †*Howittacanthus*, and †*Traquairichthys*, which lacks pelvic fins.

Class OSTEICHTHYES—bony fishes and tetrapods (= Euteleostomi of Nelson, 2006)

Skeleton, in part at least, with bone (endochondral or membrane bone); skull with sutures; lung(s) usually present, functioning either as air-breathing organs or as buoyancy-controlling swimbladders or both; intestinal spiral valve in only a few lower groups.

The Osteichthyes (bony fishes) comprise the remaining two monophyletic classes of the teleostomes. In the 2006 edition of this book, the group was called the Euteleostomi, because it was thought that the older historical use of the name Osteichthyes would mislead readers into thinking of it as a paraphyletic assemblage of fishes exclusive of tetrapods. However, it is increasingly widely accepted that tetrapods, including ourselves, are simply modified bony fishes, and so we are comfortable using the taxon Osteichthyes as a clade, which now includes all tetrapods, as also used by Rosen et al. (1981) and subsequently by many vertebrate paleontologists (e.g., Janvier, 1996, and Ahlberg, 2001) and some others. This taxon includes all Sarcopterygii (the lobe-finned fishes including tetrapods) and all Actinopterygii (the ray-finned fishes).

The term Euosteichthyes was used by Wiley (1979) for the Osteichthyes less the coelacanthiforms, but that term is not used here because coelacanthiforms are regarded as members of the Sarcopterygii.

THE FOLLOWING THREE TAXA are among those often classified as stem-group osteichthyans (e.g., by Dupret et al., 2014; Brazeau and Friedman, 2015), although others have placed them as very primitive actinopterygians (e.g., Zhu et al., 2009).

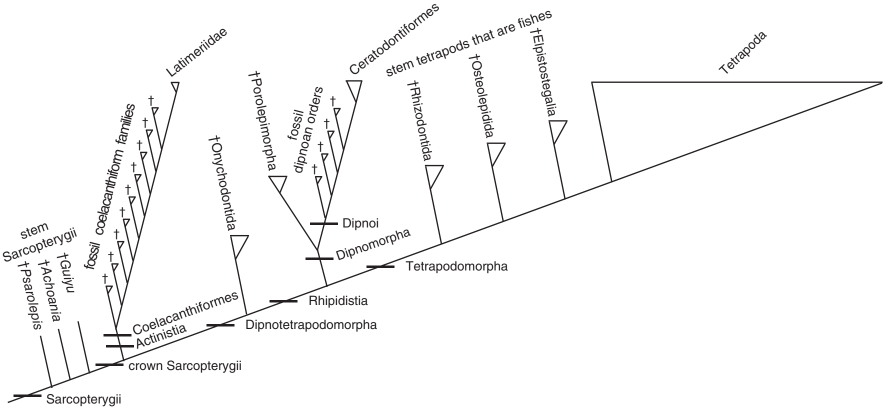
†*Lophosteus.* Late Silurian to Early Devonian. Scales and other bone fragments of this widely distributed genus are among the oldest known fossils of osteichthyans. Botella et al. (2007) described jaws and teeth for the first time, classifying them in the osteichthyan stem group.

†*Andreolepis.* This Late Silurian genus is known mainly by disarticulated scales and dermal bone fragments, but these have been intensively studied (e.g., Chen et al., 2012). †*Andreolepis* is regarded as one of the oldest and most primitive osteichthyans (e.g., Zhu et al., 2009).

†Order DIALIPINIFORMES. Early Devonian; marine. Schultze and Cumbaa (2001) described articulated skeletons from northern Canada; they and others (e.g., Zhu et al., 2009; Giles, Darras et al., 2015) classified this genus as a primitive actinopterygian, but others (e.g., Friedman and Brazeau, 2010; Dupret et al., 2014; Friedman, 2015) have placed it as a stem osteichthyan. It is of great interest for many reasons, including its possession of a diphycercal tail similar to that of coelacanths. One genus, †*Dialipina*.

Subclass SARCOPTERYGII—lobe-finned fishes and tetrapods

The Sarcopterygii, as used here, form the monophyletic taxon that includes several fish groups, both recent and fossil, and the tetrapods. All the included fishes are thus more closely related to tetrapods than they are to other fishes. The closest sister group to the tetrapods among living fishes is probably the lungfishes (not the coelacanths), although there are differing theories. In the past, the term Sarcopterygii has been variously used; some workers used it to include only fishes conventionally called crossopterygians and dipnoans (the lobe-finned fishes). We use the term to include also the tetrapods as have many earlier authors (e.g., see Nelson, 1994). Synapomorphies recognized by Cloutier and Ahlberg (1996) include: peg on rhombic scales broad; premaxilla not forming part of orbit; tectal bones present; more than four sclerotic plates; dermohyal present; squamosal and preopercular bones separate; branchiostegal rays one per side; two infradentaries; jugal canal present; mandibular canal not passing through dentary; endoskeletal supports in pectoral fins single ("humerus") articulating with girdle; basal plates present in dorsal fin supports. Unlike most other fishes, sarcopterygians have true enamel in their oral teeth (Smith, 1989).



Phylogeny of the main groups of Sarcopterygii.

In an exciting find, Zhu and Yu (2002) described a fossil sarcopterygian fish from the Early Devonian of China, †*Styloichthys*, that showed characteristics suggesting it might be close to the last common ancestor of tetrapods and lungfishes. It appears to bridge the morphological gap between stem-group sarcopterygians (see below) and primitive tetrapodomorphs or dipnoans.

Some earlier views of relationships among crossopterygians, lungfishes, and tetrapods were given in Nelson (1994). The present classification of the non-tetrapods is largely from Cloutier and Ahlberg (1996). Much information on this group is in Long (1995, 2011), Janvier (1996), Maisey (1996), Schultze and Cloutier (1996), Ahlberg (2001), and Clack (2002).

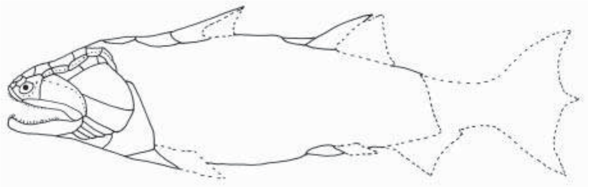
The extant Sarcopterygii are recognized here with two subclasses, having about 30,500 species, of which 8 species are fishes.

There are many important early fossil genera, of which we highlight three examples. Phylogenetic analyses usually recover these as stem-group Sarcopterygii (e.g., Dupret et al., 2014; Zhu et al., 2009; Davis et al., 2015) but some (e.g., Long et al., 2015) have published phylogenies placing some of them as stem actinopterygians.

†*Psarolepis.* This primitive fish from the Early Devonian was described as a stem osteichthyan or stem sarcopterygian (Zhu et al., 1999) although Long (2001) pointed to numerous resemblances between it and †Onychodontiformes, suggesting it might instead be a primitive member of that group.

†*Achoania.* This genus, known by cranial remains from the Early Devonian of China, had an eyestalk, a feature previously known from placoderms (Zhu et al., 2001).

†*Guiyu.* This important Late Silurian fossil from China is among the very few early osteichthyans known by articulated skeletal remains (Zhu et al., 2009). Until now its caudal region remained unknown.



THE REMAINING SARCOPTERYGIANS are members of crown-group Sarcopterygii.

Infraclass ACTINISTIA—coelacanths (Coelacanthida)

As per Cloutier and Ahlberg (1996), Actinistia contain the following synapomorphies: rostral organ present; posterior coronoid well developed and oriented vertically; articulation of symplectic with articular present; intercentra not ossified. Apart from certain very primitive fossils (mentioned above), the Actinistia are generally agreed to be the sister group of all other Sarcopterygii (including tetrapods). They are classified in a single order, and the families, most of which are extinct, are listed in approximate phylogenetic sequence.

Order COELACANTHIFORMES (17)—coelacanths. Caudal fin diphycercal, consisting of three lobes; external nostrils, no choana; lung enclosed in concentric calcified plates in many; branchiostegals absent; lepidotrichia never branched; lepidotrichia in tail equal to number of radials or somewhat more numerous; anterior dorsal fin in front of center of body.

The order is recognized with nine families (Cloutier and Ahlberg, 1996), eight with only fossil members, and one with fossil members and two living species. Much of the classification of Cloutier and Ahlberg (1996) is based on the 1993 study of H.-P. Schultze. Dutel et al. (2015) provided a revised phylogenetic estimate. There is a good fossil record of this group from the Late Devonian to the Late Cretaceous. The majority of species were marine, but some were fresh water. Forey (1998) gave extensive information on this order.

†Family MIGUASHAIIDAE. Late Devonian of Miguasha, Quebec. This important coelacanth is among the most primitive known (Cloutier, 1996; Cloutier and Ahlberg, 1996). Unlike other actinistians, its caudal fin is not symmetrical. One genus and species, †*Miguashaia bureaui*.

†Family DIPLOCERCIDAE. Devonian and Mississippian; one genus †*Diplocercides* (synonym †*Nesides*). Gess and Coates (2015) named the new genus †*Serenichthys* to contain a species represented by juvenile coelacanths with similarities to †*Diplocercides*, but did not classify it in this family.

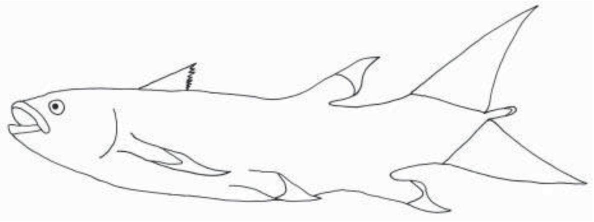
†Family HADRONECTORIDAE. Carboniferous; e.g., †*Hadronector*, and †*Polyosteorhynchus*.

†Family RHABDODERMATIDAE. Primarily Carboniferous; possibly paraphyletic; e.g., †*Caridosuctor* and †*Rhabdoderma*.

†Family LAUGIIDAE. Early Triassic to Early Cretaceous, fresh water and marine. Occipital neural arches expanded; pelvic fins thoracic; pelvic bones fused at midline; caudal fin longer (more rays) dorsally than ventrally. Genera include †*Belemnocerca*, †*Coccoderma*, and †*Laugia*; e.g., Wendruff and Wilson, 2013).

†Family WHITEIIDAE. Triassic, marine, worldwide. Arratia and Schultze (2015) proposed a revised diagnosis and membership for the †Whiteiidae; e.g., †*Atacamaia*, †*Axelia*, †*Piveteauia*, †*Wimania*, and †*Whiteia*.

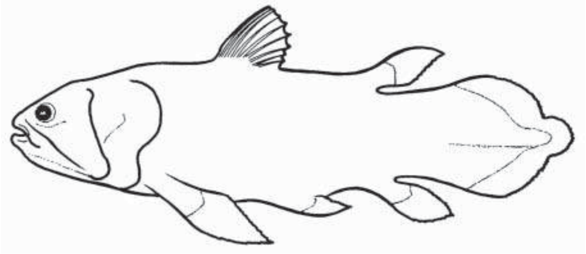
†Family REBELLATRICIDAE. Early Triassic of Western Canada, marine. One genus and species, †*Rebellatrix divaricerca*. Unlike others, these coelacanths were fast-swimming pursuit predators as evidenced by their stiff, strongly forked caudal fin (Wendruff and Wilson, 2012).



†Family COELACANTHIDAE. Perhaps one genus (Dutel et al., 2015), †*Coelacanthus*.

†Family MAWSONIIDAE. Triassic and Jurassic; e.g., †*Alcoveria*, †*Axelrodichthys*, †*Chinlea*, †*Diplurus*, and †*Mawsonia*. This family includes some of the largest known coelacanths. Recent studies suggest that they are sister to Latimeriidae (e.g., Dutel et al. 2012; Dutel, Herbin, and Clément, 2015).

Family LATIMERIIDAE (59)—gombessas or coelacanths. Marine; off southern Africa (Mozambique, Madagascar, and Comoros Archipelago) and Indonesia (Celebes Sea, north of Sulawesi).



Lung vestigial in adults; fatty organ providing buoyancy; livebearing (ovoviviparous). Length of adults up to 1.8 m.

Coelacanths were long known from the fossil record before any extant species were discovered; thus, they are often cited as the classic example of a "living fossil." The first living species to be discovered, *Latimeria chalumnae* (Gombessa), known from South Africa, the Comoros Archipelago, and off Mozambique, was for decades thought to be the sole extant member of the family Latimeriidae.

The first specimen was trawled off the Chalumna River, near East London, South Africa, in December 1938, recognized as important by museum biologist Marjorie Courtenay-Latimer, and later named by J. L. B. Smith in 1939. After fourteen years and much distribution of posters, Smith obtained the second specimen from off the Comoros. Inhabitants of the Comoros catch them, often unintentionally, when fishing for other species.

There is much interest in the unusual head-standing behavior of *L. chalumnae*, filmed by Hans Fricke in a submersible at 170–200 m depth (the species ranges between about 150–400 m). Later observations showed aggregations of the species within undersea caves. The species also has an unusual mode of swimming, especially for a fish with a notochord instead of vertebrae, in keeping the body rigid and moving its opposing fins in opposite phase.

It is the only living chordate with an intracranial joint, also found in other coelacanths, porolepiforms, and osteolepidiforms. As described by Chang in a 1991 study discussing its phylogenetic importance, the intracranial joint is a plesiomorphic character of sarcopterygians with mobility reduced in porolepiforms and lost in dipnoans. This joint divides the neurocranium into an orbitosphenoid anterior half and an otico-occipital posterior half, allowing the anterior half (and upper jaw) to be elevated and then lowered. The paired basicranial muscle increases bite force by lowering the anterior half of the neurocranium during prey capture (Dutel, Herbin, Clément, and Herrel, 2015).

The lung in *Latimeria* has recently been shown to be present in embryos based on CT scans, but vestigial in adults, although enclosed by small, scattered, hard plates thought to be homologous with the concentric calcified plates enclosing the lung in many fossil coelacanths. The fatty organ, once supposed to be a lung, is a separately developing organ (Cupello et al., 2015).

Events leading to the discovery of the second extant species (*Latimeria menadoensis*) are also the stuff of legend. They began with the sighting by Arnaz and then Mark Erdmann during their honeymoon, of a coelacanth in an Indonesian fish market in Manado, Sulawesi, on 18 September 1997, and the subsequent preservation of a second specimen on 30 July 1998. These events are documented in a 1999 issue of *Environmental Biology of Fishes.* The new species was named by Pouyaud et al. (1999).

One extant genus *Latimeria* with two species, *L. chalumnae* and *L. menadoensis.* In addition there are Jurassic and Cretaceous fossil genera, e.g., †*Holophagus*, †*Libys,* †*Macropoma,* †*Megalocoelacanthus*, †*Swenzia*, and †*Undina*. All taxa recognized here in the family Latimeriidae were recognized in the Coelacanthidae in Nelson (1994). Reasons for splitting the two families were given by Cloutier and Ahlberg (1996). †*Megalocoelacanthus* includes giant, toothless coelacanths from the marine Late Cretaceous of North America (Dutel et al., 2012).

Infraclass ONYCHODONTIDA

†Order ONYCHODONTIFORMES (Struniiformes). Middle to Late Devonian. Position uncertain but hypothesized to be sister to the remaining sarcopterygians (including tetrapods). Excellently preserved fossils are known from Gogo, Australia. Long (2001) suggested that †*Psarolepis* (see above) may be the sister taxon to †Onychodontiformes.

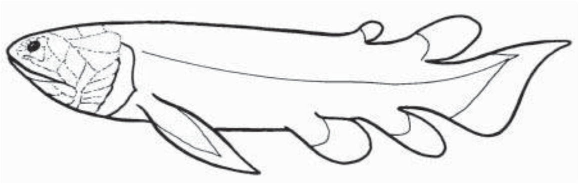
†Family ONYCHODONTIDAE. Devonian. Diagnosable by a median extrascapular that abuts the lateral extrascapulars (Cloutier and Ahlberg, 1996). Extremely well-preserved partial skeletons of †*Onychodus* are known from Gogo, Australia (Long, 2001, 2011); e.g., †*Grossius*, †*Luckius*, †*Onychodus*, †*Qingmenodus*, †*Strunius*.

Infraclass DIPNOMORPHA

†Superorder POROLEPIMORPHA

†Order POROLEPIFORMES (Holoptychiiformes). Body plump; pectorals inserted relatively high on body; thick rhombic cosmoid scales to thin round scales; dendrodont plicidentine present; prespiracular present; subsquamosals present; buccohypophysial foramen of parasphenoid double; otic canal passes through growth center of postparietal; no pineal foramen. Porolepiforms are often very common fossil vertebrates in Devonian sedimentary rocks, perhaps because of their robust bones and scales (e.g., Cloutier and Schultze, 1996). They are usually placed as the sister group to the Dipnoi.

†Family POROLEPIDAE. Devonian; e.g., †*Porolepis*.



†Family HOLOPTYCHIIDAE. Devonian; e.g., †*Holoptychius*, †*Glyptolepis*, †*Laccognathus*, †*Quebecius*.

Superorder DIPNOI (Dipterimorpha, Dipnoiformes of Cloutier and Ahlberg, 1996)

This superorder was originally named by Müller (1845) and includes all lungfishes. See Nelson (1994) for references to the older literature, especially for the major contributions of such continuing workers as P. Ahlberg, M.-M. Chang, R. Cloutier, A. Kemp, and H.-P. Schultze (see also the major study of vertebral columns by Arratia et al., 2001). The taxonomy here is based mostly on Cloutier and Ahlberg (1996), who recognize three synapomorphies: B-bone present; width of submandibularis broad; labial cavity present.

The following genera are considered to be primitive, early members of the Dipnoi: †*Youngolepis*, †*Powichthys*, and †*Glyptolepis*.

†Order DIABOLEPIDIFORMES. Early Devonian. One family, arguably the sister group of all other Dipnoi.

†Family DIABOLEPIDIDAE. Early Devonian. One genus and species, †*Diabolepis speratus*, known only from skull remains.

†Order DIPNORHYNCHIFORMES. Devonian. Two families.

†Family URANOLOPHIDAE. Early Devonian; one genus and species, †*Uranolophus wyomingensis*.

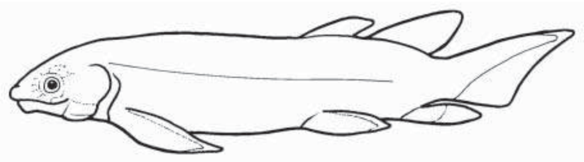
†Family DIPNORHYNCHIDAE. Early–Middle Devonian, e.g., †*Dipnorhynchus*, †*Speonesydrion*.

†Family CHIRODIPTERIDAE. Middle-Late Devonian, e.g., †*Chirodipterus*, †*Gogodipterus*.

†Order Dipteriformes. Devonian; about seven families.

†Family STOMIAHYKIDAE. Middle to Late Devonian; e.g., †*Stomiahykus*, †*Archaeonectes*.

†Family DIPTERIDAE. Devonian; e.g., †*Dipterus*, †*Grossipterus*.



†*Palaeospondylus.* Middle Devonian. Thomson et al. (2003) clarified a long-standing puzzle as to the identity of †*Palaeospondylus gunni*, a tiny (5–60 mm) and abundant vertebrate fossil from the Achanarras Quarry, Caithness, Scotland, first discovered in 1890. They showed that it is the larval stage of a lungfish, most probably †*Dipterus valenciennesi*.

†Family CHIRODIPTERIDAE. Middle-Late Devonian; e.g., †*Chirodipterus*, †*Gogodipterus*.

†Family RHYNCHODIPTERIDAE. Middle to Late Devonian; e.g., †*Griphognathus*, †*Rhynchodipterus*, †*Soederberghia*. Long-snouted lungfishes with denticulated palates.

†Family PHANEROPLEURIDAE. Middle to Late Devonian; e.g., †*Phaneropleuron,* †*Scaumenacia*, †*Pentlandia*.

†Family FLEURANTIIDAE. Middle to Late Devonian; e.g., †*Andreevichthys*, †*Barwickia*, †*Fleurantia*, †*Jarvikia*. Lungfishes with elongated snouts and wide mouth gapes.

†Order CTENODONTIFORMES. Carboniferous.

†Family URONEMIDAE. Carboniferous; one genus, †*Uronema*.

†Family CTENODONTIDAE. Carboniferous. The family was named by Woodward (1891:250); in bivalves there is a family "Ctenodontidae Whörmann, 1893," but the bivalve name appears to be the junior homonym. Genera include †*Ctenodus* and †*Tranodis*. Sharp and Clack (2013) recently reviewed the morphology of †*Ctenodus*.

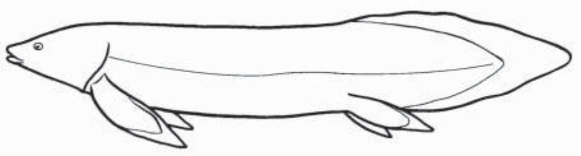
Order CERATODONTIFORMES (18)—living lungfishes and their fossil relatives. All three extant families are placed in this order, without suborders. Rather than recognizing a separate suborder for the African and South American lungfishes, we include them in the sequence of ceratodontiform families. Listing them as the last two families in the sequence is sufficient to show that they are each other's closest relatives, and collectively sister to Neoceratodontidae.

†Family ARGANODONTIDAE. Triassic; e.g., †*Arganodus*.

†Family CERATODONTIDAE. Triassic to Cenozoic; e.g., †*Ceratodus*, †*Paraceratodus*. Likely paraphyletic; many forms known only by their tooth plates.

†Family ASIATOCERATODONTIDAE. Triassic; e.g., †*Asiatoceratodus*.

Family NEOCERATODONTIDAE (60)—Australian lungfishes. Triassic to Recent; fresh water.



Scales large; paired fins stout, with numerous rays.

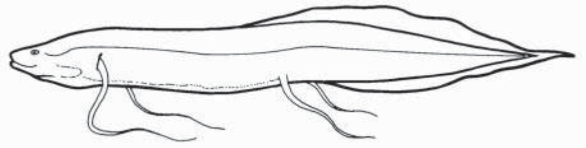
One extant species, *Neoceratodus forsteri*. Miles (1977) and Cloutier and Ahlberg (1996) recognized the family Neoceratodontidae containing the extant Australian lungfish. The Triassic †*Epiceratodus* is also placed in this family (Miles, 1977; Cloutier and Ahlberg, 1996).

Family LEPIDOSIRENIDAE (61)—South American lungfishes. Fresh water; Brazil and Paraguay.

Five gill arches and four gill clefts; body very elongate. Pectoral and pelvic fins filamentous, without rays; scales small; swimbladder (lungs) paired; larvae with external gills; adults estivate in dry season.

One species, *Lepidosiren paradoxa*. This was the first living lungfish to be formally described, in 1837.

Family PROTOPTERIDAE (62)—African lungfishes. Fresh water; Africa.



Six gill arches and five gill clefts; body moderately elongate. Maximum length about 1.8 m.

One genus, *Protopterus*, with four species.

†Infraclass RHIZODONTIDA (Rhizodontimorpha)

†Order RHIZODONTIFORMES. One family.

†Family RHIZODONTIDAE. Late Devonian to Pennsylvanian. Cloutier and Ahlberg (1996) provide two synapomorphies for the group: depressed lamina of cleithrum present; and length of proximal unsegmented part of lepidotrichium much greater than segmented part. Rhizodontids probably lacked a choana since they have two pairs of external nostrils. Genera include †*Barameda*, †*Notorhizodon*, †*Pycnoctenion*, †*Propycnoctenion*, †*Rhizodus*, †*Sauripterus*, †*Screbinodus*, and †*Strepsodus*.

†Infraclass OSTEOLEPIDIDA

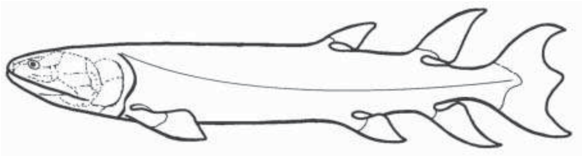
†Order OSTEOLEPIDIFORMES. Body slender; pectorals usually inserted low on body; thick, rhombic scales; pineal foramen present. About five families (based on work of H.-P. Schultze, 1993, and Cloutier and Ahlberg, 1996). *Gogonasus* is included within the osteolepidiforms, but it is of uncertain position as are several other genera.

†Family CANOWINDRIDAE. Devonian; e.g., †*Canowindra*, †*Marsdenichthys*.

†Family MEGALICHTHYIDAE. Devonian; e.g., †*Cladarosymblema, †Ectosteorhachis,* †*Megalichthys*.

†Family OSTEOLEPIDIDAE. Devonian; e.g., †*Osteolepis*, †*Thursius*.

†Family TRISTICHOPTERIDAE. Devonian; e.g., †*Cabonnichthys*, †*Eusthenodon*, †*Eusthenopteron, †Tristichopterus*.

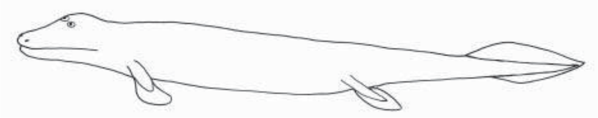


†Family RHIZODOPSIDAE. Devonian; e.g., †*Rhizodopsis*.

†Infraclass ELPISTOSTEGALIA

†Order ELPISTOSTEGALIFORMES. One family.

†Family ELPISTOSTEGALIDAE (†PANDERICHTHYIDAE). Median supraorbital ridges present (Cloutier and Ahlberg, 1996). These are fishes with paired fins that had evolved to become leg-like, while still retaining fin rays.



Genera include †*Elpistostege* and †*Panderichthys* (Cloutier and Ahlberg, 1996; Schultze, 1996), along with the more recently discovered †*Tiktaalik*, one of the most remarkable, tetrapod-like fishes ever discovered and represented by well-preserved fossil material from Arctic Canada (Daeschler et al., 2007; Shubin et al., 2014).

Infraclass TETRAPODA—tetrapods

This taxon, of about 30,500 extant species, includes the amphibians, mammals, reptiles, and birds, along with their many fossil relatives. The earliest known tetrapod fossils, such as †*Acanthostega* and †*Ichthyostega*, had well-developed limbs complete with digits (six to eight digits per limb, rather than five) instead of paired fins, yet they were aquatic. Additional characters proposed by Cloutier and Ahlberg (1996) are: paired nasals meeting in the skull midline; extrascapulars absent; opercular and subopercular bones absent; lateral gular absent.

Clack (2000) reviewed what was known to that date of the transition of tetrapods from water to land. Tetrapods appear in the fossil record in the Late Devonian. The most complete skeletons of aquatic or semi-aquatic Devonian tetrapods are from eastern Greenland.

Subclass ACTINOPTERYGII—ray-finned fishes

Scales ganoid, cycloid, or ctenoid (scales absent in many groups); spiracle usually absent; pectoral radials (actinosts) attached to the scapulocoracoid complex except in Polypteriformes; interopercle and branchiostegal rays usually present; gular plate usually absent; internal nostrils absent; nostrils relatively high up on head. The condition of the neural spines shows basic differences within the actinopterygians. In chondrosteans, some taxa possess paired neural spines throughout the vertebral column, the assumed primitive state; others, including *Polypterus*, have median neural spines in the caudal region; most teleosts have median neural spines anteriorly.

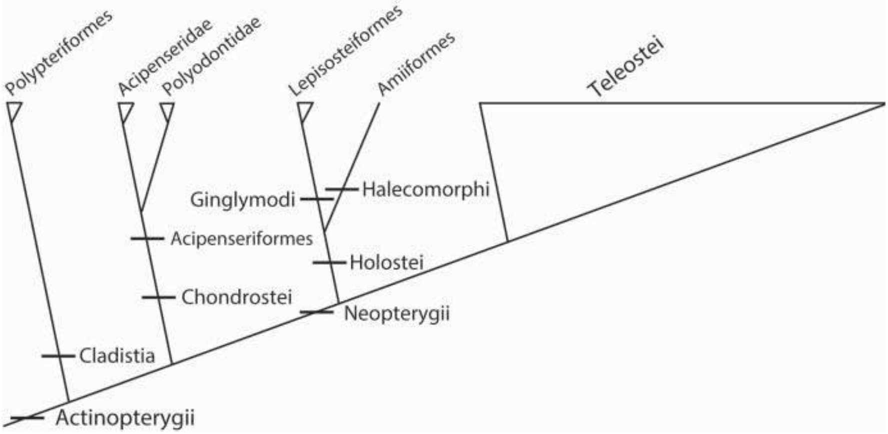
The subclass Actinopterygii, one of the major vertebrate taxa, is not diagnosed by strong derived character sets, but is nevertheless thought to be monophyletic. The earliest fossil remains are of scales of the Late Silurian †*Andreolepis*, †*Ligulalepis*, †*Naxilepis*, †*Lophosteus*, and †*Orvikuina*; in addition, there is Devonian material of, for example, †*Cheirolepis*, †*Dialipina* (see above), †*Howqualepis*, †*Limnomis*, and †*Moythomasia* (see, e.g., Choo, 2015). There is an Early Devonian endocranium of a specimen tentatively assigned to the actinopterygian genus †*Ligulalepis* (Basden and Young, 2001), and abundant

Carboniferous material of, for example, †*Aesopichthys,* †*Cyranorhis,* †*Discoserra,* †*Guildayichthys,* †*Kalops,* †*Melanecta,* †*Mesopoma,* †*Mimia,* †*Proceramala,* †*Wendyichthys,* and †*Woodichthys* (Cloutier and Arratia, 2004). Photographs and descriptions of many fossil taxa are given in Frickhinger (1991). Many of the above genera have not been satisfactorily classified in families and orders. A recent discovery (Giles, Darras et al., 2015) is of the complete skull including braincase and branchial arches of a Late Devonian actinopterygian from France, †*Raynerius.*

Actinopterygii are the sister taxon of the Sarcopterygii. We infer that at some time there was a common ancestor of both of these major lineages, and there are some interesting fossils, such as †*Psarolepis,* that show combinations of actinopterygian and sarcopterygian characters (Cloutier and Arratia, 2004; Zhu and Yu, 2004). Genera *incertae sedis* include the Cretaceous †*Diplospondichthys,* known from the same locality as the acanthomorph †*Spinocaudichthys* (Filleul and Dutheil, 2004).

Actinopterygian relationships were reviewed by Lauder and Liem (1983). The early diversification of actinopterygians was examined by Cloutier and Arratia (2004), who gave a historical review of previous phylogenetic hypotheses. Springer and Johnson (2004) produced a monograph with anatomical drawings and insights into the relationships of teleostome fishes, with emphasis on the Actinopterygii and especially the acanthomorphs.

A major problem in understanding actinopterygian phylogeny is that we still have much to learn about the homologies of various characters (Cloutier and Arratia, 2004). Much work is needed in studying fossils in a phylogenetic context and in knowing more about the origin and development of characters.



Phylogeny of the main extant groups of Actinopterygii.

Actinopterygians are recognized here with three subclasses, 67 orders, 469 families, 4,440 genera, and about 30,500 species. About 44% of the species are known only or almost only from fresh water.

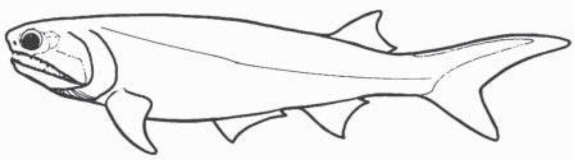
There are many fossil actinopterygian taxa, and many of those belong to the stem group (as opposed to crown-group Actinopterygii). The arrangement of stem-group fossil actinopterygians given by Cloutier and Arratia (2004) is largely followed here. There is typically a comb-like branching pattern of these fossil taxa, with each listed order being approximately the sister to all those following. However, beyond that approximation, no strictly phylogenetic classification is attempted or intended.

Three taxa that have sometimes been included as very primitive stem actinopterygians (†*Lophosteus*, †*Andreolepis*, and †*Dialipina*) were listed earlier (see above) as possible stem-group osteichthyans.

†Family HAPLOLEPIDAE. (with two Pennsylvanian genera, †*Haplolepis* and †*Pyritocephalus*) is an early family not otherwise classified here.

†Coccolepis. The morphology of †*Coccolepis bucklandi*, an *incertae sedis* form, was described by Hilton et al. (2004).

†Order CHEIROLEPIDIFORMES. Devonian. One family, the Devonian †Cheirolepididae with one genus, †*Cheirolepis*.



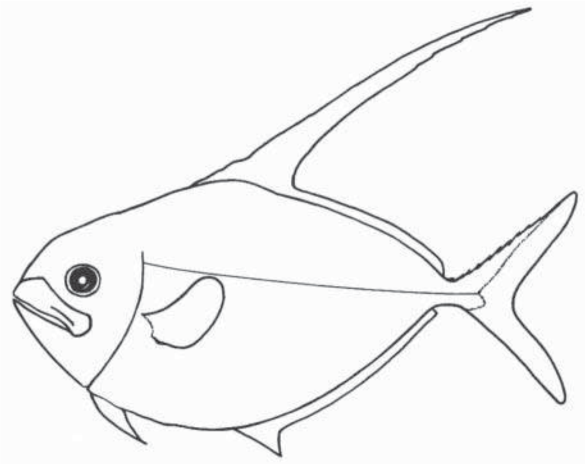
One of its species, †*C. canadensis*, may hold the record for having the largest number of pelvic fin rays, up to 124 (Arratia and Cloutier, 1996). This taxon is highly important because it is well studied and is regarded as the sister group for all remaining actinopterygians (e.g., Cloutier and Arratia, 2004; Swartz, 2009; Zhu et al., 2009; Friedman, 2015; Choo, 2015).

†Order PALAEONISCIFORMES. This group is almost certainly a paraphyletic assemblage of primitive actinopterygians. In many primitive palaeoniscids, the cheekbones form a solid unit (the maxilla, preopercles, and suborbitals are firmly united), the hyomandibula is oblique, the eyes are large and far forward, and the tail is strongly heterocercal. More advanced forms had a hyomandibula in the vertical plane and a breakup of the cheekbones. This permitted more flexibility in the oral-branchial chamber. The dorsal lobe of the tail became reduced to an abbreviated heterocercal tail. Numerous other evolutionary trends can be noted in proceeding from the chondrostean level of organization to the holostean level.

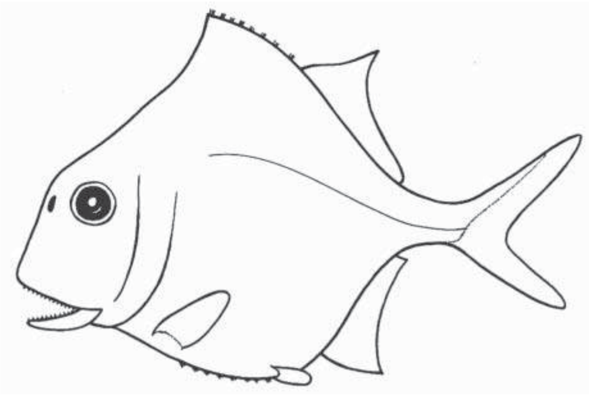
The problematic relationships in this complex and diverse group were addressed by Cloutier and Arratia (2004) and by Mickle (2012, 2013). Families or genera placed in this heterogeneous group include †Aeduellidae, †Acrolepidae (with, for example, †*Acrolepis* and possibly †*Boreosomus* and †*Pteronisculus*), †Amblypteridae (†*Amblypterus* and †*Paramblypterus*) (Dietze, 2000), †Birgeriidae (e.g., †*Birgeria*), †*Canobius*, †Commentryidae, †Elonichthyidae, †Palaeoniscidae, †Pygopteridae, †Rhabdolepidae (includes the Devonian †*Osorioichthys*), †Rhadinichthyidae and the related †Aesopichthyidae (Poplin and Lund, 2000; Cloutier and Arratia, 2004), and †Stegotrachelidae (with, e.g., the Devonian †*Stegotrachelus* and †*Tegeolepis*) (e.g., Mickle, 2012).

†Order DORYPTERIFORMES. Body deep and mostly scale-less; pelvic fin in front of pectorals (jugular); caudal peduncle very narrow. One family.

†Family DORYPTERIDAE. One Late Permian genus, †*Dorypterus*.



†Order PLATYSOMIFORMES. Mississippian to Early Triassic, worldwide, marine and fresh water. Body deep and compressed. Two families.



†Family PLATYSOMIDAE. Mississippian to Triassic; e.g., †*Chirodus* (sometimes classified in the family †Chirodontidae), †*Paranaichthys*, †*Platysomus* (e.g., Dias, 2012).

†Family BOBASATRANIIDAE. Early Triassic; e.g., †*Bobasatrania*, known from Canada, Greenland, Madagascar, and Switzerland.

†Order TARRASIIFORMES. Mississippian. Dorsal and anal fins continuous with the diphycercal caudal fin; pelvic fins absent; scales variously reduced or absent; body elongate; pectoral fins with a rounded fleshy lobe; frontal bones distinct (e.g., Taverne, 1996). One family.

†Family TARRASIIDAE. Mississippian; e.g., †*Palaeophichthys*, †*Tarrasius*. Sallan (2012) commented on the tetrapod-like regionalization of the axial skeleton in †*Tarrasius*.

†Order GUILDAYICHTHYIFORMES. Mississippian. One family.

Lund (2000) found in a cladistic analysis a stable sister group relationship between *Polypterus* and the †Guildayichthyiformes as a highly derived group within the Paleozoic Actinopterygii, and he rediagnosed the Cladistia as a superorder to reflect this relationship. However, we here follow the placement of Cloutier and Arratia (2004), reflecting a close relationship between the †Tarrasiidae and the †Guildayichthyidae.

†Family GUILDAYICHTHYIDAE. Mississippian, marine. Highly compressed, discoidal bodies, tall rhombic "ganoid" scales with peg-and-socket joints.

Two genera, †*Guildayichthys* and †*Discoserra*, from Montana (Lund, 2000).

†Order PHANERORHYNCHIFORMES. Pennsylvanian. One family.

†Family PHANERORHYNCHIDAE. Pennsylvanian. Body superficially like that of a sturgeon. One genus, †*Phanerorhynchus*.

†Order SAURICHTHYIFORMES. Permian to Jurassic. One family.

†Family SAURICHTHYIDAE. Permian to Jurassic. Body elongated, median fins far posteriorly, jaws long and anteriorly pointed; e.g., †*Acidorhynchus* (synonyms †*Belonorhynchus* and †*Saurorhynchus*) and †*Saurichthys*.

THE FOLLOWING TAXA are often referred to as subholosteans:

†Order REDFIELDIIFORMES. Triassic and Early Jurassic, fresh water. Body fusiform; mouth terminal or subterminal; dorsal and anal fins positioned far back, opposite one another, and with fin rays more numerous than radials; branchiostegal rays reduced to one or two plate-like bones; single external naris surrounded by a distinctive "premaxilla," rostral, nasal, and adnasal bones.

About 15 genera, herein treated as belonging to one family.

†Family REDFIELDIIDAE. Triassic to Jurassic; e.g., †*Brookvalia*, †*Dictyopyge*, †*Helichthys*, †*Redfieldius*, and †*Schizurichthys*.

†Order PTYCHOLEPIDIFORMES. Triassic to Jurassic. One family.

†Family PTYCHOLEPIDIDAE. Triassic to Jurassic; e.g., †*Boreosomus*, †*Ptycholepis*.

THE FOLLOWING FOUR ORDERS may represent stem-group Neopterygii rather than stem-group Actinopterygii (e.g., Xu et al., 2015).

†Order PHOLIDOPLEURIFORMES. Triassic. One family.

†Family PHOLIDOPLEURIDAE. Triassic; e.g., †*Australosomus*, †*Pholidopleurus*.

†Order PERLEIDIFORMES. Triassic. Perhaps five families.

†Family CEPHALOXENIDAE. Triassic; e.g., †*Cephaloxenus*.

†Family CLEITHROLEPIDIDAE. Triassic; e.g., †*Dipteronotus*.

†Family COLOBODONTIDAE. Triassic; e.g., †*Colobodus*, †*Procheirichthys*.

†Family PERLEIDIDAE. Triassic; e.g., †*Perleidus,* †*Endennia*.

†Family PLATYSIAGIDAE. Triassic; e.g., †*Helmolepis*.

†Order LUGANOIFORMES. Triassic. One family.

†Family LUGANOIDAE. Triassic; e.g., †*Luganoia*.

†Order PERLEIDIFORMES. Triassic and Early Jurassic. Example families placed in this probably artificial/paraphyletic group are †Cephaloxenidae, †Colobodontidae, †Platysiagidae (e.g., Neuman and Mutter, 2005), †Peltopleuridae, †Cleithrolepidae, and †Perleididae (e.g., †*Aetheodontus*, †*Dipteronotus*, and †*Meridensia*, e.g., Tintori, 1990; Bürgin, 1992). Tintori and Sassi (1992) provided evidence for a sequenced ranking of †*Australosomus*, †Peltopleuriformes (with †*Peltopleurus*, †*Habroichthys*, and †*Thoracopterus*, the latter placed in the family †Thoracopteridae and thought to be capable of gliding), †*Cleithrolepis*, †*Perleidus*, †*Luganoia*, and the Neopterygii (see below). Xu et al. (2015) placed many of these as stem-group Neopterygii in their revision of the Triassic †*Plesiofuro*, which they did not assign to a family. Further studies on members placed here include those of Bürgin (1996), Lombardo and Tintori (2004), and Mutter (2004).

ALL OF THE REMAINING TAXA are members of the crown-group Actinopterygii.

Infraclass CLADISTIA

Order POLYPTERIFORMES (Brachiopterygii) (19)—bichirs. This taxon has in the past been thought by some workers to be a member of the Sarcopterygii or at least to be more closely related to them than to the Actinopterygii; they are regarded here as the sister group of all other actinopterygians. This latter view has some support from Britz and Bartsch (2003) and possibly Venkatesh et al. (2001).

Family POLYPTERIDAE (63)—bichirs. Freshwater; Africa.

Rhombic ganoid scales; spiracular opening large but canal lost; dorsal fin consisting of 5–18 finlets, each with a single spine to which is attached one or more soft rays; pectoral fin rays supported by numerous ossified radials which attach to a cartilaginous plate and two rods, thence to the scapula and coracoid; a pair of gular plates, no branchiostegals; maxilla firmly united to skull; intestine with spiral valve; lungs partially used in respiration; vertebrae with ossified centra and neural canal. Maximum length about 90 cm, most species less than 30 cm.

Polypterids have many primitive characters that are unknown in other living Actinopterygii and many autapomorphies (Britz and Johnson, 2003). Among the latter, they have only four rather than the usual five gill arches. Of various hypotheses concerning the homology of the posterior-most arch of polypterids, Britz and Johnson (2003) make a convincing argument that it represents the fourth arch of other Actinopterygii and that the fifth arch is absent. Britz and Bartsch (2003) discussed rib homology in gnathostomes and the unique rib type of polypterids.

Suzuki et al. (2010) completed a phylogeny of bichirs based on mtDNA. Near et al. (2014) concluded that modern species of polypterids diversified in the Neogene even though the Cladistia are very old. Graham et al. (2014) studied spiracular air breathing in polypterids and found that up to 93% of their air breaths involved spiracular breathing. *Erpetoichthys* and *Polypterus* have achieved body elongation not by the usual addition of caudal segments but by adding abdominal vertebrae, leading Ward and Kley (2012) to compare anteroposterior positioning of their internal body organs.

Two genera with at least 14 extant species. In addition, there are fossils in Africa as old as mid Cretaceous and, perhaps, from the Late Cretaceous and Early Paleocene in South America (e.g., †*Dagetella,* †*Latinopollis*—a replacement name for †*Pollia,* †*Sainthilairia,* and †*Serenoichthys*) (references to studies of fossils and extant forms, other than those already given, include Gayet et al., 1995; Dutheil, 1999; Murray, 2000; Stewart, 2001; and Gayet et al., 2002).

Erpetoichthys (synonym *Calamoichthys*) *calabaricus* (reedfish or ropefish). Body eel-like; pelvics absent. The single species is confined to coastal areas adjacent to the Gulf of Guinea.

Polypterus (bichirs). Body elongate; pelvics present. At least 13 species (e.g., Gosse, 1988; Hanssens et al., 1995; Daget et al., 2001; Britz, 2004a). There is need for a revision to determine how many of the additional nominal species might be valid. Britz (2004a) named a new species of *Polypterus, P. teugelsi.* Schliewen and Schäfer (2006) described the new species *P. mokelembembe.*

Infraclass CHONDROSTEI

Palatoquadrates with anterior symphysis; gill arch dentition confined to first two hypobranchials and upper part of first arch; interhyal hypertrophied; preopercular canal in a series of ossicles, mandibular canal short or absent; body scaling reduced to tiny isolated elements.

The classification differs slightly from Grande and Bemis (1991) in that Chondrosteidae were included as a separate suborder within Acipenseriformes by those authors.

†Order CHONDROSTEIFORMES. Jurassic. One family. The chondrosteids are considered to be the primitive sister group of the Acipenseriformes (Grande and Bemis, 1991, 1996).

†Family CHONDROSTEIDAE. Jurassic of Europe. Mouth subterminal, anterior part of palatopterygoid club shaped, trunk scales completely absent, vertebral and supraneural elements extremely reduced or lost. Two genera, †*Chondrosteus* (1 species) and †*Strongylosteus* (1 species), and perhaps †*Gyrosteus*.

Order ACIPENSERIFORMES (20)—paddlefishes and sturgeons. Opercle lost; autogenous branchiostegal rays reduced in number to one-three (†*Chondrosteus* has 8-10); endocranium with extensive rostrum; rostrum with median ventral bony keel (Grande and Bemis, 1991). Additional traits mostly primitive include: caudal fin heterocercal; gulars absent; skeleton largely cartilaginous; fin rays more numerous than their basals; intestine with spiral valve.

Extant representatives in two families with six genera and 27 species (Grande and Bemis, 1996; Bemis et al., 1997).

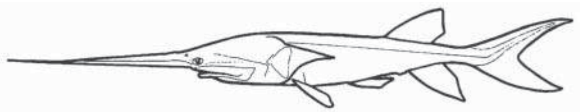
†Suborder Peipiaosteiformes. Extinct relatives of sturgeons and paddlefishes.

†Family PEIPIAOSTEIDAE. *Incertae sedis.* Two or more genera, †*Peipiaosteus* and †*Stichopterus*, and probably †*Spherosteus* and †*Yanosteus*, extending back to the Late Jurassic (Grande and Bemis, 1996; Bemis et al., 1997).

Suborder Acipenseroidei. Opercle lost, gill cover made up primarily by the subopercle; one to three elements that may be homologous to the branchiostegal rays of other actinopterygians; endocranium with an extensive rostrum.

Peng et al. (2007) estimated the age and biogeography of major clades of sturgeons and paddlefishes.

Family POLYODONTIDAE (64)—paddlefishes. Freshwater, rarely brackish; China and United States.



Small stellate bones making up lateral supports for paddle; series of elongate dorsal and ventral median rostral bones (Grande and Bemis, 1991). Additional characters: body lacking the large scutes of acipenserids but with small "scales" in some regions, such as the caudal peduncle and caudal fin, and large *Psephurus* with trunk "scales"; minute barbels on snout; gill rakers long and in the hundreds and widely gaping jaws in the plankton-feeding *Polyodon* (shorter and fewer in number with small protrusible jaws in all other paddlefish genera); teeth minute; spiracle present; gill cover greatly produced posteriorly. Maximum length perhaps up to 3 m, attained in *Psephurus gladius.* Chromosome number diploid or tetraploid (see below for differences in Acipenseridae; Peng et al. 2007; Crow et al., 2012). Grande and Bemis (1991, 1996) and Grande et al. (2002) described and reviewed this family and its included taxa.

†SUBFAMILY PROTOSEPHURINAE. Pelvic fin spine present; three or four branchiostegal elements present; small opercle present; other diagnostic characters in Grande et al. (2002). One genus, †*Protopsephurus* (Early Cretaceous, China, the oldest and most primitive paddlefish known and sister to all other members; Grande et al. 2002).

SUBFAMILY POLYODONTINAE. Pelvic fin spine absent; only a single branchiostegal element; opercle lost, subopercle forming the main gill-cover bone; subopercle with well-developed elongate spine-like projections forming a strongly serrated posterior margin (Grande and Bemis, 1991).

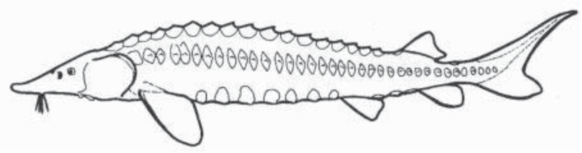
The fossil and living species of Polyodontinae were described in detail by Grande and Bemis (1991) (as Polyodontidae). There are two living species.

Polyodon spathula. Paddlefish. United States (Mississippi drainage). Plankton-feeding, with a nonprotrusible mouth. Crow et al. (2012) reported that an independent whole-genome duplication occurred in the lineage of the American Paddlefish.

Psephurus gladius. Chinese Paddlefish. China (Yangtze River and lower reaches of some other rivers and adjacent sea). Piscivorous, with a protrusible mouth.

Fossil taxa are †*Paleopsephurus* (Early and Late Cretaceous, fresh water, Montana and Wyoming, and considered to be the primitive sister group to the remaining polyodontid taxa), †*Crossopholis* (early Eocene, freshwater, Wyoming, and the sister group to *Polyodon*), and †*Polyodon tuberculata* (early Paleocene, freshwater, Montana).

Family ACIPENSERIDAE (65)—sturgeons. Anadromous and fresh water; Northern Hemisphere.



Five rows of bony scutes or plates on body; mandibular sensory canal lost entirely; pectoral fin with anterior spinous ray made up of fused rays (Grande and Bemis, 1991). Additional traits include: four barbels in front of mouth; mouth inferior and protrusible; gill rakers fewer than 50; teeth absent in adults; swimbladder large. The freshwater Kaluga, *Huso dauricus,* and the anadromous Beluga, *H. huso,* are among the largest if not the largest fish in fresh water. The latter definitely reaches 4.2 m, and longer lengths have been reported for both species.

According to Birstein et al. (1997) and Peng et al. (2007), the chromosome number is highly variable. In addition to diploid species with 110–130 chromosomes, many other sturgeons are tetraploid, with one, *Acipenser mikadoi,* having about 500 chromosomes.

The historical biogeography of sturgeons was explored by Choudhury and Dick (1998). Dillman et al. (2007) completed a mtDNA study of phylogeny of Scaphirhynchinae and other sturgeons, supporting the monophyly of *Pseudoscaphirhynchus* and *Scaphirhynchus,* but did not find them to be each other's closest relatives. Neither Dillman et al. (2007) nor Birstein et al. (2002) recovered clades consistent with the morphologically recognized subfamilies and tribes (see below). *Acipenser* itself was recovered as paraphyletic by both studies. The type species of *Acipenser, A. sturio,* was found to be the sister group of all other extant sturgeons by Dillman et al. (2007), but not by Birstein et al. (2002).

Four extant subfamilies with four genera and 25 species (Bemis et al., 1997; Birstein and Bemis, 1997). Many of the species are difficult to identify. Two fossil genera, the Late Cretaceous †*Protoscaphirhynchus* from Montana and the Late Cretaceous †*Priscosturion* also from Montana (originally named †*Psammorhynchus,* a name later found to be preoccupied by a flatworm). †*Proscosturion* was placed in its own subfamily by Grande and Hilton (2006, 2009).

SUBFAMILY ACIPENSERINAE. One genus, *Acipenser.* Northern Hemisphere. Gill membranes joined to isthmus, mouth transverse. Seventeen species, five of which occur in North America (Grande and Bemis, 1996; Bemis et al., 1997; Hilton et al., 2011). Birstein et al. (2005) argue for unrecognized species diversity in the Caspian Sea area.

In the previous edition, there were two tribes, with *Scaphirhynchus* and *Pseudoscaphirhynchus* in a second tribe. Those two genera are now in separate subfamilies (Hilton et al., 2011).

SUBFAMILY SCAPHIRHYNCHINAE. One genus, *Scaphirhynchus.* Mississippi basin. Caudal peduncle long, depressed, and completely armored. Three species.

SUBFAMILY PSEUDOSCAPHIRHYNCHINAE. One genus, *Pseudoscaphirhynchus.* Aral Sea and its drainage. Caudal peduncle short, slightly depressed, and not completely armored. Three species.

Subfamily Husinae. One genus, *Huso.* Adriatic Sea to Caspian Basin; Amur River. Gill membranes joined to one another, mouth crescentic. Two species.

NEOPTERYGII

This clade, unranked here, is characterized by: fin rays equal in number to their supports in dorsal and anal fins; premaxilla with internal process lining the anterior part of nasal pit; symplectic developed as an outgrowth of hyomandibular cartilage. In addition, the spermatozoa of neopterygians has lost a plesiomorphic feature of vertebrates—the acrosome (several species, however, have acrosome-like structures) (Jamieson, 1991).

It is generally agreed that the neopterygian fishes (Holostei including both gars and bowfins, plus Teleostei) are a monophyletic group. Their fossil record may extend as far back as the Late Permian if †*Acentrophorus* is a stem neopterygian. See above for additional taxa suggested by some to be stem neopterygians.

The next order is of uncertain placement as to infraclass within Neopterygii despite significant interest in its relationships (e.g., Poyato-Ariza and Wenz, 2002; Nursall, 2010).

†Order PYCNODONTIFORMES. Late Triassic to Eocene. This group of reef- or lagoon-dwelling fishes with crushing (durophagous) dentition lived primarily around the Tethys Sea and its extensions as the Atlantic opened during the Jurassic. Well-known fossil sites such as the Eocene Monte Bolca site in northern Italy and the Late Jurassic Solnhofen site in southern Germany have added many of the specimens. Nursall (1996) and Poyato-Ariza and Wenz (2002) presented phylogenetic analyses of the pycnodontiforms and a revised taxonomy.

The families recognized in recent literature are †Gibbodontidae, †Gyrodontidae (e.g., †*Gyrodus*), †Mesturidae, †Brembodontidae, †Pycnodontidae (with several subfamilies such as †Nursalliinae and †Proscinetinae), †Coccodontidae (with †*Coccodus* the only benthic member of the order), †Hadrodontidae, and †Trewavasiidae (Nursall, 1996, 1999a,b; Kriwet, 1999, 2004b; Poyato-Ariza and Wenz, 2002, 2004).

Infraclass HOLOSTEI (gars, bowfins, and relatives)

Grande (2010), in a morphological study of gars and their close relatives, advocated recognition once again of the Holostei, a taxon containing both Lepisosteiformes and Amiiformes and the sister group of the teleosts; this group had fallen out of favor, but its revival is also in agreement with several recent broad-scale molecular phylogenies (e.g., Near et al., 2012a; Broughton et al., 2013). One result of this rearrangement is that a major clade recognized in the previous edition, the Halecostomi, combining the Teleostei with the

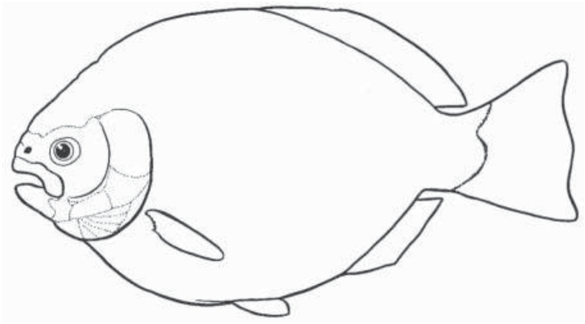
Halecomorphi (bowfins and fossil relatives, but without the gars), is no longer recognized as valid.

Division GINGLYMODI

This group includes gars (Lepisosteiformes) along with fossil relatives such as the †Semionotiformes and †Macrosemiiformes. Grande (2010) made a detailed study of gars and their relatives, placing the Ginglymodi once again within the Holostei that includes also the living bowfin *Amia calva.* López-Arbarello (2012) produced a phylogenetic analysis of Ginglymodi and concluded that there were two main clades, one containing macrosemiiforms plus semionotiforms, and the other containing lepisosteiforms. Two more recent phylogenetic studies are those of Thies and Waschkewitz (2015) and Gibson (2013b).

†Order DAPEDIIFORMES. Late Triassic to Late Jurassic. Thies and Waschkewitz (2015) erected this order to include the single family Dapediidae. The relationships of the order are in doubt as it might belong within Ginglymodi as Thies and Waschewitz concluded and as listed here, or in Halecomorphi, or be sister to both.

†Family DAPEDIIDAE. Body deep to nearly circular in outline; circumorbital bones including infraorbitals and suborbitals; vertical arm of preopercular variably covered by suborbitals; dorsal and anal fins long; gular present. Late Triassic to Early Jurassic; in marine and freshwater deposits; North America, Europe, and India.



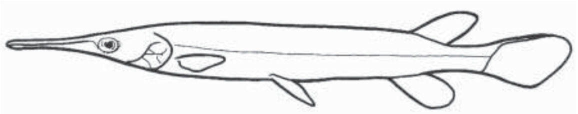
Genera include †*Dapedium* (†*D. pholidotum* was redescribed by Thies and Waschkewitz, 2015), †*Hemicalypterus*, †*Heterostrophus*, †*Paradapedium*, †*Sargodon*, and †*Tetragonolepis* (e.g., Thies and Hauff, 2011).

Order LEPISOSTEIFORMES (21)—gars. One extinct and one extant family.

The following genera, formerly in †Semionotiformes, belong within Lepisosteiformes according to López-Arbarello (2012): †*Araripelepidotes*, †*Isanichthys*, †*Lepidotes*, †*Pliodetes*, and †*Sheenstia.*

†Family OBAICHTHYIDAE. Early Cretaceous of Brazil, e.g., †*Obaichthys*, with two species (Brito et al., 2000). The family was named by Grande (2010).

Family LEPISOSTEIDAE (66)—gars. Freshwater, occasionally brackish, very rarely in marine water; eastern North America, Central America (south to Costa Rica), and Cuba.



Body and jaws elongate; mouth with needle-like teeth; abbreviated heterocercal tail; heavy ganoid scales, about 50–65 along lateral line; dorsal fin far back, with few rays; three branchiostegal rays; interoperculum absent; two or more supratemporal bones on each side; maxilla small and immobile; supramaxilla absent; myodome absent; vomer paired; swimbladder vascularized (thus permitting aerial respiration); vertebrae opisthocoelous (anterior end convex, posterior end concave, as in some reptiles and unlike all other fish except the blenny *Andamia*).

The heavily armored predaceous gars usually occur in shallow, weedy areas. Maximum length about 3.0 m, attained in *Atractosteus spatula.*

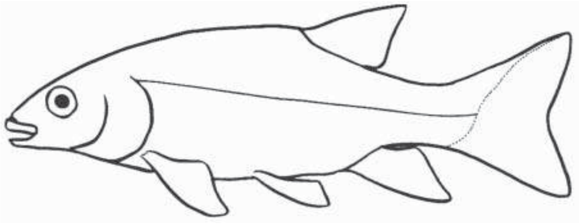
The northernmost limit is reached by *Lepisosteus osseus* in southern Quebec; the southernmost limit is reached by *A. tropicus* in Costa Rica. This is also the only species that ranges to Pacific slope drainages (from southern Mexico to Honduras). *Atractosteus tristoechus* is known to enter marine water around Cuba and the Isle of Pines.

Two genera, *Lepisosteus* and *Atractosteus*, with seven species (e.g., Nelson et al., 2004, which lists six of the seven). Grande (2010) reviewed the fossil and extant gars. *Lepisosteus* has four species, with about 14–33 small, pear-shaped gill rakers, and *Atractosteus* has three species, with about 59–81 large, laterally compressed gill rakers. Fossil species (primarily Cretaceous and Eocene) of *Lepisosteus* are known from North America, South America, Europe, and India (extant species are restricted to North America); fossil species of *Atractosteus* are known from North America, South America, Europe, and Africa (extant species are restricted to North America, Cuba, and Central America). There are several fossil genera, e.g., †*Cuneatus,* †*Dentilepisosteus,* †*Masillosteus,* †*Obaichthys,* and †*Oniichthys* (e.g., Micklich and Klappert, 2001; Grande, 2010).

†Order SEMIONOTIFORMES. Triassic to Cretaceous. Extant gars and the fossil †Semionotidae were sometimes recognized in the same order, either under the ordinal name Lepisosteiformes or Semionotiformes (e.g., Nelson, 1976, 1994). In contrast, Nelson (1984) placed them in separate orders and we do so now following the scholarly and highly detailed work of Grande and Bemis (1998) and Grande (2010).

†***Sangiorgioichthys.*** This Triassic genus from Europe and China was previously in †Semionotidae but is now *incertae sedis* in Semionotiformes according to López-Arbarello et al. (2011).

†Family SEMIONOTIDAE (Lepidotidae). Dorsal ridge scales present; epiotic with a large posteriorly directed process; mouth small; body fusiform; dorsal and anal fins short. Triassic to Cretaceous.



Composition of this family was reduced to the single genus †*Semionotus* by López-Arbarello (2012). Soon after, Gibson (2013a,b) added the new genus †*Lophionotus* as sister to †*Semionotus.*

†Family CALLIPURBECKIDAE. Late Triassic to Early Cretaceous. This family was named by López-Arbarello (2012) to contain genera previously in †Semionotidae.

Genera include †*Callipurbeckia,* †*Macrosemimimus,* †*Paralepidotus,* †*Semiolepis,* †*Tlayuamichin*; e.g., Tintori (1996), López-Arbarello and Alvarado-Ortega (2011), López-Arbarello (2012), Gibson (2013).

†Order MACROSEMIIFORMES. Jurassic and Cretaceous; one family. Arratia and Schultze (2012) named the *incertae sedis* macrosemiiform †*Voelklichthys.*

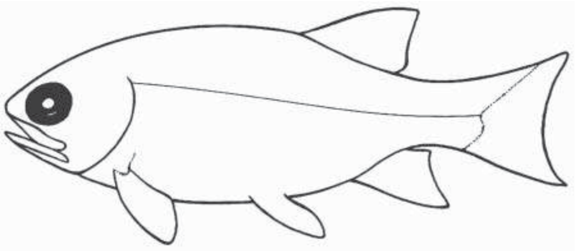
†Family MACROSEMIIDAE. Europe, Mexico, and North Africa.

Genera include †*Agoultichthys,* †*Enchelyolepis,* †*Histionotus,* †*Legnonotus,* †*Macrosemius,* †*Macrosemiocotzus,* †*Notagogus,* and †*Propterus* (González-Rodríguez et al., 2004; González-Rodríguez and Reynoso, 2004; Murray and Wilson, 2009).

Division HALECOMORPHI

Taxa that belong to or are related to this group, and placed in the Halecomorphi (then ranked as subdivision) in the work of Grande and Bemis (1998), include (with rankings of Grande and Bemis, 1998) order †Parasemionotiformes (†Parasemionotidae—includes †*Parasemionotus,* in figure below, and †*Watsonulus*), †Ionoscopiformes (†Ionoscopidae, †Oshuniidae, and †Ophiopsidae), and Amiiformes (†Caturidae, †Liodesmidae, †Sinamiidae, and Amiidae) (for more information see Maisey, 1991; Lambers, 1995; Grande and Bemis, 1998; Arratia, 2004).

†Order PARASEMIONOTIFORMES. This important group was diverse and widely distributed in the Triassic. Genera include †*Albertonia*, †*Ospia*, †*Parasemionotus*, and †*Watsonulus*.



†Order IONOSCOPIFORMES. Another diverse, widely distributed, and important group known from the Triassic, Jurassic, and Cretaceous, first recognized as an order by Grande and Bemis (1998). Genera include †*Ophiopsis*, †*Panxianichthys*, †*Placidichthys*, †*Quetzalichthys*, †*Robustichthys*, and †*Teoichthys* (e.g., Applegate, 1988; Brito, 2000; Alvarado-Ortega and Espinosa-Arrubarrena, 2008; Lane and Ebert, 2015).

Order AMIIFORMES (22)—bowfins. Ossified ural neural arches reduced to 2 or fewer; opisthotic bone lost; pterotic bone lost (Grande and Bemis, 1998). Most amiids were apparently fresh water, while most non-amiid amiiforms were marine. The following taxa are among those most closely related to the living Bowfin *Amia calva*.

†Suborder Caturoidei. Acrodin cap on larger jaw teeth sharply carinate; maxilla slender and rod-like; branchiostegals 22 or more per side; heamal spines broadly spatulate transversely; preural haemal and neural spines strongly inclined to nearly horizontal; paired block-like ural neural arch ossifications (Grande and Bemis, 1998). One family. †*Gymnoichthys* from the Triassic of China was originally described as a primitive neopterygian, but Tan and Jin (2013) argued that it is a primitive caturoid.

†Family CATURIDAE. Triassic to Cretaceous; e.g., †*Amblysemius*, †*Caturus*.

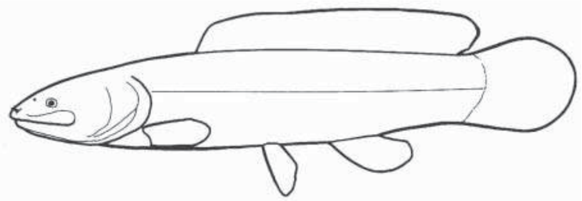
Suborder Amioidei. Posterior margin of caudal fin rounded; loss of fringing fulcra from median fins; reduced number of caudal fin rays articulating with each hypural (characters given for Sinamiidae plus Amiidae by Grande and Bemis 1998). Three families.

†Family LIODESMIDAE. Early Jurassic; e.g., †*Liodesmus*.

†Family SINAMIIDAE. Early Cretaceous. Single median parietal; three pairs of extrascapulars; dermopterotics short (Grande and Bemis, 1998). One or two genera, †*Sinamia* and its possible junior synonym †*Ikechaoamia*, with eight species (Peng et al., 2015).

Family AMIIDAE (67)—bowfins. The one extant species is freshwater; central North America.

Solid perichordally ossified, drum-shaped diplospondylous centra; occiput extending posterior to proximal ends of exoccipitals; anteriorly projecting spine-like processes on neural and or haemal arches; three or more lateral pits on each side of most centra (Grande and Bemis, 1998). Additional characters are: dorsal fin base long, with about 48 rays; large median gular plate and 10–13 branchiostegal rays; swimbladder can function as a lung; no pyloric caeca. Maximum length about 90 cm.



The only extant species is *Amia calva.* Fossil amiids are many (e.g., †*Amiopsis,* †*Calamopleurus,* †*Cratoamia,* †*Cyclurus,* †*Melvius,* †*Pachyamia,* †*Solnhofenamia,* and †*Vidalamia*) and known primarily from freshwater deposits of Cretaceous and Cenozoic age; the oldest fossils are of Jurassic age (Maisey, 1991; Grande and Bemis, 1998, 1999; Forey and Grande, 1998). There are also many extinct species of *Amia.* Recently described fossils include †*Cratoamia gondwanica* by Brito et al. (2008) and a Miocene species of *Amia* from Japan by Yabumoto and Grande (2013).

Four subfamilies are recognized by Grande and Bemis (1998), and that work should be consulted for further information (including the unusual biogeographical history of members of the subfamily †Vidalamiinae).

Division TELEOSTEOMORPHA

The Teleosteomorpha were named by Arratia (2001) to include all extant teleostean fishes plus all fossil taxa more closely related to extant teleosteans than to any other extant group of fishes. Thus, teleosteomorphs are a "total-group" taxon: they include all crown-group teleosteans plus all stem-group teleosteans. The crown-group teleosteans are named the Teleocephala (see below). The taxon Teleostei, also listed below, is neither a total-group nor a crown-group taxon but an apomorphy-based taxon, containing all fossil and extant teleosteomorphs that possess a particular suite of derived characteristics. The Teleostei defined this way include all teleocephalans plus some, but not all, of their stem-group fossil relatives.

†*Prohalecites* is the oldest stem teleost (i.e., the earliest fossil teleosteomorph) according to Arratia (2013); it is known from strata at the Middle/Late Triassic boundary.

†Subdivision ASPIDORHYNCHEI

This clade was proposed but not named by Arratia (2013) as the sister group of all other teleosteomorphs. The orthography of its name reflects its sister-group relationship to Subdivision Teleostei.

†Order ASPIDORHYNCHIFORMES. One family.

†Family ASPIDORHYNCHIDAE. Late Jurassic and Cretaceous. Body elongate with a long, slender snout; dorsal and anal fins opposite one another and placed posteriorly; interoperculum absent; maxillae free. Appearance superficially like needlefishes. Most were marine. Lengths up to 1 m were common. Brito (1999) presented strong evidence from the caudal skeleton that these fishes are in fact stem teleosts.

Four genera, †*Aspidorhynchus*, †*Belonostomus*, †*Jonoichthys*, and †*Vinctifer* (Maisey, 1991:170–89; Brito, 1999; Arratia, 2004, 2013; Gouiric-Cavalli, 2015).

†Order PACHYCORMIFORMES. One family. The morphology of pachycormiforms is poorly known and fragmentary. However, according to Friedman et al. (2010) and Arratia and Schultz (2013), the monophyly of the group is supported by several characters including a median rostrodermethmoid separating the premaxillary bones; pectoral-fin rays branched distally and with Y-type bifurcation; and a hypural plate.

†Family PACHYCORMIDAE. Early Jurassic to late Late Cretaceous; Europe, Cuba, and South America during the Jurassic; cosmopolitan as a family (e.g., †*Protosphyraena*) in Cretaceous seas.

Genera include †*Asthenocormus*, †*Bonnerichthys*, †*Euthynotus*, †*Hypsocormus*, †*Leedsichthys* (which reached an exceptionally large size and was likely a filter feeder; Liston et al., 2013), †*Notodectes*, †*Orthocormus*, †*Pachycormus*, †*Prosauropsis*, and †*Protosphyraena*, and †*Sauropsis* (e.g., Arratia and Lambers, 1996; Liston, 2004; Arratia, 2004; Friedman et al., 2010, 2013a; Arratia and Schultz, 2013; Liston, 2013; Gouiric-Cavalli and Cione, 2015).

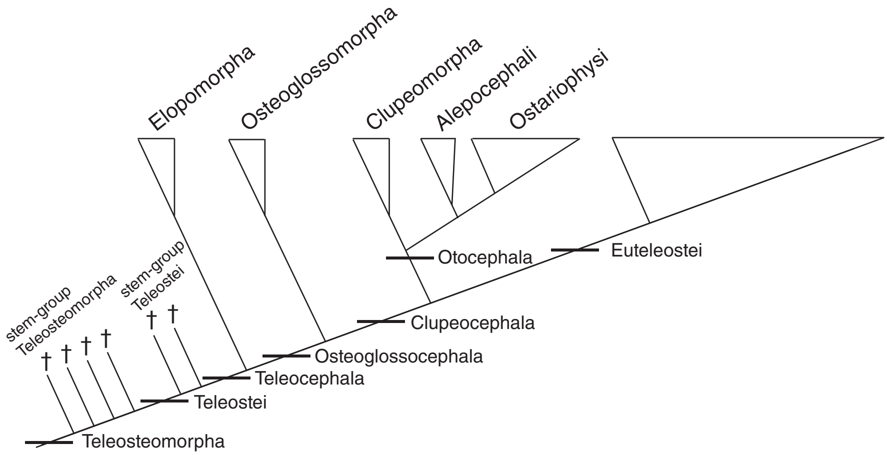
Subdivision TELEOSTEI

The monophyly of Teleostei is supported by both morphological (e.g., de Pinna, 1996a) and molecular evidence (e.g., Near et al., 2012a; Betancur-R. et al., 2013a). This is the group that is usually meant by the colloquial term "teleosts." The first modern classification of Teleostei was that of Greenwood et al. (1966). Patterson (1968) subsequently demonstrated that teleosts as defined on the basis of their caudal fin skeleton are a monophyletic group, and Patterson and Rosen (1977) defined the teleosts as a group of halecostomes with the ural neural arches elongated as uroneurals, basibranchial toothplates unpaired, and premaxilla mobile. In addition, Arratia and Schultze (1990) demonstrated that the teleost urohyal is distinctive, being formed as an unpaired ossification of the tendon of the sternohyoideus muscle.

A summary of some earlier work on teleost monophyly and boundaries was given by de Pinna (1996a), and a summary of more recent work can be found in Arratia (1997, 1999, 2004). At least 27 anatomical synapomorphies were found by de Pinna (1996a) to support monophyly of the total group, when defined as the most inclusive group of actinopterygians not including *Amia* and relatives (the Halecomorphi) and *Lepisosteus* and relatives (the Ginglymodi). Arratia has added much to our understanding of the basal members and their phylogeny (e.g., Arratia, 1997, 1999, 2004).

In the following classification, we present several groups of primitive fossil (stem-group) teleosts first. These are followed by the four lineages that include all living teleosts (the crown-group teleosts, collectively termed the Teleocephala by de Pinna, 1996a). The four groups of crown teleosts are treated here as cohorts, the Osteoglossomorpha, Elopomorpha, Otocephala (= Ostarioclupeomorpha), and Euteleostei. Contrary to Patterson and Rosen (1977), these four taxa are sequenced according to the sister-group relationships postulated by Arratia (1991), who found elopomorphs, rather than osteoglossomorphs, to be the sister group of all other crown-group teleosts. This change was originally made on the grounds that the caudal skeleton of *Elops* is more primitive than that of the osteoglossomorphs. Although this relationship was challenged by Patterson (1998) (see also the rebuttal by Arratia, 1998) as well as by the works of Filleul (2000), Inoue and Miya (2001), Inoue et al. (2003), Wang et al. (2003) and Broughton (2010), the detailed morphological work of Arratia (1997, 1999, 2004) plus the recent molecular studies of Near et al. (2012a, 2013), Betancur-R. et al. (2013a), and Broughton et al. (2013) further support the view that elopomorphs are the sister group of the others. This arrangement is also more consistent with the early appearance of elopomorphs in the fossil record (Arratia, 1997).

Teleosts probably arose in the Early or Middle Triassic, about 250–230 million years ago, shortly before the Late Triassic appearance in the fossil record of the first teleosts, the †Pholidophoridae (note that these are stem teleosts, even though they are the oldest in the apomorphy-based taxon Teleostei) in the Late Jurassic (Arratia, 2013). Teleosts have a rich fossil record (e.g., Patterson, 1993; Arratia, 1997, 1999, 2004). Several early fossil groups of uncertain relationships and not otherwise mentioned are given in Nelson (1994) and the above works of G. Arratia.

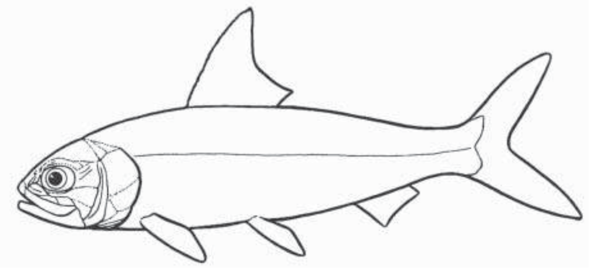


Phylogenetic relationships of the major groups of Teleostei discussed in the text and followed here.

Teleosts are the most species-rich and diversified group of all the vertebrates. They dominate in the world's rivers, lakes, and oceans. About 29,585 extant species, of which about 10% are new in the last ten years, comprising about 96% of all extant fishes, and placed in 63 orders, 469 families, and about 4,610 genera.

THE FOLLOWING FOSSIL ORDERS are stem-group teleosts arranged in approximate phylogenetic sequence.

†Order PHOLIDOPHORIFORMES. Late Triassic. Arratia (2013) recently reviewed the pholidophoriforms, and found a core monophyletic group with a single family, all members of which are Late Triassic in age.



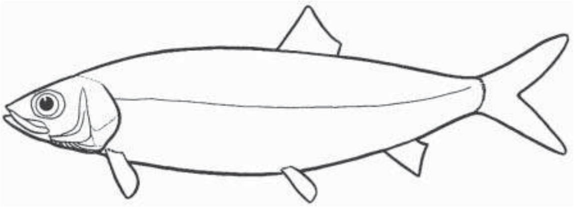
†Family PHOLIDOPHORIDAE. Marine, Late Triassic of Europe. This family was recently revised by Arratia (2013), and contains at least seven genera: †*Annaichthys*, †*Knerichthys*, †*Parapholidophorus*, †*Pholidoctenus*, †*Pholidophoretes*, †*Pholidophorus*, and †*Pholidorhynchodon*.

†Order DORSETICHTHYIFORMES. This order is named herein to include the single family †Dorsetichthyidae. Formerly thought to be part of the †Pholidophoriformes, it is more closely related to crown teleosts than that order but more basal than †Leptolepidiformes according to Arratia (2013).

†Family DORSETICHTHYIDAE. Early Jurassic, Britain. This family is named here to include the single genus and species †*Dorsetichthys bechei*, formerly classified in †*Pholidophorus* but assigned to a separate genus by Arratia (2013).

†Order LEPTOLEPIDIFORMES. Formerly a paraphyletic assemblage of primitive teleosts, this order is now restricted to one family with one genus and species (Arratia, 2013). Taxa formerly included are now placed as relatives of various other primitive teleostean groups.

†Family LEPTOLEPIDIDAE. Marine, Early Jurassic of Europe. There is now just a single genus and species, †*Leptolepis coryphaenoides*, in this family (e.g., Arratia, 2013), which formerly was a wastebasket for assorted primitive fossil teleosts.



†Order CROSSOGNATHIFORMES. This order contains fishes formerly classified separately, but now grouped together as stem Teleostei (e.g., Arratia and Tischlinger, 2010; Arratia, 2013).

†Family VARASICHTHYIDAE. Jurassic of South America; e.g., †*Bobbichthys*, †*Domeykos,* †*Luisichthys,* †*Protoclupea,* †*Varasichthys*.

†Family CROSSOGNATHIDAE. Cretaceous of Europe and North America. Two genera, †*Crossognathus*, †*Apsopelix*. Premaxilla very small; palatine without teeth and jaw teeth small; palatine very elongate.

†Family NOTELOPIDAE. Cretaceous of South America; one genus, †*Notelops*.

†Family PACHYRHIZODONTIDAE. Cretaceous to Paleogene of the Mediterranean region and North and South America. Antorbital lost or completely fused with the first infraorbital; never more than six hypurals. Ten genera including †*Aquilopiscis*, †*Elopopsis*, †*Goulmimichthys*, †*Greenwoodella*, †*Michin*, †*Nardopiscis*, †*Pachyrhizodus,* †*Platinx* (the only crossognathiform from Paleocene-Eocene), †*Rhacolepis*, and †*Tingitanichthys*.

†Order ICHTHYODECTIFORMES. Jurassic and Cretaceous. An endoskeletal ethmopalatine bone in floor of nasal capsule; uroneurals covering lateral faces of preural centra; anal fin long, usually with 24–37 rays and opposite the posteriorly situated dorsal fin of 10–18 rays. Most were marine and probably predators of other fishes. The predaceous †*Gillicus* reached 1.5 m, and †*Xiphactinus* reached at least 4 m. Maisey (1991) and Cavin et al. (2013) reviewed this order. We follow Cavin et al. (2013) for within-group relationships of ichthyodectiforms and Arratia and Tischlinger (2010) and Arratia (2013) for their systematic position currently as the sister group of crown teleosts.

†Family ALLOTHRISSOPIDAE. Jurassic and Cretaceous; e.g., †*Allothrissops,* †*Cooyoo,* †*Heckelichthys,* †*Occithrissops,* †*Thrissops,* and †*Unamichthys*. This family is a paraphyletic series of basal ichthyodectiforms according to Cavin et al. (2013), who declined to assign them to families. The family †Allothrissopidae is retained here until the family-level taxonomy is revised. The Middle Jurassic †*Occithrissops* (placed in its own family by Nelson, 2006) is the oldest known ichthyodectiform.

†Family CLADOCYCLIDAE. Cretaceous of Brazil, Italy, Lebannon and Morocco. e.g., †*Chirocentrites,* †*Chiromystus,* †*Cladocyclus*, and †*Eubiodectes* (e.g., Cavin et al., 2013; Berrell et al., 2014).

†Family SAURODONTIDAE. Cretaceous of Europe, North America and Middle East. e.g., †*Gillicus,* †*Prosaurodon,* †*Saurodon,* †*Saurocephalus*, and †*Vallecillichthys* (e.g., Cavin et al., 2013).

†Family ICHTHYODECTIDAE. Early to Late Cretaceous of North America, Europe, Africa. The name means "fish-biters"; e.g., †*Ichthyodectes,* †*Ghrisichthys,* †*Xiphactinus* (e.g., Cavin et al., 2013).

The following two genera are Jurassic stem-group teleosts that, although similar and both freshwater fishes, are of uncertain familial and ordinal relationships.

†*Luisiella.* from Argentina (Sferco et al., 2015).

†*Cavenderichthys.* from Australia (e.g., Bean, 2006).

The following two orders are of uncertain phylogenetic position within Subdivision Teleostei. They may be stem-group or crown-group teleosts.

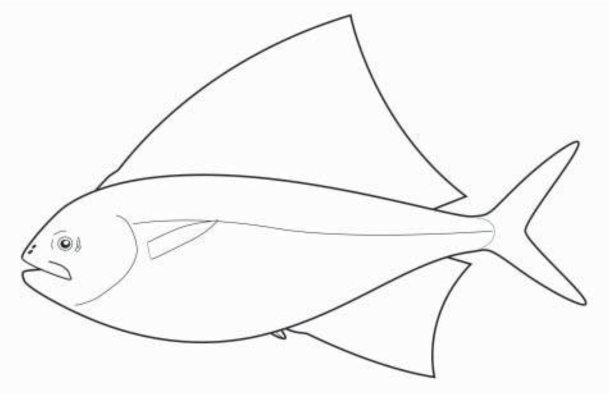
†Order TSELFATIIFORMES. Cretaceous. Body deep; mouth bordered by premaxilla and maxilla; dorsal fin extending along most of back; pectoral fins inserted high on body; pelvics absent or present with six or seven rays; caudal fin deeply forked with 18 principal rays; palate toothed; most fin rays unsegmented.

Much work on this group has been conducted by Taverne (e.g., Taverne, 2000). Taverne and Gayet (2004) placed tselfatiiforms in the Clupeocephala, but Forey et al. (2003) listed them as Elopomorpha. Their interrelationships require more study.

†Family Plethodidae (= Bananogmiidae) e.g., †*Plethodus*.

†Family Protobramidae e.g., †*Abisaadichthys*, †*Eusebichthys*, and †*Protobrama*.

†Family Tselfatiidae e.g., †*Tselfatia*.



†Order ARARIPICHTHYIFORMES. Early Cretaceous.

†Family ARARIPICHTHYIDAE. Early Cretaceous of Brazil, Mexico, Morocco, and Venezuela. Body deep; dorsal and anal fins with long base; pelvic fins and skeleton absent; pectoral fins attached low on body; caudal fin forked; teeth in jaws absent; premaxilla protractile and forming border of upper jaw; supramaxilla present; supraorbitals absent.

Maisey and Blum in Maisey (1991) did not find evidence to support earlier suggestions that †*Araripichthys* is an acanthopterygian or a beryciform, but note some similarities between this taxon and the lampriforms, a group of basal acanthomorphs. They also cast doubt on original reports that it had spiny fin rays. Maisey and Moody (2001) cast further doubt on an acanthomorph relationship for the genus. A fourth species was recently discovered in Mexico (Alvarado-Ortega and Brito, 2011).

One genus, †*Araripichthys*, with four species.

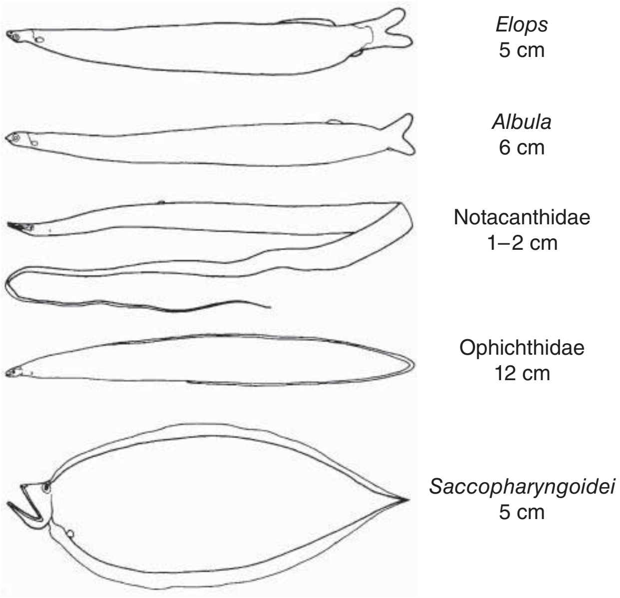
Supercohort TELEOCEPHALA—crown-group Teleostei

Teleocephala were named by Mario de Pinna (1996) in *Interrelationships of Fishes* and given supercohort rank by Wiley and Johnson (2010). There is a long-standing controversy about which clade of Teleocephala is sister to all others, the so-called “basal” clade. We accept the morphological (including fossil) evidence of Arratia (e.g., 2013), supported by some recent molecular studies (e.g., Near et al. 2012a, Betancur-R. et al., 2013a) that Elopomorpha, rather than Osteoglossomorpha, are the sister clade of all other Teleocephala.

Cohort ELOPOMORPHA

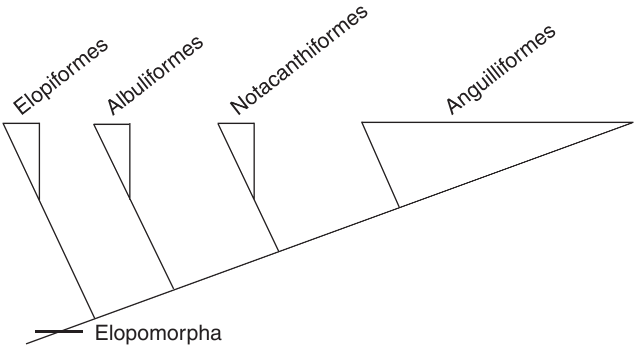
Elopomorpha as recognized here include four orders: Elopiformes (tenpounders), Albuliformes (bonefishes), Notacanthiformes (halosaurs and deep-sea spiny eels) and Anguilliformes (eels). The order Saccopharyngiformes previously recognized by, e.g., Nelson (2006) is now the suborder Saccopharyngoidei within the order Anguilliformes. As listed by Wiley and Johnson (2010) the Elopomorpha are diagnosed by: presence of a leptocephalus larva (ribbon-like, totally unlike the adult); prenasal ossicles present; sternohyoideus originating on the cleithrum; compound neural arch formed from a cartilage over the first preural and first ural centrum; unique spermatozoa and proximal centriole morphology (Greenwood et al., 1966; Forey, 1973; Arratia, 1996, 1997; Forey et al., 1996). Additional elopomorph characters include: swimbladder not connected with ear (in *Megalops*, however, it does lie against the skull); no *recessus lateralis*; hypurals on three or more ural centra; branchiostegals usually more than 15; parasphenoid toothed (except in some notacanthoids).

During metamorphosis from the leptocephalus to the juvenile body form, the fish shrinks greatly in length. Larvae commonly reach 10 cm and may be as long as 2 m. D. G. Smith in Böhlke (1989, vol. 2) gave keys and descriptions for the leptocephali of this group.



Representative leptocephalus larvae of elopomorphs; typical maximum lengths are indicated for each.

Some historical notes on the classification of the elopomorphs were given in Nelson (1994), and older classifications based on adult characters recognized markedly different relationships of the taxa given here. The relationships among the members of this group are based largely on the common occurrence of a leptocephalus larval stage (Greenwood et al., 1966). However, not all authors accepted the larva as a valid indicator of affinity and questioned the monophyly of Elopomorpha. For example, rather than the leptocephalus larvae representing a derived condition, Hulet and Robins in Böhlke (1989), argued it to be a primitive condition and therefore of limited systematic significance. Contrary to Forey et al. (1996), Filleul and Lavoué (2001) concluded that the morphological characters used to support the monophyly of the Elopomorpha are mostly weak and proposed a new hypothesis of relationships based on nucleotide sequences of ribosomal RNA 18S, 16S, and 12S. They concluded that the Elopomorpha are not monophyletic, and considered elopiforms, anguilliforms, albuliforms, and notacanthiforms as four monophyletic, *incertae sedis* taxa among basal teleosts. However, Wang et al. (2003), in an analysis of 12S rRNA sequences, confirmed a monophyletic Elopomorpha, and concluded that *Elops* and *Megalops* share a common ancestor and are basal (extant) Elopomorpha, and that *Albula* and *Notacanthus* together form the sister group of the Anguilliformes; however, they also concluded that the Congroidei are not monophyletic and neither are the Anguilliformes without the Saccopharyngiformes. Inoue et al. (2004) also supported the monophyly of the Elopomorpha, as do the current molecular phylogenies of Near et al. (2012a) and Betancur-R. et al. (2013a). Dornburg et al. (2015) assumed the monophyly of Elopomorpha, focusing instead on relationships of some elopomorph fossils with the extant clades, although they did not sample many anguilliforms; their results also are in general agreement with the groups recognized here. Overall, based on both morphological and molecular data, we accept the monophyly of Elopomorpha, but recognize that the internal relationships of the group may change with additional and targeted study.



Phylogenetic relationships among the four orders of Elopomorpha.

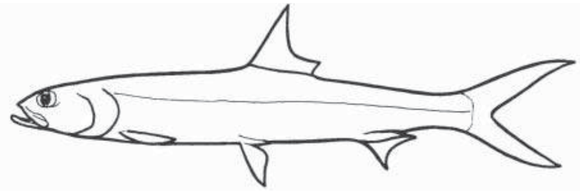
The fossil genera †*Eichstaettia* (late Late Jurassic) and †*Anaethalion* (mid to late Late Jurassic) (Arratia, 1991, 2000) may be the oldest and most primitive known elopomorphs. Other fossil elopomorphs not mentioned below include †*Davichthys*, †*Lebonichthys*, and the albuloids †*Brannerion* and †*Osmeroides*; these and others were reviewed by Forey et al. (1996) and Arratia (1997, 2000).

Four orders, 24 families, 169 genera, and about 986 species. All but six species are marine or primarily marine.

Order ELOPIFORMES (23)—tenpounders. Pelvic fins abdominal; body slender, usually compressed; gill openings wide; caudal fin deeply forked; caudal fin with seven hypurals; scales cycloid; mesocoracoid and postcleithra present; gular plate well developed (median); branchiostegals 23–35; mouth bordered by premaxilla and toothed maxilla; upper jaw extending past eye; tip of snout not overhanging mouth (mouth terminal or superior). Leptocephali small, maximum length about 5 cm, with a well-developed, forked, caudal fin, a posterior dorsal fin, and about 53–86 myomeres (see Smith in Böhlke, 1989:961–972).

Two families, two genera, and nine species. The Late Jurassic genus †*Elopsomolos* from Germany is an early fossil of this order (Arratia, 2000).

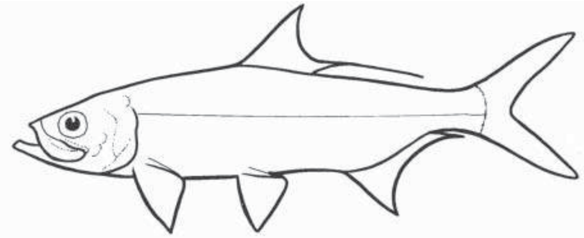
Family ELOPIDAE (68)—tenpounders (ladyfishes). Mainly marine (rarely brackish and freshwater); tropical and subtropical oceans.



Body rounded (little compressed); mouth terminal; pseudobranchiae large; branchiostegals 27–35; dorsal-fin rays usually 20–25, the last ray not elongate; anal-fin rays usually 13–18; pelvic-fin rays usually 12–16, no conus arteriosus; lateral-line tubes unbranched; lateral-line scales usually 95–120; insertion of pelvic fin beneath or posterior to origin of dorsal fin; vertebrae 63–79. Maximum length 1.0 m, attained in *Elops machnata.*

One genus, *Elops*, with seven species (e.g., Smith, 2003), including one described recently (McBride et al., 2010) from the Western Atlantic.

Family MEGALOPIDAE (69)—tarpons. Mainly marine (enters freshwater); tropical and subtropical oceans.



Body compressed; mouth terminal or superior; pseudobranchiae absent; branchiostegals 23–27; dorsal-fin rays 13–21, the last ray elongate; anal-fin rays usually 22–29; pelvic-fin rays 10 or 11; conus arteriosus present; lateral-line tubes branched (radiating over surface of lateral-line scales); the only elopiforms with the swimbladder contacting skull (but no intimate association between the swimbladder and the perilymphatic cavity as in clupeoids and notopteroids). Maximum length about 2.4 m, attained in *Megalops atlanticus.*

Two species, as follows:

Megalops cyprinoides. Indo-West Pacific (Africa to Society Islands). Pelvic-fin insertion beneath dorsal-fin origin; dorsal-fin rays 17–21; lateral-line scales 37–42; vertebrae 67 or 68; expanded arm of the intercalar forming the entire wall of the large otic bulla.

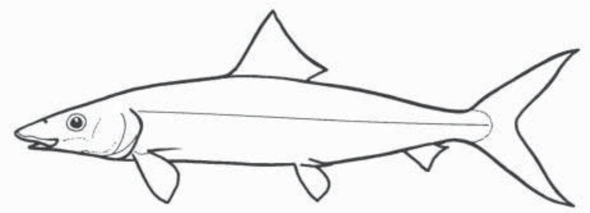
Megalops atlanticus (= Tarpon atlanticus). Western Atlantic (North Carolina, rarely north to Nova Scotia, to Brazil and offshore, and off tropical West Africa, rarely to southern Europe. Pelvic-fin insertion in advance of dorsal-fin origin; dorsal-fin rays 13–16; lateral-line scales 41–48; vertebrae 53–57; intercalar not forming part of lateral wall of otic bulla.

Order ALBULIFORMES (24)—bonefishes. Mandibular sensory canal lying in open groove in dentary and angular bones (in all other elopomorphs the groove is roofed; in *Albula* there is a small roof in the angular). Wiley and Johnson (2010) recognized three characters proposed by Forey et al. (1996) as possible synapomorphies of the order: ectopterygoid with dorsal process, subepiotic fossa, presence of a fenestra within the hyomandibular-metapterygoid suture.

One family, two genera, and about 12 species.

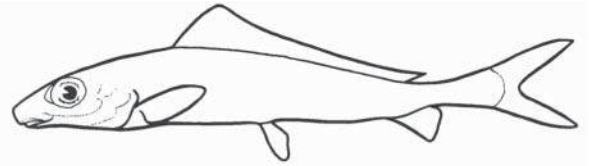
Family ALBULIDAE (70)—bonefishes. Marine; tropical seas. Maximum length about 105 cm, attained in *Albula vulpes*. Two subfamilies.

SUBFAMILY ALBULINAE. Most tropical seas (rarely brackish and freshwater). Dorsal-fin base short, 16–21 rays (last ray of dorsal fin prolonged into a filament in *Albula nemoptera*); branchiostegals 10–16; gill rakers 15–17; lateral-line scales 66–84; vertebrae 69–80; small median gular plate; maxilla and basihyal toothless; crushing dentition on parasphenoid.



One genus, *Albula,* with ten species (e.g., Smith, 2003; Nelson et al., 2004; Kwun and Kim, 2011; Pfeiler et al., 2011).

SUBFAMILY PTEROTHRISSINAE. Eastern Atlantic (Gulf of Guinea) and Japan. Dorsal-fin base long, about 55–65 rays; branchiostegals 6; lateral-line scales 85–112; vertebrae about 107; gular plate absent; maxilla each with six or seven small teeth.



One genus, *Istieus* (synonym *Pterothrissus*), with two species: *I. belloci* from tropical west Africa and *I. gissu* from Japan. C. R. Robins in Böhlke (1989:9–23) noted the 1973 evidence of Forey for synonymizing the genus *Istieus*, based on fossil species, with the similar extant species, but not all authorities accept the synonymy (e.g., Eschmeyer and Fricke, 2015).

Order NOTACANTHIFORMES (25)—halosaurs and deep-sea spiny eels. Body eel-like; posteriorly directed spine on dorsal edge of rear of maxilla; premaxilla and maxilla bordering upper jaw; connective tissue structure intercalated between pterygoid and maxilla; gill membranes separate; pectoral fins relatively high on body; pelvic fins abdominal, with 7–11 rays (the two fins are usually connected by a membrane); anal-fin base long and merged with what remains of the caudal fin; caudal fin skeleton reduced or absent; tail easily regenerated when lost; branchiostegals 5–23; swimbladder present. Some have photophores.

Smith (1979) and Smith in Böhlke (1989:955–959) described the leptocephalus larva. The 300 or more myomeres are V-shaped. A caudal fin is absent; instead there is a single postcaudal filament (Smith, 1979). The dorsal fin is short, consisting of about 10 rays, and is located in the anterior half of the body. The larvae, which can be exceptionally large, reach a length of up to 2 m before metamorphosis. Generic names applied to notacanthoid larvae include *Tilurus* and *Tiluropsis.*

Specimens have been collected between 125 and 4,900 m, but most occur at depths of 450–2,500 m.

Two families, six genera with about 27 species (e.g., Sulak, 1977; Smith, 2003).

Family HALOSAURIDAE (71)—halosaurs. Deepsea; worldwide.

Maxilla and premaxilla toothed; branchiostegal membranes completely separate, rays 9–23; dorsal fin entirely anterior to anus, with 9–13 soft rays, no spines; lateral line cavernous and extending full length of body, lateroventrally; scales relatively large, fewer than 30 longitudinal rows on each side.

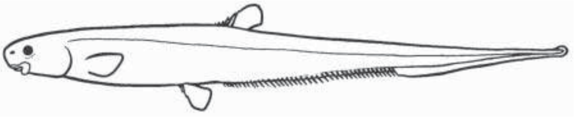
Three genera with 16 species. *Halosaurus*, with nine species, occurs in many areas of the Atlantic, Indian, and Pacific, usually confined to continental margins. *Halosauropsis macrochir* is in the Atlantic, western Pacific, and Indian. *Aldrovandia*, with six species, is in the Atlantic, Indian, and western and central Pacific. In addition, fossils such as the Late Cretaceous †*Echidnocephalus*, are known.

Family NOTACANTHIDAE (72)—deep-sea spiny eels. Deep-sea; worldwide.

Branchiostegal membranes at least partly joined; at least part of the dorsal fin posterior to the anus; lateral line not cavernous and well up on the side; scales relatively small, more than 50 longitudinal rows occur on each side; some genera with as many as three spine-like rays in each pelvic fin.

Three genera with 11 species. The common name "spiny eels" is commonly applied also to the African freshwater family Mastacembelidae in the order Synbranchiformes (see below).

Lipogenys. Mouth small, toothless, and suctorial; lower jaw short, lying within the sucker-like opening; branchiostegals 5–7; gill rakers absent; pectoral girdle lacking cleithrum and supracleithrum; dorsal-fin base short, with 9–12 rays (the first few spine-like); anal-fin base long, with the first 32–44 rays spine-like, total rays about 116–136; pyloric caeca 5–7; vertebrae about 228–2347



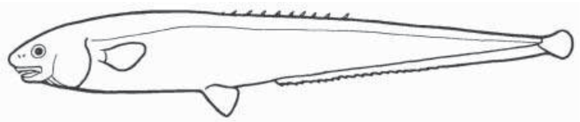
One species, *Lipogenys gilli*, deep-sea, in the Western North Atlantic and off Japan (Nakabo et al., 1991).

In contrast to *Lipogenys*, the following two genera have mouth normal in size, maxilla toothless but premaxilla and dentary toothed; branchiostegals 6–13; gill rakers well developed; cleithrum and supracleithrum well ossified.

Polyacanthonotus. Dorsal fin with 26–41 isolated spines and no conspicuous soft rays; vertebrae 224–290.

Four species known from the southern Bering Sea, North Pacific, New Zealand, Caribbean, Mediterranean, and North Atlantic at 500–3,753 m depth (Sulak et al., 1984; Crabtree et al., 1985).

Notacanthus. Dorsal fin with 6–15 isolated spines and no conspicuous soft rays.



Six species and probably worldwide.

Order ANGUILLIFORMES (Apodes) (26)—eels. Pelvic fins and skeleton absent; pectoral fins and girdle absent in some; pectoral fins, when present, approximately mid-lateral in position; dorsal and anal fins confluent with caudal fin (or nearly so in *Protanguilla*; caudal fin rayless or lost in some); scales usually absent or, if present in extant eels (*Protanguilla*, synaphobranchids, and *Anguilla*) they are cycloid and embedded; gill openings usually narrow; gill arches elongate and gills posteriorly; gill rakers absent (except *Protanguilla*; Johnson et al., 2012); pyloric caeca absent; maxilla toothed, bordering mouth; both premaxillae, the vomer, and ethmoid fused into a single bone (except premaxillae autogenous in *Protanguilla*); branchiostegals 6–49; swimbladder with pneumatic duct present; oviducts absent; opisthotic, orbitosphenoid, mesocoracoid, gular plate, posttemporal, postcleithra, supramaxilla, and extrascapular bones absent; metapterygoid absent except *Protanguilla* among extant eels; symplectic fused with quadrate during development, except *Protanguilla* and Cretaceous eels (Johnson et al., 2012). All or most of the gonads are in the tail (post anal) in some groups (e.g., Heterenchelyidae and Synaphobranchidae) (Fishelson, 1994; Johnson et al. 2012).

Johnson et al. (2012) proposed numerous synapomorphies uniting all eels, including Cretaceous fossils, and others uniting only crown-group eels. Cretaceous eels that may be stem-group taxa include †*Abisaadia,* †*Anguillavus,* †*Hayenchelys,* †*Luenchelys,* and †*Urenchelys* (Forey et al., 1996, 2003; Johnson et al., 2012). Cretaceous eels (except for †*Anguillavus*) had already lost the pelvic fin and girdle, including the primitive Cretaceous eel †*Libanechelys* described by Taverne (2004).

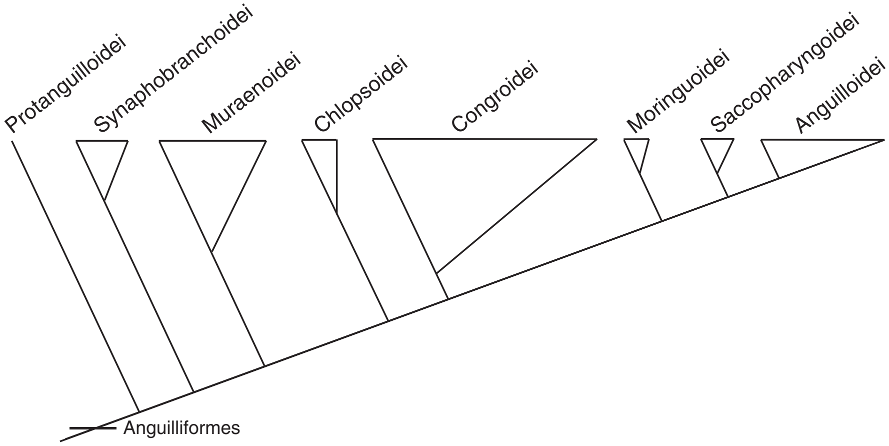
Many eels are specialized for wedging through small openings, although many others are adapted to a pelagic existence, or to burrowing in soft substrates, rotational feeding, or knotting around prey. Mehta et al. (2010), comparing morphological correlates of body elongation in a phylogenetic context, found that major groups of eels achieved long bodies and advanced behaviors in unique ways.

The leptocephalus larva of anguilliforms differs from that of elopiforms and notacanthiforms in having the caudal fin small and round, continuous with the dorsal and anal fins (the many-rayed dorsal and anal fins are usually very inconspicuous). As in notacanthiforms, there are usually more than 100 myomeres. Considerable morphological diversity exists among the pelagic leptocephalus larvae, and problems still exist in identifying them to species. Selective pressures on larval characters have evidently been different than those for adult characters (as is true for many marine larvae); the larvae and adults give the appearance of having evolved independently. Although a few leptocephali are known to exceed 50 cm, most are less than 20 cm long before metamorphosis, when there is a loss of many larval features (detailed in, e.g., Smith, 1979), and a contraction in length. Further information on eel leptocephali and keys to their identification may be found in Smith (1979) and the chapters by D. G. Smith in Böhlke (1989, vol. 2). Extensive work on leptocephali has also been done by such workers as Peter H. J. Castle (e.g., Castle and Raju, 1975).

Recent molecular studies (e.g., Inoue, Miya, and Miller et al., 2004, 2010; Johnson et al., 2012; Santini et al., 2013; Tang and Fielitz, 2012;

Chen et al., 2013) suggest that some of the relationships among suborder- and family-groups differ from those adopted in earlier editions of this book and reviews such as that of Wiley and Johnson (2010). For the present edition, we are adopting the basic arrangement in Inoue, Miya, and Miller et al. (2010), which is generally supported by other molecular and morphological studies, including those of Johnson et al. (2012), Santini et al. (2013), and Tang and Fielitz (2012). We also accept the position of the newly discovered primitive cave eel, *Protanguilla,* as the likely sister group of all other eels (Johnson et al., 2012).

There are eight suborders containing 19 families, 159 genera, and about 938 species, most of which are marine. Members of several families occur in fresh water, and about six species are known only from fresh water.



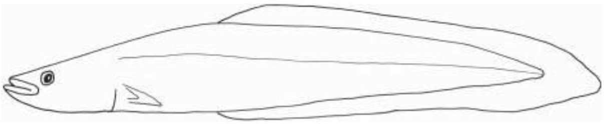
Suggested phylogenetic relationships among the suborders of Anguilliformes (eels).

Suborder Protanguilloidei. This suborder contains only the recently discovered primitive eel genus *Protanguilla.* Johnson et al. (2012) concluded, based on analysis of whole mitogenomic sequences and especially on its retention of primitive morphological features (see also Springer and Johnson, 2015), that *Protanguilla* warrants recognition as a "living fossil" of the true eels. Other studies, using exclusively molecular data (Santini et al., 2012; Tang and Fielitz, 2013), proposed that *Protanguilla* is the sister group of the Synaphobranchoidei.

One monotypic family and one species.

Family PROTANGUILLIDAE (73)—primitive cave eels. Marine, Palau.

Body relatively short; gill opening terminating as ovoid tube with fringed collar; pseudobranch present; toothed gill rakers present; premaxillae present, symplectic autogenous, and metapterygoid present (all three unique among extant eels but seen in Cretaceous eels); vomer with small, ovoid, autogenous toothplate; hypurals three and four not fused to each other; total vertebrae 87 or fewer (Johnson et al., 2015; Springer and Johnson, 2015).



The only known species, *Protanguilla palau*, was found in 2009 in an undersea cave in the Western Pacific Ocean, on a fringing reef of the Republic of Palau.

Suborder Synaphobranchoidei. As per several molecular studies (e.g., Inoue, Miya, and Miller et al., 2010), the family Synaphobranchidae is placed in its own suborder. This assignment differs from Nelson (2006) who placed it within Congroidei.

One family, three subfamilies, twelve genera, and about 38 species (Robins and Robins in Böhlke, 1989:207–253; Chen and Mok, 1995; Sulak and Shcherbachev, 1997).

Family SYNAPHOBRANCHIDAE (74)—cutthroat eels. Marine; Atlantic, Indian, and Pacific.

Gill openings low on body, at or below insertion of pectoral fin (this fin is absent in a few species); vertebrae 110–205; third hypobranchial directed forward from midline, meets third ceratobranchial at a sharp angle; larvae with diagonally elongated eyes (termed telescopic), lens at anterodorsal end.

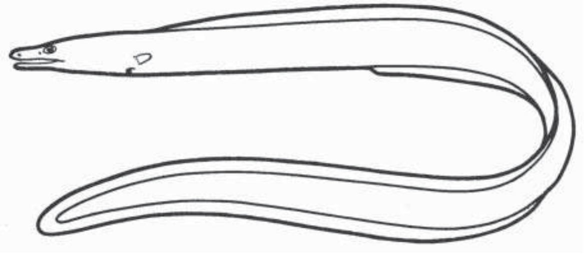
There are three subfamilies.

SUBFAMILY SIMENCHELYINAE (SNUBNOSE OR PUGNOSE PARASITIC EEL). Body especially slimy, with scales embedded in skin; snout blunt and rounded with terminal slit-like mouth; pectoral fin moderate in size; palatopterygoid arch (arcade) complete (absent or only a splinter-like pterygoid present in members of the other subfamilies). Maximum length about 60 cm.

The sole species occurs between 365 and 2,620 m. It is essentially worldwide from tropical to temperate latitudes. It is reported to be a scavenger on other fishes (especially halibut), or even to burrow into other fishes (e.g., Shortfin Mako; Caira et al., 1997) and live as an internal parasite.

One species, *Simenchelys parasiticus.*

SUBFAMILY ILYOPHINAE (DYSOMMATINAE) (ARROWTOOTH EELS OR MUSTARD EELS). Lower jaw shorter than upper; body scaleless (except in some *Ilyophis*); pectoral fin absent in some species of *Dysomma* and the monotypic *Thermobiotes*; head shape depressed and relatively rounded; some teeth relatively long.



Seven genera, *Atractodenchelys* (2), *Dysomma* (12), *Dysommina* (2), *Ilyophis* (6), *Linkenchelys* (1), *Meadia* (2), and *Thermobiotes* (1), with a total of 26 species.

SUBFAMILY SYNAPHOBRANCHINAE (CUTTHROAT EELS). Lower jaw longer than upper; body scaled (usually naked in *Haptenchelys texis*); head shape compressed and relatively pointed; teeth small and needle-like; branchial apertures confluent or only slightly separated in most; ventral region dark-colored and dorsal region pale, a pattern opposite to the usual one.

Four genera, *Diastobranchus* and *Haptenchelys* (one species each), *Histiobranchus* (three species), and *Synaphobranchus* (six species; e.g., Melo, 2007), with 11 species.

Suborder Muraenoidei. Mouth large; frontals not fused to each other; marked reduction in gill-arch elements and lateral line; eyes of normal size. In other suborders, frontals can be fused and eyes can be significantly larger or smaller. Molecular studies including those in Johnson et al. (2012) and Santini et al. (2013) recover this group as monophyletic and distinct from Anguilliformes.

Three families, 19 genera, and about 213 species.

Family HETERENCHELYIDAE (75)—mud eels. Marine; tropical, Atlantic (and Mediterranean) and eastern Pacific.

Pectoral fin absent; mouth large; gill openings low on body; dorsal fin origin over gill opening; lateral line obsolete. Members of this family appear to burrow (head first).

Two genera, *Panturichthys* (dermal crest on top of head, inner row of maxillary teeth complete or nearly so, and 109–136 vertebrae) with four species and *Pythonichthys* (synonym *Heterenchelys*) (no crest, inner row of maxillary teeth incomplete, and 141–227 vertebrae) also with four species (e.g., D. G. Smith in Böhlke, 1989:48–54). Smith et al. (2012) reviewed the eight species in the family.

Family MYROCONGRIDAE (76)—myroconger eels. Marine; eastern tropical Atlantic, St. Helena, and Pacific.

Gill openings small but not greatly restricted; basibranchials greatly reduced; body strongly compressed; pectoral fin present; posterior nostril high on head, level with upper margin of eye; lateral line incomplete, 5–7 pores at anterior end of canal in branchial region above pectoral fin.

One genus, *Myroconger,* with five species (D. G. Smith in Böhlke, 1989:89–103; Castle and Bearez, 1995; Karmovskaya, 2006).

Family MURAENIDAE (Heteromyridae) (77)—moray eels. Marine, some species in or occasionally entering fresh water; tropical and temperate seas.

Gill openings restricted to small roundish lateral openings; lateral-line pores on head, up to two in branchial region, but none on body; branchial arches reduced with basibranchials greatly reduced; fourth branchial arch strengthened and modified as pharyngeal jaws; pectoral fins absent (some other eels have lost the pectoral fin, but only morays have a greatly reduced fin in the larval stage—Smith, 1979); posterior nostril high on head (usually above front portion of eye); most with long fang-like teeth; vertebrae usually 110–200. Maximum length 3.0 m.

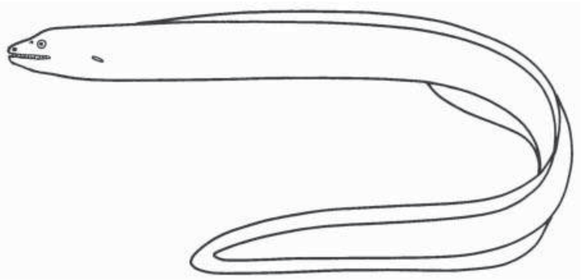
Some morays, such as species of *Gymnothorax,* are involved in ciguatera fish-poisoning (e.g., Lewis et al., 1991), which occurs largely between 35°N and 34°S and results from eating any one of a large variety of marine fish species that are ciguatoxic. It is suspected that plankton-feeding fishes acquire the toxicity first by feeding on organisms such as dinoflagellates; they then are consumed by predators. The toxin is passed up the food chain and its concentration magnified in apex predators (e.g., *Caranx, Gymnothorax, Lutjanus, Mycteroperca,* and *Sphyraena*).

About 16 genera with about 200 species (E. Böhlke, McCosker, and J. Böhlke in Böhlke, 1989:104–206; Böhlke and Randall, 2000; Böhlke and McCosker, 2001; Smith, 2002; Reece et al., 2010). There are about 150 Indo-Pacific species and 50 Atlantic species.

SUBFAMILY UROPTERYGIINAE. Hypobranchials in first and second arches ossified; dorsal and anal fins confined to tip of tail (as they are also in the larvae).

Five genera, *Anarchias* (11 species), *Channomuraena* (2), *Cirrimaxilla* (1), *Scuticaria* (2), and *Uropterygius* (20), with 36 species.

SUBFAMILY MURAENINAE. No ossified hypobranchials; vertical fins not confined to tip of tail (usually the dorsal fin origin is above the gill opening or forward, but in three species it begins over the anus or behind).

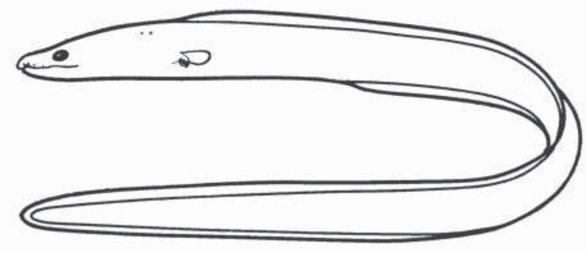


Miller (1987) described knotting behavior as a mode of feeding in species of *Echidna* and *Gymnothorax* (in aquarium observations), otherwise known in fishes only in hagfishes. The eels also employed rotational feeding, known also in *Anguilla*. *Gymnothorax polyuranodon* regularly occurs in fresh water in Indonesia and perhaps in Fiji and part of Australia.

About 11 genera: *Diaphenchelys*, *Echidna*, *Enchelycore*, *Enchelynassa*, *Gymnomuraena*, *Gymnothorax* (synonym *Lycodontis*; some with a single branchial pore; e.g., Lavenberg, 1992), *Monopenchelys*, *Muraena*, *Pseudechidna*, *Rhinomuraena*, and *Strophidon* with about 164 species.

Suborder Chlopsoidei. Frontals not fused; branchial arches reduced; gill openings restricted to small roundish lateral openings; lateral-line pores on head, one or two in branchial region, but none on body; pectoral fins absent in some (e.g., in the six species of *Chlopsis* and the similar appearing *Robinsia catherinae*); posterior nostril displaced ventrally, all but *Kaupichthys nuchalis* of the western Atlantic with posterior nostril opening into the lip; vertebrae usually 100–150. One family.

Family CHLOPSIDAE (Xenocongridae) (78)—false morays. Marine; tropical and subtropical, Atlantic, Indian, and Pacific. Formally within the suborder Muraenoidei (e.g., Nelson, 2006).



Characters are as listed for the suborder.

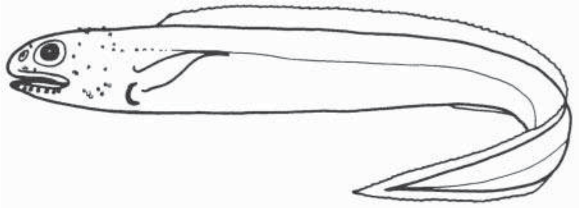
Eight genera, *Boehlkenchelys*, *Catesbya*, *Chilorhinus*, *Chlopsis*, *Kaupichthys*, *Powellichthys*, *Robinsia*, and *Xenoconger*, with 22 species (e.g., D. G. Smith in Böhlke, 1989:72–97; Tighe, 1992; Tighe and McCosker, 2003).

Suborder Congroidei. Frontals fused to each other; pharyngeal elements ossified. Evidence for this group was given by Regan (1912) based on fusion of the frontals, and supported by Nelson (1966), who recognized substantially the same membership as the present volume. Synaphobranchoids were separated from congroids by Nelson (1966) on gill-arch characters (see above). Molecular studies (e.g., Johnson et al., 2012; Santini et al., 2013) now generally agree with these divisions.

Five families, 105 genera, and about 572 species.

Family DERICHTHYIDAE (79) (includes Colocongridae)—longneck or narrowneck and shorttail eels. Marine; Atlantic, Indian, and Pacific. Derichthyidae were named by Gill (1884) when he reported the discovery of *Derichthys serpentinus*. The Colocongridae (*Coloconger* and *Thalassenchelys*) were included with the Derichthyidae in a single clade in several recent molecular analyses, including those of López et al. (2007), Johnson et al. (2012), and Tang and Fielitz (2012).

In *Derichthys* (narrowneck eels) and *Nessorhamphus* (duckbill oceanic eels), a series of short, parallel ridges on the head may form part of a sensory system (similar ridges occur also in some Nemichthyidae); branchial region not expanded, with body behind gill opening somewhat compressed; pectoral fins present, well developed in some; dorsal fin origin behind tip of pectoral fin; anus well behind midlength; lateral line virtually complete; vertebrae 125–163; adults mesopelagic to bathypelagic. Maximum length in *Derichthys* and *Nessorhamphus* about 60 cm.



In *Coloconger* (shorttail eel, shown above, the least elongate anguilliform apart from *Protanguilla*) the body is stubby and the snout blunt; lateral line complete, most pores in short tubes; vomerine teeth absent. *Thalassenchelys* is known only from leptocephalus larvae. See D. G. Smith in Carpenter and Niem (1999:1671–1672).

Derichthys containing one species with a short snout, *Nessorhamphus* containing two species with relatively long snouts (C. Robins in Böhlke, 1989:420–31), *Coloconger*, with seven species, and *Thalassenchelys* with two nominal species (e.g., Löpez et al., 2007).

Family OPHICHTHIDAE (80)—snake eels and worm eels. Marine, continental shelf, some species in or occasionally entering fresh water; coastal areas of tropical to warm temperate oceans, rarely in midwater.

Posterior nostril usually within or piercing upper lip; branchiostegals numerous (15–49 pairs) and overlapping along the midventral line (so-called "jugostegalia" or "accessory branchiostegals"), forming a bulging, basket-like structure in the ventral wall of the throat; neural spines poorly developed or absent; hyomandibulae usually vertical or backwardly inclined (inclined obliquely forward in the large-eyed, pelagic *Benthenchelys*); median supraorbital pore in frontal sensory canal; pectoral fins present or absent; vertebrae 110–270.

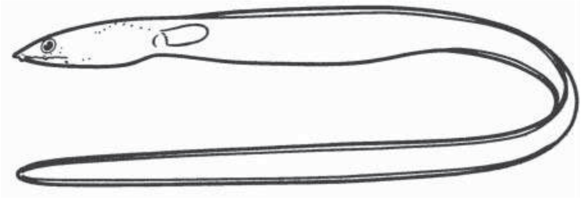
Ophichthids, with their stiffened tail, burrow tail first; they are thought to move through the sediment equally well going forward or backward (unlike the head-burrowing heterenchelyids and moringuids). Some members are especially sharp-tailed, an adaptation for rapid burrowing. Found from shore to over 800 m depth, but most at less than 200 m. (e.g., D. G. Smith and McCosker in Carpenter and Niem, 1999:1662–1663).

Two subfamilies with 59 genera and about 319 species (e.g., McCosker, E. Böhlke, and J. Böhlke in Böhlke, 1989:254–412; Castle and McCosker, 1999; McCosker and Rosenblatt, 1998; McCosker and Chen, 2000; McCosker and Randall, 2001, 2005; McCosker and Robertson, 2001; McCosker, 2007, 2010; McCosker and Ross, 2007; Ji and Kim, 2011; Hibino et al., 2013).

SUBFAMILY MYROPHINAE (WORM EELS). Gill openings midlateral, opening constricted; caudal fin rays conspicuous and still confluent with dorsal and anal fins, tail tip flexible; pectoral fin present or absent; coloration uniform, often darkened dorsally.

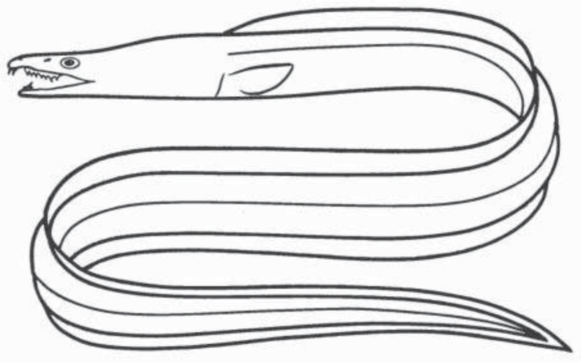
Fourteen genera, *Benthenchelys*, *Ahlia*, *Asarcenchelys*, *Glenoglossa*, *Mixomyrophis*, *Muraenichthys*, *Myrophis*, *Neenchelys*, *Pseudomyrophis*, *Pylorobranchus*, *Schismorhynchus*, *Scolecenchelys*, *Schultzidia*, and *Skythrenchelys* with about 59 species. In *Glenoglossa* (Angler Snake Eel) the glossohyal of the tongue is greatly elongated into a lure complete with 'eyespot'.

SUBFAMILY OPHICHTHINAE (SNAKE EELS). Gill openings midlateral to entirely ventral, opening unconstricted; tail tip a hard or fleshy finless point used in burrowing, rudimentary caudal-fin rays visible in some genera; pectoral fin present or absent, anal fin absent in some, dorsal fin absent in some and all fins absent in *Apterichtus*, *Cirricaecula*, and *Ichthyapus*; coloration highly variable, uniform to spotted or striped or barred.



Forty-five genera, e.g., *Apterichtus* (synonym *Verma*), *Bascanichthys*, *Caecula*, *Callechelys*, *Cirrhimuraena*, *Dalophis* (freshwater in Africa), *Echelus*, *Echiophis*, *Ethadophis*, *Ichthyapus*, *Lamnostoma* (with four western Pacific species generally found in fresh water), *Leiuranus, Letharchus, Myrichthys, Mystriophis, Ophichthus, Ophisurus, Phaenomonas, Pisodonophis*, and *Yirrkala* with about 260 species.

Family MURAENESOCIDAE (81)—pike congers. Marine; tropical, Atlantic, Indian, and Pacific.



Teeth well developed, especially on the vomer; pectorals well developed; eyes large and covered with skin; dorsal fin origin over or slightly before pectoral base; lateral line conspicuous; vertebrae 120–216.

As noted by Smith in (1989:432–440), this family is poorly diagnosed and is of uncertain affinity.

Six genera, *Congresox, Cynoponticus, Gavialiceps, Muraenesox, Oxyconger*, and probably *Sauromuraenesox*, with fifteen species (e.g., Karmovskya, 1993).

Family NETTASTOMATIDAE (82)—duckbill eels. Marine; Atlantic, Indian, and Pacific.

Head and snout elongate and narrow; mouth enlarged; tail greatly attenuated; pectoral fin usually absent in adults (present only in *Hoplunnis*); vertebrae usually 190–280. Maximum length about 1 m. This family of tropical and warm temperate fishes is poorly known; it is thought to be most closely related to the *Uroconger* lineage of congrids.

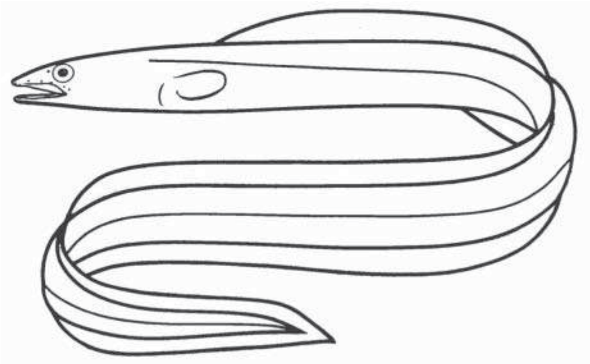
Six genera, *Facciolella, Hoplunnis, Nettastoma, Nettenchelys, Saurenchelys*, and *Venefica*, with 42 species (e.g., D. G. Smith in Böhlke, 1989:568–612; Karmovskaya, 1999).

Family CONGRIDAE (83)—conger eels. Marine; tropical to temperate, Atlantic, Indian, and Pacific.

Lateral line complete; pectoral fin usually present; branchiostegals 8–22; vertebrae 105–225.

Three subfamilies with 30 genera and about 194 species (e.g., D. G. Smith in Böhlke, 1989:460–567; Castle and Randall, 1999; Smith and Karmovskaya, 2003; Greenfield and Niesz, 2004; Karmovskaya and Smith, 2008).

SUBFAMILY CONGRINAE. Dorsal and anal fin rays segmented; pectoral fin well developed; posterior nostril at or above mideye level.



About 22 genera: e.g., *Acromycter*, *Conger* (= the older but suppressed generic name *Leptocephalus*), *Gnathophis*, *Hildebrandia*, *Lumiconger* (a luminescent eel off northern Australia described in 1984), *Macrocephenchelys* (this genus was once placed in its own family), *Rhechias*, *Rhynchoconger*, *Uroconger*, and *Xenomystax*.

SUBFAMILY HETEROCONGRINAE (GARDEN EELS). Dorsal and anal fin rays unsegmented; pectoral fin minute or absent; body very elongate and slender; mouth short and lower jaw projecting beyond upper. Garden eels hover above their sand burrows in large colonies (giving the appearance of a garden), with their tail down, the body relatively straight, and the head up.

Two genera, *Gorgasia* and *Heteroconger*.

SUBFAMILY BATHYMYRINAE. Dorsal and anal fin rays unsegmented; pectoral fin well developed; posterior nostril below mideye level. Although there is molecular support (e.g., Lópèz et al., 2007; Johnson et al., 2010; Tang and Fielitz, 2012) for including *Heteroconger* and/or *Gorgasia* in a clade with *Paraconger* and/or *Ariosoma*, there also is morphological evidence to support the two subfamilies, albeit as close relatives.

Six genera, *Ariosoma*, *Bathymyrus*, *Chiloconger*, *Kenyaconger*, *Parabathymyrus*, and *Paraconger*.

Suborder Moringuoidei. Frontals unfused; gill openings low on body; dorsal fin begins far behind head; dorsal and anal fins reduced to low folds posteriorly; pectoral fin small to feeble; eyes small and covered with skin; sensory pores on head confined to lower jaw; vertebrae 98–180. Many of the features are adaptations to their fossorial life (they burrow head first). *Moringua* has been found in fresh water.

Family MORINGUIDAE (84)—spaghetti eels. Marine, rarely in fresh water; tropical, Indo-Pacific and western Atlantic.

Body moderately to extremely elongate, cylindrical; posterior nostril anterior to eye; anus posterior to midlength; dorsal-fin origin near or behind midlength; pectoral fin present.

Two genera, *Moringua* (12) with greatly elongate body, and the moderately elongate *Neoconger* (3) with 15 species (e.g., D. G. Smith in Böhlke, 1989:55–71; D. G. Smith in Carpenter and Niem, 1999:1637–1638).

Suborder Saccopharyngoidei (Lyomeri). Highly aberrant eels; opercular bones, branchiostegals, ribs, and swimbladder absent; caudal fin absent or rudimentary; gill openings ventral; dorsal and anal fins long; hyomandibula attached to neurocranium by only one condyle; jaws and quadrate greatly elongate; gape of mouth extending well posterior to eye; pharynx highly distensible (accommodating extremely large prey); leptocephalus larvae deep-bodied with myomeres V-shaped rather than W-shaped (e.g., D. G. Smith in Carpenter and Niem, 1999:1693–1697).

The Saccopharyngoidei were a separate order in Nelson (2006). Recent studies (e.g., Johnson et al., 2012; Tang and Fielitz, 2012; Santini et al., 2013) suggest that they are a highly modified group closely related to the Anguilloidei.

Four families, 5 genera and 28 species.

Family CYEMATIDAE (85)—bobtail snipe eels. Marine (bathypelagic); Atlantic, Indian, and Pacific.

Body relatively short, compressed; lateral-line pores absent; eye small to vestigial; maxillae present; caudal fin present, tip of tail blunt. Fewer reductive characters than in other saccopharyngoids. Maximum length about 15 cm.

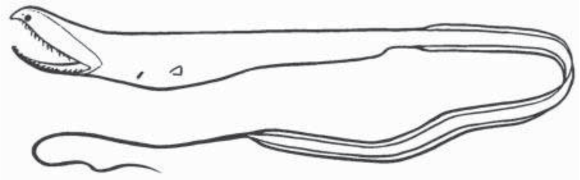
Two monotypic genera—*Cyema* (body black; long, nonocclusible upper and lower jaws) and *Neocyema* from the South and North Atlantic (body bright reddish-orange; pectoral skeleton absent, although a rayless fin is present; myomeres prominently visible; described as paedomorphic by Castle, 1977; see also DeVaney et al., 2009).

Family MONOGNATHIDAE (86)—onejaw gulpers. Marine; Atlantic and Pacific.

Upper jaw absent (i.e., no maxilla; premaxilla also absent as in other extant eels except *Protanguilla*); pectoral fins absent; dorsal and anal fins without skeletal supports; rostral fang with connected glands; abdomen distensible, often protruding posterior to anus. Maximum length 15.9 cm. Most of the 70 known specimens were taken below 2,000 m.

One genus, *Monognathus*, with about 15 species (e.g., Nielsen and Hartel, 1996).

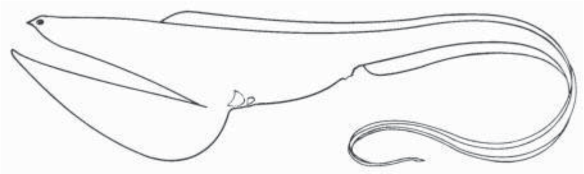
Family SACCOPHARYNGIDAE (87)—swallowers. Marine; Atlantic, Indian, and Pacific.



Head large and deep; body greatly elongated including greatly elongated, attenuated tail ending in luminous caudal organ; eye small; snout short; mouth greatly enlarged by posterior extension of jaws, gape extending far behind eye; jaws with curved teeth; gill openings closer to end of snout than to anus; pectoral fins well developed; vomer and parasphenoid absent; vertebrae about 150–300. Maximum length about 2 m.

One genus, *Saccopharynx*, with about 10 species (Tighe and Nielsen, 2000).

Family EURYPHARYNGIDAE (88)—gulpers or pelican eels. Marine; tropical and temperate, Atlantic, Indian, and Pacific.



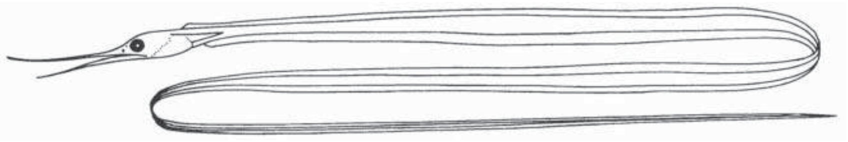
Head large; body greatly elongated with attenuated tail ending in expanded luminous caudal organ; gill openings small, closer to anus than to end of snout; mouth enormous; jaws large with numerous minute teeth; oral cavity very large but stomach not greatly distensible; pectoral fins minute; vertebrae 100–125. Maximum length about 75 cm.

One species, *Eurypharynx pelecanoides* (e.g., Nielsen et al., 1989). When announcing its discovery, Vaillant (1882) reported it to have six pairs of gill clefts and five branchial bars. D. G. Smith in Carpenter and Niem (1999:1695–1696) reported that the gulper eel engulfs mainly smaller invertebrates, expelling water before swallowing.

Suborder Anguilloidei. This group of three families is suggested by some molecular studies including Inoue, Miya, Miller, et al. (2010), and by morphological evidence including a similar pattern of shape, ossification, fusion, and loss in the basibranchials (e.g., Nelson, 1966).

Three families, seven genera, and about 40 species.

Family NEMICHTHYIDAE (89)—snipe eels. Marine (bathy- and mesopelagic); Atlantic, Indian, and Pacific.

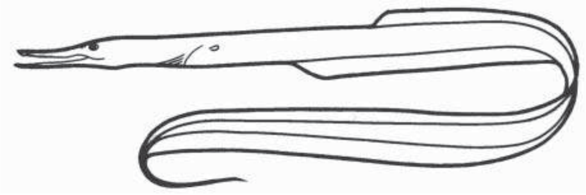


Extremely long, nonocclusible upper and lower jaws (except in fully mature males), with upper jaw longer than lower; body very elongate; pectoral fin present; dorsal and anal fins confluent with caudal; eyes large; preopercle absent; frontals fused or only partially fused in some; lateral line complete; anus a short distance behind pectoral fin (*Avocettina*) or under pectoral fin (the other two genera); vertebrae 170–220 in *Labichthys* and *Avocettina* to over 750 in *Nemichthys* (species of *Nemichthys* have a caudal filament that is frequently lost and thus precludes accurate counts). *Labichthys* and *Avocettina* have a small caudal fin rather than a caudal filament. Longitudinal dermal ridges on the head behind the eye are present in the latter two genera but lacking in *Nemichthys* (D. G. Smith in Carpenter and Niem, 1999:1678–1679).

Snipe eels are reported to orient themselves vertically (diverging jaws upward) at >300 m depth, and have been suggested to use their long jaws to entangle antennae of crustacean prey (Mead and Earle, 1970). Male snipe eels, smaller than females, undergo a transformation at sexual maturity with, for example, the jaws shortening and teeth being lost. The two sexes of some species were at one time placed in separate genera and even in separate suborders (Nielsen and Smith, 1978).

Three genera, *Avocettina* (about four species), *Labichthys* (two species), and *Nemichthys* (three species), with about nine species (D. G. Smith and J. G. Nielsen in Böhlke, 1989:441–59).

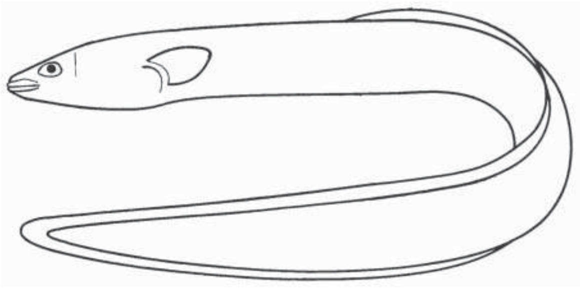
Family SERRIVOMERIDAE (90)—sawtooth eels. Marine; midwater (pelagic) tropical to temperate, Atlantic, Indian, and Pacific.



Jaws extremely elongate and slender; vomerine teeth in two or more rows; gill openings widely open dorsally; branchiostegals 6 or 7; color usually blackish with silvery sides; vertebrae 137–170.

Two genera, *Serrivomer* (eight species, dorsal-fin origin slightly posterior to anus) and the monotypic *Stemonidium* (dorsal-fin origin over or slightly anterior to anus), with about nine species (Clarke, 1984; Tighe in Böhlke, 1989:613–27).

Family ANGUILLIDAE (91)—freshwater eels. Usually catadromous; tropical and temperate seas except eastern Pacific and southern Atlantic, and freshwater in coastal areas of eastern North America (including the St Lawrence River system and Lake Ontario) and Central America (rarely occurring in Atlantic side of Colombia), Europe and Mediterranean area (including northernmost Africa), eastern Africa, India to SE Asia to Japan, Australia, and New Zealand.



Minute embedded scales present; lower jaw slightly protruding; gill opening crescentic, lateral; lateral line complete on body and head; pectoral fins well developed; vertebrae 100–119.

Adult anguillids live in fresh water or in estuaries. They stop feeding at maturity, when they move from fresh water out to sea. The leptocephali move back to coastal areas and estuaries, undergo metamorphosis as glass eels, and enter fresh water as elvers (remaining as elvers until pigmentation develops). The spawning biology and location of freshwater eels was long a mystery (Tsukamoto, 2009) but has recently been clarified by the collection of spawning adults and newly hatched larvae of the Japanese Eel and Giant Mottled Eel from oceanic spawning areas such as the West Mariana Ridge in the Pacific (Tsukamoto, 2011). The North American (*Anguilla rostrata)* and European (*A. anguilla*) freshwater eels appear to spawn in the Sargasso Sea area.

A cladistic hypothesis of relationships among the species (Lin et al., 2001) was converted into an areagram by Parenti (2008a), who concluded that at least two clade of species exhibit antitropical distributions. Minegishi et al. (2005) reconstructed the phylogeny of 18 species and subspecies of the genus *Anguilla*, finding that *A. mossambica* is the most basal species, and that the other species formed three geographically separated clades corresponding to the Atlantic, Oceania, and the Indo-Pacific regions. A more recent molecular phylogenetic study (Inoue et al., 2015) agreed that freshwater eels (Anguillidae) are highly derived anguilliforms and likely originated from midwater-dwelling ancestors that inhabited deep ocean regions.

Two genera, *Anguilla*, with 22 species (e.g., Smith in Böhlke, 1989:24–47; Watanabe et al., 2009), and *Neoanguilla*, with one species from Nepal (Shrestha, 2008).

OSTEOGLOSSOCEPHALA

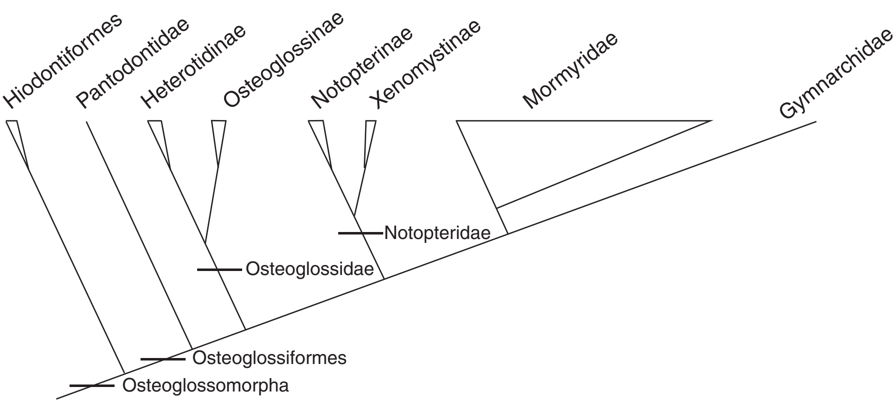
Arratia (2010b) proposed this name for the clade comprising the cohort Osteoglossomorpha and all higher teleosts. In the present treatment it is unranked.

Cohort OSTEOGLOSSOMORPHA

This is a clade of primitive teleosteans with extant representatives in five biogeographic regions and extinct representatives on six continents. Notable members include *Arapaima gigas*, the largest fresh water fish in South America and one the largest fish in existence, *Gymnarchus niloticus*, which produces electrical discharges in the water via electrical organs, and *Heterotis niloticus*, which is able to breath atmospheric air. Britz (2004b) made some interesting observations on their reproduction and early life history. Most osteoglossomorphs exhibit some kind of parental care (mouthbrooding occurs in *Osteoglossum* and *Scleropages*). Unlike most teleosts, adult osteoglossomorphs, except *Pantodon* and *Hiodon*, which do not exhibit parental care, possess only the left ovary, the right being absent.

Morphological and paleontological studies of osteoglossomorphs and their subgroups include those of Li and Wilson (1996), Li et al. (1997), Hilton (2003), Wilson and Murray (2008), Zhang (2006), Hilton and Grande (2008), Hilton and Britz (2010), and Forey and Hilton (2010). Molecular phylogenetic studies include those of Lavoué et al. (2000) on mormyrids, Inoue et al. (2009) on notopterids, and Lavoué and Sullivan (2004) on osteoglossomorphs. The main difference between the morphological and molecular results concerns the position of the Butterflyfish *Pantodon buccholzi*. Lavoué and Sullivan (2004) placed it as the sister group to all other Osteoglossiformes, whereas the morphological studies generally disagreed among each other as to its proper placement.

On the other hand, when they attempt to date phylogenetic events, the molecular studies often postulate anomalously early lineage splitting times, such as origin of Hiodontiformes by the end of the Paleozoic (e.g., Inoue et al., 2009). Such very early dates find no support in the fossil record (they are earlier by a geological period than the oldest fossils that can be considered as stem-group teleosts, i.e., the oldest teleosteomorphs) and we consider such extraordinarily early dates for the origin of Osteoglossomorpha or its early diversification to be highly unlikely.



Relationships of the extant groups of Osteoglossomorpha.

There are numerous fossil members of the Osteoglossomorpha, including fishes from China, Africa, Europe, and the Americas. Although extant osteoglossomorphs are entirely freshwater fishes, as also are most fossil osteoglossomorphs, a few fossil osteoglossomorphs seem to have lived in marine waters (e.g., some species of †*Phareodus*).

Wiley and Johnson (2010) listed possible synapomorphies for Osteoglossomorpha which include: epibranchial bones absent; sixteen principal branched caudal rays; one epural; full spine on the first preural centrum; supraorbital absent; posterior opening of mandibular sensory canal placed lateral to the angular of the jaw; presence of a "shearing bite"; second infraorbital triangular or rectangular in shape and smaller than third infraorbital. As concluded by Wiley and Johnson (2010) the synapomorphies diagnosing Osteoglossomorpha reflect the particular fossil taxa used in analyses with Recent taxa (e.g., Hilton, 2003; Zhang, 2006; Wilson and Murray, 2008). Further study including all taxa of well-preserved fossil osteoglossomorphs is warranted.

Two extant orders and six extant families.

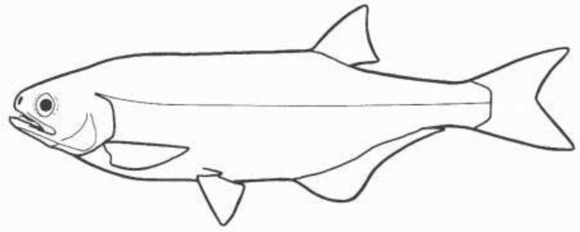
†Order LYCOPTERIFORMES. Late Jurassic to Early Cretaceous; freshwater; Asia.

†Family LYCOPTERIDAE. This family contains the well-known genus †*Lycoptera*, at one time thought to be related to hiodontiforms. Li and Wilson (1996), on the basis of four synapomorphies, regarded the †Lycopteridae as stem-group osteoglossomorphs, sister to all extant clades. That conclusion was supported by Zhang (1998). Although Hilton (2003) was not able to resolve whether it belonged in that position or was related to *Eohiodon* + *Hiodon*, we here consider it to be an order of stem-group osteoglossomorphs.

In addition to †*Lycoptera*, the fossil genera †*Jiuquanichthys* and †*Kuyangichthys* of Early Cretaceous age are also possibly stem-group osteoglossomorphs (Li and Wilson, 1996; Zhang, 1998).

Order HIODONTIFORMES (27)—mooneyes. Nasal bones tubular and strongly curved; dermosphenotic triradiate. Placement of the Hiodontidae in its own order rather than in the Osteoglossiformes, as formerly done (Nelson, 1994), follows Li and Wilson (1996) and Hilton (2003). This is also supported by molecular studies cited above. Fossil hiodontiforms are increasingly numerous and include †*Yanbiania* and †*Plesiolycoptera* from the Early Cretaceous of China (Li, 1987; Li and Wilson, 1996; Li et al., 1997; Zhang, 1998).

Family HIODONTIDAE (92)—mooneyes. Freshwater; North America (primarily Mackenzie, Saskatchewan, Mississippi, and St. Lawrence river systems).



Opercle with posterodorsal recurved process; subopercular present; anal fin sexually dimorphic, moderately long (23–33 rays), and not confluent with the well-developed forked caudal fin; pelvic fins distinct, with seven rays; 7–10 branchiostegals; lateral-line scales about 54–61. Length up to 51 cm.

Two species: *Hiodon tergisus* (Mooneye) with 11 or 12 principal dorsal-fin rays and ventral keel not extending in front of pelvic fins; and *Hiodon alosoides* (Goldeye) with 9 or 10 principal dorsal-fin rays and ventral keel extending in front of pelvics. Several species of the fossil genus †*Eohiodon*, which Hilton and Grande (2008) suggest is a synonym of *Hiodon*, are known from diverse Eocene deposits in Western North America.

Order OSTEOGLOSSIFORMES (28)—bonytongues. Intestine passing posteriorly to left of esophagus and stomach; parasphenoid and tongue bones usually with well-developed teeth and forming a shearing bite (mesopterygoid and usually ectopterygoid also toothed); premaxilla small and fixed to skull; no supramaxilla; caudal fin skeleton with large first ural centrum and no urodermals, one or more epurals fused with uroneurals; caudal fin with 16 or fewer branched rays; nasal capsule rigid, no antorbital-supraorbital system for pumping water over olfactory epithelium; epipleural intermuscular bones absent; one or two pyloric caeca, one caecum in *Pantodon* and two in other osteoglossiforms.

The osteoglossomorph †*Ostariostoma*, from the Late Cretaceous or early Paleocene freshwater deposits of Montana was assigned to the family †Ostariostomidae. It was placed by Li and Wilson (1996) in their suborder Notopteroidei (they provisionally also included the Paleocene †*Thaumaturus*), but was found to be the sister group of all non-hiodontiform osteoglossomorphs by Hilton (2003). Subsequently, the latter position was accorded to the Early Cretaceous †*Xixiaichthys* from China by Zhang (2004). The Cretaceous †*Palaeonotopterus* from Morocco was thought to be related to either mormyrids or notopterids by Cavin and Forey (2001); however, Taverne (2004) suggested that more phylogenetic work is needed before we can be confident of its relationships.

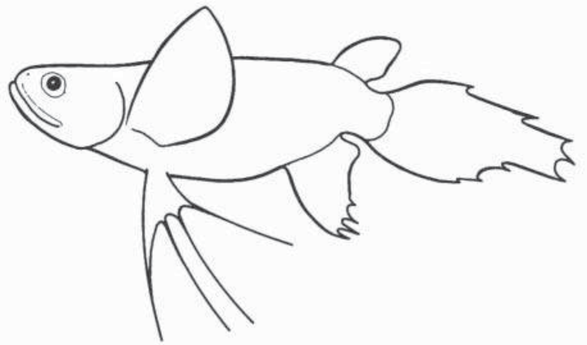
The phylogenetic study of Li and Wilson (1996) suggested that the Osteoglossidae be placed in the suborder Osteoglossoidei, and that Notopteridae, Mormyridae, and Gymnarchidae be placed in the suborder Notopteroidei. In contrast, Hilton (2003) found that mormyrids are the sister group of notopterids + osteoglossids. Herein we have not used the categories of suborder or superfamily to express detailed relationships.

According to Lavoué and Sullivan's (2004) molecular analysis, the Pantodontidae are the sister group of all other extant osteoglossiforms.

Five families, about 31 genera and 244 species. All species occur in fresh water; only some notopterids enter brackish water.

Family PANTODONTIDAE (93)—butterflyfishes. Freshwater; Africa.

Pelvic fins located under pectoral fins; swimbladder that can act as air-breathing organ; eight branchiostegals; greatly enlarged pectoral fins; suboperculum absent; interoperculum sometimes absent; 30 vertebrae. Length up to 10 cm.



One genus with one living species, *Pantodon buchholzi* (Butterflyfish) of tropical western Africa.

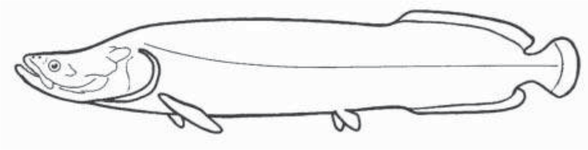
Taverne and Capasso (2012) described a possibly marine pantodontid, †*Prognathoglossum kalassyi,* from Cretaceous (Cenomanian) of Lebanon.

Family OSTEOGLOSSIDAE (94)—osteoglossids or bonytongues. Freshwater; circumtropical, South America, Africa, and Southeast Asia to northern Australia. Most osteoglossids are omnivorous or carnivorous.

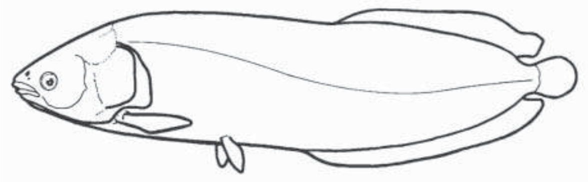
Maxilla toothed; no intracranial penetration of swimbladder; six pelvic-fin rays; pelvic fins distinctly behind base of pectoral fins; some possess a suprabranchial organ and can utilize atmospheric air; lateral-line scales 21–55; 60–100 vertebrae.

Four genera and perhaps sixteen species. A number of fossils are recognized: e.g., †*Joffrichthys* from the Paleocene of Alberta, †*Phareodus* from the Eocene of Wyoming, and †*Brychaetus* of the Paleocene and Eocene of Europe and Africa. Additional fossils were listed by Li and Wilson (1996), Hilton (2003), and Zhang (2004).

SUBFAMILY HETEROTIDINAE. No mandibular barbels; branchiostegals 10 or 11 (*Arapaima*) or 7–9 (*Heterotis*).

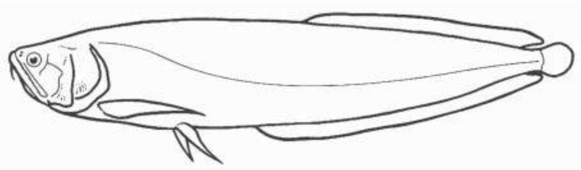


Perhaps six species, including *Arapaima gigas* (Pirarucú) of South America, shown here. In addition, Castello and Stewart (2008) and Stewart (2013a) have argued for recognition of the species *Arapaima agassizii, A. mapae,* and *A. arapaima*, and Stewart (2013b) has also named the new species *A. leptosoma. Arapaima gigas*, one of the world's largest species of scaled freshwater fish, grows to about 2–2½ m in length, although larger specimens probably existed before modern fisheries.



Heterotis niloticus (shown here), of western Africa, lacks parasphenoid teeth and has reduced tongue teeth, grows to almost a meter in length, and has a unique spiral epibranchial organ that aids in concentrating and swallowing food.

SUBFAMILY OSTEOGLOSSINAE. *Osteoglossum* and *Scleropages* have: mandibular barbels; 10–17 branchiostegals.



Osteoglossum bicirrhosum (Silver Arowana, aruana, or arawana), shown here, and *O. ferreirai* (Black Arowana), both of South America, have 42–57 dorsal-fin rays.

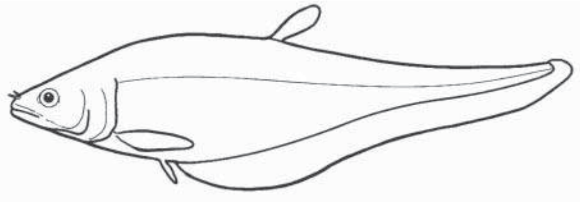
Scleropages has perhaps seven species. *Scleropages jardinii* of northern Australia and New Guinea, *S. leichardti* of the Fitzroy River in Queensland, Australia, and *S. formosus* of Southeast Asia (including Sumatra and Borneo) have about 20 dorsal-fin rays. Three other nominal species have now been named by Pouyaud et al. (2003). Roberts (2012) also described *S. inscriptus* from Myanmar (Burma). Mu et al. (2012) used mtDNA to reconstruct the phylogeny and geographical relationships of osteoglossids and supported the established morphological relationships of the group. The high amount of genetic variation in Southeast Asian populations of *S. formosus* provides some support for recognizing multiple species.

Family NOTOPTERIDAE (95). featherfin knifefishes or Old World knifefishes. Freshwater, sometimes brackish; Africa to Southeast Asia.

Maxilla toothed; anterior prongs of the swimbladder passing forward to ear lateral to skull (intracranially in *Xenomystus* and *Papyrocranus*) (also in mormyrids); anal fin long (94–141 rays or 100 or more rays in anal and caudal combined) and confluent with reduced caudal fin; dorsal fin small to absent; pectoral-fin rays 11–17; pelvic fins small (3–6 rays) to absent; subopercular absent; lateral-line scales 120–180; ventral scutes 25–52; vertebrae 66–86; body color uniform, with numerous small spots, with wavy stripes, or with large ocellated spots above anal fin; length perhaps up to 1.5 m in *Chitala chitala* and *C. lopis*.

Four genera and ten species (Roberts, 1992). Inoue et al. (2009), on mtDNA evidence agreed with Lavoué and Sullivan (2004) as to a division into two clades recognized here as subfamilies, one Southeast Asian and the other African. There are several fossil notopterids including the otolith-based †*Notopteridarum* from India (Rana, 1988), and †*Palaeonotopterus* from the Cenomanian (early Late Cretaceous) of Morocco (Forey, 1997; Cavin and Forey, 2001), which has been suggested to be the sister group to other notopterids.

SUBFAMILY NOTOPTERINAE. Two genera and seven species, Southeast Asia.



Notopterus. Mandible with two rows (versus one or none) of strongly developed serrations. One species, southern and Southeast Asia from India to Sumatra and Java.

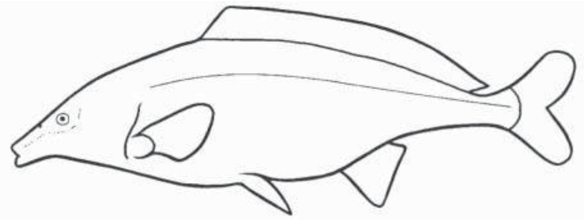
Chitala. Craniodorsal profile concave (vs. convex, straight, or slightly concave). Formerly ranked as a subgenus of *Notopterus.* Six species, Pakistan and India to Sumatra and Borneo.

SUBFAMILY XENOMYSTINAE. Two genera and three species; equatorial Africa.

Papyrocranus. Pelvic fin absent (versus present with 3–6 rays); well-developed intracranial extensions of the swimbladder. Two species, West Africa, primarily from Senegal to Nigeria and the Congo Basin.

Xenomystus. Dorsal fin absent (vs. present with 6–11 rays along a short base); branchiostegals 3 (versus 6–9); gill rakers rudimentary (versus 10–15). One species, tropical Africa (primarily Nile, Chad, Niger, and Congo basins).

Family MORMYRIDAE (96)—elephantfishes. Freshwater; tropical Africa and Nile.



Anal, caudal, and pelvic fins present; caudal peduncle narrow; caudal fin deeply forked; teeth present on parasphenoid and tongue; 6–8 branchiostegals; dorsal-fin rays 12–91; anal-fin rays 20–70; dorsal and anal fins usually opposite and placed back on body; vertebrae 37–64.

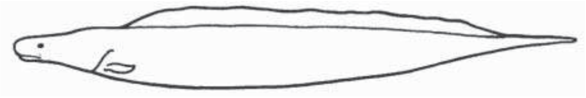
The mouth is extremely variable in mormyrids. In some there is a very elongate proboscis-like snout with a terminal mouth (e.g., *Gnathonemus curvirostris*); in a few there is an elongate lower jaw (e.g., *Gnathonemus petersii*), whereas in others there is a rounded snout with an undershot mouth (e.g., *Marcusenius*). The fish shown above has a moderately developed proboscis-like snout. Some bottom-feeding mormyrids have a chin barbel that is absent in the mid-water species. Length reported up to 1.5 m; the maximum length in most species is 9–50 cm.

Some mormyrids and the one gymnarchid are known to generate weak electric fields and to be capable of detecting extremely weak charges. They are primarily nocturnal fishes and may use these fields to locate objects or food, but there is also evidence that mormyrids communicate with each other electrically, have very specific signal patterns used during courtship, and that there has been rapid evolution in signal patterns driven by sexual selection during the radiation of some species flocks (e.g., in *Paramormyrops*; Arnegard et al., 2010).

Mormyrids appear to have considerable learning ability. Their brain size (largely the cerebellum), relative to body weight, is comparable to that of humans. There is evidence that the family Mormyridae is paraphyletic without the inclusion of *Gymnarchus*; both groups share the following: maxilla toothless; cerebellum enormous; eyes usually small; electric organs derived from caudal muscles; intracranial penetration of swimbladder; flagellum lost in spermatozoa (Jamieson, 1991).

About 21 genera (e.g., *Brienomyrus*, *Campylomormyrus*, *Gnathonemus*, *Hippopotamyrus*, *Hyperopisus*, *Ivindomyrus*, *Marcusenius*, *Mormyrops*, *Mormyrus*, *Petrocephalus*, *Pollimyrus*, and *Stomatorhinus*) with a total of about 216 species (Kramer and van der Bank, 2000; Kramer et al., 2004; Sullivan and Hopkins, 2005, on a new species of *Stomatorhinus*). The following recent papers describe nine new species of *Petrocephalus*: Lavoué et al. (2010), Lavoué (2011), Kramer et al. (2012), and Lavoué and Sullivan (2014).

Family GYMNARCHIDAE (97)—abas. Freshwater; tropical Africa and Nile River.



Anal, caudal, and pelvic fins absent; teeth absent from parasphenoid and tongue; four branchiostegals; body elongate; dorsal fin long (183–230 rays), which can be used for locomotion (they can move forward or backward equally well by passing reversible wave-like movements along the fin while keeping the body rigid); vertebrae 114–120; eyesight weak; able to generate and detect electric fields used for identifying prey and surroundings; length reported up to 1.5 m but usually less than 0.9 m.

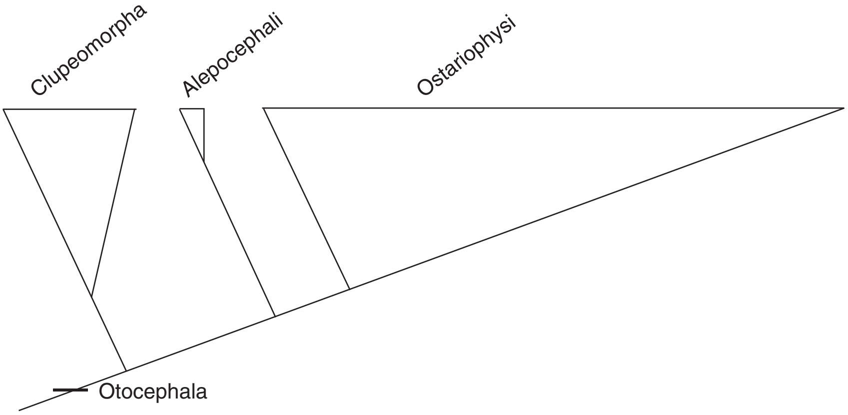
One species, *Gymnarchus niloticus* (Aba).

CLUPEOCEPHALA

The remaining two subdivisions, the Otocephala (= Ostarioclupeomorpha) and the Euteleostei, are placed together as sister groups in the clade Clupeocephala following Patterson and Rosen (1977). This relationship is supported by both morphological (e.g., Arratia, 2010b) and molecular (e.g., Broughton, 2010; Near et al., 2012a; Betancur-R. et al., 2013a) evidence. Arratia (2010b) concluded, after a critical analysis of proposed morphological synaporphies, that the following three characters unambiguously unite the Clupeocephala: early ossification of autopalatine; hyoidean artery piercing ventral hypohyal; toothplate of last pharyngobranchial or pharyngobranchial cartilage 4 corresponding to growth of only one toothplate. Additional characters provided by Wiley and Johnson (2010) include: articular and angular bones fused, retroarticular excluded from joint with quadrate; neural arch of first ural centrum reduced or absent; two anterior uroneurals present as long separated elements; and six or fewer hypurals. The Clupeocephala are not given formal rank here because we have sequenced groups at the subdivision rank to indicate phylogenetic relationships among major clades of crown-group teleosts.

Cohort OTOCEPHALA (= OSTARIOCLUPEOMORPHA, OTOMORPHA)

Strong evidence has existed for some time for a close relationship between Clupeomorpha and Ostariophysi, based on both molecular and morphological evidence (e.g., Lê et al., 1993; Lecointre and Nelson, 1996; Arratia, 1997, 1999, 2004, 2010b; Zaragueta-Bagils et al., 2002; Near et al., 2012a; and Betancur-R. et al., 2013a, among others). However, they are likely to no longer be, in the strict sense, sister groups if the Alepocephali (see below) are more closely related to one of them or the other. In that case, the group would include all three taxa.



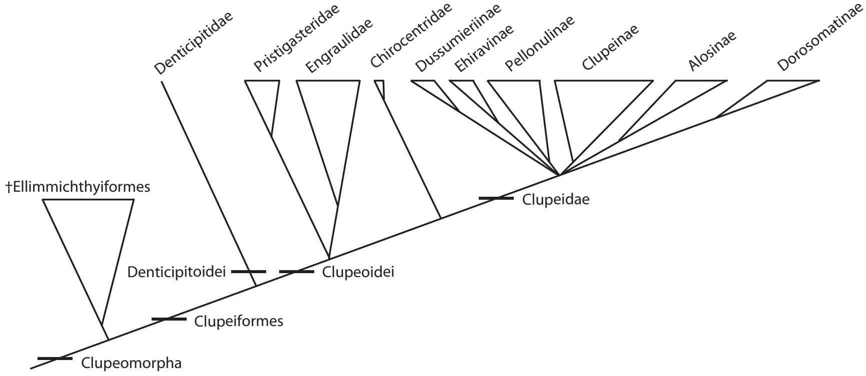
Phylogeny of major groups of Otocephala

Based on morphological studies, three names have been applied to the Clupeomorpha + Ostariophysi grouping: Otocephala by Johnson and Patterson (1996), Ostarioclupeomorpha by Arratia (1996, 1997), and Otomorpha by Wiley and Johnson (2010). The name adopted here for this subdivision, Otocephala, refers to the possession of an otophysic (hearing) connection between swimbladder and inner ear in most members. The name Ostarioclupeomorpha is node-based, referring to the last common ancestor of the Clupeomorpha and the Ostariophysi, then considered to be each other's sister groups; it was first used in the 1996 doctoral dissertation of Arratia and published later (Arratia, 1997:153). Wiley and Johnson (2010) used the name Otomorpha at a different rank for the same group. They cited the following, as supporting characters: fusion of median extrascapular to parietals; autopalatine ossifying early in ontogeny; and bases of hypurals 1 and 2 not united by cartilage during development.

As discussed below, the Otocephala might also now include a third superorder, the Alepocephali, containing only the order Alepocephaliformes (slickheads, etc.), which were formerly placed within order Argentiniformes as suborder Alepocephaloidei. Near et al. (2012a) and Betancur-R. et al. (2013a), among others, have supported the new relationship with molecular studies. Betancur-R. et al. (2013a) provided a classification grouping Alepocephali within Otocephala (= their Otomorpha). Morphological character support for Otocephala with the inclusion of Alepocephali is still wanting.

Superorder CLUPEOMORPHA

Otophysic (swimbladder to inner ear) connection comprising a pair of anterior extensions of the swimbladder that enter the skull through the exoccipital and extend into the prootic and often into the pterotics within the lateral wall of the braincase to connect with the utriculus of the inner ear (unlike that occurring in any other group); second hypural fused at base to first ural centrum in all stages of development, but the first hypural free at its base from first ural centrum (autogenous); single pelvic scute present at insertion of the pelvic fin (inconspicuous in adult *Chirocentrus*) and most species with series of median scutes along abdomen before and behind pelvic fin; dorsal scutes with a median keel; branchiostegals usually fewer than 7, rarely up to 20; body compressed in most; pneumatic duct extending from swimbladder to gut at or near stomach (opening into the dorsal wall of the stomach, relatively anteriorly, in most Engraulidae, Pristigasteridae, and in *Dussumieria*, and in some the duct extends from the swimbladder to the anus); jaws not protrusible; usually two supramaxillae (Patterson and Rosen, 1977; Grande, 1985).



Phylogenetic relationships of major groups of Clupeomorpha

Several lines of clupeomorphs, both fossil and extant, have members that are double-armored; that is, they have predorsal as well as ventral scutes. In some of these there is only one or two predorsal scutes (double-armored engraulids of the Indo-Pacific), while in others there is a series (†*Paraclupea*, †*Diplomystus*, †*Ellimmichthys*, †*Knightia*, *Hyperlophus*, *Potamalosa*, *Ethmidium*, †*Gosiutichthys*, and †*Clupanodon*). The double-armored feature has evolved or been lost independently several times, although most or all members of the fossil-only order †Ellimmichthyiformes are double-armored, and some even have additional median scutes behind the dorsal fin.

The late Early Cretaceous (Albian) fossil †*Erichalcis*, formerly thought to be a primitive clupeomorph (Forey, 1975), has now been shown (Hermus et al., 2004) not to be a clupeomorph, and to be more likely (Arratia, 2010) a primitive euteleostean (although another unnamed fish from the same deposit is a clupeomorph). The Late Cretaceous †*Ornategulum* is a possible clupeomorph of uncertain position (Forey, 2004; Alvarado-Oretega, 2014), as is †*Horseshoeichthys* (Newbrey et al., 2010; Murray and Wilson, 2013). Forey (2004) considered the Early Cretaceous †*Spratticeps* to be sister to the extant Clupeiformes plus fossils such as †*Santanaclupea*. Recently, Alvarado-Ortega (2014) described †*Ranulfoichthys*, another Albian-aged basal clupeomorph that he argued was the most primitive known clupeomorph.

There are two major clades within the Clupeomorpha, one fossil-only clade, the †Ellimmichthyiformes, and one containing the crown-group clupeomorphs, both fossil and extant, in the order Clupeiformes.

†Order ELLIMMICHTHYIFORMES. No recessus lateralis (infraorbital canal not merging with preopercular canal but extending through dermosphenotic); lateral line complete; patch of teeth on parasphenoid similar to that in *Osteoglossum*; large foramen in anterior ceratohyal; parietals meeting at midline between supraoccipital and frontals.

Zaragüeta Bagils (2004) raised biogeographical questions and gave stratigraphic and geographic occurrences for genera and species known till then. †Ellimmichthyiformes represent a great Cretacous radiation of mostly marine clupeomorphs, having been found in Lebanon, Morocco, Spain, UK, Brazil, Mexico, USA, Canada, and China (Murray and Wilson, 2013).

Earlier phylogenetic studies were by Grande (1985), Chang and Maisey (2003), Forey (2004), and Alvarado-Ortega et al. (2008), the last of whom recognized a second fossil family, †Sorbinichthyidae. The present classification follows Murray and Wilson (2013), who named a third family, †Armigatidae, and divided the order into two suborders.

†Suborder Armigatoidei. One family.

†Family ARMIGATIDAE. Late Cretaceous to Eocene; freshwater and marine of Lebanon, Portugal, USA, and China.

Two genera, †*Armigatus* and †*Diplomystus*, with at least six species. Uniting these two genera within †Armigatidae, instead of including †*Diplomystus* in †Paraclupeidae, follows Murray and Wilson (2013).

†Suborder Ellimmichthyoidei. Two families.

†Family SORBINICHTHYIDAE. Late Cretaceous; freshwater and marine; Lebanon and Morocco.

This family was named by Bannikov and Bacchia (2000) to contain the species †*Sorbinichthys elusivo* from Lebanon, notable for its extremely elongated second dorsal-fin ray and second pectoral-fin ray. A second species from Morocco was named by Murray and Wilson (2011). †Sorbinichthyidae are the sister group to the †Paraclupeidae (Murray and Wilson, 2013).

†Family PARACLUPEIDAE (= Ellimmichthyidae). Early Cretaceous to middle Eocene; freshwater and marine.

Subrectangular dorsal scutes; ventral scutes extending from isthmus to anus; pelvic fin, as far as known, in advance of dorsal fin; two supramaxillary bones; parhypural fused to first preural centrum; lateral line complete. Some species had a very deep body. Based originally on fossils of †*Paraclupea chetungensis* from China (Chang and Chou, 1977; Chang and Grande, 1997), the family as recognized here (Wilson and Murray, 2013) has at least nine fossil genera in five subfamilies, listed in approximate phylogenetic sequence:

†SUBFAMILY SCUTATOSPINOSINAE. †*Kwangoclupea* and †*Scutatospinosa* (one species each). Cretaceous of Africa and Brazil.

†SUBFAMILY THORECTICHTHYINAE. †*Thorectichthys* (two species). Cretaceous of Morocco.

†SUBFAMILY ELLIMMINAE. †*Ellimma* (one species). Cretaceous of Brazil.

†SUBFAMILY ELLIMMICHTHYINAE. †*Ellimmichthys*, †*Rhombichthys*. Cretaceous of Brazil, Africa, and the Middle East.

†SUBFAMILY PARACLUPEINAE. Two lineages: tribe †Paraclupeini with †*Paraclupea* and †*Tycheroichthys* (one species each) from China and Canada, and tribe †Triplomystini with †*Triplomystus* (three species) from Lebanon and Mexico. Late Cretaceous.

Order CLUPEIFORMES (29)—herrings. Recessus lateralis present (part of the otophysic connection in which various sensory canals merge within a chamber in the otic region of the neurocranium, not known in any other group); parasphenoid teeth absent; no large foramen on the anterior ceratohyal; parietals separated by the supraoccipital. Most are plankton feeders, with long and sometimes very numerous gill rakers that serve as straining devices. This group is very important in the world's commercial fisheries.

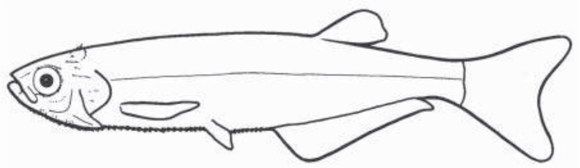
The higher classification of the order Clupeiformes presented here is based primarily on the work of Grande (1985) and works cited therein, with more recent contributions by others (e.g., Di Dario 2002, 2009; Di Dario and de Pinna, 2006). Some recent molecular phylogenetic studies (e.g., Li and Ortí, 2007; Lavoué et al., 2007, 2014) do not differ greatly from this arrangement at the level of suborders and families, but the molecular studies present many differences at subfamily and genus level within the Clupeidae. There have also been several studies (Ishiguro et al., 2005; Lavoué et al., 2007) suggesting a new phylogenetic assignment of the (former) family Sundasalangidae, which is now included within the clupeid subfamily Ehiravinae.

Lavoué et al. (2014) presented an alternative classification of the Clupeiformes, based almost solely on mitochondrial data, which we find interesting. Although a start was made by Lavoué et al. (2014) to identify morphological synapomorphies, there are still few morphological characters to support their revised classification (and no nuclear DNA studies with sufficient taxon sampling to compare with the mtDNA phylogeny). Moreover, their phylogeny did not resolve many relationships among the higher taxa within Clupeomorpha. Therefore, we have not adopted the new arrangement at this time, except for agreeing that *Sundasalanx* belongs in the Ehiravinae. In the accounts below, we note some of the major differences in the assignment of genera to families based on those mtDNA results.

Five families, about 92 genera, and 405 species. About half the species are Indo-West Pacific, and almost one-quarter are in the Western Atlantic. About 79 species occur primarily in fresh water.

Suborder Denticipitoidei. This suborder contains only a single living freshwater species and one fossil species, both from Africa, but the suborder is considered to be the sister group of all other clupeiforms (Grande 1985; Di Dario and de Pinna, 2006, De Pinna and Di Dario, 2010).

Family DENTICIPITIDAE (98)—denticle herrings. Freshwater; coastal rivers of Nigeria and Cameroon, Africa.



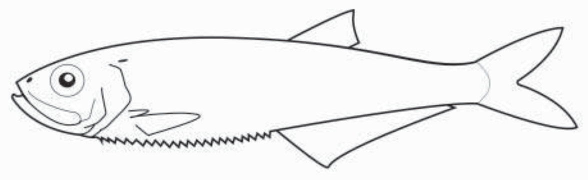
Denticles (odontodes) on all roofing bones of skull; no supramaxillae; four or five branchiostegals, first (median) pair with denticles on anterior edge; ventral half of head with "furred" appearance from small denticles; lateral line complete; ventral scutes present; 16 principal caudal fin rays; caudal skeleton with one uroneural (other clupeomorphs have three) and parhypural fused to first preural centrum; *recessus lateralis* relatively primitive, incomplete in not having a separate opening for the supraorbital laterosensory canal; postorbital bulla present; presence of a supraorbital cavern; accessory cartilage associated with the fifth ceratobranchial; branchial arches one to four with a double row of longitudinal rakers; basibranchial tooth plates absent; single upper pharyngeal tooth plate (Di Dario and de Pinna, 2006; de Pinna and Di Dario, 2010). Scales in lateral line 37–40 and vertebrae 40–41 in the living species. Maximum length 6 cm.

One species, *Denticeps clupeoides* (note that the family name is not spelled Denticepitidae). One fossil species, †*Palaeodenticeps tanganikae,* of Eocene age, is known from Tanzania, Africa (Greenwood, 1960, 1968; Murray, 2000; Murray et al., 2005).

Suborder Clupeoidei. Lateral line not extending onto body (a canal does extend beyond the gill cover and branches over one or two scales, but there are no pored lateral-line scales); single row of gill rakers on arches one–three; second and third infraphryngobranchials anteriorly reduced to long, narrow processes; 19 principal caudal-fin rays; first uroneural fused to first preural centrum (located in front of the reduced first ural centrum, which is fused to the second hypural in all clupeomorphs); parhypural usually separate from the first preural centrum. Yolk segmented (also in Bothidae). There is much diversity in the swimbladder of clupeoids, with the extreme specializations found in the pristigasterids.

The classification of this suborder is based primarily on Grande (1985), Whitehead (1985), and Whitehead et al. (1988), except that Grande (1985) and Grande and Nelson (1985) gave an elevated rank to many of the groups. Di Dario (2002, 2009) presented new morphological evidence that Pristigasteridae may be sister to a clade comprising all other clupeoids (Clupeidae + Chirocentridae + Engraulidae). The position of Chirocentridae, either closer to Clupeidae or to Engraulidae remains a subject of discussion (Di Dario, 2009).

Family PRISTIGASTERIDAE (99)—longfin herrings. Primarily marine, some freshwater in South America and southeast Asia; Atlantic, Indian, and Pacific in tropical and some subtropical seas.



Mouth usually superior, otherwise terminal; jaw teeth small, canines only in *Chirocentrodon*; abdominal scutes present; anal fin long, 30–92 rays; six branchiostegal rays; scales in lateral series about 35–55; vertebrae usually 40–55, up to 62 in *Raconda.* Pelvic fins are absent in several species as noted below. Grande (1985) recognized this taxon on the basis of having the predorsal bones orientated either vertically or inclined anterodorsally (versus being inclined posterodorsally as in nearly all other teleosts) and no notch in third hypural of the caudal skeleton (versus having a distinct notch that creates a gap with the second hypural as in most clupeomorphs). He recognized this group as a superfamily, giving family status to the following subfamilies and noted that *Ilisha,* as recognized here, is not monophyletic. Maximum length about 55 cm SL, attained in *Pellona flavipinnis* of South America; most under 25 cm.

Nine genera with 38 species (e.g., Whitehead, 1985; Randall, 1994; Munroe et al., 1999; Munroe, 2003a; de Pinna and Di Dario, 2003). Four species are freshwater; the rest are marine, occasionally entering brackish water.

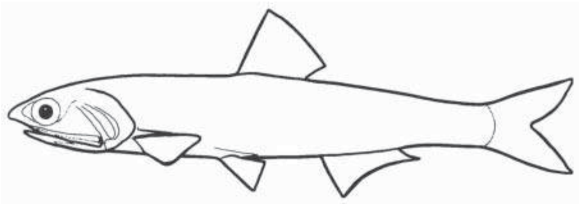
Subfamily Pelloninae. Grande (1985) recognized this group on the basis of having the maxillary-premaxillary gap covered by bone, either a toothed hypomaxilla bone or an extension of the maxilla (versus having a gap as in other clupeomorphs; the hypomaxilla is a bone that is part of the gape of the upper jaw and situated behind the premaxilla, it is also found in *Harengula*). The pelvic fin is absent in the two small species of *Neoopisthopterus* and in the single species of *Pliosteostoma.* The one small species of *Chirocentrodon* has strong conical teeth and canine-like teeth in front (there are also teeth in the gap separating the premaxillae).

Five genera, *Chirocentrodon* (1), *Ilisha* (16), *Neoopisthopterus* (shown above) (2), *Pellona* (6), and *Pliosteostoma* (1), with 26 species.

Subfamily Pristigasterinae. Grande (1985) recognized this group on the basis of having a bony process on the first pleural rib that articulates with the shoulder girdle (not known from any other teleost except *Ilisha africana,* which Grande would place in this taxon). The pelvic fin is absent in the six species of *Opisthopterus,* the three of *Odontognathus,* the single species of *Raconda* (which also lacks the dorsal fin), and usually in the single species of the exceptionally deep-bodied Amazonian *Pristigaster.*

Four genera, *Odontognathus* (3), *Opisthopterus* (6), *Pristigaster* (2), and *Raconda* (1), with 12 species.

Family ENGRAULIDAE (Engraulididae and Stolephoridae) (100)—anchovies. Marine, occasionally freshwater; Atlantic, Indian, and Pacific.



Suspensorium inclined forward with head of hyomandibula well in front of quadrate, hind tip of upper jaw (maxilla) extending well behind eye in most species and jaw articulation well behind eye; mesethmoid projecting in front of vomer and supporting a paired sensory rostral organ; snout blunt, prominent, projecting beyond tip of lower jaw in most species (only just beyond in some Old World anchovies); gill rakers 10–50 or more on lower limb of first arch, 90 or more (100 or more on both limbs) in *Anchovia*; teeth on jaws absent to well developed; 7–19 branchiostegals; scales in lateral series usually 30–60; vertebrae usually 38–49, more in *Coilia*; body often translucent and with a silver stripe down the side in some. Luminescent organs occur in *Coilia dussumieri* (found from coastal India to Java).

Most species feed on plankton (a few by filter-feeding), but a few large species are piscivorous. Most of the freshwater species occur in South America. The maximum size is 37 cm, attained by *Thryssa scratchleyi* of rivers in Papua New Guinea and those entering the Gulf of Carpentria; most species under 20 cm.

The generic composition of the two subfamilies follows Grande (1985) and Grande and Nelson (1985); however, they gave family status to these two sub-families. Whitehead et al. (1988) gave keys to the genera and descriptions of the species. In contrast to the clupeids, surprisingly few fossil anchovies are known, the oldest of the four known species being only of Miocene age (Grande and Nelson, 1985).

Seventeen genera with 146 species. At least 17 species are freshwater, occasionally entering brackish water; the others are marine, rarely entering fresh water.

SUBFAMILY COILIINAE. Scutes present in front of pelvic fin and behind pelvic fin (prepelvic scutes absent in some *Coilia*); anal fin long, 27–81 rays (*Coilia*, with the anal fin joined to the caudal fin, has 80 to about 115 rays). In addition, Grande (1985) recognized this group as being monophyletic on the basis of having lost the peg on the proximal end of the uppermost ray of the lower caudal lobe (a dorsal peg is present on the upper-middle caudal ray; in most other clupeoids there is a two-peg arrangement on the two middle rays); and loss or poor development of a notch on the distal end of the third hypural (similar to pristigasterids). *Coilia* (the rattailed anchovies) has an exceptionally long tapering body. Most species other than the 13 of *Coilia* have a terminal or superior mouth, quite different in appearance from that of other anchovies; in the extreme form the mouth may be highly oblique with the lower jaw projecting beyond the upper (e.g., *Papuengraulis micropinna* with its minute dorsal fin, and *Setipinna breviceps*).

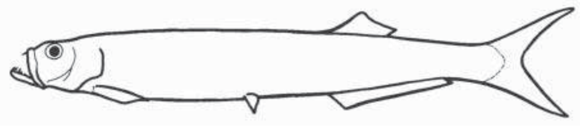
Six Indo-West Pacific genera found in eastern Africa, Asia, and Australia, *Coilia* (13), *Lycothrissa* (1), *Papuengraulis* (1), *Pseudosetipinna* (1), *Setipinna* (8), and *Thryssa* (24) (includes the subgenus *Thrissina*), with about 48 species (Grande, 1985; Whitehead et al. 1988; Peng and Zhao, 1988).

SUBFAMILY ENGRAULINAE. Scutes present in front of pelvic fin only in *Encrasicholina* and *Stolephorus*, absent behind pelvic fin; anal fin usually short, usually 13–37 rays.

Most members of this subfamily are confined to North, Central, and South America. Some species of *Engraulis* and species of two other genera occur elsewhere. The diminutive and scaleless *Amazonsprattus scintilla* of Brazil, the smallest-known clupeomorph and reaching only 19.5 mm standard length, probably belongs in this subfamily.

Eleven genera, *Amazonsprattus* (1), *Anchoa* (35), *Anchovia* (3), *Anchoviella* (16), *Cetengraulis* (2), *Encrasicholina* (5), *Engraulis* (9), *Jurengraulis* (1), *Lycengraulis* (5), *Pterengraulis* (1), and *Stolephorus* (20), with about 98 species (Grande, 1985; Whitehead et al. 1988; Kullander and Ferraris, 2003; Nizinski and Munroe, 2003; Kimura et al., 2009; Loeb and Alcantara, 2013).

Family CHIROCENTRIDAE (101)—wolf herrings. Marine; Indian (west to South Africa and the Red Sea) and western Pacific (Japan to Queensland, Australia).



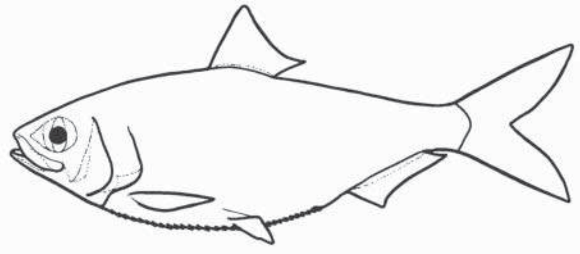
Body elongate and highly compressed; fang-like teeth in the jaws (highly predacious fish); spiral valve in intestine; 17–22 gill rakers; no pyloric caeca; scales small; dorsal fin with 16–19 rays; anal fin with 30–35 rays; pelvic fins small, with six or seven rays; pectoral fin with 13–15 rays; eight branchiostegals; pelvic scute highly reduced in adults; other abdominal scutes absent; vertebrae 69–75 (42–45 abdominal and 27–31 caudal).

Wolf herrings are voracious carnivores, unlike other clupeoids. Maximum length 100 cm.

The only fossil recognized in the Chirocentridae is the Late Cretaceous †*Gastroclupea* from Bolivia. The Chinese fossil †*Mesoclupea* was at one time placed in this family, but Grande (1985) questioned its clupeomorph affinities; Cavin et al. (2013) have suggested that it could be a basal ichthyodectiform.

Two species, *Chirocentrus dorab* and the very similar *C. nudus* (Whitehead, 1985; Munroe et al., 1999).

Family CLUPEIDAE (102)—herrings (shads, sprats, sardines, pilchards, and menhadens). Primarily marine, some freshwater and anadromous; worldwide (mostly tropical).



Two long, rod-like postcleithra in most; mouth usually terminal or nearly so or somewhat superior, usually inferior only in Dorosomatinae; teeth small or absent; abdominal scutes usually present—the Dussumieriinae (round herrings) usually lack abdominal scutes, except for a single pelvic scute; anal fin usually with 12–29 rays, up to 38 in Dorosomatinae; scales in lateral series about 40–50; usually 5–10 branchiostegals; vertebrae usually 37–59. There is much variation in body shape (from rounded to compressed). Maximum length 60 cm, attained in *Tenualosa ilisha* of India and Myanmar (marine and anadromous); most species less than 25 cm.

A valuable commercial fishery exists for clupeids in many parts of the world. Most species form schools and swim near the surface, usually in coastal waters, feeding on plankton.

There are six subfamilies in the present treatment, as in Nelson (2006). The pristigasterids and *Congothrissa* were formerly given subfamily status within the clupeids. Grande (1985) noted that the monophyly and interrelationships of at least the subfamilies Clupeinae, Alosinae, and Dorosomatinae are uncertain.

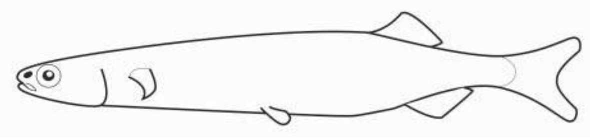
About 64 genera and 218 species. About 57 species are freshwater, occasionally entering brackish water; many others occur in the Caspian Sea, are anadromous, or otherwise extend into fresh water but are primarily marine. Fossils include †*Chasmoclupea* from the Oligocene of Egypt (Murray et al., 2005) and others listed by Grande (1985).

SUBFAMILY DUSSUMIERIINAE (ROUND HERRINGS). Pelvic scute W-shaped and no other scutes along abdomen (in other clupeids the pelvic scute, located just before the pelvic fin, has lateral ascending arms, and other scutes are usually present in front of and behind the pelvic scute).

Whitehead (1985:27) recognized *Dussumieria* and *Etrumeus* with 11–18 branchiostegals in the tribe Dussumieriini, and *Jenkinsia* and *Spratelloides* with 6 or 7 branchiostegals in the tribe Spratelloidini. Lavoué et al. (2014) classify *Jenkinsia* and *Spratelloides* in a separate subfamily Spratelloidinae.

Four genera, *Dussumieria* (2), *Etrumeus* (7), *Jenkinsia* (4), and *Spratelloides* (4), with 17 species.

SUBFAMILY EHIRAVINAE (INCLUDING SUNDASALANGIDAE). Mostly small, often paedomorphic fishes; pterotic bone receiving three different sensory canals; second hypural fused with terminal centrum at least in most; reduction of epurals to two (one in *Corica*) (Stiassny, 2002); mostly living in fresh water.



Ehiravines are miniature, paedomorphic fishes, first described by T. R. Roberts in 1981 from Southeast Asia. They were originally placed in the Osmeriformes, in their own family Sundasalangidae. They were later shown to be clupeiforms by Siebert (1997), who found a prootic bulla and a *recessus lateralis*; he suggested, on the basis of consolidation of the caudal skeleton, a relationship to the clupeid *Jenkinsia*. Recognition as a separate family of clupeiforms, as preferred by Britz and Kottelat (1999a), is not followed here, since Ishiguro et al. (2005) gave mtDNA-based phylogenetic evidence contradicting that relationship, and Lavoué et al. (2014) gave evidence that they are nested within Ehiravinae, a subfamily originally named as a family by Deraniyagala (1929) and later treated as a tribe of Pellonulinae (e.g., by Grande, 1985).

The mtDNA phylogeny of Lavoué et al. (2014) included also *Clupeonella* and *Clupeoides* within the subfamily Ehiravinae.

Eight genera, *Corica* (2), *Clupeichthys* (4), *Dayella* (1), *Ehirava* (1), *Gilchristella* (1), *Sauvagella* (2), *Spratellomorpha* (1), *Sundasalanx* (7), with about

19 species (Siebert, 1997; Britz and Kottelat, 1999a); Western Indian Ocean, South Africa, Madagascar, India, and Southeast Asia.

SUBFAMILY PELLONULINAE (FRESHWATER HERRINGS). Usually only one supramaxilla (anterior one lost); pre- and post-pelvic scutes reduced to absent; scutes present before dorsal fin in some. Most species occur in fresh water, but some are in marine waters; found only in Africa, off India, in Southeast Asia, and in Australia, with most species in lakes and rivers of West Africa.

The double-armored fossil †*Knightia*, known from presumed freshwater deposits of the middle Paleocene to middle Eocene in western North America and China, is provisionally retained in this subfamily. The monotypic *Congothrissa* of the Zaire system was originally placed in its own family, Congothrissidae.

Lavoué et al. (2014) did not recognize a separate Pellonulinae, choosing to include most of the genera within an expanded Dorosomatinae, even though there is a weakly supported clade in their study that is sister to other Dorosomatinae and contains most of the traditionally recognized pellonuline genera.

Twenty-three genera (e.g., *Clupeoides, Congothrissa, Cynothrissa, Hyperlophus, Limnothrissa, Microthrissa, Minyclupeoides, Odaxothrissa, Pellonula, Potamalosa, Potamothrissa, Spratellomorpha,* and *Stolothrissa*) with at least 44 species.

SUBFAMILY CLUPEINAE. Two supramaxillae present. Fossils include †*Gosiutichthys* of Wyoming.

Lavoué et al. (2014) include only seven genera (*Clupea, Sprattus, Strangomera, Ramnogaster, Potamalosa, Hyperlophus,* and *Ethmidium*) in their greatly restricted Clupeinae.

Sixteen genera (e.g., *Amblygaster, Clupea, Clupeonella, Escualosa, Harengula, Herklotsichthys, Lile, Opisthonema, Platanichthys, Ramnogaster, Sardina, Sardinella, Sardinops,* and *Sprattus*) with at least 72 species.

SUBFAMILY ALOSINAE (SHADS). Upper jaw with a distinct median notch or cleft; mouth terminal; jaw teeth small or absent; strong scutes along abdomen and, in *Ethmidium*, before dorsal fin. Species may be marine, freshwater, or anadromous.

Only four genera (*Alosa, Brevoortia, Sardinops,* and *Sardina*) are included in this subfamily by Lavoué et al. (2014).

Seven genera, *Alosa* (26), *Brevoortia* (6), *Ethmalosa* (1), *Ethmidium* (1), *Gudusia* (2), *Hilsa* (1), and *Tenualosa* (5), with 42 species. Almost half of the species belong to *Alosa*.

SUBFAMILY DOROSOMATINAE (GIZZARD SHADS). Upper jaw with a distinct median notch or cleft; mouth usually inferior, lower jaw flared outward; no teeth; strong scutes along abdomen and, in *Clupanodon*, before dorsal fin; last dorsal fin ray filamentous in most; gill rakers long and numerous; stomach muscular, gizzard-like, and intestine after second and last flexure with a loop; pharyngeal pouches near the fourth epibranchials that may concentrate food from the exceptionally large number of gill rakers. Species may be marine, anadromous, or freshwater. *Dorosoma* is found only in North and Central America, while the others are Indo-West Pacific (marine and freshwater).

The molecular study of Lavoué et al. (2014) included many more genera in a greatly expanded Dorosomatinae, including many listed here in Alosinae (e.g., *Ethmalosa*, *Gudusia*), Clupeinae (e.g., *Amblygaster*, *Harengula*, *Rhinosardinia*), and Pellonulinae (e.g., *Pellonula*, *Microthrissa*).

Six genera, *Anodontostoma* (3), *Clupanodon* (1), *Dorosoma* (5), *Gonialosa* (3), *Konosirus* (1), and *Nematalosa* (11), with 24 species.

Superorder ALEPOCEPHALI

In the present work, the suborder Alepocephaloidei is included in the Otocephala (see phylogenetic diagram for Otocephala above) as the superorder Alepocephali, order Alepocephaliformes, contrary to Nelson (2006) and many earlier works. Earlier morphological studies (e.g., Greenwood and Rosen, 1971; Lauder and Liem, 1983) had united alepocephaloids with the Argentiniformes based on the possession of a crumenal organ, and Diogo (2008) continued to advance that phylogenetic position in recent years based on muscle anatomy. However, numerous molecular studies (e.g., Inoue et al., 2003, Ishiguro et al., 2003; Lavoué et al., 2008; Poulsen et al., 2009; Near et al., 2012a; Betancur-R. et al., 2013a) have now placed alepocephaloids within the Otocephala, and we accept this placement.

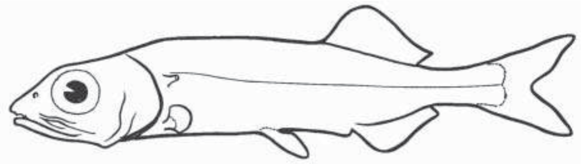
The position of alepocephaloids within otocephalans is somewhat uncertain, though recent molecular works seem to be converging on a closer relationship to Ostariophysi than to Clupeomorpha (Lavoué et al., 2008, 2014; Poulsen et al., 2009; Near et al., 2012a; Betancur-R. et al., 2013a). The taxon Alepocephali herein uses a spelling used also by Betancur-R. et al. (2013a) but at the rank of subcohort. We list the superorder in implied phylogenetic sequence, after Clupeomorpha and before (i.e., sister to) Ostariophysi, but without naming that sister pair pending further corroboration of the relationship and identification of morphological or biological synapomorphies.

Order ALEPOCEPHALIFORMES (30)—slickheads and tubeshoulders. Dorsal fin inserted well back on body; no adipose fin; no swimbladder; upper jaw with teeth except in *Leptochilichthys*; one or two supramaxillae; mouth usually large; posttemporal fossa absent; mesocoracoid present; maximum one postcleithrum; dark-colored fishes. Hatch from large eggs with direct development.

The internal classification of this taxon is based on Johnson and Patterson (1996: 311–312).

Three families with about 32 genera and 137 species.

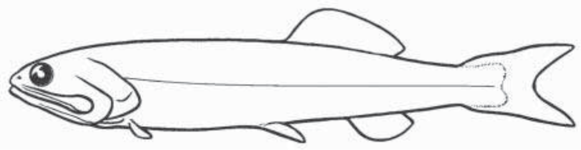
Family PLATYTROCTIDAE (Searsiidae) (103)—tubeshoulders. Marine; all oceans (absent from Mediterranean).



Black shoulder sac apparatus located under shoulder girdle produces blue-green luminous fluid, with conspicuous opening through tubular papilla just below lateral line; light organs present in many species (directed horizontally in young and ventrally in adults); subcutaneous canal system, usually connected to scale pockets by pores; pectoral-fin rays 14–28; pelvic-fin rays 6–10, pelvic fins absent in *Platytroctes apus*; swimbladder absent; branchiostegals 4–8; vertebrae 40–52. Maximum length about 30 cm. Most species occur between 300–1,000 m.

Thirteen genera, *Barbantus, Holtbyrnia, Maulisia, Mirorictus, Normichthys, Paraholtbyrnia, Pellisolus, Persparsia, Platytroctes, Sagamichthys, Searsia, Searsioides,* and *Tragularius,* with 39 species (Matsui and Rosenblatt, 1987).

Family BATHYLACONIDAE (104)—bathylaconids. Marine; tropical to temperate latitudes, circumglobal.

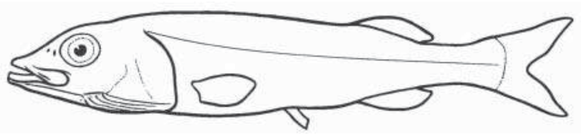


Premaxilla minute, maxilla extending well behind eyes; pectoral fin small, set low on body; branchiostegals 7–10, upper ones forming part of posterior gill cover; vertebrae unossified; large cycloid scales.

Regarded as a subfamily of Alepocephalidae in Nelson (1994). The genus *Herwigia* was formerly included in Bathylaconidae but has been placed in Alepocephalidae following molecular and morphological evidence given by Poulsen et al. (2009).

One genus, *Bathylaco* with three species known from few specimens from circumtropical waters (e.g., Iwamoto et al., 1976; Carter and Hartel, 2003). One of the three species (*B. macrophthalmus*) is on the IUCN red list of threatened species.

Family ALEPOCEPHALIDAE (105)—slickheads. Deep-sea; all oceans.



Teeth usually small; gill rakers long and numerous; shoulder sac apparatus absent; photophores present; pectoral-fin rays 7–18; branchiostegals 5–8 (12 in the pikelike *Bathyprion*); scales absent in some. Most commonly found below 1000 m.

Leptochilichthys, with three species, deep-sea, rare but widespread, was placed in its own family, Leptochilichthyidae, in Nelson (1994), but it along with the genus *Herwigia*, formerly placed in Bathylaconidae, are both grouped in Alepocephalidae by Poulsen et al. (2009) and Lavoué et al. (2008).

About 18 genera (e.g., *Alepocephalus*, *Asquamiceps*, *Aulastomatomorpha*, *Bajacalifornia*, *Bathyprion*, *Bathytroctes*, *Bellocia*, *Conocara*, *Ericara*, *Herwigia*, *Leptochilichthys*, *Leptoderma*, *Narcetes*, *Photostylus*, *Rinoctes*, *Rouleina*, *Talismania*, and *Xenodermichthys*) with at least 95 species (e.g., Markle and Merrett, 1980; Markle and Sazonov, 1996; Sazonov, 1999; Mecklenburg et al., 2002).

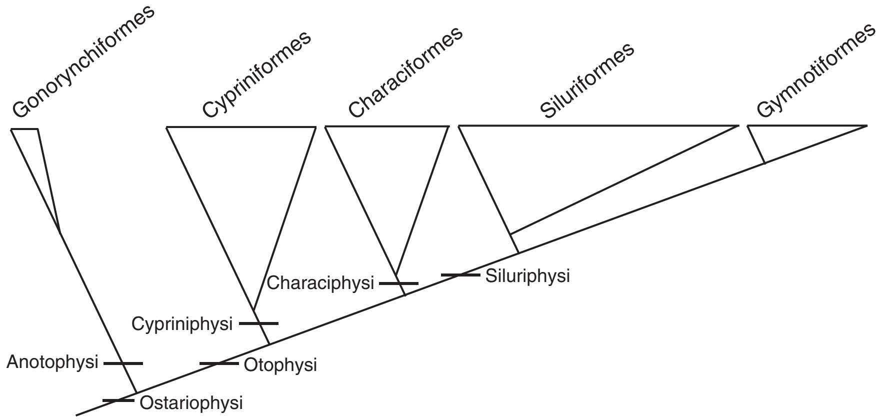
Superorder OSTARIOPHYSI

Basisphenoid absent; supramaxillae absent; unattached neural arch anterior to arch of first centrum absent; dorsomedial expansion of the anterior neural arches; loss of supraneural one; dermopalatine absent; sacculi and lagenae positioned more posteriorly, along midline; swimbladder present (except in *Gonorynchus*) and usually divided by a ductus pneumaticus into a smaller anterior chamber, which is partially or completely covered by a silvery peritoneal tunic and a larger posterior chamber (reduced or absent in some groups); multicellular horny tubercles (= breeding or nuptial tubercles or pearl organs) with keratinous cap well developed; pelvic fins, if present, abdominal. Morphological characters of various authors were reviewed by Wiley and Johnson (2010).

Fishes of this group possess a fright reaction elicited by an alarm substance (Schreckstoff). This was first documented by Karl von Frisch in 1938 and described in detail by Wolfgang Pfeiffer (e.g., 1963, 1977). The alarm substance is a pheromone that is chemically similar in all ostariophysans and produced by epidermal club cells. Injuries to the skin release the alarm substance, which is detected by the sense of smell and causes a fright (escape) reaction in nearby members of the same species (or sometimes in related species). Although widely distributed among ostariophysans, it is not universally present. Some members of the superorder lack the fright reaction but possess an alarm substance (e.g., Serrasalminae) while others lack both the alarm substance and the reaction to alarm substances of other species (e.g., Loricariidae and Gymnotiformes).

The recognition of five major lineages and their sequencing mostly follows Fink and Fink (1981). They postulated, as is still usually accepted, gymnotiforms to be siluriform relatives and characiforms to be the primitive sister group of both, with cypriniforms being the sister group to this entire assemblage.

The superorder Ostariophysi is divided into two series, the Anotophysi and the Otophysi. In old literature (e.g., Regan, 1911a, b; Berg, 1940), prior to the inclusion of gonorynchiforms (Anotophysi), the name Ostariophysi was restricted to what is herein recognized as the Otophysi.



Phylogeny of major groups of Ostariophysi.

The Late Jurassic genus †*Tischlingerichthys* from Germany was interpreted by Arratia (1999) as a primitive, stem-group ostariophysan, or possibly a stem-group anotophysan or gonorynchiform.

Five orders, about 80 families, 1,347 genera, and about 10,388 species. The three largest families—Cyprinidae (3,006), Characidae (1,306), and Loricariidae (915)—account for 5,227 (or 50%) of the species. The ostariophysans contain about 28% of the known fish species in the world while accounting for about 68% of the freshwater species. They are present on all continents and major land masses except Antarctica, Greenland, and New Zealand (Australia has a few catfishes secondarily derived from marine groups). About 123 species are marine (the chanid, the gonorynchids, half of the plotosids, and most ariids).

Series ANOTOPHYSI. One order, the sister group to all other Ostariophysi.

Order GONORYNCHIFORMES (31)—milkfishes. Orbitosphenoid absent; pterosphenoids reduced and separated; parietals small and separated by supraoccipital; quadrate condyle far forward; teeth absent on fifth ceratobranchial; Baudelot's ligament absent; three sets of intermuscular ribs including cephalic ribs; anterior rib of third vertebra enlarged and shorter than preceding ribs; first three vertebrae specialized and associated with one or more cephalic ribs; first neural arch enlarged making contact with occipital margin; second uroneural elongate anteroventrally; suprabranchial (= epibranchial) organ present (consisting of lateral pouches in the posterior part of the branchial chamber behind the fourth epibranchials); mouth small; jaws toothless; postcleithra absent; 5–6 hypurals. (Fink and Fink, 1981, Grande and Poyato-Ariza, 1999; Poyato-Ariza et al., 2010)

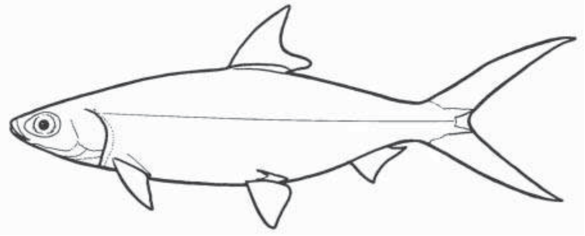
Gonorynchiform monophyly has been convincingly demonstrated using both morphological (e.g., Fink and Fink, 1981; Gayet, 1993; Poyato- Ariza, 1996a; Grande and Poyato-Ariza, 1999; Poyato-Ariza et al., 2010) and molecular data (e.g., Lavoué et al., 2005; Davis et al., 2013; Betancur et al., 2013a;

Near, Dornburg, and Friedman, 2014). Contrary to Nelson (2006) and following Grande and Poyato-Ariza (1999) and Poyato-Ariza et al. (2010), we recognize three families within the order: Chanidae, Gonorynchidae, and Kneriidae. Kneriidae are divided into two subfamilies, Phractolaeminae and Kneriinae.

Although the monophyly of the order is not in doubt, the interrelationships of its families pose an interesting problem. All morphological analyses (e.g., Fink and Fink, 1981, 1996; Gayet, 1993a, b, c; Johnson and Patterson, 1997; Grande and Poyato-Ariza, 1999; Poyato-Ariza et al., 2010) strongly support a sister-group relationship between Gonorynchidae and Kneriidae, but molecular (mtDNA and nuclear DNA) studies (e.g., Lavoué et al., 2005; Davis et al., 2013; Near, Dornburg, and Friedman, 2014) support a relationship between Chanidae and Kneriidae, with Gonorynchidae sister to those two. Davis et al. (2013) demonstrated in their study that when the morphological and molecular data are partitioned, the two data sets give incongruent results with respect to the position of gonorynchids. It seems fair to say that another look at gonorynchiform interrelationships will be worthwhile. That being said, we have decided to list the three families within Gonorynchiformes without implying a particular sister-group relationship.

Three families, seven genera, and about 37 species (of which 31 are freshwater). The order has a broad geographic distribution in marine and freshwater environments of Southeast Asia, Africa, and the Indo-Pacific.

Family CHANIDAE (106)—milkfishes. Marine and brackish (occasionally freshwater); tropical and subtropical Indian and Pacific (rare in eastern Pacific from Southern California to Peru).



Small, anteriorly directed mouth cleft; premaxilla large, very broad and laterally convex; maxilla expanded posteriorly; opercular bone expanded; suprapreopercle present. The following two subfamilies, one of them fossil-only, are recognized following Poyato-Ariza (1996a), Grande and Poyato-Ariza (1999), and Poyato-Ariza (2010).

†SUBFAMILY RUBIESICHTHYINAE. Nasal bone small but flat, not reduced to a tubular ossification; maxillary articular process very curved; preopercular limbs forming an acute angle. There are two Early Cretaceous fossil genera from Spain, †*Gordichthys* and †*Rubiesichthys* (Poyato-Ariza, 1996b; Poyato-Ariza et al., 2010). The Early Cretaceous genus †*Nanaichthys* from Brazil is thought to be the sister-group of the former two (Amaral and Brito, 2012).

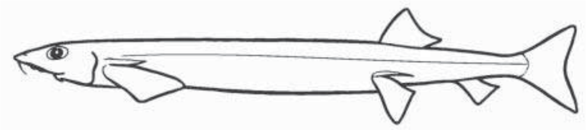
Subfamily Chaninae. Maxillary process for articulation with autopalatine present; ridge on anteroventral limb of preopercular bone present (Poyato-Ariza, 2010); body compressed; mouth terminal; upper jaw non-protractile; scales cycloid, 78–90 in lateral line; dorsal-fin rays 13–17; anal-fin rays 9–11; pelvic-fin rays 10–12; branchiostegals four; swimbladder present.

Milkfish spawn in the ocean, but metamorphosis from the ribbon-like larval stage occurs in brackish water. Young are caught close to shore and reared in coastal ponds. Breeding, however, does not occur in the ponds. Females are highly fecund and can lay millions of eggs. Adults feed primarily on algae. For a detailed study of the ossification and development of *Chanos chanos* see Arratia and Bagarinao (2010). *Chanos* is of considerable importance as a food fish in Southeast Asia. In the Philippines (where they are known as bangos, bangus, or sabalo), Indonesia, and especially in Taiwan, there is an extensive fishpond culture for them. Maximum length 1.8 m, usually 1.0 m.

Early Cretaceous fossil genera include †*Aethalionopsis* (Belgium), †*Dastilbe* (Brazil and Equatorial Guinea), †*Parachanos* (Gabon), and †*Tharrhias* (Brazil, and sister to *Chanos*).

One extant species, *Chanos chanos* (e.g., Poyato-Ariza, 1996a; Grande and Arratia, 2010).

Family GONORYNCHIDAE (107)—beaked sandfishes. Marine; Indo-Pacific, rare in southern Atlantic (e.g., St. Helena).



Tooth plates on entopterygoids and basibranchial 2; brush-like cranial intermuscular bones (Davis et al. 2013 report that such intermusculars have been observed in very large *Chanos* specimens); frontals long and narrow; modified ctenoid scales on body and head; elongation of lower limb of preopercle; body elongate; mouth inferior; protractile upper jaw; fins posteriorly placed in most. Unobservable in fossil forms, the swimbladder is lost, and a single barbel at the tip of the pointed snout is present.

One genus, *Gonorynchus,* with five species (Grande, 1999b). Total vertebrae 54–66; lateral-line scales about 160–220; dorsal-fin rays 10–12; anal-fin rays 8 or 9; pectoral-fin rays 10-11 rays; pelvic-fin rays 8-9.

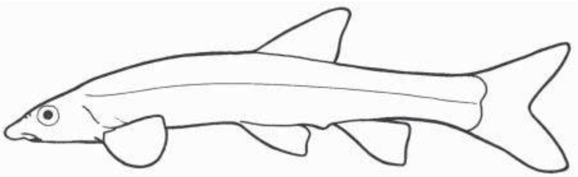
Named fossil gonorynchid genera include †*Notogoneus* (North America, Europe, Australia, some of them freshwater, Late Cretaceous to Oligocene, sister to *Gonorynchus* plus the Middle Eastern forms), the Cretaceous †*Charitosomus* (Germany, Lebanon), †*Judeichthys* and †*Ramallichthys* (Middle East), †*Charitopsis* (Lebanon), and the recently described †*Sapperichthys* (Mexico) considered to be the most primitive gonorynchid (Poyato-Ariza, 1996; Grande, T., 1996, 1999a, b; Grande, T., and Poyato-Ariza, 1999; Grande, L., and T. Grande, 2008; Grande, T., and L. Grande, 2008; Grande, T., and Arratia, 2010; Amaral et al., 2013).

Family KNERIIDAE (108)—knerias and snake mudheads. Freshwater; tropical Africa.

Parietals highly reduced or lost; foramen magnum enlarged, dorsally bounded by supraoccipital; extensions on lateral ethmoids; number of supraneurals reduced to one; fusion of haemal arch and preural centrum 2.

We recognize two subfamilies following Grande and Poyato-Ariza (1999) and Poyato-Ariza et al. (2010): Kneriinae and Phractolaeminae.

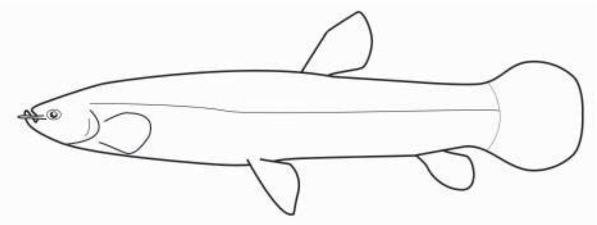
SUBFAMILY KNERIINAE. Knerias. Freshwater; tropical Africa and Nile. Mesethmoid long and slender with anterior elongate extensions; fifth basibranchial ossified in adult specimens; neural arch of first vertebra and supraocipital in contact; supraneurals greatly reduced in size or absent; mouth inferior or subterminal; upper jaw protractile; pelvic-fin rays 6–9. *Kneria* and *Parakneria* have cycloid scales and a lateral line, whereas the small and paedomorphic species of *Cromeria* and *Grasseichthys* have a naked body and lack a lateral line. Maximum length about 15 cm (attained in *Parakneria marmorata* of Angola).



Four genera with 30 species: *Kneria* (13 species), *Parakneria* (14 species), *Cromeria* (2 species, *C. nilotica* and *C. occidentalis* as recognized by Britz and Moritz, 2007), *Grasseichthys gabonensis* (1 species).

†*Mahengichthys singidaensis,* from the Eocene Mahenge deposits of Tanzania, Africa, is the first and only described fossil belonging to the subfamily Kneriinae, Tribe Kneriini, and sister to the genus *Kneria* (Davis et al., 2013).

SUBFAMILY PHRACTOLAEMINAE. Snake mudheads. Freshwater; tropical Africa (Niger Delta and Malebopool and Zaire systems). Frontals wide, and short; articular process of maxilla wider than the rest of maxilla; symplectic absent; expansion of anteroventral limbs of preopercles resulting in bones overlapping; spike-like interopercle; infraorbitals 2–4 greatly enlarged; mouth superior; quadrate positioned near anterior tip of head; protractile upper jaw; pelvic-fin rays six; cycloid scales; body elongate; dorsal and anal-fin rays about six; esophagus with numerous folds; swimbladder divided into numerous small alveoli and adapted to airbreathing; single median abdominal vein resulting from fusion of the iliac veins. Maximum length about 16 cm.



One species, *Phractolaemus ansorgii*, also known as the African Mudminnow (D. F. E. Thys van den Audenaerde, in Daget et al., 1984; Poll and Gosse, 1995), sometimes classified as a separate family.

Series OTOPHYSI. The Otophysi are diagnosed in part by the presence of a Weberian apparatus (named in honor of E. Weber, who described them in 1820). A Weberian apparatus consists of a series of modified bony elements and ligaments of the anterior four or five vertebrae that connect the swimbladder with the inner ear for sound transmission, accompanied by modifications to the otic region of the skull. Characters of the Otophysi include: ventral expansion of the anterior one or two supraneurals to form a synchondral joint with their corresponding neural arches; modification of the first neural arch elements to form the scaphium and claustrum; second neural arch to form the intercalarium; the third pleural rib to form the tripus; and the fourth pleural rib to form the os suspensorium; presence of a sinus impar, anteriorly bifurcated pelvic girdle; presence of a compound terminal centrum consisting of the first preural centrum, ural centra one, ural centrum two, anterior uroneurals and hypural two (Fink and Fink, 1981, 1996; Wiley and Johnson, 2010).

Early fossils (as old as Early Cretaceous) that may be stem otophysans include †*Chanoides macropoma*, †*Lusitanichthys*, †*Nardonoides*, and †*Santanichthys* (Patterson, 1984a, b; Malabarba and Malabarba, 2010; Mayrink et al., 2014). The genus †*Salminops* had been said to be an otophysan ostariophysan but is now Teleostei *incertae sedis* (Mayrink et al., 2015).

Fink and Fink (1981) gave strong morphological evidence for the phylogenetic relationships within the series Otophysi (comprising herein three subseries and four orders, the Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes). The Cypriniformes (in the Cypriniphysi of Fink and Fink, 1981, 1996) are sister to the Characiformes (in the Characiphysi) plus the Siluriphysi (with two orders: Siluriformes and Gymnotiformes).

Dimmick and Larson (1996) provided strong support for this phylogenetic hypothesis (as opposed to earlier views postulating different relationships), in a combined analysis of molecular data (from 160 phylogenetically informative sites from nuclear-encoded ribosomal RNA and 208 phylogenetically informative sites from the mitochondrial genes encoding ribosomal RNA and the valine transfer RNA) and 85 morphological characters and found generally high congruence between the molecular and morphological data in supporting this view of a sister-group relationship between the Gymnotiformes and Siluriformes, those two together being a sister group to the Characiformes, and of the earliest phylogenetic split within the crown-group Otophysi being the separation of Cypriniformes from all other otophysans. However, the molecular data of those authors analyzed separately produced a topology that differs from the analysis of the combined data, for example, in grouping the Characiformes and the Gymnotiformes as sister taxa (this was an earlier idea of some morphologists). Dimmick and Larson examined the sources of the incongruence between the molecular and morphological data, and found that the morphological characters in their study were significantly less homoplastic than those from nuclear encoded rRNA, which were in turn significantly less homoplastic than those from mitochondrial DNA.

In some more recent molecular studies (e.g., Ortí and Meyer, 1997; Ortí, 1997; Broughton, 2010) characiforms are hypothesized to be the sister group to gymnotiforms, while in others (e.g., Near et al., 2012a; Betancur-R. et al., 2013a) a characiform + siluriform sister-group relationship was obtained. Additionally, Nakatani et al., 2011, and Chen et al. (2013) hypothesized a paraphyletic Characiformes closer to Siluriformes than to Gymnotiformes. Because of the inconsistencies among results based on molecular and morphological data in recent years, and among various molecular studies using data from mitochondrial and/or nuclear genes, we follow herein Fink and Fink (1996) and Wiley and Johnson (2010) for otophysan ordinal relationships.

Four orders, 77 families, 1,340 genera, and 10,350 species.

Subseries Cypriniphysi. One order, the sister group to all other extant Otophysi.

Order CYPRINIFORMES (32)—carps, loaches, minnows, and relatives. Kinethmoid present (a median bone or cartilage between ascending processes of premaxillae); pre-ethmoid present and tightly articulated between vomer and mesethmoid; dorsomedial process of autopalatine present; autopalatine articulating in a socket of the endopterygoid; loss of ectopterygoid-autopalatine anterior overlap; fifth ceratobranchial (the pharyngeal bone) enlarged, with teeth ankylosed to the bone (bound by collagenous fibers to the bone in other ostariophysans with teeth, pharyngeal teeth absent in gyrinocheilids); pharyngeal teeth opposed to enlarged posterior process of basioccipital bone (which encloses the dorsal aorta) rather than to upper pharyngeal elements, the basioccipital process against which the pharyngeal teeth press usually covered by a pad (tough horny pad in cyprinids, soft pad in catostomids); elongation of the lateral process of the second vertebral centrum, projecting into somatic musculature; ascending process to premaxillae; upper jaw usually protractile; mouth (jaws and palate) always toothless; adipose fin absent (except in some cobitoids); head almost always scaleless; branchiostegals three (Fink and Fink, 1996, 1999; Wiley and Johnson, 2010; Conway et al., 2010; Conway, 2011).

Ordinal status is given here following Fink and Fink (1981). The order is divided into two main groups, usually classified either as superfamilies (as here; see Conway, 2011) or as suborders. Siebert (1987) gave valuable insights into family interrelationships. An early molecular (mitochondrial sequence) study was that of Liu et al. (2002); since then, numerous others have been published by a variety of research teams. The history of phylogenetic studies of the Cypriniformes was reviewed by Simons and Gidmark (2010), Conway et al. (2010) and Conway (2011).

Thirteen families, with about 489 genera and 4,205 species. The greatest diversity is in Southeast Asia. Cypriniforms are natively absent from Australia and South America. Members of this order are popular aquarium fishes, especially the minnows and loaches.

Superfamily Cyprinoidea. Two families, the very diverse Cyprinidae, with numerous subfamilies, hundreds of genera, and thousands of species, and the much smaller Psilorhynchidae with a single genus.

Family CYPRINIDAE (109)—minnows, carps, and loaches. Freshwater, very rarely occurring in brackish water; North America (northern Canada to southern Mexico), Africa, and Eurasia.

Pharyngeal teeth in one to three rows, never more than eight teeth in any row; absence of an uncinate process on epibranchials one and two; absence of pharyngobranchial one; pharyngobranchial two overlapping with pharyngobranchial three; barbels present or absent; upper jaw bordered only by premaxilla (i.e., maxilla excluded from gape); upper jaw usually protrusible; spinelike rays in dorsal fin in some.

Pectenocypris balaena of Borneo, a phytoplankton feeder, has over 200 gill rakers. The largest species are the tetraploid barbine *Catlocarpio siamensis* of Thailand, which is known to reach at least 2.5 m and probably 3 m, and *Tor putitora* of the Brahmaputra River (eastern India), which reaches about 2.7 m; other large Asian species (2 m or larger) include *Elopichthys bambusa* and *Barbus esocinus.* The largest North American cyprinid is *Ptychocheilus lucius* of the Colorado River. Many species are under 5 cm, including miniature danionines discussed below.

The family Cyprinidae is the largest family of freshwater fishes and, with the possible exception of Gobiidae, the largest family of vertebrates. The common name for the family most frequently used in North America is minnow, while in Eurasia it is carp. The incredible diversity in the family is reflected in the many other common names that have been applied to its genera and species, including barbel, bitterling, bleak, bream, chub, dace, goldfish, gudgeon, labeo, loach, riffle dace, roach, rudd, shiner, and tench.

Various members of this family are important as food fish, as aquarium fish, and in biological research. Species particularly widely used include the Common Carp (and koi) *Cyprinus carpio,* Goldfish *Carassius auratus,* and Zebra Danio or zebrafish *Danio* (*Brachydanio*) *rerio.* The last species is a popular aquarium fish that is being used extensively in developmental (embryological) and genetic research.

The earliest definite cyprinid fossils are of Eocene age from Asia; the earliest European and North American ones are of Oligocene age. Examples include †*Parabarbus* from the Oligocene and possibly Eocene of Kazakhstan (Sytchevskaya, 1986), the Eocene †*Palaeogobio* from China (e.g., Chang and Chen, 2008), and an Early Eocene fossil assigned to *Blicca* from England (Cavender, 1991). Cavender (1991) presented evidence that cyprinids were absent from North America in the Eocene, a time when other otophysans were present (catostomids, hypsidorids, and ictalurids), the oldest North America cyprinids being from the Oligocene. Major extinctions occurred about 40 and 38 million years ago (Eocene) in the North American faunas when a marked global cooling occurred.

Much information on this family is found in Winfield and Nelson (1991). Gilbert (1998) gave a type catalogue of recent and fossil taxa.

The recognition and composition of the subfamilies has changed over the years. Important contributions were those of Arai and Kato (2003), and chapters in Winfield and Nelson (1991) by G. J. Howes and W. J. Rainboth. Cavender (1991) and Cavender and Coburn (1992) preferred to recognize two subfamilies: those with "head usually kept relatively rigid when feeding and having relatively slow swimming movements in feeding" (Cyprininae, as also given in Nelson, 1994), and those with a "head lifting mechanism when feeding and often feeding with rapid swimming movements" (Leuciscinae, six subfamilies of Nelson, 1994). Species are being described and genera revised on a broad front.

About 367 genera and about 3,006 species.

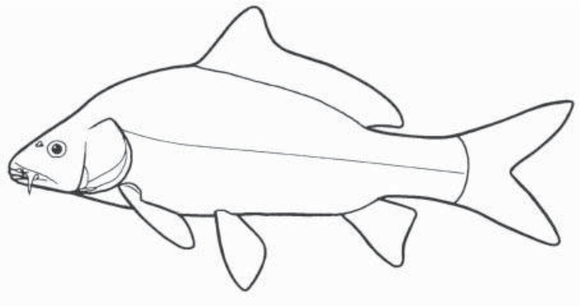
SUBFAMILY DANIONINAE. Africa and southern Eurasia, including Indonesia. Barbels absent. The composition and monophyly of this group are uncertain (e.g., Tang et al., 2010). Genera include *Amblypharyngodon, Aspidoparia, Barilius, Boraras, Chela, Danio* (synonym *Brachydanio*), *Danionella, Engraulicypris, Esomus, Fanfangia, Horadandia, Leptocypris, Mesobola, Neobola, Opsaridium, Opsarius, Paedocypris, Raiamas, Rasbora, Rasboroides, Rastrineobola, Salmostoma, Sundadanio, Tanichthys,* and *Thryssocypris.* About 319 species (Eschmeyer and Fong, 2015).

Miniaturization and truncated development is seen in several genera of danionines including *Danionella, Paedocypris,* and *Sundadanio* (e.g., Kottelat et al., 2006; Britz et al., 2011; Conway et al., 2011; Britz and Conway, 2015). One of the smallest cyprinids and among the smallest freshwater fishes is *Danionella translucida,* from lower Myanmar, in which females are ripe at 10–11 mm and the longest specimen known is 12 mm, with *D. mirifer* of upper Myanmar being only slightly larger, reaching up to 14 mm (Britz, 2003). Britz and Conway (2015) recently studied the truncated development of another miniature species from Myanmar, the Dracula Minnow, *Danionella dracula,* which has unusual morphologies such as fang-like processes from the upper jaws of males.

However, the smallest fish and arguably the smallest vertebrate known is another danionine, *Paedocypris progenetica* from Sumatra. Mature females range in size from 7.9 to 10.3 mm, and mature males from 8.2 to 10.1 mm (Kottelat et al., 2006). There is controversy over the relationships of *Paedocypris* as to whether it is nested within Danioninae (Britz and Conway, 2009, 2011; Britz et al., 2009) or is a much more primitive cyprinid (Mayden and Chen, 2010).

SUBFAMILY LABEONINAE (LABEOS). Asia and Africa. Weberian apparatus contacting skull with supraneural bones; basioccipital cross-section concave; first anal pterygiophore enlarged. e.g., *Bangana, Cirrhinus, Crossocheilus, Epalzeorhynchos* (in the aquarium trade these are called "sharks" including the flying fox and the red-tailed black shark), *Garra, Hongshuia, Labeo, Osteochilus, Rectoris,* and *Sinigarra.* Fossil *Labeo* are noted in Africa by Stewart (2001). Some species of *Labeo* and of other genera are also called "sharks." Perhaps 402 species (Eschmeyer and Fong, 2015).

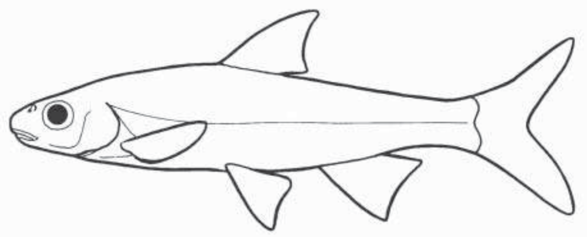
Subfamily Cyprininae (carps and goldfishes). Median rostral process of supraethmoid; most with two pairs of barbels; maxillary foramen for maxillaris nerve innervating anterior barbel; e.g., *Aaptosyax, Anematichthys, Aulopyge, Barbus, Capoeta, Carassius* (Crucian Carp and Goldfish), *Catlocarpio, Cyclocheilichthys, Cyprinion, Cyprinus* (e.g., Common Carp, koi), *Gymnocypris, Luciobarbus, Luciocyprinus, Poropuntius, Rohtee,* and *Varicorhinus* (e.g., Pasco-Viel et al., 2012; Yang et al. 2015). *Aaptosyax,* a giant but critically endangered cyprinid described in recent decades from the Mekong River (Rainboth, 1991) is included only tentatively in this subfamily as its relationships are disputed and only limited molecular evidence has been presented to date (Yang et al., 2015).



Cyprinines include many of the most important food fishes, many of the most commonly kept aquarium fishes, and many of the most troubling invasive species. About 50 species (Eschmeyer and Fong, 2015).

Subfamily barbinae. The barbels. Europe, Africa, and Asia. Mouth inferior; lower lip often swollen or modified; two pairs of barbels; often large, living near the bottom; females often with larger anal fin than males; e.g., *Acrossocheilus, Balantiocheilos, Barbus* (barbels, barbs), *Clypeobarbus, Diptychus, Haludaria, Hampala, Onchystoma, Oreichthys, Pseudobarbus, Puntius, Schizothorax* (this and its relatives, known as snow trouts, occur at high elevations), *Sinocyclocheilus* (with many cave species in China), *Semiplotus, Spinibarbus,* and *Tor.* About 744 species (Eschmeyer and Fong, 2015).

Subfamily Leuciscinae (minnows). North America and Eurasia (except, e.g., India and Southeast Asia). Includes Alburninae in this treatment. Barbels absent; maxillary foramen absent; pharyngeal teeth usually in two rows; high number of vertebrae (Howes, 1991). Several monophyletic lineages are recognized within this taxon, but the subfamily itself may not be monophyletic. *Phoxinus* was at one time recognized as being in both the Nearctic and Palearctic (Holarctic), but Strange and Mayden (2009) resurrected the genus *Chrosomis* for the Nearctic species. The phylogeny of North American Leuciscinae was analyzed by Bufalino and Mayden (2010). Gidmark and Simons (2014) reviewed North American cyprinids and recognized additional genera in this subfamily.



North American genera include *Acrocheilus, Agosia, Algansea, Aztecula, Campostoma, Chrosomis, Clinostomus, Codoma, Couesius, Cyprinella, Dionda, Eremichthys, Ericymba, Erimonax, Erimystax, Evarra, Exoglossum, Gila, Hemitremia, Hesperoleucus, Hybognathus, Hybopsis, Iotichthys, Lavinia, Lepidomeda, Luxilus, Lythrurus, Macrhybopsis, Margariscus, Meda, Moapa, Mylocheilus, Mylopharodon, Nocomis, Notemigonus* (may have affinity with Alburninae), *Notropis, Opsopoeodus, Oregonichthys, Orthodon, Pararhinichthys, Phenacobius, Pimephales, Plagopterus, Platygobio, Pogonichthys, Pteronotropis, Ptychocheilus, Relictus, Rhinichthys, Richardsonius, Semotilus, Siphateles, Snyderichthys, Stypodon, Tampichthys,* and *Yuriria* (based on Nelson et al., 2004). Old world genera in this clade include *Abramis* (bream), *Acanthobrama, Achondrostoma, Alburnoides, Alburnus* (bleak) (synonym *Chalcalburnus*) (type genus of the subfamily Alburninae, recognized in Nelson, 1994), *Anaecypris, Aspius, Atrilinea, Ballerus, Blicca, Chondrostoma* (nase), *Delminichthys, Elopichthys, Hypophthalmichthys, Iberochondrostoma, Iberocypris, Kottelatia, Ladibesocypris, Leucaspius, Leuciscus* (e.g., the ide, formerly in the genus *Idus*), *Luciobrama, Leucos, Ochetobius, Oreoleuciscus, Pachychilon, Parachondrostoma, Pelasgus, Pelecus, Petroleuciscus, Phoxinellus, Phoxinus, Protochondrostoma, Pseudaspius, Pseudochondrostoma, Pseudophoxinus, Rasbosoma, Rhynchocypris* (synonym *Eupallasella*), *Rutilus* (roach), *Sarmarutilus, Scardinius* (rudd), *Squalius, Telestes, Tribolodon, Tropidophoxinellus,* and *Vimba* (e.g., Kottelat and Freyhof, 2007a).

There are about 564 species in the subfamily (Eschmeyer and Fong, 2015).

SUBFAMILY ACHEILOGNATHINAE. Eurasia (including Japan, absent from central Asia). Ovipositor in females (eggs usually laid in mantle cavity of unionid bivalves); males with tubercle-bearing plates; uroneurals absent; coracoid foramen reduced or absent; deep, compressed bodies. Three genera, *Acheilognathus, Rhodeus* (bitterlings), and *Tanakia,* with about 75 total species (Eschmeyer and Fong, 2015).

SUBFAMILY GOBIONINAE (GUDGEONS). Eurasia. One pair of barbels; derived sensory canal patterns and frontal and supraoccipital morphology; benthic fishes usually with flat belly, inferior mouth, and laterally spread pectoral fins (Kottelat and Freyhoff, 2007b). The phylogeny of Gobioninae was reconstructed by Tang et al. (2011), who recognized three or more main clades. All genera except *Gobio* (gudgeons) restricted to eastern Asia (including Japan). For example, *Coreius, Gnathopogon, Gobio, Gobiobotia, Microphysogobio, Pseudogobio, Pseudorasbora, Romanogobio, Sarcocheilichthys* (type of the nominal subfamily Sarcocheilichthyinae), *Saurogobio,* and *Squalidus,* with 201 total species (Eschmeyer and Fong, 2015).

SUBFAMILY TINCINAE. Southeast Asia. One pair of barbels; supraorbital and infraorbital sensory canals separated; scales small and deeply embedded (Howes, 1991; Kottelat and Freyhof, 2007). Two genera with four species, *Tinca* (*T. tinca,* the Tench) of Eurasia, and *Tanichthys* (3), which may be its closest relative (Tang et al., 2010; Chang et al., 2014).

MOST MEMBERS OF THE FOLLOWING FOUR SUBFAMILIES, formerly thought to be Danioninae (also referred to as Rasborinae in some works), have been grouped together based on molecular evidence by several studies, including those of Wang et al. (2007), Fang et al. (2009) and Tang et al. (2010). Wang et al. (2007) used the existing name Xenocyprinae for the entire clade. Fang et al. (2009) called them "ex-Danioninae," and then Liao et al. (2011) suggested using Opsariichthyinae, a name coined by Rendahl (1928) to also include *Zacco.* Tang et al. (2013), using molecular data, but a different method of analysis, synonymized all four of these under the subfamily name "Oxygastrinae Bleeker, 1860a," arguing that this name had priority over all others. However, we disagree about the nomenclature. "Oxygastrinae" is based on Bleeker's (1860a, b) term Oxygastri, which is not an available family-group name, as also pointed out recently by Kottelat (2013) and by Van der Laan et al. (2014).

When Bleeker (1860a, b) used Oxygastri to describe a small group of genera, he included the genus *Chela* in both publications, but he did not (separately) include *Oxygaster,* because, as he (1860b) made clear, he regarded *Chela* as a senior synonym of *Oxygaster.* Basing the name on a genus then considered invalid (a junior synonym) disqualified Oxygastri, even with corrected spelling, from being made available as a family-group taxon (ICZN 1999, Articles 11.7.1, 64) in Bleeker's publications. Kottelat (2013) also suggested (plausibly, in our view) that Bleeker intended it to be a descriptive term, and not a family-group name based on a type genus. Bleeker himself did not use the name in his later work, as Tang et al. (2013) admitted. Therefore, we are confident that Tang et al. (2013) and others are mistaken in using that name, and we use Opsariichthyinae herein for the subfamily that contains it. Pending a greater consensus about the details of their relationships, which are not agreed upon by different studies, we provisionally retain all four separate subfamilies.

SUBFAMILY OPSARIICHTHYINAE. Eastern Asia. *Macrochirichthys, Opsariichthys, Oxygaster, Zacco.* Tang et al. (2011) include also *Aphyocypris, Candidia, Nicholsicypris, Nipponocypris, Parachela, Pararasbora, Parazacco,* and *Yaoshanicus* in this clade. This subfamily name would apply to a clade that contained all four of these subfamilies if monophyly of the entire clade is confirmed.

SUBFAMILY CULTRINAE. Eastern Asia. Barbels absent; vomer extending anterior to ethmoid to floor kinethmoid cavity; parasphenoid flattened anteriorly with deep ventral groove; sensory canal as prominent ridge on platform formed mostly by parietal; belly keel-like; body compressed (Howes, 1991). For example, *Chanodichthys*, *Culter*, *Erythroculter*, *Hemiculter*, and *Parabramis*.

SUBFAMILY SQUALIOBARBINAE. East Asia. Large cyprinids with enlarged subtemporal fossa; palatine articulating with lateral border of supraethmoid; enlarged intercalar; divided levator posterior muscle. *Ctenopharyngodon* (*C. idella*, Grass Carp), *Mylopharyngodon* (1), and *Squaliobarbus* (1) (e.g., Howes, 1961; Kottelat and Freyhof, 2007).

SUBFAMILY XENOCYPRINAE. East Asia. Pharyngeal teeth compressed, six teeth in main row. For example, *Aristichthys*, *Hypophthalmichthys* (Bighead Carp and Silver Carp, introduced into North America, India, and Southeast Asia), and *Xenocypris*. Miocene fossils include †*Eoxenocypris* and †*Xenocyproides* (Chang et al., 1996).

Family PSILORHYNCHIDAE (110)—mountain carps. Freshwater mountain streams; Bangladesh, Nepal and adjacent India to western Myanmar (former Burma) and China.

Mouth small, subterminal; jaws with sharp horny edges, lips fleshy; barbels absent; gill openings narrow; ventral surface of head flattened; dorsal fin with 10–12 rays (7–9 branched) and anal fin with two unbranched and five branched rays; pectoral fin with at least four unbranched rays; lateral line complete, with 31–50 scales; pharyngeal bone with one row of four teeth; swimbladder reduced. Maximum length about 8 cm. Given in Nelson (1994) as a subfamily of Cyprinidae. Conway (2011) analyzed the osteology and morphology-based relationships of *Psilorhynchus* and recommended continued use of the family name.

One genus, *Psilorhynchus* (synonym *Psilorhynchoides*), with twenty species, of which the majority have been named in recent decades (e.g., Yazdani et al., 1993; Vishwanath and Manojkumar, 1995; Conway and Britz, 2010; Conway and Kottelat, 2007).

Superfamily Cobitoidea. The arrangement of families follows Siebert (1987), with some modifications after Conway (2011) and Kottelat (2012). Catostomids are usually regarded as the sister group to the remaining extant cobitoids (e.g., Conway, 2011). The cobitids and balitorids were recognized as a monophyletic group by Sawada (1982), in part, because the opisthotic is absent and the orbitosphenoid is in contact with the supraethmoid-ethmoid complex. Conway (2011) also included Nemacheilidae in this group.

One fossil-only family; 11 extant families with about 121 genera and 1,179 species.

†Family JIANGHANICHTHYIDAE. Freshwater, Eocene, China. Adults deep-bodied; caudal fin forked; dorsal and anal fins emarginate; first anal principal ray branched; sensory canal in frontal bone-enclosed posteriorly but roofed by bony shelf anteriorly; maxilla with three anterior processes; 4th pleural rib of Weberian apparatus short with hooked end; pharyngeal bones lacking enlarged teeth.

This fossil-only family of freshwater fishes was recently named by Liu et al. (2015). Its precise relationships to the extant families are uncertain, but it clearly represents a separate, very distinct lineage. One genus with one species, †*Jianghanichthys hubeiensis.*

THE NEXT TWO FAMILIES ARE UNITED IN A CLADE BY SOME recent studies (e.g., Saitoh et al., 2006; Conway, 2011).

Family GYRINOCHEILIDAE (111)—algae eaters. Freshwater mountain streams; Southeast Asia. These fishes are used extensively in home aquaria.

Pharyngeal teeth absent; ventral mouth as sucking organ used to attach onto objects; gill slit consisting of a dorsal and ventral opening, inhalent aperture entering into gill chamber above the exhalent aperture; no barbels; number of gill rakers about 140; lateral-line scales 39–43. Feeds exclusively on algae. Size up to 30 cm.

One genus, *Gyrinocheilus*, with three species (Roberts and Kottelat, 1993).

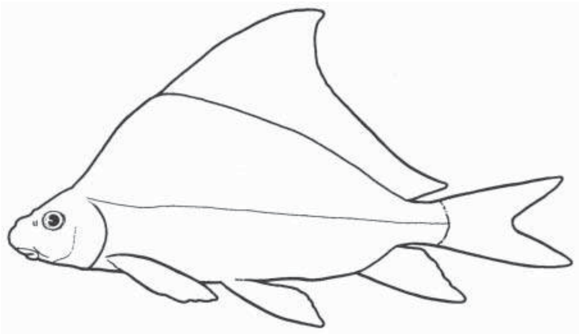
Family CATOSTOMIDAE (112)—suckers. Freshwater; China, northeastern Siberia, North America.

Basioccipital process finely fenestrated; decending ventral process of second vertebral centrum and outer arm of the os suspensorium sutured forming a transverse plate, mandibular portion of the preopercular-mandibular canal absent; row of 16 or more pharyngeal teeth; lips usually thick and fleshy with plicae or papillae; upper jaw usually bordered by premaxilla and maxilla; 18 (9+9) principle caudal rays; tetraploids. Maximum length about 1.0 m, less than 60 cm for most species.

Thirteen genera with 78 species (about 45 species placed in the genera *Catostomus* and *Moxostoma*). In Nelson (1994), three subfamilies were recognized following Smith (1992); here, an additional subfamily is recognized based on Harris and Mayden (2001) and Harris et al. (2002). Several more recent molecular studies have attempted to resolve internal relationships of catostomids (Doosey et al. 2010; Chen and Mayden, 2012; Clements et al., 2012), but none has been comprehensive both with genetic loci or taxa sampled.

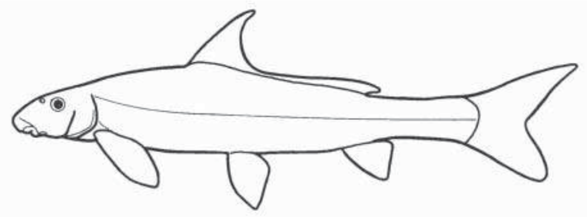
Smith (1992:800) reviewed the Asian and North American fossil record. Fossil genera include †*Amyzon* from North America and China (with a suggested relationship to ictiobines; Wilson, 1977; Bruner, 1991a; Smith, 1992; Liu et al., 2016), †*Vasnetzovia* from Asia, and †*Plesiomyxocyprinus* from China (Liu and Chang, 2009), all of Eocene age. Bruner (1991b) compiled a bibliography to the family, and Gilbert (1998) made a type catalogue of recent and fossil taxa.

SUBFAMILY MYXOCYPRININAE. Twelve to 14 anal-fin rays; 52–57 dorsal-fin rays; 47–55 lateral-line scales; body relatively deep.



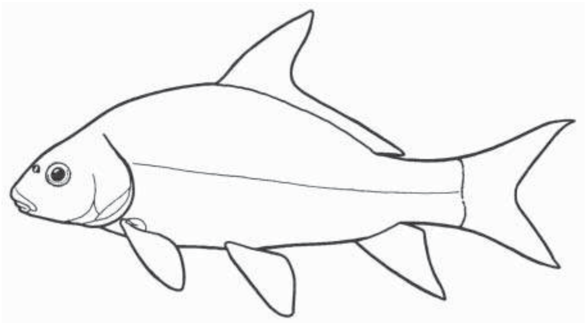
One species, *Myxocyprinus asiaticus*, primarily in Yangtse and Hwang Ho drainages, eastern China.

SUBFAMILY CYCLEPTINAE. Seven anal-fin rays; 28–37 dorsal-fin rays; 51–59 lateral-line scales.



One genus, *Cycleptus* (blue suckers), with two species, Mississippi and adjacent gulf coastal drainages of southern United States and Mexico.

SUBFAMILY ICTIOBINAE. Seven to 11 anal-fin rays; 22–32 dorsal-fin rays; 33–43 lateral-line scales; 115–190 pharyngeal teeth (the highest of all catostomids; Eastman, 1977). Canada to Guatemala (absent from Pacific drainages). The northernmost species is *Carpiodes cyprinus* (North Saskatchewan and Red Deer rivers, Alberta); the southernmost is *Ictiobus meridionalis* (Guatemala).



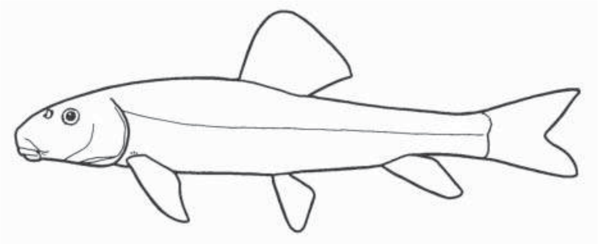
Two genera, *Carpiodes* (3, quillback and carpsuckers) and *Ictiobus* (5, buffaloes), with eight species.

SUBFAMILY CATOSTOMINAE. Seven anal-fin rays; 10–18 dorsal-fin rays; 30–120 lateral-line scales. Northeastern Siberia, Alaska, and northern Canada to Mexico. The northernmost species is *Catostomus catostomus* (rivers adjacent to the Arctic coastline); the southernmost is probably *Moxostoma congestum* (northeastern Mexico).

Nine genera and 67 species.

TRIBE ERIMYZONTINI. The lateral line is incomplete or absent. Two genera, *Erimyzon* (4, chubsuckers) and *Minytrema* (1), with five species, eastern Canada and United States.

TRIBE CATOSTOMINI. Mostly Western North America. Lateral line present; more than 50 lateral-line scales. Most suckers are benthic feeders and have a ventral mouth, but species of *Chasmistes* (lake suckers) are midwater planktivores and have a large, terminal mouth.



Two species are particularly widespread: *Catostomus catostomus* (Longnose Sucker) extends from New York to eastern Siberia and *C. commersonii* (White Sucker) extends from Georgia to British Columbia.

Four genera, *Catostomus* (27, with subgenera *Catostomus* and *Pantosteus*), *Chasmistes* (5), *Deltistes* (1), and *Xyrauchen* (1), with 34 species. The genus *Catostomus* may be paraphyletic (Harris et al., 2002).

TRIBE THOBURNIINI. Eastern Canada and United States. Swimbladder posterior chamber reduced in size. Two genera, *Hypentelium* (3, hog suckers) and *Thoburnia* (3, paraphyletic if all species included), with six species, Considered monophyletic by Harris and Mayden (2001).

TRIBE MOXOSTOMATINI. Lateral line present; fewer than 50 lateral line scales. Most of the species live in eastern and central Canada and United States and in Mexico. One, *Moxostoma macrolepidotum*, which is particularly widespread, extends from easternmost United States to Alberta. One genus, *Moxostoma* (synonyms *Lagochila*, based on Smith, 1992, and *Scartomyzon*, based on Harris et al., 2002) (redhorses and jumprocks), with 22 species. The extinct Harelip Sucker, *Moxostoma lacerum* (*Lagochila lacera*), has not been collected for over 100 years and is not included in the generic species counts.

THE REMAINING NINE FAMILIES of Cobitoidea constitute the loaches. The first two, the Botiidae and Vaillantellidae, were united in a clade by Conway (2011).

Family BOTIIDAE (113)—botiid loaches. Freshwater; Asia, from India to China and Japan, including Sumatra, Java, and Borneo. Several species are popular aquarium fishes. Kottelat (2012) raised the former cobitid subfamily Botiinae to family rank.

Two pairs of rostral barbels; cephalic lateral-line system inconspicuous; caudal fin deeply forked; body compressed.

Eight genera, *Ambastaia* (2), *Botia* (10) (e.g., zebra loach *B. striata*), *Chromobotia* (1) (the clown loach *C. macracanthus*), *Leptobotia* (14), *Parabotia* (12), *Sinibotia* (6), *Syncrossus* (5) (e.g., tiger loach *S. bermorei*), and *Yasuhikotakia* (7), with about 57 species (Kottelat, 1998, 2004a, 2012).

Family VAILLANTELLIDAE (114)—long-fin loaches. Borneo and Sumatra (Kottelat, 2012). Greatest diversity in southern Asia; bottom dwellers. Maximum length about 40 cm.

Dorsal fin long, with 59-71 rays (Nalbant and Banarescu, 1977; Conway et al., 2010).

One genus, *Vaillantella*, with three species.

THE REMAINING FAMILIES were recognized as distinct by Kottelat (2012).

Family COBITIDAE (115)—loaches. Freshwater; Eurasia and Morocco.

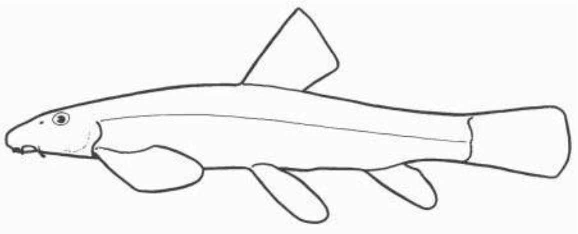
Coronomeckelian absent; orbitosphenoid not in contact with pterosphenoid; endopterygoid reduced to a rod and articulating loosely with metapterygoid; concave posteroventral edge of opercle; horizontal and descending processes of the fourth pleural rib from the lateral and posterior surfaces of the swimbladder; fusion of the first preural centrum to the parhypural and hypural one; fusion of the second preural centrum to the last haemal arch (Conway at al., 2010); body worm-like to fusiform; mouth subterminal; 3–6 pairs of barbels present; erectile spine below eye (anterior in *Acantopsis*); one row of pharyngeal teeth; one pair of rostral barbels (rarely absent); cephalic lateral-line system conspicuous; caudal fin usually rounded or slightly emarginate (forked in *Acantopsis* and some *Lepidocephalichthys*).

Popular aquarium species belong to such genera as *Acantopsis* (horse-face loach), *Pangio* (e.g., kuhli or coolie loaches), and *Misgurnus* (e.g., weatherfishes, including a color form of the Japanese weather loach called the golden dojo). *Misgurnus* has been widely released and is now invasive in many locations including North America and Australia.

The accepted spelling of the family name is Cobitidae, not Cobitididae as introduced into the literature in 1980 (Opinion 1500 of the International Commission on Zoological Nomenclature, 1988, stemming from a case published in the Bulletin of Zoological Nomenclature in December 1986 by M. Kottelat).

About 21 genera, e.g., *Acantopsis, Acanthopsoides, Bibarba, Canthophrys* (synonym *Somileptus*), *Cobitis, Iksookimia, Kichulchoia, Koreocobitis, Kottelatlimia, Lepidocephalichthys, Lepidocephalus, Microcobitis, Misgurnus, Neoeucirrhichthys, Niwaella, Pangio* (synonym *Acanthophthalmus*), *Paralepidocephalus, Paramisgurnus, Protocobitis, Sabanejewia,* and *Theriodes* with about 195 species (e.g., Kottelat et al., 1993, 1998, 2012; Roberts, 1997).

Family BALITORIDAE (Homalopteridae) (116)—hillstream or river loaches. Freshwater; Eurasia.

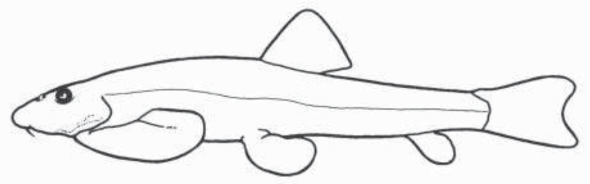


Three pairs of barbels present near mouth; exoccipitals separated from each other by the supraoccipital; interhyal absent; mesocoracoid fused with an enlarged cleithrum; enlargement of pelvic basipterygium; enlargement of pleural rib connected to pelvic basipterygium; gill opening restricted or not; paired fins enlarged with adhesive pads on ventral surface, orientated horizontally; pelvic fin separated or united under belly. These fishes, commonly known as the hill-stream loaches, have the body and head flattened, mouth subterminal, and paired fins adapted as adhesive organs. They are found in fast-flowing mountain streams from India through Southeast Asia including Sumatra, Java, and Borneo, to China and Taiwan.

According to Sawada (1982), balitorids and nemacheilids may be recognized as a separate lineage from cobitids by differences in the Weberian apparatus (e.g., by the Y-shaped tripus, the most posterior element of the Weberian ossicles). Nelson (1994) recognized two tribes that in earlier literature had been recognized as distinct at the family or subfamily level, the balitorines (= homalopterines) (with two or more unbranched anterior rays in both pectoral and pelvic fins) and gastromyzontines (single unbranched anterior ray in pectoral and pelvic fins). We now also separate the gastromyzontines from the balitorids as a third family following Kottelat (2012).

About 14 genera, e.g., *Balitora* (12) (see figure), *Balitoropsis* (10), *Bhavania* (1), *Cryptotora* (1), *Hemimyzon* (16), *Homaloptera* (11), *Homalopteroides* (6), *Homalopterula* (6), *Jinshaia* (3), *Lepturichthys* (2), *Metahomaloptera* (3), *Sinogastromyzon* (20), and *Travancoria* (2), with about 93 species (e.g., Tan and Martin-Smith, 1998; Freyhof, 2003; Freyhof and Serov, 2000; Kottelat, 1998, 2000a, 2001a,b, 2004b, 2012 and references therein).

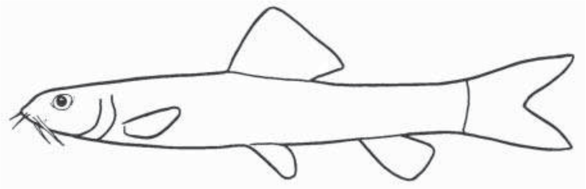
Family GASTROMYZONTIDAE (117)—gastromyzontid or sucker loaches. China and Southeast Asia. Formerly included within Balitoridae, the family is now considered distinct by Kottelat (2012) and herein.



Pectoral and pelvic fins modified into sucker organs for clinging to objects in fast-flowing streams; single unbranched anterior ray in pectoral and pelvic fins.

At least 18 genera, e.g., *Annamia* (1), *Beaufortia* (16), *Erromyzon* (4), *Formosania* (10), *Gastromyzon* (36) (lower figure), *Glaniopsis* (4), *Hypergastromyzon* (2), *Katibasia* (1), *Liniparhomaloptera* (4), *Neogastromyzon* (6), *Paraprotomyzon* (4), *Parhomaloptera* (1), *Plesiomyzon* (1), *Protomyzon* (4), *Pseudogastromyzon* (9), *Sewellia* (13), *Vanmanenia* (16), *Yaoshania* (1), with about 125 species.

Family NEMACHEILIDAE (118)—stone loaches. Eurasia and Ethiopia. The previous subfamily Vaillantellinae was raised to family status (see above) by Kottelat (2012).



Prepalatine present; no spine under or before eye; two pairs of rostral barbels and one pair of maxillary barbels; body elongate, rounded, or compressed; mouth subterminal; single unbranched ray in pectoral and pelvic fins; adipose-like fin present in some; scales present or absent.These loaches occur throughout much of Eurasia, with greatest diversity in the Indian subcontinent, Indochina, and China. One species occurs in Africa, in the Lake Tana drainage in Ethiopia. Several cave species are known from Iran, India, China, Thailand, and Malaysia (e.g., Proudlove, 2005). At least 42 genera, e.g., *Aborichthys, Acanthocobitis, Barbatula* (synonym *Orthrias*), *Heminoemacheilus, Lefua, Nemacheilus, Neonoemacheilus, Oreonectes, Paracobitis* (synonym *Adiposia*), *Pteronemacheilus, Schistura* (which contains the majority of species), *Traccatichthys, Triplophysa,* and *Yunnanilus* (synonym *Eonemachilus*), with at least 618 species (e.g., Sawada, 1982; Kottelat, 1998, 2000a, 2012; Freyhof and Serov, 2001; Vishwanath and Laisram, 2001; Bohlen and Slechtová, 2011).

The following three families were also recognized as distinct in Kottelat's (2012) review of world loaches, and possibly related to Balitoridae, Gastromyzontidae, and Nemacheilidae according to a molecular study by Bohlen and Šlechtová (2009).

Family BARBUCCIDAE (119)—fire-eyed loaches. Borneo and Thailand. This family was newly named by Kottelat (2012). One genus, *Barbucca,* with two species. Bohlen and Šlechtová (2009) found *Barbucca* to be close to Balitoridae, Serpenticobitidae, and Gastromyzontidae.

Family ELLOPOSTOMATIDAE (120)—sturgeon-mouthed loaches. Borneo and Thailand (Kottelat 2012). Snout squarish or oblique (vs rounded or pointed in other loaches); mouth very small, ventral, and highly protrusible; eyes very large; one pair of barbels; 35-38 pharyngeal teeth (vs 8-25 in others); see Roberts (1972). This family was named by Bohlen and Šlechtová (2009). One genus, *Ellopostoma,* with two species.

Family SERPENTICOBITIDAE (121)—serpent loaches. Mekong River basin of Southeast Asia. Mouth small, inferior; suborbital spine present; body with 7–8 regular, dark, vertical bars. The genus was named by Roberts (1997) and the family was named by Kottelat (2012). One genus, *Serpenticobitis*, with three species. Bohlen and Šlechtová (2009) found *Serpenticobitis* to be possibly the sister group to Gastromyzontidae.

Subseries Characiphysi. This clade, originally named by Fink and Fink (1981) to contain three orders, herein contains only the order Characiformes. Its sister group is the Siluriphysi (below). For character support see Fink and Fink (1996).

Order CHARACIFORMES (33)—characins. Teeth usually well developed and multicuspid (most are carnivores); replacement teeth on premaxillary and dentary forming in crypts; auditory foramen of prootic present; dorsomedial opening into posttemporal fossa present (Wiley and Johnson, 2010); adipose fin usually present; body almost always scaled (scales almost totally lacking in adults of the characid tetra *Gymnocharacinus bergii* of Argentina, which also lacks an adipose fin and is the most southerly known characiform); ctenoid or ctenoid-like scales in some; pelvic fin present (with 5–12 rays); anal fin short to moderately long (fewer than 45 rays); lateral line often decurved, sometimes incomplete; upper jaw usually not truly protractile; pharyngeal teeth usually present, but not usually specialized as in cypriniforms (anostomids have highly modified pharyngeal teeth); barbels absent; branchiostegals 3–5; usually three postcleithra; first hypural separated from the centrum by a gap in adults; usually 19 principal caudal-fin rays. Maximum length about 1.4 m, attained by *Hydrocynus goliath* of the Congo. At the opposite extreme, many members are under 3 cm, and the smallest reach a maximum size of about 13 mm.

Some members of this order are extremely colorful (many are silvery). Many species are popular aquarium fishes (often known as tetras). In South America, many are also important food fishes (e.g., *Brycon*).

Fossils include †*Paleohoplias* and †*Tiupampichthys* from South America (Gayet et al., 2003), †*Eocitharinus* (possibly in Citharinoidei) and †*Mahengecharax* (and possibly sister to the Alestiidae) from Africa (Murray, 2003a, b), and †*Sorbinicharax* (of the fossil family †Sorbinicharacidae) from the latest Cretaceous of Europe (Taverne, 2003; Otero et al., 2008). A Late Cretaceous partial jaw from Canada (Newbrey et al., 2009) was identified as a characiform because of the distinctive details of a complex interdigitating joint at the symphysis between its lower jaws. These European and North American fossil records show that the Characiformes were not restricted to the Southern Hemisphere during the Mesozoic.

The order contains at least 24 families, about 520 genera, and about 2300 species. All extant characins are confined to fresh water. More than 200 species occur in Africa, with the remainder in southwestern United States, Mexico, and Central and South America. The African members comprise three lineages—the citharinoids, the alestiids, and the one species of *Hepsetus.* Numbers of species for Central and South America taxa were listed by Reis et al. (2003).

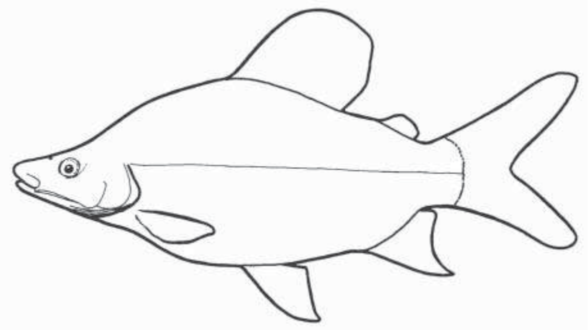
The classification of this large assemblage of poorly known species, with much morphological diversity and where convergent evolution is common remains controversial. The history of phylogenetic hypotheses for this order was reviewed by Vari (1998), Dahdul (2010), and Malabarbara and Malabarbara (2010). A comprehensive morphological phylogeny is that of Buckup (1998) and that classification was closely followed by Nelson (2006). Other recent molecular phylogenetic papers include those of Calcagnotto et al. (2005) and Oliveira et al. (2011). The last mentioned study suggested some rearrangements of family groups, some of which we adopt here. Some other major aspects remain unchanged in this edition, including the basic division into two suborders.

Suborder Citharinoidei. Teeth bicuspidate; second and third postcleithra fused; neural arch of fourth vertebra autogenous; premaxillary ascending process absent; scales ctenoid (cycloid in *Citharinus*); pelvic-fin rays relatively numerous.

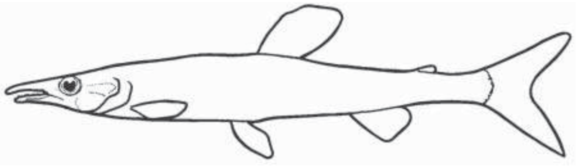
Fink and Fink (1981) and Buckup (1998) postulated this group to be the primitive sister group to all other characiforms, with *Xenocharax* being the most primitive member. That hypothesis is also supported by molecular studies including those of Ortí and Meyer (1997), Calcagnotto et al. (2005) and Oliveira et al. (2011).

Two families with twenty genera and about 109 species.

Family DISTICHODONTIDAE (122)—distichodontids. Freshwater; Africa.

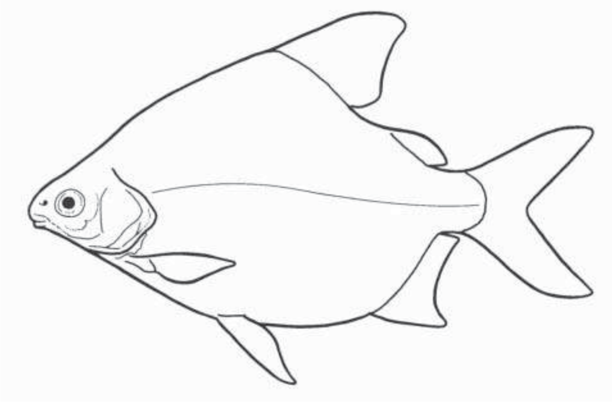


There are two typical morphotypes. One consists of those members with non-protractile upper jaws; they are micropredators and herbivores. Their body shape varies from deep (as in figure above) to shallow. The other consists of species with a movable upper jaw; they are carnivores, eating the fins of other fishes or the whole fish. Their body is usually elongate (as in figure below). This latter group was frequently recognized as a subfamily or family (Ichthyboridae). Maximum length 83 cm, attained in *Distichodus niloticus*.



Seventeen genera, *Belonophago, Congocharax, Distichodus, Dundocharax, Eugnathichthys, Hemigrammocharax, Hemistichodus, Ichthyborus, Mesoborus, Microstomatichthyoborus, Nannaethiops, Nannocharax, Neolebias, Paradistichodus, Paraphago, Phago,* and *Xenocharax,* with about 101 species (Daget and Gosse in Daget et al., 1984:184–211).

Family CITHARINIDAE (123)—citharinids. Freshwater; Africa.



Maxilla reduced and lacking teeth; body deep; dorsal and anal fins relatively long, dorsal with 16–24 rays and anal with 19–31 rays. Maximum length about 84 cm.

Three genera with eight species, *Citharinus* with six and the monotypic *Citharinops* and *Citharidium* (J. Daget in Daget et al. 1984:212–16).

Suborder Characoidei. This suborder contains all other characiforms, constituting the vast majority of taxa, at least 22 families, perhaps 500 genera, and 2200 or more species. Monophyly is supported by both morphological and molecular evidence (see above).

Superfamily Crenuchoidea. One family.

Family CRENUCHIDAE (124)—South American darters. Freshwater; eastern Panama and South America.

Paired foramina in the frontal bones, posterodorsally to the orbits (pronounced in Crenuchinae but very small in the Characidiinae). Crenunchids are relatively small, usually under 10 cm SL.

Both subfamilies were recognized as subfamilies of a large Characidae in Nelson (1994); they are placed here as a monophyletic group in the family Crenuchidae following Buckup (1998, 2003).

Twelve genera and 85 species.

SUBFAMILY CRENUCHINAE. Enlarged lateral frontal foramina (Buckup, 1998, lists additional synapomorphic features supporting monophyly for this taxon).

Poecilocharax lacks an adipose fin. Maximum length only 5.7 cm TL. Northern South America.

Two genera, *Crenuchus* (1) and *Poecilocharax* (2), with three species.

SUBFAMILY CHARACIDIINAE. Anal fin with fewer than 14 rays. Buckup (1993a), lists some 13 synapomorphic features supporting monophyly for this taxon and provides a diagnosis for the then known genera and species. Eastern Panama and South America south to northern Argentina and Uruguay). Some species of *Characidium* have the remarkable ability to climb waterfalls by using their paired fins to cling to the underside of rocks (Buckup et al., 2000). As noted by these authors, some species of *Awaous* and reportedly of Trichomycteridae, Astroblepidae, Rivulidae, and Balitoridae are able to surmount waterfalls (adult *Entosphenus* and juvenile *Galaxias* apparently can also surmount falls and/or dams).

Ten genera, *Ammocryptocharax* (4), *Characidium* (56), *Elachocharax* (4), *Geryichthys* (1), *Klausewitzia* (1), *Leptocharacidium* (1), *Melanocharacidium* (9), *Microcharacidium* (3), *Odontocharacidium* (1), and *Skiotocharax* (1), with about 82 species (Buckup, 1993b, 2003).

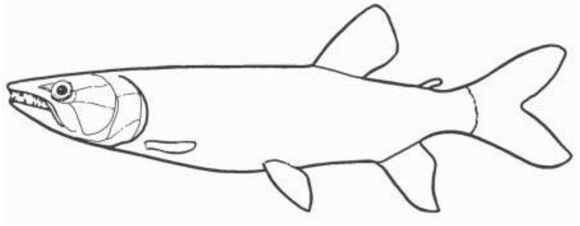
Superfamily Alestoidea. The orthography of the superfamily name is corrected to correspond to that of the type family. Two families, twenty genera and about 123 species.

Family ALESTIDAE (ALESTIIDAE) (125)—African tetras. Freshwater; Africa.

Buckup (1998) gave reasons for recognition as a separate family; had been considered a subfamily of Characidae in Nelson (1994) and Weitzman and Malabarba (1998).

About 19 genera, e.g., *Alestes*, *Brycinus*, *Bryconaethiops*, *Clupeocharax*, *Hemigrammopetersius*, *Hydrocynus*, *Ladigesia*, *Micralestes*, *Nannopetersius*, *Petersius*, *Phenacogrammus*, *Rhabdalestes*, and *Tricuspidalestes*, with about 118 species in total (Géry, 1995; Murray and Stewart, 2002).

Family HEPSETIDAE (126)—African pikes. Freshwater; tropical Africa.



Elongate pike-like body; long snout and large mouth with a few large canines and smaller pointed teeth; dorsal fin with seven rays placed before origin of anal fin which has nine rays (each also with two rudimentary rays); pelvic fin with nine rays; lateral-line scales 49–58, cycloid; adipose fin present.

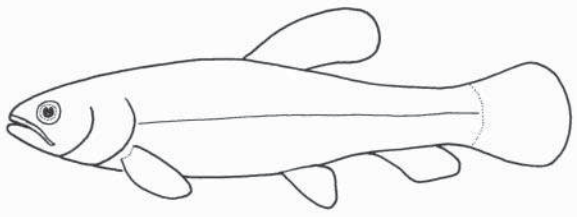
Maximum length 65 cm SL. Eggs are laid in a nest of floating foam. This species is considered to be a gamefish.

One genus and perhaps five species, including *Hepsetus odoe* (T. R. Roberts in Daget et al., 1984:138–39; Poll and Gosse, 1995; Skelton, 2001).

Superfamily Erythrinoidea. The oldest available family-group name (Van der Laan et al., 2014) within this superfamily appears to be Erythrinidae Valenciennes, 1847, which is the basis for the superfamily name Erythrinoidea adopted here.

Molecular evidence (Oliveira et al., 2011, fig. 4) suggested the existence of this clade, which includes Anostomidae, Chilodontidae, Curimatidae, Cynodontidae, Erythrinidae, Hemiodontidae, Parodontidae, Prochilodontidae and Serrasalmidae. The sequence in which the families are listed approximates their suggested phylogenetic relationships. Nine families with about 56 genera and about 466 valid species.

Family ERYTHRINIDAE (127)—trahiras. Freshwater; South America.

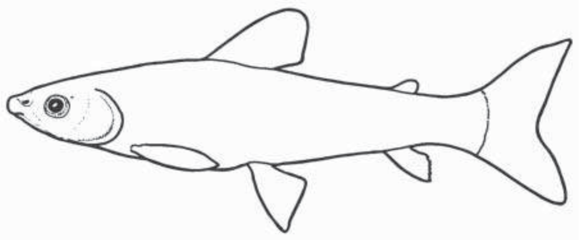


Gape long, extending beyond anterior margin of orbit; body cylindrical; five branchiostegals; pectoral-fin rays relatively few, 9–14; dorsal fin with 8–15 rays (plus three rudimentary ones), origin in front of anal fin and usually over pelvic fins (males of *Erythrinus* can have an elongated dorsal fin); anal fin short, 10–11 rays; adipose fin absent; caudal fin rounded; scales relatively large, 34–47 in lateral line; numerous teeth on palate.

Some are predators. Some can breathe air and move across land between ponds. They show some resemblance to *Amia* in body shape. Maximum length about 1.0 m, attained in *Hoplias lacerdae* and *H. macrophthalmus.*

Three genera, *Erythrinus* (2), *Hoplerythrinus* (3), and *Hoplias* (9), with 16 species (Oyakawa, 2003).

Family PARODONTIDAE (128)—parodontids. Freshwater, benthic; mountain streams of eastern Panama and most of South America.

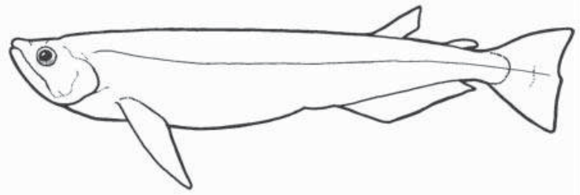


Peculiar fishes with ventral mouths and teeth modified for scraping algae off rocks; premaxillaries highly mobile and greatly enlarged; adipose eyelid absent; lateral line scales 35–43; pectoral fins expanded and flattened; vertebrae 35–41. Maximum length usually 15 cm.

Formerly considered a subfamily of Hemiodontidae. Recognized here following Buckup (1998) as forming a polytomy with two other clades of the Charocoidei, the Anostomoidea and all other characiforms (his clade 9, recognized in six superfamilies and 11 families).

Three genera, *Apareiodon* (15), *Parodon* (14), and *Saccodon* (3), with about 32 species (Pavanelli, 2003).

Family CYNODONTIDAE (129)—cynodontids. Freshwater; South America.

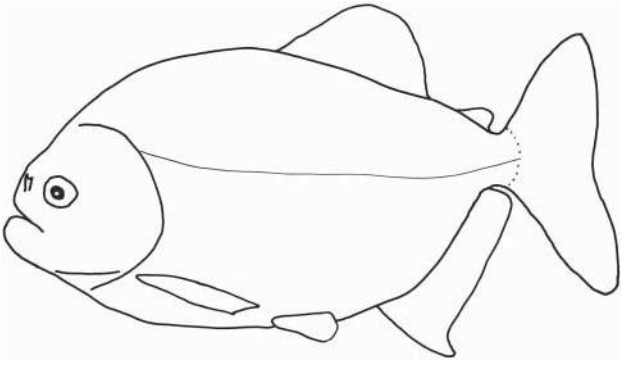


Mouth oblique; well-developed canines (saberlike in some); pectoral fins relatively large. Maximum length 65 cm. Two subfamilies were formerly recognized, Cynodontinae for *Cynodon*, *Hydrolycus*, and *Rhaphiodon* with the largest species and those with the longest canines, and Roestinae for *Gilbertolus* and *Roestes*. The Roestinae are now a subfamily of Acestrorhynchidae (see below).

Three genera, *Cynodon* (3), *Hydrolycus* (4), and *Rhaphiodon* (1, upper figure) with 8 species (Toledo-Piza, 2003).

THE NEXT TWO FAMILIES were hypothesized by Oliveira et al. (2011) to be a clade. Serrasalmidae were classified as a subfamily of Characidae by Nelson (2006).

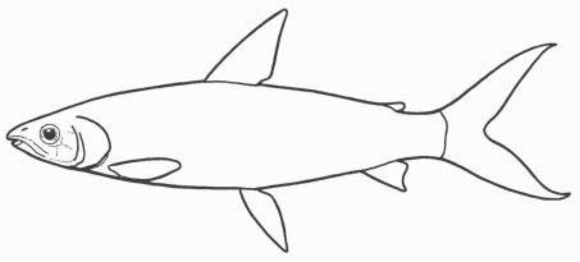
Family SERRASALMIDAE (130)—pacus, silver dollars, and piranhas. South America (introduced to other areas) (pacus, silver dollars, and piranhas). Maximum length about 80 cm SL.



Piranhas are thought to be mostly carnivorous, but other members of the family are mainly herbivorous (M. Jégu in Réis et al., 2003).Thompson et al. (2012) produced a molecular phylogeny of the family. Lundberg et al. (1986) described fossils of a living species of *Colossoma* from the Miocene, suggesting a very conservative history for a specialized herbivorous fish. Fossils from the Miocene of a very large, meter-long piranha called *Megapiranha*, said to be a link between pacus and piranhas, were found recently in Argentina (Cione et al., 2009). Whether it was carnivorous or herbivorous is still debated.

Sixteen genera, e.g., *Acnodon* (3), *Catoprion* (1), *Colossoma* (1), *Metynnis* (11), *Mylesinus* (3), *Myleus* (15), *Myloplus* (11), *Piaractus* (5), *Pristobrycon* (5), *Pygocentrus* (4), *Serrasalmus* (28), and *Tometes* (2), with about 92 species (Jégu in Reis et al., 2003:182–196).

Family HEMIODONTIDAE (131)—hemiodontids. Freshwater, usually pelagic; northern South America, south to the Paraná-Paraguay Basin.



Body subcylindrical to fusiform (and fast swimming fishes); adipose eyelid well developed; teeth absent on lower jaw in adults; gill membranes free; adipose eyelid present; lateral-line scales 50–125; pectoral-fin rays 18–23; 9–11 branched pelvic rays; most species with round spot on side of mid-body and stripe along lower lobe of caudal fin; vertebrae 40–45. Langeani (1998) listed synapomorphies for the family and its lower taxa. Maximum length about 30 cm SL.

Five genera with about 31 species, with several undescribed species (Langeani, 2003).

SUBFAMILY ANODONTINAE. *Anodus* has jaw teeth absent; numerous elongate gill rakers, up to 200 on first arch (more than any other characoid) depending on fish size; pharyngeal structures specialized for filter feeding on plankton, while *Micromischodus sugillatus* is the only hemiodontid with teeth on lower jaw throughout life.

Two genera, *Anodus* (2, synonym *Eigenmannina*) and *Micromischodus* (1), with three species (Langeani, 2003).

SUBFAMILY HEMIODONTINAE. Two tribes with three genera and about 28 species.

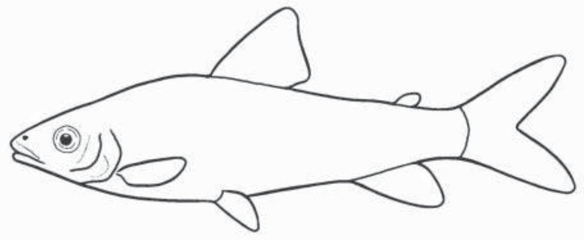
TRIBE HEMIODONTINI. One genus, *Hemiodus* (synonyms *Hemiodopsis* and *Pterohemiodus*), with about 21 species (Langeani, 2003).

TRIBE BIVIBRANCHIINI. The only characiform with a highly protrusible upper jaw having a unique mechanism of protrusion (especially pronounced in *Bivibranchia*); premaxilla minute and firmly attached to anterior end of maxilla. *Bivibranchia* also has a number of other derived modifications, including a unique elaboration of the glossopharyngeal and vagus nerves.

Two genera, *Argonectes* (2) and *Bivibranchia* (synonym *Atomaster*, 5), with about seven species (Langeani, 2003).

THE NEXT TWO FAMILIES recognized here, Anostomidae and Chilodontidae, have been proposed to form a monophyletic group (Vari, 1983) though results from some molecular analyses (e.g., Oliveira et al., 2011) have neither confirmed nor strongly rejected the grouping. Mandible relatively short; upper and lower pharyngeal dentition enlarged; two or more cusps on all pharyngeal teeth; single tooth row on each jaw. Many of the species swim in an oblique head-down position, hence the common name headstanders for the group. Most species are herbivores or detritovores.

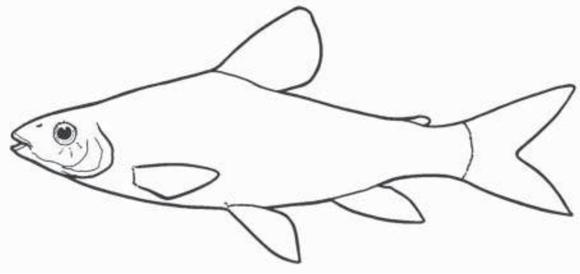
Family ANOSTOMIDAE (132)—toothed headstanders. Freshwater; southern Central America and South America.



Mouth small, nonproctractile (upturned in many species); series of only three or four teeth in upper and lower jaws; premaxilla (especially the ascending process) enlarged, much larger than the maxilla (which is excluded from the gape), and with enlarged teeth; body usually elongate; anal fin short, usually with fewer than 11 branched rays. Maximum length 80 cm SL.

Fourteen genera, *Abramites* (2), *Anostomoides* (3), *Anostomus* (5), *Gnathodolus* (1), *Hypomasticus* (8), *Laemolyta* (9), *Leporellus* (4), *Leporinus* (90), *Petulanos* (3), *Pseudanos* (5), *Rhytiodus* (4), *Sartor* (3), *Schizodon* (16), and *Synaptolaemus* (2), with at least 155 species (Garavello and Britski, 2003). A comprehensive osteological analysis and resulting phylogeny was published by Sidlauskas and Vari (2008).

Family CHILODONTIDAE (133)—headstanders. Freshwater; northern South America.



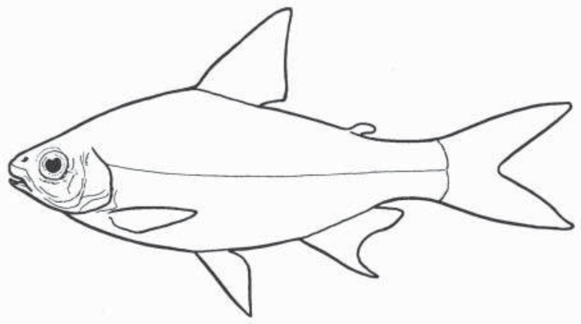
Premaxilla relatively small, maxilla much enlarged; uppermost of three postcleithra typical of the order missing; 7–10 branched dorsal-fin rays; lateral-line scales about 25–31; sixth lateral-line scale smaller than the other scales; highly modified pharyngeal apparatus; single series of relatively small teeth movably attached to jaws. Maximum length 18 cm.

Two genera, *Caenotropus* (4) and *Chilodus* (4), with eight species (Vari and Raredon, 2003).

THE FOLLOWING TWO FAMILIES constitute a clade according to both morphological (Vari, 1983, 1989; Buckup, 1998) and molecular (e.g., Oliveira et al., 2011) evidence. These two families were recognized in Nelson (1994) as subfamilies of the Curimatidae. They share a large sac-like muscular epibranchial organ that extends dorsal to the medial elements of the dorsal portions of the gill arches; and reduction or loss of dentition on the fifth upper pharyngeal tooth plate and loss on the ceratobranchial. Many of the synapomorphies uniting them are associated with food gathering and manipulation. Typically detritivorous.

About 11 genera and 124 species.

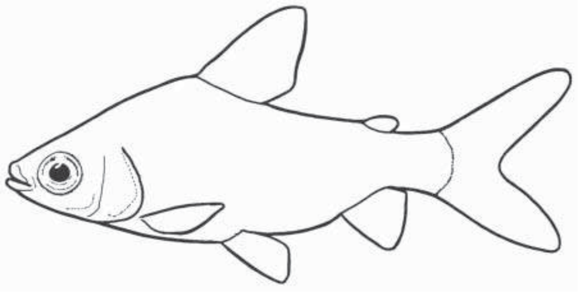
Family CURIMATIDAE (134)—toothless characiforms. Freshwater; southern Costa Rica to northern Argentina.



Jaw teeth absent (*Anodus* is the only other characiform lacking jaw teeth); enlarged lagenar capsule; gill rakers absent or poorly developed; four branchiostegal rays; branchiostegal membranes united to isthmus; vertebrae usually 30–36. Body form ranges from fusiform to deep-bodied and compressed; most are mullet-like in shape. Curimatids are microphagous fishes. Maximum length about 32 cm, attained in *Curimata mivartii.*

Eight genera, *Curimata* (synonym *Acuticurimata*), *Curimatella, Curimatopsis, Cyphocharax, Potamorhina* (synonyms *Gasterotomus, Suprasinelepichthys*), *Psectrogaster, Pseudocurimata,* and *Steindachnerina* (synonyms *Cruxentina, Curimatorbis*), with about 103 species (e.g., Vari, 1991, 1992a, b, 2003a, Vari et al., 2010). The eight genera that are currently recognized were keyed in Vari (1992b).

Family PROCHILODONTIDAE (135)—flannel-mouth characiforms. Freshwater; South America, primarily the northern half, south to Ecuador and Brazil.



Mouth protractile, forming a sucking disc (lips enlarged); jaw teeth present, numerous and small; predorsal spine present. Superficially resemble the cyprinid *Labeo.* Maximum length 74 cm TL., attained in *Prochilodus lineatus.*

Three genera, *Ichthyoelephas* (2), *Prochilodus* (13), and *Semaprochilodus* (6), with about 21 species (Vari, 1983; Castro and Vari, 2003).

Superfamily Characoidea. There are currently five families in this very large superfamily.

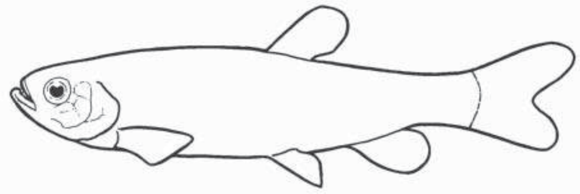
THE FOLLOWING TWO FAMILIES constitute a group that is suggested by Oliveira et al. (2011) to be sister to all remaining Characoidea. Those authors also proposed numerous other changed taxonomic groups that we find interesting and often plausible; however, because the changes are radical, not all suggestions have been followed at this time; where appropriate they are discussed in the text. The sequence in which families are listed below approximates that implied by the phylogeny of Oliveira et al. (2011).

Family LEBIASINIDAE (136)—pencil fishes. Freshwater; Costa Rica, Panama, and South America. This is the sister group to Ctenoluciidae on molecular evidence (Oliveira et al., 2011).

Gape short, usually not reaching orbit; three or four branchiostegals; adipose fin present or absent; anal fin with 8–14 rays; dorsal fin in front of anal fin, usually over pelvic fins (often behind in the Pyrrhulinini, which also have an elongate upper caudal fin lobe); scales large, 17–33 in longitudinal series.

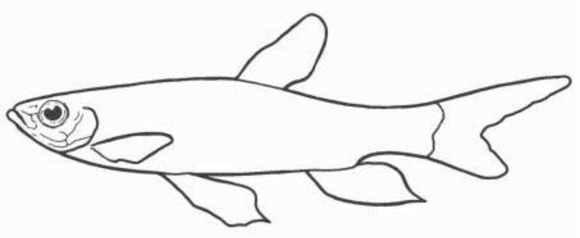
Two subfamilies with seven genera (*Derhamia* with one species is not assigned to subfamily) and about 77 species (Weitzman and Weitzman, 2003).

SUBFAMILY LEBIASININAE. Four branchiostegals; maxilla relatively long.



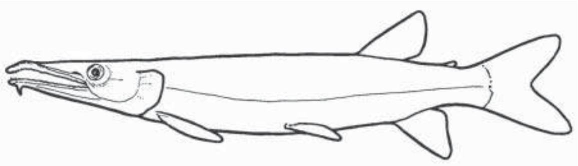
Two genera, *Lebiasina* (18) and *Piabucina* (9), with about 27 species.

SUBFAMILY PYRRHULININAE. Three branchiostegals; maxilla short.



Two tribes are recognized: Pyrrhulinini, with about 29 species, in *Copeina* (2), *Copella* (9), and *Pyrrhulina* (18); and Nannostomini, which contains the one genus of pencilfishes, proper, *Nannostomus* (20, synonym *Poecilobrycon*).

Family CTENOLUCIIDAE (137)—pike-characids. Freshwater; Panama and South America.



Elongate pike-like body, including having anal fin and usually the dorsal fin set far back on body; carnivorous; scales spinoid; pelvic fin with eight rays. Maximum length at least 67.5 cm SL.

Two genera, *Boulengerella* (5) and *Ctenolucius* (2), with seven species (Vari, 1995, 2003b).

Family ACESTRORHYNCHIDAE (138)—acestrorhynchids. Freshwater; South America (greatest diversity in Orinoco and Amazon basins).

Body elongate, pike-like body, and covered with small scales. Maximum length 40 cm SL.

SUBFAMILY ACESTRORHYNCHINAE. One genus, *Acestrorhynchus,* with 14 species.

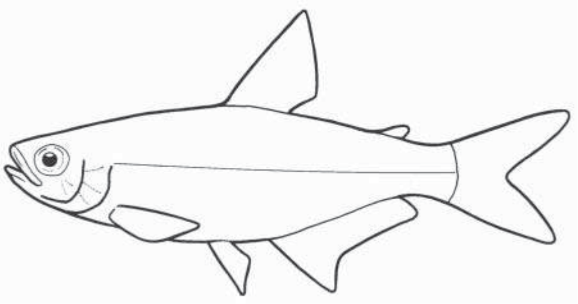
SUBFAMILY HETEROCHARACINAE. Mirande (2009) recognized this subfamily. Four genera, *Heterocharax* (3), *Gnathocharax* (1), *Lonchogenys* (1), and *Hoplocharax* (1), with six species.

SUBFAMILY ROESTINAE. Mirande (2009, 2010) did not study these two genera, previously placed within Cynodontidae (see above), but Oliveira et al. (2011) gave molecular evidence for placing them as a subfamily within the Acestrorhynchidae. Two genera, *Roestes* (3) and *Gilbertolus* (3), with six species.

Family CHARACIDAE (139)—characins. Freshwater; southwestern Texas, Mexico, and Central and South America.

Orbitosphenoid small, slender and separated from parasphenoid; rhinosphenoid present; lateral-line canal on caudal-fin membrane present; anterior ventral procurrent caudal-fin rays fused in laminar medial bone; attachment of medial tendon of A1 section of adductor mandibulae on quadrate near its articulation with preopercle (Mirande, 2010). Mirande (2009, 2010) published a detailed morphological phylogenetic analysis of the family.

This large and diversified family includes many fishes that are widely used in home aquaria and as food, a blind cavefish in Mexico (*Astyanax jordani* and *Astyanax* sp.) and Brazil (*Stygichthys typhlops*) (Proudlove, 2005), and a species that has dispersed into Texas, United States (*Astyanax mexicanus*).



The composition of this family has greatly changed with the removal of the formerly recognized subfamilies Crenuchinae and Characidiinae, now recognized in the family Crenuchidae, and the removal of African taxa (the formerly recognized Alestiinae, now a family). This now leaves the osteoglossids as the only completely freshwater fish family indigenous to both Africa and South America (some nandids enter brackish water, and cyprinodontids and cichlids have a few members that enter marine water).

A large number of taxa are *incertae sedis* as to subfamily, perhaps 500–600. Reis et al. (2003:212) preferred to emphasize that the relationships of many characids are too poorly known to recognize artificial subfamilies. Reis et al. (2003:104–105) listed nine species as *incertae sedis* in Characidae while Lima et al. in Reis et al. (2003:106–169), listed 88 genera containing 620 species as *incertae sedis*. More recently, some of those genera have been allocated to families as indicated below. Some of the remaining *incertae sedis* genera (with approximate numbers of species) are *Astyanax* (142, see note below), *Bramocharax* (4), *Exodon* (1), *Gymnocharacinus* (1), *Gymnocorymbus* (3, black tetras), *Hemigrammus* (figure above) (54), *Hyphessobrycon* (135, synonyms include *Megalamphodus*), *Jupiaba* (27), *Moenkhausia* (75), *Oligosarcus* (19), *Paracheirodon* (3, recognized at one time in *Hyphessobrycon*, cardinal, green neon, and neon tetras), *Pristella* (1), *Probolodus* (1), *Rachoviscus* (2), and *Stygichthys* (1). There have been many changes in the species recognized in the genus *Astyanax*, the most species-rich in the order, over the last several years (Reis et al., 2003): for example, *A. jordani* of Mexico (originally described in *Anoptichthys*), often treated as a synonym of *A. mexicanus*, is now recognized as valid; and *A. fasciatus*, described from Brazil, has been identified more recently in southern Mexico populations and has been introduced into the United States (Witmer and Fuller, 2011).

Much of the information on the subfamilies considered to be monophyletic by Reis et al. (2003:170–230) is from individual chapters in that work, written by specialists, and cited below.

SUBFAMILY IGUANODECTINAE. South America. Three genera, *Bryconops* (19), *Iguanodectes* (8), and *Piabucus* (3), with 30 species (Moreira in Reis et al., 2003:172–173).

Oliveira et al. (2011) suggest that the following two groups are closely related to each other as well as to *Engraulisoma* (1), *Lignobrycon* (1) and *Triportheus* (18), three genera that were formerly *incertae sedis*.

SUBFAMILY AGONIATINAE. South America (primarily in the Amazon basin). Resemble clupeiforms in body shape and color. One genus, *Agoniates*, with two species (Lima and Zanata in Reis et al., 2003:170).

SUBFAMILY CLUPEACHARACINAE. South America. Elongate body with midventral keel and long anal fin. One species, *Clupeacharax anchoveoides* (Lima in Reis et al., 2003:171).

SUBFAMILY BRYCONINAE. Southern Mexico (i.e., *Brycon guatemalensis*) to Argentina. Maximum length about 70 cm SL. Four genera, *Brycon* (75), *Chilobrycon* (1), *Henochilus* (1), and *Salminus* (2), with about 79 species (Lima in Reis et al., 2003:174–181). A recent molecular phylogenetic study of this group was that by Abe et al. (2014), who suggested that *Brycon* is paraphyletic, several species being closer to *Chilobrycon*, and that *Henochilus* is a junior synonym of *Brycon*.

SUBFAMILY STETHAPRIONINAE (SILVER DOLLAR TETRAS). South America (mainly Colombia to Argentina). Body deep; anteriorly directed spine preceding first dorsal-fin ray. Maximum length 9 cm. Six genera, *Brachychalcinus* (5), *Gymnocorymbus* (3), *Orthospinus* (1), *Poptella* (4), and *Stethaprion* (2), *Stichonodon* (1), with 16 species (Reis.in Reis et al., 2003:209–211).

SUBFAMILY RHOADSIINAE. Nicaragua and Costa Rica to Ecuador and Peru. Longest dorsal-fin ray may reach caudal fin in adult males. Maximum length 13.6 cm SL. Four genera, *Carlana* (1), *Nematocharax* (2), *Parastremma* (3), and *Rhoadsia* (2), with eight species (Cardosa in Reis et al., 2003:213–214).

SUBFAMILY CHARACINAE. Southern Mexico to South America (to La Plata basin). Maximum length 24 cm SL. About twelve genera, e.g., *Acanthocharax* (1), *Acestrocephalus* (8), *Bryconexodon* (2), *Charax* (16), *Cynopotamus* (12), *Exodon* (1), *Galeocharax* (3), *Phenacogaster* (20), *Priocharax* (2), and *Roeboexodon* (2), *Roeboides* (21), with more than 88 species (Lucena and Menezes in Reis et al., 2003:200–208).

Subfamily Tetragonopterinae. South America. Body deep; anal-fin base long. Most genera previously placed in this subfamily, as in Nelson (1994), are now placed as *incertae sedis* in Characidae because there is no evidence that they form a monophyletic group. One genus, *Tetragonopterus*, with eight species (Reis in Reis et al., 2003:212).

Subfamily Aphyocharacinae. South America. Eight genera, *Aphyocharax* (12), *Inpaichthys* (1), *Leptagoniates* (2), *Paragoniates* (1), *Phenagoniates* (1), *Prionobrama* (2), *Rhacoviscus* (2), *Xenagoniates* (1) with 22 species (Lima in Reis et al., 2003:197–199).

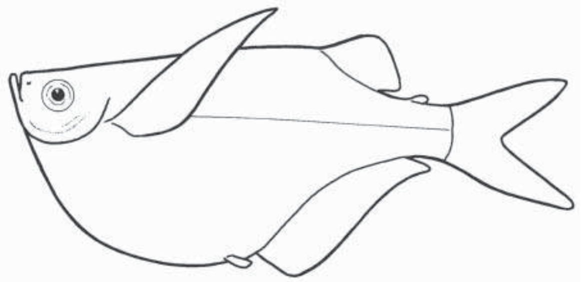
Subfamily Aphyoditeinae. The monophyly of this subfamily, supported most recently on morphological grounds by Mirande (2010), has been questioned on molecular results by Tagliacollo et al. (2012). Eight genera, *Aphyodite* (1), *Paarecbasis* (1), *Leptobrycon* (1), *Microschemobrycon* (7), *Aphyocharacidium* (2), *Oxybrycon* (1), *Axelrodia* (3), and *Tyttobrycon* (5), with 21 species.

Subfamily Cheirodontinae. Costa Rica and South America (to northern Argentina and including Trinidad). Two tribes are recognized: Cheirodontini with secondary sexual specializations in males of the ventral procurrent caudal-fin rays, and Compsurini, which are inseminators, where sperm is apparently transferred to the ovaries of females. Maximum length 6 cm, attained in *Spintherobolus papilliferus*. Sixteen genera, e.g., *Cheirodon* (10), *Compsura* (2), *Odontostilbe* (17), *Serrapinnus* (9), and *Spintherobolus* (4), with about 62 species (L. R. Malabarba in Reis et al., 2003:215–221).

Subfamily Gymnocharacinae. Monophyly of this subfamily was supported by Mirande (2010). Four genera, *Gymnocharacinus* (1), *Grundulus* (3), *Nematobrycon* (2), and *Coptobrycon* (1), with seven species.

Subfamily Stevardiinae (Glandulocaudinae). Costa Rica and South America (to northern Argentina and including Trinidad). Males with a putative pheromone pumping mechanism in the caudal region; internal fertilization in all known species are inseminators, as are those of the above-mentioned members of the tribe Compsurini, but with differing details. This is now a large group, with 44 genera, e.g., *Argopleura* (4), *Bryconamericus* (51), *Corynopoma* (1), *Creagrutus* (64), *Diapoma* (2), *Gephyrocharax* (12), *Glandulocauda* (2), *Hemibrycon* (19), *Knodus* (16), *Mimagoniates* (6), *Pseudocorynopoma* (2), *Tyttocharax* (3), and *Xenurobrycon* (4), with 438 species (Weitzman in Reis et al., 2003:222–230). Many of the genera in this group were listed by Nelson (2006) as *incertae sedis* within Characidae.

Family GASTEROPELECIDAE (140)—freshwater hatchetfishes. Freshwater; Panama and South America (absent in Chile). This family was placed within Characidae close to Salmininae and Bryconinae by a recent molecular study (Oliveira et al., 2011).



Strongly compressed head and body with protruding bony and muscular breast region; lateral line extremely short, extending to tail, or curved downward to approach origin of anal fin; dorsal-fin rays 10–17; anal-fin rays 22–44; pelvic fins and associated bones minute: teeth on third pharyngobranchial absent, four or five branchiostegals; adipose fin present (in larger species) or absent (in smaller species); frontal bone bearing a strong longitudinal ridge; posttemporal and supracleithrum fused into a single bone; cleithra of each side fused; no postcleithra. Maximum length about 6.8 cm SL.

These fishes are capable of jumping out of the water and making short flights.

Three genera, *Carnegiella* (4), *Gasteropelecus* (3), and *Thoracocharax* (2), with nine species (Weitzman and Palmer, 2003).

Subseries Siluriphysi. The Siluriphysi are ranked here as the third and last subseries within series Otophysi. The clade was unranked when it was named by Fink and Fink (1996) to contain two orders, Siluriformes and Gymnotiformes. Siluriphysi are the sister group to the subseries Characiphysi containing the single order Characiformes. Fink and Fink (1996) reviewed the extensive character support for the Siluriphysi. See the discussion above under series Otophysi concerning alternative phylogenies. Siluriformes + Gymnotiformes are diagnosed by a suite of characters discussed in Fink and Fink (1981) and listed in Wiley and Johnson (2010). These characters include the absence of the intercalar, sclerotic, and supraorbital bones; eye of adults reduced in size; ectopterygoids reduced in siluroids or absent in gymnotoids; presence of a single pharyngeal toothplate; Baudelot's ligament robust and bifurcated distally; all rib elements (especially the fourth and tripus) projecting from their centra at an angle close to horizontal; flanges on dorsal and ventral halves of pectoral-fin rays about equal in size; separate middle radial ossifications absent from all dorsal and anal fin pterygiophores; when present, principal caudal fin ray count usually 9/9 or fewer, rather than 10/9; and neural complex exhibiting development of cartilaginous bridges between supradorsals 3 and 4 of each side that fuse with supraneural 3 cartilage (Hoffman and Britz, 2006).

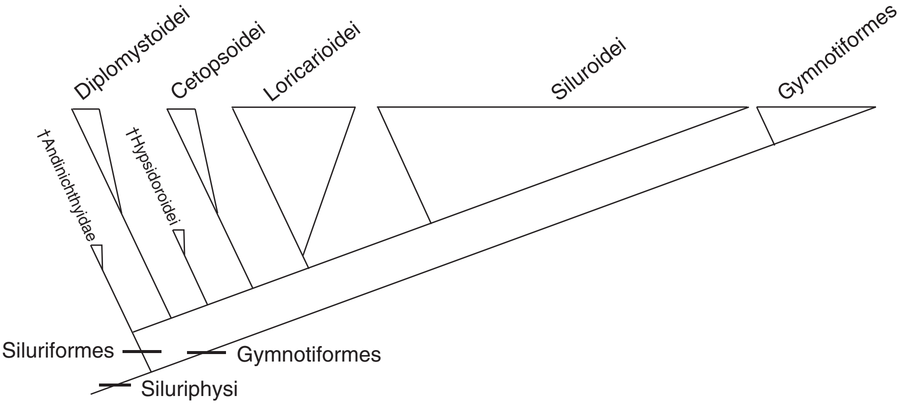
Order SILURIFORMES (Nematognathi) (34)—catfishes. Symplectic, subopercular, basihyal, and intermuscular bones absent; parietals presumed fused to supraoccipital; mesopterygoid very reduced; preopercle (with no horizontal limb) and interopercle relatively small; posttemporal presumably fused to supracleithrum; vomer often toothed (as are the pterygoid and presumed palatine); adipose fin usually present; spine-like (= spinous) rays often present at the front of the dorsal and pectoral fins (referred to as spines in family descriptions) (the dorsal fin of most catfishes technically has two spines—the first being very short and forming a locking mechanism for the second spine, which is usually the only one referred to in the family descriptions); body naked or covered with bony plates; normally up to four pairs of barbels on head, one nasal, one maxillary, and two on chin (i.e., on the lower jaw or mandible), the nasal and chin barbels may be variously absent; maxilla toothless and small, functioning with small autopalatine for precisely moving the maxillary barbel (except in Diplomystidae and the extinct †Hypsidoridae); principal caudal-fin rays 18 or fewer (most with 17, i.e., i,7-8,i); caudal skeleton varying between having six separate hypural plates to complete fusion of caudal elements; air-breathing organs in Clariidae and Heteropneustidae. Vertebrae are as few as 15 in some pangasiids to over 100 in some clariids, not including the Weberian vertebrae (Arratia et al., 2003). In contrast to other teleosts, where the urohyal forms as an unpaired ossification of the tendon of the sternohyoideus muscle, in siluriforms a“parurohyal” results from paired ossifications of the tendons, which then fuse in early ontogeny (Arratia et al. 2003). The Weberian apparatus of catfishes is described in detail by Chardon et al. (2003). For specific characters (e.g., os suspensoria lacking posteromedial process; parapophysis of second centrum absent; transformator process of tripus separated posteriorly by width of complex centrum) see Fink and Fink (1996) and Wiley and Johnson (2010). The many cave species are listed in Proudlove (2005).

Several catfish species are known to be poisonous or venomous (Perrière and Goudey-Perrière, 2003, gave a detailed review). They can inflict severe wounds with their spines (primarily those of the pectoral fin) and inject a poison produced by glandular cells in the epidermal tissue covering the spines. Most species are passive stingers (e.g., *Noturus*). Some, such as *Heteropneustes fossilis* of India, which has a painful and potentially dangerous sting, have an aggressive behavior with records of attacks on humans and other fishes. Stings from *Plotosus lineatus* may result in death.

In many areas, catfishes are popular sports fishes and valued food items. They are also widely used as tropical aquarium fishes. All members of this order are appropriately referred to as catfishes, despite attempts for marketing purposes to restrict use of the term to one family (Nelson et al., 2002). The largest catfish is *Silurus glanis* which commonly reaches 3 m in length; a pangasiid and pimelodid are also known to reach exceptionally large sizes. Many catfishes have a maximum length of under 12 cm.

Extensive information on all aspects of catfishes may be found in various chapters in Arratia et al. (2003); for example, apart from papers cited below, chapters 1 and 4 by G. Arratia give, respectively, an overview of the catfish head skeleton and of the postcranial skeleton, and chapter 5 by B. G. Kapoor, B. Khanna, R. Diogo, E. Parmentier, and M. Chardon reviews the internal anatomy. A detailed review of higher-level names was given by Ferraris and de Pinna (1999). Ferraris (2007) more recently produced a detailed checklist and type catalog for Siluriformes including fossil taxa.

Valuable reviews of past classifications, as well as information on the groups, are found in de Pinna (1998), Diogo (2003a), and Teugels (2003). The classification here is modified from that in de Pinna (1998) and that work, based largely on his 1993 unpublished Ph.D. dissertation, should be consulted for many synapomorphies of clades. The family descriptions below do not necessarily give diagnostic features. Parts of the classification are based on the molecular results of Sullivan et al. (2006) though that work left many deeper nodes within Siluroidei unresolved.



One view of relationships among the main subgroups of Siluriphysi.

Forty families with about 490 genera and about 3,730 species. Of these, about 2,053 species (excluding strictly marine ones of Ariidae) occur in the Americas. Two families, Ariidae and Plotosidae, consist largely of marine species, but they have representatives that are frequently found in brackish and coastal waters and sometimes only in fresh water. Other catfish families are freshwater groups, although some have species that can invade brackish water.

Including Eocene or Oligocene fossils from Antarctica (Grande and Eastman, 1986), catfishes are now known from all continents. The sister group of the Siluriformes is usually considered to be the Gymnotiformes (see above under Otophysi and Siluriphysi) although some preliminary molecular phylogenies place them as sister to Characiformes (e.g., Betancur-R. et al., 2013a) or sister to characoid characiforms (e.g., Nakatani et al., 2011).

As noted by Ferraris in Reis et al. (2003:254), *Conorhynchos conirostris* of Brazil was formerly not assigned to any family and was placed *incertae sedis*, but Sullivan et al. (2006) have now found evidence that it is close to or in Heptapteridae. See also Sullivan et al. (2013) for additional evidence that *Conorhynchos* is close to Heptapteridae and another *incertae sedis* genus, *Phreatobius*, is close to Pseudopimelodidae and Pimelodidae.

A new family of catfishes was described by Rodiles-Hernandez et al. (2005), the Lacantuniidae, erected for a single species from southern Mexico.

A molecular phylogenetic and biogeographic study (Lundberg et al., 2007) later concluded that *Lacantunia* indeed represents a separate family, closest to Claroteidae and surprisingly in an unnamed clade of catfishes with African distributions.

Another unusual new catfish from western India was named by Vincent and Thomas (2011). *Kryptoglanis glanis* is a stygobitic (groundwater-dwelling) catfish with developmentally truncated morphology (Lundberg et al., 2014) and assigned to a new family by Britz et al. (2014).

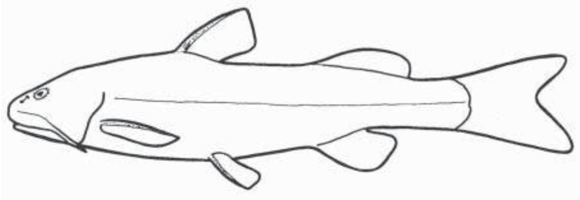
The fossil record, beginning in the late Late Cretaceous (fossils are known from all continents except perhaps Australia), was reviewed by Gayet and Meunier (2003). The checklist and type catalog of Ferraris (2007) also lists fossils. Some fossil taxa not placed in the families below include an unnamed genus of late Late Cretaceous age from Bolivia; fossils assignable to the Arioida (sensu Lundberg, 1993), Late Cretaceous, Bolivia; †*Bucklandium*, Eocene, England; †*Fajumia*, Eocene, Egypt; and the so-called "titanoglanis," not formally named, from the Eocene of Arkansas (Gayet and Meunier, 2003).

†Family ANDINICHTHYIDAE. Late Cretaceous to Paleocene, Bolivia, based on skeletal fragments. Extrascapular canal perhaps present (a primitive feature and unique among catfishes); dermal skull bones ornamented. Genera include †*Andinichthys,* †*Incaichthys,* and †*Hoffstetterichthys*.

Suborder Diplomystoidei. This may be the primitive sister group of all other extant catfishes (Grande, 1987; Diogo, 2004; Diogo and Peng, 2010). Sullivan et al. (2006) and Betancur-R. et al. (2013a) in molecular analyses suggested instead that they are sister to Siluroidei, and that Loricarioidei are sister to all other extant catfishes. The molecular studies unfortunately could not sample one of the most important primitive catfish clades, the fossil-only †Hypsidoroidei.

†Family BACHMANNIIDAE. Eocene, South America. One genus and species. The primitive catfish †*Bachmannia chubutensis* Dolgopol de Saez, 1941, was redescribed by Azpelicueta and Cione (2011), who suggested that it is the sister group of the Diplomystidae. See also Pereira (1988).

Family DIPLOMYSTIDAE (141)—velvet catfishes. Freshwater; southern South America, Chile and Argentina.



The only extant catfish family with teeth on a well-developed maxilla, 18 principal caudal-fin rays, and lagenar otolith equal in size to or larger than utricular otolith; only maxillary barbels present; skin covered with papillae; no bony plates; dorsal fin with spine and 6 or 7 soft rays; anal fin with 9–12 principal rays; adipose fin present; pectoral fin with spine. Maximum length 32 cm SL.

Two genera, *Diplomystes* (3) and *Olivaichthys* (3), and six species (Arratia, 1987; Ferraris, 2003a; Lundberg et al., 2004). Diplomystid fossils have been identified as pectoral spines from the late Late Cretaceous of Argentina and Bolivia, although identification is based on primitive characters (Lundberg, 1998; Gayet and Meunier, 2003).

†***Suborder Hypsidoroidei.*** Eocene. One family.

†Family HYPSIDORIDAE. Eocene of North America. Teeth on a well-developed maxilla (similar to the condition in diplomystids); one suprapreopercle; six infraorbital bones; 17 principal caudal-fin rays.

Two species, †*Hypsidoris farsonensis* from the early middle Eocene of Wyoming and †*H. oregonensis* from the middle Eocene of Oregon (Grande 1987; Grande and de Pinna, 1998). The fossils of †*H. farsonensis* are exceptionally well preserved and yield a wealth of anatomical information; Grande (1987) concluded that they are the sister group of all catfishes except Diplomystidae.

Suborder Cetopsoidei. The one family is sister to all extant catfishes except Diplomystidae according to de Pinna (1993), Hardman (2005), and de Pinna et al. (2007), or forms a trichotomy with the †Hypsidoridae and a clade of all remaining catfishes according to de Pinna (1998). Alternative phylogenetic positions for the Cetopsidae are as sister to Siluroidei (Diogo, 2004), in a polytomy at the base of all Siluroidei (Sullivan et al., 2006), or in an effective polytomy (key nodes having very weak support) among most Siluroidei (Betancur-R. et al., 2013a).

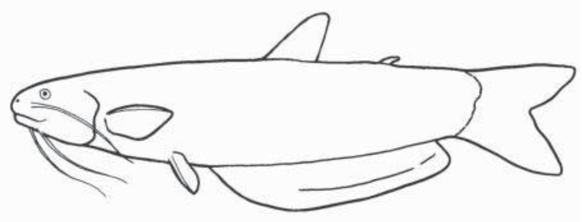
Family CETOPSIDAE (142)—whale catfishes. Freshwater; South America.

Body naked; three pairs of barbels (no nasals); anal fin with long base, usually 20–49 rays; body naked and lacking bony plates; pectoral and dorsal fins lacking spines (except in a few cetopsines).

The families Helogeneidae and Cetopsidae (as recognized in Nelson, 1994) were united by de Pinna and Vari (1995) and this was followed in de Pinna (1998) and de Pinna et al. (2007). They are recognized here as subfamilies.

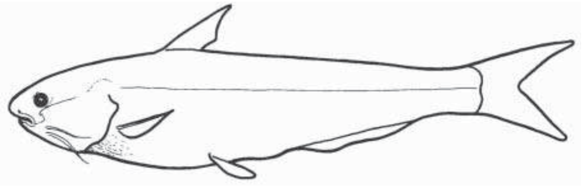
Five genera (see below) with 42 species (Vari and Ferraris, 2003; Vari et al., 2005; Vari and Ferraris, 2009).

Subfamily Helogeneinae. Dorsal fin base short, with about five soft rays and no spine; no spine in pectoral fin; adipose fin, if present, small (present or absent within some species); caudal fin with 15 or 16 principal rays; 12 or 13 branchiostegal rays; vertebrae 41–45 (including the 5 Weberian vertebrae). Maximum length about 7 cm SL.



One genus, *Helogenes* (synonym *Leyvaichthys*), with four species (Vari and Ferraris, 2003; de Pinna et al., 2007).

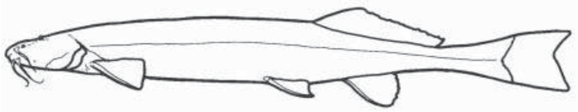
Subfamily Cetopsinae. No adipose fin; swimbladder highly reduced and enclosed in bony capsule; dorsal fin far forward. Maximum length about 26 cm SL.



Four genera, *Cetopsis* (including *Bathycetopsis*, *Hemicetopsis* and *Pseudocetopsis*) (21), *Cetopsidium* (7), *Denticetopsis* (7), and *Paracetopsis* (3, synonym *Cetopsogiton*), with about 38 species (Vari and Ferraris, 2003). Vari et al. (2005) made generic changes and described new species; de Pinna et al. (2007) revised the family and made additional changes to taxonomy.

Suborder Loricarioidei. Six families with 159 genera and 1.453 species. Loricarioids may be sister to all other extant catfishes (Sullivan et al., 2006) or sister to Siluroidei among extant catfish groups (Diogo, 2004, 2010).

Family TRICHOMYCTERIDAE (Pygidiidae) (143)—pencil catfishes or parasitic catfishes. Freshwater; Costa Rica, Panama, and throughout South America.



Body naked and elongate; chin (mental) barbels usually absent; nasal barbel usually present but on anterior nostril rim rather than on the posterior nostril rim as in many siluroids; usually two pairs of maxillary barbels; usually no adipose fin; opercle usually with spines. Pelvic fins have been lost in at least three lineages: *Eremophilus*, Glanapteryginae, and *Miuroglanis*.

The common name "parasitic catfishes" is derived from the habits found in species of two subfamilies. Members of the Vandelliinae are hematophagous and pierce the skin of living fishes or other animals and gorge themselves on blood; some live on blood obtained within the gill cavities of other fishes. In addition, individuals of *Vandellia* (a candiru) of Brazil are known to enter the urethra of humans with serious consequences for both the fish and the person (see review by de Carvalho, 2003, of a book on the candiru). Members of the Stegophilinae feed on the mucus and scales of other fishes. This family and the Nematogenyidae are probably sister groups (de Pinna, 1998).

Eight subfamilies provisionally recognized, with about 41 genera and about 273 species (de Pinna, 1998; de Pinna and Wosiacki, 2003; Teugels, 2003).

SUBFAMILY COPIONODONTINAE. Brazil. Adipose fin well developed; origin of dorsal fin in anterior half of body; maxilla articulating with lower jaw. Two genera, *Copionodon* (3) and *Glaphyropoma* (2) and 5 species (de Pinna and Wosiacki, 2003). This group and the Trichogeninae may be part of a trichotomy with the remaining trichomycterids (de Pinna, 1998; Bichuette et al., 2008).

SUBFAMILY TRICHOGENINAE. Brazil. Anal fin long, with more than 30 rays. One genus, 2 species, *Trichogenes longipinnis* and *T. claviger* from southeastern Brazil (de Pinna and Wosiacki, 2003; de Pinna et al., 2010).

SUBFAMILY TRICHOMYCTERINAE. Central and South America. Eight genera, *Bullockia* (1), *Eremophilus* (1), *Hatcheria* (1), *Ituglanis* (22), *Rhizosomichthys* (1), *Scleronema* (3), *Silvinichthys* (5), and *Trichomycterus* (about 160), with about 194 species (de Pinna and Wosiacki, 2003; Wosiacki and Garavello, 2004; Bichuette and Trajano, 2004; Fernández and de Pinna, 2005; Campos-Paiva and Costa, 2007; Wosiacki and de Pinna, 2008; Barbosa and Costa, 2010; Fernández and Vari, 2012; Bichuette and Rizzato, 2012; Fernández et al., 2013). They occur from near sea level to 4,500 m elevation. Some of the species in the unusually widespread genus *Trichomycterus* can inhabit torrential streams. One species, *T. catamarcensis* from the Andes of Argentina, lacks the pelvic fins and girdle. This subfamily may not be a monophyletic assemblage and is thus in need of revision (de Pinna, 1998; Datovo and Bockmann, 2011).

SUBFAMILY VANDELLIINAE. South America. About four genera, *Paracanthopoma* (1), *Paravandellia* (2, synonyms *Branchioica* and *Pleurophysus*), *Plectrochilus* (3), and *Vandellia* (3), with about nine species (de Pinna and Wosiacki, 2003; Teugels, 2003; Fernández and Schaefer, 2009).

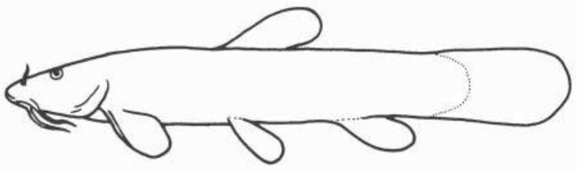
SUBFAMILY STEGOPHILINAE. South America. Coronoid process of dentary oriented horizontally; wing-like posterior projection at distal tip of premaxilla; posterodorsal process of hyomandibula medial to main lamina of the bone; mouth opening a wide, crescent-shaped disc (DoNascimiento, 2015). These catfishes feed on scales, mucus, or skin of other fishes. There are 12 genera, *Acanthopoma* (1), *Apomatoceros* (1), *Haemomaster* (1), *Henonemus* (5), *Homodiaetus* (4), *Megalocenter* (1), *Ochmacanthus* (5), *Parastegophilus* (2), *Pseudostegophilus* (2), *Pareiodon* (1), *Schultzichthys* (2), and *Stegophilus* (3), with about 28 species (de Pinna and Wosiacki, 2003; Teugels, 2003; DoNascimiento and Provenzano, 2006).

SUBFAMILY TRIDENTINAE. South America. Anal fin relatively long, more than 15 fin rays. About four genera, *Miuroglanis* (1), *Tridens* (1), *Tridensimilis* (2), and *Tridentopsis* (3), with about seven species (de Pinna and Wosiacki, 2003; Teugels, 2003).

SUBFAMILY GLANAPTERYGINAE. South America. Pectoral fin with three or four rays; principal caudal-fin rays 11 or fewer; pelvic skeleton and fin present or absent within *Glanapteryx anguilla*, both absent in the other species; dorsal fin present in only the two species of *Listrura*; anal fin absent in *G. anguilla*; hypurals completely fused. They have a transparent body and are sand-dwelling. Four genera, *Glanapteryx* (2), *Listrura* (6), *Pygidianops* (4), and *Typhlobelus* (5), with about 17 species (de Pinna and Wosiacki, 2003; Teugels, 2003; Schaefer et al., 2005; Villa-Verde et al., 2012; de Pinna and Zuanon, 2013).

SUBFAMILY SARCOGLANIDINAE. South America. Six genera and 11 species most are monotypic, *Ammoglanis* (3), *Malacoglanis* (1), *Microcambeva (3), Sarcoglanis* (1), *Stauroglanis* (1), and *Stenolicmus* (2), undescribed species are known (de Pinna and Wosiacki, 2003; Teugels, 2003; Mattos et al., 2008; Mattos and Lima, 2010). Poorly known, specialized, minute catfishes. Most known only from a few specimens from the Amazon Basin. (Costa et al., 2004; Mattos et al., 2010).

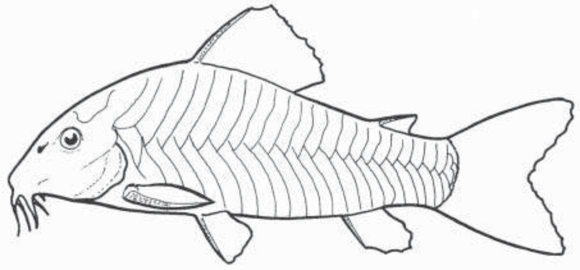
Family NEMATOGENYIDAE (144)—mountain catfishes. Freshwater; central Chile.



Body naked and elongate; three pairs of barbels present, chin (mental) barbel, single maxillary barbel, and a short nasal barbel on each side; no adipose fin; opercle lacking spines; dorsal fin in midbody, over pelvic-fin origin; pectoral spine serrated on posterior margin. This family and the Trichomycteridae may be sister groups (de Pinna, 1993, 1998); the molecular phylogeny of Sullivan et al. (2006) could not resolve their relationships relative to Trichomycteridae and remaining families within Loricarioidei.

One species, *Nematogenys inermis* (de Pinna, 2003; Teugels, 2003). The fossil species †*Nematogenys cuivi* is known from the Miocene of Chile (Azpelicueta and Rubilar, 1998).

Family CALLICHTHYIDAE (145)—callichthyid armored catfishes. Freshwater; Panama and South America.



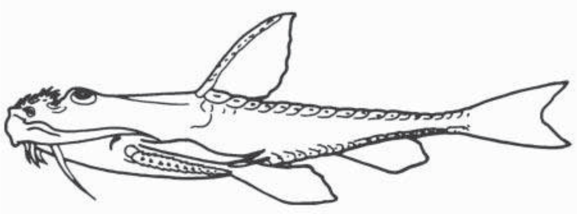
Body with two rows of overlapping bony plates on each side; swimbladder encased in bone; mouth small and ventral; one or two pairs of well-developed barbels present, and shorter processes usually on upper jaw and on lower jaw; dorsal and pectoral fins with strong spine; spine at anterior border of adipose fin. Some species can move short distances on land by utilizing air in vascular hindgut.

Two subfamilies with nine genera and about 202 species (Reis, 2003c). De Pinna (1993) and Sullivan et al. (2006) found them to be the first in a sequence of successive sister groups among the remaining families of Loricarioidei (Callichthyidae, Scoloplagidae, Astroblepidae, Loricariidae). Reis (1998) discussed the fossil record and biogeography of this taxon. *Corydoras* appears in the fossil record in the late Paleocene of Argentina, and *Hoplosternum* is reported from the Miocene of Colombia (Lundberg ,1997).

SUBFAMILY CALLICHTHYINAE. Snout area depressed. Five genera, *Callichthys* (4), *Dianema* (2), *Hoplosternum* (3, synonym *Cataphractops*), *Lepthoplosternum* (6), and *Megalechis* (2) with 17 species (Reis, 2003c; Reis et al., 2005; Reis and Kaefer, 2005).

SUBFAMILY CORYDORADINAE. Snout area compressed or rounded. Four genera, *Aspidoras* (about 20 species), *Brochis* (1), *Corydoras* (about 160 species), and *Scleromystax* (4) with about 185 species (Reis, 2003c; Britto et al., 2009).

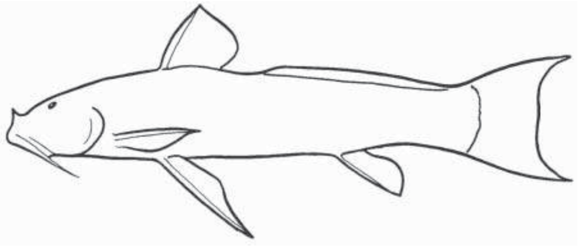
Family SCOLOPLACIDAE (146)—spiny dwarf catfishes. Freshwater; South America (Peru, Bolivia, Brazil, and Paraguay).



Body with two bilateral series of odontode-bearing plates and one midventral series of plates; rostral plate with numerous recurved odontodes; odontodes on many other parts of body; dorsal fin with stout smooth spine and 3–5 soft rays; anal fin with 5 or 6 soft rays; adipose fin absent; caudal fin with 10–12 principal rays; vomer absent; exoccipitals absent. Maximum length about 20 mm SL. This is among the most recently discovered families of catfishes in the sense that the first species in it was not described until 1976. The Lacantuniidae (discussed below) and the recently proposed family Kryptoglanidae (see above under Siluridae) were discovered more recently.

One genus, *Scoloplax*, with six species (Schaefer, 2003a; Rocha et al., 2008; Rocha et al., 2012).

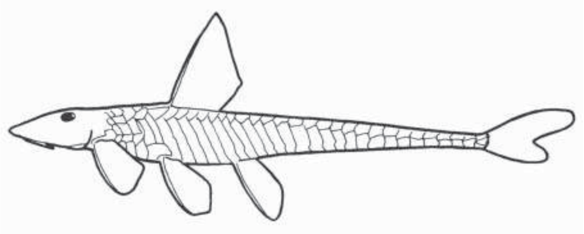
Family ASTROBLEPIDAE (Argidae) (147)—climbing catfishes. Freshwater; Panama and South America (Andean region).



Body naked or almost naked; suctorial mouth disc present as in virtually all loricariids; two pairs of barbels present, maxillary and nasal; adipose fin present or absent; dorsal fin with a spine and 6 or 7 soft rays; dorsal-fin spine lacking locking mechanism (a locking mechanism is present in the related callichthyids and loricariids); anal fin with 4–6 rays; relatively short intestine; 34 vertebrae (17 + 17). Some members are able to live in torrential mountain streams, up to 3500 m, and climb the faces of waterfalls. Maximum length about 30 cm.

One genus, *Astroblepus*, with at least 56 species (Schaefer, 2003b; Schaefer et al., 2011). Schaefer and Buitrago-Suárez (2002) described skin and fin-ray odontodes and skin surface features of Andean species.

Family LORICARIIDAE (148)—suckermouth armored catfishes. Freshwater; Costa Rica, Panama and South America.



Body with bony plates; mouth ventral, with or without noticeable barbels; ventral lip papillose; adipose fin, when present, usually with a spine at anterior border; relatively long intestine; 23–38 vertebrae. Members of this family may be found from low elevations to swift-flowing streams up to 3,000 m. "Pleco" or "plecostomus" is a name used in the aquarium trade for species in several genera of this family.

This is the largest family of catfishes, with more species being described every year. The recognition of seven subfamilies and their composition is based on de Pinna (1998) and Reis et al. (2003), which in turn closely followed, with modifications, the classical study of Isbrücker (1980) (and co-authors such as Hans Nijssen). In Nelson (1994), *Lithogenes* was placed in the Astroblepidae.

About 106 genera and about 915 species, with one of the species *incertae sedis* from that in the following list (Reis et al., 2003:318–400). Information on the subfamilies listed below is from the individual chapters in Reis et al. (2003:170–230) written by specialists as follows: Neoplecostominae (C. J. Ferraris, Jr.), Hypoptopomatinae (S. A. Schaefer), Loricariinae (C. J. Ferraris, Jr.), Ancistrinae (S. Fisch-Muller), and Hypostominae (C. Weber).

Dermal plates of loricariids occur as fossils in the Eocene or Oligocene of Brazil, and other remains from South America are of Miocene age (Gayet and Meunier, 2003). †*Taubateia paraiba* is a named fossil loricariid from the late Oligocene or early Miocene of Brazil (Malabarba and Lundberg, 2007).

SUBFAMILY LITHOGENEINAE. Three species, *Lithogenes valencia* (described in 2003 and may be extinct), *L. villosus* and *L. wahari* (Provenzano et al., 2003; Schaefer and Provenzano, 2008).

SUBFAMILY NEOPLECOSTOMINAE. Five genera and 48 species. All but *Neoplecostomus* were described after the 2006 volume. *Isbrueckerichthys* (5), *Neoplecostomus* (14), *Kronichthys* (3), *Pareiorhaphis* (22), *Pareiorhina* (6), with seven species in southeastern Brazil. (Pereira and Britto, 2012; Roxoi et al., 2012; Azevedo-Santos and Roxo, 2015).

SUBFAMILY HYPOPTOPOMATINAE. Some 21 genera, e.g., *Acestridium, Eurycheilichthys, Hisonotus, Hypoptopoma, Microlepidogaster, Otocinclus, Otothyris, Oxyropsis, Parotocinclus, Pseudotocinclus, Rhinolekos* and *Scizolecis*, with about 140 species. Schaeffer (1991) proposed a phylogeny based on osteological characters. See also Carvalho and Reis, 2009.

SUBFAMILY LORICARIINAE. About 34 genera, e.g., *Apistoloricaria, Crossoloricaria,* Dasyloricaria, *Farlowella, Harttia, Loricaria, Loricariichthys, Pseudohemiodon, Reganella, Rineloricaria, Spatuloricaria,* and *Sturisoma*, with 238 species.

SUBFAMILY ANCISTRINAE. About 29 genera, e.g., *Ancistrus* (synonym *Xenocara*), *Chaetostoma, Hemiancistrus, Hypancistrus, Lasiancistrus, Lithoxus, Lipopterichthys, Megalancistrus, Panaque, Parancistrus, Pseudacanthicus,* and *Pseudancistrus*, with about 276 species (e.g., Armbruster, 2004; Armbruster and Provenzano, 2000; Fisch-Muller et al., 2012).

SUBFAMILY HYPOSTOMINAE. 13 genera, e.g., *Hypostomus* (synonyms *Cochliodon* and *Plecostomus*) (*H. watwata* lives in brackish water), *Peckoltia, Pogonopoma,* *Pterygoplichthys (includes Liposarcus* and *Glyptoperichthys), Rhinelepis,* and *Squaliforma*, with 202 species. (Weber, 2003; Armbruster and Werneke, 2005; Armbruster, 2004, 2008; Cardoso et al., 2012; Webber et al., 2012).

SUBFAMILY DELTURINAE. Two genera, *Delturus* (4) *and Hemipsilichthys* (3) with 7 species, removed from *Hypostominae* by Reis et al. (2006).

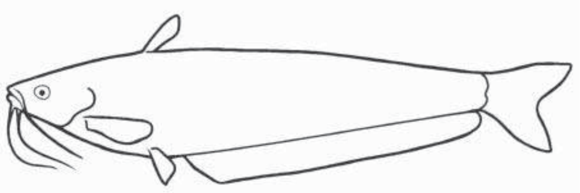
Incertae sedis: *Nannoplecostomus eleonorae,* Central Brazil, considered to be the smallest loricariid catfish known (Ribeiro et al., 2012).

Suborder Siluroidei. This large group of catfishes is yet to have its relationships satisfactorily worked out, though the evidence for its monophyly appears strong (e.g., de Pinna, 1993; Diogo, 2004; Sullivan et al., 2006). Many family-group taxa are recognized but, with a few exceptions, their higher-level relationships are uncertain. The list below begins with families of uncertain placement within the suborder. Next are listed families for which there is preliminary evidence of membership in one of several larger clades, though formal taxonomic recognition of those clades is premature. Following those tentative groupings, named superfamilies containing multiple families are listed where there is stronger evidence of relationships.

Thirty-two families, 323 genera, and 2,227 species.

THE FOLLOWING THREE FAMILIES are of uncertain placement within the suborder Siluroidei.

Family SILURIDAE (149)—sheatfishes. Freshwater; Europe and Asia.



Dorsal fin usually with fewer than seven rays, sometimes absent, not preceded by a spine; anal fin with axis of each ray aligned between pterygiophores instead of opposite the following pterygiophore; paired hemitrich bases of dorsal and anal-fin rays clasping distal radial and contacting anterior margin of following pterygiophore; anal-fin base very long, 41–110 rays; adipose fin absent; pelvic fins small, sometimes absent; nasal barbel absent, one or two pairs of barbels on lower jaw, and maxillary barbels usually long (Wiley and Johnson, 2010; Lundberg et al., 2014). Monophyly of this family was established by Bornbusch (1995) on the basis of such characters as the autopalatine reduced to a small nodule.

The Siluridae were in a basal polytomy in Siluroidei in the results of Sullivan et al. (2006). De Pinna (1993) had earlier suggested a relationship to the following four families plus some others, while Diogo (2004) suggested a basal position (after Cetopsidae) within Siluroidei.

The largest species of siluriform is the commercially important European wels, *Silurus glanis*, which commonly reaches 3 m (maximum recorded length

5 m and weight 330 kg). This species is native in Europe east of the Rhine, and in some areas occurs in brackish water and in inland saline seas.

A problematic, groundwater-dwelling species, *Kryptoglanis shajii,* included here tentatively in Siluridae, was recently discovered (Vincent and Thomas, 2011) and has since been studied with computed tomography (Lundberg et al., 2014). It was described osteologically as well as made the basis of the proposed new monotypic family Kryptoglanidae by Britz et al. (2014). Its precise relationships remain in doubt, apart from assignment to Siluroidei and being perhaps sister to or within Siluridae.

About 13 genera, *Belodontichthys, Ceratoglanis, Hemisilurus, Kryptoglanis, Kryptopterus* (glass catfish), *Micronema, Ompok, Phalacronotus, Pinniwallago, Pterocryptis* (includes *Hito*), *Silurichthys, Silurus* (*Parasilurus* may be a synonym), and *Wallago,* with about 107 species (Bornbusch, 1995; Rainboth, 1996; Teugels, 2003; Ng and Kottelat, 2013a,b). Only two species, both in the large genus *Silurus,* occur in Europe. Fossils are not common until the Miocene (Gayet and Meunier, 2003), and include †*Silurus altus* from the Miocene or Pliocene of Russia.

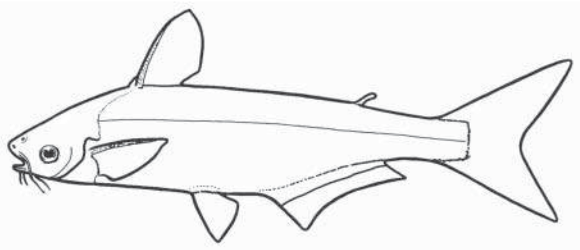
Family AUSTROGLANIDIDAE (150)—rock catfishes. Freshwater; southern Africa.

Three pairs of barbels (nasal pair absent); strong dorsal and pectoral spines; adipose fin small.

Formerly placed in Bagridae, but recognized as a separate family by Mo (1991), de Pinna (1998), and Diogo (2004). Diogo and Bills (2005) studied the osteology and myology of the head and pectoral girdle. This small family was grouped with Ariidae and Claroteidae by Diogo (2004), but its phylogenetic position was not evaluated by Hardman (2005) or by Sullivan et al. (2006).

One genus, *Austroglanis,* with three species (Teugels, 2003).

Family PANGASIIDAE (151)—shark catfishes. Freshwater; southern Asia (Pakistan to Borneo).



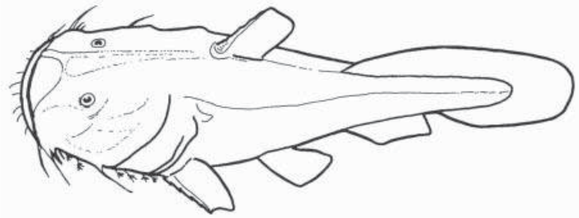
Usually two pairs of barbels (maxillary and one pair of mandibular or mental barbels present, nasal barbels always absent, only maxillary barbels in adult *Pangasianodon gigas*); body compressed; adipose fin present, small, never confluent with caudal fin; dorsal fin far forward with one or two spines and 5–7 soft rays; anal fin with 26–46 rays; vertebrae 39–52. Maximum length about 3 m and maximum weight 300 kg, attained in the plant-eating, toothless (in adults) *Pangasianodon gigas.*

The Pangasiidae were grouped with Schilbeidae by de Pinna (1998) and Diogo (2004), but recovered as distant from Schilbeidae and in a basal polytomy of Siluroidei by Sullivan et al. (2006).

Four genera, *Helicophagus* (3), *Pangasianodon* (2, including *P. gigas*, the endangered giant Mekong catfish), *Pangasius* (23), and *Pseudolais* (2), with 30 species (Rainboth, 1996; Teugels, 2003). An Eocene fossil from Indonesia was assigned to *Pangasius* (as †*P. indicus*) by Sanders (1934) but has not recently been re-studied (Gayet and Meunier, 2003; Ferraris, 2007). The extinct genus †*Cetopangasius* (species †*C. chaetobranchus*) is based on Miocene fossils from Thailand (Roberts and Jumnongthai, 1999).

THE NEXT THREE CATFISH FAMILIES may be related based on morphological and/or molecular evidence, though evidence remains preliminary. The Chacidae and Plotosidae were included (with others) in a clade by de Pinna (1993) and a similar grouping was supported by Diogo (2004; Diogo and Peng, 2010). The fifth family, Ritidae, was formerly a subfamily of Bagridae, but the two are not closely related on molecular evidence and there is weak support for a relationship between Ritidae and Plotosidae (Sullivan et al., 2006).

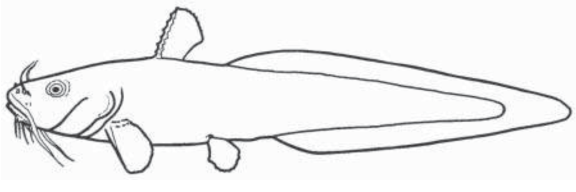
Family CHACIDAE (152)—squarehead, angler, or frogmouth catfishes. Freshwater; eastern India to Borneo.



Head broad, long, and depressed; body compressed posteriorly; mouth terminal, very wide; three or four pairs of small barbels (nasals if present, minute); eyes very small; dorsal fin with one short spine and four soft rays; anal fin with 8–10 soft rays; pectoral fin with one serrated spine and four or five soft rays; pelvic fins large, with six rays; adipose fin confluent with caudal fin; gill rakers absent; branchiostegal rays 6–8; vertebrae 31–35 (14–16 abdominals). Maximum length about 24 cm. On occasions, *Chaca* uses its maxillary barbels to lure prey fish closer to its large mouth. Diogo et al. (2004c), found new autapomorphies.

One genus, *Chaca*, with four species (Brown and Ferraris, 1988; Teugels, 2003; Ng and Kottelat, 2012).

Family PLOTOSIDAE (153)—eeltail catfishes. Marine, brackish, and freshwater; Indian Ocean and western Pacific from Japan to Australia and Fiji.



Body eel-like, tail pointed or bluntly rounded; usually four pairs of barbels; no adipose fin; caudodorsal fin rays may extend far forward (i.e., two dorsal fins, the second of which is confluent with the caudal), and lower procurrent caudal rays join the long anal fin to form a continuous fin; branchiostegal rays 7–14. As with some other catfishes, some of these can inflict painful wounds.

Ten genera, *Anodontiglanis* (1), *Cnidoglanis* (1), *Euristhmus* (5), *Neosiluroides* (1), *Neosilurus* (11), *Oloplotosus* (3), *Paraplotosus* (3), *Plotosus* (9), *Porochilus* (4), and *Tandanus* (2), with about 40 species (Allen and Feinberg, 1998; Ng and Sparks, 2002; Teugels, 2003). About half of the species are freshwater and occur in Australia and New Guinea.

Family RITIDAE (154)—ritas and nanobagrids. Freshwater; South Asia and Southeast Asia (Indochina, Borneo, and Sumatra). Ritidae are recognized here at the family level for the first time.

Ritas have pectoral and dorsal spines enlarged; eyes dorsolateral; anal fin short (Talwar and Jhingran, 1991). Nanobagrids are very small, less than 50 mm adult length, with reduced supraoccipital process and reduced nuchal-plate element; posterior cranial fontanel large and prominent (Ng, 2010).

Existence of this clade, formerly a subfamily of Bagridae (Mo, 1991), was supported by the results of Ng (2003). Sullivan et al. (2006) found *Rita* to be not a member of the Bagridae or even of their larger clade of mostly Asian families; however, there was weak support for a relationship to Plotosidae. Note that they did not examine DNA of *Nanobagrus*.

Two genera, *Nanobagrus* (7) and *Rita* (6). Fossil species of *Rita* are known from the Pliocene of India (Gayet and Meunier, 2003).

THE FOLLOWING SEVEN CATFISH FAMILIES were suggested by Sullivan et al. (2006, 2008) to belong to a large, unnamed clade of mostly Asian families based on molecular evidence. Some of these are distinct family-group taxa (e.g., subfamilies) recognized earlier on morphological grounds (e.g., Mo, 1991; Talwar and Jhingran, 1991; Jayaram, 2005), but with suggested changes to their relationships. Within this grouping, several families (Amblycipitidae, Akysidae, Sisoridae, Erethistidae, Aspredinidae) were grouped in Sisoroidea by de Pinna (1996b), but Friel (1994) and more recently Sullivan et al. (2006) removed Aspredinidae and placed them in Doradoidea, as done here.

Family AILIIDAE (155)—Asian "schilbeids". Freshwater and brackish water; widely distributed in continental South and Southeast Asia including India, Bangladesh, Nepal, Burma, and Yunnan.

Dorsal fin absent; adipose fin small; anal fin very long, 58–90 rays; eyes small, ventrolateral (Talwar and Jhingran, 1991).

This clade was formerly a subfamily within Schilbeidae (Mo, 1991; Talwar and Jhingran, 1991). Two genera were included by some (Sullivan et al., 2006) whereas Van der Laan (2015) included six.

Six genera: *Ailia* (1), *Clupisoma* (9), *Eutropiichthys* (6), *Laides* (2), *Proeutropiichthys* (3), and *Silonia* (2), with 23 species.

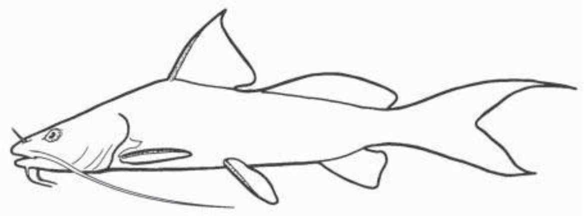
Family HORABAGRIDAE (156)—imperial or sun catfishes. Freshwater; India and Southeast Asia.

Characters and generic composition for this family remain to be adequately understood, but its existence separate from Bagridae seems likely.

Horabagridae were recognized by Mo (1991) on morphological grounds as distinct from Bagridae and Schilbeidae and containing *Horabagrus*, *Platytropius*, and *Pseudeutropius*. De Pinna (1993) and Jayaram (2005) recognized *Horabagrus* in its own family or subfamily (respectively), while Hardman (2005) found molecular evidence to recognize a family with the same three genera included by Mo (1991). Sullivan et al. (2006) sampled DNA of *Horabagrus* and *Pseudeutropius*, finding them to be a distinct clade close to Bagridae. Betancur-R. et al. (2013a) also sampled *Horabagrus* and *Pseudeutropius*, which they labeled as Schilbeidae where they were formerly classified, again finding the two genera to be sister to Bagridae.

Perhaps four genera, *Horabagrus* (3, including Günther's catfish *H. brachysoma*), *Pachypterus* (=*Neotropius*) (3) (included here by Van der Laan, 2015), *Platytropius* (2), and *Pseudeutropius* (4), with about 12 species.

Family BAGRIDAE (157)—bagrid catfishes. Freshwater; Africa and Asia (to Japan and Borneo).



Dorsal fin preceded by a spine, usually with 6 or 7 soft rays (rarely 8–20) (except in *Olyra,* which lacks a spine and has seven or eight soft rays); adipose fin present and highly variable in size between species; pectoral spine serrated; body naked; usually four pairs of well-developed barbels. Some species are kept as aquarium fishes, while others are large and important as food fishes. Maximum length about 1.5 m.

Nelson (1994) divided the family following the work of Mo (1991) into three families, the Claroteidae (with two subfamilies, Claroteinae and Auchenoglaninae, Africa, both now families), Austroglanididae (one genus, Africa), and Bagridae (with the African *Bagrus* with the Asian genera in separate subfamilies).

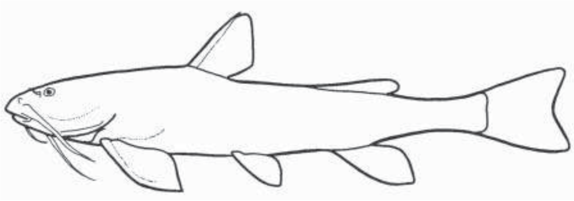
Since then, studies such as those by de Pinna (1998), Ng (2003), and Sullivan et al. (2006) have led to further changes, e.g., the family Olyridae (see lower figure) is now included within Bagridae, whereas a number of other groups have been removed. For example, the former subfamily Ritinae for *Rita* and *Nanobagrus* is now the separate family Ritidae, and the genera *Horabagrus, Neotropius* (junior synonym of *Pachypterus*)*, Platytropius,* and *Pseudeutropius* are now in the separate family Horabagridae.

About 19 genera, e.g., *Bagrichthys* (7), *Bagroides* (2), *Bagrus* (11), *Batasio* (17), *Chandramara* (1), *Coreobagrus* (2), *Hemileiocassis* (1), *Hyalobagrus* (3), *Hemibagrus* (41), *Leiocassis* (13), *Mystus* (45), *Olyra* (6, lower figure), *Pelteobagrus* (4), *Pseudobagrus* (31), *Pseudomystus* (19), *Rama* (1), *Sperata* (4), *Sundolyra* (1), and *Tachysurus* (12), with about 221 species (Talwar and Jhingran, 1991; Teugels, 2003; Ng, 2003, 2010; Arunachalam et al., 2013). *Sundolyra* was named by Ng et al. (2015). See also Yang and He (2008) for a phylogeographic study of *Hemibagrus* and the effect of sea-level changes on South China biogeography.

The oldest fossil bagrids are from the Paleocene of Niger, Africa (genera †*Eomacronies* and †*Nigerium*) (Murray, 2000; Gayet and Meunier, 2003). Eocene fossils from Egypt include †*Fajumia* and †*Socnopaea*; †*Eaglesomia* is known from Nigeria, and †*Eomacronies* from Niger (Murray, 2000). The Miocene †*Nkondobagrus* is from Uganda (Gayet and Meunier, 2003). Bagrid fossils are common in India beginning in the Eocene (Gayet and Meunier, 2003) and some have been assigned to the African genera †*Fajumia* and †*Socnopaea* (Sahni and Mishra, 1975). Eocene †*Gobibagrus* has been reported from Mongolia, along with Miocene fossil species of *Mystus* from China and of *Pseudobagrus* from Japan (Gayet and Meunier, 2003). †*Hemibagrus major* is based on Miocene fossils from Thailand (Roberts and Jumnongthai, 1999; Ng and Kottelat, 2013c).

Superfamily Sisoroidea. Four families: Akysidae, Amblycipitidae, Sisoridae, and Erethistidae. This clade was proposed to be part of the unnamed “Big Asia” clade of Sullivan et al. (2006) on molecular evidence.

Family AKYSIDAE (158)—stream catfishes. Freshwater; southeastern Asia.



Dorsal fin with a strong spine and a short base, usually four or five soft rays.

Five genera (given below) with at least 67 species. The two subfamilies were ranked as families in Nelson (1994). The family is sister to the clade of Sisoridae, Erethistidae, and Aspredinidae in de Pinna (1996b, 1998), but Sullivan et al. (2008) included Amblycipitidae rather than Aspredinidae among close relatives.

SUBFAMILY AKYSINAE. Body with unculiferous tubercles arranged in longitudinal rows, a median middorsal row and usually four lateral rows; dorsal fin with usually five soft rays; adipose fin present and moderate; pectoral fin with strong spine, anterior margin with notch visible dorsally and usually serrated posteriorly; gill openings relatively narrow; eyes small; four pairs of barbels.

Two genera, *Akysis* (24) and *Pseudobagarius* (14) and 48 species (Ng and Kottelat, 1998, 2004; Ng and Freyhof, 2003; Ng and Siebert, 2004; Ng and Sabaj Pérez, 2005; Ng and Rainboth, 2005; Page et al., 2007).

SUBFAMILY PARAKYSINAE. Dorsal fin with 4 soft rays; pectoral spine nonserrate; anal fin with 8–13 soft rays; four pairs of barbels, mandibular barbels usually with short accessory barbels; gill rakers absent; lateral-line pores absent; head and body covered with rounded tubercles, arranged in longitudinal rows (*Acrochordonichthys* and *Breitensteinia*) or evenly distributed and not in rows (*Parakysis*); adipose fin absent (*Breitensteinia* and *Parakysis*) or present and long (*Acrochordonichthys*); eyes minute; vertebrae 30–32 (abdominals 16–19). Primarily Malay Peninsula, Sumatra, Sarawak, and western and southern Borneo.

Three genera, *Acrochordonichthys* (10), *Breitensteinia* (3), and *Parakysis* (6), with 19 species (Ng and Ng, 2001; Vidthayanon and Ng, 2003; Ng and Siebert, 1998; Ng and Kottelat, 2003).

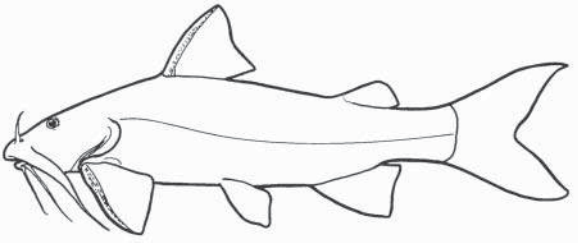
Family AMBLYCIPITIDAE (159)—torrent catfishes. Freshwater; southern and eastern Asia (Pakistan across northern India to Malaysia and to Korea and southern Japan).

Dorsal fin covered by thick skin; adipose fin present, confluent with caudal fin in some species; dorsal-fin base short, spine in fin weak; anal-fin base short, with 9–18 rays; four pairs of barbels; lateral line poorly developed or absent. These small fish inhabit swift streams.

Sullivan et al. (2008) presented molecular evidence that *Liobagrus* and *Xiurenbagrus* are more closely related to Akysidae than to *Amblyceps*. However, they also drew attention to the apparently strong morphological support (numerous unique and unreversed synapomorphies) for retaining them in Amblycipitidae. This issue evidently requires additional study.

Four genera, *Amblyceps* (18), *Liobagrus* (13), *Nahangbargus* (1) and *Xiurenbagrus* (2), with about 34 species (Chen and Lundberg, 1995; Ng and Kottelat, 2000; Ng, 2001; Ng and Wright, 2009, 2010; Wu et al., 2013).

Family SISORIDAE (Bagariidae) (160)—sisorid catfishes. Freshwater; southern Asia (from Turkey and Syria to South China and Borneo, primarily in Oriental region).



Body usually with small unculiferous tubercles; adipose fin present (confluent with caudal in some genera and consisting of a small spine in the elongate *Sisor*); dorsal-fin base short, fin with or without a spine; adhesive apparatus in thoracic region present or absent; four pairs of barbels (however, the monotypic *Sisor* has one maxillary pair and five pairs on the lower jaw). Mostly small forms occurring in mountain rapids; maximum length 2 m.

The composition of this family as recognized in Nelson (1994) was changed by de Pinna (1996b), who removed six taxa into a new family, Erethistidae.

Seventeen genera with at least 202 species (de Pinna 1996b; Roberts and Ferraris, 1998; Roberts, 2001; Diogo et al., 2002; Diogo, 2003a; Guo et al., 2005; Thomson and Page, 2006; Ng, 2010).

SUBFAMILY SISORINAE. Four genera, *Bagarius* (4), *Gagata* (8), *Gogangra* (2), and *Sisor* (6), with about 20 species. The oldest fossil, named †*Bagarius gigas* by Sanders (1934), is from the Eocene of Sumatra.

SUBFAMILY GLYPTOSTERNINAE. Thirteen genera, *Chimarrichthys* (1), *Creteuchiloglanis* (4), *Euchiloglanis* (4), *Exostoma* (7, includes *Coraglanis*), *Glaridoglanis* (1), *Glyptosternon* (4), *Glyptothorax* (96), *Myersglanis* (2), *Oreoglanis* (21), *Parachiloglanis* (1), *Pareuchiloglanis* (20), *Pseudecheneis* (19), and *Pseudexostoma* (2), with about 182 species. (Li et al., 2007; Zhou et al., 2011).

Family ERETHISTIDAE (161)—erethistid catfishes. Freshwater; southern Asia.

Pectoral girdle with long coracoid process extending beyond base of pectoral fin; most are small, cryptically colored fishes, with tuberculate skin; nostrils close together; dorsal fin with strong spine and without thick covering of skin (e.g., Thomson and Page, 2006).

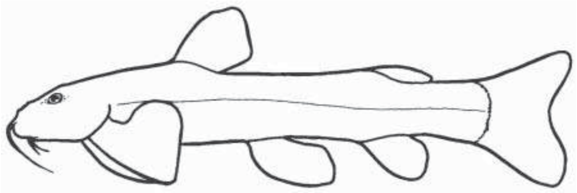
The family Erethistidae was established by de Pinna (1996b) to include genera previously placed in Sisoridae. Two subfamilies were recognized, Continae for genus *Conta,* and Erethistinae for the other five genera. See above under superfamily Sisoroidea. Sullivan et al. (2006, 2008) found molecular evidence that *Nangra*, included here, is closer to *Erethistes* than to Sisoridae where it formerly was classified.

Eight genera, *Ayarnangra* (1), *Caelatoglanis* (1), *Conta* (2), *Erethistes* (1), *Erethistoides* (10), *Hara* (9), *Nangra* (5), and *Pseudolaguvia* (16), with about

45 species (de Pinna, 1996b; Diogo et al., 2003; Britz and Ferraris, 2003; Ng and Kottelat, 2005; Thomson and Page, 2006).

THE NEXT SEVEN FAMILIES OF CATFISHES (Amphilidae, Malapteruridae, Mochokidae, Schilbeidae, Auchenoglanididae, Claroteidae, and Lacantuniidae) have been suggested by Sullivan et al. (2006) and Lundberg et al. (2007), based largely on molecular evidence, to belong to a large, diverse, but unnamed clade of mostly African catfishes, dubbed "Big Africa" by Sullivan et al. (2006).

Family AMPHILIIDAE (162)—loach catfishes. Freshwater; tropical Africa.



Three pairs of barbels (nasal barbels absent); dorsal and anal-fin bases short; dorsal and pectoral fin spine absent (weakly developed in Leptoglaninae and *Trachyglanis*); adipose fin present (with a short spine, modified scute, in *Trachyglanis*); pterygoid and posttemporal absent. Widespread in tropical Africa but commonest in streams at high elevations; most of the species can cling to rocks in fast-flowing streams. Maximum length 19 cm, but most species are less than 12 cm.

Three subfamilies, 13 genera with 93 species (Diogo, 2003b; Teugels, 2003; Roberts, 2003). There has been doubt about the content of this family as recognized, but evidence for monophyly of this family and of its three subfamilies was given by Diogo (2003b).

SUBFAMILY AMPHILIINAE. Body relatively short, appearing similar to homalopterids; bony plates and nuchal shield absent; mouth subterminal.

Two genera, *Amphilius* (28) and *Paramphilius* (4) with 32 species. (Skelton, 2007).

SUBFAMILY LEPTOGLANINAE. Maxilla exceptionally elongated; proximal radials completely fused (versus not fused as is the primitive condition found in most siluriforms).

Five genera, *Dolichamphilius* (2), *Leptoglanis* (2), *Psammphiletria* (2), *Tetracamphilius* (4), and *Zaireichthys* (18), with 28 species. (Eccles et al., 2011).

SUBFAMILY DOUMEINAE. Body elongate; bony plates often developed along body, nuchal shield present; mouth inferior.

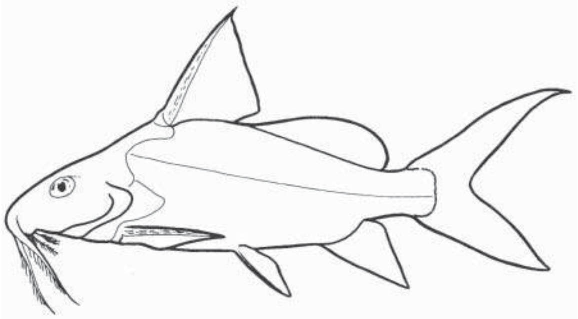
Six genera, *Andersonia* (1), *Belonoglanis* (2), *Congoglanis* (4) *Doumea* (9), *Phractura* (13), and *Trachyglanis* (4), and with 33 species. (Skelton, 2007; Ferraris et al., 2010, 2011; Ferraris and Vari, 2012).

Family MALAPTERURIDAE (163)—electric catfishes. Freshwater; tropical Africa and Nile.

Electrogenic organ present, derived from anterior body musculature and lining the body cavity; dorsal fin absent; fin spines absent; adipose fin far back; caudal fin rounded; three pairs of barbels (nasal pair absent); pectoral girdle loosely attached to skull; swimbladder with an elongate posterior chamber, two chambers in *Malapterurus* and three in *Paradoxoglanis.* Produce strong stunning electrical current; some other catfishes have electroreceptive systems, but only malapterurids have a well-developed electrogenic organ. Maximum length about 1.0 m SL (all species of *Paradoxoglanis* are much smaller).

Two genera, *Malapterurus* (18) and *Paradoxoglanis* (3), with 21 species (Norris, 2002) (this family has had a large increase in species recognized since Nelson, 1994, with 14 new species described in Norris, 2002).

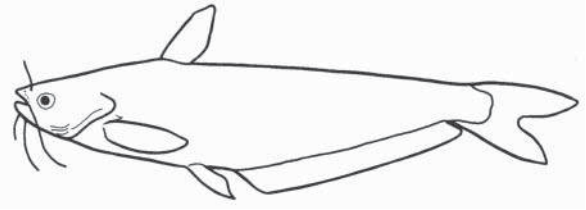
Family MOCHOKIDAE (164)—squeakers or upside-down catfishes. Freshwater; Africa.



Adipose fin usually very large; anal fin with fewer than 10 rays; dorsal and pectoral-fin spines usually strong and with a locking mechanism; three pairs of barbels, nasal barbels absent and mandibular barbels may have numerous branches; some with lips and part of barbels modified into an oral sucker (*Atopochilus*, *Chiloglanis,* and *Euchilichthys*); the two species of *Mochokus* of the Nile system have a rayed adipose fin. Maximum length 72 cm. Monophyly was addressed by Mo (1991) and Day et al. (2013).

Ten genera, e.g., *Atopochilus* (7), *Atopodontus* (1), *Chiloglanis* (49), *Euchilichthys* (5), *Microsynodontis* (12), *Mochokus* (4) (synonym *Acanthocleithron*), and *Synodontis* (131), with 209 species (e.g., Teugels, 2003; Ng, 2004; Friel and Vigliotta, 2008, 2011; Day et al., 2013). The genus *Synodontis* occurs as fossils from Africa beginning in the Oligocene.

Family SCHILBEIDAE (SCHILBIDAE) (165)—schilbeid or butter catfishes. Freshwater; Africa.



Dorsal fin usually present (with short base and a spine, absent in *Parailia*); adipose fin usually present; anal-fin base very long, not confluent with caudal, 24–90 rays; usually four pairs of barbels. The pelvic fin is occasionally absent in species of several genera. Members of this family tend to swim in open water.

As with some other family names, there is disagreement on the correct spelling. The spellings Schilbeidae and Schilbidae are both used, including previous editions of this book (Schilbidae in Nelson, 1984, and Schilbeidae in Nelson, 1976, 1994, and 2006). We continue to use Schilbeidae as recommended by Eschmeyer (1998), and Van Der Laan et al. (2014), although Ferraris and de Pinna (1999) and Ferraris (2007), following Steyskal (1980), favored the spelling Schilbidae.

A close relationship between Schilbeidae and Pangasiidae was suggested by Pinna (1993) and Diogo et al. (2004d), yet Sullivan et al. (2006) placed Schilbeidae in their African clade sister to Claroteidae and close to Auchenoglanidae. The Schilbeidae may be monophyletic after removal of Asian genera which, on molecular evidence (Sullivan et al., 2006; Betancur-R. et al. 2013a), have been suggested to belong with other Asian families, including *Pseudeutropius* and *Horabagrus* (both in Horabagridae close to Bagridae), as well as *Ailia, Ailiichthys* and *Laides* among others (in Ailiidae in an Asian group with Akysidae, Amblycipitidae, Bagridae, Erethestiidae, Horabagridae, Ritidae, and Sisoridae). Note, however, that Betancur-R. et al. (2013a) used *Pseudeutropius* for their DNA sample of Schilbeidae; *Pseudeutropius* is now in Horabagridae (see above), and thus they did not have a true schilbeid in their analysis.

About 5 genera, *Irvineia* (2), *Parailia* (5), *Pareutropius* (4), *Schilbe* (21), and *Siluranodon* (1), with 33 species (e.g., Talwar and Jhingran 1991). Fossils in *Schilbe* are known from the Miocene of Kenya (Stewart, 1995).

Family AUCHENOGLANIDIDAE (166)—auchenoglanidids. Freshwater; Africa.

Anterior nostrils on anteroventral side of upper lip; caudal fin rounded.

Earlier placed in the Bagridae (as in Nelson, 1994), this group was considered a subfamily of Claroteidae by Mo (1991) as followed by Teugels (2003), but recognized by de Pinna (1998), supported by molecular data (Sullivan et al., 2006) as a distinct family.

Six genera, *Anaspidoglanis* (4), *Auchenoglanis* (37), *Liauchenoglanis* (1, may be a synonym of *Notoglanidium*), *Notoglanidium* (9), *Parauchenoglanis* (18), and

Platyglanis (1, endemic to Cameroon and the type locality of the Sanaga River Basin), with about 70 species (Teugels, 2003; Geerinckx et al., 2004). Fossils of *Auchenoglanis* are known from the Miocene of Africa (Gayet and Meunier, 2003; Geerinckx et al., 2013).

Family CLAROTEIDAE (167)—claroteids. Freshwater; Africa.

Dentary with ventral process at symphysis; body moderately elongate; four pairs of barbels; dorsal and pectoral fins with strong spines; adipose fin present. Formerly placed in Bagridae, but recognized in a separate family by Mo (1991). The Auchenoglanididae, formerly a subfamily of Claroteidae, are now considered to be a closely related separate family.

Eight genera, *Amarginops* (1), *Bathybagrus* (6), *Chrysichthys* (42), *Clarotes* (2), *Gephyroglanis* (3), *Lophiobagrus* (4), *Paradiglanis* (1) (the Somalian giant catfish, considered a junior synonym of *Clarotes* by some workers) and *Phyllonemus* (3), with as many as 62 species (Teugels, 2003, based on Mo, 1991).

Fossil claroteids include two species of *Chrysichthys* from Africa): the Eocene †*C. mahengeensis* Murray and Budney, 2003, from Tanzania and the Pliocene †*C. macrotis* Van Neer, 1994, from Uganda, along with the monotypic genus †*Eaglesomia*, containing †*E. eaglesomei* from Nigeria (White, 1934; Gayet and Meunier, 2003).

Family LACANTUNIIDAE (168)—Chiapas catfishes. Freshwater; southern Mexico.

Palatine bone highly modified; palatine cartilage hypertrophied; fifth infraorbital large, anteriorly convex, and remote from sphenotic process; lateral margins of frontal, lateral ethmoid, and sphenotic bones thick at origins of enlarged adductor mandibulae and levator arcus palatini muscles; skull roof constricted and flat; cone-shaped “pseudo-pharyngobranchial” bones; enlarged axe-shaped uncinate process dorsally from third epibranchial; swimbladder with paired, spherical unencapsulated diverticulae from anterodorsal wall (Rodiles-Hernández et al. 2005).

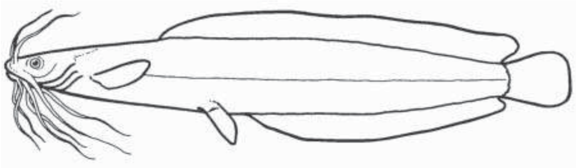
This family was erected by Rodiles-Hernández et al. (2005) for a single, newly discovered species found in the Río Lacantún, tributary to the Río Usumacinta, Chiapas, southern Mexico. Although it has many unique, autapomorphic characters, their morphological analysis could not place it precisely except to put it within the suborder Siluroidei. Using molecular analysis, Lundberg et al. (2007) suggested that the family’s closest relatives were Claroteidae and other members of an unnamed clade of families with African origins, and that its lineage originated in the Late Cretaceous. Scenarios involving vicariance or dispersal to account for its present occurrence in the Americas are an interesting problem without an easy solution.

One monotypic genus, *Lacantunia enigmatica*.

THE REMAINING SILUROID FAMILIES are grouped in five superfamilies for which there is stronger morphological and molecular evidence: Clarioidea, Arioidea, Doradoidea, Ictaluroidea, and Pimelodoidea (e.g., Sullivan et al., 2006).

Superfamily Clarioidea. Mo (1991) and Teugels and Adriaens (2003), and Sullivan et al. (2006) suggested a close relationship between Clariidae and Heteropneustidae, and Sullivan et al. (2006) recognized the superfamily Clarioidea for the same two families based on molecular evidence. Both families possess air-breathing organs (Graham, 1977), the Clariidae with a unique respiratory organ developed from branchial arches, although sometimes greatly reduced (Teugels and Adriaens, 2003), and the Heteropneustidae with a lung-like outgrowth from the pharynx (Sullivan et al., 2006). Two families, 16 genera, and about 120 species.

Family CLARIIDAE (169)—airbreathing catfishes. Freshwater; Africa, Syria, and southern and western Asia (Philippines to Java).

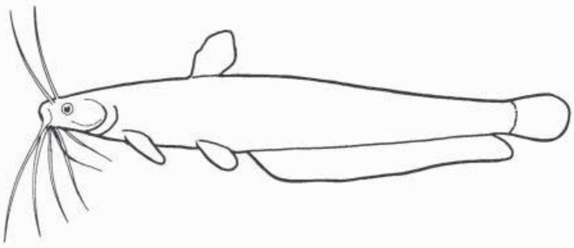


Dorsal fin base very long, usually with more than 30 rays, not preceded by a spine, separate or continuous with caudal fin; pectoral and pelvic fins variously absent in some species; caudal fin rounded; gill openings wide; usually four pairs of barbels; air-breathing labyrinthic organ arising from gill arches.

Some members of this family can move short distances over land. One species of walking catfish, the widespread *Clarias batrachus* has been introduced into southern Florida waters, where it thrives. Members of three African genera (*Gymnallabes*, *Channallabes*, and *Dolichallabes*) have a marked burrowing habit, have small eyes, and reduced or absent pectoral and pelvic fins. *Uegitglanis* (sometimes placed in Uegitglanididae) of Somali Republic, *Horaglanis* of India, and one species of *Clarias* in southwestern Africa are blind (Proudlove, 2005). Clariidae and Heteropneustidae are sister taxa (e.g., Mo, 1991; Teugels and Adriaens, 2003) and could be recognized as subfamilies, but we retain them as separate families. See Agnese and Teugles (2005) and Jansen et al. (2006) for insight into possible familial interrelationships.

About 15 genera, *Bathyclarias* (8, Africa), *Channallabes* (6, Africa), *Clariallabes* (16, Africa), *Clarias* (60, Africa and Asia), *Dinotopterus* (1, Africa), *Dolichallabes* (1, Africa), *Encheloclarias* (7, SE Asia), *Gymnallabes* (2, Africa), *Heterobranchus* (4, Africa), *Horaglanis* (3, India), *Platyallabes* (1, Africa), *Platyclarias* (1, Africa), *Tanganikallabes* (3, Africa), *Uegitglanis* (1, Africa), and *Xenoclarias* (1, Africa; *X. eupogon* is an endemic to Lake Victoria and is on the verge of extinction due to predation by Nile perch and climate change) with about 115 species (Teugels and Adriaens, 2003). The greatest diversity occurs in Africa. Clariid fossils (mostly from Africa in the genus *Clarias* and *Heterobranchus*) appear first in the Eocene. In Asia they are known from the Miocene and Pliocene (Gayet and Meunier, 2003).

Family HETEROPNEUSTIDAE (Saccobranchidae) (170)—airsac catfishes. Freshwater; Pakistan to Thailand (primarily India, Ceylon, and Myanmar).



Body elongate, compressed; head greatly depressed, strongly resembling that of clariids; four pairs of barbels; long air sac, serving as a lung, extends posteriorly from the gill chamber; dorsal fin short, without a spine; adipose fin absent or represented as a low ridge.

The pectoral spines have an associated venom gland, and the fish is considered dangerous to persons wading in its territory.

One genus, *Heteropneustes*, and five species (Menon, 1999; Rema Devi and Raghunathan, 1999; Hossain et al., 2013).

Superfamily Arioidea. The Anchariidae and Ariidae may be each other's closest relatives (de Pinna, 1993; Diogo, 2005; Sullivan et al., 2006).

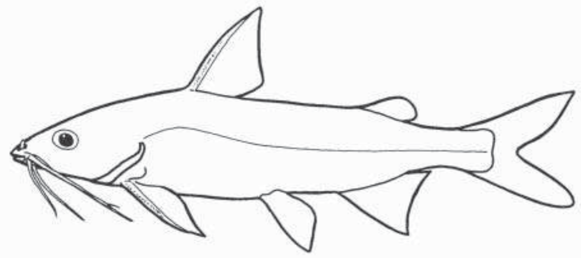
Family ANCHARIIDAE (171)—Malagasy catfishes. Freshwater, endemic to Madagascar.

Fringed barbels; reduced anterior nuchal plate (Ng and Sparks, 2005).

This family was revised by Ng and Sparks (2005), who described a second species of *Ancharius* and erected the new genus *Gogo* for *G. brevibarbis* (formerly in *Ancharius*) along with three new species. *Ancharius* was said to be related to Ariidae by de Pinna (1993) and Diogo (2005). According to Sullivan et al. (2006), *Gogo* also is related to Ariidae, but *Ancharius* was not included in the latter study.

Two genera, *Ancharius* (2) and *Gogo* (4), with six species.

Family ARIIDAE (Tachysuridae) (172)—sea catfishes. Mainly marine (to 100 m depth), many fresh or brackish water; worldwide, tropical to warm temperate.



Caudal fin deeply forked; adipose fin present; usually three pairs of barbels, rarely two (no nasal barbels); some bony plates on head and near dorsal fin origin; pectoral and dorsal fins with a spine; anal fin with 14–40 soft rays; in most, if not all species, the male carries the relatively large eggs in its mouth until hatching.

Many species of the sea catfishes enter fresh water and some only occur in fresh water. For example, in the United States, Mexico, and Central and South America about 43 species of the genera *Ariopsis* (*A. felis*), *Arius, Aspistor, Bagre, Cathorops, Galeichthys, Genidens, Hexanematichthys, Notarius,* and *Potamarius* occur in fresh water (some exclusively) or at least extend into brackish river mouths from the ocean (Marceniuk and Ferraris, 2003, using a classification that is based on the 2003 doctoral dissertation of the senior author; Nelson et al., 2004). The divergent *Doiichthys* from freshwater in New Guinea has sometimes been placed in its own family, Doiichthyidae.

Marceniuk and Menezes (2007) reviewed the family and redefined its genera. Ariidae were placed in Doradoidea in de Pinna (1998), but moved to the Bagroidea as sister to Claroteidae in Nelson (2006). Here they are not included with either of those groups and are treated (with Anchariidae) as unplaced within Siluroidei as suggested by Sullivan et al. (2006). Betancur-R. (2009) sampled broadly from the genera to produce a molecular phylogeny that suggested that New World ariines are paraphyletic while Old World ariines are monophyletic with subgroups distributed in different regions. Species within Ariidae are often divided among three subfamilies, Bagreinae containing only *Bagre,* Galeichthyinae containing only *Galeichthys,* and Ariinae containing the rest. Subfamily designations are not however used here.

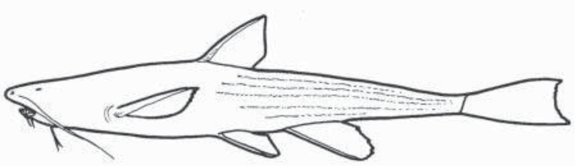
About 30 genera, e.g., *Amissidens, Amphiarius, Ariopsis, Arius* (synonym *Tachysurus*), *Aspistor, Bagre, Batrachocephalus, Brustiarius, Carlarius, Cathorops, Cephalocassis, Cinetodus, Cochlefelis, Cryptarius, Doiichthys, Galeichthys, Genidens, Hemiarus, Hexanematichthys, Ketengus, Nedystoma, Nemapteryx, Netuma, Notarius* (synonym *Sciadeops*), *Occidentarius, Osteogeneiosus, Plicofollis, Potamarius, Potamosilurus,* and *Sciades* with about 150 species (Marceniuk and Ferraris, 2003; Teugels, 2003; Aceroa and Betancur-R., 2006, 2007; Marceniuk and Menezes, 2007; Betancur-R. et al., 2007, 2008; Marceniuk et al. 2012).

Many fossils of Ariidae are recognized by their fin spines. Fossils of ariids are first recognized in the Late Cretaceous of South America, and are common on most continents by the Eocene (e.g., fossils of the extant genus *Ariopsis* from Africa: Murray, 2000; Gayet and Meunier, 2003).

Superfamily Doradoidea. A grouping of Aspredinidae, Auchenipteridae, and Doradidae is suggested by molecular results of Sullivan et al. (2006). Diogo et al. (2004b) and Hardman (2005) also supported the hypothesis that Doradidae and Auchenipteridae are closely related.

Three families, 61 genera, and 345 species.

Family ASPREDINIDAE (173)—banjo catfishes. Freshwater (some brackish); tropical South America.



Body naked except for large tubercles arranged in longitudinal rows; no adipose fin; body depressed anteriorly; opercular aperture reduced to a slit; dorsal spine-locking mechanism absent in most species; 10 or fewer caudal-fin rays. Maximum length about 38 cm SL, attained in *Aspredo aspredo*; most species less than 15 cm.

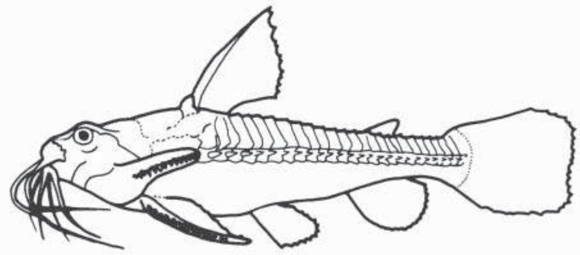
Thirteen genera with 39 species (de Pinna, 1998; Diogo et al., 2001; Friel and Lundberg, 1996; Friel, 2003). Much information from these studies was based on the 1994 Ph.D. dissertation of John Friel of Duke University. *Micromyzon akamai* (Friel and Lundberg, 1996) lacks eyes. *Acanthobunocephalus* may be sister to the remaining taxa (and hence would not belong in the subfamily Bunocephalinae).

SUBFAMILY BUNOCEPHALINAE. Six genera, *Acanthobunocephalus* (1), *Amaralia* (1), and *Bunocephalus* (10), *Micromyzon* (1), *Pseudobunocephalus* (6) *Pterobunocephalus* (2) with 21 species.

SUBFAMILY ASPREDININAE. Three genera, *Aspredinichthys* (2), *Aspredo* (1), and *Platystacus* (1), with four species.

SUBFAMILY HOPLOMYZONTINAE. Four genera, *Dupouyichthys* (1), *Ernstichthys* (3), *Hoplomyzon* (3), and *Xyliphius* (7), with 14 species.

Family DORADIDAE (174)—thorny catfishes. Freshwater; South America (primarily in Brazil, Peru, and the Guianas).



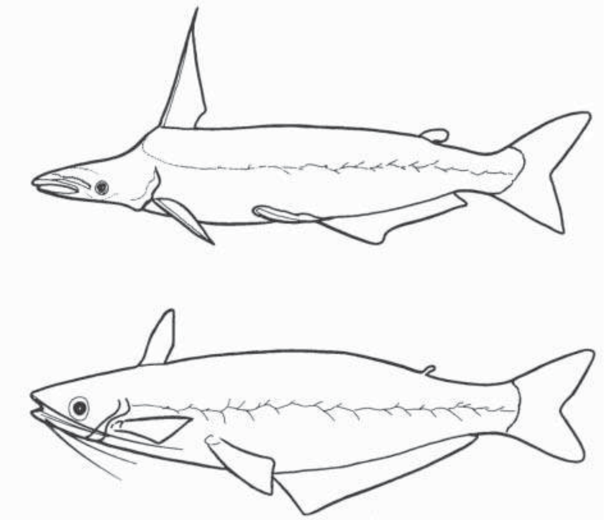
Body with row of lateral bony plates, most with spines (*Liosomadoras morrowi* lacks lateral bony plates and *Doraops zuloagai* has them only on the posterior portion of the body). Three pairs of barbels (no nasals), mandibular barbels with branches in some; dorsal fin with spine and 4–6 soft rays; adipose fin usually present. Doradids are also called "talking catfishes" because of their sound production, made either by movements of the pectoral spine or by vibrating the swimbladder. Maximum length about 120 cm FL.

A molecular phylogeny of doradids was produced by Arce et al. (2013).

About 32 genera, *Acanthodoras* (3), *Agamyxis* (2), *Anduzedoras* (1), *Amblydoras* (5), *Anadoras* (4), *Astrodoras* (1), *Centrochir* (1), *Centrodoras* (2), *Doraops* (1), *Doras* (5), *Franciscodoras* (1), *Hassar* (5), *Hemidoras* (2), *Hypodoras* (1), *Kalyptodoras* (1), *Leptodoras* (12), *Lithodoras* (1), *Megalodoras* (2), *Merodoras* (1), *Nemadoras* (5), *Opsodoras* (4), *Orinocodoras* (1), *Ossancora* (4), *Oxydoras* (3, includes *Pseudodoras*), *Physopyxis* (3), *Platydoras* (4), *Pterodoras* (2), *Rhinodoras* (5), *Rhynchodoras* (3), *Scorpiodoras* (2), *Tachydoras* (5), and *Wertheimeria* (1), with about 93 species (Sabaj and Ferraris, 2003; Birindelli et al., 2007; Higuchi et al., 2007; Sousa and Birindelli, 2011).

The oldest undoubted doradid fossils are partial skulls of *Oxydoras* from the Miocene of Venezuela, Peru, and Argentina (Lundberg, 1998).

Family AUCHENIPTERIDAE (175)—driftwood catfishes. Freshwater (one species in brackish water); Panama and tropical South America (to Argentina).



Body naked (dorsal region of body between head and dorsal fin with sutured bony plates beneath the skin); usually three pairs of barbels (nasal barbels absent), maxillary pair longest; strong spine in pectoral and dorsal fins; adipose fin present but small, rarely absent. Internal insemination probably in all species.

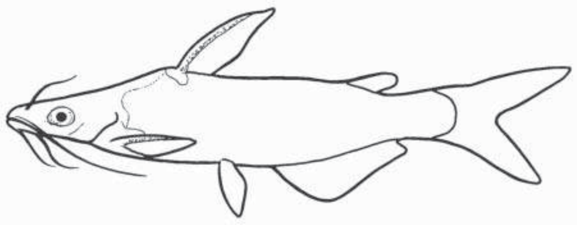
This family now includes the previously recognized family Ageneiosidae (the bottlenose or barbelless catfishes with *Ageneiosus* and *Tetranematichthys*; Ferraris, 2003b). Fossils include Miocene remains from Argentina (Arratia and Cione, 1996). Two subfamilies with 21 genera and about 115 species (Ferraris, 2003b).

Subfamily Auchenipterinae. About 17 genera, e.g., *Ageneiosus* (upper figure), *Asterophysus, Auchenipterus* (lower figure), *Epapterus, Entomocorus, Liosomadoras (removed from Doradidae) Pseudauchenipterus, Spinipterus, Tetranematichthys, Trachelyichthys, Trachelyopterus,* and *Trachycorystes,* with 73 species (Ferraris, 2003b; Reis and Borges, 2006; Akama and Ferraris, 2011).

Subfamily Centromochlinae. Soares-Porto (1998) gave details on the synapomorphies in showing monophyly and relationships of this group. Four genera, *Centromochlus* (13), *Gelanoglanis* (4), *Glanidium* (8), and *Tatia* (17), with 42 species (Ferraris, 2003b; Vari and Ferraris, 2013).

Superfamily Ictaluroidea. A close relationship between Cranoglanididae and Ictaluridae was suggested by Diogo (2004), Hardman (2005), and Sullivan et al. (2006).

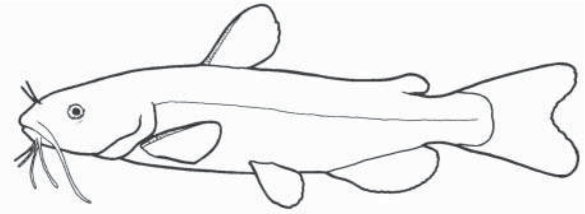
Family CRANOGLANIDIDAE (176)—armorhead catfishes. Freshwater; Asia, China and Vietnam (mainly large rivers).



Dorsal fin short, six (rarely five) branched rays and one spine; anal fin with 35–41 rays; pectoral with a spine; each pelvic fin with 12–14 rays; caudal fin deeply forked; eyes large; body compressed and naked; rough bony plates on top of head; vomer without teeth; four pairs of barbels. Similar to *Pseudobagrus.*

One genus, *Cranoglanis*, and five species (Teugels 2003).

Family ICTALURIDAE (Ameiuridae) (177)—North American catfishes. Freshwater; North America (southern Canada to Guatemala).



Four pairs of barbels on head; skin naked; dorsal (except in *Prietella*) and pectoral fins with a spine; dorsal fin usually with six soft rays; pelvic fin with 7–10 rays; palate toothless except in fossil *Astephus.* Four species of blind (eyeless) catfishes are known; two (*Satan* and *Trogloglanis*) from deep artesian wells and associated ditches near San Antonio, Texas, and two (*Prietella*) from northeastern Mexico. Monophyly and phylogenetic relations of the genera were shown by Lundberg (1992) and relationships among species of *Ameiurus* discussed in (Hardman and Page, 2003). Maximum length about 1.6 m, attained in *Ictalurus furcatus* and *Pylodictis olivaris.*

Seven genera, *Ameiurus* (7, bullheads), *Ictalurus* (10, five of which occur only in Mexico and Guatemala, channel catfishes), *Noturus* (29, including one recently extinct, stonecat, and madtoms, which have a poison gland at base of pectoral spine), *Prietella* (2), *Pylodictis* (1, Flathead Catfish), *Satan* (1), and *Trogloglanis* (1), with a total of about 51 species (including one recently extinct) (Nelson et al., 2004; Hardman, 2004).

Grande and Lundberg (1988) reviewed the Eocene fossils from North America in the genus †*Astephus*, concluding that †*Astephus* is sister to all other ictalurids. *Ictalurus* occurs as fossils of Oligocene age from Saskatchewan, while Oligocene fossils of *Ameiurus* occur in Colorado. Gilbert (1998) gave a type catalogue of recent and fossil taxa.

Superfamily Pimelodoidea. Although not recovered by de Pinna (1993) and not recognized by Nelson (2006), a monophyletic assemblage of three subfamilies (Heptapterinae, Pimelodinae, and Pseudopimelodinae) was suggested by Diogo et al. (2004a). A similar group with three members, now ranked as families, was recovered in the molecular studies of Hardman (2005) and Sullivan et al. (2006), the latter study adding also the problematic Brazilian genus *Conorhynchos* close to or within Heptapteridae. Lundberg et al. (2011) and Sullivan et al. (2013) also recognized the Pimelodoidea as monophyletic. The *incertae sedis* genus *Phreatobius*, with three species, is also included here but its family placement is uncertain (Sullivan et al., 2013).

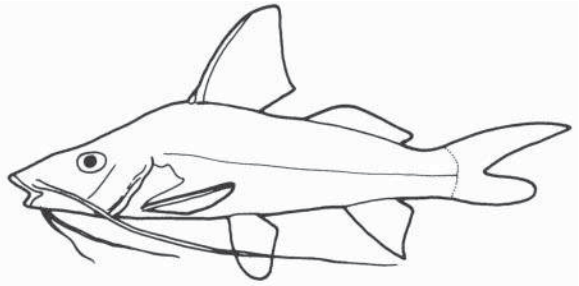
Family HEPTAPTERIDAE (178)—heptapterids. Freshwater; Mexico to South America.

Skin usually naked; three pairs of barbels; adipose fin large; caudal fin deeply forked. Unfortunately for field identification, members of this family cannot always be separated from members of the former Pimelodidae by external features (the above features are not unique to this family; synapomorphies are given in Lundberg et al., 1991a; de Pinna, 1998; Bockmann and Guazzelli, 2003; Shibatta, 2003a).

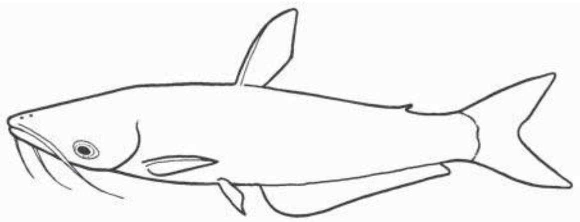
This family is equivalent to the previously recognized Rhamdiinae (placed in Pimelodidae, with the nominal genera listed in Lundberg et al., 1991a) plus the Heptapterinae of de Pinna (1998). The diversity of this group is still poorly known (Bockmann and Guazzelli, 2003).

About 25 genera, e.g., *Acentronichthys, Brachyglanis, Brachyrhamdia, Cetopsorhambia, Chasmocranus, Conorhynchos* (formerly unplaced but included here after Sullivan et al., 2006, 2013), *Gladioglanis, Goeldiella, Heptapterus, Imparfinis, Leptorhamdia, Mastiglanis, Myoglanis, Nemuroglanis, Pimelodella* (synonyms *Caecorhamdella* and *Typhlobagrus*), *Rhamdella, Rhamdia,* and *Taunayia,* with roughly 209 species (Shibatta, 2003a; Bockmann and Guazzelli, 2003; Weber et al., 2003; Trajano et al., 2004; Bockmann and Miguelarena, 2008; Ribeiro et al., 2011).

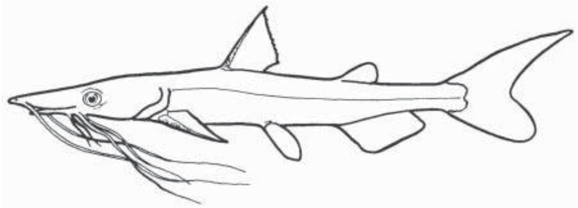
Family PIMELODIDAE (179)—long-whiskered catfishes. Freshwater; Panama and South America (north to southernmost Mexico).



Body naked; adipose fin present; three pairs of barbels (no nasal barbels); pectoral and dorsal-fin spines present or absent; adipose fin well developed. Maximum length about 2.8 m FL, attained in *Brachyplatystoma filamentosum.*



This family now includes the previously recognized family Hypophthalmidae (lookdown catfishes or loweye catfishes with four species of *Hypophthalmus* (middle figure), thought to be most closely related to *Parapimelodus,* part of the *Pimelodus* group) (de Pinna, 1998; Lundberg and Littmann, 2003).



In Nelson (1994), three subfamilies were recognized, Rhamdiinae, Pimelodinae, and Pseudopimelodinae, with members of the first and last now placed elsewhere. Lundberg et al. (2011) studied the intra- and inter-relationships of the Pimelodidae. See above under superfamily Pseudopimelodoidea for further discussion.

About 32 genera, e.g., *Bergiaria, Brachyplatystoma, Calophysus, Goslinia, Hypophthalmus* (middle figure), *Luciopimelodus, Leiarius, Megalonema, Parapimelodus, Phractocephalus, Pimelodina, Pimelodus* (upper figure), *Sorubim* (lower figure), *Sorubimichthys,* and *Zungaro* (synonym *Paulicea*), and at least 112 species (de Pinna, 1998; Lundberg and Littmann, 2003; Lundberg et al., 2011).

The listed works discuss various lineages of this family. †*Steindachneridion iheringi* is an extinct species in an extant genus from the Oligocene or Miocene of Brazil. Other fossil pimelodids are common beginning in the Miocene in South America (Gayet and Meunier, 2003).

Family PSEUDOPIMELODIDAE (180)—bumblebee catfishes. Freshwater; South America.

Wide mouth; small eyes; barbels short. Some are popular aquarium fishes, noted for their body coloration of dark brown blotches. Formerly part of Pimelodidae.

Six genera, *Batrochoglanis* (5), *Cephalosilurus* (4), *Cruciglanis* (1), *Lophiosilurus* (1), *Microglanis* (23), *Pseudopimelodus* (5), with 39 species (Shibatta 2003a,b).

Order GYMNOTIFORMES (35)—Neotropical knifefishes. Body eel-like (compressed or cylindrical); pelvic girdle and fins absent; dorsal fin absent (but see family Apteronotidae); adipose fin absent; anal fin extremely long (more than 100 rays and extending from near pectoral-fin origin to near posterior tip of body) and employed in forward and backward movements; caudal fin absent or greatly reduced (present only in the apteronotids); restricted gill openings; anal opening under head or pectorals; basal pterygiophores to anal fin with only one section (radial) and a hemispherical cartilaginous head that articulates the fin rays (allowing them to move in a circular motion); electric organs present; suboperculum absent; ectopterygoid absent; autopalatine not ossified; maxilla rudimentary (except *Electrophorus*), maxillary teeth absent; endopterygoid teeth few or none; claustrum of Weberian complex absent; alarm substance (Schrekstoff) absent.

The electric organs are derived from muscle cells in most groups (myogenic), or from nerve cells in adult apteronotids (neurogenic). Like catfishes, gymnotiforms are nocturnal. They probably arose in the Neotropical region. They are thought, on the basis of a cladistic study by Fink and Fink (1981, 1996), to be the sister group to the siluriforms (see above under Otophysi), a position that is supported by numerous morphological synapomorphies (see discussion above under series Otophysi).

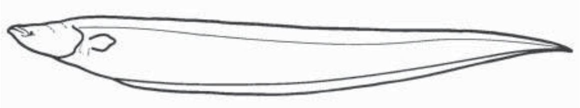
Five families, 33 genera, and at least 208 species (Albert and Crampton, 2005). The classification follows Albert and Campos-da-Paz (1998), Albert (2001), and Albert and Crampton (2005). See the family Sternopygidae below for the only known fossil species.

Suborder Gymnotoidei. One family, two genera, *Gymnotus* (38) and the monotypic *Electrophorus electricus* equaling 39 species (Albert and Crampton, 2005).

Family GYMNOTIDAE (181)—nakedback knifefishes. Freshwater; North (southern Mexico only), Central, and South America.

Body rounded or partially so (adult body depth greater than half the body width at the anal-fin origin); body cavity very long with 31–51 (more than 100 in

Electrophorus) precaudal vertebrae. Maximum length about 2.2 m TL, attained in *Electrophorus electricus*; species of *Gymnotus* reach up to 100 cm. The common name in English for the family is appropriate for the order but is retained here.



Gymnotus (banded knifefishes). Small scales present; mouth superior; anal fin terminating at a point near the tip of the tail; body subcylindrical; weak electrical discharge. The genus *Gymnotus*, currently with 38 species (Campos-da-Paz, 2003; Crampton and Albert, 2004; Albert and Crampton, 2003a, 2005; Fernandes et al., 2005; Cognato et al., 2007; Maxime et al., 2011) is substantially more diverse than previously recognized (e.g., Nelson, 1994, recognized only three species). This is the most widespread genus of the order, extending from southern Mexico (*G. maculosus*) to Argentina (*G. inaequilabeatus*) and also to Trinidad (*G. carapo*). Albert et al. (2005) reconstructed the phylogeny and biogeography of the many species of *Gymnotus*, and commented on the evolution and function of the patterns of the pigment bands, which characterize lineages. The ancestors of the species in Middle America and South America were the earliest divergence.

Electrophorus electricus (electric eel). The single species of *Electrophorus* was formerly recognized in the family Electrophoridae (electric knifefish), but was placed with the gymnotids in its own suborder; placement here in the same family with *Gymnotus* is based on studies demonstrating their close relationship (Albert and Campos-da-Paz, 1998, Albert, 2001). *Electrophorus* is unique among gymnotiforms in having large electric organs producing lethal discharges (up to 600 volts) for stunning prey (high voltage, low amperage), vascularized oral respiratory organ (they can breathe air), and continuous addition of vertebrae throughout life. In addition: scales absent; mouth terminal; anal fin continuing to the tip of the tail; body rounded. Northern South America (primarily Orinoco and Amazon River basins).

Suborder Sternopygoidei. Body compressed (rarely cylindrical); precaudal vertebrae 12–26 (except *Sternopygus*, which can have as many as 30). Two superfamilies, four families, 31 genera, and 169 species.

Superfamily Rhamphichthyoidea. Two families.

Family RHAMPHICHTHYIDAE (182)—sand knifefishes. Freshwater; South America.

Teeth absent on oral jaws; snout elongate; nostrils relatively close together. The common name tubesnout knifefishes may also be used for this group.

Three genera, *Gymnorhamphichthys* (6), *Iracema* (1), and *Rhamphichthys* (9), with 16 species (Ferraris, 2003c; Albert and Crampton, 2005; Carvalho et al., 2011).

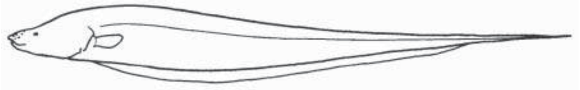
Family HYPOPOMIDAE (183)—bluntnose knifefishes. Freshwater; Panama and South America.

Teeth absent on oral jaws; snout relatively short, not tubular; nostrils well separated; anal-fin origin below or posterior to pectoral-fin base. Maximum length only 35 cm, attained in *Brachyhypopomus brevirostris*; the smallest gymnotiform is *Hypopygus lepturus,* reaching only 9 cm TL. The common names grass and leaf knifefishes may also be used for this group.

Eight genera, *Akawaio* (1), *Brachyhypopomus* (13), *Hypopomus* (1, synonym *Parupygus*), *Hypopygus* (8), *Microsternarchus* (1), *Procerusternarchus* (1), *Racenisia* (1), *Steatogenys* (3), and *Stegostenopos* (1), with 30 species (Albert and Crampton, 2003b, 2005; Giora and Malabarba, 2009; Maldonado-Ocampo et al., 2013; Cox et al., 2014).

Superfamily Apteronotoidea (Sinusoidea). Two families.

Family STERNOPYGIDAE (184)—glass knifefishes. Freshwater; Panama and South America.



Villiform teeth present on the upper and lower jaws; infraorbital bone series complete, bones enlarged, partial cylinders with slender osseous arches, and with an enlarged sensory canal; snout relatively short; eye relatively large (diameter equal to or greater than distance between nares); anal-fin origin at isthmus. *Eigenmannia vicentespelaea* of Brazil is the only cave-inhabiting gymnotiform (Proudlove, 2005). Maximum length 140 cm, attained in *Sternopygus macrurus.*

Alves-Gomez et al. (1995) gave preliminary molecular evidence, supported by phenotypic data, that the Sternopygidae might be di-phyletic, with *Sternopygus* (Sternopygidae s.s.) being a much more primitive lineage not closely related to some of the other genera in the group. For the remaining genera they proposed the family name Eigenmanniidae. That suggestion has not been widely adopted. The broad-scale molecular study of Betancur-R. et al. (2013a) did not help resolve the issue because of limited taxon sampling and weak nodal support.

The only known gymnotiform fossil, the late Miocene †*Humboldtichthys* (formerly †*Ellisella*) *kirschbaumi* from Bolivia, belongs to this family; as with living gymnotiforms, it could regenerate its caudal skeleton (Gayet and Meunier, 2000; Albert and Crampton, 2005). Species of sternopygids are also known as rattail knifefishes.

Six genera, *Archolaemus* (6), *Distocyclus* (2), *Eigenmannia* (8), *Japigny* (1), *Rhabdolichops* (10), and *Sternopygus* (9), with about 36 species (Albert, 2003a; Albert and Crampton, 2005; Correa et al., 2006; Meunier et al., 2011).

Family APTERONOTIDAE (185)—ghost knifefishes. Freshwater; Panama and South America.

Small caudal fin (with fin rays) present that is not united to the anal fin; fleshy dorsal organ (a longitudinal strip attached to posterodorsal midline, resembling an adipose fin); neurogenic electric organ in adults. Maximum length 1.3 m, attained in *Apteronotus magdalenesis.*

Fourteen genera, *Adontosternarchus* (6), *Apteronotus* (23, synonyms *Tembeassu* and *Ubidia*), *Compsaraia* (2), *Magosternarchus* (2), *Megadontognathus* (2), *Orthosternarchus* (1), *Pariosternarchus* (1), *Parapteronotus* (1), *Platyurosternarchus* (2), *Porotergus* (3), *Sternarchella* (6), *Sternarchogiton* (5), *Sternarchorhamphus* (1), and *Sternarchorhynchus* (32), with about 87 species (Albert, 2001, 2003b; Albert and Crampton, 2005, 2006; de Santana and Crampton, 2006; de Santana et al., 2007; Triques, 2011; de Santana and Vari, 2012).

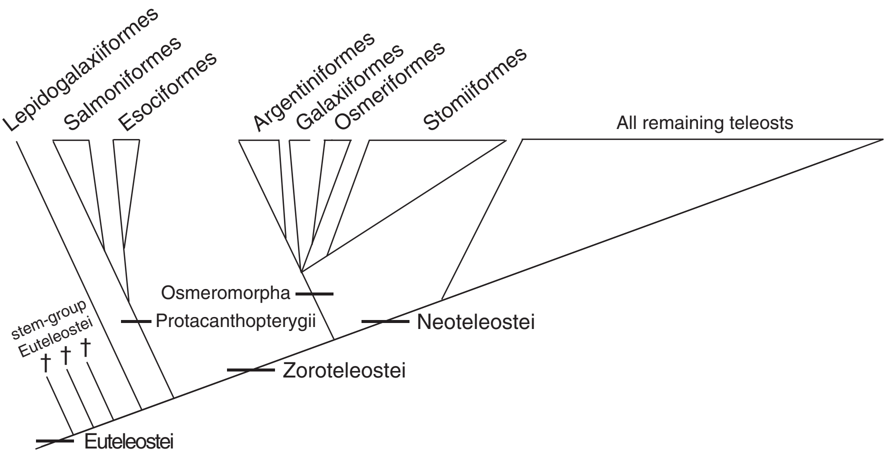
Cohort EUTELEOSTEI

This cohort contains all the remaining teleost fishes. As noted by Johnson and Patterson (1996) and Wiley and Johnson (2010), the monophyly of this group is supported by the pattern of supraneural development, presence of a stegural with an anterodorsal membrane outgrowth, and presence of caudal median cartilages. Strong support for Euteleostei is also seen in molecular-sequence studies including those of Zaragüeta-Bagils et al. (2002), Ishiguro et al. (2003), Osinov and Lebedev (2004), Li et al. (2010), Burridge et al. (2012), Near et al. (2012a), Betancur-R. et al. (2013a), and Campbell et al. (2013).

The monotypic genus *Lepidogalaxias* of Western Australia, formerly classified among Galaxioidei (which were usually then in Osmeriformes), is now regarded as the sister group of all other extant members of the cohort Euteleostei (see discussion below). Among those other extant Euteleostei, the Superorder Protacanthopterygii (Salmoniformes plus Esociformes) is sister to all other euteleosts, which are an unranked taxon called the Zoroteleostei. The latter group in our treatment includes the superorder Osmeromorphi plus all higher teleosts in the unranked taxon Neoteleostei.

Stem-group fossil euteleosts include the Late Jurassic †*Leptolepides* (Arratia, 1996, 1997) from Germany, along with the late Early Cretaceous †*Erichalcis* (Hermus et al., 2004; Arratia, 2008) from Canada, and the Late Cretaceous †*Avitosmerus* (Fielitz, 2002; Murray and Cumbaa, 2015) also from Canada.

Fifty orders, 351 families, 3,160 genera, and 19,799 species.



Possible relationships among the more primitive groups of the Cohort Euteleostei.

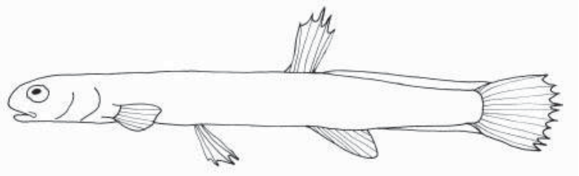
Order LEPIDOGALAXIIFORMES (36)—salamanderfishes. One monotypic family. For characters see the family Lepidogalaxiidae.

The phylogenetic position of *Lepidogalaxias* has been subject to much debate. Williams (1997) regarded *Lepidogalaxias* as the sister group to Galaxiidae + Aplochitonidae. Waters et al. (2000) argued that it is not a galaxiid, and that an esocoid relationship might be possible (at least they could not reject such a hypothesis), a view previously suggested by Rosen (1974). Johnson and Patterson (1996) presented evidence that *Lepidogalaxias* and the other galaxiids form a monophyletic group (however, a number of characters in *Lepidogalaxias* were interpreted as reversals). Nelson (2006) adopted most conclusions of Johnson and Patterson (1996) and placed Lepidogalaxiidae and Galaxiidae into synonomy. Wilson and Williams (2010) then suggested that *Lepidogalaxias* might be sister to all osmeriforms (then including argentinoids and galaxioids).

However, recent molecular work (Li et al., 2010; Burridge et al., 2012; Near et al. 2012a; Betancur-R. et al., 2013a) now strongly supports the idea that *Lepidogalaxias* is the sister to all other euteleosts. Although it shares some osteological and myological characters with galaxiids, its preopercular sensory canal is in a bony tube opening by a pore (Wilson and Williams, 2010), a primitive state more consistent with it not being a member of the Zoroteleostei (see below). Rosen (1974) and Fink (1984) were correct to remove *Lepidogalaxias* from the galaxioids, although their suggested alternative placements are not currently favored. Herein we accept the strong molecular evidence for a basal position of *Lepidogalaxias* within Euteleostei.

Family LEPIDOGALAXIIDAE (186)—salamanderfishes. Freshwater; southwestern Australia.

Body elongate and slender; dorsal fin posterior to pelvic fin, above anal fin; no adipose fin; dorsal-fin rays 5–7; anal-fin rays 11 or 12; scales very thin; males with modified anal-fin rays and a sheath of scales over anal fin base, facilitating direct transfer of sperm to female for internal fertilization; gill rakers 4–7; eyes lacking eye muscles (in compensation for the inability to rotate the eye in its socket, the fish has an unusual ability to bend its neck downwards and sideways); vertebrae 44–47.



This ancient lineage from the early radiation of Euteleostei survives drought periods by burrowing into damp sand. Maximum SL about 6.7 cm.

One species, *Lepidogalaxias salamandroides* (Salamanderfish) (Berra, 1997; Berra and Pusey, 1997).

Superorder PROTACANTHOPTERYGII

Originally a much larger assemblage of fishes when proposed in the landmark volume on teleostean relationships by Greenwood et al. (1966), the Protacanthopterygii have been greatly reduced in scope over the following decades, beginning with the work of Rosen (1973a, 1985). Nelson (1984) recognized Protacanthopterygii with one order, Salmoniformes, containing four suborders. In Nelson (1994) the same content was recognized, but with a different arrangement classified in three orders. Much of the work immediately prior to Johnson and Patterson (1996), and employed in Nelson (1994), was by Fink (1984), Rosen (1985), and Sanford (1990). In Nelson (2006), the overall composition of Protacanthopterygii followed Nelson (1994), but the recognized orders and sequence changed again. Esociformes were retained in Protacanthopterygii even though Johnson and Patterson (1996) had advocated that they be positioned as sister to the Neoteleostei.

A very restricted membership for Protacanthopterygii, with only salmoniforms and esociforms as sister groups, was also supported by the morphological work of Williams (1987) and by Wilson and Williams (2010). Morphological characters supporting the Protacanthopterygii include: unique anteroventral process on hyomandibular bone in primitive members (lost in some more derived genera of salmoniforms), and loss of a ligamentous connection between the maxilla-mandibular ligament and the adductor mandibulae muscle (possibly reversed in *Prosopium*; Wilson and Williams, 2010).

The sister-group relationship between salmoniforms and esociforms, albeit joined in Protacanthopterygii in one study or another by various other taxa such as argentinoids, galaxioids, osmeroids, and/or stomiiforms, has also been supported by several molecular studies (Zaragueta-Bagils et al., 2002; Broughton, 2010:fig. 1; Near et al., 2012a; Betancur-R., et al. 2013a). However, there is no general agreement among such studies as to which of the additional taxa should be included in Protacanthopterygii. The more restricted membership for Protacanthopterygii, consisting of only of salmoniforms and esociforms as sisters, has also been supported by some molecular studies, many of them with diverse taxon sampling and relatively strong nodal support (e.g. Ishiguro et al., 2003; López et al., 2004; Broughton, 2010:fig. 2; Burridge et al., 2012; Campbell et al., 2013). Here we have adopted the more restricted membership of two orders, because it has significant molecular and morphological support.

Two orders with 3 families, 15 genera, and about 335 species.

Order SALMONIFORMES (37)—trout, salmon, and whitefish. This order contains only the family Salmonidae. Cretaceous fossils that may be related to salmoniforms include †*Kermichthys* and †*Paravinciguerria,* studied by L. Taverne in the 1990s.

Family SALMONIDAE (187)—trout, salmon, and whitefish. Freshwater and anadromous; Northern Hemisphere.

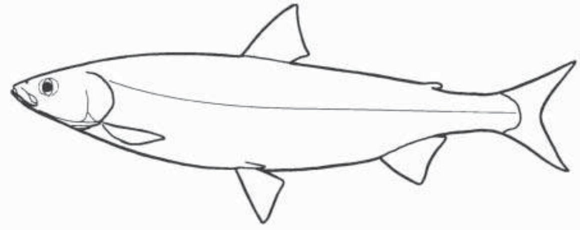
Deep posterior myodome with eye musculature passing through and attaching to trunk muscles; adipose fin present; mesocoracoid present; gill membranes extending far forward, free from isthmus; basihyal teeth present; pelvic axillary process present; vertebral centra pitted; last three vertebrae turned up; 11–210 pyloric caeca; 7–20 branchiostegal rays; vertebrae 50–75; tetraploid karyotype; parr marks in young of most species. Maximum length up to 1.5 m. This family has high value in sport and commercial fisheries.

Many biological species exist that are not named (e.g., of whitefishes and char). However, there is a serious problem of how many nominal species to recognize as valid (according to various species definitions). Some workers might combine various species (for an example, see Nelson et al., 2004:208–209), which others might split. The basic classification of this group is similar to that in Nelson (1994), which was largely consistent with the morphological works of Norden (1961), Kendall and Behnke (1984), Sanford (1990), Stearley and Smith (1993), and Wilson and Li (1999). These morphological studies and the supertree review by Wilson and Williams (2010), along with some molecular work (e.g., Osino and Lebedev, 2004) agreed that the sequenced cladistic relationships are Coregoninae, Thymallinae, and Salmoninae, with the latter two being sister groups. However, several molecular studies have placed Thymallinae closer to Coregoninae than to Salmoninae, although usually with a short branch length (e.g., Betancur-R. et al., 2013a; Campbell et al., 2013). Herein we are continuing to list the three subfamilies as before, while acknowledging that the placement of Thymallinae remains controversial.

Some authors prefer to recognize two of the subfamilies at the family level, e.g., Coregonidae and Salmonidae (containing the subfamilies Thymallinae and Salmoninae) (e.g., Johnson and Patterson, 1996; Sanford, 2000), or all three at the family level (e.g., Reshetnikov et al., 1997). We here recognize subfamilies within a single family, and given the controversy about the relationships of *Thymallus,* we continue to recognize three subfamilies. A listing of species by broad geographic areas is found in Kottelat (1997), Reshetnikov et al. (1997), and Nelson et al. (2004).

Three subfamilies with 10 genera and up to 223 species.

SUBFAMILY COREGONINAE (WHITEFISHES AND CISCOES). Fewer than 16 dorsal-fin rays; scales large, fewer than 110 along lateral line; no teeth on maxilla; vomer usually small and without teeth; orbitosphenoid present; suprapreopercular absent. Three genera and as many as 88 species.



Prosopium (round whitefishes). Small mouth with weak or no teeth; single flap between nostrils; basibranchial plate present; young with parr marks. Freshwater; northern Northern Hemisphere; six species. One species occurs in both northern North America and Siberia; three are endemic to Bear Lake, Utah-Idaho, one of which is cisco-like.

Coregonus (*lake whitefishes and ciscoes*)—Small mouth with weak or no teeth; two flaps between nostrils; no basibranchial plate; young without parr marks. Freshwater (occasionally anadromous along Arctic coastline), northern Northern Hemisphere; up to 80 species.

Formerly, subgenera *Coregonus* (lake whitefishes) and *Leuciscus* (ciscoes) were recognized, but recent studies (e.g., Politov et al., 2004) suggest that cisco-like characters have been acquired independently. Whitefishes usually have subterminal mouth, maxillae usually not extending beyond front margin of eye, and are bottom and plankton feeders, whereas ciscoes usually have a superior or terminal mouth, maxillae normally extending beyond front margin of eye, and are usually plankton feeders. In North America there is good separation between the two groups in gill-raker number; the lake whitefishes almost always have 35 or fewer gill rakers, the ciscoes 36 or more. In Eurasia, however, one lake whitefish (*C. muksun*) usually has 51–56 gill rakers, whereas one cisco (*C. tugun*) has 25–39.

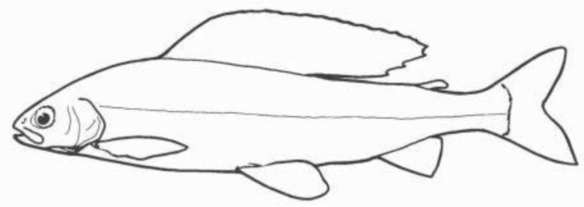
Circumpolar, but most species in northwestern Eurasia. Large lakes often contain endemic radiations in the form of species complexes, such as the *C. lavaretus* complex in Eurasia and the *C. clupeaformis* complex in North America.

Stenodus. Two species are recognized, *Stenodus leucichthys* (Inconnu) and *S. nelma.* Large mouth with many small teeth on jaws, vomer, and palatine; two flaps between nostrils. Anadromous; Arctic Asia and North America.

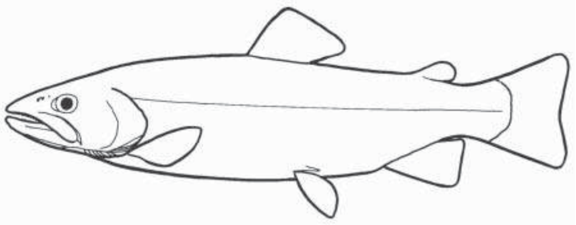
SUBFAMILY THYMALLINAE (GRAYLINGS). More than 17 dorsal-fin rays; teeth on maxilla; orbitosphenoid absent; suprapreopercular absent.

One genus, *Thymallus* (graylings), freshwater; Northern Hemisphere; up to 14 species, mostly in Eurasia, but only one in North America (*T. arcticus*).

Affinities between North American and Eurasian grayling were covered by Stamford and Taylor (2004). A molecular study of the genus *Thymallus* was completed by Froufe et al. (2005).



Subfamily Salmoninae (trout and salmon). Fewer than 16 dorsal-fin rays; scales small, more than 110 along lateral line; teeth on maxilla; orbitosphenoid present (sometimes absent in *Salvethymus svetovidovi*); suprapreopercular present. Six genera and perhaps 121 species.



Relationships within Salmoninae have been examined with both morphological and molecular data (see references for Salmonidae, above).

Certain species, such as *Salvelinus fontinalis*, *Salmo trutta*, and *Oncorhynchus mykiss* (synonym *Salmo gairdneri*), have been introduced virtually throughout the world. Species of Salmoninae that are called "trouts" are mostly those that spend most of their lives in fresh water and usually do not die after spawning. Some so-called trouts belong to distinct genera such as *Brachymystax* and *Hucho* (see below). Some others are really chars (genus *Salvelinus*), and still others are isolated, usually landlocked populations, some of them recognized as distinct species, of Atlantic trout/salmon (genus *Salmo*) or of Pacific salmon (genus *Oncorhynchus*).

Genera of Salmoninae are:

Brachymystax. Perhaps three species including *B. lenok* (lenok). Freshwater; northern Asia to Korea (Holcík et al., 1988).

Hucho (huchen or taimen). Freshwater and anadromous; northern Asia to Japan, Danube basin of Europe; perhaps four species (Holcík et al., 1988).

Salvelinus (chars or charrs). Biological information on the species of this genus and some problems of char taxonomy are presented by Behnke (2002).

Subgenus *Salvethymus.* One species, *S. svetovidovi* (Longfin Char), described by I. A. Chereshnev and M. B. Skopets in 1990, known only from Lake El'gygytgyn, a cold, clear, ultraoligotrophic lake formed in a meteorite crater about 3.5 million years ago and having been a refugium during the Pleistocene glaciation. This planktivore is unique among salmonines in several features; for example, it has an unusually high number of gill rakers and very reduced orbitosphenoid (sometimes absent) and basisphenoid. Reasons for not recognizing *Salvethymus* at the generic level, as proposed by Chereshnev and Skopets (they also recognized *Baione* and *Cristivomer* as genera), are given in Nelson (1994), based on Behnke (1989).

Subgenus Baione. Two species, *Salvelinus fontinalis,* Brook Trout (freshwater and anadromous, eastern North America), and *S. namaycush,* Lake Trout (freshwater, northern North America, recognized by some in the subgenus or genus *Cristivomer*).

Subgenus Salvelinus. Freshwater and anadromous; Northern Hemisphere. About eight species (e.g., Arctic Char, Dolly Varden, and Bull Trout). Perhaps the northernmost record for any freshwater fish is that for anadromous and freshwater Arctic Char in Lake Hazen, Ellesmere Island, Canada. The work of Stearley and Smith (1993) suggested that several species recognized here belong in the *Baione* lineage; for example, in their cladogram, Bull Trout and Lake Trout are sister species. E. B. Taylor and colleagues have done many studies on hybridization and its significance in char species (e.g., Taylor, 2004). Up to 52 species.

Parahucho. Erected as a monotypic subgenus by Vladykov in 1963, this is a separate lineage according to the 1995 molecular study by R. B. Phillips and colleagues and by some of the results of Crespi and Fulton (2004). Wilson and Williams (2010) in a supertree analysis suggested that it was sister to *Salmo* and *Oncorynchus.*

Salmo. Freshwater and anadromous; North Atlantic basin (northeastern North America and Europe) and European Arctic. Fall spawning. Commercially important species include the Atlantic Salmon (*S. salar*) and Brown Trout (*S. trutta*), both with numerous anadromous and freshwater populations that have been named as separate species (e.g., Kottelat and Freyhof, 2007; Susnik et al., 2007; Turan et al., 2011, 2012). Nominal subgenera that are probably derived, landlocked populations of the genus *Salmo* include *Acantholingua* (*A. ohridanus*), *Salmothymus* (*S. obtusirostris*), and *Platysalmo* (*P. platycephalus*) (see also Wilson and Williams, 2010). Up to 41 species.

Oncorhynchus (*Pacific trouts and Pacific salmon*). About 17 species.

Stearley and Smith (1993) provided evidence that the subgenus *Rhabdofario,* previously used for several Pacific trout species, is paraphyletic, with the four extant species forming separate branches on a comb-like cladogram.

Pacific salmon comprise an important fishery, and a great deal is known of their biology. They are a rich source of material for studies in diversity. They have a strong homing ability, usually returning to their natal streams for spawning. *Oncorhynchus masou* (Masu Salmon or Cherry Salmon) and *O. rhodurus* (Amago) are the most "trout-like"; the latter nominal species is probably conspecific with *O. masou*—both occur only in far eastern Asia. *Oncorhynchus kisutch* (Coho Salmon) and *O. tshawytscha* (Chinook Salmon) are somewhat intermediate between the Japanese endemics and the next three species. *Oncorhynchus keta* (Chum Salmon) and *O. gorbuscha* (Pink Salmon) usually spawn in the lower reaches of rivers and are the most "marine-like." Individuals of *O. gorbuscha* have a rigid two-year life span, with one or the other or both of the even- and odd-year stocks existing allochronously in the same stream. Individuals of other species have variable lifespans: those of *O. nerka* (Sockeye Salmon) live as long as eight years in their northern range (Alaska). In this species the anadromous form (sockeye) has, throughout most of its range, given rise to freshwater populations (kokanee), which occur in sympatry or allopatry (usually in so-called "landlocked" lakes, though connected to the sea by rivers) with the parental anadromous form. All individuals of the last five species and all anadromous individuals die after spawning; some non-anadromous *O. masou* may repeat spawn. Wilson et al. (2009) reconstructed the history of inland populations of *O. clarki* using mtDNA, recognizing six subspecies in western USA and Mexico.

Fossils include i) the Eocene †*Eosalmo*, the oldest salmonid and the primitive sister group to all other salmonines, combining characters of Thymallinae and Salmoninae (Wilson and Williams, 1992, 2010; Stearley and Smith, 1993), with two species, †*E. driftwoodensis* from North America (Wilson 1977, Wilson and Li, 1999, Wilson and Williams, 2010) and †*E. kamchikensis* from eastern Siberia (Sytchevskaya, 1986); ii) †*Brachymystax bikinensis* of Oligocene age (Sytchevskaya, 1986); iii) the giant Miocene †*Oncorhynchus rastrosus* from Oregon and California, a very large-bodied filter feeder that had over 100 gill rakers; iv) †*Oncorhynchus ketopsis*, also Miocene, from Oregon (Eiting and Smith, 2007); and v) the southernmost known salmonid, †*Oncorhynchus australis*, from the Pliocene of Mexico (Stearley and Smith, 1993). These and related fossils demonstrate that Salmoninae are at least as old as early Eocene, and that *Oncorhynchus* arose at least six million years ago.

Order ESOCIFORMES (Haplomi, Esocae) (38)—pikes and mudminnows. Maxilla toothless but in gape of mouth; no adipose fin; dorsal and anal fins located posteriorly; no breeding tubercules; no pyloric caeca; no mesocoracoid; cheek and operculum scaled; one postcleithrum; basibranchial tooth plate in two parts; ossification of middle radials on only central pterygiphores of dorsal and anal fins (*Esox* and *Umbra*), or not ossified at all (*Dallia* and *Novumbra*); paired elongate proethmoids (Rosen, 1974; Johnson and Patterson, 2010).

Two families, four genera, and at least 12 species. There is one fossil-only family recognized.

The crown-group Esociformes consist of two families, Esocidae (*Esox*, *Novumbra* and *Dallia*) and Umbridae (*Umbra*). The Umbridae formerly (Wilson and Veilleux, 1982; Nelson, 2006) included also *Novumbra* and *Dallia*, but based on molecular results, López et al. (2000, 2004) found *Dallia* and *Novumbra* to be more closely related to *Esox* than to *Umbra*, with *Novumbra* being the living sister group to *Esox*. This new arrangement is accepted here.

†Family PALAEOESOCIDAE. This extinct family contains the Eocene-Miocene genus †*Palaeoesox* and possibly the Paleocene-Eocene genus †*Boltyshia*, both from Europe (Sytchevskaya 1976; Gaudant 2012).

Family ESOCIDAE (188)—pikes. Freshwater; Northern Hemisphere.

Opercle truncated dorsally; one small supramaxilla; subopercle sickle-shaped; vomer and palatines strongly toothed; scales with few strong, anterior radii.

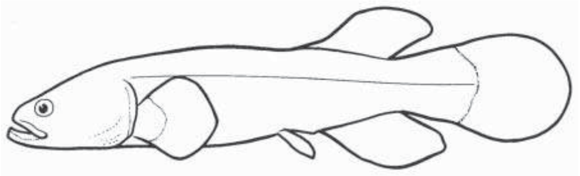
The oldest members of the family are fossil species of the Late Cretaceous †*Estesox* and †*Oldmanesox* (Wilson et al., 1982). The oldest known fossil species of the genus *Esox*, †*E. tiemani*, is from Paleocene formations of about 62 million years ago in Alberta (Wilson, 1984); it is relatively similar in appearance to *E. lucius*, more so than some Cenozoic species of *Esox* from Eurasia. The oldest pike found outside North America is from the early Eocene of China (Chang and Zhou, 2002). L. Grande (1999) described an early Eocene fossil from North America, †*E. kronneri*, that appears to belong to the subgenus *Kenoza*, the first appearance of that subgenus in the fossil record, and briefly reviewed both fossil and extant species of *Esox*. †*Esox kronneri* lived during one of the warmest periods of reconstucted Cenozoic climates, the Early Eocene Thermal Maximum, although other fossil esocids seem to have responded to warm climates by living farther north (Newbrey et al., 2008).

Three genera with about nine species.

Novumbra. Caudal fin truncate; two mandibular canal pores present; three temporal canal pores; one epural in caudal fin skeleton; pectoral-fin rays 18–23; pelvic-fin rays six or seven; dorsal-fin rays 12–15; anal-fin rays 11–13; lateral-scales 52–58; vertebrae 37–40.

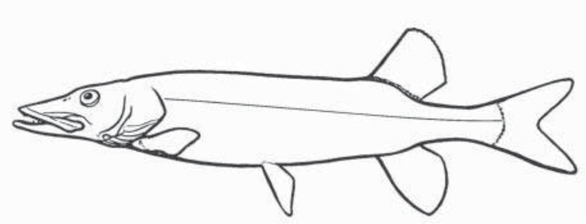
One species, *Novumbra hubbsi* (Olympic Mudminnow), confined to the Olympic Peninsula in western Washington, occurring primarily in the Chehalis system. There is one fossil species, †*Novumbra oregonensis*, from the Oligocene of Oregon (Cavender, 1969).

Dallia. Rounded caudal fin; pectoral-fin rays 29–38; pelvic-fin rays usually two or three (rarely none or one); dorsal-fin rays 10–16; anal-fin rays 11–16; lateral-line scales 76–100; vertebrae 40–42; Baudelot's ligament ossified (the only esociform with it ossified); intercalar and postcleithrum absent; much of pectoral skeleton unossified (all based on *Dallia pectoralis*, in the strict sense).



One to three species, *D. pectoralis* (Alaska Blackfish), in northeastern-most Siberia and Alaska (see the population study based on mtDNA by Campbell and López, 2014) and two nominal species *D. admirabilis* and *D. delicatissima* from northeastern Siberia (pelvic-fin rays absent in some specimens of the latter). Mecklenburg et al. (2002) recognized all nominal species as synonyms of *D. pectoralis* but noted other workers who recognize three species. Cavender (1969) noted but did not formally name a fossil *Dallia* from the Miocene of Alaska.

Esox. Posttemporal canal present; anterior part of palatine articulating with premaxilla to form a toothed biting surface of the upper jaw; maxillary articulation process present; depressible teeth on dentary, vomer and palatine; toothplates on basibranchial one and two; anterior supraneural expanded; lateral line complete; presence of notched or cardioid scales along lateral line; caudal fin forked, with 40–50 rays (17 branched, rarely 16); infraorbital canal with eight or more pores; 6 preopercular canal pores; branchiostegal rays 10–20; vertebrae 46–68 (T. Grande et al., 2004). Maximum length 1.4 m, obtained in *Esox masquinongy*.

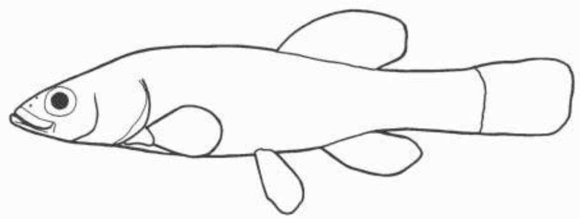


Seven recognized species divided between two subgenera.

Subgenus *Esox* (i.e., pikes). *Esox lucius* (the Northern Pike), with a circumpolar distribution, *E. reicherti* (the Amur Pike), from Siberia, *E. masquinongy* (the Muskellunge) from North America, and *E. cisalpinus* (= *E. flaviae,* the Southern Pike of Europe) native to Italy. Infraorbital canal complete; posttemporal fossa covered by parietals; vomer greater than 50% of parasphenoid length; abdominal vertebrae 39–48; caudal vertebrae 17–21; three epurals present in caudal fin skeleton; 5–9 mandibular canal pores; pelvic-fin rays 10–13; lateral-line scales, 36–59.

Subgenus *Kenoza* (i.e., pickerels). *E. niger* (Chain Pickerel), and *E. americanus,* which has two subspecies (Redfin Pickerel and Grass Pickerel) all endemic to North America (L. Grande, 1999; T. Grande et al., 2004). Abdominal vertebrae 32–39; caudal vertebrae 13–18; two epurals present in the caudal fin skeleton; four mandibular canal pores present; infraorbital canal discontinuous; total vertebrae 46–55; expansion of second neural arch in the transverse plane and rostrocaudally; notched scales present between pelvic fins; dorsal-fin rays 13–21; anal-fin rays 11–18; pelvic-fin rays 8–11; lateral-line scales, 78–140. Grande et al. (2004) and López et al. (2004) found strong support for the monophyly of the genus, and for the monophyly of the subgenera *Esox* (pikes) and *Kenoza* (pickerels).

Family UMBRIDAE (189)—mudminnows. Freshwater; parts of Northern Hemisphere.



Pectoral-fin rays 11–16; pelvic-fin rays 5–7; dorsal-fin rays 13–17; anal-fin rays 7–10; lateral-scales 30–36; vertebrae 32–37; mandibular canal absent in *Umbra limi* and *U. pygmaea*, present in *U. krameri*; 2 mandibular canal pores; extrascapular and pottemporal canals absent. Can breath atmospheric air using a modified swimbladder.

Until recently, the Umbridae included also the genera *Dallia* and *Novumbra* (e.g., Wilson and Veilleux, 1982, who studied the osteology of all three genera), but *Dallia* and *Novumbra* are now in Esocidae (e.g., López et al., 2000, 2004). One genus*, Umbra*, with three species: *U. limi* in east-central North America, *U. pygmaea* in the eastern United States, and *U. krameri* in southeastern Europe.

ZOROTELEOSTEI (ZOROTELEOSTS). All of the remaining taxa of Euteleostei were named the Zoroteleostei by Wilson and Williams (2010) in recognition of the possession, in most primitive members of included clades, of a completely open or ventrally open preopercular sensory canal. The name means "pure teleosts." When it was named, some of its members were thought to be related in ways different from those adopted here, but with one exception the membership has not changed. The exception is *Lepidogalaxias*, earlier thought to be a galaxioid, but now regarded as being sister to all other crown-group Euteleostei and here separated from Zoroteleostei and from Protacanthopterygii (see above) in the Order Lepidogalaxiiformes. The new position for *Lepidogalaxias* solves a problem, because in *Lepidogalaxias* the preopercular sensory canal, though greatly reduced, is enclosed in a bony tube with at least one pore opening (Wilson and Williams, 2010). Thus it is no longer necessary to postulate a reversal in this character for *Lepidogalaxias*. Rosen (1985) had earlier proposed a somewhat similar group (also without *Lepidogalaxias*, which he had argued was related to salmoniforms; Rosen 1974), with the following additional zoroteleostean characters: acellular endoskeletal bone; toothed alveolar process on premaxilla lying under the maxilla; neural spine of caudal skeletal centrum PU2 shorter than that of PU3.

Superorder OSMEROMORPHA

A clade that includes Argentiniformes, Galaxiiformes, Osmeriformes, and Stomiiformes was recovered by Burridge et al. (2012), sister to all higher teleosts. Some members of this putative clade have been classified either as separate lineages (e.g., Galaxiiformes in the phylogeny of Near et al., 2012a) or as closer to the salmoniforms and esociforms—i.e., within Protacanthopterygii—(e.g., Argentiniformes by Near et al. 2012a; Argentiniformes and Galaxiiformes by Betancur-R. et al. 2013a). We recognize here that there is a clade, within Zoroteleostei and sister to Neoteleostei, that includes Osmeriformes and probably others. Betancur-R. et al. (2013a) recognized a clade that they called Stomiatii containing only Osmeriformes and Stomiiformes, but in their tree it is not sister to Neoteleostei and it does not include either Argentiniformes or Galaxiiformes. Therefore, we here designate the new superordinal taxon Osmeromorpha, containing four orders.

Order ARGENTINIFORMES (39)—marine smelts. Adipose fin usually present; caudal fin forked; dorsal fin near body center; maxillae and premaxillae (when present) toothless; supramaxilla absent; mouth usually small; endopterygoid teeth absent; metapterygoid reduced; basibranchials 1–3 toothless; pharyngobranchials 2 and 3 toothless; accessory neural arch absent; uroneural one without membranous anterodorsal outgrowth; branchiostegal rays 2–7; lateral line scales 40–70; swimbladder, when present, physoclistous; mesocoracoid present or absent. The following three characters were previously thought to indicate relationship to alepocephaloids. In the present arrangement they are considered convergent: complex posterior branchial structure ("epibranchial" organ), termed the "crumenal organ;" distal parts of anterior 1–4 epineurals descended; caudal medial cartilages supporting lowermost ray of upper caudal lobe (Johnson and Patterson, 1996; Wiley and Johnson, 2010).

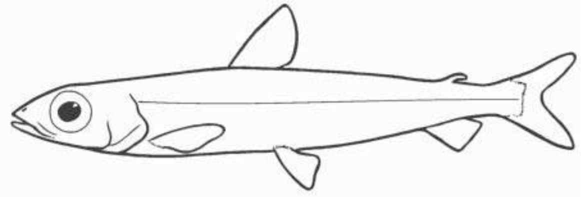
Many are bathypelagic. Color usually silvery. They hatch from small eggs (about 1–3 mm diameter) with gradual larval development, then transform to demersal juvenile.

Studies on this taxon include those by Kobyliansky (1990, 1998), Johnson and Patterson (1996) and Patterson and Johnson (1997a, b), Mecklenburg et al. (2002), Carter and Hartel (2003), Wiley and Johnson (2010). Nelson (2006), following Johnson and Patterson (1996), recognized the two suborders of argentiniforms: Argentinoidei and Alepocephaloidei (slickheads). This classification was followed by Wiley and Johnson (2010). However, there is now strong evidence that the alepocephaloids do not belong here; see the above treatment of Otocephala for a discussion of the new phylogenetic placement of alepocephaloids.

Taverne (1982) assigned the Early Cretaceous genera †*Nybelinoides* and †*Pattersonella* to the Argentinidae. Younger records include species of Oligocene-Miocene age from marine deposits in the Caucasus (Prokofiev, 2005).

Three families, 21 genera, and about 87 species.

Family ARGENTINIDAE (190)—argentines or herring smelts. Marine; Atlantic, Indian, and Pacific.



Eyes not tubular; adipose fin over anal fin base; postcleithra and mesocoracoid present; dorsal-fin origin in front of pelvics; pectoral-fin base on ventrolateral surface; dorsal-fin rays 10–14; anal-fin rays 10–17; pectoral-fin rays 11–25; pelvic-fin rays 10–15; branchiostegal rays 4–6; vertebrae 43–70 (most with 46–55).

Two genera, *Argentina* and *Glossanodon*, with about 27 species.

Family OPISTHOPROCTIDAE (191)—barreleyes or spookfishes. Marine; tropical to temperate, Atlantic, Indian, and Pacific.

Eyes usually tubular; pectoral-fin base on side; pelvic-fin base on side in some; adipose fin in some; photophores in some; most lack swimbladder; frontals fused; parietals not meeting on midline (true also for bathylagids); branchiostegal rays 2–4.

Eight genera, *Bathylychnops*, *Dolichopteroides*, *Dolichopteryx*, *Ioichthys*, *Macropinna*, *Opisthoproctus*, *Rhynchohyalus*, and *Winteria*, with about 19 species.

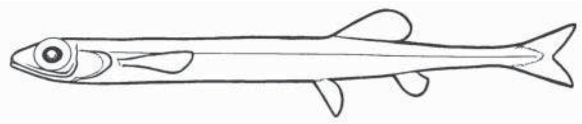
Family MICROSTOMATIDAE (192)—pencilsmelts. Marine; tropical to temperate seas, Atlantic, Indian, and Pacific (extending from the subarctic to the Antarctic).

Lateral line and lateral-line-scales extending onto tail; postcleithra present; mesocoracoid absent; pectoral-fin base on side; dorsal-fin rays 9–12; anal-fin rays 7–10; pectoral-fin rays 7–14; pelvic-fin rays 8–12; branchiostegal rays 3 or 4; vertebrae 41–50.

Three genera with about 20 species.

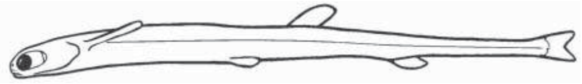
Nansenia. Adipose fin present; dorsal fin in front of pelvics. Seventeen species found from the subarctic to the subantarctic.

Microstoma—No adipose fin; dorsal fin behind pelvics.



One or two species.

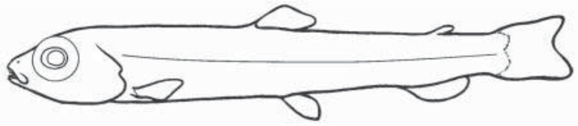
Xenophthalmichthys—No adipose fin; dorsal-fin origin behind pelvic-fin insertion; eyes tubular (protruding anteriorly); pectoral-fin base well up on side, fin with 7 rays; pelvic fin with 7 or 8 rays.



One or two species.

Family BATHYLAGIDAE (193)—deepsea smelts. Subarctic to Antarctic.

Adipose fin present or absent; postcleithra and mesocoracoid absent; pectoral-fin base near ventral surface; dorsal-fin rays 6–13; anal-fin rays 10–28; pectoral-fin rays 7–16; pelvic fin-rays 6–11; branchiostegal rays 2; vertebrae 38–55.



Eight genera, *Bathylagichthys* (5), *Bathylagoides* (3), *Bathylagus* (7), *Dolicholagus* (1), *Leuroglossus* (3), *Lipolagus* (1), *Melanolagus* (1), and *Pseudobathylagus* (1), with about 22 species.

Order GALAXIIFORMES (40)—galaxiiforms. Usually no pyloric caeca; no mesocoracoid; no supramaxillae; 18 or fewer principal caudal-fin rays; no upturned vertebrae. These cold-water fishes form the dominant element in the freshwater fish fauna of the Southern Hemisphere. One family.

Previously, retropinnids were thought to be closely related. However, Waters et al. (2002), in a mitochondrial DNA analysis, concluded that retropinnids and osmerids are sister taxa, a conclusion supported by several later molecular studies.

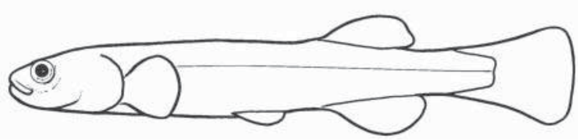
Family GALAXIIDAE (194)—galaxiids. Freshwater and diadromous; Australia, New Zealand, New Caledonia, southernmost Africa, and southern South America.

Principal caudal-fin rays 16 or fewer; caudal fin with 12–14 branched rays; scales absent, but lateral line present; no horny keel along abdomen; maxillary, vomerine, palatine, and basibranchial teeth absent; hypurals 5; gonads paired; cucumber odor absent. Freshwater and diadromous; Australia, New Zealand, New Caledonia, southernmost Africa, and southern South America.

Anderson (1998) described a possible fossil galaxiid, †*Stompooria,* from the Late Cretaceous in South Africa; he also noted other papers on fossil *Galaxias* from New Zealand. Lee et al. (2007) reviewed the galaxiid fossil record and described the Miocene †*Galaxias effusus* also from New Zealand.

Seven genera and 50 species. We here recognize three subfamilies, with Galaxiinae sister to Aplochitoninae and Lovettiinae, following the phylogeny of Burridge et al. (2012).

SUBFAMILY GALAXIINAE. No adipose fin; dorsal fin posteriorly placed near tail (originating above pelvics in *Paragalaxias*); caudal fin usually truncate to emarginate (forked or rounded in some); pelvic fins absent in most *Neochanna*; branchiostegal rays 5–9; pyloric caeca 0–6 (usually 2); vertebrae 37–66. Maximum length 58 cm, attained in *Galaxias argenteus* of New Zealand; most species are less than 20 cm.



Most members are confined to fresh water, although some species are partially anadromous, having larvae that descend streams after hatching, and spend some time in the ocean. The 16-cm *Galaxias maculatus* is peculiar among galaxiids in New Zealand in that ripe adults usually migrate down streams and spawn in estuarine grasses in upper tidal flats during spring tides. The eggs usually hatch after two weeks in subsequent high tides when they are reimmersed in water, and the larvae are washed out to sea (they have been found as far as 700 km from shore). The species is marginally catadromous (with a lunar rhythm), although landlocked populations are known. The juveniles of several species of *Galaxias* can move up damp rock faces or dams and *G. brevipinnis* of New Zealand is particularly good at moving upstream in rapid waters. Species of *Neochanna* (mudfishes) can live in swamps and are able to aestivate during dry periods. The term whitebait is applied to the transparent immature fry of fish that move from the sea into rivers at approximately six months of age. In New Zealand, several species of *Galaxias* constitute the whitebait commercial and recreational fishery.

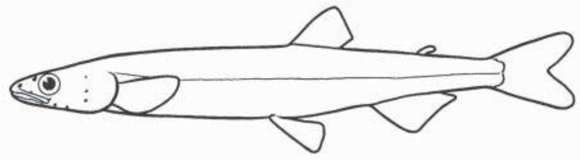
Species abundance is greatest in Australia, especially in Tasmania and southeastern Australia, and in New Zealand. The variable *Galaxias zebratus* occurs in South Africa (two or more species may be represented, McDowell, 2001), and the only species of *Nesogalaxias* occurs in the uplands of New Caledonia. The most widespread species, *G. maculatus,* occurs in Australia, Tasmania, Lord Howe Island, New Zealand, Chatham Islands, and southern South America (Chile, Patagonia, Tierra del Fuego, and Falkland [Malvinas] Islands). Berra (2001) and Wallis and Waters (2003) gave details on the distribution of galaxiid fishes.

Five genera, *Brachygalaxias*, *Galaxias* (synonym *Nesogalaxias*), *Galaxiella*, *Neochanna*, and *Paragalaxias*, with about 47 species (e.g., McDowall, 1990, 1997, 2003; McDowall and Wallis, 1996; McDowall and Chadderton, 1999; Waters et al., 2000; Ling and Gleeson, 2001; Wallis et al., 2001; McDowall and Waters, 2002).

SUBFAMILY LOVETTIINAE. Adipose fin reduced but present; dorsal fin anteriorly placed, above pelvic fin, with 7–9 rays; caudal fin forked; branchiostegal rays usually 5 or 6; pyloric caeca absent; maxilla excluded from gape; postcleithrum present; vertebrae 52–58. Maximum length about 7.7 cm.

One species, *Lovettia sealii*, anadromous, known only from Tasmania (McDowall, 1990). *Lovettia* and a few *Galaxias* constitute the Tasmanian whitebait fishery.

SUBFAMILY APLOCHITONINAE. Adipose fin present; dorsal fin anteriorly placed, above pelvic fin, with 11–14 rays; caudal fin forked; branchiostegal rays 3 or 4; pyloric caeca long, 1 or 2; maxilla almost excluded from gape; postcleithrum absent; vertebrae 64–73. Maximum length 38 cm, attained in *Aplochiton taeniatus*.



One genus, *Aplochiton*, with two species, freshwater and diadromous, from southern Chile, parts of western Argentina in the Andes, Tierra del Fuego, and the Falkland (Malvinas) Islands (McDowall, 1990).

Order OSMERIFORMES (41)—freshwater smelts. Posterior shaft of vomer short; mesopterygoid teeth reduced; articular absent or reduced; pterosphenoid usually with ventral flange; maxilla included in gape of mouth; adipose fin present or absent; radii absent on scales; loss of basisphenoid and orbitosphenoid bones.

Osmeriforms spawn in fresh water except for *Osmerus eperlanus*, and perhaps one or two salangines; only some salangines and *Nesogalaxias* occur in tropical regions.

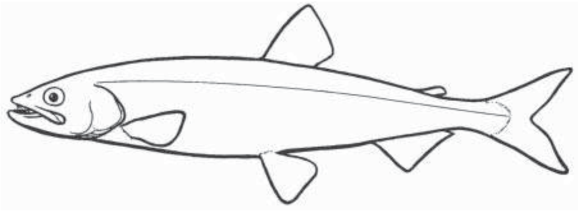
López et al. (2004) gave molecular evidence supporting a close relationship of this order with Stomiiformes (see below). The phylogeny of Burridge et al. (2012) contained two clades here classified as suborders, Osmeroidei (Osmeridae, Plecoglossidae, and Salangidae) and Retropinnoidei (Prototroctidae and Retropinnidae).

Possible fossils include the piscivorous marine Late Cretaceous †*Spaniodon* (Taverne and Filleul, 2003).

Recognized with two suborders, 5 families, 20 genera, and about 47 species.

Suborder Osmeroidei. Egg surrounded by an adhesive anchor membrane. The Sundasalangidae, previously placed here, are now placed in the Clupeidae.

Family OSMERIDAE (195)—Northern Hemisphere smelts. Marine, anadromous, and coastal freshwater; Northern Hemisphere in Arctic, Atlantic, and Pacific.



Palatine bone dumbbell shaped; notch in dorsal margin of opercle; pelvic axillary process absent; adipose fin present; lateral line present, but usually incomplete; dorsal-fin rays 7–14; anal-fin rays usually 11–17, but up to 23 in *Mallotus*; pelvic-fin rays eight (one additional short ray in *Mallotus*); principal caudal rays 19 (17 branched), caudal fin forked; branchiostegal rays 5–10; teeth on premaxilla, maxilla, dentary, and inner mouth bones in extant species; mesocoracoid present; pyloric caeca 0–11; vertebrae 51–78. Color silvery. Maximum length about 40 cm; most species less than 20 cm. *Mallotus villosus* is circumpolar, occurring almost throughout the range of the family.

Key older fossil osmerids are the European †*Enoplophthalmus* of Oligocene-Miocene age (Gaudant and Reichenbacher, 1998), and the Miocene †*Austromallotus* from the Caucasus (Prokofiev, 2005). †*Speirsaenigma* (see below), originally described in Osmeridae close to *Plecoglossus*, is now in Plecoglossidae (Wilson and Williams, 2010).

Six genera with 15 species. Genera, listed in approximate phylogenetic sequence, are *Hypomesus* (5), *Mallotus* (Capelin) (1), *Osmerus* (4), *Thaleichthys* (Eulachon) (1), *Allosmerus* (1), and *Spirinchus* (3). Saruwatari et al. (1997) reviewed the genus *Mallotus*.

Family PLECOGLOSSIDAE (196)—Ayu or sweetfish. Freshwater and anadromous from Japan, Korea, Taiwan, and China.

The single species *Plecoglossus altivelis* (Ayu) differs from other osmeroids in having more than 300 pyloric caeca, preopercular canal partly closed; laterally projecting dorsal flange on maxilla; lateral shelf on ectopterygoid (Wilson and Williams, 2010). The mouth changes developmentally from one with normal teeth in juveniles to one with many, fine, comb-like teeth on the outer margins of its jaws in adults, during a switch from zooplanktivory to algal grazing or filtering (Howes and Sanford, 1987). Most Ayu live only one year, dying after spawning. Anadromous individuals spawn in the lower reaches of rivers with the newly hatched fish drifting into the ocean. This is a commercially important fish, as are some other smelt, and it is also produced in aquaculture.

One monotypic genus, *Plecoglossus*. The oldest fossil is the Paleocene-age freshwater fish †*Speirsaenigma lindoei* from Alberta, Canada, which retained strong jaw teeth in adults (Wilson and Williams, 1991, 2010).

Family SALANGIDAE (197)—icefishes or noodlefishes. Anadromous and freshwater, Sakhalin, Japan, Korea, China, to northern Vietnam.

Scales absent, body translucent or transparent, extremely slender and small, skeleton mostly cartilaginous, retaining larval features as adults.

Seven genera, *Hemisalanx*, *Leucosoma*, *Neosalangichthys*, *Neosalanx*, *Protosalanx*, *Salangichthys*, and *Salanx* (shown in figure), with about 20 species.

Suborder Retropinnoidei. Freshwater and brackish water (some partially marine); New Zealand, Chatham Islands, southeastern Australia, and Tasmania.

Adipose fin present; caudal fin forked, with 16 branched rays; cycloid scales present, but no lateral line on body; small horny keel along midventral abdomen, in front of anus; vomerine, palatine, and basibranchial teeth present; branchiostegal rays usually five or six; pyloric caeca absent; only left gonad present; cucumber odor to body in most species when captured (this has also been detected in some osmerids).

Two families, three genera, and five or six species.

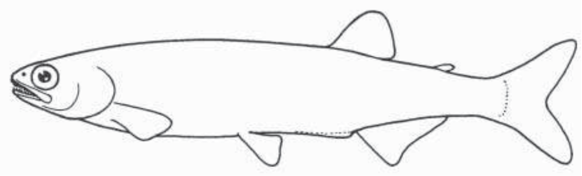
Family PROTOTROCTIDAE (198)—southern graylings. Marine and freshwater; Australia, Tasmania, and New Zealand.

Dorsal fin forward, above pelvic fin; maxilla toothless; horny shelf surrounding lower jaw; vertebrae 62–72. Length up to 35 cm.

One or two species, *Prototroctes maraena*, in southeastern Australia and Tasmania. Another species of this genus, *P. oxyrhnchus* from New Zealand, may be extinct (McDowall, 1990). There are Pleistocene fossils of *Prototroctes* from New Zealand (McDowall et al., 2006).

Family RETROPINNIDAE (199)—southern smelts. Marine and freshwater; South Australia, New Zealand.

Dorsal fin posterior to pelvics and a little in front of anal fin origin; maxilla sometimes with teeth; vertebrae 45–63. Maximum length about 15 cm, usually less than 10 cm. These small silvery fishes occur in coastal seas, estuaries and lowland rivers, and inland lakes and rivers.



Two genera, *Retropinna* (3) and *Stokellia* (1), with about four species. *Retropinna* has about three highly variable species, one in Australia (southern Queensland to eastern South Australia), one in Tasmania, and one in New Zealand (including the Chatham Islands; in some areas of New Zealand, both diadromous and lake-resident forms occur, and in at least one drainage there appears to be reproductive separation of the two forms); *Stokellia anisodon* is endemic to the South Island of New Zealand (McDowall, 1990).

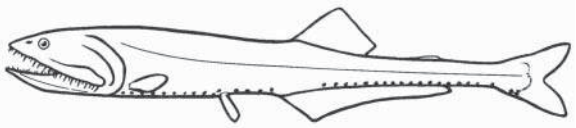
Order STOMIIFORMES (Stomiatiformes) (42)—dragonfishes. Luminescent organs (photophores) present; chin barbel present in some; premaxilla and maxilla in gape of mouth—both have teeth; mouth extending past eye in most; scales, if present, cycloid and easily lost; pectoral, dorsal, or adipose fins absent in some; ventral adipose fin present in some; pelvic-fin rays 4–9; branchiostegal rays 5–24. Color in most is dark brown or black; some are silvery (primarily some Gonostomatoidei). Mostly tropical to temperate; many are deep-sea.

Rosen (1973a) first proposed recognition of this group at the ordinal level. Major contributions to this group were made by R. H. Gibbs, Jr., in the 1960s to 1980s, and by W. L. Fink and S. H. Weitzman in the 1970s and 1980s. Monophyly of the stomiiforms was supported by Fink and Weitzman (1982) and Harold and Weitzman (1996) based on various synapomorphic characters, such as the unique (for teleosts) histology of the photophores and the type of tooth attachment. Harold (2003) provided keys to western Atlantic taxa. There have been few molecular studies with broad taxon sampling that focus on Stomiiformes. A dissertation (DeVaney, 2008) suggested numerous differences from the current arrangement in terms of the families to which genera belong, but is unpublished and we have not followed it here. Kenaley et al. (2013) published a molecular phylogeny containing some similar conclusions, though focused on Stomiidae.

Five families, 52 genera, and about 414 species. All species are marine. Possible fossil stomiiforms were discussed by Fink (1985) and references therein.

Suborder Gonostomatoidei. Four bony pectoral-fin radials (except one in *Cyclothone*); serial photophores with lumen or duct; true gill rakers present; jaw teeth small, all about equal in size.

Family GONOSTOMATIDAE (200)—bristlemouths. Marine; Atlantic, Indian, and Pacific.



Body elongate, never extremely compressed; adipose fins present or absent; anal-fin rays 16–69; branchiostegal rays, 12–16, 4–6 on epihyal (= posterior ceratohyal); 8–16 branchiostegal photophores; photophores on isthmus; vertebrae 29–94.

Eight genera, *Bonapartia* (1), *Cyclothone* (13), *Diplophos* (5), *Gonostoma* (2), *Manducus* (2), *Margrethia* (2), *Sigmops* (5), and *Triplophos* (1), with 31 species (Miya, 1994; Miya and Nishida, 2000, Harold, 1998, 2003). Harold (1998) suggested that *Cyclothone* is probably a synonym of *Gonostoma* but did not change the classification. *Cyclothone* occurs in virtually all seas including the Antarctic has one of the greatest abundances of individuals of any vertebrate genus.

Family STERNOPTYCHIDAE (201)—marine hatchetfishes. Marine; Atlantic, Indian, and Pacific.

Six to 10 branchiostegal rays, three on epihyal (= posterior ceratohyal); 3–7 (usually six) branchiostegal photophores; pseudobranch present (reduced or lost in most other stomiiforms).

†*Eosternoptyx* is a recently described Eocene fossil sternoptychid from Iran (Afsari et al., 2014). Other fossil members include the Eocene †*Polyipnoides*, the Oligocene †*Horbatshia*, and the Miocene †*Dicosternon*, all from Europe

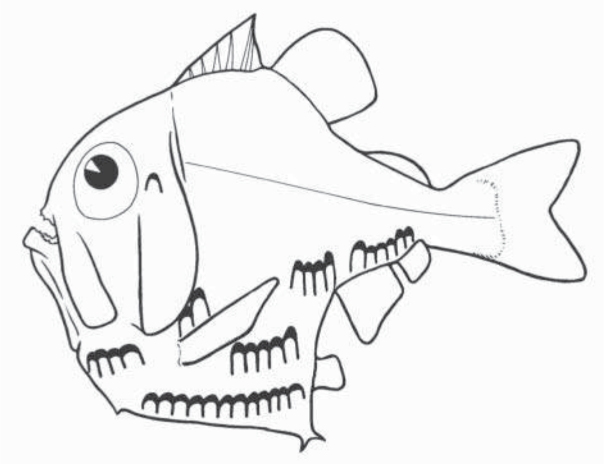
Ten genera and about 73 species.

SUBFAMILY MAUROLICINAE. Body elongate, never extremely compressed; adipose fin present or absent; 19–38 anal-fin rays; photophores present on isthmus, six on branchiostegal membrane. This taxon is probably paraphyletic (Harold and Weitzman, 1996).

Seven genera, *Araiophos* (1), *Argyripnus* (7), *Danaphos* (1), *Maurolicus* (15), *Sonoda* (2), *Thorophos* (2, synonym *Neophos*), and *Valenciennellus* (2), with about 30 species (e.g., Parin and Kobyliansky, 1996; Harold and Lancaster, 2003; Harold, 2003).

SUBFAMILY STERNOPTYCHINAE (MARINE HATCHETFISHES). Body deep and extremely compressed; mouth nearly vertical; preopercular spine; eyes sometimes telescopic; abdominal keel-like structure; blade in front of the dorsal fin composed of specialized dorsal pterygiophores; anal fin sometimes divided, rays 11–19; dorsal-fin rays 8–17; vertically orientated pelvic bones; adipose fin rarely absent (e.g., in *Polyipnus latirastrus*).

Three genera, *Argyropelecus* (7, broadly worldwide, high-sea pelagic, usually 100–600 m), *Sternoptyx* (4, broadly worldwide, high-sea pelagic, 500–1,500 m), and *Polyipnus* (32, usually coastal, 50–400 m; most species in the western Pacific), with 43 species (e.g., Harold, 1994, 2003).



Sternoptychinae (see previous page).

Suborder Phosichthyoidei. Three bony pectoral fin radials (rarely 0–2 in some genera with reduced pectoral fins); branchiostegal rays 10 (*Bathophilus*) to 28 (*Heterophotus*).

Family PHOSICHTHYIDAE (Photichthyidae) (202)—lightfishes. Marine; Atlantic, Indian, and Pacific.

General body shape similar to the gonostomatids; serial photophores having a lumen and a duct; gill rakers well developed in young and adults; usually two supramaxillaries; adipose fin present except in *Yarrella*; 10–16 dorsal-fin rays; 12–33 anal-fin rays; 11–22 branchiostegal rays, 4–7 on epihyal; barbel on lower jaw absent. This taxon is probably paraphyletic. Reasons for now accepting Phosichthyidae as the spelling of the family name are given in Nelson et al. (2004).

Seven genera, *Ichthyococcus*, *Phosichthys* (synonym *Photichthys*), *Pollichthys*, *Polymetme*, *Vinciguerria*, *Woodsia*, and *Yarrella*, with about 24 species (e.g., Parin and Borodulina, 1990; Harold, 2003). *Vinciguerria*, like *Cyclothone* (see above under Gonostomatidae) is one of the most numerous in individuals of any vertebrate genus.

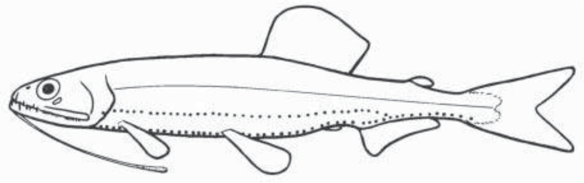
Family STOMIIDAE (203)—barbeled dragonfishes. Marine; Atlantic, Indian, and Pacific.

No true gill rakers in adults; one infraorbital bone (other stomiiforms have 2–6); one or no supramaxillaries; mesopterygoid reduced in size or absent; photophores without ducts or lumen; mental barbel in most, associated with hyoid apparatus; pectoral-fin rays absent in *Tactostoma*, *Idiacanthus*, *Photostomias*, and some species of *Eustomias*; most are darkish in color. Schnell et al. (2010) studied in detail the ontogeny of the junction between the cranium and the vertebral column.

Fink (1985) combined six "barbeled" families formerly recognized in the superfamilies Stomioidea and Astronethoidea into the one family, Stomiidae, as recognized here. The following sequence of taxa reflects Fink's (1985) cladogram. Harold (2003) recognized all six higher level taxa given below as separate families.

About 27 genera and about 286 species (e.g., Parin and Borodulina, 1998, 2003; Clarke, 2001; Harold, 2003; Sutton and Hartel, 2004).

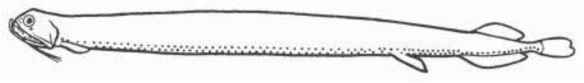
SUBFAMILY ASTRONESTHINAE (SNAGGLETOOTHS). Scales absent; dorsal-fin origin over or behind pelvic-fin insertion but well ahead of anal-fin origin; dorsal adipose fin present except in *Rhadinesthes decimus*; ventral adipose fin present in many, in front of anal fin; barbel on chin; dorsal-fin rays 9–21; anal-fin rays 12–28. Maximum length about 30 cm. Parin and Borodulina (2003) recognized 47 species in the deepsea oceanic genus *Astronesthes* and regarded *Eupogonesthes* as a sister genus.



Six genera, *Astronesthes*, *Borostomias*, *Eupogonesthes*, *Heterophotus*, *Neonesthes*, and *Rhadinesthes*, with about 59 species.

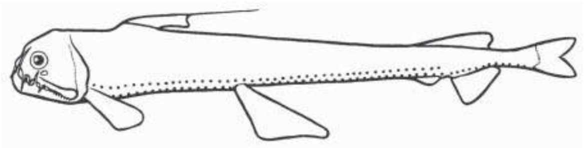
SUBFAMILY STOMIINAE. Scales present (or body marked with scale-like hexagonal pattern).

TRIBE STOMIINI (SCALY DRAGONFISHES). Body elongate; dorsal-fin origin far behind pelvics, above anal fin; long barbel on chin; no adipose fin.



One genus, *Stomias* (synonym *Macrostomias*), with 10 or 11 species (e.g., Fink and Fink, 1986).

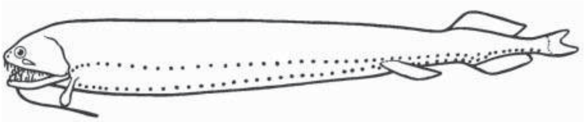
TRIBE CHAULIODONTINI (VIPERFISHES). Dorsal fin well in advance of pelvics, shortly behind head; first dorsal-fin ray greatly elongated; fang-like teeth on premaxilla and lower jaw; short chin barbel present in some; adipose fins present behind dorsal fin and in front of anal fin; dorsal-fin rays 5–7; anal-fin rays 10–13.



According to DeVaney (2008) and Kenaley et al. (2013), *Chauliodus* does not belong in Stomiidae, but those two studies gave different placements for this genus.

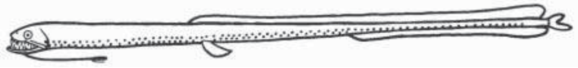
One genus, *Chauliodus*, with nine species.

Subfamily Melanostomiinae (scaleless black dragonfishes). Scales absent; dorsal fin origin far behind pelvic fin, over anal fin; dorsal adipose fin absent except in *Chirostomias*; most with barbel on chin; supracleithrum absent in *Eustomias*.



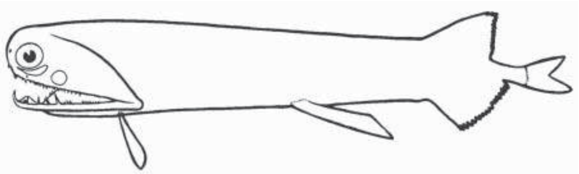
Fifteen genera, *Bathophilus* (16), *Chirostomias* (1), *Echiostoma* (1), *Eustomias* (116), *Flagellostomias* (1), *Grammatostomias* (3), *Leptostomias* (12), *Melanostomias* (16), *Odontostomias* (2), *Opostomias* (2), *Pachystomias* (1), *Photonectes* (17), *Tactostoma* (1), *Thysanactis* (1), and *Trigonolampa* (1), with about 191 species. More than one-half of the species are contained in *Eustomias* (Sutton and Hartel, 2004, give 115 species for this genus, noting that most species can only be identified by the mental barbels). Fink (1985) recognized a clade comprising the genera *Bathophilus*, *Grammatostomias*, and *Eustomias*, which is the sister group to the remaining stomiids, comprising the herein recognized malacosteines and *Pachystomias*.

Subfamily Idiacanthinae (black dragonfishes). Body eel-like; dorsal fin extremely elongate, more than one-half the body length and with 54–74 rays; anal fin-rays 29–49; each dorsal and anal-fin ray flanked by a spur; scales absent; pectoral fins absent in adult; chin barbel only in females; adult males retain some larval characters; eyes on very elongate stalks in larvae allowing for an increase in field of vision.



One genus, *Idiacanthus*, with three species. According to Fink (1985), the sister group of this genus is *Tactostoma*.

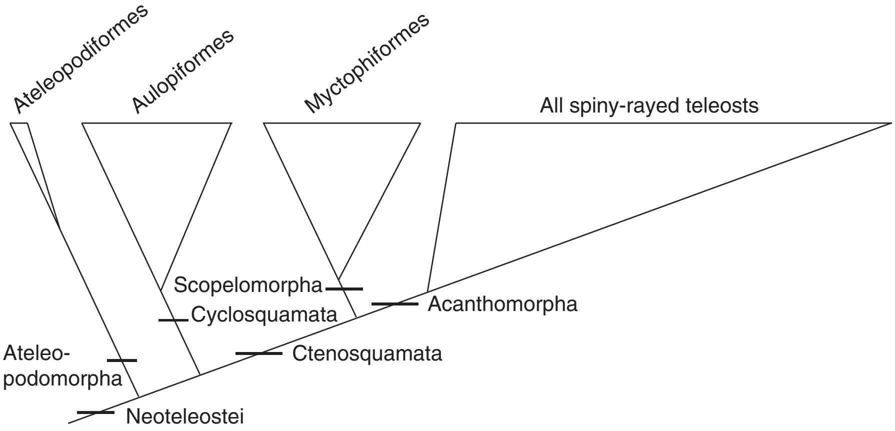
Subfamily Malacosteinae (loosejaws). Jaws elongated, longer than skull; floor of mouth absent; dorsal-fin origin far behind pelvic fin, over anal fin; adipose fin and scales absent; chin barbel in most; pectoral fins absent in some; dorsal-fin rays 14–28; anal-fin rays 17–32.



Three genera, *Aristostomias* (6), *Malacosteus* (2), and *Photostomias* (6) (synonym *Ultimostomias*), with 14 species. Fink (1985) includes *Pachystomias* in a clade with these three genera.

NEOTELEOSTEI (NEOTELEOSTS). The six superorders Ateleopodomorpha, Cyclosquamata, Scopelomorpha, Lamprimorpha, Paracanthopterygii, and Acanthopterygii comprise the Neoteleostei, a monophyletic group not given formal rank here. Stomiiformes were formerly included within Neoteleostei as sister to all other members (e.g., Rosen 1973a; Stiassny, 1986, 1996; Johnson and Patterson, 1993), but in the present work they are treated in the Osmeromorpha (see above). Neoteleostei (then including stomiiforms) were diagnosed as monophyletic by Rosen (1973a) on the basis of three synapomorphies, one of which is the retractor dorsalis muscle (= Rosen's retractor arcuum branchialium—RAB). This character may still be valid although it is arguably also found in stomiiforms. Additional characters that have been used to diagnose this more inclusive group include: Type 4 tooth attachment; insertion of the third levator on the fifth upper pharyngeal toothplate; and presence of a transverse epibranchial 2 (Johnson, 1992; Wiley and Johnson, 2010). Although not usually considered a synapomorphy, most neoteleosts have ascending and articular premaxillary processes on the premaxillae.

The monophyly of Neoteleostei, excluding Stomiiformes, is highly supported (though not by Miya et al., 2003) in numerous molecular studies (e.g., Li et al., 2010; Broughton, 2010; Davis, 2010; Burridge et al., 2012; Near et al., 2012a; Betancur-R. et al., 2013a). Here we accept the results of these corroborating molecular studies and, in a change from Nelson (2006), include Stomiiformes within the Osmeromorpha (see above), the postulated sister group to the Neoteleostei. The effects of removing stomiiforms on the morphological character support for the Neoteleostei have not been investigated in detail.

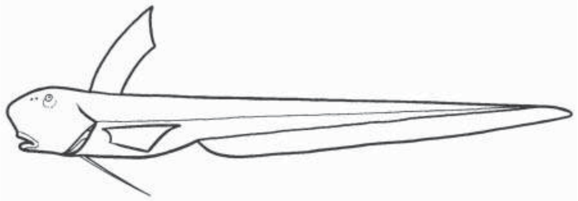


Suggested relationships among early-branching lineages of Neoteleostei.

Superorder ATELEOPODOMORPHA

Order ATELEOPODIFORMES (43)—jellynose fishes. Once placed within Lampriformes (e.g., Nelson 1976, 1984), they were suggested by Olney et al. (1993) to be in an unresolved trichotomy with stomiiforms and eurypterygians. In contrast, Miya et al. (2003) found them to be the sister group of the Lampriformes. Numerous other molecular studies (e.g., Davis, 2010) in recent years (and see citations above under Neoteleostei) place them as the sister group of all other neoteleosts (after removal of Stomiiformes from Neoteleostei; see above).

Family ATELEOPODIDAE (204)—jellynose fishes. Marine; Caribbean Sea, eastern Atlantic, Indo-West Pacific, and eastern Pacific off Panama and Costa Rica.



Snout gelatinous; head large and bulbous; Caudal fin reduced, united, except in *Guentherus,* with the long anal fin; anal-fin rays 70 or more; pelvic fin of adults with single elongate ray on throat (young specimens have up to 10 rays); dorsal fin short-based with 3–13 rays (usually 9–13); skeleton largely cartilaginous; branchiostegals 7. Maximum length about 2 m.

Four genera, *Ateleopus* (5), *Ijimaia* (4), *Parateleopus* (1), and *Guentherus* (2), with 12 or 13 species (e.g., Smith and Heemstra, 1986; Moore, 2003). As noted by Moore (2003), the family is in great need of revision.

EURYPTERYGII (EURYPTERYGIANS). The remaining five superorders of neoteleosts (Cyclosquamata, Scopelomorpha, Lamprimorpha, Paracanthopterygii, and Acanthopterygii) compose Rosen's (1973a) Eurypterygii. Rosen recognized two subsections, the Cyclosquamata for the Aulopiformes and the Ctenosquamata for the higher eurypterygians. The sister-group relationship of the Cyclosquamata and Ctenosquamata was accepted by Fink and Weitzman (1982) and by Lauder and Liem (1983), with Stiassny (1986) and Johnson (1992) also supporting a monophyletic Eurypterygii as viewed by Rosen (1973a). However, many of Rosen's (1973a) synapomorphies for the Eurypterygii seem not to be valid, and Johnson (1992) later gave three synapomorphies that he considered valid (i.e., fusion of the base of the ventral hemitrich of the medial pelvic fin ray to the medial pelvic radial, fusion of a toothplate to the third epibranchial, and presence of an interoperculohyoid ligament). In addition, Wiley and Johnson (2010) included the following two characters from Springer and Johnson (2004) to diagnose eurypterygians: presence of a transverse epibranchial 4, and inclusion of the second pharyngobranchial in the attachment of the transversus dorsalis. The combined molecular and morphological study of Davis (2010), as well as the recent molecular studies of Li et al. (2010), Near et al. (2012a), and Betancur-R. et al. (2013a) also support eurypterygian monophyly. Keivany (2014a,b,c,d) surveyed osteology among various eurypterygian taxa.

A fossil taxon not otherwise mentioned, included here as Eurypterygii *incertae sedis,* is the †Cheirotricidae (Patterson, 1993; Dietze, 2009).

Superorder CYCLOSQUAMATA

This superorder contains only one order. Many of its members are well represented in the fossil record beginning in the Cretaceous.

Order AULOPIFORMES (44)—lizardfishes. Specializations in the gill arches include: elongation of the uncinate process of the second epibranchial, third pharyngobranchial lacking cartilaginous condyle for the articulation of second epibranchial, epibranchial four with a expanded proximal end capped with a large cartilage band and an uncinate process in the center, and the presence of epibranchial five. Additional characters include: epipleurals originating on vertebra two, one or more epipleurals displaced dorsally into horizontal septum, swimbladder absent, medial processes of pelvic girdle fused. (Rosen, 1973a; Johnson, 1992; Baldwin and Johnson, 1996; Sato and Nakabo, 2002a,b; Davis, 2010).

The classification of the extant families of aulopiforms follows Davis (2010) who conducted a total evidence analysis of five protein coding gene regions plus 138 morphological characters from Baldwin and Johnson (1996) with the modifications of Sato and Nakabo (2002a). The major differences between the two morphological studies is that Sato and Nakabo (2002a) i) recognized the two clades formerly in *Chlorophthalmus* as being unrelated to one another (Baldwin and Johnson, 1996, had not included species of the clade now recognized as *Paraulopus*), ii) differed in the phylogenetic position of *Bathysauroides,* iii) assigned family status to *Bathysauroides* and *Bathysauropsis* (Baldwin and Johnson, 1996, while placing them in separate suborders, did not assign them to any family), and iv) recognized a different sequence for the alepisauroid families. Baldwin and Johnson (1996) considered Aulopidae to be the most primitive family, while Sato and Nakabo (2002a) found that position to belong to their new family, Paraulopidae.

According to Davis (2010), Chlorophthalmoidei are paraphyletic. The monotypic Paraulopidae are recovered as a separate lineage but not the most primitive; instead the Aulopoidei, which Baldwin and Johnson (1996) called the Synodontoidei, a name also used by Davis (2010), are sister to all other aulopiforms. In addition, giganturoids were found to be sister to ipnopids, while chlorophthalmoids are sister to notosudoids + alepisauroids.

The families Aulopidae, Chlorophthalmidae, Ipnopidae, Pseudotrichonotidae, Paraulopidae, and Synodontidae are predominantly benthic. Species in the remaining families tend to be pelagic to bathypelagic. Many aulopiforms are synchronous hermaphrodites (Davis and Fielitz, 2010).

Fifteen families with 47 genera and about 261 species.

The next two listed suborders and the families †Cimolichthyidae and †Enchodontidae, which are placed here in the suborder Alepisauroidei following Fielitz (2004), containing marine Cretaceous fishes, were placed in the suborder †Enchodontoidei by Nelson (1994). They are recognized here following Patterson (1993) and Fielitz (2004). Members have the maxilla as a long, narrow strut in the gape (maxilla excluded from gape in the other members of this order). Goody (1969) divided the members of this taxon among four suborders, and Rosen (1973a) suggested a relationship to the alepisauroids. Genera of uncertain relationships include †*Serrilepis*, †*Yabrudichthys*, and †*Nardorex* (Taverne, 1985, 2004). There is a need for additional studies similar to that of Fielitz (2004) that also involve a broad range of extant taxa.

†***Suborder Ichthyotringoidei.*** Three families.

†Family ICHTHYOTRINGIDAE. Including Apateopholidae; e.g., †*Apateodus* (e.g., Newbrey and Konishi, 2015) and †*Ichthyotringa*.

†Family DERCETIDAE. At least seven genera of Cretaceous fishes with a very long snout and elongate and shallow body: †*Benthesikyme*, †*Cyranichthys*, †*Dercetis*, †*Dercetoides*, †*Hastichthys*, †*Pelargorhynchus*, †*Rhynchodercetis*, and †*Stratodus* (Taverne, 1990; Chalifa, 1989).

†Family PRIONOLEPIDIDAE. One genus, †*Prionolepis*.

†***Suborder Halecoidei.*** One family.

†Family HALECIDAE. At least three genera including †*Halec*, †*Hemisaurida*, and †*Phylactocephalus* (Goody, 1969).

Suborder Aulopoidei (=Synodontoidei). Separation of ceratobranchial five from the main body of the fourth basibranchial cartilage by a cartilaginous tail or a trail of small nubbins of cartilage extending posteriorly; anterior ceratohyal with autonenous cartilage along ventral margin; six or more basibranchials on posterior ceratohyal; distal end of the first one to three epineurals displaced ventrally; accessory neural arch present; all ribs ossified in membrane bone; proximal portion of most principal caudal-fin rays with modified segment; caudal median cartilages absent; neural and haemal spines of preural centra two and three expanded; five hypurals, the sixth lost or fused; adults with one epural; and posterior pelvic processes elongate and widely separated (Baldwin and Johnson, 1996; Wiley and Johnson, 2010; Davis, 2010).

The limits and relationships of this clade were revised by Johnson et al. (1996) and Baldwin and Johnson (1996); they altered our understanding of this group in finding characters supporting aulopoids (their synodontoids) as the most primitive of extant aulopiforms. This relationship was supported by Davis (2010). Contrary to Nelson (2006) and following Davis (2010), Paraulopidae are not a member of Aulopoidei (= Synodontoidei) but placed within their own suborder Paraulopoidei, sister to the remaining aulopiforms.

Three families, 9 genera and 84 species.

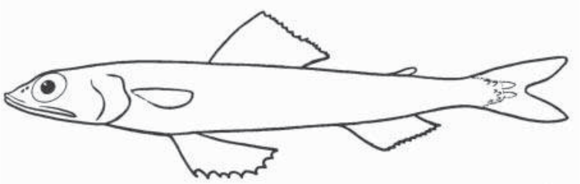
Family SYNODONTIDAE (205)—lizardfishes. Marine (rarely brackish); Atlantic, Indian, and Pacific.

Supramaxilla small (two in *Saurida* and one in *Harpadon*) or absent; gill rakers present as toothplates; fifth ceratobranchial V-shaped with median limb robust; quadrate with produced anterior limb; quadrate cartilage separated into two condyles; metapterygoid extended anteriorly over posterior portion of ectopterygoid; branchiostegals 8–26; vertebrae 39–67; dioecious mode of reproduction (Baldwin and Johnson, 1996; Davis, 2010).

The subfamily Bathysaurinae with *Bathysaurus*, formerly recognized in this family, is now placed in its own family below.

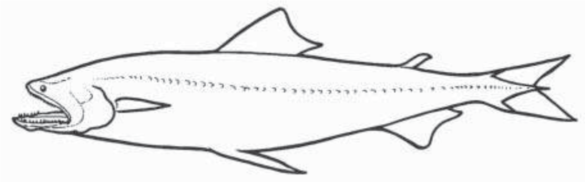
Four genera with about 70 species.

SUBFAMILY SYNODONTINAE (LIZARDFISHES). Scales along lateral line not enlarged; dorsal-fin rays 10–15; anal-fin rays 8–16; adipose fin usually present. Maximum length about 60 cm.



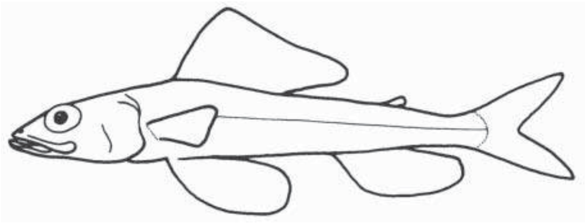
Two genera, *Synodus* (synonym *Xystodus*) and *Trachinocephalus* (maybe a synonym of *Synodus*), with about 44 species (e.g., Waples and Randall, 1988; Russell 1999, 2003).

SUBFAMILY HARPADONTINAE (BOMBAY DUCKS). Nine pelvic-fin rays (eight in other members of family); dorsal and anal-fin rays 9–15.



Two genera, *Harpadon* (5, shown in figure) and *Saurida* (21), with about 26 species (e.g., Okiyama, 1984; Russell 1999, 2003). *Harpadon* is secondarily pelagic and has a naked head and body except for scales along the lateral line and on part of the posterior half of the body. This subfamily is Indo-Pacific; some species of *Harpadon* enter brackish water.

Family AULOPIDAE (206)—flagfins. Marine; tropical and subtropical waters, Atlantic (including the Mediterranean) and Pacific.



Two supramaxillae; body slender; fulcral scales on caudal peduncle; dorsal-fin origin in front third of body, fin with 14–22 rays; anal-fin rays 9–13; pelvic fin thoracic, nine rays; pectoral fin lateral, 11–14 rays; scales on head and body, cycloid or ctenoid; orbitosphenoid present; vertebrae 36–53.

This family was placed in monotypic suborder Aulopoidei in Nelson (1994), with the family name orthography being Aulopodidae.

Four genera, *Aulopus* (4) for the Atlantic species and *Hime* (5), *Latropiscis* (1), and *Leptaulopus* (2) for the Pacific species, with about 12 species (e.g., Parin and Kotlyar, 1989; Thompson, 1998; Gomon et al., 2013). Baldwin and Johnson (1996) found no evidence supporting recognition of *Hime* as a valid genus, and in the past it was often regarded as a junior synonym of *Aulopus*. Its recognition here follows Thompson's (1998) study of additional characters, although he does note that further study of variation of these characters is required in order to better support this conclusion.

Family PSEUDOTRICHONOTIDAE (207)—sand-diving lizardfishes. Marine; Izu Peninsula, Japan, and Saya de Malha Bank, Indian Ocean.

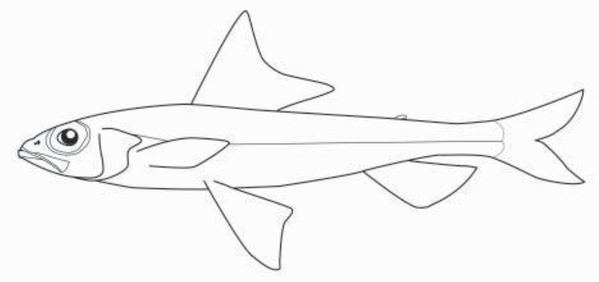
Body slender and cylindrical; mouth relatively small, upper jaw bordered only by premaxillaries and slightly protrusible; lateral line complete, midlateral; cycloid scales, 46–48 in lateral line; dorsal fin single, with about 33 soft rays; anal-fin rays 13–15; pectoral fin with 11 rays; pelvic fin beneath origin of dorsal, with seven long rays; caudal fin with 19 principal rays; adipose fin absent; photophores absent; no swimbladder; orbitosphenoid and mesocoracoid absent; two supraneurals; six branchiostegals; 23 or 24 abdominal vertebrae and 25 or 26 caudal vertebrae. Maximum length about 9 cm SL. Individuals of the one species have been observed to dive into the sand.

Two species are recognized. However, Parin (1992), in reporting one specimen from the Indian Ocean at 110 m as a new species (*Pseudotrichonotus xanthotaenia*), found only minor differences with the specimens from Japan. The two species might well be conspecifics despite the geographic distance separating them.

One genus with two species, *Pseudotrichonotus altivelis* (Japan) and *P. xanthotaenia* (Indian ocean).

Suborder Paraulopoidei. One family.

Family PARAULOPIDAE (208)—cucumber fishes. Marine; tropical to temperate, benthic, outer continental shelf and upper continental slopes, Indian and western Pacific (southern Japan and Emperor Seamounts south to Australia and New Zealand).



Dorsal-fin rays 10 or 11; anal-fin rays 8–11; pectoral-fin rays 13–20; pelvic-fin rays 9; pored lateral line scales 40–52; vertebrae usually 39–46; in addition, Sato and Nakabo (2002a) recognized this clade based on six apomorphies, primarily characters in the branchial arches, intermuscular bones, caudal skeleton, and pelvic girdle. See Davis (2010) for a character analysis (e.g., presence of a bony ridge on dorsal surface of pharyngobranchial three; lacrimal anterior to orbit oriented horizontally; epicentrals ossified anteriorly but ligamentous posteriorly; small urodermal present in upper caudal lobe). Maximum length 35 cm.

One genus, *Paraulopus*, with 14 species (Sato and Nakabo, 2002a,b, 2003).

Suborder Alepisauroidei. This suborder contains all remaining aulopiforms; they are classified here in a phylogenetic sequence of superfamilies.

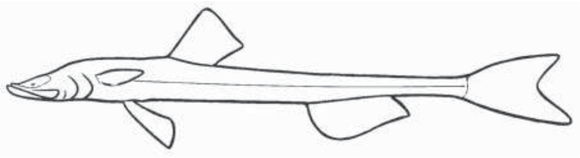
Superfamily Ipnopoidea. Four families according to the combined analysis of Davis (2010).

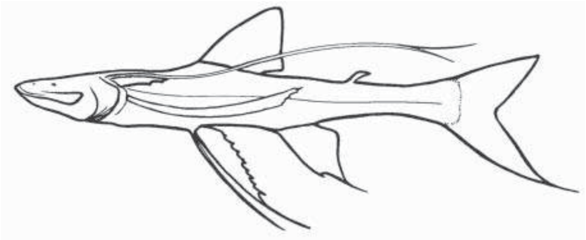
Family IPNOPIDAE (209)—deepsea tripod fishes. Marine; temperate and tropical oceans.

Small to medium sized fishes; body slender; mouth large, reaching far behind eye; lower jaw with fleshy tip; teeth minute, needle-shaped (Paxton and Niem, 1999).

Two subfamilies, six genera, and about 32 species.

SUBFAMILY IPNOPINAE (DEEPSEA TRIPOD FISHES). Marine; Atlantic, Indian, and Pacific. Eyes minute (first four genera listed here) or plate-like, directed dorsally, and lens-less (*Ipnops*); pseudobranch absent in adult; tip of upper jaw extending behind orbit; pyloric caeca absent; dorsal-fin rays 8–16; anal-fin rays 7–19; pectoral rays 9–24; branchiostegals 8–17; vertebrae 44–80. *Bathypterois* (spiderfishes) has elongated pectoral, pelvic, and caudal rays.



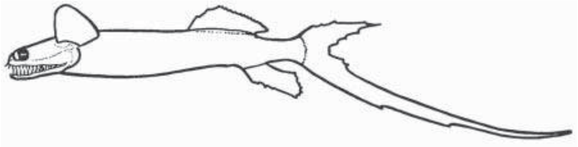


Five genera, *Bathymicrops (4), Bathypterois* (19, synonym *Benthosaurus*) (figured this page), *Bathytyphlops* (2, synonym *Macristiella*), *Discoverichthys* (1) and *Ipnops* (3, figured previous page), with about 29 species (e.g., Nielsen and Merrett, 1992; Paxton and Niem, 1999; Sato and Nakabo, 2002a; Thompson, 2003a).

SUBFAMILY BATHYSAUROPSINAE (BATHYSAUROPSINES). Marine; mesobenthic, widespread. *Bathysauropsis gracilis* is circumglobal, subtropical, and the other two are Indo-West Pacific, tropical (Shcherbachev and Pakhorukov, 2002). This genus has been placed in Ipnopidae (e.g., K. J. Sulak in Smith and Heemstra, 1986; Nelson, 1994) or in its own family (Sato and Nakabo, 2002a). Evidence from Davis (2010) suggests that this genus is sister to Ipnopidae.

One genus with three species, *Bathysauropsis gigas, B. gracilis,* and *B. malayanus* (Shcherbachev and Pakhorukov, 2002).

Family GIGANTURIDAE (210)—telescopefishes. Marine; Atlantic, Indian, and Pacific.



Eyes large, tubular, and directed forward; mouth large, extending well behind eyes; sharp depressible teeth in mouth; greatly expandable stomach; pectoral fins high on body, above gill opening, with 30–43 rays; skin loose; body scaleless; pelvic fin, adipose fin, and branchiostegals in larvae but lost during transformation; caudal fin forked with some rays in lower lobe greatly elongated; no premaxilla, orbitosphenoid, parietal, symplectic, gill rakers, posttemporal, supratemporal, or cleithrum; no swimbladder. Color silvery. The loss of many characters that generally appear late in fish morphogenesis suggests a neotenous condition for these fish. The transformation from larvae to juveniles, commencing about 25–34 mm, is exceptionally striking among teleosts (R. K. Johnson, 1984; Johnson and Bertelsen, 1991). Maximum length 22 cm SL.

One genus with two species, *Gigantura chuni* and *G. indica* (synonyms *Rosaura rotunda* and *Bathyleptus lisae*) (Johnson and Bertelsen, 1991; Paxton and Niem, 1999; Thompson, 2003a).

Family BATHYSAUROIDIDAE (211)—largescale deep-sea lizardfish. Marine; Western Pacific.

Eyes slightly elliptical; palatine teeth more prominent than premaxillary teeth; basihyal with two rows of large teeth; gill rakers as toothplates; anus much closer to pelvic fins than to anal fin; 16–17 pectoral-fin rays; adipose fin inserting above anterior part of anal-fin base; caudal vertebrae few (5–7) (Baldwin and Johnson, 1996).

Bathysauroides has sometimes been classified in Ipnopidae (e.g., Paxton and Niem, 1999). Baldwin and Johnson (1996:399) noted similarities with *Bathysaurus*, and, acknowledging the evidence was weak, placed both in the Giganturoidei. The placement of *Bathysauroides* here is uncertain.

One species, *Bathysauroides gigas* (e.g., Nakabo, 2002:364; Sato and Nakabo, 2002a).

Family BATHYSAURIDAE (212)—deepsea lizardfishes. Marine; circumglobal, generally deeper than 1000 m, tropical to temperate latitudes.

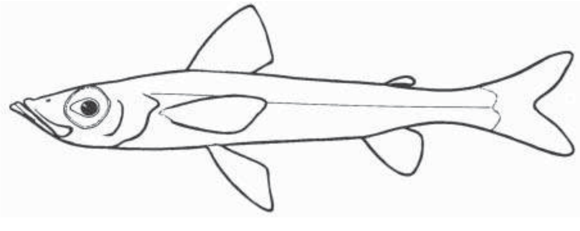
Head very depressed; upper jaw long, extending well past rear of eye; scales along lateral line enlarged; dorsal-fin rays 15–18; anal-fin rays 11–14; pectoral-fin rays 15–17; pelvic-fin rays 8; dorsal adipose fin present or absent; branchiostegal rays 8–13. These bottom-dwelling deepsea fishes are hermaphrodites. Maximum length 78 cm SL.

The one genus was previously recognized in the Synodontidae. Johnson et al. (1996), in a detailed analysis of synapomorphies, showed that its relationships were outside the Synodontoidei; Baldwin and Johnson (1996) placed it in it own family in the suborder Giganturoidei. Although the cladistic results of Sato and Nakabo (2002a) differ from those of Baldwin and Johnson (1996), there is agreement on the placement given here.

One genus, *Bathysaurus* (synonym *Macristium*), with two species (e.g., Russell 2003).

Superfamily Chlorophthalmoidea. One family (Davis, 2010) with two genera and about 17 species.

Family CHLOROPHTHALMIDAE (213)—greeneyes. Marine; tropical to temperate, deepsea benthic, Atlantic, Indian, and Pacific.



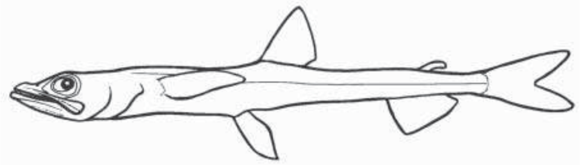
Single elongate supramaxilla; one condyle for the articulation of the hyomandibula with the skull; monoecious mode of reproduction; eyes large, normal; pseudobranch present; tip of upper jaw not extending beyond orbit; outer tooth patch exposed to the outside on tip of lower jaw; A1 and

A2 components of the adductor mandibulae fused; pyloric caeca present; dorsal-fin rays 9–13; anal-fin rays 7–11; pectoral-fin rays 15–19; branchiostegals 8; vertebrae 38–50.

Two genera, *Chlorophthalmus* (15) and *Parasudis* (2), with about 17 species (e.g., Sato and Nakabo, 2002a; Thompson, 2003a).

Superfamily Notosudoidea. One family (Davis, 2010), three genera, and 17 species.

Family NOTOSUDIDAE (Scopelosauridae) (214)—waryfishes. Marine; Subarctic to Subantarctic.

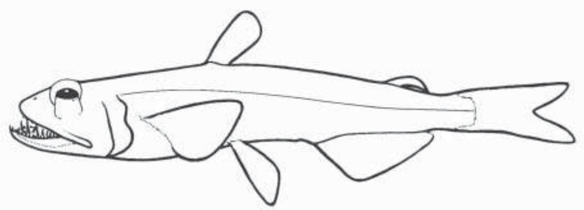


Dorsal-fin rays 9–14; anal-fin rays 16–21; pectoral-fin rays 10–15; lateral-line scales 44–65; no swimbladder; no photophores; larvae with maxillary teeth (all other larvae of the order lack teeth); vertebrae 42–66.

Three genera, *Ahliesaurus* (2), *Luciosudis* (1), and *Scopelosaurus* (14, synonym *Notosudis*), with 17 species (Bertelsen et al., 1976; Paxton and Niem, 1999; Thompson, 2003a).

Superfamily Alepisauroidea. Five extant families, 24 genera, and about 94 species.

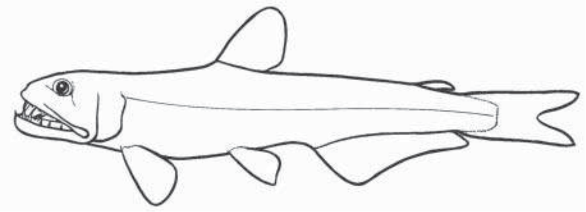
Family SCOPELARCHIDAE (215)—pearleyes. Marine; Antarctic, Atlantic, Indian, and Pacific (absent from Arctic Ocean and Mediterranean Sea).



Cycloid scales present on entire body and postorbital region, 40–65 along lateral line; strong teeth on tongue, usually hooked; large tubular eyes, directed upward or upward and slightly forward; dorsal-fin rays 5–10; anal-fin rays usually 17–27 (up to 39); pectoral-fin rays 18–28; two postcleithra; no swimbladder; vertebrae 40–65. Adults usually occur at depths between 500–1,000 m, larvae of most species usually between 100–200 m. Maximum length about 23 cm, attained in two species of *Benthalbella*. Davis (2015) reconstructed the phylogeny, finding *Benthalbella* to be sister to the remaining genera, and named the new genus *Lagiacrusichthys* for a species formerly in *Benthalbella*.

Five genera, *Benthalbella* (4), *Lagiacrusichthys* (1), *Rosenblattichthys* (4), *Scopelarchoides* (5), and *Scopelarchus* (4), with 18 species (e.g., Johnson, 1982; Paxton and Niem, 1999; Thompson, 2003a).

Family EVERMANNELLIDAE (216)—sabertooth fishes. Marine; Atlantic, Indian, and Pacific.



Normal scales lacking on head and body; three distinct bands of muscle tissue—epaxial, midlateral, and hypaxial—externally visible on the tail; teeth absent on tongue; anteriormost palatine tooth very elongate; eyes small to large, tubular in most species; dorsal-fin rays 10–13; anal-fin rays 26–37; pectoral-fin rays 11–13; no swimbladder; vertebrae 45–54. The sabertooth fishes are mesopelagic predators, occurring primarily in tropical and subtropical waters and absent from cold water areas. Maximum length about 18 cm.

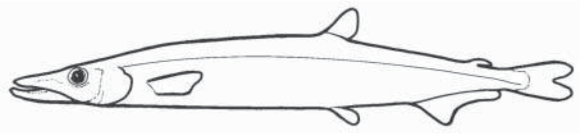
Three genera, *Coccorella* (2), *Evermannella* (5), and *Odontostomops* (1), with eight species (Johnson, 1982; Paxton and Niem, 1999; Thompson, 2003a).

Family SUDIDAE (217)—sudid barracudinas. Marine, bathypelagic, circumtropical.

Pectoral fins greatly enlongated; tip of lower jaw distinct curved upward; larvae with enlarged pectoral fins and head spines; dorsal-fin soft rays 12–16 (e.g., Davis, 2010).

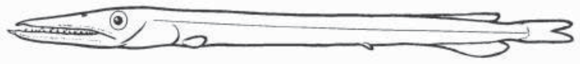
One genus (*Sudis*) with two species *Sudis atrox* and *S. hyalina.*

Family PARALEPIDIDAE (218)—barracudinas. Marine; all oceans, Arctic to Antarctic.



Dorsal-fin origin in middle of trunk, fin rays 7–16 (fin absent in *Anotopterus,* but adipose fin well developed); anal-fin base long, with 20–50 rays (14–16 in *Anotopterus*); pectoral-fin rays 11–17; body scales present or absent; no swimbladder; vertebrae 53–121. Superficially resemble sphyraenids. Maximum length about 1 m.

Genera were previously assigned to subfamilies, based in part on whether the pectoral fins were small and short and vertebrae 60–121 or whether the pectoral fins were large and elongate (about head length or longer), but subfamilies are not recognized here. Much earlier systematic work on this family was by R. K. Johnson, A. Post, and R. R. Rofen.



Anotopterus pharao (Daggertooth), recognized in its own family, Anotopteridae, in Nelson (1994), as sister to the Paralepididae, is now placed in this family (e.g., Davis, 2010).

Most recently, Ghedotti et al. (2015), provided evidence to separate the Paralepididae as treated here from the new "naked barracudina" family Lestidiidae (with *Lestidiops*, *Lestidium*, *Lestrolepis*, and *Macroparalepis*; see below).

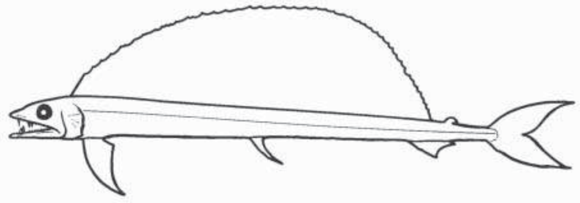
Paralepididae with seven genera, *Anotopterus* (4), *Arctozenus* (1), *Dolichosudis* (1), *Notolepis* (2), *Paralepis* (4), *Stemonosudis* (11), and *Uncisudis* (4) (synonym *Pontosudis*), and about 27 species (Sato and Nakabo, 2002a; Thompson, 2003a; Fukui and Ozawa, 2004).

†Family Enchodontidae. Fielitz (2004) found that the following Late Cretaceous fossil taxa form a monophyletic group, which he treated as suborder Enchodontoidei, and found it to be the sister group to the extant Alepisauridae (*Alepisaurus* and *Omosudis*), a position judged reasonable by Davis (2010). The fossil group is treated here as a family, sequenced to recognize its proposed relationship to Alepisauridae. Fielitz placed the enchodontid genera in four subfamilies but two are recognized here.

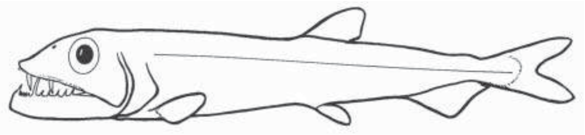
†SUBFAMILY CIMOLICHTHYINAE. One genus, †*Cimolichthys*, sister to all other enchodontids (enchodontoids of Fielitz 2004). †*Cimolichthys* was a common predator in Late Cretaceous seas that often reached large body sizes, e.g., total lengths well over a meter.

†SUBFAMILY ENCHODONTINAE. Five genera, †*Enchodus*, †*Eurypholis*, †*Palaeolycus*, †*Parenchodus*, †*Rharbichthys*, and †*Saurorhamphus*. This subfamily was classified as a family by Fielitz (2004), who found †*Parenchodus* to be nested within †*Enchodus*. A recent study by Cavin (2012) et al. (2012) returned †*Parenchodus* to generic status as the sister group to †*Enchodus*. Chalifa (1996) gave anatomical details on a large †*Enchodus*.

Family ALEPISAURIDAE (219)—lancetfishes. Marine; Atlantic, Indian, and Pacific.



Body slender (covered with pores in *Alepisaurus*); scales and light organs absent; dorsal fin in *Alepisaurus* high and extending along most of body (originating over opercle and with 29–48 rays), in *Omosudis* only 9–12; anal fin low with 12–18 rays; pelvics abdominal with 8–10 rays; mouth large; teeth well developed, palatines especially long; vertebrae in *Alepisaurus* 47–51, 39–41 in the shorter *Omosudis*; swimbladder absent. Length up to 2 m in *Alepisaurus*, 20 cm in *Omosudis*.



Omosudis was recognized in its own family, Omosudidae, by Nelson (1994).

Four genera, *Alepisaurus* (2 *A. ferox*, upper figure) *Anotopterus* (3), *Magnisudis* (3) and *Omosudis* (1, *O. lowei*, lower figure), with nine species (e.g., Paxton and Niem, 1999; Thompson, 2003a; Davis, 2010).

Family LESTIDIIDAE (220)—naked barracudinas. Marine; tropical and temperate oceans, worldwid .

Bioluminescent organ derived from hepatopancreatic tissue in some, uniquely among vertebrates (Ghedotti et al., 2015).

Harry (1953) was the first to use the family-group name as the tribe Lestidiini. Ghedotti et al. (2015), citing also Davis (2010) and Davis and Fielitz (2010), recognized this clade at the family level.

Four genera, *Lestidiops* (16), *Lestidium* (4), *Lestrolepis* (3), *Macroparalepis* (7), with about 30 species.

CTENOSQUAMATA (CTENOSQUAMATES). Rosen (1973a) recognized two taxa for his subsection Ctenosquamata—the Scopelomorpha for the myctophiforms and the Acanthomorpha for the remaining taxa of teleosts. Johnson (1992) concluded that the only synapomorphy that is unique to and unreversed in the ctenosquamates is the absence of the fifth upper pharyngeal toothplate and the associated third internal levator muscle. Wiley and Johnson (2010) cited four additional characters from Stiassny (1996) that have been used to diagnose Ctenosquamata. They are: two posterior ceratohyal branchiostegals present; craniotemporalis absent; supraorbital bones absent; neural arches of first vertebra fused. The molecular study of Miya et al. (2003) also supported ctenosquamate monophyly, as did more recent molecular studies such as Near et al. (2012a) and Betancur-R. et al. (2013a).

Superorder SCOPELOMORPHA

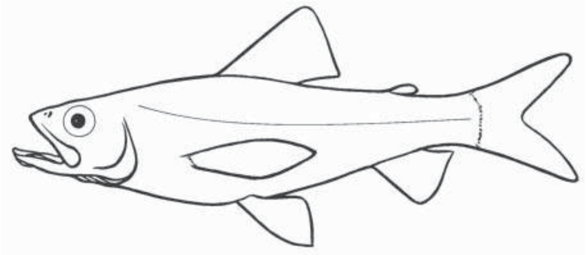
The Scopelomorpha with the single order Myctophiformes are the sister group to the Acanthomorpha.

Order MYCTOPHIFORMES (45)—lanternfishes. Deep-sea pelagic and benthopelagic fishes. Differ from the Aulopiformes in having the upper pharyngobranchials and retractor muscles like those of generalized paracanthopterygians (Rosen, 1973a:452). Other characteristics are: head and body compressed; eyes lateral (dorsolateral in the myctophid *Hierops*); mouth usually large and terminal; adipose fin present; usually 8 pelvic-fin rays; usually 7–11 branchiostegals.

Stiassny (1996), in addition to giving synapomorphies supporting monophyly of this order (e.g., large tooth plate fused to proximal face of fourth ceratobranchial; first centrum with enlarged cone-like parapophysis; first external levator reduced or absent; median dorsal keel present on mesethmoid), listed synapomorphies supporting monophyly of the two families and presented a phylogenetic diagram of the genera. Poulsen et al. (2013) presented a mitochondrial sequence study that largely supported early ideas about phylogeny.

Two families, 36 genera, and about 254 species.

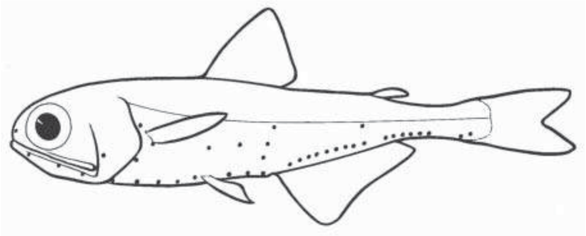
Family NEOSCOPELIDAE (221)—blackchins. Marine; Atlantic, Indian, and Pacific.



Trilobate rostral cartilage; enlarged bony protuberance on median process of maxilla; head and body compressed; long slender supramaxilla present; subocular shelf absent; origin of anal fin far behind dorsal-fin base; photophores present in *Neoscopelus*; scales cycloid except in *Solivomer*, which has ctenoid scales on body; swimbladder absent only in *Scopelengys*; vertebrae 29–35. Maximum length about 30 cm.

Three genera, *Neoscopelus* (3), *Scopelengys* (2), and *Solivomer* (with one species known only from the Philippine Islands), with six species (Nafpaktitis, 1977; Paxton and Hulley,1999; Hartel and Craddock, 2003).

Family MYCTOPHIDAE (222)—lanternfishes. Marine; all oceans, Arctic to Antarctic.



Cartilaginous supporting plate below the adipose fin; small supramaxilla present in some genera; subocular shelf present; origin of anal fin under or short distance behind dorsal-fin base; small photophores arranged in groups and rows on head and body (except in one species); scales usually cycloid (ctenoid in four species); swimbladder present (except in adults of a few species); vertebrae 28–45.

Myctophids are heavily consumed by numerous marine fishes and mammals. Most undergo a diurnal migration of several hundred meters. During the daytime the peak abundance of most species is between 300 and 1,200 m, while at night it is between 10 and 100 m.

About 33 genera with at least 248 species (Paxton et al., 1984; Paxton and Hulley, 1999; Zahuranec, 2000; Craddock and Hartel, 2003).

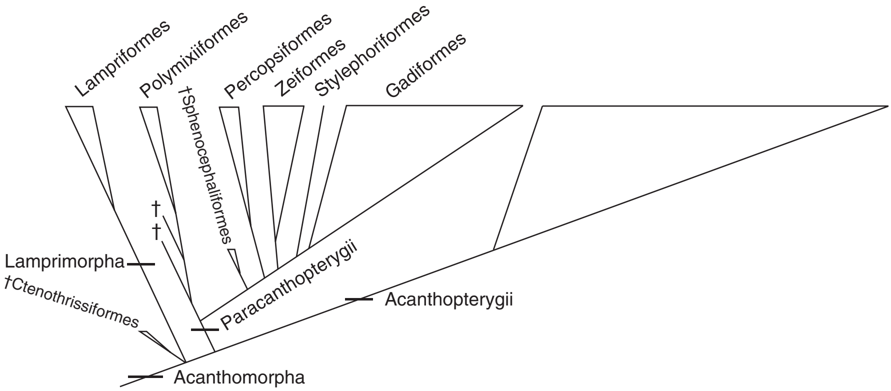
SUBFAMILY MYCTOPHINAE. About 13 genera (e.g., *Benthosema, Centrobranchus, Diogenichthys, Electrona, Gonichthys, Hygophum, Krefftichthys, Loweina, Metelectrona, Myctophum, Protomyctophum, Symbolophorus,* and *Tarletonbeania*).

SUBFAMILY LAMPANYCTINAE. About 20 genera (e.g., *Bolinichthys, Ceratoscopelus, Diaphus, Gymnoscopelus, Hintonia, Idiolychnus, Lampadena, Lampanyctodes, Lampanyctus, Lampichthys, Lepidophanes, Lobianchia, Nannobrachium, Notolychnus, Notoscopelus, Parvilux, Scopelopsis, Stenobrachius, Taaningichthys, and Triphoturus*).

ACANTHOMORPHA (ACANTHOMORPHS)—SPINY-RAYED FISHES. Rosen (1973a) recognized this taxon for all remaining teleosts, where many members have true fin spines in the dorsal, anal, and pelvic fins. Stiassny (1986) and Johnson and Patterson (1993) gave further evidence of the monophyly of the acanthomorphs. The molecular studies of, for example, Wiley et al. (2000), Miya et al. (2003), Li et al. (2009), Near et al. (2012a), Betancur-R. et al. (2013a), and Chen et al. (2014) also support acanthomorph monophyly.

Morphological characters diagnosing Acanthomorpha include: median palato-maxillary ligament absent; palato-vomerine ligament divided; dorsal limb of posttemporal firmly bound to epioccipital; medial pelvic process distally ossified; anterior and medial infracarinales separate; median rostral cartilage bound to premaxillary ascending process by well-developed rostro-premaxillary ligaments; dorsal and anal-fin spines present in most; first centrum with anterior surface bearing distinct facets that articulate with exoccipital condyles; and median caudal cartilages absent (Hartel and Stiassny, 1986; Stiassny, 1986; Johnson and Patterson, 1993; Rosen, 1985; Fujita, 1990; Wiley and Johnson 2010).

Johnson and Patterson (1993) presented arguments for regarding the lampriforms as the sister group to the remaining acanthomorphs. This provisional relationship is accepted here partly because molecular studies do not agree amongst themselves (e.g., Near et al., 2012a; Miya and Nishida, 2015; Betancur-R. et al. 2013a). In naming higher monophyletic groupings, Johnson and Patterson (1993) introduced the Euacanthomorpha for the polymixiiforms and higher taxa (Acanthomorpha less Lampridiformes in their terminology) and Holacanthopterygii for the Paracanthopterygii and higher taxa (Euacanthomorpha less Polymixiiformes; see also Wiley and Johnson, 2010). Concerning the former, their group had mostly similar contents to the Paracanthopterygii plus higher acanthomorphs in the present work, but their Paracanthopterygii did not include Polymixiiformes. Concerning the latter, we consider the polymixiiforms to be a member of the Paracanthopterygii; thus the Holacanthopterygii are not recognized as valid herein.



Suggested relationships of major early-branching groups of Acanthomorpha, including some important fossil taxa.

Our treatment of Acanthomorpha uses a phylogenetic sequence of three superorders for the following groups: Lamprimorpha, Paracanthopterygii, and Acanthopterygii. The last of these is further divided into two groups at the series rank: Berycida and the very diverse Percomorpha.

There is a rich fossil record of marine acanthomorphs beginning in the early Late Cretaceous. Stewart (1996) documented a variety of Cretaceous fossil occurrences in North America. Wilson and Murray (1996) described †*Xenyllion zonensis*, a paracanthopterygian from the Fish Scale Zone of western Canada, and grouped it with the genus †*Sphenocephalus* in the family †Sphenocephalidae (now in the order †Sphenocephaliformes), the type genus of which was discussed in detail by Rosen and Patterson (1969). †*Xenyllion*, when named, was the oldest known acanthomorph fossil; it was collected from rocks immediately above the Albian/Cenomanian boundary, making it of very early Late Cretaceous age (about 100 million years before present). A second species of †*Xenyllion* was discovered (Stewart, 1996) and has also now been redescribed and named (Newbrey et al., 2013). Gonzalez-Rodriguez et al. (2013) recently described additional diminutive and primitive acanthomorphs, including monocentrid-like armored Beryciformes (†*Handuichthys* and †*Pseudomonocentris*) and another armored genus of less certain relationships (†*Dalgoichthys*) from beds of very late Albian or very early Cenomanian age in Mexico. All of the earliest acanthomorphs known so far are of very small fishes, though the species of †*Sphenocephalus*, which lived millions of years later, are much larger.

The oldest Cretaceous acanthomorph recorded from a freshwater deposit is the *incertae sedis* †*Spinocaudichthys oumtkoutensis*, described from the early Late Cretaceous (Cenomanian) of Morocco (Filleul and Dutheil, 2001, 2004).

Another very interesting but taxonomically problematic fossil acanthomorph is the genus †*Asineops*, containing only one fossil species, †*Asineops squamifrons* of Eocene age from the Green River Formation of Wyoming (Rosen and Patterson, 1969; Grande, 1984; Borden et al., 2013), and the only member of the †Asineopidae. The genus is known also by fossil scales from the Paleocene (Wilson, 1980). †*Asineops* has a dorsal fin of 7–10 spines and 11 or 12 soft rays; the anal fin has two or three spines and 8–11 soft rays.

Other fossil acanthomorph taxa of uncertain placement include the Cretaceous †Aipichthyidae, †Aipichthyoididae, †Dinopterygiidae, †Pharmacichthyidae, †Pycnosteroididae, and †Stichocentridae (e.g., Patterson, 1993b; Otero and Gayet, 1995; Murray and Wilson, 2014). See below under Lamprimorpha for a possible placement of most of these fossil taxa.

†Order CTENOTHRISSIFORMES. These are well-preserved fossil acanthomorphs of basal but otherwise uncertain position, including the marine Late Cretaceous genera †*Aulolepis* and †*Ctenothrissa.* †*Pattersonichthys* also may be closely related to ctenothrissiforms. Rosen (1973a) thought it possible that ctenothrissiforms are the "primitive sister group of the paracanthopterygian-acanthopterygian assemblage" and classified them with that assemblage under the Acanthomorpha. How closely they are related to lamprimorphs is unknown.

Superorder LAMPRIMORPHA

The superorder Lamprimorpha is thought to be the first in a sequence of three superorders of Acanthomorpha, being sister to the superorder Paracanthopterygii plus the superorder Acanthopterygii (as discussed above). Its orthography was "Lampriomorpha" in the previous edition, or "Lampridomorpha" by some authorities, and although simplified herein it is still intentionally different from "Lampromorpha," which is the name of a clade of cuckoo birds.

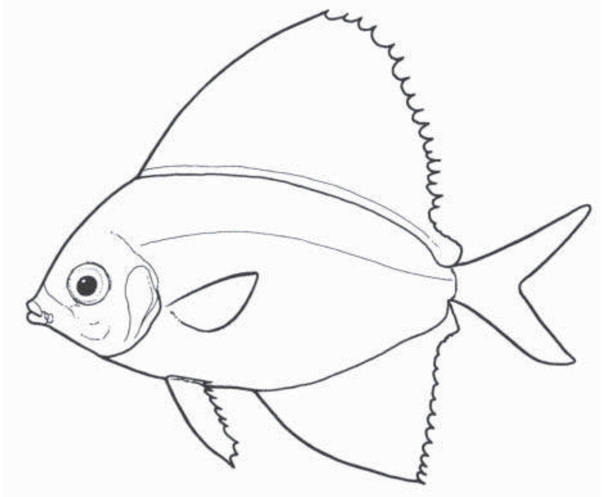
Rosen (1973a) established that lampriforms are not percomorphs, as previously believed, but instead are basal acanthomorphs. Strong evidence that they are the sister group to all other acanthomorphs (euacanthomorphs) was presented by Olney et al. (1993) and Johnson and Patterson (1993). Positioning them as basal acanthomorphs was also supported by the molecular evidence of Wiley et al. (2000), Near et al. (2012a), and Betancur-R. et al. (2013a), among others. The study of Wiley et al. (1998), based on morphological and molecular evidence, confirmed monophyly of the order and, though only for the five lampriform species they studied, agreed with the phylogenetic results of Olney et al. (1993). Davesne et al. (2014) and Delbarre et al. (2015) have made a case that the formerly *incertae sedis* families †Aipichthyidae, †Aipichthyoididae, †Pharmacichthyidae, and †Pycnosteroididae are all Cretaceous relatives of Lamprimorpha.

Order LAMPRIFORMES (Lampridiformes, Allotriognathi) (46)—opahs. No true spines in fins; premaxilla excludes maxilla from gape; unique type of protrusible upper jaw (maxilla, instead of being ligamentously attached to the ethmoid and palatine, slides in and out with the highly protractile premaxilla); absence of the anterior palatine prong and the anterior palatomaxillary process; mesethmoid positioned posterior to lateral ethmoids; elongate ascending process of premaxillae and large rostral cartilage inserts into frontal vault; insertion of the first dorsal pterygiophore anterior to the first neural spine; second ural centrum fused posteriorly to the upper hypural plate; pelvic fins with 0–17 rays; swimbladder, when present, physoclistous; orbitosphenoid present in some (Olney et al., 1993; Wiley and Johnson, 2010).

The deep-bodied members with symmetrical caudal fins and well-developed skeletons—the lamprids and veliferids—are referred to as the bathysomes. The other five families, with long ribbon-like bodies with dorsal fins extending from the head to the tail and asymmetrical caudal fins and weak skeletons, are referred to as the taeniosomes. These two groups were formally recognized in Regan's 1907 classification as the Bathysomi and the Taeniosomi. According to the cladogram of Olney et al. (1993), the former is paraphyletic while the latter is monophyletic.

Fossil lampriforms include †*Bajaichthys* (family not assigned), †*Palaeocentrotus*, †*Veronavelifer*, and the lamprid-like †Turkmenidae (with long pelvic fins of 7–10 rays), along with †*Turkmene* and †*Danatinia* of the late Paleocene and †*Analectis* of the Lower Oligocene (see Nelson 1994, for references). Olney et al. (1993) and Patterson (1993a,b) discussed and listed these fossils. For orthography of ordinal name, see Lampridae below. Six families with 11 genera and about 22 species. There are no freshwater species in this order. The families are sequenced to reflect the sister-group relationships recognized by Olney et al. (1993).

Family VELIFERIDAE (223)—velifers. Marine, usually near-shore; Indian and western part of mid-Pacific.

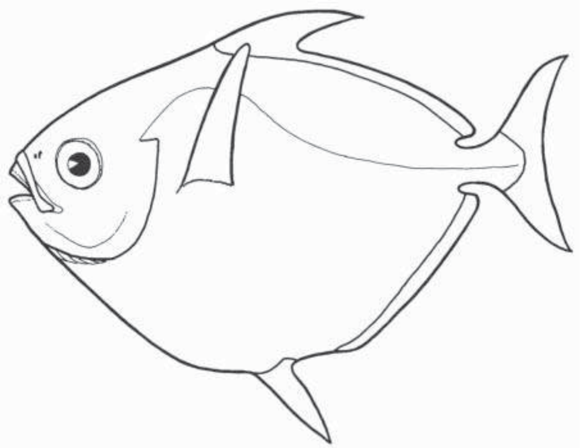


Body deep and compressed; pelvic fins with seven to nine rays (no spine); dorsal and anal fins long, total number of spines plus soft rays in dorsal fin 32–44, and in anal fin 25–35; dorsal and anal-fin bases with scaly sheaths; teeth absent; swimbladder bifurcate posteriorly, the two horns extending far beyond anus; six branchiostegal rays; vertebrae 33 or 34 (16 abdominal and 17 or 18 caudal). Maximum length about 40 cm.

†*Veronavelifer* is an Eocene fossil found in northern Italy that is relatively similar to the extant *Metavelifer multiradiatus*; the only other fossil veliferoid is †*Palaeocentrotus* (family Palaeocentrotidae) of the Eocene in Denmark.

Two monotypic genera, *Velifer* and *Metavelifer* (e.g., Smith and Heemstra, 1986).

Family LAMPRIDAE (Lamprididae) (224)—opahs. Marine pelagic; Atlantic, Indian, and Pacific.



Body oval-shaped and compressed; foramen magnum enclosed in cranial condyle; lateral line arched high in front; dorsal and anal fins long (dorsal with 48–56 rays and anal with 33–42 rays); pelvic fin rays 12–17; minute cycloid scales; vertebrae 43–46. Its diet consists primarily of squids, octopuses, and crustaceans. Maximum length up to 1.8 m.

The orthography of the family has been changed from Lamprididae to Lampridae. There is a desire to have stability in the orthography of family names, while following provisions of the code of the International Commission of Zoological Nomenclature as given in the fourth edition of the "International Code of Zoological Nomenclature". There is currently much disagreement for some families as to whether the suffix should be "ididae" or "idae." For the present case, Lampridiformes and Lamprididae have been the forms used in most recent literature by specialists and were used in Nelson (1994) in the belief, based on the work of Patterson in Olney et al. (1993), that this form was grammatically correct. However, the latter seems not to be accurate, and Eschmeyer (1998, Online) employed the forms Lampriformes and Lampridae. We now follow Eschmeyer (1998).

Two species, *Lampris guttatus* (worldwide) and *L. immaculata* (cold and temperate waters of Southern Hemisphere) (Parin and Kukuyev, 1983; Collette, 2003a).

The remaining four families form a monophyletic group and share the following features: body very thin and ribbon-like; anal fin short or absent; pelvic fin rays 0–10; six or seven branchiostegal rays; swimbladder, when present, does not extend past the anus; each dorsal fin ray has more than one lateral spine at its base; one or two fang-like teeth present on the vomer; suborbital series absent except for the lachrymal and second suborbital (jugal); frontal bones separated by a groove; vertebrae 62–200. According to Olney et al. (1993), the lophotids and radiicephalids are sister groups, and the trachipterids and regalecids are sister groups.

Family LOPHOTIDAE (225)—crestfishes. Marine; most oceans.

Body with small deciduous cycloid scales (sometimes appearing naked); supraoccipital spine enlarged and supporting first dorsal-fin pterygiphore; anal fin small, near caudal and with 5–20 rays; pelvic fin, absent or with 2–6 rays; dorsal fin very long with about 220–392 rays and originating above or before tip of snout; swimbladder present; ink sac present, which discharges into cloaca; vertebrae 124–200. The extinct †*Protolophotus* is known from Oligocene deposits in Iran. Maximum length about 200 cm.

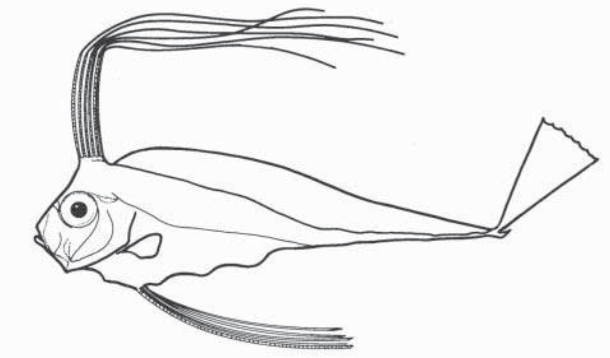
Two genera, *Lophotus* and *Eumecichthys* (e.g., Olney, 2003), and probably four species.

Family RADIICEPHALIDAE (226)—tapertails. Marine; central and eastern Atlantic and off New Guinea.

Body elongate and laterally compressed, tapering to a thin caudal filament (caudal fin with small upper lobe of four rays and long, slender lower lobe of seven rays); elongate haemal spines on preural centra 4–6; dorsal fin with 152–159 rays; anal fin vestigial, with seven rays; pectorals and pelvics each with up to nine rays (pelvic rays tend to be lost during development); scales along lateral line but absent on rest of body; ribs present; swimbladder well developed; brown ink sac, which discharges into the cloaca (the ink, like that of *Lophotus*, may serve to blind would-be predators); cloaca about one-third along total length from snout; vertebrae 114–121 (36–39 abdominal + 77–82 caudal), of equal length. Maximum length about 70 cm.

One species, *Radiicephalus elongatus*, known from only a few specimens (e.g., Olney, 2003).

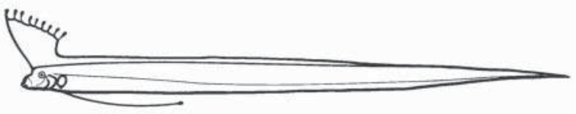
Family TRACHIPTERIDAE (227)—ribbonfishes. Marine; Arctic, Atlantic (including Mediterranean), Indian, and Pacific.



Body naked, with deciduous cycloid scales, or with deciduous modified ctenoid scales (tubercles may also be present); no anal fin; caudal fin long and at a right angle to the body, consisting of upper lobe only (*Desmodema* has the few caudal rays parallel to the caudal peduncle); pelvic fins with 1–10 rays; dorsal fin very long, originating distinctly behind tip of snout; eyes large; teeth present; ribs absent; swimbladder rudimentary or absent; vertebrae 62–111. Allometric growth results in various body shapes during growth (including the loss of the pelvic fins during metamorphosis in *Desmodema*). Maximum length about 1.7 m, attained in *Trachipterus altivelis*.

Three genera, *Desmodema* (2 species), *Trachipterus* (about 6,including King-of-the-Salmon), and *Zu* (2), with about 10 species (e.g., Olney, 2003).

Family REGALECIDAE (228)—oarfishes. Marine; all oceans.



Scales absent; no anal fin; pelvic fin very elongate, slender, with one ray; dorsal fin very long, originating distinctly behind tip of snout, with 260–412 rays, the first few rays being elongate and bright red; eye small; no teeth; swimbladder absent; vertebrae about 143–170. *Regalecus glesne* (Oarfish or King-of-the-Herring) has 40–58 gill rakers; *Agrostichthys parkeri* (Streamer Fish) has 8–10 gill rakers. This group is probably responsible for many reports about sightings of supposed sea-serpents. Maximum length up to about 8 m, attained in *R. glesne*, longest of the bony fishes.

Two genera, *Regalecus* (2) and *Agrostichthys* (1), with three species (e.g., Olney 2003).

The Euacanthomorpha of Johnson and Patterson (1993) included almost all the fishes beyond this point, but they were arranged differently than they are here. For example, Polymixiiforms were separated from paracanthopterygians but are not here, some former paracanthopterygian taxa (Ophidiiformes, Batrachoidiformes, and Lophiiformes) are now in Acanthopterygii, and some former acanthopterygians (Zeiformes) are now in Paracanthopterygii. In addition, the monotypic Stylephoriformes were then in Lampriformes but are now in Paracanthopterygii (see below). The taxon Holacanthomorpha of the same authors is not considered valid because it combined some but not all Paracanthopterygii in a group with Acanthopterygii.

Superorder PARACANTHOPTERYGII

The monophyly and taxonomic composition of the superorder Paracanthopterygii have been debated since the group was named by Greenwood et al. (1966). Its original membership included Batrachoidiformes, Gadiformes (including Ophidioidei and Zoarcoidei), Gobiesociformes, Lophiiformes, and Percopsiformes (Amblyopsidae, Aphredoderidae, Percopsidae). Since then, various authors have suggested including the Polymixiiformes, Gobiiformes, Indostomidae, Myctophiformes, Stylephoridae, and Zeiformes within the suborder, and removing the batrachoidiforms, bythitoids, gobiesocoids, lophiiforms, ophidioids, and zoarcoids to Percomorpha (e.g., Rosen and Patterson, 1969; Banister, 1970; Freihofer, 1970; Wiley et al., 2000; Chen et al., 2003; Miya et al., 2003, 2005; Holcroft, 2004, 2005; Dettai and Lecointre, 2005; Smith and Wheeler, 2006).

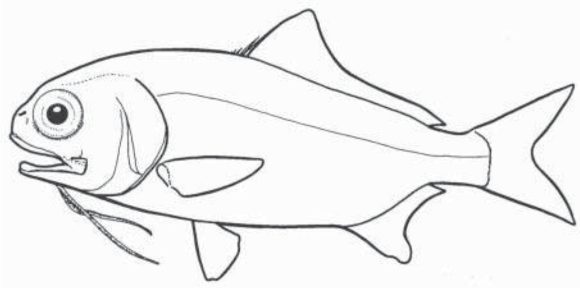
Wiley et al. (2000) for the first time recovered gadiforms and zeiforms as sister groups in a total-evidence analysis of 27 taxa, using a matrix composed of 38 morphological characters drawn from Johnson and Patterson (1993) and 1,674 base pairs from two ribosomal gene fragments (572 bp from mitochondrial 12S, and 1,112 bp of nuclear 28S). They recovered this novel clade as sister to an "acanthopterygian-like" clade, with both collectively the sister group of Percopsiformes. Miya et al. (2007), in a mitochondrial molecular study, recovered the supposed lampriform *Stylephorus* in a novel position as sister to the Gadiformes. *Stylephorus* was subsequently placed in a new order, Stylephoriformes. Their Bayesian analysis of mitogenomic data suggested a paracanthopterygian clade consisting of ((Polymixiiformes + Percopsiformes) + ((Gadiformes + Stylephoriformes) + Zeiformes)).

More recently, Grande et al. (2013) and Borden at al. (2013) recovered Polymixiiformes as sister to a Paracanthopterygii comprising Percopsiformes + [Zeiformes (*Stylephorus* + Gadiformes)]. Polymixiids + paracanthopterygians were in turn found to be sister to the acanthopterygians (beryciforms, ophidioids, batrachoidiforms, percomorphs, lophiiforms). Other molecular studies (e.g., Near et al., 2012a; Betancur-R. et al., 2013a; Miya and Nishida, 2014; and Chen et al., 2014) have also consistently recovered a group comprising percopsiforms, gadiforms, *Stylephorus*, and zeiforms, but the placement of Polymixiiformes among acanthomorphs varied in these studies. Here we follow the phylogenetic relationships proposed in the molecular and morphological studies of Borden et al. (2013) and Grande et al. (2013) and, like Miya et al. (2005), Miya and Nishida (2014), and Chen et al. (2014), we now explicitly include *Polymixia* within the Paracanthopterygii.

The 667 or so living species are placed in about 109 genera, 21 families, and five orders. The orders are listed in hypothesized phylogenetic sequence. There are numerous fossil taxa discussed below.

Order POLYMIXIIFORMES (47)—beardfishes. Few groups have shifted back and forth as frequently as this one. They were formerly placed within the Beryciformes by many workers employing differing methods, though Rosen and Patterson (1969) drew many parallels with paracanthopterygians and the acanthomorph stem lineage. Later works such as those of Stiassny (1986) and Johnson and Patterson (1993) gave evidence that Polymixiiformes could be the sister group to all other acanthomorphs. Some large-scale molecular studies disagreed as to their placement, finding them variously to be sister to percopsiforms (e.g., Miya et al., 2005; Near et al., 2012a), sister to paracanthopterygians (lacking data on stylephoriforms; Miya et al., 2003), sister to percopsiforms within Paracanthopterygii (again lacking data on stylephoriforms; Miya et al., 2005); sister to Acanthopterygii (e.g., Betancur-R. et al., 2013a); or sister to percopsiforms, gadiforms, and zeiforms (also lacking data on stylephoriforms; Chen et al. 2014). The more taxonomically-focused studies of Borden et al. (2013) and Grande et al. (2013) found molecular and morphological support for a sister-group relationship between Polymixiiformes and the other Paracanthopterygii, including stylephoriforms. As noted by Stiassny (1986), *Polymixia* is unique in having a palato-premaxillary ligament passing between maxillary lateral processes, rather than between contralateral palatines. Regardless of its precise phylogenetic position, it is one of the most plesiomorphic acanthomorph genera still extant. Patterson (1993a) concluded, "If there is an acanthomorph equivalent of the living monotremes amongst mammals, it is *Polymixia* … ".

Family POLYMIXIIDAE (229)—beardfishes. Marine; tropical and subtropical Atlantic, Indian (primarily off Natal), and western Pacific.



Body moderately elongate and compressed; pair of hyoid barbels; dorsal fin continuous, with 4–6 spines and 26–38 soft rays; anal fin with four short spines and 13–17 soft rays; pelvic fins subabdominal, with one spine-like ray and six soft rays; 16 branched caudal rays; about 33–38 lateral-line scales; four branchiostegal rays; 11–21 gill rakers; two simple, flat supramaxillae; subocular shelf, orbitosphenoid, and basisphenoid present; three epurals; three widely spaced supraneurals; usually 29 or 30 vertebrae. This is the only acanthomorph retaining two sets of intermuscular bones, epipleurals (what are generally termed epipleurals in acanthomorphs are now thought to be homologous with the epineurals of lower teleosts; Johnson and Patterson, 1993). Maximum length 38 cm. Beardfishes usually occur between 180 and 640 m depth.

One genus, *Polymixia,* with 10 species (e.g., Moore, 2003). Fossils appear first in the Cenomanian (early Late Cretaceous) and include such Cretaceous marine genera such as †*Berycopsis,* †*Dalmatichthys,* †*Magrebichthys,* †*Omosoma,* and †*Omosomopsis* (e.g., Murray and Wilson, 2014).

†Order SPHENOCEPHALIFORMES. Late Cretaceous. One family. This fossil group was once thought to be related to the living North American freshwater percopsiforms and was placed within that order as suborder †Sphenocephaloidei by Rosen and Patterson (1969). Patterson and Rosen

(1989) later considered it to be sister to all other paracanthopterygians, a group of taxa that they termed the anacanthines, on the basis of both groups sharing the following characters: "gadoid notch" present—a cavity behind the high postmaxillary process of the premaxilla (not present in all anacanthines, however); first vertebra with a pair of high facets off the centrum that articulate with the forwardly displaced exoccipital condyles; second and third vertebrae foreshortened (sometimes only the second centrum is foreshortened in anacanthines). Currently, the anacanthines are regarded as a polyphyletic assemblage, but †sphenocephaliforms are still likely to be basal members of the true Paracanthopterygii, most likely sister to all paracanthopterygians except for Polymixiiformes (Murray and Wilson, 1999; Borden et al., 2013; Grande et al., 2013).

†Family SPHENOCEPHALIDAE. Marine. Late Cretaceous. Sphenocephalids retain a single pair of slender supramaxillae (*Polymixia* has two, other paracanthopterygians have none); large spines at posteroventral angle of preopercle; opercle with distinctive dorsal excavation and recurved spine; supraneurals reduced to one; adipose fin present.

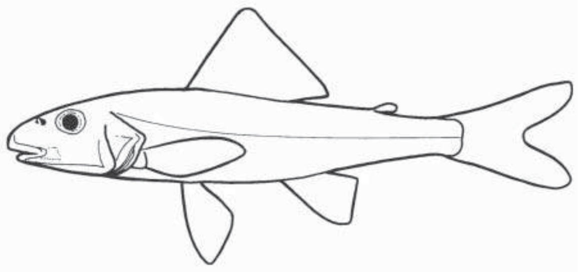
Two genera with four species: †*Sphenocephalus*, with two species, middle Late Cretaceous of Europe, and †*Xenyllion*, with two very small species, early Late Cretaceous of North America (Wilson and Murray, 1996; Stewart, 1996; Newbrey et al., 2013).

Order PERCOPSIFORMES (48)—trout-perches. Premaxilla non-protractile; diamond-shaped opercle (also observed in †sphenocephaliforms); enlarged intercalars; ectopterygoid and palatine with teeth; transverses dorsales and obliquii dorsales combined with a trapezoid appearance in dorsal view; obliquus dorsalis 4 extending posteriorly, passing dorsal to the articulation between the uncinate processes and third and fourth epibranchials to insert on the levator process of the fourth epibranchial; pelvic fins, if present, behind pectorals and with 3–8 soft rays; spines (normally weak) usually present in dorsal fin; many species with ctenoid scales; six branchiostegal rays; 16 branched caudal rays; orbitosphenoid, basisphenoid, and suborbital shelf absent; vertebrae 28–35.

Monophyly of this order has been questioned by several authors (e.g., Murray and Wilson, 1999) with suggestions that amblyopsids may be more closely related to anacanthines or to gobioids (Poly and Proudlove, 2004). However, contrary to the above, Smith and Wheeler (2006), Dillman et al. (2011), Borden et al. (2013), and Grande et al. (2013) recovered a monophyletic percopsiform lineage, which is consistent with conclusions of Springer and Johnson (2004) and Springer and Orrell (2004) based on eight specializations of the dorsal gill arches and musculature (see above).

Three families, seven genera, and ten species. All are confined to fresh water and all are from North America.

Family PERCOPSIDAE (230)—trout-perches. Freshwater; northern North America, primarily Alaska to Quebec and southward to Missouri and Kentucky.



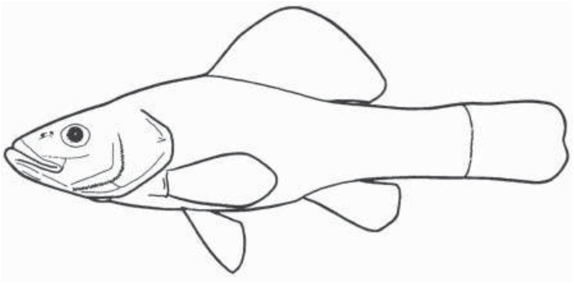
Alveolar premaxillary process broadly arched; vomer toothless; ctenoid and cycloid scales; head naked; adipose fin present; dorsal fin with one or two spines and 9–12 soft rays; anal fin with one or two spines and six or seven soft rays; pelvic fin subthoracic, with eight rays; lateral line complete or nearly so, scales 43–60; anus in front of anal fin; vertebrae 33–36. Maximum length 20 cm, attained in *Percopsis omiscomaycus*.

Two species, the widespread *Percopsis omiscomaycus* and the more restricted *Percopsis* (synonym *Columbia*) *transmontana* of the Columbia River drainage in Washington, Oregon, and Idaho.

The family is well represented by fossil genera from North America (e.g., Rosen and Patterson, 1969; Murray and Wilson, 1996; Poly, 2004a) in the Paleocene (†*Lateopisciculus*, †*Massamorichthys*) and Eocene (†*Amphiplaga*, †*Erismatopterus*). Another Eocene genus, †*Libotonius*, with two species, is sometimes classified in the separate family †Libotoniidae (e.g., Murray and Wilson, 1999) or included within the Percopsidae (e.g., Wilson, 1977; Borden et al., 2013).

†Family MCCONICHTHYIDAE. †*Mcconichthys longipinnis*, a freshwater early Paleocene fish from Montana, was considered by L. Grande (1988) to form a trichotomy with the gadiforms and the pediculates (lophiiforms and batrachoidiforms—but the latter two groups are no longer included within the Paracanthopterygii). Murray and Wilson (1999) considered it to belong within Percopsiformes as a stem lineage, while Grande et al. (2013) recovered it as more closely related to Aphredoderidae. This is currently the oldest named fossil percopsiform.

Family APHREDODERIDAE (231)—pirate perches. Freshwater; eastern United States, primarily lowlands of Atlantic drainage from Long Island southward, Gulf of Mexico slope, Mississippi Valley, and part of Great Lakes drainage.

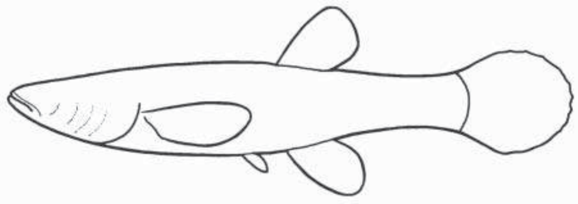


Ctenoid scales; sides of head scaly; eyes normal; dorsal fin with three or four spines and 10 or 11 soft rays; anal fin with two or three spines and 5–7 soft rays; pelvic fin subthoracic, with seven rays; anus between gill membranes in adults; adipose fin absent; lateral line absent or incomplete; vomer toothed; premaxilla segmented.

The anus is in the normal position in juveniles, just ahead of the anal fin, and moves forward during the growth of the fish. Also, in young pirate perch, the third anal ray becomes transformed from a soft ray to a spine during growth. Young individuals thus appear to have two spines and eight soft rays; adults have three spines and seven soft rays. Maximum length about 13 cm.

One species, *Aphredoderus sayanus* (Poly 2004b).

Family AMBLYOPSIDAE (232)—cavefishes. Freshwater; southern and eastern United States.



Cycloid scales; head naked; eyes small to rudimentary; dorsal fin with 0–2 spines and 7–12 soft rays; anal fin with 0–2 spines and 7–11 soft rays; pelvic fins usually absent (present only in *Amblyopsis spelaea*, where they are small, abdominal, and with 0–6 rays); sensory papillae in rows on the head, body, and tail; myodome lost; anus between gill membranes in adults; adipose fin absent; lateral line absent or incomplete; vomer toothed; premaxilla segmented; vertebrae 27–35.

All the species, except *Chologaster cornuta* of the Atlantic coastal plains, usually live in caves in limestone formations. *Chologaster cornuta* and *Forbesichthys agassizii* are the only species with functional eyes. The other four species are blind. Maximum length about 9 cm, attained in *Amblyopsis spelaea*.

Niemiller and Fitzpatrick (2007) and Niemiller, McCandless et al. (2012) completed molecular phylogenies for subterranean populations of *Typhlichthys subterraneus* and *Amblyopsis spelaea*, respectively, and reported finding cryptic diversity. Niemiller, Near, and Fitzpatrick (2011) resurrected *Typhlichthys eigenmanni* and identified populations representing up to 15 putative cryptic species.

Six genera, *Amblyopsis* (2), *Chologaster* (1), *Forbesichthys* (1), *Speoplatyrhinus* (1), *Troglichthys* (1), and *Typhlichthys* (2), with eight species (Nelson et al., 2004; Poly and Proudlove, 2004; Proudlove, 2005; Parenti, 2006; Chakrabarty et al., 2014).

Order ZEIFORMES (49)—dories. Metapterygoid reduced in size; exoccipital facets narrowly spaced; first proximal radial of dorsal fin enlarged dorsoventrally; contact between the first proximal radial of dorsal fin and first neural arch and spine; dorsal, anal, and pectoral-fin rays unbranched;

accessory caudal fin elements present in some groups; three and one-half gills (seven hemibranchs); no open gill slit between fourth and fifth branchial arches; palatine teeth absent; vomerine teeth present; caudal fin usually with 11 branched rays (13 in grammicolepidids); dorsal fin with 5–10 spines and 22–36 soft rays; body usually thin and deep; jaws usually greatly distensible; no orbitosphenoid; simple posttemporal fused to skull; swimbladder present; vertebrae usually 30–44.

The classification of Zeiformes (after the removal of caproids) follows Tyler et al. (2003). However, contrary to Johnson and Patterson (1993) and Nelson (2006), there is overwhelming molecular and some morphological support for the placement of Zeiformes within Paracanthopterygii, where they are closely aligned with Gadiformes and Stylephoriformes (Wiley et al., 2000; Grande et al., 2013; Borden et al., 2013; Chen et al., 2014; Miya and Nishida, 2014).

Most zeiform species are deepsea fishes; some, however, may occur at 100–300 m.

The earliest fossil zeiform is †*Cretazeus rinaldii* (family †Cretazeidae), described by Tyler et al. (2000), a mid Late Cretaceous species and the oldest in the order. For a discussion of additional zeiform fossil taxa see Tyler and Santini (2005) and Santini et al. (2006).

Six families with about 16 genera and 33 species. There are no freshwater species.

Suborder Cyttoidei. Recognized after Tyler et al. (2003).

Family CYTTIDAE (233)—lookdown dories. Marine; southeast Atlantic and Indo-West Pacific (e.g., from South Africa to off Australia and New Zealand).

Ascending process of premaxilla extending back to about one-half into orbit; scute-like scales present from isthmus to pelvic-fin base; no ossified ribs (convergent with *Cyttomimus*); ossified epineurals on some anterior vertebrae (convergent with *Zeus* + *Zenopsis*); no large buckler scales present along bases of dorsal and anal fins or along ventral midline; dorsal fin with 8–10 spines and 28–36 soft rays.

One genus, *Cyttus*, with 3 species.

Suborder Zeoidei. This suborder (as Zeioidei) was recognized in Nelson (1994) but also included *Cyttus*.

Family OREOSOMATIDAE (234)—oreos. Marine; Antarctic, Atlantic, Indian, and Pacific. Known primarily from South Africa and southern Australia.

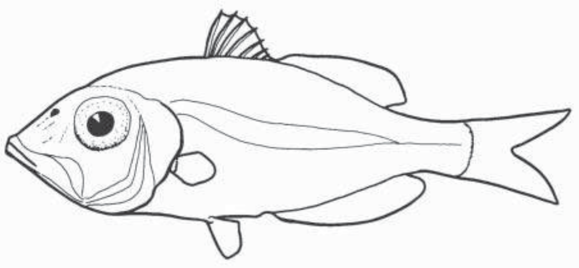
Body very deep and compressed; mouth upturned, protractile; eyes large; scales small, cycloid or ctenoid; young with conical scutes on parts of body; extended prejuvenile stage present with a unique combination of several derived morphologies (Tyler et al., 2003); pelvic fin with one spine and 5–7 soft rays; dorsal fin with 5–8 spines and 28–36 soft rays; anal fin with 2–4 spines and 26–33 soft rays; pectoral-fin rays 17–22; vertebrae 34–43. Maximum length about 50 cm.

Most species occur between 400–1,800 m.

Tyler et al. (2003) recognized two subfamilies, Pseudocyttinae for *Pseudocyttus maculatus*, and Oreosomatinae for the other three genera.

Four genera, *Allocyttus* (4), *Neocyttus* (4), *Pseudocyttus* (1), and *Oreosoma* (1), with about nine or 10 species (C. Karrer in Smith and Heemstra, 1986; Heemstra, 2003a; Tyler et al., 2003).

Family PARAZENIDAE (235)—smooth dories. Marine; scattered localities in the western Atlantic and the Indo-Pacific.



Large haemal spine vacuities present in several posterior abdominal vertebrae; pelvic fin with no spine and 7–9 soft rays.

Three genera with four species.

SUBFAMILY PARAZENINAE. Body compressed and elongate; premaxillaries extremely protractile; two dorsal fins, the first with eight spines, second with 26–30 soft rays; anal fin with one spine and 31 soft rays; pectoral fin with 15 or 16 rays; pelvic fins thoracic (origin behind pectoral fin origin), with one unbranched ray and six branched rays; 34 vertebrae. The species has only one lateral line, rather than two as previously thought (Kotlyar, 2001).

One species, *Parazen pacificus*, and perhaps an undescribed species in the western Atlantic (Kotlyar, 2001).

SUBFAMILY CYTTOPSINAE. Dorsal fin with six or seven spines (rarely eight); buckler-like scales present from isthmus to anus; pectoral fin with 13–15 rays; pelvic-fin base under or slightly in front of pectoral-fin base, fins with nine rays.

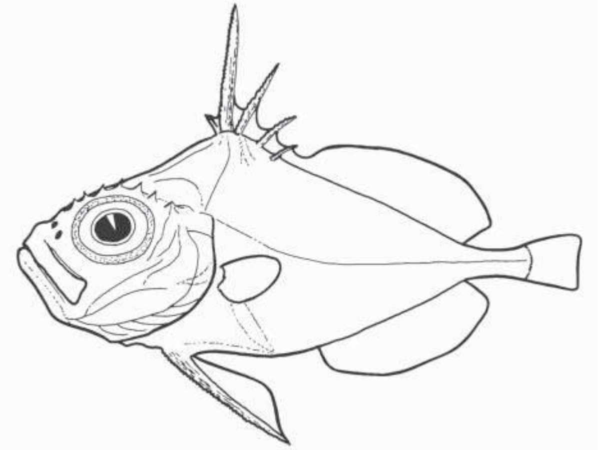
Two genera, *Cyttopsis* (2) and *Stethopristes* (1), with about three species (Tyler et al., 2003).

Family ZENIONTIDAE (Zenionidae) (236)—armoreye dories. Marine; Atlantic, Indian, and Pacific.

Scales on most of body rounded to squarish; dentary with multiple serrations behind symphysis; serrations present along posterior border of supracleithrum; beryciform foramen represented by a deep concavity on the dorsal surface of the ceratohyal; alveolar process of premaxilla ventrally indented; second anal fin spine short. Pectoral-fin rays 12–18; anal-fin spines when present 1 or 2; vertebrae 25–27; branchiostegal rays 7–8. (Tyler et al., 2003).

Three genera, *Capromimus* (1), *Cyttomimus* (2), and *Zenion* (4) (synonym *Cyttula*), with about seven species (e.g., Heemstra, 2003a) (the first two genera were placed in Zeidae and the latter in Macrurocyttidae in Nelson, 1994).

Family GRAMMICOLEPIDIDAE (237)—tinselfishes. Marine; scattered parts of Atlantic and Pacific.



Scales narrow and greatly elongate vertically; fifth ceratobranchial toothless.

Three genera, three species.

SUBFAMILY MACRUROCYTTINAE. Pelvic fin, in addition to the spine, with two inconspicuous soft rays; spinous dorsal elevated, with five spines (strong, all but one relatively short); soft dorsal rays 27, and anal fin with 22 soft rays; pectoral rays 15. Luzon (Philippines).

One species, *Macrurocyttus acanthopodus.*

SUBFAMILY GRAMMICOLEPIDINAE. Proximal end of parhypural laterally expanded as specialized pegs; scales on body greatly elongate vertically; basisphenoid present as a short shaft at front of roof of posterior myodome (Tyler et al., 2003); mouth small, nearly vertical; dorsal fin with 5–7 spines and 27–34 soft rays; anal fin with two spines and 27–35 soft rays; row of spines along each side of dorsal and anal-fin bases; pelvic fin with one spine and six soft rays; caudal fin with 13 branched rays; vertebrae 37–46.

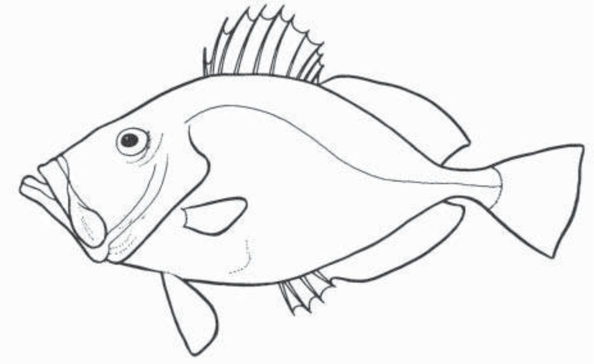
Two monotypic genera, *Grammicolepis* (synonym *Daramattus*) *brachiusculus* and *Xenolepidichthys dalgleishi.*

Family ZEIDAE (238)—dories. Marine; Atlantic, Indian, and Pacific.

Large buckler scales with posteriorly directed processes present along bases of dorsal and anal fins; otolith small and trilobed; Baudelot's ligament attached to exoccipitals; ventral end of supracleithrum deeply forked; ossified ribs on most abdominal vertebrae; accessory caudal fin elements present (Tyler et al., 2003;

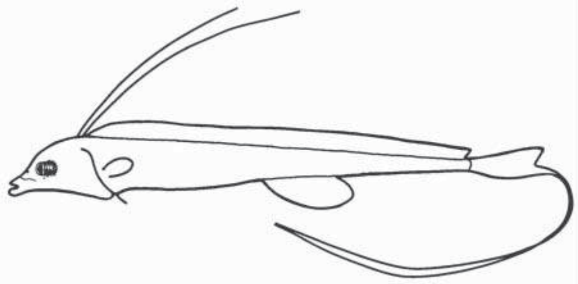
Borden et al., 2013; Grande et al., 2013). Dorsal fin with 9–10 spines and 22–26 soft rays; anal fin with 4 spines and 20–23 soft rays in *Zeus*, and three spines and 24–26 soft rays in *Zenopsis*, Also known as John dory and St. Peter fish.

Two genera, *Zenopsis* (4) and *Zeus* (2), with about six species.



Order STYLEPHORIFORMES (50)—tube-eyes or thread-tails. Recent molecular studies (e.g., Miya et al., 2007; Grande et al., 2013; Betancur-R. et al., 2013a; Miya and Nishida, 2014) strongly suggest that *Stylephorus* is closely related to gadiforms and not nested within lampriforms. This placement is accepted here although morphological support for this relationship is wanting.

Family STYLEPHORIDAE (239)—tube-eyes or thread-tails. Marine abyssal; most oceans.



Body ribbon-like; dorsal fin extending from nape to tail, with 115–124 rays; anal fin short, 15–17 rays; pectoral-fin rays 10 or 11 and unbranched, base horizontal; pelvic fin with only one ray; caudal fin in two parts, upper with five rays and lower with two extremely elongate rays; branchiostegal rays reduced to five; eyes large, telescopic, may be directed forward or upward; mouth small and protractile; teeth small; no swimbladder; about 50 vertebrae. This fish swims in a vertical position, head uppermost. It occurs at depths of about 300–800 m. Maximum length 31 cm.

Probably one species, *Stylephorus chordatus* (e.g., Olney, 2003).

Order GADIFORMES (51)—cods and hakes. Pelvic fins, when present, inserted below or in front of pectorals (thoracic or jugular, rarely behind in Macrouridae) with up to 11 rays; scapular foramen present between the scapula and coracoid; basihyal lost; no true spines in the fins; most with long dorsal and anal fins; scales usually cycloid, rarely ctenoid; premaxilla forms the entire margin of upper jaw, protractile in some; ectopterygoid toothless; orbitosphenoid and basisphenoid absent; single hyomandibular condyle; intercalar enlarged; levator arcus palatini laterally to adductor mandibulae A2; branchiostegal rays 6–8; posterior vertebral reduction results in posterior dorsal and anal pterygiophores exceeding the number of caudal vertebrae; presence in many species of accessory caudal skeletal elements, often called XY bones, between neural and/or hemal spines; swimbladder without pneumatic duct (the swimbladder is absent in *Melanonus* and *Squalogadus*). Gadiforms have a unique, pince-nez shaped saccular otolith; in most gadiforms, with the exception of phycines (Nolf and Steurbaut, 1989), there is a collicular crest above the ostium-cauda junction of the crista inferior (Endo, 2002; Grande et al., 2013; Borden et al., 2013).

This order consists of many important commercial fishes that constitute over one quarter of the world's marine fish catch. Much information on various members is found in Cohen (1989), with keys to many of the species and much distributional and other data provided by Cohen et al. (1990). Different concepts of the composition of Gadiformes have existed as a result of various hypotheses of relationships and philosophy of classification. For example, Berg (1940) recognized it as a relatively compact group, containing only four families: Muraenolepididae, Moridae, Bregmacerotidae, and Gadidae (which included *Gaidropsarus* and *Merluccius*). The Macrouridae and Macrouroididae were placed in a separate order. At the opposite extreme, Nelson (1976), following Greenwood et al. (1966) and Rosen and Patterson (1969), recognized two additional suborders that are now excluded—the Ophidioidei (= Ophidiiformes) and Zoarcoidei. Although there is general agreement on the monophyly of Gadiformes with its present composition, there is disagreement on its classification as revealed in various studies (e.g., Cohen, 1989; Endo, 2002; von der Heyden and Mathee, 2008; Roa-Varón and Ortí, 2009; Grande et al., 2013; Betancur-R. et al., 2013a).

Two of the most recent and comprehensive phylogenetic works and classifications are that of Endo (2002) based exclusively on morphology (with non-zeiform outgroups but some percopsiforms) and that of Roa-Varón and Ortí (2009) based on molecular data (with zeiform, percopsiform, *Polymixia* outgroups). Although both studies support the monophyly of Gadiformes as well as the monophyly of most subgroupings, the two studies differ significantly with respect to within-gadiform relationships. For example, Endo (2002) recovered Melanonoidei, consisting only of Melanonidae, as the basal gadiform, sister to Macrouroidei + Gadoidei, while Roa-Varón and Ortí (2009) reported a Gadiformes consisting of a trichotomy among Muraenolepidoidei (i.e., Muraenolepididae), Macrouroidei and Gadoidei. The basal gadiform group was suggested to be Muraenolepidoidei, but could not be resolved with confidence, and the other major clades were only weakly supported. All of the families and several subfamilies that are currently recognized (e.g., Endo, 2002; Nelson, 2006) were recovered as monophyletic. Here we follow Endo (2002), except for the few clades that are strongly supported by molecular evidence.

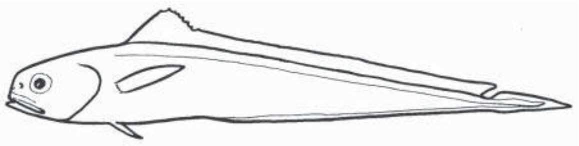
The fossil record of gadiforms and their relatives is discussed in several chapters in Cohen (1989), and Kriwet and Hecht (2008). The oldest skeletal fossils of any gadiform are a macrourid of Paleocene age from Antarctica (Kriwet and Hecht, 2008).

Thirteen families, 84 genera, and about 613 species. Only one species (*Lota lota*) is confined to fresh water, while a second species (*Microgadus tomcod*) has some populations that are confined to fresh water.

Suborder Melanonoidei. Supraoccipital excluded from margin of foramen magnum; unique cranial neuromast pattern and innervation consisting of numerous fang-like structures on the skin, innervated by the ramus canalis lateralis via a complex nerve network; anteriorly positioned brain with the telencephalon and anterior part of mesencephalon being anteriorly displaced beyond the cranial vault thus lying in the orbital cavity formed by pterosphenoids; enlarged pterosphenoids contacting the lateral ethmoids (Howes, 1993; Endo, 2002; Wiley and Johnson, 2010).

One family with one genus and two species.

Family MELANONIDAE (240)—pelagic cods. Marine, bathypelagic; Atlantic, Indian, Pacific, and subantarctic.



Intercalar small, single long-based dorsal fin with 72–78 rays; anal fin with 50–58 rays; barbel absent; otophysic connection absent, vertebrae 58–62. Maximum length 15 cm.

One genus, *Melanonus*, with two species.

Suborder Macrouroidei. Transverse median process of pelvic girdle extended almost transversally, facing its contralateral member in the midline (Endo, 2002). According to Endo (2002) members of the suborder also lack caudal fin skeletons, but this conclusion may hide complexity given that at least in some larvae and juveniles for some of these groups (eg. *Steindachneria*; Fahay, 1989), caudal elements are present although their homology is unidentified.

Four families, about 36 genera, and at least 395 species.

Family STEINDACHNERIIDAE (241)—luminous and southern hakes. Marine; Gulf of Mexico, Caribbean, and Guianan shelf off northeastern South America.

Anus between pelvic fins and far forward of urogenital pore, which is immediately anterior to the anal fin (in larvae the anus is near the origin of the anal fin); elaborate light organ system on head and body; nostrils nearer to eye than to tip of snout; vomerine teeth arranged in a single U-shaped row; first dorsal fin with one spine and 7 to 9 rays; second dorsal fin with 123 or more rays; anal fin with 123 to more than 125 rays; pectoral fins with 14–17 rays; caudal fin and skeleton extremely reduced, tail tapering to a fine point.

One species, *Steindachneria argentea.*

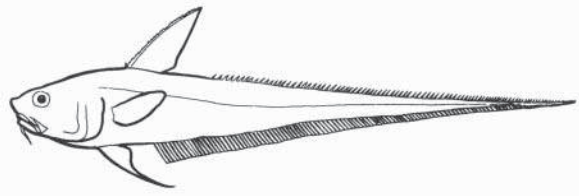
Family BATHYGADIDAE (242)—rattails. Nearly worldwide, tropical to subtropical seas, except the eastern Pacific; depths primarily 200–2,700 m.

Second dorsal fin rays longer than those of anal fin, starting close behind first dorsal fin; mouth wide and terminal; snout rounded; 7 branchiostegal rays; abdominal vertebrae 11–13; scales without spinules. Maximum length 65 cm.

Bañón et al. (2013) revised Bathygadidae from the eastern North Atlantic.

Two genera, *Bathygadus,* with the chin barbel small to absent (13 species), and *Gadomus,* with a distinct barbel (13 species). Scale fossils of †*Palaeobathygadus* were reported from the Oligocene of California, and of †*Probathygadus* from Oregon by David (1956). †*Bolbocara* is known by skeletal fossils from the Miocene of California (Jordan, 1927).

Family MACROURIDAE (Coryphaenoididae) (243)—grenadiers (rattails). Marine; deepwater, Arctic to Antarctic.



First dorsal fin short with a spike-like first ray closely followed by a spinous second ray and 7 to 12 soft rays; second dorsal-fin rays much shorter than those of anal fin, a gap between its origin and that of first dorsal fin; mouth terminal to subterminal; teeth variable from fang-like to minute villiform bands; branchiostegal rays 6 or 7; abdominal vertebrae 10–15; scales with spinules in most species; ventral light organ in many species; barbel present or absent. Basically worldwide except absent in high Arctic. Maximum length 150 cm, attained in *Albatrossia pectoralis.*

About 29 genera (e.g., *Albatrossia, Cetonurus, Coelorinchus* (synonym *Coelorhynchus*), *Coryphaenoides, Hymenocephalus, Hymenogadus, Lepidorhynchus, Lucigadus, Kumba, Macrourus, Malacocephalus, Mataeocephalus, Mesobius, Nezumia, Odontomacrurus, Pseudonezumia* (synonym *Paracetonurus*), *Sphagemacrurus, Trachonurus* and *Ventrifossa*) and about 364 species (e.g., Cohen et al., 1990; Iwamoto and Williams, 1999; Merrett and Iwamoto, 2000; Iwamoto, 2003; Satoh et al., 2006; McMillan et., al 2012). Many new species continue to be described.

Family TRACHYRINCIDAE (244)—whiptails and trachyrincines. Marine, most oceans. Two subfamilies, four genera, nine species.

SUBFAMILY MACROUROIDINAE (WHIPTAILS). Basically worldwide in tropical to temperate waters, bentho- to bathypelagic. Single low dorsal fin; mouth subterminal; head enlarged; chin barbel absent; seven branchiostegal rays; pelvic fins either rudimentary with 5 rays or absent; no light organ;. Maximum length 40 cm.

Two monotypic genera, *Macrouroides inflaticeps* (pelvic fin absent) and *Squalogadus modificatus* (small pelvic fin of five rays).

SUBFAMILY TRACHYRINCINAE (TRACHYRINCINES). Almost worldwide in temperate waters. Second dorsal-fin rays usually somewhat longer than those of anal fin, starting close behind first dorsal fin; mouth wide and subterminal; snout long and pointed; prominent fossa in temporal region; seven branchiostegal rays; body scales spinous; a row of keeled scutes along dorsal and anal fins; pelvic-fin rays 3 to 4 in *Idiolophorhynchus* and 6 to 7 in *Trachyrinchus*; abdominal vertebrae 14; no light organ. Maximum length 60 cm.

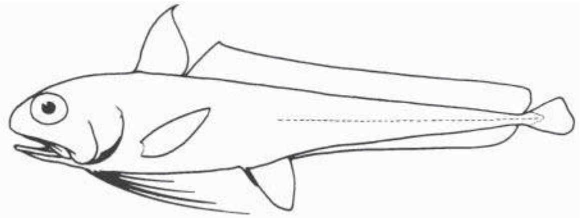
Two genera, the monotypic *Idiolophorhynchus andriashevi*, lacking a chin barbel, and *Trachyrincus*, with six species having a small barbel.

Suborder Gadoidei. Presence of X and Y bones in the caudal skeleton (Endo, 2002; Grande et al., 2013; Borden et al., 2013).

Eight families, 57 genera at least 282 species.

THE FOLLOWING FOUR FAMILIES (i.e., Euclichthyidae, Moridae, Macruronidae, Merlucciidae) are *incertae sedis* within Gadoidei.

Family EUCLICHTHYIDAE (245)—eucla cod. Marine; benthopelagic off New Zealand and Australia.



Two dorsal fins, nearly contiguous, the first high and with a short base of 12–15 rays and the second extending to base of the caudal fin with 74–77 rays; anal fin long, with large anterior lobe of about 15 rays and the remainder with about 77 rays; no chin barbel; pelvic fins under head and with four long rays, the longest reaching the anus; pelvic girdle inserted between the cleithra (it is farther back in almost all other gadiforms); caudal fin small but distinct, externally asymmetrical with rays of lower lobe extended; lateral ethmoid wing transversely convex (Howes, 1991); presence of lateral ethmoid suspensorial ligament (Howes, 1988); about 70 vertebrae. Maximum length about 35 cm.

One species, *Euclichthys polynemus* (Cohen et al., 1990).

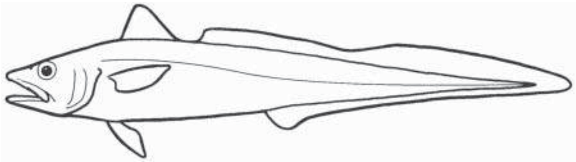
Family MORIDAE (246)—deepsea cods, codlings, hakelings. Marine, deep water; all seas (rarely in brackish water).

One or two, rarely three, dorsal fins; one or two anal fins; fins lacking spines; caudal fin always separate from dorsal and anal fins; spine of first vertebra tightly connected to a narrow crest at rear of skull; chin barbel present or absent; head of vomer toothless or with minute teeth; swimbladder in contact with auditory capsules (otophysic connection); light organ in some; vertebrae 41–72.

What appears to be a remarkable case of disjunct distribution occurs in *Halargyreus johnsonii*, a species with an antitropical distribution in the Atlantic and Pacific Oceans (Cohen et al., 1990).

Currently 18 genera (*Antimora*, *Auchenoceros*, *Eeyorius*, *Eretmophorus*, *Gadella*, *Guttigadus* (with junior synonym *Paralaemonema*), *Halargyreus*, *Laemonema*, *Lepidion*, *Lotella*, *Mora*, *Notophycis*, *Physiculus*, *Pseudophycis*, *Rhynchogadus*, *Salilota*, *Svetovidovia*, and *Tripterophycis*) with about 108 species (e.g., Cohen et al., 1990; Long and McCosker, 1998).

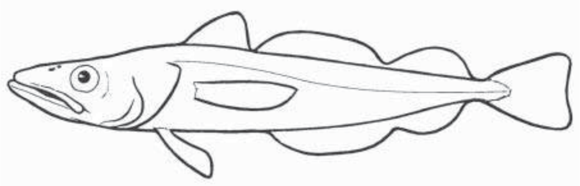
Family MACRURONIDAE (247)—southern hakes. Marine; Atlantic and Southern Hemisphere (primarily off southern South Africa, southern South America, southern New Zealand, and southern Australia).



Body elongate, strongly compressed; retroarticular with anteroventral prolongation; prootic forms a wall across midline; adductor arcus palatini originates from the ventral palatine fossa. Pectoral fin high on body, level with eye.

Three genera, *Lyconus, Macruronus,* and *Lyconodes,* with about seven species. *Lyconodes argenteus* is perhaps extinct. It should be noted that, based on mtDNA (regions of COI and Cyt*b*), von der Heyden and Matthee (2008) resurrected the family Lyconidae, consisting of *Lyconus pinnatus* and *L. brachycolus*, and assigned it as sister to Macruronidae. Additional work is needed to test this relationship.

Family MERLUCCIIDAE (248)—merlucciid hakes. Marine; Atlantic (both sides and including the Mediterranean Sea and parts of the Black Sea), southwesternmost Indian, eastern Pacific (from British Columbia to tip of South America), and New Zealand.



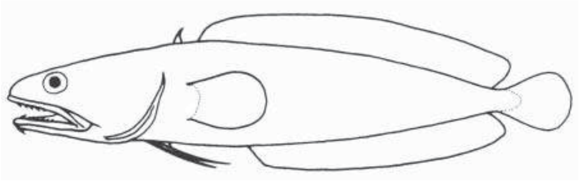
Two dorsal fins, first with 8–13 rays (first principal dorsal ray is spinous—a pseudospine) and second notched and with 34–46 rays; anal fin with 35–46 rays, notched; caudal fin separate from dorsal and anal fins; no chin barbel; mouth terminal, large, and with long teeth; teeth on head of vomer, none on palatines; seven pelvic rays; seven branchiostegal rays; no pyloric caeca; anus and urogenital pore close together; enlarged vertebral parapophyses; medial prootic shelves forming a pseudo-posterior myodome; lateral-line scales 101–171; vertebrae 48–58.

The common names usually applied to various species of *Merluccius* throughout the world are hake and whitings. However, as is often the case with common names, they are also variously applied to species of other families (e.g., hake for the phycid *Urophycis*; whiting for some other gadiforms and for sillaginids).

One genus, *Merluccius*, with 16 species (Cohen et al., 1990; von der Heyden et al., 2007; Machado-Schiaffino et al., 2009; Siva-Segundo et al., 2011). Fossils include the Eocene †*Rhinocephalus* from Britain, and the Oligocene †*Merluccius errans* from the Caucasus.

Superfamily Gadoidea. We recognize Ranicipitidae, Bregmacerotidae, and Gadidae, the latter with four subfamilies. All families were observed to have X and Y bones (Borden et al., 2013). 24 genera and at least 80 species.

Family RANICIPITIDAE (249)—tadpole cods. Marine, shallow coastal waters; northeastern Atlantic, Norwegian coast to British Isles and Bay of Biscay. IUCN Red Listed as a threatened species (Fernandes et al., 2014).

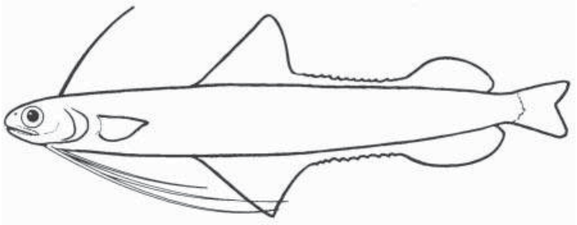


Two dorsal fins, the first with three short rays; one anal fin, base long and fin not indented; anteriorly inclined hyomandibular head without pores or lateral line; upper jaw protruding past lower; chin barbel present. Maximum length about 30 cm.

Recognition of *Raniceps* at the family level in Nelson (1994) and as the sister group to the remaining gadiforms followed D. F. Markle in Cohen (1989). On the other hand, Howes in Cohen (1989), Endo (2002), Roa-Varón and Ortí (2009), and Grande et al. (2013) considered it to be a relatively advanced gadiform.

One species, *Raniceps raninus*.

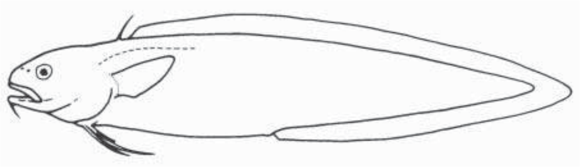
Family BREGMACEROTIDAE (250)—codlets. Marine, rarely in estuaries; tropical and subtropical seas.



Two dorsal fins and one long anal fin (first dorsal fin on nape and consisting of one elongate ray, second dorsal and anal fins with large notch in middle); chin barbel absent; dorsal maxilla-premaxillary ligament absent; scales relatively large, 40–89 along side; head of vomer toothed; plate on epibranchial 3 toothless; postcleithrum with a mid-posterior expansion; pelvic fins under head and with five rays, outer three as elongate free filaments; lateral line for most of its length extending along dorsal margin of body; a few pyloric caeca; swimbladder not in contact with auditory capsules; 43–59 vertebrae. Maximum length about 12 cm.

One genus, *Bregmaceros*, and about 14 species (Harold and Johnson, 2003; Torii et al., 2003, 2004). Fossils of *Bregmaceros* occur in the Miocene of the Caucasus and the Pliocene of Italy.

Family MURAENOLEPIDIDAE (251)—eel cods and moray cods. Marine; Southern Hemisphere, cold temperate, primarily Antarctic, continental shelf.



Caudal fin connected with anal and second dorsal fins; two dorsal fins, the first with only one or two rays and the second with 127–141 rays, and one anal fin with 98–112 rays; gill openings narrow, extending upward only to level of pectoral bases; pectoral radials 10–13 (usually four in other gadiforms); pectoral fin rays 37 or 38; chin barbel present; head of vomer toothless; pyloric caeca absent; vertebrae 67–85. Maximum length 40 cm. X and Y bones were reported by Endo (2002) in *Muraenolepis*. This observation was not confirmed by Grande et al. (2013).

Two genera, *Muraenolepis* (8) and *Notomuraenobathys* (1) with nine species.

Family GADIDAE (252)—cods. Marine with one Holarctic freshwater species; Arctic, Atlantic, and Pacific.

First dorsal fin posterior to head; head of vomer toothed; swimbladder not connected with auditory capsules. Maximum length about 1.8 m, attained by the Atlantic *Gadus morhua*.

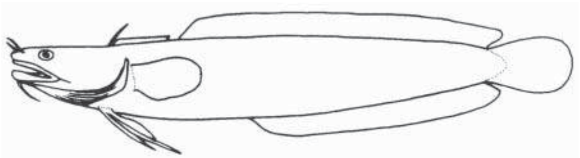
Four subfamilies, 20 genera and about 56 species. The area of greatest diversity is the Atlantic. Fossil gadids are common from the Oligocene and later.

Endo (2002) recognized four subfamilies in Gadidae as follows: Phycinae, Gaidropsarinae, Lotinae, and Gadinae. This taxon composition is supported by Teletchae et al. (2005), Roa-Varón and Ortí (2009), Grande et al. (2013), and Betancur-R. et al. (2013a). There is general agreement that the subfamily Gadinae, as recognized here, is the most advanced taxon in the order.

Subfamily Phycinae (phycid hakes). Atlantic (including the Gulf of Mexico and Mediterranean). Two dorsal fins, first with 8–13 rays and second with 43–68 rays; one anal fin; pelvic fin with two highly elongated rays; no barbels on snout (but chin barbel present).

Two genera, *Phycis* with three species and *Urophycis* with 8 species.

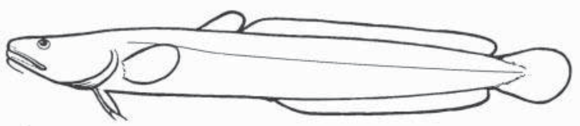
Subfamily Gaidropsarinae (rocklings). Primarily from the northern Atlantic, including the Mediterranean, but also in the Southern Hemisphere (e.g., off New Zealand and Tasmania). Three dorsal fins barely separated from each other (the first with a single thickened unsegmented ray; the second with small, unsegmented rays in a fleshy ridge that rises within a groove; and the third with segmented rays in an elongate fin); 2–4 prominent individual barbels on snout (rudimentary barbels may also be present), in addition to the one at the tip of the lower jaw.



Gaidropsarines have often been included within the Lotinae.

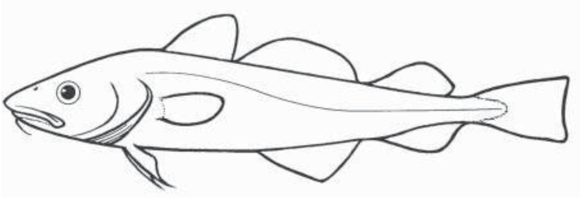
Three genera, *Gaidropsarus* (13), *Ciliata* (3), and *Enchelyopus* (1), with 17 species.

Subfamily Lotinae (Burbot, Cusk, and lings). Marine and freshwater; North Atlantic region. One or two dorsal fins and one anal fin; chin barbel always present but no barbels on snout; caudal fin rounded; egg with oil globule; X and Y bones secondarily lost.



Three genera, *Brosme* (1), *Lota* (1), and *Molva* (3), with five species. *Brosme brosme*, the Cusk or Tusk, lives in the North Atlantic off Canada, Greenland, Iceland, and northern Europe. *Lota lota*, the Burbot, is found in the northern parts of Eurasia and North America, and is the only completely freshwater member of the Gadiformes. The three species of *Molva* (lings) occur in the coastal regions of the northern North Atlantic, including the Mediterranean, and the Arctic.

Subfamily Gadinae (cods and haddock). Arctic to temperate waters of the Northern Hemisphere. Three dorsal fins and two anal fins; chin barbel usually present; X and Y bones secondarily lost; caudal fin truncate or slightly forked; egg without an oil globule. Very important commercially.



Microgadus tomcod of the Atlantic coast of North America can spawn in fresh water, and some freshwater populations are known. *Boreogadus* and *Arctogadus* are found with Arctic sea ice; the former can also be found in Arctic estuaries and lagoons. Evolution of geographical and ecological distributions of the Gadinae was investigated by Owens (2015).

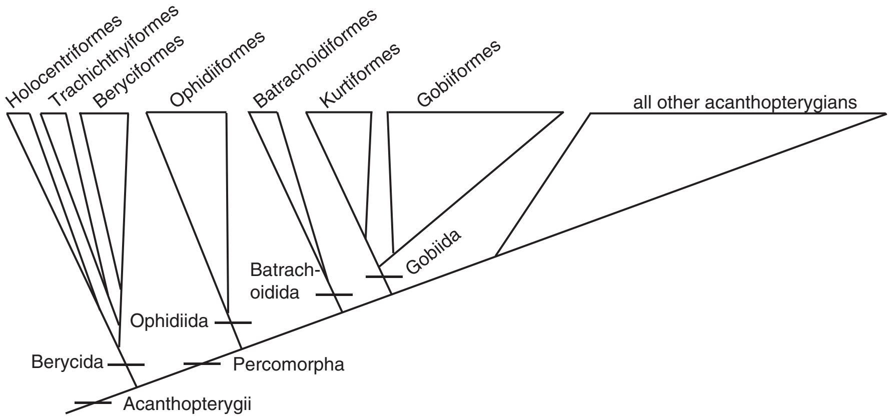
Twelve genera, *Arctogadus*, *Boreogadus*, *Eleginus*, *Gadiculus*, *Gadus*, *Melanogrammus*, *Merlangius*, *Microgadus*, *Micromesistius*, *Pollachius*, *Theragra*, and *Trisopterus*, with about 23 species.

Superorder ACANTHOPTERYGII

Greenwood et al. (1966) gave equal rank to the Atherinomorpha and their Acanthopterygii. Rosen and Patterson (1969) combined them under the taxon Acanthopterygii, and Rosen (1973a) defined the latter by the loss, reduction or migration of insertion of the posterior bundle of the retractor arcuum branchialium muscle so that the RAB inserts on the third pharyngobranchial, and the reduction of the articular surface of the fourth epibranchial with the enlargement of the second and third epibranchials as principal supports of the upper pharyngeal dention. As described by Lauder and Liem (1983), acanthopterygians have a more mobile upper jaw than the teleosts below this level (except for the Lampriformes). This is due largely to the presence of a well-developed ascending process on the premaxilla. There is a secondary loss of the forward movement of the jaw (protrusibility) in several acanthopterygian lines. In most actinopterygians, Baudelot's ligament (the ligamentous support of the pectoral skeleton attached to the supracleithrum) originates on the basioccipital. In stephanoberyciforms and a very few derived acanthopterygians (e.g., agonids, champsodontids, and some zoarcoids), Baudelot's ligament originates on the first vertebra (Johnson and Patterson, 1993; Wiley and Johnson, 2010).

Within the actinopterygians, Johnson and Patterson (1993) recognized a novel set of interrelationships. They regarded the Stephanoberyciformes as the most basal acanthopterygian, followed by the Zeiformes and Beryciformes, as the first three sequential branches of acanthopterygians. In addition, they recognized a new taxon Smegmamorpha: comprised of Synbranchiformes, Mugilomorpha, Elassomatidae, and Gasterosteiformes in an unresolved polytomy. The smegmamorphs were diagnosed by one character (i.e., the first epineural originating at the tip of a transverse process on the first vertebra). Smegmamorpha, Scorpaeniformes, and higher taxa composed the Percomorpha of Johnson and Patterson (1993). Smegmamorpha were a controversial group from the onset. Many morphologists doubted their monophyly, and the early molecular studies of Wiley et al. (2000), Roe et al. (2002), Miya et al. (2003), and Chen et al. (2003) failed to support its monophyly.

Here we do not recognize the Smegmamorpha, and the basal groups within the Acanthopterygii differ somewhat in contents and significantly in their relationships from those in Johnson and Patterson (1993).



Major clades within Acanthopterygii are here recognized at the rank of series and sequenced to indicate probable relationships.

Some 34 orders, 284 families, 2,422 genera, and 14,797 species (24% limited to freshwater).

Series BERYCIDA. The series Berycida includes three orders: Holocentriformes (Holocentridae), Trachichthyiformes (Anoplogastridae, Diretmidae, Anomalopidae, Monocentridae, Trachichthyidae), and Beryciformes (berycoids and stephanoberycoids). This group was suggested to be monophyletic by Near et al. (2012a) but was paraphyletic in Betancur-R. et al. (2013a) and Chen et al. (2014). There are no known stem-group fossils of Berycida, but the crown-group fossil record begins in the early Cenomanian (early Late Cretaceous); key fossils are mentioned below.

Three orders, 14 families, 52 genera, and at least 255 species.

Order HOLOCENTRIFORMES (52)—squirrelfishes. For characters see the Holocentridae and its subfamilies. One family with two subfamilies, 8 genera and 83 species.

Fossil genera include the Late Cretaceous †*Alloberyx*, †*Caproberyx*, †*Paracentrus*, and †*Trachichthyoides*. Cenozoic fossils include †*Africentrum*, †*Berybolcensis*, †*Eoholocentrum*, †*Holocentrites*, and †*Tenuicentrum*. Gallo-Da-Silva and De Figueiredo (1999) included the Cretaceous †*Pelotius hesselae* in the Holocentriformes because of the presence of four spines in the anal fin, seven pelvic-fin rays and two dorsal fins.

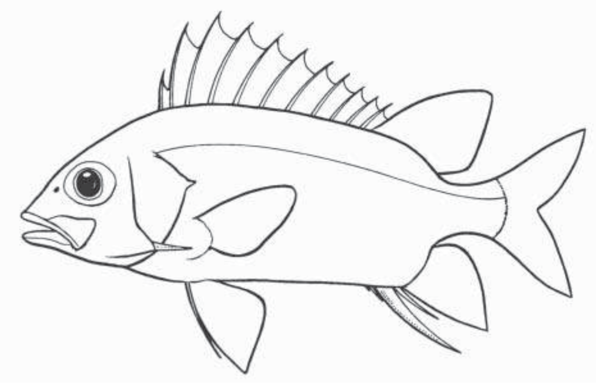
Family HOLOCENTRIDAE (253)—squirrelfishes. Tropical marine; Atlantic, Indian, and Pacific.

Pelvic fin with one spine and 5–8 (usually seven) soft rays; long dorsal fin with spiny portion (10–13 spines) and soft-rayed portion (11–17 rays) divided by a notch; anal fin with four spines and 7–16 soft rays; caudal fin forked, with 18 or 19 principal rays; scales large and ctenoid (extremely rough); eyes large; opercle with spiny edge; vertebrae 26 or 27; color usually reddish.

Squirrelfishes are mostly nocturnal, usually hiding in crevices or beneath ledges of reefs in the daytime (along with cardinalfishes, bigeyes, and sweepers). Most species occur between the shoreline and 100 m, rarely over 200 m. Adults tend to remain close to the bottom. Maximum length about 61 cm, attained in *Sargocentron spinifer.*

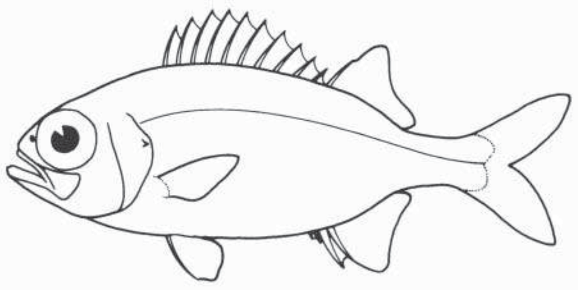
Two monophyletic subfamilies (e.g., Dornburg et al., 2012), eight genera and about 83 species (e.g., Kotlyar, 1996; Randall, 1998; Randall and Greenfield, 1996; Randall and Yamakawa, 1996; Greenfield, 2003).

Subfamily Holocentrinae (squirrelfishes). A strong spine present at angle of preoperculum (sometimes a toxin is associated with this spine); longest anal spine usually longer than or equal to longest dorsal spine; anal-fin soft rays 7–10; swimbladder tubular, extending entire length of body (contacting the skull in a few species).



Three genera and 40 species—*Flammeo* (1), *Holocentrus* (2), *Neoniphon* (4), and *Sargocentron* (33).

Subfamily Myripristinae (soldierfishes). No enlarged preopercular spine (except in the Atlantic *Corniger spinosus*, which has two enlarged spines at the corner of the preopercle); longest anal spine usually shorter than longest dorsal spine; anal-fin soft rays 10–16; swimbladder constricted in anterior third to form two more or less separate chambers (anterior section with two anterolateral projections).



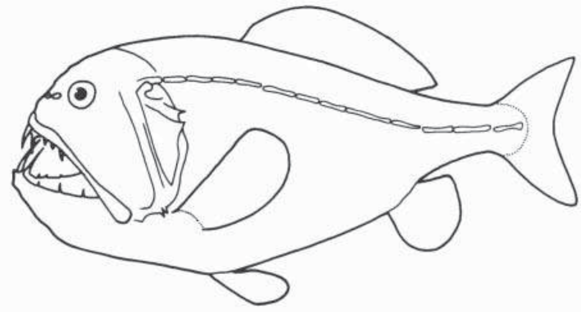
Five genera and 43 species—*Corniger* (1), *Myripristis* (28), *Ostichthys* (11), *Plectrypops* (2), and *Pristilepis* (1).

Order TRACHICHTHYIFORMES (53)—roughies. The recognition of this clade with the subclades given below is based on the cladogram of Moore (1993). According to Moore (1993), diagnostic characters of Trachichthyiformes (his Trachichthyoidei) include a distinctive X pattern of frontal ridges; presence of complete bony arches over the lachrymal and at least infraorbital three; and a small ethmoid confined to the area between the dorsomedial portions of the lateral ethmoids. Baldwin and Johnson (1995) and Konishi and Okiyama (1997), based on larval characters, supported the monophyly of this group.

Five families, 20 genera, and about 68 species.

Suborder Anoplogastroidei. Spines present on parietals, frontals, and preoperculum of larva. Two families.

Family ANOPLOGASTRIDAE (254)—fangtooths. Marine, bathypelagic; Atlantic, Indian, and Pacific.



Body short, deep, and compressed; numerous long fang-like teeth on jaws in adults; eye small, diameter less than snout length; scales small or minute;

lateral line an open groove (partly covered by scales); fins without spines, dorsal with 16–20 rays and anal usually with 7–9 rays; pelvic fin with seven soft rays, the first unbranched; pectoral fin with 13 to 16 rays; Baudelot's ligament absent; subocular shelf absent, but instead there is a distinctive thickening of the entire upper portion of the third infraorbital where the shelf would normally be found (Moore, 1993); neural spines steeply slanted; vertebrae 25–28. Maximum length about 16 cm.

One genus, two species, *Anoplogaster cornuta* and *A. brachycera* (Kotlyar, 1996, 2003; Moore, 2003).

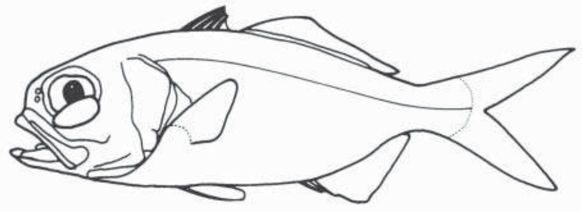
Family DIRETMIDAE (255)—spinyfins. Marine; Atlantic, Indian, and Pacific.

Eyes very large; jaws do not extend behind eye; one supramaxilla; no lateral line; dorsal and anal fins without spines, dorsal rays 24–30 and anal rays 19–22; pelvic fin with laminar spine and six soft rays; sharp edge to abdomen formed by ventral scutes; branchiostegal rays seven or eight; vertebrae 20–32. Maximum length 37 cm.

Three genera, *Diretmichthys* (1), *Diretmoides* (2), and *Diretmus* (1), with four species (Kotlyar, 1996; Moore, 2003).

Suborder Trachichthyoidei. Neural arch of second preural centrum unfused; absence of the fourth pharyngobranchial toothplate. Three extant families and one extinct.

Family ANOMALOPIDAE (256)—flashlight or lanterneye fishes. Marine; scattered warm-water localities, primarily Indo-Pacific.



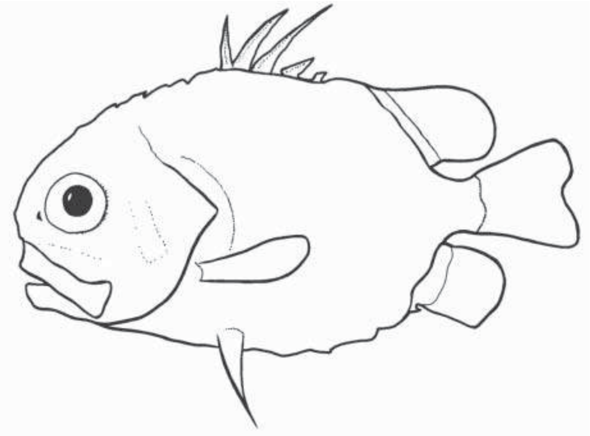
Luminous organ with symbiotic bacteria beneath eye with rotational and shutter mechanism for controlling light emission (hence the common name, lanterneye or flashlight fishes); pelvic fin with one spine and five or six soft rays; dorsal fin with 2–6 spines and 14–19 soft rays, spinous and soft portions continuous (*Photoblepharon* only) or with notch; anal fin spines two or three and soft rays 10–13; short subocular shelf; vertebrae 25–30. Blinking action of the light organ assists in avoiding predation and is controlled by rotation of the luminous organ downward, erection of a black membrane over it, or by both mechanisms (Johnson and Rosenblatt, 1988). Maximum length about 27 cm, attained by the planktivore, *Anomalops katoptron*. Also known as lanterneye fishes.

Six genera—the western Pacific *Anomalops* (1), Indo-West Pacific *Photoblepharon* (2), the Caribbean *Kryptophanaron* (1), the Pacific *Parmops* (2, known from Fiji and Tahiti), and the eastern Pacific *Phthanophaneron* (1, the Gulf of California), and the South Pacific *Protoblepharon* (2, from off Rarotonga, Cook Islands and eastern Taiwan)—with nine species (Kotlyar, 1996; Baldwin et al., 1997; Johnson and Rosenblatt, 1988; Johnson et al., 2001; Moore, 2003; Ho and Johnson, 2012).

†Family PSEUDOMONOCENTRIDAE (Pseudomonocentrididae). Marine; Muhi quarry, Zimapan, State of Hidalgo, Mexico; El Doctor Formation; Albian/Cenomanian, mid-Cretaceous. Body covered with large, heavy plate-like scales. Pelvic and anal fins each with one large spine; dorsal-fin spines appear to be absent; ornamented dermosphenotic fused with the autosphenotic; large opercle sutured with a small, narrow subopercle; ossified sclerotic bones absent; supramaxillary bone absent. These are among the oldest known fossil acanthomorphs. If the fossil beds from which they came are Albian rather than Cenomanian, they will represent the oldest fossil acanthomorphs.

Two monotypic genera †*Handuichthys interopercularis* and †*Pseudomonocentris microspinosus*. Although these two fossil species have monocentrid-like characters, González-Rodríguez et al. (2013) placed them in their own family. A third armored genus from the same deposit, †*Dalgoichthys*, was placed as Acanthomorpha *incertae sedis* (González-Rodríguez et al. 2013).

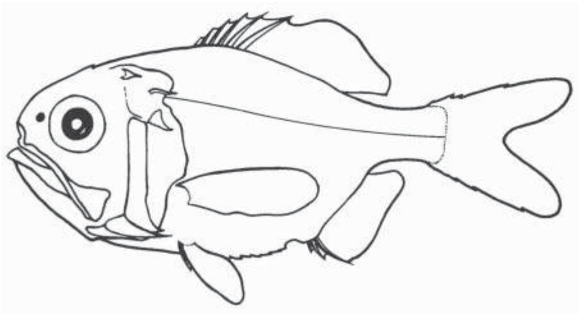
Family MONOCENTRIDAE (Monocentrididae) (257)—pinecone fishes. Marine; tropical and subtropical, Indian and Pacific. They occur primarily at depths of 30–300 m.



Body covered with large, heavy plate-like scales; phosphorescent (luminous bacteria) light organs on lower jaw; pelvic fin with one large spine and two to four small soft rays; two dorsal fins, the first with 4–7 strong spines alternating from side to side and the second with 9–12 soft rays; anal fin with 10–12 soft rays (no spines); pectoral fin with 13–15 rays; branchiostegal rays eight. Maximum length about 21 cm. According to Moore (1993) only Monocentridae and Trachichthyidae have a subocular shelf restricted to the third infraorbital.

Two genera, *Cleidopus* (1) and *Monocentris* (3), with four species (Kotlyar 1996).

Family TRACHICHTHYIDAE (258)—roughies. Marine; Atlantic, Indian, and Pacific at about 100–1,500 m, mostly in deep water.



Distinct spine at angle of preopercle; posteriorly pointing spine on posttemporal bone (also found in *Centroberyx*); pelvic fin with one normal spine and six or seven soft rays; dorsal fin with 3–8 spines and 10–19 soft rays; anal fin with two or three spines and 8–12 soft rays; caudal fin usually with 4–7 procurrent spines on each lobe; abdomen with median ridge of scutes; scales variable between species (e.g., thick and spiny to thin and cycloid); body very deep in the Australian *Trachichthys* and the widespread *Gephyroberyx* and *Hoplostethus* (shown in figure) to only moderately deep; some species with luminescence. Maximum length about 55 cm.

Some members of this family are called roughies, such as the widespread Orange Roughy, *Hoplostethus atlanticus*, which has been important in the commercial fisheries in many areas but because recruitment is slow, stock depletion easily occurs. Others are called slimeheads. Late Cretaceous fossils include †*Antarctiberyx* from Antarctica described by L. Grande and Chatterjee in 1987, †*Lissoberyx* from Italy described by L. Taverne in 2003, and †*Hoplopteryx* from Britain and Lebanon (Forey et al., 2003).

Eight genera, *Aulotrachichthys* (8), *Gephyroberyx* (2), *Hoplostethus* (30), *Optivus* (3), *Paratrachichthys* (3), *Parinoberyx* (1), *Sorosichthys* (1), and *Trachichthys* (1), with about 49 species (e.g., Kotlyar, 1995 1996; Moore, 1993, 2003).

Order BERYCIFORMES (54)—beryciforms. Although we do not exclude Holocentriformes from the Berycida (see above), we do combine the trachichthyoids, stephanoberycoids, and the berycoids in one clade (e.g., Betancur et al., 2013a), as the second and third orders in the sequence (Holocentriformes, Trachichthyiformes, and Beryciformes). Subgroups of Beryciformes are arranged mostly following Moore (1993).

Beryciformes have two suborders (Stephanoberycoidei and Berycoidei), eight families, about 24 genera, and 104 species.

Suborder Stephanoberycoidei—prickle-fishes. Body usually roundish; palate toothless; skull bones, in general, exceptionally thin; orbitosphenoid absent (except present in *Hispidoberyx*); subocular shelf absent; supramaxilla absent or reduced; extrascapula, when present, greatly enlarged, partially or entirely covering the parietal (Johnson and Patterson, 1993; Wiley and Johnson, 2010); abdominal haemal arches absent; exoccipital facets widely separated and not contacting each other such that the foramen magnum is at the dorsal margin of the basioccipital facet; dorsal fin originating posterior to the midbody and opposite the anal fin (Moore, 1993).

In Nelson (2006) this group had ordinal status and contained the family Melamphaidae. However multiple molecular studies (e.g., Betancur et al., 2013a) place the Melamphaidae as the sister group of the Berycidae.

Moore (1993) included all the stephanoberyciforms and most of the beryciforms (but not the Berycidae or the Holocentridae) in his order Trachichthyiformes (including the one-time lampridiform but later stephanoberyciform taxa Mirapinnidae and Megalomycteridae, now both synonymized with Cetomimidae), on the basis of the following characters: ocular sclera absent (most other acanthomorphs have two ossified sclera circling the eyeball); neural arch of first vertebrae fused to underlying centrum; one (the posterior) supramaxilla. Johnson and Patterson (1993), however, argued that the Trachichthyiformes as recognized by Moore (1993) were paraphyletic. Instead, they recognized the Stephanoberyciformes as the sister group to all remaining acanthomorphs and placed the Trachichthyoidei of Moore (1993) with the Berycidae and Holocentridae, recognizing the resulting group (minus stephanoberyciforms) as the Beryciformes. Their beryciforms were the third clade to diverge within acanthomorphs (zeiforms were second). Colgan et al. (2000) questioned the monophyly of the Stephanoberyciformes based on DNA sequences.

More recently, Near et al. (2012a) recovered a group (labeled Beryciformes) with three clades each composed of a few representatives of the three orders of the present work, but with the relationships (stephanoberyciforms (holocentriforms, beryciforms)). With weak nodal support but better taxon sampling, Betancur-R. et al. (2013a) removed holocentriforms from Beryciformes but recovered separate clades of beryciforms corresponding to stephanoberycoids and berycoids. Chen et al. (2014), sampling only a few species, recovered the relationships (trachichthyiforms (stephanoberycoids, berycoids), (holocentroids, higher acanthomorphs)).

Clearly these molecular results are not yet converging on a consensus. In view of the continuing uncertainties, especially concerning the relationships of holocentriforms, we here combine stephanoberycoids and berycoids in a single order and follow mostly Moore's (1993) arrangement of the stephanoberycoid families.

Six families with about 17 genera and about 31 species (with many undescribed species). All species are marine.

Superfamily Stephanoberycoidea. Following Moore's (1993) study, the Stephanoberycoidea (unnamed in Moore 1993) have the following character: Y-shaped frontal crest pattern. Nelson (2006) placed Gibberichthyidae close to Rhondeletiidae within Cetomimoidea following Paxton's (2001). Here we revert to Moore's grouping pending stronger evidence to the contrary.

Three families, 6 genera and 7 species.

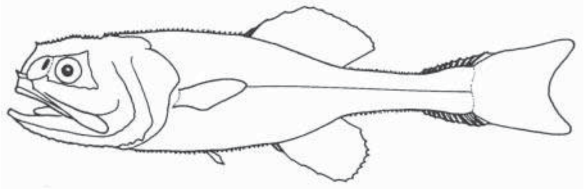
Family GIBBERICHTHYIDAE (259)—gibberfishes. Marine; tropical western Atlantic, western Indian, and western and southwestern Pacific.

Pectoral fins with 13 to 15 rays; pelvic fin subabdominal, with one spine and five or six soft rays (prejuvenile with elongate appendage off third pelvic ray); adults with semi-isolated series of 5–8 short spinous rays before soft dorsal fin and four or five before anal fin (about 7–9 soft rays in each fin); fusion of infraorbitals 2 + 3; scales cycloid, about 28–34 in lateral line; vertical rows of papillae on sides of body over the vertical lateral line tubes; swimbladder present and partially filled with fat; 28–31 vertebrae. Maximum length about 12 cm. Larvae have been found between near-surface waters and 50 m, while adults have been captured primarily between 400 and 1,000 m.

Kasidoron, once given family status (Kasidoridae), is the larva of *Gibberichthys pumilus.*

One genus, *Gibberichthys,* with two species known from relatively few specimens (Moore, 2003; Kotlyar, 1996, 2004b).

Family STEPHANOBERYCIDAE (260)—pricklefishes. Marine; tropical and subtropical western parts of Atlantic, Indian (off South Africa), and Pacific.



Spines, if any, in dorsal and anal fins, weak; each fin with about 10–14 soft rays; pelvic fin abdominal or subabdominal, with five soft rays, no spine; caudal fin with 8–11 procurrent spines (these precede the principal rays dorsally and ventrally); scales smooth or spiny; lateral line faint; 30–33 vertebrae.

Four monotypic genera: *Acanthochaenus* (Atlantic and off Durban, South Africa), *Abyssoberyx* (Northeast Atlantic), *Malacosarcus* (Pacific), and *Stephanoberyx* (Atlantic) (Moore, 2003; Kotlyar, 1996, 2004c; Merrett and Moore, 2005). All are known from relatively few specimens.

Family HISPIDOBERYCIDAE (261)—hispidoberycids. Marine; northeastern Indian Ocean and South China Sea.

Spinulose scales; operculum with a long, stout spine; palatine and vomerine teeth present; dorsal fin with four or five spines and 10 soft rays; anal fin with three spines and nine soft rays; pelvic fin with one spine and six or seven soft rays; lateral-line scales 32–34; vertebrae 34.

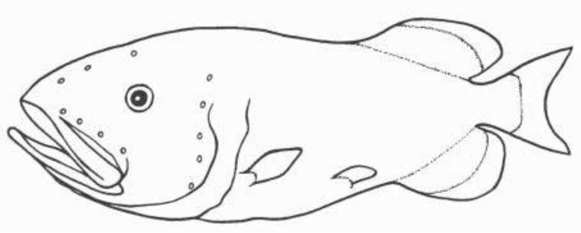
One species, *Hispidoberyx ambagiosus* (Kotlyar, 1996, 2004d).

Superfamily Cetomimoidea (whalefishes). Complete loss of fin spines. The taxonomic history of this group was reviewed in Nelson (1984) and Moore

(1993) and references therein. The current classification mostly follows the conclusions of Moore (1993), some of which were expressed by Rosen (1973a). The families Mirapinnidae and Megalomycteridae, placed in this superfamily by Nelson (2006), have since been synonomized with Cetomimidae (Johnson et al., 2009; see below). The families of whalefishes have the following features: body whale-shaped; mouth very large and stomach highly distensible; eyes well developed to degenerate; lateral line made up of enormous hollow tubes; dorsal and anal fins far back on body and opposite one another; no swimbladder; orbitosphenoid absent; supramaxilla absent or reduced; color usually orange and red on a black body. Bathypelagic. Length up to 39 cm.

Three families, about 11 genera, and about 24 species (e.g., Paxton, 1989; Moore, 1993; Paxton et al., 2001; Johnson et al., 2009).

Family RONDELETIIDAE (262)—redmouth whalefishes. Marine; oceanic.



Box-shaped head; skin smooth without external body scales; lateral line system composed of a number of pores in each of a series of 14–26 vertical rows; one dorsal fin with 13 to 16 soft rays; anal fin with 13 to 16 soft rays; pectoral fins with 9 to 11 rays; pelvics subabdominal with five or six rays; caudal fin with 19 principle rays, three epurals and six hypurals; vertebrae 24–27. Maximum length about 11 cm.

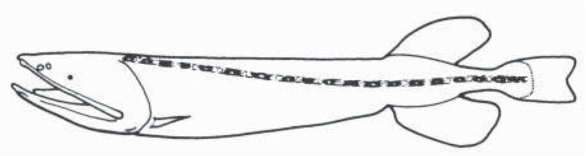
Two species, *Rondeletia bicolor* and *R. loricata* (e.g., Kotlyar, 1996; Paxton and Trnski, 2003).

Family BARBOURISIIDAE (263)—red (redvelvet) whalefishes. Marine; parts of Atlantic (including Gulf of Mexico where first found), Indian, and Pacific.

Mouth very large, jaws extending far behind eye; teeth small and closely set on jaws, vomer and ectopterygoid; palatine toothless; presence of 8 supraneurals anterior to the dorsal fin; presence of 7 infraorbitals, not counting the dermosphenotic. Fins without spines; pectoral fins with 13 or 14 rays; pelvic fins subabdominal, with six rays; skin spiny; dorsal-fin rays 19–22; anal-fin rays 15–18; vertebrae 40–43. Color reddish-orange. Maximum length 39 cm SL.

One species, *Barbourisia rufa* (Paxton and Bray in Smith and Heemstra, 1986; Paxton et al., 2001; Paxton, 2003).

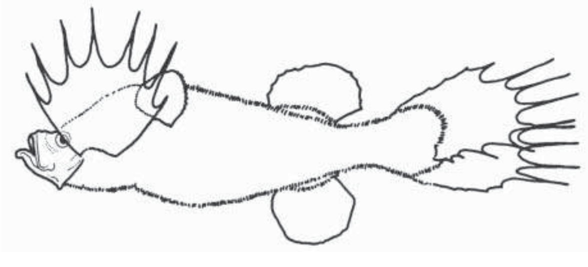
Family CETOMIMIDAE (264)—flabby whalefishes. Marine; oceanic.



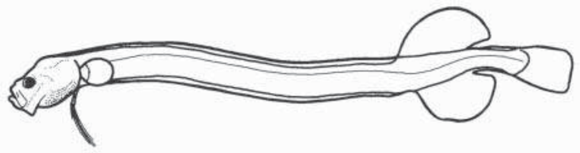
Pelvic fins absent; skin loose and scaleless; eyes reduced or rudimentary; three or four gills; no photophores present, but cavernous, glandular tissue of unknown function often present around anus and dorsal and anal-fin bases; pleural ribs absent; vertebrae 38–59. Live color brown or orange with brilliant orange or red jaws and fins. Maximum length 39 cm, attained in a species of *Gyrinomimus.*

Members of this family are second only to the anglerfish family Oneirodidae in being the most species-rich family in the bathypelagic zone (1,000 m–4,000 m) and may be the most abundant one below 1,800 m (Paxton, 1989). The cavernous tissue, at one time thought to secrete a luminous substance (Harry, 1952), is present in all genera except *Procetichthys* and *Rhamphocetichthys*, being most extensive in *Gyrinomimus*, *Cetomimus*, and *Ditropichthys* (Paxton, 1989).

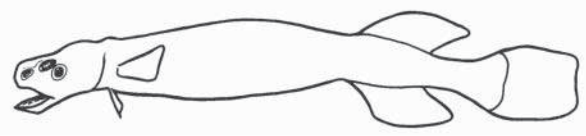
Nine genera, *Cetichthys* (2), *Cetomimus* (8), *Cetostoma* (1), *Danacetichthys* (1), *Ditropichthys* (1), *Gyrinomimus* (5), *Notocetichthys* (1), *Procetichthys* (1), and *Rhamphocetichthys* (1), with about 21 species (more undescribed), most known from only a few specimens (e.g., Paxton, 1989, 2003). The monotypic *Procetichthys*, with a large nasal organ and the eye with a lens in specimens over 10 cm (versus small nasal organ and eye without lens in specimens over 10 cm) is often placed in one subfamily and the other eight genera in second subfamily.



In a most interesting study by Johnson et al. (2009), the family Mirapinnidae (hairyfish, tapetails), and the family Megalomycteridae (bignose fishes) were found to be the larvae and males, respectively, of fishes within the family Cetomimidae known only from female specimens. In that study, *Mirapinna esau* (formerly in subfamily Mirapinninae, family Mirapinnidae) was determined to be the postlarval form of *Procetichthys kreffti* (figured above) and *Parataeniophorus bertelseni* (formally subfamily Eutaeniophorinae, family Mirapinnidae) is the larva of *Ditropichthys storeri* (figured below).



Molecular data also suggest that larval *Eutaeniophorus* (formerly subfamily Eutaeniophorinae, family Mirapinnidae) and the male *Ataxolepis* (formerly family Megalomycteridae) (figured below) are embedded within the genera *Cetomimus* and *Gyrinomimus*.



Based on the convincing evidence presented by Johnson et al. (2009) we agree with synonomizing the families Mirapinnidae and Megalomycteridae with Cetomimidae. Considerable work is still necessary to link the three life stages: larval forms of the genus *Parataeniophorus* and males of the genera *Ataxolepis*, *Cetomimoides, Megalomycter,* and *Vitiaziella* to the females of Cetominidae.

Suborder Berycoidei—bigscales and alfonsinos. The two families are sister groups in recent molecular studies (e.g., Betancur-R. et al., 2013a).

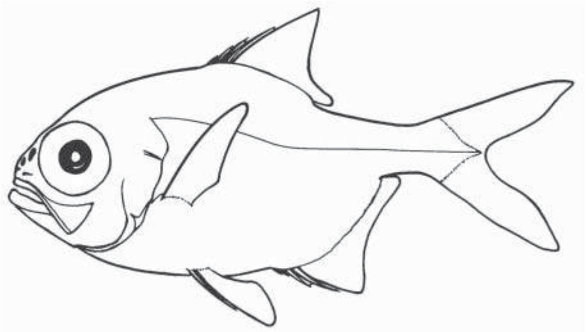
Two families with 7 genera and 73 species. All species are marine.

Family MELAMPHAIDAE (265)—bigscale fishes. Marine, bathypelagic; most oceans (absent from Arctic and Mediterranean).

Head large; eyes small in most species; jaws long, extending to or beyond posterior margin of eye; teeth small; palate toothless; dorsal fin single, 1–3 weak spines preceding 9 to 18 soft rays; anal fin with one spine and 7 to 10 soft rays; pelvic fin thoracic or subthoracic, with one spine and 6–8 soft rays; caudal fin with three or four procurrent spines; scales usually large, cycloid, and deciduous; no lateral line (one or two pored scales at most); 24–31 vertebrae; small fish total length to about 16 cm.

Five genera, *Melamphaes* (27), *Poromitra* (22), *Scopeloberyx* (9), *Scopelogadus* (4), and *Sio* (1), with 63 species (Moore, 2003; Kotlyar, 1996, 2004a, 2008a,b, 2009, 2011a,b, 2012).

Family BERYCIDAE (266)—alfonsinos. Marine; Atlantic, Indian, and western and central Pacific.



Body ovate and compressed; eyes very large; pelvic fin with one spine and 7–13 soft rays; dorsal fin without notch, with 4–7 spines increasing in length from first to last, and 12–20 soft rays; anal fin with four spines and 12–17 (*Centroberyx*) or 25–30 (*Beryx*) soft rays; lateral-line scales 39–51 (*Centroberyx*) or 66–82 (*Beryx*); 24 or 25 vertebrae. Most species occur between 200–600 m.

Two genera, *Beryx* (3) and *Centroberyx* (7), with ten species (e.g., Kotlyar, 1996; Moore, 2003).

Series PERCOMORPHA. The Percomorpha were recognized by Rosen (1973a) as the most derived euteleostean clade, but the clade's contents have changed somewhat over the years since. Problems and changes were reviewed by Johnson (1993). As per Johnson (1993) followed by Wiley and Johnson (2010), Percomorpha (= Percomorphacea) consisted of Smegmamorpha (comprising the mugilomorphs, atherinomorphs, gasterosteiforms, synbranchiforms, and elassomatids) and 23 additional orders placed within Percomorpha as *incertae sedis.* The concept of the Smegmamorpha did not achieve a consensus among morphologists, and many recent molecular studies (e.g., Miya et al., 2003, 2005; Near et al., 2012a; Wainwright et al., 2012; Betancur-R. et al., 2013a) have provided strong evidence that it is not a natural group. It is thus not recognized here. Morphological characters that support the monophyly of Percomorpha include: second ural centrum present; pelvic fins with fewer than six soft rays; absence of free pelvic radials; and seventeen principal caudal fin rays in a i,8,7,i pattern (Wiley and Johnson, 2010).

The Percomorpha in the present work are divided into groups in a suggested phylogenetic sequence at the subseries rank: Ophidiida, Batrachoidida, Gobiida, Ovalentaria, followed by the remaining acanthopterygians with hypothesized but mostly unnamed groupings.

Fossil percomorphs were covered in Patterson (1993). Some treated in recent literature include: i) †*Priscacara* (Priscacaridae) and †*Mioplosus*, freshwater Eocene percoid genera from North America, (e.g., Grande, 2001); ii) †*Eoserranus,* †*Indiaichthys,* †*Nardoichthys,* and †*Saldenioichthys* (e.g., Arratia et al., 2004); iii) †Asianthidae (†*Asianthus,* †*Eosasia,* and †*Pauranthus*) from the Upper Paleocene of Turkmenistan that may form a monophyletic assemblage together with the families Priacanthidae and Caproidae (Sytchevskaya and Prokofiev, 2003); iv) †*Tungtingichthys* (Chang and Huanzhang, 1998); v) and †Sorbinipercidae (†*Sorbiniperca scheuchzeri*) (Tyler, 1999); vi) †*Synagropoides,* a possible acropomatid from the Eocene of the Northern Caucasus (Bannikov, 2002); and vii) †Eocottidae (†*Eocottus* and †*Bassania*) from the Eocene of Monte Bolca, Italy (Bannikov, 2004b). Many other important studies have been done on perciform fossils, such as: i) Micklich (1996) on middle Eocene †*Amphiperca,* †*Palaeoperca,* and †*Rhenanoperca,* ii) Otero and Gayet (1999) on the Plio-Pleistocene †*Semlikiichthys,* and iii) Chen et al. (1999) on *Coreoperca* and *Siniperca.* The latter two genera, with cycloid scales, have extant species in eastern Asia; they are usually classified in their own family Sinipercidae (Roberts, 1993), members of which are known from fresh water except for the probably marine Miocene sinipercid †*Inabaperca taniurai* (Yabumoto and Uyeno, 2000).

Percomorpha include 31 orders with 270 families, 2,212 genera, and 13,173 species.

Subseries Ophidiida. The single contained order Ophidiiformes was classified in Paracanthopterygii by Nelson (2006) and earlier authors cited therein, but *incertae sedis* within “Percomorphacea” by Wiley and Johnson (2010). The Ophidiiformes are classified here in the subseries Ophidiida and are now regarded (e.g., by Miya et al., 2005, Near et al., 2012a, and Betancur-R. et al., 2013a) as the sister group of all other extant Percomorpha.

Order OPHIDIIFORMES (55)—cusk-eels. Pelvic fins, when present, inserted at level of preopercle or farther anterior (mental or jugular), one or two soft rays in each, and occasionally with a spine; base of dorsal and anal fins long, extending to and usually joined with caudal fin; nostrils paired on each side; dorsal and anal fin pterygiophores more numerous than adjacent vertebrae (the ratio being about 1.8:1).

Some of the past disagreement about the phyletic relationships and taxonomic rank of this group was reviewed by Nelson (1994) (also, see the discussion above under Paracanthopterygii). The following internal classification is based on Nielsen et al. (1999), except that they did not include the family Parabrotulidae.

Two suborders (Ophidioidei and Bythitoidei), five families, 119 genera, and about 531 species. The fifth family, Parabrotulidae, is only provisionally retained here. About five species, all bythitids, are limited to fresh water or weakly brackish water.

Suborder Ophidioidei. Anterior nostril well above upper lip in most species; oviparous, males lack an external intromittent organ; caudal fin usually present and connected with dorsal and anal fins (appearing as one continuous fin and tapering to a point).

Family CARAPIDAE (267)—pearlfishes. Marine; Atlantic, Indian, and Pacific.

Larvae (planktonic vexillifer stage) with a vexillum (long, deciduous, thread-like first dorsal-fin ray); anal-fin rays longer than opposing dorsal-fin rays; anus of adults and anal-fin origin far forward, behind head and usually beneath pectoral fin (which is rarely absent); scales absent; gill openings wide and extending far forward; teeth on jaws, vomer, and palatines; no spines on opercular bones; branchiostegal rays 6 or 7; supramaxillary absent; about 85–145 vertebrae.

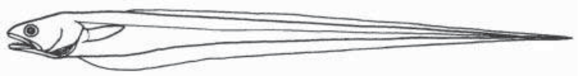
Although subfamilies were not recognized in Nielsen et al. (1999), we retain them here as given in Nelson (1994), based on the 1990 cladistic classification of Markle and Olney (1990).

Eight genera and 36 species (Nielsen et al., 1999; Olney, 2003).

SUBFAMILY PYRAMODONTINAE. Basically circumtropical, north to Japan and Gulf of Mexico and south to New Zealand and Chile. Pectoral fin nearly as long as head, rays 24–30; upper jaw protractile; anal-fin pterygiophores modified into a visceral cradle consisting of alternately bending pterygiophores; some pleural ribs present; precaudal vertebrae 12–15.

Three genera, *Eurypleuron* (2), *Pyramodon* (4, pelvics present) and *Snyderidia* (1, pelvics absent), with seven species (Nielsen et al. 1999).

SUBFAMILY CARAPINAE (FIERASFERIDAE). Tropical and temperate seas (south to New Zealand, South Georgia Island, and southern Chile). Pectoral fin usually much shorter than head length and with 23 or fewer rays (absent in the three species of the subgenus *Encheliophis* of the genus *Encheliophis*); interarcual element ossified (also ossified in synbranchids); pelvic fins and girdle absent (the girdle is present in at least most larvae); upper jaw nonprotractile; no pleural ribs; precaudal vertebrae 17–35.



Many species of pearlfishes (also known as fierasfers) have the interesting habit of hiding in living animals. Some live in sea cucumbers, but apparently there is no evidence as reported that they may eat the cucumber's internal organs in a parasitic fashion. Others are commensal with starfish, sea cucumbers, clams, and tunicates (known as inquiline behavior, "living as a tenant"). Similar molluscan inquiline behavior, with scallops, is also known in the red hake, *Urophycis chuss.* Pearlfishes, whether free-living, commensal, or parasitic, pass through two distinct larval stages. The vexillifer, or first, larval stage is pelagic; the tenuis, or second, larval stage, perhaps absent or abbreviated in the free-living species, is demersal. In this stage the vexillum is gone, the head is relatively small, and total length is reduced. Except in the free-living species, individuals can enter the host in the tenuis stage. References on which most of the above is based were given in Nelson (1994).

Maximum length about 30 cm, attained by *Echiodon drummondii* and *Carapus bermudensis.*

Four genera, the parasite-like *Encheliophis* (7), the free-living *Echiodon* (13), and the commensal genera *Carapus* (synonym *Disparichthys,* erected for one specimen that was collected from a brook in New Guinea and described in 1935 as an eel in its own family; a second species was added in 1938 from a specimen collected off Cuba) (5) and *Onuxodon* (3), and with a total of 28 species (Nielsen et al., 1999). Parmentier et al. (2000) proposed changes to the generic diagnoses and species composition of *Carapus* and *Encheliophis.* See Parmentier et al. (2010) for a revision of *Encheliophis.*

SUBFAMILY TETRAGONDACNINAE. Marine, deep waters off Sumatra. First neural spine with wing-like process larger than second neural spine; no rocker bone; no predorsal bone; no supraneurals; no upper jaw teeth; caudal-fin rays 11; precaudal vertebrae 13; scales present.

One genus, *Tetragondacnus* with one species (*T. spilotus*). This monotypic subfamily was introduced by Anderson and Satria (2007) for a new genus and species based on a single specimen.

Family OPHIDIIDAE (268)—cusk-eels. Marine; Atlantic, Indian, and Pacific.

Dorsal-fin rays usually equal to or longer than opposing anal-fin rays; anus and anal fin origin usually behind tip of pectoral fin; scales present; some with one or more spines on opercle; supramaxillary present; larvae without a vexillum; pelvics rarely absent. Maximum lengths about 1.6 m, attained by *Genypterus capensis,* and 2.0 m, attained in *Lamprogrammus shcherbachevi.*

Four subfamilies with 50 genera and about 258 species (Nielsen et al., 1999; Lea and Robins, 2003). Fossils include the Tertiary †*Ampheristus* and †*Hoplobrotula.*

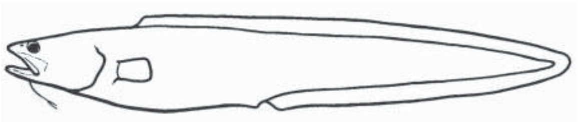
SUBFAMILY BROTULINAE. Circumtropical. Barbels present on chin and snout.

One genus, *Brotula* (brotulas), with six species.

SUBFAMILY BROTULOTAENIINAE. Circumtropical. No barbels on chin or snout; scales in the form of small prickles.

One genus, *Brotulotaenia,* with four species. *Lamprogrammus* may be better placed in this subfamily rather than in the non-monophyletic Neobythitinae (Fahay and Nielsen, 2003).

SUBFAMILY OPHIDIINAE. Considered monophyletic by Nielsen et al. (1999). No barbels on snout or chin; pelvic fins far forward; cycloid scales present (in regular rows or at oblique angles to each other); slender, elongate filament of bone extending anteriorly from junction of ventral arms of cleithra.



Eight genera, one tribe, Lepophidiini (30 species), with *Cherublemma* (1), *Genypterus* (6), and *Lepophidium* (23), and the other, Ophidiini (35) species), with *Chilara* (1), *Ophidion* (27), *Otophidium* (4), *Parophidion* (2), and *Raneya* (1), with about 65 species. (Robins et al., 2012).

Subfamily Neobythitinae. Littoral to the greatest depths at which fish have been obtained (the deep-sea record being for *Abyssobrotula galatheae* obtained at 8,370 m in the Puerto Rico Trench). No barbels on snout or chin; cycloid scales present; no filament of bone extending anteriorly from junction of ventral arms of cleithra; pelvic fins absent in at least adults of the five species of the virtually circumtropical *Lamprogrammus*; eye lens minute or absent in *Leucicorus* and eye minute in *Typhlonus*. This subfamily is possibly not monophyletic.

About 40 genera: *Abyssobrotula* (1), *Acanthonus* (1), *Alcockia* (1), *Apagesoma* (3), *Barathrodemus* (2), *Barathrites* (2), *Bassogigas* (2), *Bassozetus* (13), *Bathyonus* (3), *Benthocometes* (2), *Dannevigia* (1), *Dicrolene* (15), *Enchelybrotula* (2), *Epetriodus* (1), *Eretmichthys* (1), *Glyptophidium* (6), *Holcomycteronus* (6), *Homostolus* (1), *Hoplobrotula* (3), *Hypopleuron* (1), *Lamprogrammus* (5), *Leucicorus* (2), *Leuciobrotula* (6), *Leptobrotula* (1), *Mastigopterus* (1), *Monomitopus* (14), *Neobythites* (52), *Neobythitoides* (1), *Penopus* (2), *Petrotyx* (2), *Pycnocraspedum* (5), *Porogadus* (13), *Selachophidium* (1), *Sirembo* (3), *Spectrunculus* (2), *Spottobrotula* (2), *Tauredophidium* (1), *Typhlonus* (1), *Ventichthys* (1), and *Xyelacyba* (1), with about 183 species (Nielsen et al., 2006; Nielsen et al., 2008; Uiblein et al., 2008; Nielsen et al., 2010).

Suborder Bythitoidei. Anterior nostril immediately above upper lip in most species; viviparous, males with an external intromittent organ; caudal fin connected with dorsal and anal fins or separate.

Family BYTHITIDAE (269)—viviparous brotulas. Marine (rarely in brackish and freshwaters); Atlantic, Indian, and Pacific.

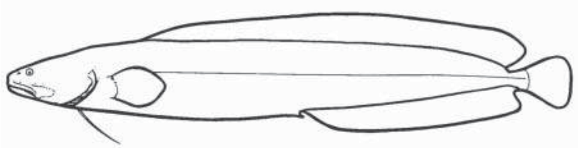
Scales usually present; swimbladder present; opercular spine usually present and strong; pyloric caeca present; precaudal vertebrae 9–22. One species of *Bythites* is known from a thermal vent in the Galapagos Rift Zone. In contrast to ophidiids, several species of bythitids extend into shallow water. About five species are confined to freshwater or weak brackish water.

About 53 genera with 211 species (Nielsen et al., 1999; Møller et al., 2004a,b; Møller et al., 2005).

Subfamily Bythitinae. Caudal fin united with dorsal and anal fins; pelvic fins absent in *Bellottia* and *Hephthocara*. The six blind to partially blind species of *Lucifuga* (placed in Brosmophycinae in Nielsen et al., 1999) live in limestone caves and sinkholes in waters ranging in salinity from fresh to highly saline; four species occur in Cuba, one in the Bahamas, and one in the Pacific in the Galapagos (Nielsen et al., 1999; Proudlove, 2005).

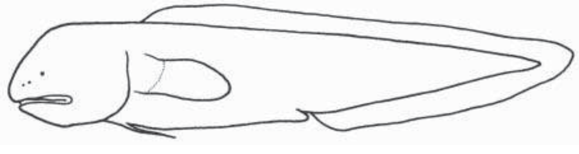
About 22 genera: *Acarobythites* (1), *Anacanthobythites* (2), *Bellottia* (5), *Bythites* (3), *Calamopteryx* (3), *Cataetyx* (12), *Diplacanthopoma* (9), *Ematops* (1), *Grammonus* (11), *Hastatobythites* (1), *Hephthocara* (2), *Microbrotula* (7), *Olgibichthys* (7), *Parasaccogaster* (3), *Pseudogilbia* (1), *Pseudonus* (2), *Saccogaster* (8), *Stygnobrotula* (1), *Thermichthys* (1), *Thalassobathia* (2), *Timorichthys* (2), and *Tuamotuichthys* (3), with about 87 species (e.g., Møller et al., 2004a; Møller et al., 2006; Nielsen et al., 2010; Nielsen, 2011; Nielsen and Schwarzhans, 2011).

SUBFAMILY BROSMOPHYCINAE. Caudal fin separate from dorsal and anal fins. One species of *Ogilbia* lives in brackishwater caves and crevices in the Galapagos, and one species of *Typhliasina* (*T. pearsei*, placed in *Ogilbia* in Nielsen et al., 1999, and Nelson et al., 2004) lives in fresh water caves in the Yucatan. Two tribes were recognized by Nielsen et al. (1999), Brosmophycinini and Dinematichthyini (with most of the genera; males exhibit a copulatory organa and 1-2 pairs of pseudoclaspers)).



About 31 genera: *Alionematichthys* (11), *Beaglichthys* (3), *Bidenichthys* (3), *Brosmodorsalis* (1), *Brosmolus* (1), *Brosmophycis* (1), *Brosmophysiops* (1), *Brotulinella* (1), *Dactylosurculus* (1), *Dermatopsis* (5), *Dermatopsoides* (4), *Diancistrus* (28), *Didymothallus* (3), *Dinematichthys* (2), *Dipulus* (3), *Eusurculus* (3), *Gunterichthys* (3), *Fiordichthys* (2), *Lapitaichthys* (1), *Lucifuga* (7), *Majungaichthys* (2), *Mascarenichthys* (3), *Melodichthys* (1), *Monothrix* (1), *Nielsenichthys* (1), *Ogilbia* (18), *Paradiancistrus* (4), *Porocephalichthys* (1), *Typhliasina* (1), *Ungusurculus* (5), and *Zephyrichthys* (1), with about 124 species (e.g., Møller et al., 2004b, 2006).

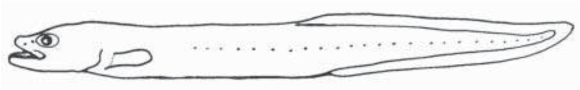
Family APHYONIDAE (270)—aphyonids, blind cusk-eels. Marine; Atlantic, Indian, and Pacific.



Scales absent; swimbladder absent; dorsal and anal fins confluent; dorsal-fin origin posterior, well behind pectoral fin; eyes poorly developed; opercular spine weak or absent; no sensory pores on head; pyloric caeca absent; pelvics jugular, one ray in each (absent in a few species); ovaries bilobed; precaudal vertebrae 26–48 (total of 68–86 vertebrae). A number of neotenic characters are present. Most species occur in depths exceeding 700 m.

Six genera, *Aphyonus* (4), *Barathronus* (10), *Meteoria* (1), *Nybelinella* (2), *Parasciadonus* (2), and *Sciadonus* (4), with 23 species (Nielsen et al., 1999).

Family PARABROTULIDAE (271)—false brotulas. Marine; scattered parts of Atlantic, Indian, and Pacific.



Scales absent; body eel-like; mouth small, lower jaw protruding in front of upper; dorsal and anal fins confluent with caudal fin, dorsal fin with 37–50 rays, caudal fin with 4–6 rays, and anal fin with 34–43 rays; dorsal-fin origin posterior, well behind pectoral fin; two nostrils on each side of head; no sensory pores on head (neuromasts free); pelvic fins absent; pectoral fin small, with 6–8 rays; ovaries bilobed; vertebrae 54–73. Maximum length about 6 cm.

Nelson (1994) noted reasons for and against placing the parabrotulids near the zoarcids or, as here, the aphyonids. Nielsen et al. (1999) did not regard them as ophidiiforms. The issue of their correct phylogenetic position remains unresolved because of a lack of recent detailed studies and because broad-scale molecular phylogenies such as that of Betancur-R. et al. (2013a) have not sampled them.

Two genera, *Parabrotula* (2) and *Leucobrotula* (1), with three species (Miya and Nielsen 1991).

Subseries Batrachoidida. This series contains a single order (toadfishes) with one family. Patterson and Rosen (1989) considered the batrachoidiforms and lophiiforms to be sister groups and applied the term Pediculati to include both orders. That group is no longer considered valid. Concerning recent ideas about their phylogenetic relationships, see the discussions within Paracanthopterygii and Ophidiida.

The fossil genus †*Bacchiaichthys*, of late Late Cretaceous age, was named by Bannikov and Sorbini (2000) for specimens from proto-Mediterranean (Tethys Sea) deposits at Trieste, northeastern Italy. Though its relationships need more study, it cannot be placed currently within the crown-group batrachoidiforms (Carnevale and Collette, 2014), and it might prove to be a stem-group member of the Batrachoidida and/or Batrachoidiformes, which it resembles in overall body form, configuration of the first dorsal fin, absence of a supraneural, lack of anal fin spines, and rounded caudal fin with reduced number of rays. It also has a similar structure of the caudal skeleton, with the epaxial plate fused to the second ural centrum and the hypaxial plate fused to the compound first ural centrum plus first preural centrum and parhypural (Carnevale and Collette, 2014). Further research is needed to test this hypothesis.

Order BATRACHOIDIFORMES (Haplodoci) (56)—toadfishes. Head large, broad, depressed; body tapered, usually scaleless (small cycloid scales in some), with photophores in some; eyes on top of head and directed upwards; mouth large, bordered by premaxilla and maxilla, often with barbels or fleshy flaps, and moderately strong teeth on jaws and roof of mouth; spines on opercle and often on subopercle; glandular tissue may be present in opercular region or on or near pectoral fin; swimbladder well developed; lateralis system very well developed with single or multiple lateral lines, each pore usually surrounded by two tentacles; dorsal fins separated, first with two or three spines, second with up to 40 soft rays; anal fin with up to 39 rays; pectoral fins large, broad-based; presence of five pectoral radials, the uppermost unossified in some species; pore (foramen) in axil of pectoral fin in some; pelvic fins jugular, with one spine and three soft rays; three pairs of gills; gill membrane broadly joined to isthmus; branchiostegal rays six; pectoral radials four or five; vertebrae 25 to 47; upper hypurals with peculiar intervertebral-like basal articulation with rest of caudal skeleton; no ribs, epiotics, parietals, or intercalars; no pyloric caeca; larvae with very large yolk sac bearing an adhesive disc on its verntral surface. Maximum size at least 57 cm.

Most are drab colored. Some can produce audible sounds with the swimbladder and can live out of water for several hours.

Carnevale and Collette (2014) reviewed the fossil record of the Batrachoidiformes. Except possibly for †*Bacchiaichthys* (see above), stem-group batrachoidiforms are so far undocumented, though likely to be at least as old as mid Late Cretaceous given the phylogenetic position of the clade. The oldest fossil evidence of the order currently is otoliths of early Eocene age from France. Modern batrachoidid subfamilies and genera began to appear in the Miocene, again mostly based on otoliths. There are also two fossil toadfish genera based on skeletons of Miocene age; both are members of the Halophryninae (see below).

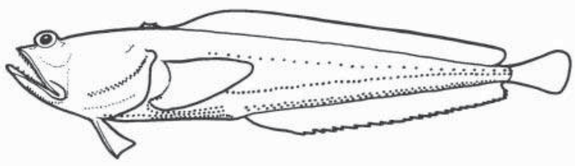
One family, 23 genera, and 101 species.

Family BATRACHOIDIDAE (272)—toadfishes. Marine (primarily coastal benthic; rarely entering brackish water, a few species confined to freshwater); Atlantic, Indian, and Pacific. Toadfishes generally occur on sand and mud bottoms, although species of *Sanopus* occur in coral reefs.

Greenfield et al. (2008) recently reviewed the toadfishes and erected a fourth subfamily, Halophryninae, containing most of the genera formerly in Batrachoidinae. Subfamilial diagnostic characters below are mostly from that work.

Four subfamilies with 23 genera and 83 species.

SUBFAMILY PORICHTHYINAE. Eastern Pacific and Western Atlantic. Two solid dorsal-fin spines with no venom glands; subopercular spines absent; canine teeth present.

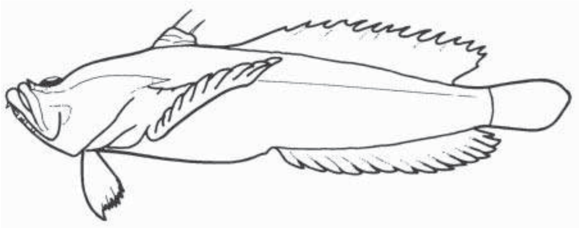


Two genera with 14 species.

Aphos. Photophores absent; canines on vomer. One species, southeastern Pacific off Peru and Chile (Walker and Rosenblatt, 1988; Greenfield et al., 2008).

Porichthys (midshipmen). Numerous photophores (this is one of the few shallow-water fishes with photophores); canines on vomer; four lateral lines. Thirteen species, eight along the eastern Pacific (British Columbia to Ecuador and Galapagos Islands) and five along the western Atlantic (Virginia to Argentina, but generally absent from the West Indies) (Walker and Rosenblatt, 1988). Maximum length 43 cm, in *P. myriaster.*

SUBFAMILY THALASSOPHRYNINAE. Eastern Pacific and western Atlantic. Two dorsal-fin spines; no subopercular spines; dorsal and opercular spines hollow and connected to venom glands capable of producing extremely painful wounds; canine teeth absent; body scaleless; no photophores; lateral line single or absent; pectoral fin rays 13–18.

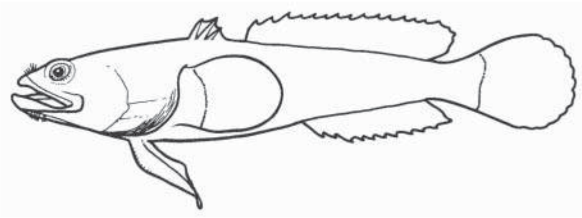


Two genera with 11 species (e.g., Collette, 1973; Greenfield et al., 2008).

Daector. Second dorsal-fin rays 22–33; anal-fin rays 21–30; distinct glands with pores between bases of upper 3–7 pectoral-fin rays on inner surface of fin (similar to *Opsanus*); vertebrae 31–40. Four tropical eastern Pacific marine species plus *D. quadrizonatus* from Caribbean-drainage fresh water in northwestern Colombia.

Thalassophryne. No distinct glands on pectoral fin; second dorsal-fin rays 17–21; anal-fin rays 16–20; vertebrae 26–30. Five western Atlantic marine species (Panama and South America), plus *T. amazonica,* a freshwater species known only from the Amazon River.

SUBFAMILY BATRACHOIDINAE. New World, off the coasts of the Americas. Three dorsal-fin spines; dorsal and opercular spines not hollow and lacking connection to venom glands; one to three subopercular spines; photophores and canine teeth absent; upper accessory pectoral-fin radial fully ossified; medial suture between epihyal and ceratohyal; ventral edge of cratohyal rounded where it joins epihyal; dorsal side of joint between dentary and articular about equal height and rounded; dorsal edge of quadrate flat where it meets metapterygoid.



Six genera, *Amphichthys* (1), *Batrachoides* (9), *Opsanus* (6), *Potamobatrachus* (1), *Sanopus* (6), and *Vladichthys* (1), with about 24 species (e.g., Collette, 1995a, 2001, 2003a; Greenfield, 1996, 1998; Greenfield et al., 1994; Greenfield and Smith, 2004; Greenfield et al., 2008).

SUBFAMILY HALOPHRYNINAE. Old World. Three dorsal-fin spines; dorsal and opercular spines not hollow and not connected to venom glands; one to two subopercular spines and one to three filaments; photophores and canine teeth absent; foramina absent in median process of pelvic bone; median process of pelvic bone not joined to pelvic bone along its entire length; ventral edge of ceratohyal square where it joins epihyal; dorsal edge of quadrate not flat where it meets metapterygoid; usually one or three lateral lines.

This subfamily was named by Greenfield et al. (2008) to contain most of the genera previously in the subfamily Batrachoidinae, which now contains only New World genera.

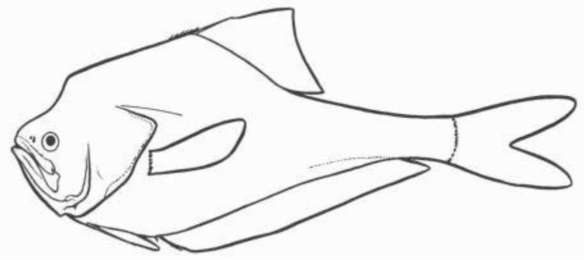
Allenbatrachus (3), *Austrobatrachus* (2), *Barchatus* (2), *Batrachomoeus* (5), *Batrichthys* (2), *Bifax* (1), *Chatrabus* (synonym *Tharbacus*) (3), *Colletteichthys* (3), *Halobatrachus* (1), *Halophryne* (4), *Perulibatrachus* (4) (a replacement name for *Parabatrachus,* preoccupied by the fossil sarcopterygian genus †*Parabatrachus*), *Riekertia* (1), and perhaps *Triathalassothia* (2), with about 52 species (Greenfield et al., 2008; Greenfield, 2012a,b, 2014; Greenfield et al., 2012). *Triathalassothia* is of somewhat uncertain subfamilial assignment (Greenfield et al., 2008).

The only known fossil skeletons of Batrachoidiformes are both Miocene members of the Halophryninae from deposits of late stages of the proto-Mediterranean. A previously known fossil, newly assigned by Carnevale and Collette (2014) to the extant subfamily Halophryninae, comes from the southern margin of the Tethys Sea in Algeria. †*Zappaichthys* is an extinct genus of Halophryninae from deposits of the Paratethys Sea in Austria (Carnevale and Collette, 2014).

Subseries Gobiida. The Gobiida contain two orders, Kurtiformes and Gobiiformes, and are sister to all of the groups that follow. This clade was suggested by the molecular phylogeny of Betancur-R. et al. (2013a) and supported although not fully tested by Thacker and Roje (2009) and Agorreta et al. (2013). Johnson (1993) had earlier mentioned similar grid-like patterns of sensory papillae on the head and body of kurtids, apogonids, and gobioids (see characters of Kurtiformes, below) but the details of their distribution among various gobiiforms were not explored.

Order KURTIFORMES (57)—nurseryfishes and cardinalfishes. Two families, Kurtidae and Apogonidae. A close relationship between kurtids and apogonids was suggested by Johnson (1993) based on similar dorsal gill-arch elements, such as the second epibranchial having no direct articulation with the second pharyngobranchial, the articular head of the third pharyngobranchial expanded and broader than that of the fourth, and the fourth pharyngobranchial cartilage absent. As well, the eggs in both groups bear filaments around the micropyle that allow them to form a mass that is mouth brooded in apogonids but carried on the supraoccipital hook in kurtids. In addition, in both there are horizontal and vertical rows of sensory papillae on the head and body, often in a grid pattern. Somewhat similar patterns may occur in some gobiiforms (Johnson, 1993). The families Kurtidae and Apogonidae are sister groups in some molecular phylogenies (e.g., Betancur-R. et al., 2013a) but successive sisters to Gobiiformes in some others (e.g., Thacker, 2009; Chakrabarty et al., 2012; Agorreta et al., 2013).

Family KURTIDAE (273)—nurseryfishes. Brackish and freshwater (rarely marine), in Indo-Malay area and parts of Australia.

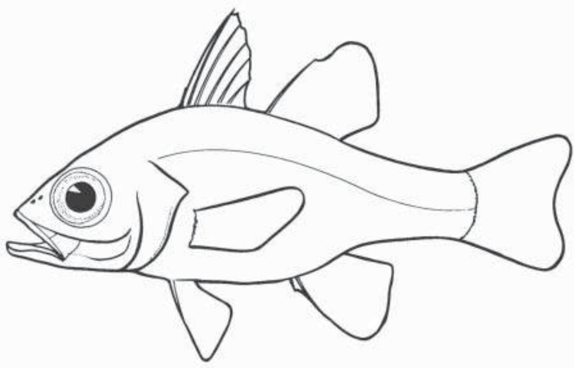


Males with occipital hook, used for carrying eggs on the head; scales small and cycloid; lateral line short and rudimentary; mouth large; dorsal fin single, with spines and soft rays; anal fin with two spines and 31–47 soft rays; pelvic fins with one spine and five soft rays; caudal fin deeply forked; ribs expanded, partly enclosing the anterior portion of the swimbladder and entirely enclosing the posterior portion. Maximum length 60 cm, attained in *Kurtus gulliveri*.

Much information on these fascinating fishes with an unusual method of parental care is contained in many works by T. M. Berra (e.g., Berra, 2001, 2003; Berra and Humphrey, 2002; Berra and Neira, 2003).

One genus, *Kurtus*, with two species. *Kurtus gulliveri* has 44–47 soft rays in the anal fin and is found in southern New Guinea and northern Australia; *K. indicus* has 31 or 32 soft rays in the anal fin and is found in the Indo-Malay area (e.g., India, China, Borneo) (e.g., Berra, 2001, 2003).

Family APOGONIDAE (274)—cardinalfishes. Marine, some brackish water, a few in streams in the tropical Pacific; Atlantic, Indian, and Pacific.



Two separated dorsal fins, the first with 6–8 spines and the second with one spine and 8–14 soft rays (*Paxton* has a continuous dorsal fin); anal fin with two spines and 8–18 soft rays; scales usually ctenoid, but cycloid in several groups and absent in *Gymnapogon*; seven branchiostegal rays; usually 24 vertebrae (10 + 14). Several other families have widely separated dorsal fins, but this is the only one in which the distal radial of the last spine is short (versus elongate) (Johnson, 1993). Species of *Siphamia* have a ventral luminous organ. Many of the species are mouthbreeders; it is suspected that in some only the males incubate the eggs, whereas in others it is only the females. Most species are nocturnal. Maximum length is usually about 20 cm, and most are less than 10 cm.

The nine species of *Glossamia* are found only in fresh water; they occur primarily in New Guinea but also in Australia. A few species of *Apogon* occur in estuaries and the lower reaches of rivers. The relatively deep dwelling (60–290 m) *Apogon gularis* is unique among apogonids in having the anus located just behind the origin of the pelvic fins. Baldwin and Johnson (1999) supported the recognition of the following two subfamilies. Thacker and Roje (2009) published a preliminary molecular phylogeny of these fishes and discussed their bioluminescent organs.

About 33 genera and 347 species.

SUBFAMILY APOGONINAE. Oral incubation of eggs in many species.

Some 29 genera (e.g., *Amioides* (1), *Apogon* (105), *Apogonichthyoides* (22), *Apogonichthys* (3), *Archamia* (2), *Astrapogon* (3), *Cercamia* (2), *Cheilodipterus* (16), *Foa* (7), *Fowleria* (7), *Glossamia* (11), *Holapogon* (1), *Jaydia* (3), *Lachneratus* (1), *Lepidamia* (1), *Neamia* (4), *Nectamia* (9), *Ostorhinchus* (59), *Phaeoptyx* (3), *Pristiapogon* (5), *Pristicon* (3), *Pterapogon* (2), *Rhabdamia* (7), *Siphamia* (23), *Sphaeramia* (2), *Taeniamia* (12), *Vincentia* (5), *Zapogon* (1), and *Zoramia* (6.)), with 326 species (Fraser, 2000, 2005, 2008, 2012, 2013a,b; Gon, 2003; Gon and Randall, 2003a,b; Mabuchi et al., 2006; Baldwin et al., 2009; Fraser and Allen, 2010, 2011; Gon and Bogorodsky, 2010; Gon and Allen, 2012; Gon et al., 2013a,b). *Amioides* is considered valid (Yamanoue, 2009).

Subfamily Pseudamiinae. Large canine teeth always present on dentary and premaxillae; lateral line incomplete or absent; scales cycloid or absent. *Gymnapogon urospilotus* has exceptionally large, fast-swimming, and conspicuous larvae (Leis et al., 2015).

Four genera, *Gymnapogon* (8), *Paxton* (1), *Pseudamia* (7), and *Pseudamiops* (5), with 21 species (e.g., Baldwin and Johnson, 1999).

Order GOBIIFORMES (58)—gobies. The Gobiiformes were formerly treated as suborder Gobioidei within the order Perciformes, but molecular evidence (e.g., Betancur-R. et al., 2013a) and some morphological characters (see above under Kurtiformes) now place them with Kurtiformes (herein grouped as subseries Gobiida). Parietals absent; infraorbitals, except for the lachrymal, unossified or absent; lateral-line system reduced to variably developed cephalic canals except in the primitive *Rhyacichthys* (free neuromasts may be involved); swimbladder usually absent; gill membranes usually joined to isthmus; barbels on head in some; no pyloric caeca; spinous first dorsal with typically 4–10 flexible spines; second dorsal and anal with first element typically spinous, and variable number of soft rays; pelvic fins below pectorals, with one spine and usually four or five soft rays, often united; unique sperm gland; vertebrae 25–35 (exceptions to certain characters occur in some Gobiidae). At least some gobiiforms have eggs with attachment filaments (Kramer and Patzner, 2008), like those of Ovalentaria (discussed below).

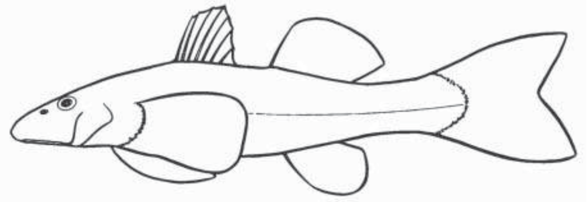
This order comprises over two thousand species with varied ecological specializations and life history traits, presenting a challenge in elucidating relationships among members. The sheer diversity of this suborder hampered a broad and comprehensive survey of morphological characters. Recent molecular phylogenies incorporate many taxa but use different molecular markers and taxa, and resulting clades are undiagnosed by synapomorphies, thus presenting a challenge when attempting to resolve inconsistencies among studies. Consequently, there is at present no consensus on the familial classification of gobioid fishes. The sister group of gobioids is also uncertain, but phylogenies recovered from molecular data identify Apogonidae and Kurtidae. There is an immense literature, very little of which could possibly be incorporated here. We adopt the largely consistent phylogenies and classifications proposed by Thacker and Hardman (2005), Thacker (2009), and Agorreta et al. (2013). We also include the new family Thalasseleotridae proposed by Gill and Mooi (2012), and tentatively retain the family Milyeringidae recently revived by Chakrabarty (2010), thus recognizing eight families within the Gobioidei: Rhyacichthyidae, Milyeringidae, Odontobutidae, Eleotrididae, Butidae, Thalasseleotrididae, Gobionellidae, and Gobiidae.

Our knowledge of gobiiform systematics and diversity is rapidly expanding with contributions such as those of Thacker (2003, 2009, 2011, 2013); Keith et al. (2005); Thacker and Hardman (2005); Kottelat (2007, 2011); Smith and Sparks (2007); Mendel et al. (2008); Mejri et al. (2009, 2011); Neilson and Stepien (2009); Thacker and Roje (2009); Chakrabarty (2010); Larmuseau et al. (2010); Mooi and Gill (2010); Gill and

Hoese (2011); Thacker et al. (2011); Agorreta and Rüber (2012); Chakrabarty et al. (2012); Hoareau et al. (2012); Maxfield et al. (2012); and Agorreta et al. (2013).

Eight families, about 321 genera, and approximately 2167 species. Many gobioids, probably over 200, occur in fresh water (for example, in New Guinea and Africa).

Family RHYACICHTHYIDAE (275)—loach gobies. Freshwater streams; Indo-Australian Archipelago (e.g., Java, Sulawesi, and New Guinea), New Caledonia, Philippines, China, and Solomon Islands.



Head depressed, tail compressed; mouth inferior with fleshy upper lip; eyes small; pelvic fins widely separated; pectoral fins very broad, with 21 or 22 rays; lower surface of head and anterior part of body, with the paired fins, form an adhesive disc; dorsal fins well separated, first with seven feeble spines and second with one spine and eight or nine soft rays; anal fin with one feeble spine and eight or nine soft rays; three epurals; lateral-line system on body and head well developed (a primitive feature unique within the order); lateral-line scales (ctenoid) about 27–40; six branchiostegal rays; caudal fin lunate. The fish superficially resembles the homalopterids in appearance and habit, with strong adaptations to freshwater streams. They are thought to be among the most primitive gobies. Maximum length about 32 cm.

One or two genera, *Rhyacichthys* (2), and possibly *Protogobius* (1), with a total of three species. Thacker and Hardman (2005) regarded *Rhyacichthys aspro* as the most primitive member of the Gobioidei based on a mitochondrial DNA phylogeny.

Family ODONTOBUTIDAE (276)—freshwater sleepers. Freshwater; northern Vietnam, China, Korea, Japan, and Russia.

This family may be distinguished from other gobioid families by the following characters: scapula large, excluding proximal radial from contact with cleithrum (as in *Rhyacichthys*); six branchiostegal rays (as in *Rhyacichthys* and eleotrids); pelvic fins unfused; two epurals; no lateral line (*Rhyacichthys* is the only gobioid with a lateral line) (e.g., Thacker, 2009).

This family, once placed in the eleotrids and formerly considered of doubtful monophyly (e.g., Ahnelt and Göschl, 2004), or sister to all gobiiforms except for Rhyacichthyidae (Thacker and Hardman, 2005), has also been said to be perhaps sister to Rhyacichthyidae, the two families together being sister to all other Gobiiformes (Agorreta et al., 2013). However, Tornabene et al. (2013a) presented a nuclear DNA phylogeny suggesting that Odontobutidae are closer to Rhyacichthyidae, the two together being sister to all other gobioids.

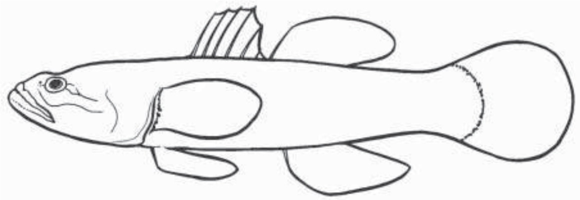
Six genera, *Micropercops* (3), *Neodontobutis* (5), *Odontobutis* (8), *Perccottus* (1), *Sineleotris* (3), and *Terateleotris* (1), with 21 species (Kottelat, 1998; Shibukawa et al., 2001; Chen et al., 2002; Nguyen and Nguyen, 2011).

Family MILYERINGIDAE (277)—blind cave gobies. Caves and sinkholes of Western Australia (Larson et al.. 2013) and Madagascar (Sparks and Chakrabarty, 2012).

The family was named by Whitley (1945) and recently revived by Chakrabarty (2010). *Milyeringa veritas* was until recently the lone member of the family. Chakrabarty (2010) named a second species (*M. brooksi*), and Smith and Chakrabarty (2012) then revised the Malagasy cavefish genus *Typhleotris*, assigning it also to the family. Larson et al. (2013) then synonymized *M. brooksi* with *M. veritas*, and named another new species, *M. justitia* from Barrow Island, Western Australia. They did not recognize the family as distinct but could not test the family's monophyly owing to limited outgroup selection in their analysis. The blind cave gobies (and the Rhyacichthyidae, above) may be related to the Odontobutidae (Thacker and Hardman, 2005; Thacker, 2009; Larson et al., 2013) but evidence for that position is not strong. Chakrabarty et al. (2012) found them to be related to Eleotridae based on mitochondrial DNA, whereas Tornabene et al. (2013) presented a nuclear DNA phylogeny suggesting that, although Rhyacichthyidae and Odontobutidae might be closely related to each other, Milyeringidae are a distinct clade more closely related to all other gobioids.

Two genera, *Milyeringa* (2) and *Typhleotris* (3), with five species (Chakrabarty, 2010; Sparks and Chakrabarty, 2012; Larson et al., 2013).

Family ELEOTRIDAE (Eleotrididae) (278)—spinycheek sleepers. Marine, brackish, and freshwater; most tropical and subtropical areas (rarely temperate areas). The Indo-Pacific xenisthmids are now included within Eleotridae.



Pelvic fins separate (no sucking disc), bases close together or united (there is considerable variation in the degree of union or separation of the pelvic fins, and sleepers and gobies cannot always be neatly separated on the basis of this character alone); mouth never inferior; spinous dorsal with 2–8 flexible spines; scales cycloid or ctenoid; six branchiostegal rays; two epurals; vertebrae 25–28. Maximum length about 60 cm, attained in *Dormitator maculatus*.

Eleotrids extend as far north as the Atlantic coast of the United States and as far south as Stewart Island, New Zealand. Six species occur in New Zealand freshwaters in swift streams, and the larvae are thought generally to drift downstream to the ocean (McDowall, 1990).

Recent studies include: Gill and Randall (1994); Pezold and Cage (2002); Thacker et al. (2006); Winterbottom and Gill (2006); Thacker (2009); Chakrabarty (2010); Caires and de Figueiredo (2011); Chakrabarty et al. (2012); Keith et al. (2012); Caires (2013); Larson et al. (2013); Pouyaud et al. (2013). The Xenisthmidae, formerly a separate family, are now synonymized with Eleotridae (e.g., Thacker, 2003).

Worldwide and found mostly in freshwater and mangrove environments. Twenty-six genera, e.g., *Allomogurnda* (8), *Allomicrodesmus* (1), *Belobranchus* (2), *Bunaka* (1), *Calumia* (4), *Dormitator* (5), *Eleotris* (30), *Erotelis* (4), *Giuris* (1), *Gobiomorphus* (9), *Gobiomorus* (3), *Guavina* (2), *Gymnoxenisthmus* (1), *Hemieleotris* (2), *Hypseleotris* (16), *Kimberleyeleotris* (2), *Leptophilypnus* (3), *Microphilypnus* (4), *Mogurnda* (25), *Paraxenisthmus* (2), *Philypnodon* (2), *Ratsirakia* (1), *Rotuma* (1), *Tateurndina* (1), *Tyson* (1), and *Xenisthmus* (8), with 139 species.

The Late Oligocene fossil genus †*Pirskenius* from freshwater deposits of Bohemia is related to the Eleotridae according to Přikryl (2014).

Family BUTIDAE (279)—butid sleepers. Freshwater and estuarine, tropical Indo-Pacific and West Africa

Six branchiostegals; pelvic fins unfused; two epurals (Thacker 2009).

Formerly treated as a subfamily of Eleotridae, they are now considered a distinct family. Some molecular phylogenies place them close to Oxudercidae (= Gobionellidae) and Gobiidae (e.g., Thacker and Hardman, 2005; Thacker, 2009; Agorreta et al., 2013; Tornabene et al., 2013) while others place them as sister to Oxudercidae + Gobiidae (Chakrabarty et al., 2012).

Ten genera: *Bostrychus* (9), *Butis* (6), *Incara* (1), *Kribia* (4), *Odonteleotris* (3), *Ophiocara* (2), and *Oxyeleotris* (17), *Parviparma* (1), *Pogoneleotris* (1), and *Prionobutis* (2) with 46 species. Recent species descriptions include those by Hoese and Kottelat (2005); Larson (2008); and Pouyaud et al. (2013).

Family THALASSELEOTRIDIDAE (280)—ocean sleepers. Marine, Western Pacific from temperate Australia and New Zealand. The orthography of the name is as in Gill and Mooi (2012), who regarded the family as the sister group to the Gobiidae *sensu lato* (i.e., Oxudercidae + Gobiidae herein).

First gill slit restricted or closed with broad membrane connecting hyoid arch to ceratobranchial 1.

Two genera, *Thalasseleotris* (2), and *Grahamichthys* (1), with three species (e.g., Gill and Mooi, 2012; Hoese and Roberts, 2005).

Family OXUDERCIDAE (= GOBIONELLIDAE) (281)—*Gobionellus*-like and mudskipper gobies. Near worldwide in temperate and tropical waters, freshwater to marine, usually inshore, shallow, euryhaline, often muddy or silty habitats (except *Gnatholepis*, which lives on coral reefs).

Suspensorium more elongate and gracile than that of Gobiidae (Thacker, 2013); like Gobiidae they have five branchiostegal rays and a ventral process projecting from ceratobranchial 5; pelvic fins fused; one or two epurals (Thacker, 2009).

Recognition of this family, which includes the members of several former subfamilies of the Gobiidae, is based on the phylogenetic work of Thacker (2003, 2009, 2013), Thacker and Roje (2011), Chakrabarty et al. (2012), and Agoretta et al. (2013). These studies found molecular evidence to support the division of the family Gobiidae into two major clades, recognized here as the families Oxudercidae (= Gobionellidae of some authors) and Gobiidae. Four formerly recognized gobiid subfamilies—Gobionellinae, Oxudercinae (including the mudskippers), Amblyopinae, and Sicydiinae—are here included within the family Oxudercidae. According to Springer (1978) and Gill and Mooi (2012), the family-group name Oxudercidae Günther, 1861, has priority over the family-group name Gobionellidae (used by Thacker, 2009, and others). Both the Oxudercidae and the Gobiidae are highly diverse, with many genera and potentially many subgroups. Although there is preliminary evidence mostly from molecules for monophyletic subgroups, we have not recognized them taxonomically owing to the unsettled nature of their generic contents and resulting doubt about the correct names to be applied.

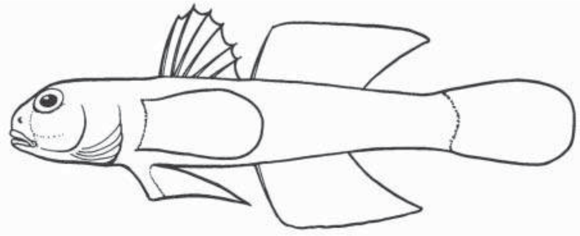
The Oxudercidae contain about 86 genera and about 598 species. Many of the species occur in fresh water. Several gobies live on wet beaches and may spend several days out of water. Some of the land gobies, such as the mudskippers, *Boleophthalmus, Periophthalmus,* and *Periophthalmodon,* can move over land with considerable speed. Their eyes, placed on top of the head on short stalks and capable of being elevated or retracted, are well adapted for vision in air. *Gillichthys mirabilis,* which usually remains in the water, comes to the surface when the water is low in oxygen and gulps air, which is held in the highly vascularized buccopharynx for respiratory exchange.

The freshwater *Pandaka pygmaea* and *Mistichthys luzonensis,* of Luzon, Philippines, are among the shortest known freshwater fishes, with females maturing as short as about 10–11 mm (see also small species of the family Gobiidae, below, and for possibly the smallest known fish see the discussion of *Paedocypris progenetica* and other species in the Cyprinidae, subfamily Danioninae).

About 86 genera including: *Acanthogobius* (6), *Akihito* (2), *Amblychaeturichthys* (2), *Awaous* (19), *Boleophthalmus* (6), *Brachyamblyopus* (1), *Brachygobius* (9), *Chlamydogobius* (6), *Clariger* (6), *Clevelandia* (1), *Cotylopus* (2), *Ctenogobius* (22), *Eugnathogobius* (9), *Eutaeniichthys* (1), *Evorthodus* (2), *Gillichthys* (3), *Gnatholepis* (10), *Gobionellus* (7), *Gobiopterus* (9), *Gymnogobius* (16), *Hemigobius* (2), *Ilypnus* (2), *Karsten* (1), *Lepidogobius* (1), *Mistichthys* (1), *Mugilogobius* (32), *Odontamblyopus* (5 spp.), *Oligolepis* (6), *Oxuderces* (2), *Paedogobius* (1), *Pandaka* (7), *Papuligobius* (2), *Parapocryptes* (2), *Periophthalmus* (18), *Periophthalmodon* (3), *Pseudapocryptes* (2), *Pseudogobius* (8), *Pseudorhinogobius* (1), *Pterogobius* (4), *Quietula* (1), *Redigobius* (14), *Rhinogobius* (63), *Sicyopterus* (35), *Sicyopus* (9), *Smilosicyopus* (7), *Stenogobius* (27), *Stigmatogobius* (7), *Stiphodon* (33), *Taenioides* (13), *Tamanka* (2), *Tridentiger* (9), *Trypauchen* (2), *Typhlogobius* (1), *Wuhanlinigobius* (2), and *Zappa* (1), with a total of about 598 species.

Many papers have been published on Oxudercidae recently (Murdy, 1989, 2006; Parenti and Maciolek, 1996; Watson and Allen, 1999; Watson, 2000; Murdy, 2002, 2003; Murdy and Shibukawa, 2003; Keith and Marquet et al., 2004; Keith and Watson et al., 2004, 2005, 2006, 2007a,b, 2009, 2010, 2011; Pezold, 2004a,b; Jenkins and Boseto, 2005; Keith and Marquet, 2005, 2007; Larson, 2005, 2010; Watson et al., 2005, 2007; Chen and Fang, 2006; Sparks and Smith, 2006; Watson and Kottelat, 2006; Watson, 2008; Mejri et al., 2009, 2011; Maeda et al., 2011; Swift et al., 2011; Thacker and Roje, 2011; Larson and Buckle, 2012; Lindstrom et al., 2012; Cui et al., 2013; Huang et al., 2013; Lynch et al., 2013; Thacker, 2013).

Family GOBIIDAE (282)—gobies. Marine, brackish, or rarely freshwater; most tropical and subtropical areas. Phylogenetic studies cited above under Gobiiformes and Oxudercidae strongly suggest that the remaining gobies constitute a clade of derived gobies. Some authors continue to recognize it as a subfamily within a larger Gobiidae.



Suspensorium less elongate and stouter than that of Oxudercidae; epurals one or none (Thacker, 2013); pelvic fins absent, or present but unfused, or fused to form an adhesive disc; spinous dorsal, when present, separate from soft dorsal and with four to ten flexible spines (but see note about wormfishes, above); scales cycloid or ctenoid (rarely absent); some species with prominent head barbels; five branchiostegal rays; ventral process projecting from ceratobranchial 5.

The family as recognized here now includes the former members of several nominal families: the Indo-Pacific Kraemeriidae (sanddivers), which burrow into the sand leaving only the head protruding; both subfamilies of Microdesmidae—the eel-like Microdesminae, or wormfishes with compressed body, long and continuous dorsal fin composed of 10–28 spines and 23–61 soft rays (figured below); the Ptereleotrinae or dartfishes with near vertical mouth, first dorsal with six spines and second dorsal with 9–36 soft rays; and the small, extremely neotenic Schindleriidae (infantfishes), some adults having a transparent body, reduced ossification, and functional pronephros (embryonic kidney). Johnson and Brothers (1993; see also Gill and Mooi, 2010) aligned *Schindleria* with the (then) Gobioidei, a position now also supported by molecular phylogenies placing them within the family Gobiidae (Thacker, 2009; Agorreta et al., 2013).

The Gobiidae, even with the Oxudercidae excluded, are still among the most species-rich of marine fish families, and are often the most abundant fishes in freshwater habitats on oceanic islands. Some species that occur in fresh water spawn in the ocean and are thus catadromous like the anguillids. Together with blenniids, they form a dominant element of the small-fish fauna in benthic habitats of tropical reefs. Most species occur in the tropical Indo-West Pacific, but the family extends well into temperate waters of both the Northern and Southern hemispheres.

Most gobies are free living and typically occur singly or in small schools. Some gobies live in close association with other invertebrate animals; the majority of these occur in coral reef ecosystems. They are obligate dwellers within hard and soft corals, as well as sponges (e.g., *Bryaninops, Paragobiodon, Pleurosicya, Risor*). About 120 species of gobies (e.g., *Amblyeleotris, Cryptocentrus*) inhabit burrows of alpheid shrimps. Many species of *Elacatinus* feed on ectoparasites of other fishes. Some gobies exhibit sequential hermaphroditism (e.g., *Gobiodon*), and many also have parental care.

Like the Oxudercidae, this family also contains some of the world's smallest fishes. The scaleless *Trimmatom nanus*, described by Winterbottom and Emery (1981) from the Chagos Archipelago in the Indian Ocean, is among the shortest gobiids and one of the shortest known vertebrates, mature females reaching only 8–10 mm SL. Some species of the marine *Eviota* are only slightly larger. Watson and Walker (2004) reported that *Schindleria brevipinguis* males (now in Gobiidae) averaged 7.7 mm in length and a gravid female measured 8.4 mm and weighed only 1 mg. Maximum length is up to 50 cm in *Glossogobius giuris* (D. F. Hoese in Smith and Heemstra, 1986).

About 189 genera and about 1,359 species, e.g., *Aboma* (1), *Acentrogobius* (20), *Amblyeleotris* (38), *Amoya* (4), *Anatirostrum* (1), *Ancistrogobius* (4), *Asterropteryx* (8), *Aulopareia* (4), *Barbulifer* (5), *Barbuligobius* (1), *Bathygobius* (28), *Benthophilus* (18), *Bryaninops* (16), *Buenia* (2), *Callogobius* (25), *Cristatogobius* (5), *Croilia* (1), *Cryptocentroides* (3), *Cryptocentrus* (35), *Didogobius* (7), *Drombus* (10), *Egglestonichthys* (3), *Ego* (1), *Elacatinus* (24), *Elotrica* (1), *Evermannia* (4), *Evermannichthys* (5), *Eviota* (87), *Gladiogobius* (3), *Glossogobius* (28), *Gobiodon* (26), *Gobiopsis* (14), *Gobiosoma* (16), *Gobitrichinotus* (2, with fused pelvics), *Gobius* (26), *Gobulus* (4), *Gorogobius* (2), *Gunnellichthys* (7), *Hazeus* (3), *Hetereleotris* (17), *Heteroplopomus* (1), *Istigobius* (10), *Kelloggella* (5), *Knipowitschia* (17), *Koumansetta* (2), *Kraemeria* (7), *Lophogobius* (3), *Lotilia* (2), *Luposicya* (1), *Lythrypnus* (20), *Microdesmus* (16), *Microgobius* (15), *Millerigobius* (1), *Minysicya* (1), *Myersina* (9), *Neogobius* (4), *Nes* (1), *Nesogobius* (4), *Obliquogobius* (6), *Opua* (1), *Oxymetopon* (5), *Padogobius* (2), *Paragunnellichthys* (2), *Paratrimma* (2), *Pariah* (1), *Parkraemeria* (1), *Parrella* (5), *Phyllogobius* (1), *Pleurosicya* (18), *Ponticola* (13), *Porogobius* (1), *Priolepis* (34), *Psilotris* (6), *Ptereleotris* (20), *Rhinogobius* (1), *Risor* (1), *Robinsichthys* (1), *Schindleria* (3), *Signigobius* (1), *Silhouettea* (10), *Stonogobiops* (7), *Sueviota* (4), *Tasmanogobius* (3), *Tigrigobius* (11), *Trimma* (74), *Trimmatom* (7), *Valenciennea* (15), *Vanderhorstia* (25), *Varicus* (3), *Vomerogobius* (1), *Yoga* (1), *Wheelerigobius* (2), *Yongeichthys* (3), *Zebrus* (1), and *Zosterisessor* (1).

There is an extensive recent literature on Gobiidae and its recently synonymized subgroups (e.g., Rennis and Hoese, 1987; Johnson and Brothers, 1993; Greenfield and Randall, 1999; Thacker, 2000; Hoese and Reader, 2001; Thacker and Cole, 2002; Winterbottom, 2002; Guimarães et al., 2004; Keith, Marquet and Watson., 2004; Keith, Watson and Marquet, 2004; Shibukawa and Suzuki, 2004; Van Tassell and Baldwin, 2004; Watson and Walker, 2004; Williams and Lecchini, 2004; Hoese and Larson, 2005, 2006, 2010; Huyse and Volckaert, 2005; Chen et al., 2006; Winterbottom, 2006; Freyhof and Naseka, 2007; Kon et al., 2007; Randall et al., 2007; Victor, 2007; Kovačić and Engín, 2008; Kovačić and Schliewen, 2008; Sazima et al., 2008; Yang et al., 2008; Hoese and Allen, 2009, 2011; Hoese and Motomura, 2009; Joyeux et al., 2009; Neilson and Stepien, 2009; Randall and Colin, 2009; Randall and Lobel, 2009; Gill and Mooi, 2010; Greenfield and Randall, 2010, 2011; Greenfield and Suzuki, 2010, 2011, 2012, 2013; Suzuki et al., 2010; Ahnelt, 2011; Bogorodsky et al., 2011; Greenfield and Jewett, 2011, 2012; Kovačić et al., 2011; Swift et al., 2011; Thacker and Roje, 2011; Tornabene and Pezold, 2011a,b; Chen et al., 2012a,b; Greenfield and Allen, 2012; Greenfield and Winterbottom, 2012; Hoese and Stewart, 2012; Shibukawa et al., 2012; Suzuki et al., 2012; Tornabene et al., 2012, 2013a,b,c; Delventhal and Mooi, 2013; Greenfield and Erdmann, 2013; Hastings and Findley, 2013; Herler et al., 2013; and Kovačić and Bogorodsky, 2013a,b).

Subseries Ovalentaria. The subseries Ovalentaria is a very diverse, presumed monophyletic group of acanthopterygians, named by W. L. Smith and T. J. Near in Wainwright et al. (2012). This taxon is based on a molecular phylogeny and there are no morphological characters yet evaluated in detail to support it, though Smith and Near in Wainwright et al. (2012) made suggestions about possible morphological and developmental character support (see below).

With lesser taxon sampling, Ovalentaria are also supported by Li et al. (2009), who gave the ordinal name Stiassnyiformes to a clade combining Mugiloidei, Plesiopidae, Blenniiformes, Atherinomorpha, and Cichlidae. Molecular results of Betancur-R. et al. (2013a) also supported the monophyly of the Ovalentaria with virtually identical membership to that proposed by Smith and Near in Wainwright et al. (2012), and with strong support for the basal node of the group.

According to Smith and Near in Wainwright et al. (2012), most members of the group (e.g., Blenniidae, Gobiesocidae, Opistognathidae, Grammatidae, Plesiopidae; Kramer and Patzner, 2008) are characterized by demersal eggs with adhesive filaments extending from the egg surface (e.g., Britz, 1997; and other references cited in Wainwright et al., 2012). In some members, reproduction is by live bearing (e.g., embiotocids, zenarchopterids, many cyprinodontiforms, and some labrisomids); in others, the eggs are secondarily pelagic but still with adhesive filaments (e.g., exocoetids, some belonids). However, the correlation is not perfect. Mugilids, included in Ovalentaria, lack the egg filaments, while Kurtiformes and some Gobiiformes, not included in Ovalentaria, possess egg filaments (e.g., Kramer and Patzner, 2008).

Many members also have the following reductive characters, of doubtful phylogenetic significance: loss of interarcual cartilage; loss of supraneurals; reduced number of pharyngobranchials; reduced number of branchiostegals; and fusion of caudal-fin elements (Johnson, 1984; Rosen and Patterson, 1990; Johnson, 1993; Parenti, 1993; Smith and Wheeler, 2004).

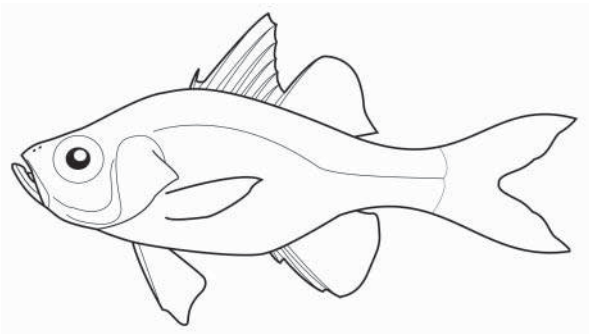
Members of the subseries Ovalentaria as classified here include the monophyletic infraseries Atherinomorpha (Atheriniformes, Cyprinodontiformes, and Beloniformes) together with the following additional taxa, related in some way to the Atherinomorphs but with less certain detailed affinities. These include the Polycentridae, Cichliformes (including Pholidichthyidae), Pomacentridae, Ambassidae, Embiotocidae, Congrogadinae, Plesiopidae, Pseudochromidae, Grammatidae, Opistognathidae, Mugiliformes, Blennioidei, and Gobiesocidae. Some of the Ovalentaria were classified as the series Mugilomorpha and the series Atherinomorpha in the previous edition of this book, whereas others were dispersed among various perciform orders and suborders.

The Syngnathiformes, Scombriformes, and a few other taxa were not included in Ovalentaria but also suggested to be a distinct clade based on molecular evidence by Wainwright et al. (2012), Near et al. (2012a), and Betancur-R. et al. (2013a). They are listed below, after Ovalentaria, unnamed and unranked, because their monophyly is considered less supported.

In the molecular phylogenies of Wainwright et al. (2012) and Betancur-R. et al. (2013a), the sister group to the Ovalentaria was thought tentatively to be a group that included the Synbranchiformes, Anabantiformes, Carangiformes, Istiophoriformes, and Pleuronectiformes, also listed and discussed below but unnamed and unranked.

THE FOLLOWING EIGHT FAMILIES are *incertae sedis* as to order within Ovalentaria based on low support values for relevant nodes in molecular phylogenies (e.g., Betancur-R. et al., 2013a). They are listed here in alphabetical order.

Family AMBASSIDAE (Chandidae) (283)—Asiatic glassfishes. Marine, brackish, and freshwater; Indo-West Pacific (freshwater in Madagascar and India to the Australian region).

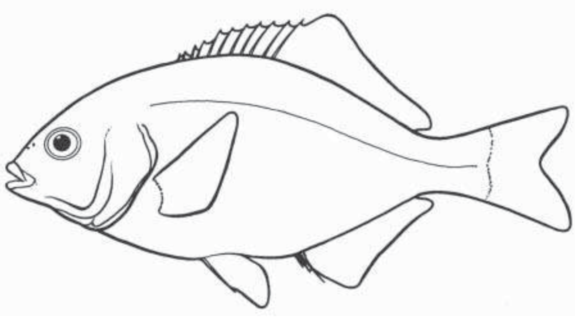


Many species with semitransparent body; scales entirely absent in the transparent *Gymnochanda filamentosa*; dorsal fin usually with seven or eight spines and 7–11 soft rays; anal fin with three spines and 7–11 soft rays; vertebrae usually 24 or 25. *Paradoxodacna piratica* is a scale-eater. Maximum length about 26 cm.

The family name Chandidae was used in Nelson (1994). The family names Ambassidae, Chandidae, and Bogodidae were discussed by Anderson and Heemstra (2003) and Kottelat (2003). An alternative phylogenetic position for Ambassidae was suggested by Otero (2004) as sister to Centropomidae, a family somewhat doubtfully included in a putative clade sister to Ovalentaria (see below).

Seven genera, *Ambassis* (20), *Chanda* (1), *Denariusa* (1), *Gymnochanda* (5), *Paradoxodacna* (1), *Parambassis* (19), and *Tetracentrum* (3), with 50 species (e.g., Roberts, 1994; Kottelat, 1995, 2003; Anderson and Heemstra, 2003).

Family EMBIOTOCIDAE (284)—surfperches. Coastal marine (rarely in fresh water); North Pacific.



Dorsal fin continuous, with 6–11 spines (except 15–19 in *Hysterocarpus traski*) and 9–28 soft rays; anal fin with three spines and 15–35 soft rays; lateral line high on body, complete (but not on caudal fin); scales cycloid, generally 35–75 in lateral line; caudal fin forked. Viviparous (impregnation by the male is aided by the thickened forward end of the anal fin, and embryos may rely on connections to maternal tissue for developmental requirements). Maximum length about 45 cm, attained in *Rhacochilus toxotes.*

Eighteen species occur in the Pacific off western North America with one in fresh water (Nelson et al., 2004), and three or four occur off Japan and Korea. *Hysterocarpus traski* lives in fresh water in California (but reduced from its former range and rarely extending into brackish-water estuaries). *Cymatogaster aggregata,* an otherwise marine species, extends into estuaries and the lower portions of coastal rivers in North America.

Thirteen genera, *Amphistichus* (3), *Brachyistius* (2), *Cymatogaster* (1), *Ditrema* (3), *Embiotoca* (2), *Hyperprosopon* (3), *Hypsurus* (1), *Hysterocarpus* (1), *Micrometrus* (2), *Neoditrema* (1), *Phanerodon* (2), *Rhacochilus* (2), and *Zalembius* (1), with about 24 species (based, in part, on references given in Nelson, 1994; Katafuchi and Nakabo, 2007).

Family GRAMMATIDAE (Grammidae) (285)—basslets. Marine; tropical western Atlantic.

Lateral line on body interrupted or absent; pelvic fin with one spine and five soft rays; spines in dorsal fin 11–13; eggs with filaments. Maximum length about 10 cm.

Species of this family and some members of the above few families (e.g., *Pseudochromis* and *Liopropoma*) are especially colorful and are popular as marine aquarium fishes.

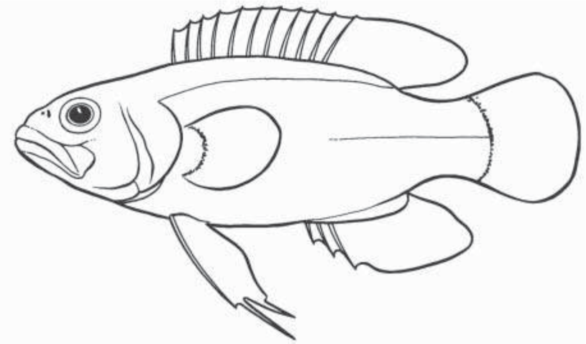
Two genera, *Gramma* (5, West Indies) and *Liopogramma* (8, tropical western Atlantic), with 13 species (e.g., Gilmore, 1997; Sazima et al., 1998).

Family PLESIOPIDAE (286)—roundheads. Marine; Indo-West Pacific.

Third branchiostegal ray extending farther posteriorly than adjacent rays resulting in a projection on the margin of the branchiostegal membrane (except in *Calloplesiops*); lateral line incomplete or disjunct. Maximum length about 20 cm.

Two subfamilies, 12 genera, and 50 species (e.g., Mooi, 1995, 1999).

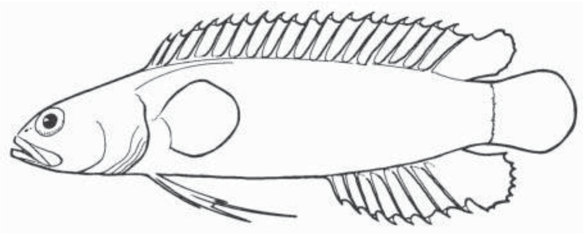
SUBFAMILY PLESIOPINAE (ROUNDHEADS OR LONGFINS). Scales on gill cover and often on top of head; dorsal fin with 11–15 spines and 6–21 soft rays; anal fin with three spines and 7–23 soft rays; pelvic fin with one spine and four soft rays. Maximum length about 20 cm.



Nelson (1994) gave the sequenced subfamily classification suggested in the 1993 cladistic study of Mooi.

Seven genera, *Assessor* (3), *Calloplesiops* (2), *Fraudella* (1), *Paraplesiops* (5), *Plesiops* (17), *Steeneichthys* (2), and *Trachinops* (4), with 34 species. Indo-Pacific, south to Tasmania.

SUBFAMILY ACANTHOCLININAE (SPINY BASSLETS). Head lacking scales or almost so; dorsal fin with 17–26 spines and 2–6 soft rays; anal fin with 7–16 spines and 2–6 soft rays; pelvic fin with one spine and two soft rays; 1–4 lateral lines; vertebrae 26–35. Maximum length about 30 cm, attained in *Acanthoclinus fuscus.*



Five genera, *Acanthoclinus* (5), *Acanthoplesiops* (6), *Beliops* (2), *Belonepterygion* (1), and *Notograptus* (2), with 16 species. Indo-West Pacific (Africa to Japan and Marshall Islands and south to New Zealand); generally less than 70 m in depth.

Family POLYCENTRIDAE (287)—South American leaffishes. Freshwater; tropical South America.

Characters (also shared with *Polycentropsis*—family Nandidae) are: eggs with a unique surface pattern of narrow ridges running radially from the micropyle; larvae with a multicellular cement gland on top of head; and adults with a unique spawning procedure (Britz, 1997). See Springer and Johnson (2004) for dorsal gill-arch musculature. Parental care is given to eggs and larvae.

Two monotypic genera *Polycentrus schomburgkii* (Guiana and the Amazon lowlands) and *Monocirrhus polyacanthus* (Trinidad to Guiana) (Britz, 1997; Berra, 2001; Britz and Kullander, 2003; Springer and Johnson, 2004).

Family POMACENTRIDAE (288)—damselfishes. Marine (rarely brackish); all tropical seas (primarily Indo-Pacific).

Nostril usually single on each side (*Chromis* and *Dascyllus* have species with double nostrils, a condition that may be difficult to see in preserved specimens); body usually high (generally terete in the plankton-pickers) and compressed; mouth small; lateral line incomplete or interrupted; anal fin with two spines (very rarely three); subocular shelf present; palate toothless; single continuous dorsal fin with 8–17 and usually 11–18 soft rays (but base of spinous portion longer than soft). Maximum length about 35 cm. Parental care of eggs by males.

Damselfishes present many problems to the taxonomist because of the many species complexes and color patterns that vary with individuals and between localities in a species. Considerable morphological diversity exists in many of the genera. The classification of this family is based primarily on Allen (1991). Tang (2001) and Jang-Liaw et al. (2002) confirmed a monophyletic Pomacentridae and subfamily Amphiprioninae (but *Premnas* was recovered within *Amphiprion*, and is thus considered a junior synonym); Chrominae and Pomacentrinae were not found to be monophyletic, but no changes are made to these subfamilies at this time.

Four subfamilies, 29 genera, and 387 species. Many new species have been described in the last two decades, primarily by G. R. Allen and by J. E. Randall.

Recent studies include Bernardi, 2011; Cooper et al., 2009; Domingues et al., 2006; Drew and Barber, 2009; Quenouille et al., 2004; Tang et al., 2004; Timm et al., 2008. The region from the Philippines to Australia has the most species.

The fossil record was reviewed by Bellwood and Sorbini (1996), Bellwood (1999), and Bannikov and Bellwood (2014). The Eocene genera from Monte Bolca, Italy, include the pomacentrids †*Palaeopomacentris,* †*Lorenzichthys,* and †*Sorbinichromis.*

SUBFAMILY AMPHIPRIONINAE (ANEMONEFISHES). Transverse scale rows 50–78 (most members of the following subfamilies have fewer than 40); all the opercles usually serrate (all the opercles not serrate in the other subfamilies); dorsal fin with 10 spines, rarely nine or 11 (most members of the following sub-families have 12–14 spines) and usually 14–20 soft rays; color variable, 0–3 white transverse bands.

These fish live in coral reefs and show a commensal relationship with large sea anemones, living about and within them for protection (nematocyst discharge is inhibited).

Two genera, *Amphiprion* (29), *Premnas* (1), with about 30 species. Found in coastal tropical Indo-West Pacific waters,

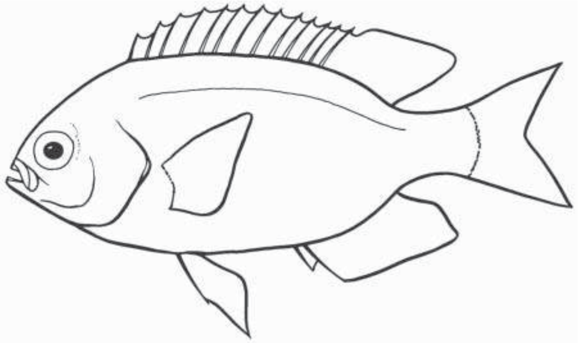
SUBFAMILY CHROMINAE. Upper and lower edges of caudal peduncle usually with two or three short spiny procurrent caudal rays. *Dascyllus* appears to have a commensal relationship with coral.

Five genera, *Acanthochromis* (1), *Altrichthys* (2), *Azurina* (2), *Chromis* (97), and *Dascyllus* (10), with about 112 species (Pyle et al., 2008; Quéro et al. 2009).

SUBFAMILY LEPIDOZYGINAE. Body elongate; upper and lower edges of caudal peduncle without projecting spiny caudal rays; small papilla-like structures on inner edge of posterior infraorbitals.

One species, *Lepidozygus tapeinosoma,* a plankton-picker found throughout much of the tropical Indo-West Pacific.

SUBFAMILY POMACENTRINAE. Body orbiculate to moderately elongate; upper and lower edges of caudal peduncle without projecting spiny caudal rays.



In the Indian Ocean and western Pacific, one of the species of *Neopomacentrus*, *N. taeniurus*, the Freshwater Demoiselle, enters estuaries and penetrates the lower reaches of streams. In the western tropical Atlantic, a species of *Stegastes*, *S. otophorus*, the Freshwater Gregory, also occurs in estuaries and the lowermost reaches of streams.

Twenty-one genera, *Abudefduf* (20, sergeant-majors), *Amblyglyphidodon* (11), *Amblypomacentrus* (3), *Cheiloprion* (1), *Chrysiptera* (33), *Dischistodus* (7), *Hemiglyphidodon* (1), *Hypsypops* (1), *Mecaenichthys* (1), *Microspathodon* (4), *Neoglyphidodon* (9), *Neopomacentrus* (16), *Nexilosus* (1), *Parma* (10), *Plectroglyphidodon* (10), *Pomacentrus* (71), *Pomachromis* (4), *Pristotis* (2), *Similiparma* (1), *Stegastes* (37) (synonym *Eupomacentrus*), and *Teixeirichthys* (1), with a total of 244 species (Allen 2004; Randall 2004).

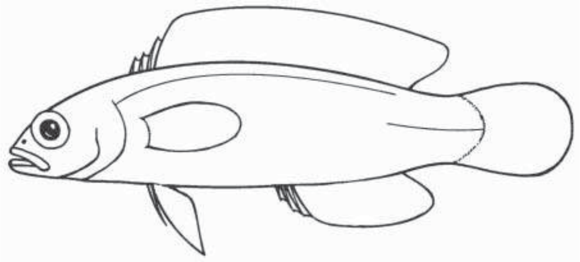
Family PSEUDOCHROMIDAE (289)—dottybacks. Marine; tropical Indo-Pacific.

Dorsal and anal fins each with one to three spines (often inconspicuous, no anal spine in congrogadines), in addition, except for congrogadines, dorsal with 21–37 soft rays and anal usually with 13–21 soft rays; pelvic fin (absent in some) with one spine and three to five soft rays, inserted below or in front of pectoral-fin base; lateral line usually interrupted or incomplete; six branchiostegal rays; no interarcual cartilage (between uncinate process of the first epibranchial and the second infrapharyngobranchial); ligamentous attachment between lower jaw and hyoid arch, unlike in most percoids; vertebrae, except in congrogadines, 26–35 (10–13 + 16–25); eggs with filaments attached to the chorion. Maximum length about 45 cm, most less than 11 cm.

Dottybacks are piscivorous, reef-dwelling fishes, often exhibiting flexible, phenotypically plastic mimicry of substrates and of other species using a wide variety of color patterns, with some able to change color within weeks of being moved to a different location. They also often show sexually dimorphic color patterns. *Pseudochromis fuscus* has recently been shown to gain multiple types of fitness benefits both by habitat-specific crypsis and by increasing access to prey such as juveniles of their model species (Cortesi et al., 2015).

Four subfamilies, 24 genera and at least 152 species (e.g., Gill, 1999, and references below).

SUBFAMILY PSEUDOCHROMINAE. Pelvic fin with one spine and five branched soft rays; head scaled; teeth on palatine; pectoral-fin rays 16–20; lateral line interrupted, two parts (one dorsoanteriorly, one midlateral posteriorly). Maximum length about 19 cm (obtained in *Labracinus*).



About ten genera: *Assiculoides* (1), *Assiculus* (1), *Cypho* (2), *Labracinus* (3), *Manonichthys* (7), *Ogilbyina* (3), *Oxycercichthys* (1), *Pholidochromis* (2), *Pictichromis* (8), and *Pseudochromis* (70), with at least 98 species (e.g., Gill and Hutchins, 1997; Gill and Randall, 1998; Gill and Allen, 2004, 2011; Gill and Edwards, 2004, 2006; Gill and Williams, 2011; Gill and Zajopnz, 2011; Gill et al., 2012a,b; Gill, 2013).

SUBFAMILY PSEUDOPLESIOPINAE. Pelvic fin with one spine and three or four simple (unbranched) soft rays; head scaled; most dorsal-fin rays simple; teeth on palatine; pectoral-fin rays 17–19; lateral line with one anterior-pored scale.

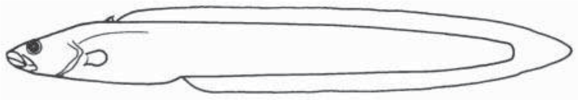
A solid foundation for monophyly of this subfamily and its genera has been laid by Gill and Edwards (1999, 2004); and Gill (2013).

Five genera, *Amsichthys* (1), *Chlidichthys* (13), *Lubbockichthys* (3), *Pectinochromis* (1), and *Pseudoplesiops* (9), with about 27 species (e.g., Gill and Edwards, 1999, 2002, 2003, 2004, 2006).

SUBFAMILY ANISOCHROMINAE. Pelvic fin with one spine and four soft rays (three branched and one simple), inserted distinctly in front of pectoral base; head naked; teeth absent on palatine; pectoral-fin rays 13–15; single lateral line along base of dorsal fin; dorsal fin with one weak spine.

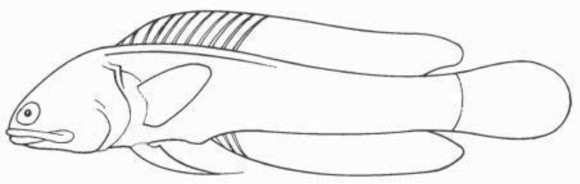
One genus, *Anisochromis*, with three species in the western Indian Ocean (Gill and Fricke, 2001).

SUBFAMILY CONGROGADINAE (EELBLENNIES). Body elongate to eel-like; body with small cycloid scales; dorsal fin with one stout spine (absent in *Congrogadus* subducens) and 32–79 rays; anal fin with no spines and 26–66 rays; dorsal and anal fins long; pelvic fin present (in eight species) (jugular and with one small spine and two to four soft rays) or absent (in 11 species); caudal fin confluent with dorsal and anal fins in a few species, slightly separated in most; mouth protractile; gill membranes united; opercle with strong, posteriorly directed spine on upper margin; one to three lateral lines, fully or partly complete (only *Halidesmus* has three and auxiliary lines may be present); palatine teeth absent, vomerine teeth present or absent; cord-like ligament extending from ceratohyal to dentary symphysis; egg surface with cruciform hooks. Maximum length about 40 cm. Eelblennies occur on coral reefs and on gravel and mud bottoms from the intertidal zone to about 140 m. Indo-West Pacific. One species is known to inhabit the insides of sponges in the Gulf of Carpentaria.



Eight genera, *Blennodesmus* (1), *Congrogadus* (6), *Halidesmus* (5), *Halimuraena* (3), *Halimuraenoides* (1), *Haliophis* (3), *Natalichthys* (3), and *Rusichthys* (2), with about 24 species (e.g., Winterbottom, 1996; Winterbottom and Randall, 1994).

Family OPISTOGNATHIDAE (290)—jawfishes. Marine; western and central Atlantic, Indian, and western and eastern Pacific (Gulf of California to Panama).



Mouth large; body with cycloid scales; eyes relatively large and high on head; head naked; pelvic fins ahead of pectorals, with one spine and five soft rays (inner three weak and branched and outer two stout and unbranched, unlike any other perciform); dorsal fin continuous, with 9–12 dorsal spines and usually 12–22 soft rays; anal fin with two or three spines and 10–21 soft rays; lateral line high, ending near middle of dorsal fin (one species has both a ventral and a dorsal lateral line); palate without teeth. The species of *Stalix* are probably unique among fishes in having the first 5–9 dorsal fin spines transversely forked distally (Smith-Vaniz, 1989). The males practice oral incubation. The eggs have filaments arranged around the micropyle. All jawfishes are burrow dwellers (usually having only their heads exposed) and use their large mouth to excavate their burrows. Maximum length about 40 cm; some species under 3 cm.

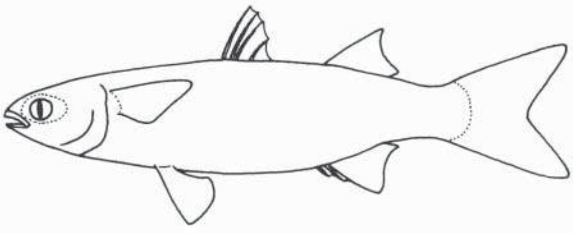
Three genera, *Opistognathus* (65), *Lonchopisthus* (4), and *Stalix* (11), with about 80 species (and many species remain to be described) (e.g., Bussing and Lavenberg, 2003; W. F. Smith-Vaniz in Smith and Heemstra, 1986; Smith-Vaniz, 1989, 1999, 2003, 2004, 2011, Smith-Vaniz et al., 2012).

THE FOLLOWING THREE ORDERS (Mugiliformes, Cichliformes including Pholidichthyidae, and Blenniiformes) are included in subseries Ovalentaria (Wainwright et al. 2012; Betancur-R. et al., 2013a) but their precise relationships within the subseries remain somewhat uncertain.

Order MUGILIFORMES (59)—mullets. There has been much disagreement concerning the relationships of the one family placed in this order. Berg (1940) placed the three families Atherinidae, Mugilidae, and Sphyraenidae in the order Mugiliformes at the subperciform level. Gosline (1971) considered the suborder Mugiloidei as a perciform and included the families Polynemidae, Sphyraenidae, Mugilidae, Melanotaeniidae, Atherinidae, Isonidae, Neostethidae, and Phallostethidae. Gosline considered his suborder Mugiloidei to be one of the most primitive perciform groups and listed it first in his perciform classification. He did this largely on the basis that all mugiloids have only a ligamentous connection and no direct articulation between the pelvic girdle and the cleithra (whereas in most other perciforms they articulate). Greenwood et al. (1966) and Nelson (1984) gave subordinal status to the first three families and placed them in the order Perciformes. In light of earlier morphological evidence relating Mugiliformes to Atherinomorpha (e.g., Stiassny, 1993) and molecular phylogenies now grouping them with

Ovalentaria, which include the Atherinomorpha (Wainwright et al. 2012; Betancur-R. et al., 2013a), Mugiliformes are here placed in Ovalentaria but with the closeness of their relationship to Atherinomorpha remaining to be determined.

Family MUGILIDAE (291)—mullets. Coastal marine and brackish water (some are freshwater); all tropical and temperate seas.



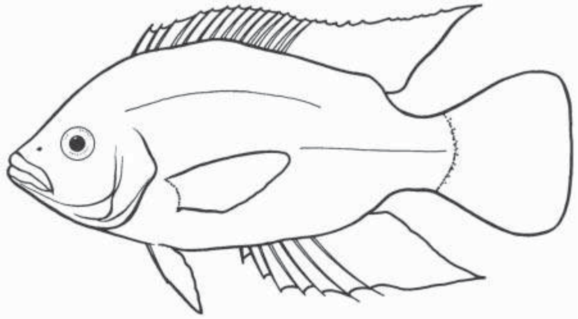
Widely separated spiny-rayed (with four spines) and soft-rayed (8–10 rays) dorsal fins; anal fin with two or three spines and 7–11 soft rays; pectoral fins high on body; pectoral girdle associated with three extrascapular bones; pelvic fins subabdominal, with one spine and five branched soft rays; lateral line absent or very faint; ctenoid scales in adults except *Myxus*, which has cycloid scales throughout life; mouth moderate in size; teeth small or absent; gill rakers long; stomach usually muscular and intestine exceedingly long; vertebrae 24–26. Oral and branchial filter-feeding mechanism involving gill rakers and a pharyngeal apparatus. Egg of typical marine, pelagic type with a single, large oil globule and a smooth surface without adhesive filament. Maximum length about 1.2 m SL. Members are also known as grey mullets (see Stiassney, 1993; Wiley and Johnson, 2010).

Liza abu is known only from fresh water and estuaries in southeastern Asia. The juveniles of many otherwise marine species extend into estuaries. Recent molecular phylogenies of the family were by Fraga et al. (2007) and Durand et al. (2012).

About 20 genera, *Agonostomus* (3), *Aldrichetta* (1), *Cestraeus* (3), *Chaenomugil* (1), *Chelon* (7), *Crenimugil* (2), *Ellochelon* (1), *Joturus* (1), *Liza* (20), *Moolgarda* (5), *Mugil* (14, synonym *Mugiloides*), *Myxus (2)*, *Neomyxus* (1), *Oedalechilus* (2), *Paramugil* (2), *Rhinomugil* (2), *Sicamugil* (2), *Trachystoma* (1), *Valamugil* (4), and *Xenomugil* (1), with about 75 species (e.g., Harrison, 2003; Menezes et al., 2010).

Order CICHLIFORMES (60)—cichlids and convict blennies.

Family CICHLIDAE (292)—cichlids. Freshwater and occasionally in brackish water; Central and South America (one species extending north to Texas), West Indies, Africa, Madagascar, Israel, Syria, coastal India, and Sri Lanka.



Single nostril on each side; lateral line interrupted, generally 20–50 scales in lateral lines but number may exceed 100; generally 7–25 spines and 5–30 soft rays in dorsal fin and 3–15 spines (3 in the majority of species) and 4–15 soft rays in the anal fin. (*Etroplus* has about 12–15 anal spines, but most other species exceeding three spines have 4–9; a few cichlids may have more than 30 soft rays in the anal fin.) No subocular shelf. Maximum length about 80 cm, attained in *Boulengerochromis microlepis* of Lake Tanganyika.

As in many families, there is much variability in body shape between some species. Most cichlids have a moderately deep and compressed body similar to *Cichlasoma* shown in the figure. However, the body can be disc shaped and have extremely high, sail-like fins, as in *Pterophyllum* (angelfishes), or low fins, as in *Symphysodon* (discus fishes); it can also be elongate, as in *Crenicichla* (pike cichlids).

Cichlids form an important group of relatively large and often colorful aquarium fishes. Many color patterns have been developed through selective breeding in some of the species for the aquarium trade. Keep in mind that the common names for the species of *Pterophyllum*, the angelfishes, can be confused with the pomacanthids, which are also known as angelfishes; the first group is freshwater and the latter is marine, and, where confusion could arise, refer to them as either the freshwater angelfishes or the marine angelfishes. There is an extensive aquaculture for several species of tilapia, especially for *Oreochromis niloticus.*

Species of the family have highly organized breeding activities (see Keenleyside, 1991). Two general forms of parental care may be recognized: i) mouthbrooders, which are usually polygamous and usually only the female carries the fertilized eggs and newly hatched eggs in the mouth; and ii) substratebrooders, which are usually monogamous and both sexes may care for the eggs. A few species combine both methods, e.g., eggs are laid and cared for on the substrate, but the newly hatched young are carried in the parent’s mouth. Mouthbrooding or oral incubation is common and appears to have arisen independently in several groups of African cichlids but is known from only a relatively few species in Central and South America. Female discus fish secrete a whitish milk-like substance from the skin to “nurse” their young.

Cichlids have attracted much attention in evolutionary biology because of the existence of species flocks in Africa. A wealth of information on the biology, adaptive radiation, and speciation of African cichlids exists. Endemic cichlids make up most of the fish fauna in the three African lakes that contain the most species of fish of any lake in the world, namely, Lake Malawi, Lake Victoria, and Lake Tanganyika. These cichlids exhibit a vast diversity of feeding habits, including species specialized to eat the scales of other fishes (e.g., Boileau et al., 2015). Berra (2001) summarized much information on the above subjects (see also Keenleyside, 1991).

Cichlids are the most species-rich non-Ostariophysan family in fresh waters worldwide (Kullander, 2003). Several species of tilapias (species of *Tilapia*, *Sarotherodon*, and *Oreochromis*) are euryhaline and can disperse along some brackish coastlines between rivers. Africa is estimated to host at least 1,600 species (see also Turner et al., 2001), four species in the Jordan Valley in the Middle East, one in Iran, three in India and Sri Lanka (also in brackish water), at least 17 on Madagascar (some also in brackish water), four in Cuba and Hispaniola (some in brackish water), 111 in North and Central America, and 291 in South America (Kullander, 2003, with figures updated from Kullander, 1998). Several authors have discussed whether or not the cichlids in various continental areas form a monophyletic group and this will not be explored here (but for a discussion of cichlid biogeography, see Chakrabarty 2004, 2006; Concheiro Pérez et al., 2007; Katongo et al., 2007; Musilová et al., 2008; Sparks, 2004a; Sparks and Smith, 2004a). MacMahon et al. (2013) used molecular data to study evolutionary rates and diversification patterns among the cichlid subfamilies in Africa and the neotropics. Friedman et al. (2013) reviewed fossil and molecular evidence that are largely congruent, agreeing with Murray (2001) in placing cichlid origins in the early Cenozoic, long after Gondwanan rifting separated South America from Africa.

There is much active work on the taxonomy and systematics of cichlids (see below). While progress is significant, there are many areas of disagreement and agreement, and a comprehensive system of assigning species to monophyletic genera has been difficult.

About 202 genera are recognized to date: e.g., *Acaronia* (2), *Abactochromis* (1), *Aequidens* (17), *Alticorpus* (5), *Amatitlania* (4), *Amphilophus* (27), *Andinoacara* (8), *Apistogramma* (85), *Astatotilapia* (8), *Astronotus* (2), *Aulonocara* (22), *Australoheros* (28), *Baileychromis* (1), *Bathybates* (7), *Benitochromis* (6), *Biotodoma* (2), *Buccochromis* (7), *Bujurquina* (17), *Caquetaia* (4), *Chetia* (6), *Chilochromis* (1), *Chromidotilapia* (11), *Cichla* (15), *Cichlasoma* (39), *Congochromis* (5), *Congolapia* (3), *Copadichromis* (25), *Crenicara* (2), *Crenicichla* (89), *Cryptoheros* (9), *Cyprichromis* (5), *Danakilia* (2), *Dicrossus* (5), *Diplotaxodon* (7), *Eclectochromis* (2), *Ectodus* (1), *Enigmatochromis* (1), *Etroplus* (3), *Fossorochromis* (1), *Geophagus* (26), *Greenwoodochromis* (2), *Guianacara* (7), *Gymnogeophagus* (11), *Haplochromis* (228), *Haplotaxodon* (2), *Hemichromis* (11), *Herichthys* (12), *Heros* (4), *Hoplarchus* (1), *Hypsophrys* (2), *Iodotropheus* (3), *Iranocichla* (1), *Julidochromis* (5), *Krobia* (4), *Lamprologus* (20), *Laetacara* (7), *Labidochromis* (18), *Lepidiolamprologus* (7), *Lestradea* (2), *Lethrinops* (24), *Maylandia* (35, possible synonym *Metriaclima*), *Melanochromis* (15), *Mikrogeophagus* (2), *Myaka* (1), *Mylochromis* (21), *Nannacara* (6), *Nanochromis* (8), *Neolamprologus* (50), *Nyassachromis* (8), *Oreochromis* (32), *Orthochromis* (14), *Otopharynx* (14), *Oxylapia* (1), *Paraneetroplus* (14), *Paratilapia* (2), *Paretroplus* (11), *Pelvicachromis* (8), *Petrochromis* (8), *Petrotilapia* (10), *Placidochromis* (43), *Plecodus* (4), *Protomelas* (15), *Pseudotropheus* (25), *Pterophyllum* (3), *Ptychochromis* (9), *Ptychochromoides* (3), *Pungu* (1), *Retroculus* (3), *Rhamphochromis* (6), *Sargochromis* (8), *Sarotherodon* (13), *Satanoperca* (8), *Stigmatochromis* (6), *Symphysodon* (3), *Taeniacara* (1), *Telmatochromis* (6), *Teleocichla* (8), *Theraps* (8), *Thorichthys* (8), *Thoracochromis* (12), *Tilapia* (44), *Tomocichla* (3), *Trematocara* (9), *Tylochromis* (18), *Tyrannochromis* (4), *Uaru* (2), *Variabilichromis* (1), *Xenochromis* (1), and *Xenotilapia* (18), with a total of about 1762 species. The African cichlid fossil record, known as early as the Eocene, was discussed by Murray (2000) and Stewart (2001).

There undoubtedly are many species yet to be described and perhaps many yet to be placed in synonymy with others. However, because an objective of this book is to provide the number of species currently recognized as valid in each family, we give the figure of 1762. Nelson (1994) and Kullander (2003) estimated at least 1,300; the increased estimate here is based largely on new species described since the last edition from Africa, southeast Asia, and Latin America. Current research in the group includes: Hulsey et al., 2004, 2011; Sparks, 2004a,b; Sparks and Smith, 2004a; Takahashi, 2004; Aibara et al., 2005; Brandstätter et al., 2005; López-Fernández et al., 2005, 2010; Lucena and Kullander, 2006; Konings and Stauffer, 2006, 2012; Kullander and Ferreira, 2006; Stauffer and Konings, 2006; Azuma et al., 2008; Renno et al., 2006; Schelly et al., 2006; Chakrabarty, 2006; Day et al., 2007; Chakrabarty and Sparks, 2007; Concheiro Pérez et al., 2007; Duftner et al., 2007; Katongo et al., 2007; Koblmüller et al., 2007, 2010; Schelly et al., 2007; Schmitter-Soto, 2007a,b; Stiassny and Schliewen, 2007; Willis et al., 2007, 2012, 2013; Musilová et al., 2008; Říčan et al., 2008; Smith et al., 2008; Cleaver et al., 2009; Oliver and Arnegard, 2010; Carvajal-Vallejos et al., 2010; Dunz and Schliewen, 2010, 2012, 2013; Ciccotto et al., 2011; Kullander, 2011a,b, 2012a,b; Lamboj and Pichler, 2012; Piálek et al., 2012; Wijkmark et al., 2012; Casciotta et al., 2013; De la Maza-Benignos and Lozano-Vilano, 2013; Friedman et al., 2013; Varella and Moreira, 2013; Malabarba et al., 2014.

Family PHOLIDICHTHYIDAE (293)—convict blenny. Marine, southwesternmost Philippines to Solomon Islands.

Body eel shaped; one nostril on each side; scales absent; pelvics below or slightly in front of pectoral base, with one thin spine and two or three soft rays, rarely absent; caudal fin rounded and joined with dorsal and anal fins; dorsal fin with 66—98 soft rays; anal fin with 49—81 soft rays; pectoral fin with 15 rays; lower pharyngeals fused into a single bone; septal bone present in interorbital area; larvae with four adhesive attachment glands between the eyes; vertebrae 71–101.

Placed in the Trachinoidei in Nelson (1994), this family is of very uncertain position. Springer and Johnson (2004), in noting previous studies associating it also with the blennioids and labroids, placed *Pholidichthys* (Pholidichthyidae) in its own suborder, as had been previously suggested by others. Here it is very provisionally included in Cichliformes on molecular evidence (e.g., Betancur-R. et al., 2013a).

One genus, *Pholidichthys*, with two species, *P. leucotaenia* Bleeker, 1856, and *P. anguis* Springer and Larson, 1996.

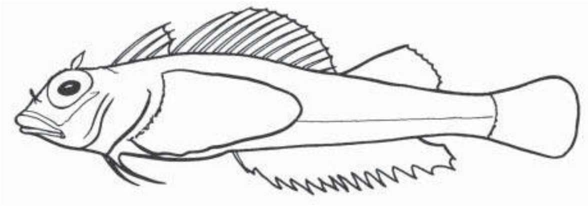
Order BLENNIIFORMES (61)—Blennies. Six families. Monophyly for this taxon is based on the following characters complexes given in Springer (1993): i) the third pharyngobranchial present but second and fourth absent and first absent or cartilaginous; uncinate process absent on first epibranchial and interarcual cartilage absent; ii) among other features of the caudal skeleton, the parhypural and hypurals 1 and 2 are fused to form a plate, and there is a dorsal hypural plate thought to comprise hypurals 3 and 4 fused to each other and to the urostylar complex; iii) pelvic fin usually with one embedded spine and two to four simple soft rays (fins absent in two species of *Plagiotremus*) and inserted in front of the pectoral-fin base, and the pelvis forming a nut-like pod open ventrally; iv) anal fin with fewer than three (0–2) spines and all soft rays simple; and v) among other features of the pectoral complex, at least some of the pectoral radials are longer than deep. Synapomorphic characters were added by Johnson (1993), Mooi and Gill (1995), and Springer and Johnson (2004). In addition, blennioids share the following: dorsal and anal-fin spine pterygiophores a single element; usually six branchiostegal rays; two nostrils on each side (except for some species of *Enchelyurus*); cirri often on head (variously on nape, above eye, on nostrils, or on margin of cephalic sensory pores).

Miocene fossils are known for several groups (references in Stepien et al., 1997:268).

Six families are recognized in this group following much earlier work by Springer (see Nelson, 1994; Springer and Johnson, 2004) who considered them to be the sole members of their Blennioidei. The families Clinidae, Labrisomidae, and Chaenopsidae were treated as one family, Clinidae, in some works, an assemblage that is probably a monophyletic group (e.g., Stepien et al., 1997; Hastings and Springer, 2009b; Lin and Hastings, 2013).

Six families, 150 genera, and at least 918 species.

Family TRIPTERYGIIDAE (294)—triplefin blennies. Marine (primarily tropical), one species occasionally in estuaries; Atlantic, Indian, and Pacific.

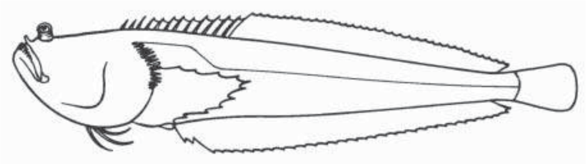


Dorsal fin divided into three distinct segments, the first two composed of spines and the third with never fewer than seven soft rays but fewer in number than the spines; no dorsal-fin spine articulating with pterygiophore serially associated with first segmented dorsal-fin ray; anal-fin spines absent to two (usually two); no cirri on nape; scales usually ctenoid, with radii in anterior field only; gill membranes broadly attached across isthmus; premaxillae protractile. Maximum length about 25 cm, most species less than 6 cm. In New Zealand, one species is known to also occur in estuaries (McDowall, 1990).

Some of the generic changes in the important work of Fricke (1997) are in error (e.g., Smith and Williams, 2002).

About 29 genera (e.g., *Acanthanectes* (2), *Apopterygion* (2), *Axoclinus* (6), *Bellapiscis* (2), *Blennodon* (1), *Bachynectes* (1), *Ceratobregma* (2), *Cremnochorites* (1), *Crocodilichthys* (1), *Cryptichthys* (1), *Enneanectes* (11), *Enneapterygius* (60), *Forsterygion* (8), *Gilloblennius* (2), *Helcogramma* (38), *Helcogrammoides* (3), *Karalepis* (1), *Lepidoblennius* (2), *Lepidonectes* (3), *Matanul* (2), *Norfolkia* (4), *Notoclinops* (3), *Notoclinus* (2), *Ruanoho* (2), *Springerichthys* (2), *Trianectes* (1), *Tripterygion* (4), *Trinorfolkia* (3), and *Ucla* (1),) with 171 species (e.g., Shen, 1994; Fricke, 1994, 1997; Williams and Fricke in Carpenter and Niem, 2001:3532–3535; Smith and Williams, 2002; Williams and Howe, 2003; Carreras-Carbonell et al., 2005, 2006; Holleman, 2005, 2007; Holleman and Bogorodsky, 2012; Rosenblatt et al. 2013). The area of greatest diversity is the Indo-West Pacific. There are relatively few species in the Atlantic.

Family DACTYLOSCOPIDAE (295)—sand stargazers. Marine (rarely brackish); warm temperate to tropical in North and South America.



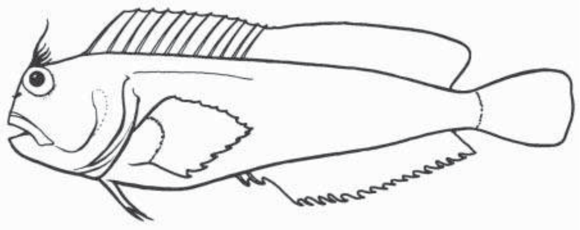
Mouth extremely oblique; lips usually fringed; upper edge of gill cover subdivided into finger-like elements; gill membranes separate and free from isthmus; eyes dorsal, somewhat protrusive (may be on stalk); pelvic fins with one spine and three soft rays, jugular; dorsal fin long, continuous or divided, with 7–23 spines and 12–36 soft rays; anal fin with 21–41 soft rays; lateral-line scales 33–73; scales cycloid; pterosphenoids absent (Springer, 1993); abdominal vertebrae 10–13 and caudal vertebrae 23–42. Maximum length 15.0 cm SL reached for *Dactylagnus mundus* Gill, 1863.

Sand stargazers frequently bury themselves in sand bottoms, similar to some trachinoids. However, unlike virtually all other teleosts, which normally pump water over the gills by alternately expanding and contracting the buccal and opercular cavities, they have evolved a branchiostegal pump that replaces the opercular pump (other benthic fishes have both). Finger-like labial and opercular fimbriae probably function to prevent particles from clogging the branchial chamber.

Nine genera, *Dactylagnus* (3), *Dactyloscopus* (20), *Gillellus* (10), *Heteristius* (1), *Leurochilus* (1), *Myxodagnus* (5), *Platygillellus* (6), *Sindoscopus* (1), and

Storrsia (1), with 48 species (e.g., Doyle, 1998; Feitoza, 2002; Williams, 2002). Nineteen species occur in the Western Atlantic (United States to Brazil) and 29 in the Eastern Pacific (Gulf of California to Chile). See Herrera et al., 2007 for a study on the development of Dactyloscopidae.

Family BLENNIIDAE (296)—combtooth blennies. Marine (rarely freshwater and occasionally brackish water, primarily tropical and subtropical); Atlantic, Indian, and Pacific.



Body naked (modified lateral-line scales in a few species); premaxillae not protractile; head usually blunt; pelvic fins present (except in two species of *Plagiotremus*), anterior to the pectorals, and with one short embedded spine (easily overlooked) and 2–4 segmented rays; palatines toothless, vomer may have teeth; jaws with comb-like teeth, fixed or freely movable (most species with at least some canine teeth); dorsal fin with 3–17 flexible spines and 9–119 segmented rays (fewer spines than soft rays in most species); pectoral rays not branched, 10–18; caudal-fin rays branched or unbranched; anal fin with two spines (the first is buried beneath genital tissue in females); basisphenoid present except in Nemophini; adults without swimbladder except in *Phenablennius*, *Omox*, and most Nemophini where it may be minute and easily overlooked; vertebrae usually 28–44 (up to 135 in *Xiphasia*). Maximum length about 54 cm, most species under 15 cm.

Many species of blenniids are involved in mimetic associations with other fishes, being similar in external appearance to the other species (e.g., Smith-Vaniz et al., 2001).

Fifty-eight genera with 397 species. The study of Williams (1990) and Bath (2001) provide a foundational understanding of relationships. Bath (2001) for example, combined the formerly recognized tribes Salariini and Parablenniini because they lacked defining characters. There have also been many studies on combtooth blennies since the 2006 edition (e.g., Springer and Allen, 2004; Smith-Vaniz, 2005; Francisco et al., 2006; Stefanni et al., 2006; Murase, 2007; Domingues et al., 2008; Almada et al., 2009; Rangel and Mendes, 2009; Javonillo and Harold, 2010; Williams and Bogorodsky, 2010; Levy et al., 2011, 2013; Smith-Vaniz and Allen, 2011, 2012; Smith-Vaniz and Rose, 2012; Pinheiro et al., 2013; Schmidt and Moccio, 2013).

SUBFAMILY SALARIINAE. Marine (rarely brackish and freshwater), primarily Indo-West Pacific. Some species can spend much of their time out of water.

Forty-two genera, *Aidablennius* (1), *Alticus* (8), *Alloblennius* (5), *Andamia* (7), *Antennablennius* (8), *Atrosalarias* (3), *Bathyblennius* (1), *Blenniella* (9), *Chalaroderma* (2), *Chasmodes* (3), *Cirripectes* (23), *Cirrisalarias* (1), *Coryphoblennius*

(1), *Crossosalarias* (1), *Dodekablennius* (1), *Ecsenius* (53), *Entomacrodus* (27), *Exallias* (1), *Glyptoparus* (1), *Hirculops* (1), *Hypleurochilus* (11), *Hypsoblennius* (16), *Istiblennius* (14), *Lipophrys* (2), *Litobranchus* (1), *Lupinoblennius* (3), *Medusablennius* (1), *Microlipophrys* (7), *Mimoblennius* (5), *Nannosalarias* (1), *Ophioblennius* (5), *Parablennius* (26), *Parahypsos* (1), *Paralticus* (1), *Pereulixia* (1), *Praealticus* (14), *Rhabdoblennius* (5), *Salaria* (5), *Salarias* (13), *Scartella* (7), *Scartichthys* (4), and *Stanulus* (2), with about 302 species.

SUBFAMILY BLENNIINAE. Marine (rarely brackish and freshwater).

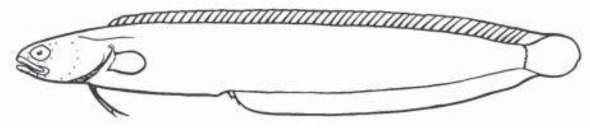
Sixteen genera, *Adelotremus* (1), *Aspidontus* (3), *Blennius* (2), *Enchelyurus* (5), *Haptogenys* (1), *Laiphognathus* (2), *Meiacanthus* (28), *Oman* (1), *Omobranchus* (21), *Omox* (2), *Parenchelyurus* (2), *Petroscirtes* (11), *Phenablennius* (1), *Plagiotremus* (11), *Spaniblennius* (2), and *Xiphasia* (2), with about 95 species.

Family CLINIDAE (297)—kelp blennies. Marine, primarily temperate in both Southern and Northern hemispheres; Atlantic, Indian, and Pacific.

Scales cycloid, with radii on all fields (scales absent only in *Clinoporus biporosus* of South Africa), and usually small and embedded; nape cirri absent (cirri may be present elsewhere on head); dorsal fin with more spines than soft rays; all fin rays simple; anal fin with two spines; cord-like ligament extending from ceratohyal to dentary symphysis. Maximum length about 60 cm, attained in *Heterostichus rostratus*, most much smaller.

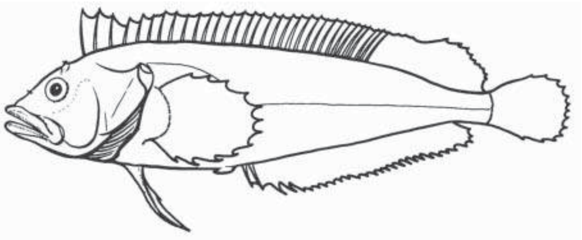
Three subfamilies provisionally recognized with 26 genera and 88 species (e.g., Zsilavecz, 2001; Hastings and Springer, 2009a,b). Unlike related families, clinids are generally absent from the tropics; there are only about four species in the tropics (in the Indo-Pacific).

SUBFAMILY OPHICLININAE. Southern Australia. Dorsal and anal fins united to caudal fin; dorsal fin continuous and without elongated anterior rays, with 36–84 spines and 1–4 soft rays; pectoral fins vestigial in several species, both pectoral and pelvic fins vestigial in *Peronedys*; no orbital cirri and nostril cirri usually absent; lateral line reduced; males with intromittent organ; ovoviviparous; body eel-shaped, especially in *Peronedys* and *Sticharium*; vertebrae 48–96 (18–35 precaudal). Maximum length 16 cm.



Four genera, *Ophiclinops* (3), *Ophiclinus* (6), *Peronedys* (1), and *Sticharium* (2), with 12 species.

SUBFAMILY CLININAE. Widespread in temperate Indo-West Pacific (including New Zealand) with about four species in the tropics. First three dorsal-fin spines usually longer than remaining spines and separated from them by a small notch; anal fin rarely attached to caudal fin; orbital and nasal cirri usually present; males with intromittent organ; ovoviviparous.

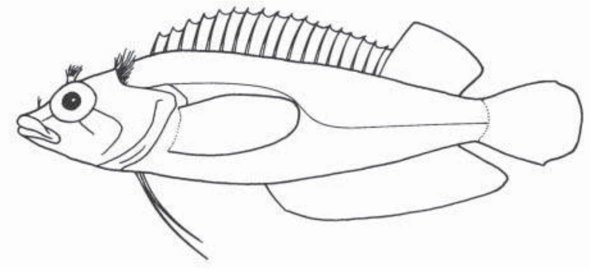


Seventeen genera, *Blennioclinus* (2), *Blennophis* (2), *Cancelloxus* (3), *Cirrhibarbis* (1), *Clinoporus* (1), *Climacoporus* (1), *Clinus* (19), *Cologrammus* (1), *Cristiceps* (3), *Ericentrus* (1), *Fucomimus* (1), *Heteroclinus* (16), *Muraenoclinus* (1), *Pavoclinus* (9), *Smithichthys* (1), *Springeratus* (3), and *Xenopoclinus* (2), with 67 species.

SUBFAMILY MYXODINAE. Temperate waters of Western Hemisphere and Mediterranean Sea. First three dorsal fin spines usually not separated from rest by notch (last two genera listed below have a deep notch between spines three and four); anal fin not attached to caudal fin; dorsal fin with 30–38 spines and 2–14 soft rays; anal fin with two spines and 18–36 soft rays; orbital and nasal cirri present; vomerine teeth present in first two genera listed below; males without an intromittent organ; oviparous; vertebrae 40–58 (precaudal 13–22).

Five genera, *Clinitrachus* (1), *Gibbonsia* (3), *Heterostichus* (1), *Myxodes* (3), and *Ribeiroclinus* (1), with about nine species. *Clinitrachus* is known only in the Mediterranean, *Ribeiroclinus* from the Atlantic coast of South America, and the others from the Pacific coast of the Americas from British Columbia to the tip of Baja California and Peru to southern Chile.

Family LABRISOMIDAE (298)—labrisomid blennies. Marine, most tropical; Atlantic and Pacific.

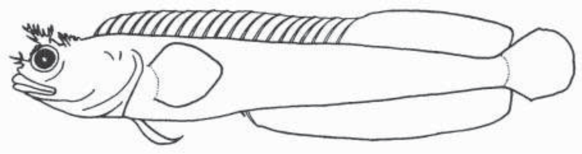


Scales cycloid, with radii only on anterior margin (scales absent in five of the six species of the New World genus *Stathmonotus* and in one species of *Neoclinus* from Taiwan) and never small and embedded; cirri often present on nape, nostril, and above eye; dorsal fin with more spines than soft rays (some species with only spines); only *Xenomedea* and eastern Pacific species of *Starksia* are viviparous, and only *Starksia* has intromittent organ in males (but of a different type than in clinids).

The monophyly of this family is uncertain; Stepien et al. (1997) found that chaenopsids form a monophyletic clade within labrisomids in their molecular analysis.

Fourteen genera: *Alloclinus* (1), *Auchenionchus* (3), *Calliclinus* (2), *Cottoclinus* (1), *Cryptotrema* (2), *Dialommus* (2), *Exerpes* (1), *Haptoclinus* (1), *Labrisomus* (21), *Malacoctenus* (22), *Nemaclinus* (1), *Paraclinus* (23), *Starksia* (37), and *Xenomedea* (1), with 118 species (e.g., Baldwin et al., 2011; Guimarães and de Bacellar, 2002; McCosker et al., 2003; Nelson et al., 2004; Sazima et al., 2009). Most species of this family occur in the tropics of North America (primarily in Central America) and South America: four species of *Neoclinus* are in the western Pacific (Taiwan to Japan), about 53 in the eastern Pacific, 47 in the western Atlantic, and two in the eastern Atlantic off Africa (one of which, a *Labrisomus*, is widespread in the western Atlantic).

Family CHAENOPSIDAE (299)—tube blennies. Warm seas of North and South America.



Body naked; no lateral line (three pores at most behind opercle); maxilla not visible externally; some species with anterior portion of dorsal fin much higher than rest; dorsal fin with 17–28 spines and 10–38 soft rays (total rays 29–57); anal fin with two spines and 19–38 soft rays; pectoral fin with 12–15 rays; caudal fin separate or variously united with dorsal and anal fins; orbital and nasal cirri variously present or absent (cirri on nape absent); palatines with teeth; head often spiny or rough; body usually elongate and compressed (as shown in figure), particularly slender (eel-like) in *Chaenopsis*. Maximum length about 16 cm, attained in various species of *Chaenopsis*, most much less.

Fourteen genera, *Acanthemblemaria* (21), *Chaenopsis* (10), *Cirriemblemaria* (1), *Coralliozetus* (6), *Ekemblemaria* (3), *Emblemaria* (16), *Emblemariopsis* (14), *Hemiemblemaria* (1), *Lucayablennius* (1), *Mccoskerichthys* (1), *Neoclinus* (11), *Protemblemaria* (3), *Stathmonotus* (7), and *Tanyemblemaria* (1), with 96 species (e.g., Rosenblatt and McCosker, 1988; Tyler and Tyler, 1997; Hastings and Robertson, 1999; Smith-Vaniz, 2000; Hastings, 2001; Williams, 2002; Ramos et al., 2003; Nelson et al., 2004; Lin and Galland, 2010; Lin and Hastings, 2011; Eytan et al., 2012). Most of the genera are amphi-American.

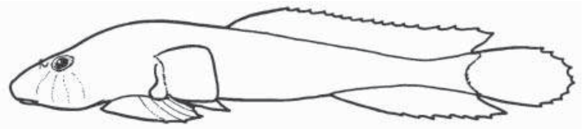
Order GOBIESOCIFORMES (62)—clingfishes. Understanding the relationship of clingfishes among acanthomorphs has been problematic, yet interesting. Rosen and Patterson (1969) included the group within Paracanthopterygii. Gosline (1970) argued, however, that Gobiesocidae probably bear some affinity with the callionymoids and possibly the notothenioids. Rosen and

Patterson (1990), following George and Springer (1980), ultimately aligned gobiesocids with blennioids. Gill-arch characters aligning these two groups are the loss of pharyngobranchial one, two, and four, and a peculiar axe-shaped third phayngobranchial (in callionymoids pharyngobranchial two is present). Springer and Johnson (2004) placed the Gobiesocidae in the suborder Callionymoidei (placed as a perciform group next to the Blennioidei). Most molecular studies recover a gobiesocid/blennioid sister-group relationship (an exception being Betancur-R. et al., 2013a, who recovered clingfishes embedded within blennioids) with callionymoids less closely related to blennioids and more closely related to syngnathiforms. In this volume, contrary to Wiley and Johnson (2010), we follow Rosen and Patterson (1990) and Conway (2015; pers. comm.) in recognizing a close relationship between clingfishes and blennies.

Family GOBIESOCIDAE (300)—clingfishes. Marine, primarily shallow water or inter-tidal, few in fresh water; Atlantic, Indian, and Pacific.

Two subfamilies, 47 genera, and 169 species.

Subfamily Gobiesocinae. Most species are shallow-water bottom-dwelling fishes. Pelvic fins modified into a thoracic sucking disc (permitting fish to adhere to substrate), with underlying pelvic bones specialized for supporting disc (pelvic skeleton highly reduced in *Alabes*); each pelvic fin with one small spine and four soft rays (rarely five); single dorsal fin without spines; head and body scaleless; branchiostegal rays 5–7 (three in *Alabes*); no circumorbital bones posterior to the lachrymal; articular process of premaxilla either fused with ascending process or absent; basibranchials one and two probably absent; supracleithrum with concave process that articulates with condyle on cleithrum (not known from other fishes); basisphenoid and orbitosphenoid absent; genital papilla behind anus; three or three and half gills; hypurals fused into a single plate; no swimbladder. The following characters apply to all gobiesocids except *Alabes*: scapula and four pectoral radials and 16–31 pectoral-fin rays; usually two postcleithra (rarely one); either common gill opening or separate opening on each side; ribs attached to the epineural ribs (an opposite relationship to that found in most fishes); total caudal-fin rays 16–27 (8–14 articulating on hypural fan); vertebrae 25–54 (11–20 + 13–33). Maximum length normally 7 cm; two species, however, reach 30 cm or slightly more—*Chorisochismus dentex* of South Africa and *Sicyases sanguineus* of Chile.



About 46 genera, e.g., *Acyrtops* (2), *Acyrtus* (3), *Apletodon* (6), *Aspasmichthyes* (2), *Aspasmodes* (1), *Aspasmogaster* (4), *Arcos* (6), *Aspasma* (1), *Briggsia* (1), *Chorisochismus* (1), *Cochleoceps* (5), *Conidens* (2), *Creocele* (1), *Dellichthys* (1), *Derilissus* (5), *Diademichthys* (1)(questionably included), *Diplecogaster* (4), *Diplocrepis* (1), *Discotrema* (3), *Eckloniaichthys* (1), *Gastrocyathus* (1), *Gastrocymba* (1), *Gastroscyphus* (1), *Gobiesox* (28) (four species of which occur in freshwater streams in Central America), *Gouania* (1), *Gymnoscyphus* (1), *Haplocylix* (1), *Kopua* (3), *Lecanogaster* (1), *Lepadicyathus* (1), *Lepadichthys* (11), *Lepadogaster* (3), *Liobranchia* (1), *Lissonanchus* (1), *Modicus* (2), *Opeatogenyus* (2), *Parvicrepis* (1), *Pherallodichthys* (1), *Pherallodiscus* (2), *Pherallodus* (2), *Posidonichthys* (1), *Propherallodus* (1), *Rimicola* (5), *Sicyases* (3), *Tomicodon* (22), and *Trachelochismus* (2), with 158 species (Briggs, 2001a,b, 2002; Williams and Tyler, 2003; Nelson et al., 2004; Fricke, 2007; Craig and Randall, 2008, 2009; Fricke et al., 2010; Moore et al., 2012; Sparks and Gruber, 2012).

Subfamily Cheilobranchinae. The 11 species of *Alabes* differ from the other members of the family in having: pelvic bones absent in three species and present in one behind the gill opening (jugular) with three reduced rays (vestigial "sucking disc" in some specimens of one species); no rays in dorsal and anal fins; scapula and pectoral fin radials and rays absent; no postcleithra; single gill opening to both gill chambers situated on midventral side of head; pleural ribs absent (epipleurals attached to vertebral centra); total caudal-fin rays 8–11 (seven or eight articulating on hypural fan); vertebrae 60–78 (e.g., Hutchins and Morrison, 2004; Hutchins, 2006).

The highly modified marine *Alabes* (synonym *Cheilobranchus*) of the Australian region was once placed in its own family Alabetidae (Cheilobranchidae).

Infraseries Atherinomorpha. Atherinomorphs are a well-established monophyletic group that was formerly a superorder separate from Acanthopterygii (Greenwood et al., 1966) or a series (Nelson, 1996), but is included here within the subseries Ovalentaria.

Opercular and preopercular margin without spines or serrations; ctenoid scales rare; branchiostegal rays 4–15; no orbitosphenoid; four cuboidal pectoral actinosts; caudal skeleton usually with two large triangular hypural plates, never more than four; swimbladder physoclistous. The protrusible upper jaw differs from that of other acanthopterygians in lacking a ball-and-socket joint between the palatine and maxilla (a feature that prevents the premaxillaries from being locked in the protruded position) and in lacking crossed rostral ligaments extending between the palatines and the heads of the premaxillaries (however, *Odontesthes* species have a different form of crossed ligaments; Dyer, 1997). A list of synapomorphic characters is given by Parenti (1993, 2005) and Wiley and Johnson (2010). They include large demersal egg with long and chorionic filaments; coupling during mating; separation of afferent and efferent circulation during development; single or double disc-like mesethmoid ossifications; supracleithrum reduced or absent; fourth epibranchial enlarged; fourth pharyngobranchial absent; supraneurals absent; saccus vasculosus absent.

Most species of this group are surface-feeding fishes, and about 75% are confined to fresh or brackish water. This taxon contains the only naturally occurring populations of unisexual (all-female) fishes; these live in the New World—the atherinid *Menidia clarkhubbsi* and members of the poeciliid genera *Poecilia* and *Poeciliopsis* (shown by A. A. Echelle and co-authors in 1983). The diversity of adaptation for internal fertilization is not found in any other higher taxon of fishes; some freshwater members of several families have independently evolved methods for internal fertilization and may lay fertilized eggs or be viviparous (e.g., Grier and Collette, 1987). The eggs of most oviparous members have one or more long chorionic filaments that adhere to the spawning substrate and, except in most exocoetoids, have conspicuous oil droplets that coalesce at the vegetal pole. Atherinomorphs have other unusual reproductive features such as the unique male testis in being of the restricted lobular type, in which spermatogonia are restricted to the distal termini of the lobules (Parenti and Grier, 2004). Delayed hatching is a common occurrence and this may be a synapomorphy (Parenti, 2005).

The concept of a monophyletic Atherinomorpha containing the present assemblage of Atheriniformes, Beloniformes (including the Adrianichthyoidei), and Cyprinodontiformes goes back to Rosen (1964), Greenwood et al. (1966), and Rosen and Patterson (1969). Few taxa have such strong evidence for monophyly as the Atherinomorpha, and the unity of this group continues to gain support and its constituent members have remained unchanged over the last 40 years. A detailed review of the phylogeny of the Atherinomorpha with emphasis on the evolution of the unusual reproductive modifications was given by Parenti (2005). The sister group of this taxon was suggested to be the Mugilidae following evidence presented by Stiassny (1990, 1993). Support for this was given by Johnson and Patterson (1993) and Wiley et al. (2000), and atherinomorph monophyly has since been corroborated by molecular studies (e.g., Setiamarga et al., 2008; Betancur-R. et al., 2013a).

Rosen and Parenti (1981) made a major contribution in recognizing Atheriniformes as sister to the Beloniformes and the Cyprinodontiformes. They argued that the spined atherinids were primitive, with spines being lost in the cyprinodontiforms. The idea of Atheriniformes as sister to the other two orders has since been supported by others (Dyer and Chernoff, 1996; Dyer, 1998) including molecular studies (e.g., Setiamarga et al., 2008; Betancur-R. et al., 2013a).

The three orders (Atheriniformes, Beloniformes, and Cyprinodontiformes) are listed in sequence to reflect phylogeny, with 24 families, 216 genera, and about 1,891 species (over 1,300 are primarily freshwater).

Order ATHERINIFORMES (63)—silversides. Usually two separated dorsal fins, the first, if present, with flexible spines, and the second preceded by a single flexible spine in most species (Parenti, 1993, suggested that the second dorsal fin is homologous with the single dorsal fin of Cyprinodontiformes); anal fin usually preceded by a spine; lateral line absent or very weak; branchiostegal rays 4–7; narial openings paired; pectoral fins inserted high on body in most; pelvic fins abdominal (most species), sub-abdominal, or thoracic in position (essentially absent in female phallostethids and highly modified in male phallostethids); parietals absent in infraorder Atherinoida, present in other taxa. Two derived larval features are preanal length of larvae between hatching and flexion less than 40% of body length (longer in members of most other eurypterygians); larvae with single middorsal row of melanophores on dorsal margin (most other atherinomorphs have two or more mid-dorsal rows). In addition, the fin rays are not evident at hatching as they are in beloniforms and cyprinodontiforms. Most species are silvery in color (and have a silvery lateral stripe), except male melanotaenioids, which can be very colorful. Maximum length about 52 cm, in the atherinopsid *Odontesthes bonariensis* (Dyer and Chernoff, 1996:44). See "infraseries Atherinomorpha" above for further comments on this order.

The following sequenced classification follows Dyer and Chernoff (1996) and Dyer (1998, 2000). Dyer and Chernoff (1996) and Dyer (1998) Synapomorphies given by Dyer and Chernoff (1996) include ventral face of vomer concave; adductor mandibulae A1 with long tendon to lactimal; presence of two anterior infraorbital bones; presence of a pelvic-rib ligament; second dorsal fin spine flexible. Also see Wiley and Johnson (2010).

Two suborders, eight families with 52 genera and about 351 species (about 210 are primarily freshwater, many also occur in brackish water, with 58 species in North American continental waters). Most atheriniforms are tropical or warm temperate and live in shallow, inshore marine or fresh waters.

Suborder Atherinopsoidei. The recognition of two suborders in the Atheriniformes reflects the cladistic results of Dyer and Chernoff (1996) showing that the Atherinopsidae are sister to the remaining families. One of the major needs in atheriniform systematics is to resolve the very different conclusions of Dyer and Chernoff (1996) from those of Aarn et al. (1998) and Aarn and Ivantsoff (1997).

Two families (Atherinopsidae and Notocheiridae), fourteen genera and 111 species.

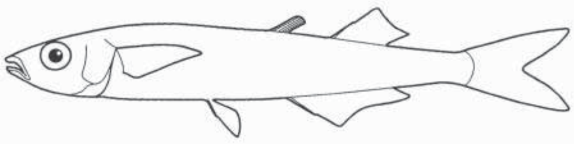
Family ATHERINOPSIDAE (301)—New World silversides. Marine (pelagic coastal) and freshwater; temperate to tropical North, Central, and South America.

Two widely separated dorsal fins, the first with 2–9 spines; pectoral fins inserted high on body. Body often translucent, with silvery lateral stripe. Diagnostic features include sphenotic postorbital process wide at base, premaxilla with narrow anterior joint. Other characters supporting monophyly of this group and as the sister group to all other atheriniforms are given in Dyer (1997, 1998) and Dyer and Chernoff (1996). Atherinopsids are most easily separated from the atherinids in having the premaxilla protractile (usually highly protractile), distal end of the premaxilla expanded, premaxilla lacking post-maxillary process, and preopercular sensory canal connecting to mandibular canal (Chernoff, 2003) (see Atherindae for opposing characters). Maximum length in most adults about 15 cm.

The Atherinopsidae, restricted to the New World, have generally been recognized as a subfamily of the Atherinidae. They were formerly removed from the Atherinidae and recognized at the family level by Saeed et al. (1994), but regarded as sister to the notocheirids, rather than as sister to all remaining atheriniforms as proposed by Dyer and Chernoff (1996).

Thirteen genera and about 110 species in two subfamilies (about 58 species are primarily marine or brackish water, as defined by spawning habitat, and about 50 are confined to fresh water). These are the only atheriniforms in the New World except for *Notocheirus* and a few atherinids (see also below under Notocheiridae).

SUBFAMILY ATHERINOPSINAE. Marine, brackish, and freshwater. Eastern Pacific and western South Atlantic, and coastal drainages.

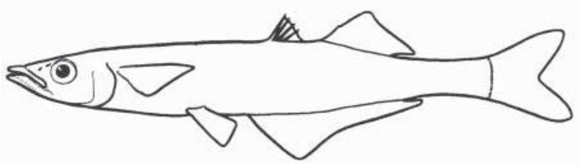


Two tribes with six genera and 30 species (Dyer 1997, 1998; Dyer and Gosztonyi, 1999; Malabarba and Dyer, 2002).

TRIBE ATHERINOPSINI. *Atherinops* (1), *Atherinopsis* (1), *Colpichthys* (2), and *Leuresthes* (2, grunions: watching grunions run is a popular night-time sport in California) with a total of six marine species, occasionally brackish water, temperate Pacific coast North America from British Columbia to Gulf of California).

TRIBE SORGENTININI. *Basilichthys* (four species, freshwater, Peru, and Chile) and *Odontesthes* (20 species, of these about eight primarily coastal marine Peru and southern Brazil south to Tierra del Fuego, and 15 primarily freshwater, Chile and southern Brazil to Patagonia, with many of the 23 also in brackish water).

SUBFAMILY MENIDIINAE. Some temperate species but primarily in the tropics with many freshwater members in Mexico and Central America.

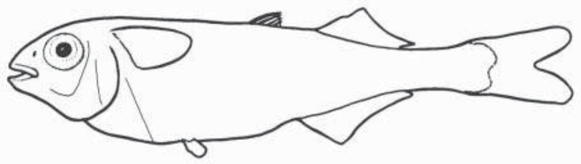


Two tribes with seven genera, and 80 species.

TRIBE MENIDIINI. *Labidesthes* (1, shown in the figure), *Menidia* (8), *Chirostoma* (23), and *Poblana* (4), with about 36 species (Barbour, 2002; Dyer, 2003). Echelle and Echelle (1984) argued that *Chirostoma* and *Poblana* are synonyms of *Menidia* (*Labidesthes* would then be the primitive sister group of the more inclusive *Menidia*). The synonymy of the three genera was not accepted by Dyer (2003) but was by Miller et al. (2005).

Tribe membradini. *Atherinella* (35 species in fresh, brackish, and coastal marine waters, with about 15 primarily marine and 20 primarily freshwater, Mexico to South America, Chernoff 1986a,b; Dyer, 2003; Nelson et al., 2004), *Membras* (six marine species), and *Melanorhinus* (three marine species, Dyer, 2003); each of the three genera has Atlantic and Pacific members.

Family NOTOCHEIRIDAE (302)—surf silversides. Marine, coastal; southern South America (Argentina and Chile). The common name is from Allen (1995).



First dorsal fin absent; epurals absent.

Saeed et al. (1994) and Aarn and Ivantsoff (1997) considered the New World *Notocheirus* to be closer to the New World Atherinopsidae, and this has been supported by the molecular phylogeny of Bloom et al. (2012).

One monotypic genus, *Notocheirus hubbsi.*

Suborder Atherinoidei. According to Dyer and Chernoff (1996), the remaining taxa form a monophyletic group, sister to the above Atherinopsidae. In their cladogram, the Notocheiridae are sister to the Atherinoida, but following Bloom et al. (2012), the Notocheiridae belong with the Atherinopsoidei (see above), and the Isonidae (formerly synonymized with the Notocheiridae by some) belong here, with the Atherinoidei. For the other families, Sparks and Smith (2004b), in a molecular study analysed by Maximum Parsimony, found the following relationships listed in approximate phylogenetic sequence: Atherionidae, Phallostethidae, Atherinopsidae, Notocheiridae, Atherinidae, and Melanotaenioidei (Pseudomugilidae, Melanotaeniidae, Bedotiidae).

Six families, 37 genera, and about 240 species.

Family ISONIDAE (303)—surf sardines. Marine, Indo-West-Pacific (South Africa to southern Japan and Australia, American Samoa, Taiwan, Hawaii, etc.)

Body depth greatest very anteriorly, at pectoral fin origin (due to elongated cleithrum and coracoids); body highly compressed; pectoral fins inserted exceptionally high on body, above lateral line and near dorsal surface; ventral abdominal edge keel-shaped, formed by ventral expansion of cleithra, post-cleithra, and pelvic girdle; upper jaw teeth confined to symphyseal portion of premaxilla; supracleithrum absent; postcleithrum and cleithrum elongated and about equal in length. Maximum length about 5 cm.

Saeed et al. (1994, 2006) recognized Isonidae separately from Notocheiridae, but Dyer and Chernoff (1996) and Sparks and Smith (2004b) concluded that they were sister groups, and thus could be in the same family, as adopted by Nelson (2006). Recent molecular studies support the earlier idea in finding that *Notocheirus* and *Iso* are not sister clades, the former being related to Atherinopsidae and the latter to Atherinidae (Bloom et al., 2012).

One genus, *Iso*, with five Indo-West Pacific species (Saeed et al., 1993, 1994; Ivantsoff 1999).

Family MELANOTAENIIDAE (304)—rainbowfishes and blue eyes. Freshwater, some in brackish water, rarely in marine water; Madagascar, New Guinea and adjacent islands, northern and eastern Australia, and parts of eastern Indonesia.

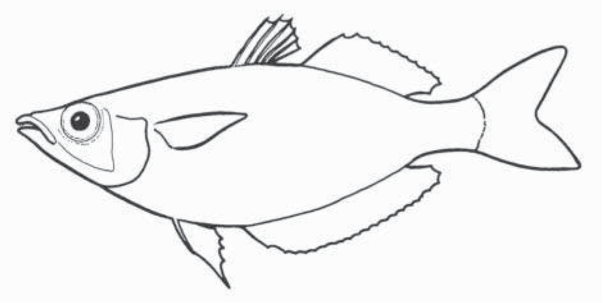
Distal premaxillary teeth enlarged (shared with telmatherinids); body compressed; dorsal fins narrowly separated, the first with 3–7 spines and the second with 6–22 rays (the first being a stout spine in some species); anal fin with 10–30 rays, the first ray a stout spine in some species; lateral line absent or weakly developed; scales relatively large, 28–60 in lateral series; innermost pelvic ray attached to abdomen by membrane along its entire length. (This is a useful character in separating rainbowfishes from silversides, but the membrane is easily broken.) Vertebrae 27–38. Most members of this family exhibit some sexual dimorphism with, for example, males usually being more colorful than females and having the median fin-ray extended (other atheriniforms except for *Quirichthys*, are monomorphic).

Seventeen genera with 140 species (some occur in marine waters but all are primarily freshwater). The four subfamilies of rainbowfishes and blue eyes have been variously recognized as separate families (e.g., Allen, 1995, Ivantsoff et al., 1997) or subfamilies of the same family (e.g., Dyer and Chernoff, 1996). They are herein placed in the same family to indicate their monophyletic relationship (e.g., Sparks and Smith, 2004b). The two terminal groups of the Melanotaeniidae of Dyer and Chenoff (1996), ranked as tribes, are ranked here equally as subfamilies, to better follow conventional practice while still maintaining phylogenetic relations, giving four subfamilies of Melanotaeniidae.

SUBFAMILY BEDOTIINAE (MADAGASCAR RAINBOWFISHES). Anal fin spine weak or absent; pterotic canal absent. Recognized as a family by Stiassny et al. (2002) but recognized as a subfamily of Melanotaeniidae, as done here, by Dyer and Chernoff (1996), who regarded this taxon as the primitive sister group of their Melanotaeniinae and Pseudomugilinae. Freshwater; Madagascar (primarily forested rivers, streams, and swamps, in central and eastern parts).

Two genera, *Bedotia* (9) (Stiassny and Harrison, 2000; Sparks, 2001) and *Rheocles* (7) (Stiassny and Rodriguez, 2001; Stiassny et al., 2002; Sparks and Rush, 2005; Loiselle and Rodriguez, 2007; Jones et al., 2010), with at least 16 species.

SUBFAMILY MELANOTAENIINAE (RAINBOWFISHES). Posttemporal canal present; strong spine preceding second dorsal fin (this spine is absent in *Cairnsichthys* and *Rhadinocentrus*). Maximum length about 12 cm. Freshwater, some in brackish water. New Guinea and small nearby islands and in Australia.



Seven genera with about 84 species (Allen, 1991; Allen and Renyaan, 1996a,b; Allen, 1997; Price, 1997; Allen, 1998; Allen and Renyaan, 1998). Most of the species are in New Guinea and a few are in common with Australia and New Guinea (*Melanotaenia* and the monotypic *Iriatherina*).

The generic relationships expressed here in three unnamed clades at the tribe level are based on Aarn and Ivantsoff (1997), though a slightly different result for the relationships among them was obtained by Sparks and Smith (2004b).

Unnamed Tribe—*Chilatherina* (about 11), *Glossolepis* (about 9), and *Melanotaenia* (about 60); e.g., Kadarusman et al. (2011, 2012), Sudarto and Pouyaud (2010).

Unnamed Tribe—*Cairnsichthys* (1) and *Rhadinocentrus* (1), each being monotypic. The sister group of this taxon, unlike that given here, was considered by Aarn and Ivantsoff (1997) to be a clade of the bedotiine genera *Bedotia* and *Rheocles*.

Unnamed Tribe—*Iriatherina werneri* (1). This clade was considered by Aarn and Ivantsoff (1997) to be sister to the above five genera and *Bedotia* and *Rheocles*. Relationship uncertain: *Pelangia mbutaensis* (1) (Allen, 1998).

SUBFAMILY PSEUDOMUGILINAE (BLUE EYES). Mesethmoid absent; fin spines tend not to be as rigid as in rainbowfishes and the second dorsal fin lacks a spine. These colorful fishes are generally much smaller than rainbowfishes with a maximum length of about 6.5 cm SL. Brackish and freshwater, generally at elevations under 100 m, rarely in marine water in mangrove swamps. New Guinea and small nearby islands and in Australia.

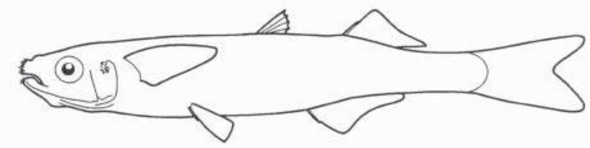
Three genera, *Kiunga* (2), *Pseudomugil* (19 species in New Guinea and Australia), and *Scaturiginichthys* (1), with 22 species (Allen, 1995; Allen and Renyaan, 1999; Ivantsoff et al., 1997; Ivantsoff, 1999).

SUBFAMILY TELMATHERININAE (CELEBES RAINBOWFISHES). Freshwater; Indonesia on Sulawesi and Misool Island off Irian Jaya (West Papua).

Aarn et al. (1998) rediagnosed this taxon on the basis of 26 characters and considered it a family phylogenetically separate from the Melanotaeniidae (subfamily Psuedomugilinae), whereas Dyer and Chernoff (1996) and Dyer (1998:522) place it as a sister group to their tribe Pseudomugilini (i.e., as one of two tribes of the Psuedomugilinae). Sparks and Smith (2004b) sampled only three species, finding one telmatherinine (*Marosatherina*) to be nested between two pseudomugilines (*Pseudomugil* spp.).

Five genera, *Kalyptatherina* (1), *Marosatherina* (1), *Paratherina* (4), *Telmatherina* (10), and *Tominanga* (2), with 18 species (Aarn et al., 1998). *Kalyptatherina* and *Marosatherina* are considered to be in one clade with the last three genera in another clade (Aarn et al., 1998). Most species are from the Malili lakes and area, of Sulawesi (e.g., Kottelat et al., 1993; Aarn et al., 1998).

Family ATHERIONIDAE (305)—pricklenose silversides. Marine (tropical and subtropical); Indian (South Africa to India) and western Pacific (southern Japan to Fiji and Australia).



Shagreen denticles present on outside of mouth area and parts of head; origin of first dorsal fin behind tip of pelvic fins; first dorsal fin with 3–6 spines, second with 1 spine and 8–13 soft rays; anal fin with 1 spine and 13–17 soft rays; midlateral scales about 40–44. Maximum length about 5.5 cm.

Previously considered a subfamily of Atherinidae; the studies of Dyer and Chernoff (1996) and Aarn and Ivantsoff (1997) strongly support its separation.

One genus, *Atherion,* with three species.

Family DENTATHERINIDAE (306)—Mercer's tusked silverside. Marine; tropical western Pacific (Philippines to northern Java, New Guinea, northeastern Australia, and Fiji).

Large lateral wings of parasphenoid beneath orbits; maxilla with large spatulate process from anterior edge; one epural; elongate ventral postcleithrum (dorsal postcleithrum absent); ectopterygoid and quadrate fused; premaxilla with a ventrally directed tusk-like process; branchiostegal rays usually 5; first dorsal fin with 5–8 spines; midlateral scales 40–43. Called "pygmy silversides" in Allen (1995).

Dentatherina was recognized in Atherinidae before Parenti's (1984) study in which she considered it and the phallostethines to be sister taxa; this hypothesis was strengthened by Dyer and Chernoff (1996) and the clade is recognized on the basis of several osteological features. Although Dyer and Chernoff (1996), Aarn and Ivantsoff (1997) and Nelson (2006) placed *Dentatherina* within Phallostethidae, we follow Ivantsoff (1999) and Parenti and Louie (1998) and recognize a distinct Dentatherinidae.

Dentatherina and the phallostethids overlap in Borneo and the Philippines, with the coastal marine *Dentatherina* extending much farther east than the largely coastal and freshwater phallostethines, which are in the western part of the Indo-Australian archipelago. The only phallostethine to occur east of

Borneo and east of Wallace's Line is a species of *Neostethus* found in Sulawesi (Parenti and Louie, 1998).

One species, *Dentatherina merceri* (e.g., Patten and Ivantsoff, 1983; Parenti and Louie, 1998; Ivantsoff, 1999).

Family PHALLOSTETHIDAE (307)—priapiumfishes. Brackish and freshwater (rarely coastal marine); Southeast Asia, from the Philippines to Thailand and Sumatra.

Males with unique bilaterally asymmetric, subcephalic copulatory organ under the throat termed the priapium (see below for description), modified primarily from pelvic skeleton; pelvic skeleton absent in females, except, primarily, in *Gulaphallus falcifer* (see Parenti 1986a, 1989); fertilization internal but development oviparous with females laying fertilized eggs; eggs with a filamentous process; anus and urogenital openings anterior, below pectoral fin in both sexes; fleshy keel extending on abdomen from urogenital opening to origin of anal fin; body compressed and transparent to translucent in life; usually two dorsal fins, the first, if present, with one or two short spines or thickened rays and second with 5–10 rays; anal fin with 13–28 rays; pectoral fin high, with 9–13 rays; two pectoral radials; scales cycloid, 28–58 in lateral series; branchiostegal rays 4–6; vertebrae 31–40.

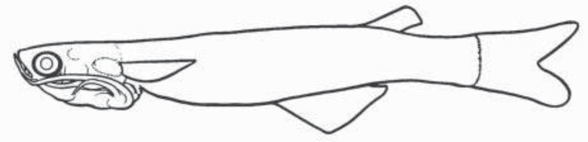
The priapium is used to hold the female during mating. This complex muscular and bony organ contains ducts from the kidney and gonads as well as terminal parts of the intestine. Parenti (1989), in identifying homologies, gives a detailed description of the priapium and its three components: i) suspensory components, ii) holding or clasping component consisting of elongate parts of the ctenactinium (or toxactinium), and iii) papillary component.

The male's body is asymmetrical with the anus and priapium being on opposite sides. In what are termed sinistral males, the anal opening is on the right side (proctal side) with the priapium being on the left side (aproctal side). In dextral males the anal opening is on the left side (proctal side) with the priapium being on the right side (aproctal side). Females have the anal opening on the mid-line. In most species the sinistral and dextral males are about in equal numbers, but a few species are predominantly sinistral or dextral (Parenti, 1986b). Unique features of the gonad structure are discussed in Grier and Parenti (1994).

Maximum length 3.7 cm SL, attained in *Gulaphallus eximus* of Luzon, Philippines.

Four genera with 23 species (Parenti, 1989, 1996, 1999; Parenti and Louie, 1998). The relationships of the member groups were well established by Parenti (1989, 1996); however, the category of subfamily employed in her studies has been altered to tribe to accommodate recognizing the dentatherinines as a subfamily of the phallosthethids.

SUBFAMILY PHALLOSTETHINAE. Jaws highly protrusible with elongate premaxillary ascending processes, priapium with a reduced second ctenactinium; shield-like pulvinulus present, covering articulation of toxactinium and proctal axial bone; skin of gular flap not perforated. *Neostethus,* which is coastal marine, brackish, and freshwater in Thailand, Malayasia, and Philippines, is thought to be sister to the clade of the other two genera, found in brackish and freshwater in Malayasia (Malay Peninsula and northern Borneo) and Thailand.

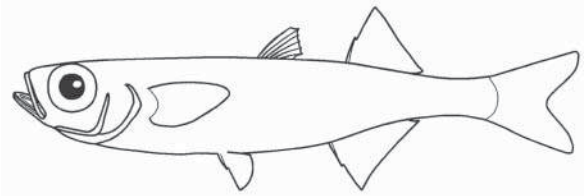


Three genera, *Neostethus* (12), *Phallostethus* (3), and *Phenacostethus* (3), with 18 species (e.g., Shibukawa et al., 2012).

SUBFAMILY GULAPHALLINAE. Jaws only slightly protrusible; priapium lacking a second ctenactinium; pulvinulus absent; adult males with a perforated gular skin flap through which anterior end of first ctenactinium projects.

One genus, *Gulaphallus,* with five species. Four species in streams on Luzon and one in brackish to coastal marine areas of Panay, Philippines.

Family ATHERINIDAE (308)—Old World silversides. Marine (pelagic coastal) and freshwater; Atlantic and Indo-West Pacific.



Two widely separated dorsal fins, the first with 2–5 spines; pectoral fins inserted high on body. Body often translucent, with silvery lateral stripe. Diagnostic features include lacrimal notch present on posterior margin (where it articulates with the condyle of the lateral ethmoid), ventral postcleithrum between first and second pleural ribs (as in atherinopsids), and ventral pelvic spine on pelvic bone (separating the abductor muscles of the pelvic spine and pelvic soft rays) (Dyer and Chernoff ,1996). Formerly included members now placed in Atherinopsidae (see Atheriniformes for reasons for separation). Most easily separated from the atherinopsids in having the premaxilla not protractile, distal end of the premaxilla narrow, premaxilla with a postmaxillary process, and preopercular sensory canal connecting to anterior infraorbital canal (Chernoff, 2003) (see Atherinopsidae for opposing characters). Maximum length about 10 cm.

Four subfamilies, 13 genera, and about 68 species. Species of this family occur primarily in the Old World, in the Indo-West Pacific, in contrast to the New World silversides of the family Atherinopsidae; however, three species of the subfamily Atherinomorinae are in the subtropical/tropical western Atlantic (southern Florida to Argentina), *Alepidomus evermanni* (endemic to

Cuba where it is primarily freshwater), *Atherinomorus stipes*, and *Hypoatherina harringtonensis* (Chernoff, 2003). According to Dyer and Chernoff (1996), the Craterocephalinae and Atherininae are sister groups, and the resulting clade is sister of the Atherinomorinae.

SUBFAMILY ATHERINOMORINAE. Five genera, *Alepidomus* (1), *Atherinomorus* (11), *Hypoatherina* (13), *Stenatherina* (1), and *Teramulus* (2), with about 28 species (e.g., Ivantsoff and Crowley, 1999; Kimura et al., 2002; Sasaki and Kimura, 2012, 2013). Mainly Indo-West Pacific and tropical western Atlantic (see family for listing of western Atlantic species).

SUBFAMILY CRATEROCEPHALINAE (HARDYHEADS). Two genera, *Craterocephalus* (*Allanetta, Quirichthys*) (26; Crowley et al., 1995; Ivantsoff and Crowley, 1999), and *Sashatherina* (1), with 27 species. Most species freshwater, some brackish and coastal marine; mainly New Guinea and Australia.

SUBFAMILY BLEHERATHERININAE. One monotypic genus, *Bleheratherina pierucciae*, New Caledonia (Aarn and Ivantsoff, 2009).

SUBFAMILY ATHERININAE. Five genera, *Atherina* (5), *Atherinason* (1), *Atherinosoma* (2), *Kestratherina* (2), and *Leptatherina* (2), with about 12 species. Freshwater and marine; primarily eastern Atlantic (including Mediterranean Sea) for the five species of *Atherina* (e.g., Francisco et al., 2008) and Australia for species of the other four genera.

Order BELONIFORMES (64)—needlefishes. Interarcual cartilage (connects the epibranchial of the first gill arch with the pharyngobranchial of the second gill arch) small or absent; second pharyngobranchial vertically oriented; small second and third epibranchials; interhyal absent; dorsal hypohyal absent; parietals small or absent; lower caudal fin lobe with more principal rays than the upper lobe. In addition, all species of this order have a fixed or nonprotrusible upper jaw. The loss of premaxillae movement is associated with the above noted loss of the interhyal and, in at least the medaka, in the secondary loss of long ascending processes of the premaxillae; it is inferred that the entire branchial apparatus has limited movement (Rosen and Parenti, 1981; Parenti, 1987, 2005, 2008).

Ordinal status for the Beloniformes is recognized here for reasons given in Nelson (1994:264). See discussion below under Adrianichthyoidei.

Two suborders, six families, 34 genera, and 283 species. About 98 species are confined to freshwater or weak brackish water. Beloniforms dominate the epipelagic region of the tropics and subtropics.

Suborder Adrianichthyoidei. Prior to the 1980s, this taxon was classified with the Cyprinodontiformes (as herein defined). Rosen and Parenti (1981) provided evidence, primarily based on characters of the gill arch skeleton and hyoid apparatus, indicating monophyly of a taxon comprising the Adrianichthyidae within the Beloniformes, and the adrianichthyids were placed within Beloniformes in the 1994 edition, in one of two suborders recognized. Li (2001) considered only the interhyal absence in both suborders of beloniforms to be valid and, on the basis of several assumed synapomorphies, placed the adrianichthyoids within the Cyprinodontiformes. Parenti (2008b) provided strong evidence for the inclusion of Adrianichthyidae within Beloniformes. The molecular studies of Near et al. (2012a) and Betancour-R. et al. (2013a) also support this relationship.

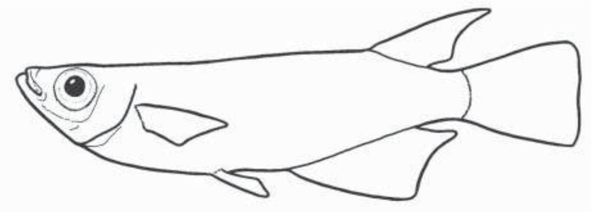
Family ADRIANICHTHYIDAE (309)—adrianichthyids. Freshwater and brackish water; India to Japan and to Indo-Australian archipelago.

Articular surface of fourth epibranchial expanded; cartilaginous ceratobranchial epiphysis branched; tooth plate on the fourth ceratobranchial absent; Meckel's cartilage about one-half the length of the dentary; jaw symphasis cartilaginous; mandibulo-lacrimal ligament absent; lateral line absent on body; narial opening paired; vomer, supracleithrum, metapterygoid, and ectopterygoid absent; rostral cartilage absent; branchiostegal rays 4–7 (Parenti, 2008b; Wiley and Johnson, 2010).

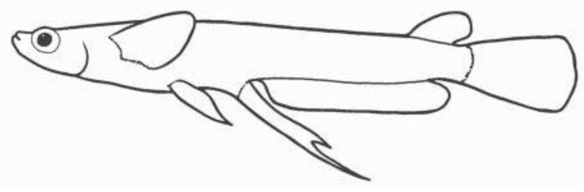
†*Lithopoecilus brouweri* from the Miocene of central Sulawesi, is tentatively placed in the Adrianichthyidae (Parenti, 2008b).

Two subfamilies with two genera and 38 species. Prior to Rosen and Parenti (1981), the three subfamilies recognized here were given family status (Oryziidae, Horaichthyidae, and Adrianichthyidae), as in Nelson (1976, 1984).

Subfamily Oryziinae (medakas or ricefishes). Jaws not tremendously enlarged; dorsal and anal fins of male (shown in figure) usually more pronounced than in female; most species with 5–7 dorsal-fin rays and 18–25 anal-fin rays; almost always egg layers. Maximum length about 9 cm. Freshwater and brackish water; India to Japan and to Indo-Australian archipelago.

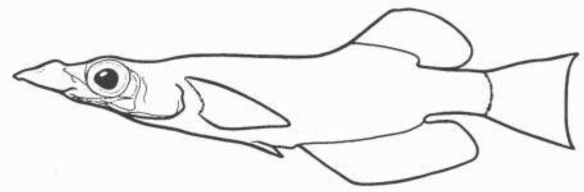


One genus, *Oryzias* (includes *Horaichthys setnai*), with about 34 species (Parenti, 1987, 2008b; Kottelat, 1990b, 2001a; Roberts, 1998a; Parenti and Soeroto, 2004; Takehana et al., 2005; Parenti and Hadiaty, 2010; Asai et al., 2011; Parenti et al., 2013).



Oryzias setnai (synonym *Horaichthys setnai*, subfamily Horaichthyinae in Nelson, 2006) is the only atherinomorph known to produce spermatophores or encapsulated sperm bundles (Grier, 1984).

SUBFAMILY ADRIANICHTHYINAE (DUCKBILLED FISHES). Jaws tremendously enlarged; scoop-shovel-type mouth; almost always egg layers, eggs held in place against belly by pelvic fins. Maximum size up to 20 cm. Freshwater; Sulawesi (= Celebes Island).



One genus, *Adrianichthys* (4, includes *Xenopoecilus*). (Kottelat, 1990b, Kottelat et al., 1993; Parenti, 2008b; Parenti and Soeroto, 2004).

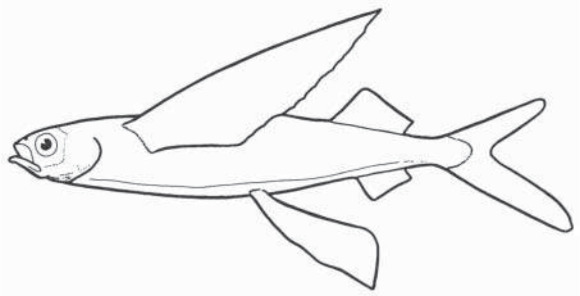
Suborder Exocoetoidei (= Belonoidei). Lateral line low on body, along ventral margin of body behind pectoral fin (absent in some freshwater hemiramphids and in *Cololabis adocetus*); narial opening single; branchiostegal rays 6–15; single lower pharyngeal tooth plate; elongate lower jaw at least in some stage of life history; basioccipital with a vertical plate-like process; no spines in fins; dorsal and anal fins placed far back on body; pectoral fin with 5–20 rays, fin inserted high on body in most species; pelvic fin with six rays, abdominal; caudal fin usually with 13 branched rays; oil droplets in egg minute or absent (Rosen and Parenti, 1981).

The suggestion of Lovejoy (2000) and Lovejoy et al. (2004) that halfbeaks and the related flyingfishes are basal to needlefishes is followed here.

Superfamily Exocoetoidea. Scales large, usually 38–60 in lateral line; mouth opening small, upper jaw never elongate; no isolated finlets; dorsal and anal fins usually with 8–18 rays each, up to 25 in *Euleptorhamphus*; teeth small; premaxillary canal absent; third pair of upper pharyngeal bones united into a palate.

Three families (Exocoetidae, Hemiramphidae, Zenarchopteridae), 20 genera, and about 194 species.

Family EXOCOETIDAE (310)—flyingfishes. Marine; tropical to warm temperate, epipelagic oceanic to coastal, Atlantic, Indian, and Pacific.



Jaws relatively short and equal in length (lower jaw produced in some juveniles); exceptionally large pectoral fins (gliding flights can be made out of water with the pectorals spread like wings) inserted high on body; pelvic fins exceptionally large in some species (thus two-winged and four-winged types can be recognized); lower lobe of caudal fin longer than dorsal lobe (fin deeply forked); juveniles of many have a pair of long, flap-like barbels (see below); swimbladder extends into haemal canal; 39–51 vertebrae. Maximum length 45 cm (attained in *Cheilopogon pinnatibarbatus californicus*); most species are less than 30 cm.

This is one of the few fish groups to actively glide in the air. There is a stepwise increase in gliding capability, with sequential changes in the caudal, pectoral, and pelvic fins, in proceeding through the cladogram of Dasilao and Sasaki (1998).

Four subfamilies (based on Collette et al., 1984), seven genera, and about 69 species. In North America there are 27 species (12 Atlantic, 19 Pacific). *Oxyporhamphus* and its subfamily Oxyporhamphinae, placed here in the previous edition, are returned to the Hemiramphidae herein (see below).

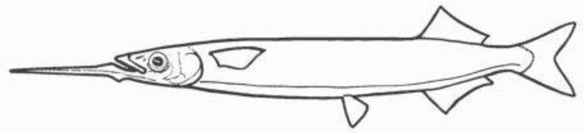
SUBFAMILY FODIATORINAE. One genus, *Fodiator,* with two species. This forms a monophyletic group to the remaining subfamilies, to which it is the sister group, based on 10 synapomorphies (Dasilao and Sasaki, 1998). The remaining taxa, except for *Hirundichthys* and *Prognichthys,* have barbels on the lower jaw in juveniles.

SUBFAMILY PAREXOCOETINAE. One genus, *Parexocoetus,* with three species. Unique in having strongly protrusible jaws and in having a process on the exoccipital directly articulating with the cleithrum (this joint between the cranium and shoulder girdle gives increased head maneuverability) (Dasilao and Sasaki, 1998).

SUBFAMILY EXOCOETINAE. One genus, *Exocoetus,* with five species.

SUBFAMILY CYPSELURINAE. Four genera, *Cheilopogon* (31, considered a synonym of *Cypselurus* in some works but Parin regarded them as separate (Parin, 1999a, 2003), *Cypselurus* (12), *Hirundichthys* (10, including *Danichthys,* a valid subgenus, and *Exonautes*), and *Prognichthys* (6), with about 59 species (e.g., Parin, 1996; 1999a,b; 2003).

Family HEMIRAMPHIDAE (311)—halfbeaks. Marine except for four freshwater species of *Hyporhamphus* (Berra 2001). Atlantic, Indian, and Pacific Oceans, Most species are coastal continental but some extend into the western and central Pacific (one species is endemic to New Zealand).



This group of halfbeaks exhibits external fertilization; upper jaw much shorter than lower (lower jaw elongate in juveniles and in most adults); premaxillae pointed anteriorly forming a triangular upper jaw; third pair of upper pharyngeal bones anklyosed into a plate; pectoral and pelvic fins short; some species with lower lobe of caudal fin longer than upper lobe (fin rounded, truncate, or forked); vertebrae 38–75 (except 18–25 in *Arrhamphus*). Maximum length about 40 cm SL, attained in *Euleptorhampus viridis.*

Hemiramphids, which are herbivorous, are one of 15 families of stomachless fish, all of which posses a pharyngeal jaw apparatus (pharyngeal mill) (Tibbetts and Carseldine, 2003). They share many pharyngeal features with cichlids (e.g., Stiassny and Jensen, 1987), but there are also many differences and at least in *Arrhamphus sclerolepis* there are departures from general euteleostean pharyngeal anatomy (Tibbetts and Carseldine, 2003). Most of the freshwater species are in the Indo-Australian region, whereas most of the freshwater needlefishes are in the Neotropical region.

Eight genera, *Arrhamphus* (2), *Chriodorus* (1), *Euleptorhamphus* (with 20–25 dorsal and anal-fin rays and 105–125 lateral-line scales) (2), *Hemiramphus* (11), *Hyporhamphus* (including *Reporhamphus*) (40), *Melapedalion* (1), *Oxyporhamphus* (2), and *Rhynchorhamphus* (4), with about 67 species (e.g., Collette et al., 1984; Collette and Su, 1986; Collette, 1995, 2004a; Banford and Collette, 2001). *Oxyporhamphus* was said to be in Exocoetidae by Dasilao et al. (1997) and Dasilao and Sasaki (1998), but is retained here in Hemiramphidae following Collette (1999, 2004a) and Lovejoy et al. (2004); it shares a vesicular swimbladder with its genetic sister genus *Hemiramphus* (Tibbetts et al., 2007).

Family ZENARCHOPTERIDAE (312)—viviparous halfbeaks. Fresh and brackish water, Asia and New Guinea.

All occur in fresh water or estuaries in the Indo-West Pacific, and have a modified anal fin (termed an andropodium and analogous to the gonopodium found in some cyprinodontiforms) for internal fertilization. The spermatozeugmata in the testes of species of *Zenarchopterus* provide a unique method of sperm packaging (Grier and Collette, 1987). Contains all the species of halfbeaks with internal fertilization; all are viviparous live-bearing except as noted below.

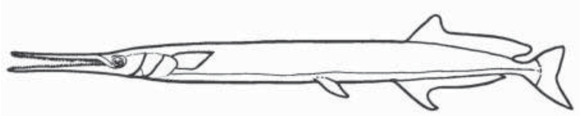
This family was considered a subfamily of Hemiramphidae in Nelson (2006). However, Lovejoy et al. (2004) gave family status to this clade; family status has been accepted by many authors since, and is followed here.

Five genera, *Dermogenys* (13), *Hemirhamphodon* (6), and *Nomorhamphus* (19), and the oviparous (laying fertilized eggs) *Tondanichthys* (1; Collette, 1995b) and *Zenarchopterus* (19 species), with about 58 species (Anderson and Collette, 1991; Meisner and Burns, 1997; Meisner and Collette, 1999; Meisner and Louie, 2000; Meisner, 2001; Collette, 2004a; Huylebrouck et al., 2012, 2014; Tan and Lim, 2013).

Superfamily Scomberesocoidea. Scales small, 70 to over 350 in lateral line; mouth opening usually relatively large, at least upper jaw slightly elongate (i.e., both jaws usually elongate); premaxillary canal present. Lovejoy (2000) concluded that the sister group of sauries (Scomberesocidae) is *Belone*, and thus that Belonidae are monophyletic only if sauries are included.

Two families, twelve genera, and 51 species.

Family BELONIDAE (313)—needlefishes. Marine and freshwater (e.g., South America, Pakistan, India, and Southeast Asia); tropical to warm temperate, epipelagic in coastal and oceanic tropical and temperate waters, Atlantic, Indian, and Pacific.

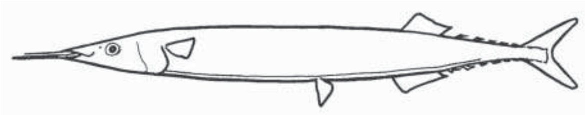


Both upper and lower jaws extend into long beaks with numerous needle-like teeth (two South American freshwater species of *Belonion* have a short upper jaw, similar to halfbeaks); mouth opening large; scales small (usually 130–350 in lateral line and easily detached); no isolated finlets behind the dorsal and anal fins; dorsal-fin rays usually 11–26, up to 43; anal-fin rays 12–39; posttemporal forked; interruptions in the cephalic lateralis system; vertebrae 52–97; general body shape superficially resembling *Lepisosteus.* One species, *Belonion apodion*, unlike the only other species in the genus, lacks the pelvic fin and girdle. Some species are capable of high jumps out of water. Maximum length about 1.5 m (reported to 2 m); several species of *Tylosurus* reach over 1 m.

At hatching, belonids have short jaws of equal length. During growth, the lower jaw first elongates forming the “halfbeak” stage; then the upper jaw elongates forming the “needlenose” stage. Lovejoy (2000) gave phylogenetic evidence that this pattern in ontogeny of passing through the flyingfish and halfbeak states is a good example of recapitulation. See above under Belonoidei for evidence that this family is not monophyletic without the inclusion of the Scomberesocidae. Lovejoy and Collette (2001) proposed multiple independent invasions of fresh water by marine taxa.

Ten genera, *Ablennes* (1), *Belone* (3), *Belonion* (2), *Petalichthys* (1), *Platybelone* (7), *Potamorrhaphis* (4), *Pseudotylosurus* (2), *Strongylura* (15), *Tylosurus* (10), and *Xenentodon* (2), with 47 species (Collette et al., 1984; Collette, 1999, 2003a,b; Collette and Banford, 2001; Lovejoy and Collette, 2001; Sant’Anna et al., 2012). About 12 species are restricted to freshwater. In North America there are 10 species (7 in Atlantic, 2 in fresh water, 5 in Pacific). The seven species of *Belonion*, *Potamorrhaphis*, and *Pseudotylosurus*, the New World clade, are South American river endemics (Lovejoy, 2000; Lovejoy and Collette, 2001), whereas the two species of *Xenentodon* are Southeast Asian river endemics, and the widespread *Strongylura* includes both freshwater (two in Central and South America and one in Asia) and marine species (Lovejoy and Collette, 2001; Collette, 2003b). Over half the species are in *Strongylura* and *Tylosurus*, the phylogeny and biogeographic history of which were estimated by Banford et al. (2004).

Family SCOMBERESOCIDAE (314)—sauries. Marine; epipelagic tropical to temperate seas.



Four to seven finlets after both dorsal and anal fins; scales small (70–91 along midline in two dwarf species and 107–148 in two large species); mouth opening relatively small, jaw length varies from long slender beaks with both jaws produced (as in *Scomberesox* and shown in figure) to relatively short beaks with lower jaw only slightly produced (small juveniles of all species have short jaws); teeth relatively small; dorsal-fin rays 14–18; anal-fin rays 16–21; swimbladder absent and ovary single in two dwarf species; vertebrae 54–70 (32–43 precaudal). Maximum length about 45 cm SL, attained in *Scomberesox saurus.*

See above under Belonoidei for molecular evidence that members of this family should be placed in Belonidae.

Two genera, *Scomberesox* and *Cololabis,* each with two species. Each genus, representing an evolutionary lineage, has one relatively large species and one dwarf that is more tropical than the large species. The classification of Collette (2003a, 2004b) and Collette et al. (1984) is followed here, but Hubbs and Wisner (1980) recognized all four species in monotypic genera, as was followed in the 1994 edition. The species are found as follows:

Scomberesox. The large species in the North Atlantic and Southern Hemisphere and the dwarf one, placed by some in *Nanichthys,* in the Atlantic and a small portion of the Indian Ocean.

Cololabis. The large species in the North Pacific and the dwarf and more tropical relative, placed by some in *Elassichthys,* in the eastern central Pacific.

In North America there are two species (one Atlantic, one Pacific).

Order CYPRINODONTIFORMES (Microcyprini) (65)—killifishes. Monophyly of this order is recognized on the basis of several derived characters: e.g., caudal fin truncate or rounded; caudal fin skeleton symmetrical, with one epural; first pleural rib on second vertebra rather than third; pectoral fin insertion ventrolateral (primitively, low-set pectoral girdle); scale-like first postcleithrum; an alveolar arm of the premaxillae; extended developmental period (Parenti, 1981; Rosen and Parenti, 1981; Costa, 1998a). In addition, they possess the following characters: lateral-line canal and pores chiefly on head, lateral line represented on body only by pitted scales; narial opening paired; branchiostegal rays 3–7; pelvic fins and girdle present or absent; upper jaw bordered by premaxilla only, protrusible; vomer usually present and supracleithrum always present; metapterygoid usually absent and ectopterygoid always absent; parietals present or absent; vertebrae 24–54. Marked sexual dimorphism with the males often brightly colored.

Members of this order are popular aquarium and experimental fishes. Rosen (1973b) presented a key to the salt-tolerant species, and Parenti (1981) gave a key to genera of most of the families. Scheel (1990) discussed the biology of the world rivulines and of some other cyprinodontiform taxa and has numerous color photographs. Lazara (2001) presented an annotated checklist, synonymy, and bibliography of the oviparous members of this order (once placed in the family Cyprinodontidae). Egg diameter varies from less than 0.3 mm to about 3 mm, and embryonic development may be less than one week to over one year (Able, 1984).

Classifications of the late 1960s through early 1980s, and followed by some authors even later, generally adopted Greenwood et al. (1966), who recognized the following families together (in their suborder Cyprinodontoidei): Oryziatidae, Adrianichthyidae, Horaichthyidae, Cyprinodontidae (including the herein recognized Aplocheiloidei, Profundulidae, Fundulidae, and two viviparous goodeid genera, *Crenichthys* and *Empetrichthys*), Goodeidae, Anablepidae, Jenynsiidae, and Poeciliidae. In a detailed anatomical study and cladistic analysis, Parenti (1981) provided evidence that this view of relationships was not correct, breaking up the Cyprinodontidae and recognizing that the viviparous families did not form a monophyletic group. While the monophyly of Parenti's (1981) nine families and recognition of two lineages, the Aplocheiloidei and Cyprinodontoidei, has been confirmed by most subsequent studies, there are changes in our understanding of the relationships of the families, based primarily on the works of Parker (1997), Costa (1998a), and Ghedotti (2000), which are given in Parenti's (2005) classification and accepted here. The largest change is that of the Goodeidae, now considered sister to Profundulidae and not to the Cyprinodontidae (Costa, 1998a).

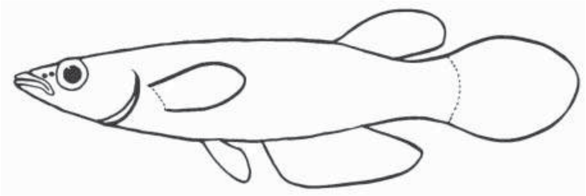
Two suborders, ten families, 131 genera, and about 1,257 species (over 996 being primarily freshwater).

Suborder Aplocheiloidei. Pelvic-fin bases inserted close together; metapterygoid present; three basibranchials; mesethmoid cartilaginous; basihyal broad anteriorly; orbital rims attached to frontals; a dorsal ray on each of the first two dorsal radials; dorsal-fin origin posterior or anterior to anal fin origin. In all other members of the order the pelvic-fin bases are not inserted close together, and they possess two basibranchials, lack the metapterygoid, and have one dorsal ray articulating with the first two radials. (Parenti, 1981).

Some members are termed "annuals." In these, adults spawn during the rainy season in temporary waters and the drought-resistant eggs with a thickened chorion may survive dry periods in diapause buried in the substrate. Hatching normally occurs during the next rainy season but may be delayed for over one year. According to Parenti (1981), the true annuals do not form a monophyletic group, and independent origins of diapause have been proposed in the rivulids (Costa, 1998b; Hrbek and Larson, 1999). Many species are particularly colorful and are popular aquarium fishes.

Three families with about 51 genera, and at least 642 species.

Family APLOCHEILIDAE (315)—Asian rivulines. Freshwater (rarely brackish); Madagascar, Seychelles, Indian subcontinent, Sri Lanka, and Indo-Malaysian archipelago to Java.



Black blotch on dorsal fin of females.

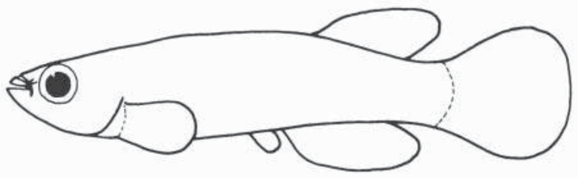
Two genera, *Aplocheilus* (7) and *Pachypanchax* (7), with at least fourteen species (Loiselle, 2006).

Family NOTHOBRANCHIIDAE (316)—African rivulines. Freshwater (rarely brackish); continental Africa (south of Sahara Desert to South Africa).

Three oblique red stripes on postorbital region of males.

At least 12 genera, e.g., *Aphyosemion* (includes *Callopanchax*, *Diapteron*, and *Scriptaphyosemion*), *Epiplatys* (includes *Aphyoplatys*), *Fundulopanchax*, *Nothobranchius*, *Pronothobranchius*, *Adamas* and *Foerschichthys*, with perhaps 258 species. Aarn and Shepherd (2001) examined some members of the lineage *Epiplatina* but with differing results from Costa (2004b). Recent studies have been mostly at the species level (e.g., Agnès et al., 2006, 2009, 2013a,b; Akum, 2007; Sonnenberg et al. 2006, 2011; Sonnenberg 2007; Valdesalici 2007; Sonnenberg and Van Der Zee, 2008; Collier et al., 2009; Costa, 2009; Sonnenberg and Busch, 2009; Wildekamp et al., 2009; Reichard, 2010; Shidlovskiy et al., 2010; Van Der Zee and Sonnenberg, 2010; Valdesalici et al., 2012; Van Der Zee et al., 2013).

Family RIVULIDAE (317)—New World rivulines. Freshwater (rarely brackish); southern Florida through much of Middle America to Uruguay and northeastern Argentina.



Supracleithrum not fused to posttemporal; first postcleithrum absent; opercular and branchiostegal membrane united and often covered with scales; pelvic fins and skeleton absent in *Rivulus nudiventris* (Costa and Brasil, 1991), and in *Simpsonichthys boitonei*, *S. parallelus*, and *S. cholopteryx* (Wilson Costa, personal communication, 2004). Maximum length 20 cm TL, most less than 8 cm, and some miniature species under 3 cm TL.

Kryptolebias marmoratus (formerly placed in *Rivulus*; Costa, 2004a), which occurs in fresh water and strongly brackish water in southern Florida and the West Indies, and one or more other species of the genus, are unique among fishes and indeed all vertebrates, in consisting of individuals with simultaneously functional ovary and testis (self-fertilizing hermaphrodites). Fertilization is internal and eggs are laid. However, internal fertilization also occurs in species of *Campellolebias* and *Cynopoecilus*, in which the anal fin is modified in males. *Kryptolebias marmoratus* also has the amazing ability to survive weeks out of water in moist environments, using the skin as a site of osmo- and iono-regulation (LeBlanc et al., 2010).

Thirty-seven genera, e.g., *Aphyolebias*, *Austrofundulus*, *Austrolebias*, *Campellolebias*, *Cynolebias*, *Cynopoecilus*, *Gnatholebias*, *Kryptolebias* (proposed by Costa 2004a for the preoccupied *Cryptolebias*, used earlier by Costa 2004b), *Leptolebias*, *Maratecoara*, *Megalebias*, *Micromoema*, *Millerichthys*, *Moema*, *Nematolebias*, *Neofundulus*, *Papiliolebias*, *Pituana*, *Plesiolebias*, *Pterolebias*, *Rachovia*, *Renova*, *Rivulus*, *Simpsonichthys*, *Spectrolebias*, *Stenolebias*, *Terranatos*, and *Trigonectes*, with about 370 species (e.g., Costa, 1998b, 2003, 2004b, 2005, 2006a,b,c,d, 2007a,b,c, 2009, 2011b, 2013; Hrbek et al., 2004, 2005; Suijker and Collier, 2006; Hrbek and Taphorn, 2008; Costa et al., 2012). The most species-rich genera are *Rivulus* and *Simpsonichthys*. Two subfamilies were established by Costa (2004a,b), Kryptolebiatinae for *Kryptolebias* and Rivulinae for all other genera.

Suborder Cyprinodontoidei. The classification in four superfamilies follows Costa (1998a) and Parenti (2004).

Superfamily Funduloidea. The Profundulidae and Goodeidae are sister taxa in the analysis of Costa (1998a), and support for this was found in the molecular study of Webb et al. (2004).

Three families, 25 genera, and about 111 species.

Family PROFUNDULIDAE (318)—Middle American killifishes. Freshwater; Atlantic and Pacific slopes of Middle America in Mexico, Guatemala, and Honduras.

Gillrakers on anterior arm of first arch 14–23; dorsal fin with 1–3 rudimentary rays and 10–16 principal rays; scales in lateral series 31–39. Fertilization external.

One genus, *Profundulus*, with eight species. All five occur in North America (Mexico).

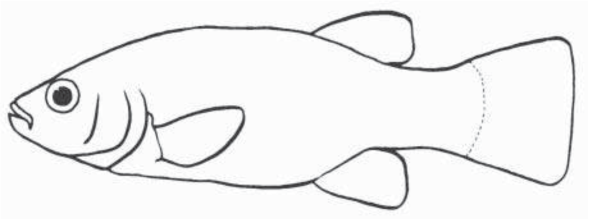
Family GOODEIDAE (319)—goodeids. Freshwater; Nevada and west central Mexico.

First two to seven middle anal radials fused to the proximal radials; dorsal processes of the maxillaries greatly reduced; distal arm of the premaxilla straight; articular reduced; ovaries united into a single median organ.

The Empetrichthyinae, formerly placed in the large and polyphyletic Cyprinodontidae, are regarded as a sister group to what was formerly regarded as the goodeids following Parenti (1981). The molecular study of Webb et al. (2004) also supported the monophyly of Goodeidae and the sister-group relationship of the Empetrichthyinae and Goodeinae. Uribe et al. (2012) described ovarian structure and oogenesis.

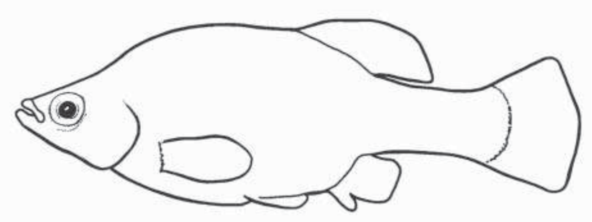
Two subfamilies, 20 genera and about 59 species.

SUBFAMILY EMPETRICHTHYINAE. Pelvic skeleton and pelvic fins absent; epibranchial Y-shaped; anal rays of males not shortened; pseudophallus not present; scales in lateral series 26–30; dorsal fin with one rudimentary ray and 11 soft rays; pectoral fin with 16 or 17 rays; vertebrae 28 or 31; fertilization external; ovaries united into a single median organ with no septum. Southern Nevada.



Two genera, *Crenichthys* (springfishes, two species) and *Empetrichthys* (poolfishes, two species from Nye County, Nevada, one of which is probably extinct).

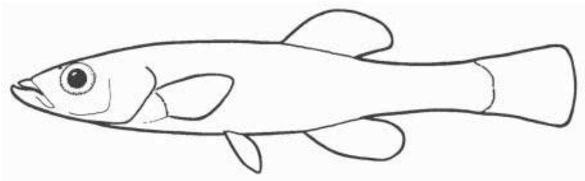
SUBFAMILY GOODEINAE. Viviparous with internal fertilization; anterior rays of anal fin in males crowded, shortened, and slightly separated by a notch from the rest of the fin (gonopodium-like structure termed a pseudophallus or andropodium); scales in lateral series 30–35; dorsal fin with one rudimentary ray and 14 or 15 soft rays; pectoral fin with 15 or 16 rays; vertebrae 37; ovaries partly united into a single median organ with a septum; eggs small and with little yolk; embryos and newborn young usually have placenta-like trophotaeniae (ribbon-like extensions from anal region associated with nutrition and respiration). Mesa Central, Mexico.



This subfamily, centered in the Rio Lerma basin, has species of many diverse body forms (deep bodied to long bodied) and feeding habits (carnivores to herbivores). Maximum length up to 20 cm. Many species are known as splitfins. Webb et al. (2004) and Doadrio and Domínguez (2004) reconstructed its phylogeny using mtDNA sequences, the latter authors finding evidence for five tribes.

Eighteen genera, *Allodontichthys*, *Alloophorus*, *Allotoca* (synonym *Neoophorus*), *Ameca*, *Ataeniobius*, *Chapalichthys*, *Characodon*, *Crenicthys*; *Girardinichthys* (synonym *Lermichthys*), *Empetrichthys*; *Goodea*, *Hubbsina*, *Ilyodon*, *Skiffia* (synonyms *Neotoca* and *Ollentodon*), *Xenoophorus*, *Xenotaenia*, *Xenotoca*, and *Zoogoneticus*, with about 55 species (Webb, 2002; Webb et al., 2004; Nelson et al., 2004; Doadrio and Domínguez, 2004).

Family FUNDULIDAE (320)—topminnows. Freshwater, brackish water, and coastal marine (rarely hypersaline); lowlands of North America from southeastern Canada to the Yucatan (Mexico), including Mississippi River drainage, Bermuda, and Cuba.



Interior (ventral) arms of maxillaries directed anteriorly, often with pronounced hooks; maxilla twisted, not straight. Dorsal fin (7–16 soft rays) in mid-body, origin in front of or near anal fin (9–15 soft rays) origin. Maximum length 30 cm.

Many species are remarkably euryhaline. *Adinia xenica* occurs in fresh water and salt marshes, as do several species of *Fundulus* such as the Mummichog, *F. heteroclitus*, which lives primarily in coastal seawater (marshes and estuaries) but also occurs in fresh water. Common names often reflect former views of relationships or otherwise cut across present family boundaries for other reasons; the accepted common name used for this family, topminnow, is also used for a poeciliid and the name killifishes is used for species in this family as well as for some cyprinodontids.

Four genera, *Adinia* (1), *Fundulus* (39, including *Plancterus* and *Xenisma*), *Leptolucania* (1), and *Lucania* (3), with about 44 species (e.g., Bernardi, 1997; Nelson et al., 2004; Ghedotti et al., 2004; Parenti and Hartel, 2011).

Superfamily Valencioidea. One family; northern Mediterranean region.

Family VALENCIIDAE (321)—Valencia toothcarps. Freshwater; southeastern Spain, Italy, and western Greece.

Elongate and attenuate dorsal process of the maxilla; rostral cartilage minute or absent; total number of rays in dorsal fin 8–11; scales in lateral series 28–34. Fertilization external.

One genus, *Valencia*, with two species (Bianco and Miller, 1989).

Superfamily Cyprinodontoidea. The superfamilies Cyprinodontoidea and Poecilioidea are thought to be sister taxa (Costa, 1998a).

Family CYPRINODONTIDAE (322)—pupfishes. Freshwater, brackish water, and coastal marine; United States, Middle America, West Indies, parts of northern South America, North Africa, and Mediterranean Anatolian region.

Dorsal processes of maxillaries expanded medially, nearly meeting in the mid-line; lateral arm of maxilla expanded. Origin of dorsal fin (10–18 soft rays) anterior to origin of anal fin (8–13 soft rays). Fertilization external. Maximum length 8 cm SL.

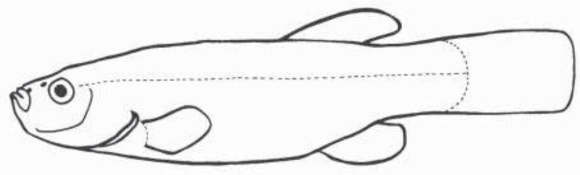
Nine genera and 131 species.

Subfamily Cubanichthyinae. Enlarged supraoccipital crest; elongate process of the autopalatine; parietals present; dorsal fin with 2 rudimentary rays and 9 principal rays, fin enlarged in males; pectoral fin with 18 rays; scales in lateral series 24–26; vertebrae 27. Cuba and Jamaica.

One genus, *Cubanichthys*, with two species (Costa 2003).

Subfamily Cyprinodontinae. Second pharyngobranchial offset relative to the third; Meckel's cartilage expanded posteriorly; parietals absent; outer jaw teeth uniserial.

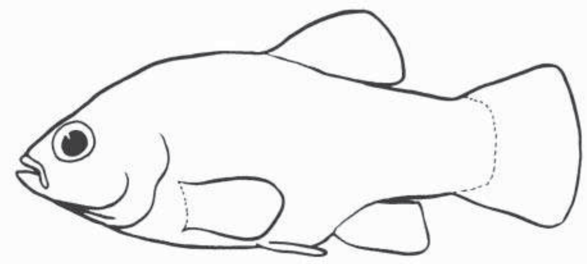
Tribe orestiini. Lower jaw robust due to medial extension of dentary; pelvic fin and pelvic skeleton, vomer, and first postcleithrum absent in species of *Orestias* (pelvic fin also absent in *Aphanius apodus*, as well as in a Miocene fossil species of *Aphanius*, Gaudant 1993); scales absent or present, 0–60 in lateral series; 26–37 vertebrae. Maximum length about 22 cm, attained in *O. cuvieri.*



The 10 or so species of *Aphanius* (probably not a monophyletic group) occur in the Mediterranean region in brackish and fresh water (e.g., North Africa, Spain, Italy, Turkey, Greece, Arabian Peninsula, and Iran). The 43 species of *Orestias* occur in high-altitude lakes in Peru, western Bolivia, and northernmost Chile along the Continental Divide (especially common in Lake Titicaca). The Eurasian and American disjunct occurrence of the freshwater members of this tribe has been considered a serious biogeographic challenge to Parenti's (1981) hypothesis of relationships (addressed by Parenti, 1981:535–38). Parker and Kornfield (1995) corroborated the relationships in a molecular study and proposed that the taxa represent a Tethyan distribution pattern. It is certainly one of the more notable cases of disjunct distributions in postulated monophyletic freshwater taxa, similar to that seen in polyodontids and *Umbra.*

Two genera, *Aphanius* (33, synonym *Kosswigichthys, Anatolichthys*), and *Orestias* (45), with about 78 species (Parenti, 1981; Costa, 2003; Blanco et al., 2006; Vila et al., 2011; Garrigos et al., 2013; Gholami et al., 2013).

Tribe cyprinodontini. Lower jaw without an anteriorly directed medial extension; first vertebra lacking neural spine, its neural arches applied to supraoccipital of skull; exoccipital condyles absent; pelvic fin and skeleton absent in *Cyprinodon diabolis* of Devil's Hole, Nevada, and in *Megupsilon aporus* of Nuevo León, Mexico, present or absent in *C. nevadensis* of Nevada and California; scales in lateral series 23–29; vertebrae 23–29. Southern and eastern United States, Middle America, and West Indies to Venezuela. Some species occur in marine and brackish water such as *Floridichthys carpio* and *Cyprinodon variegatus* (also in fresh water). Information on the biology of the species of *Cyprinodon* is given in Naiman and Soltz (1981).



Six genera, *Cualac* (1), *Cyprinodon* (about 45), *Floridichthys* (2), *Garmanella* (1), *Jordanella* (1), and *Megupsilon* (1), with about 51 species (e.g., Costa, 2003; Nelson et al., 2004; Echelle et al., 2005, 2006; Strecker, 2006; Haney et al., 2007).

Superfamily Poecilioidea. Ghedotti (2000) gave a detailed morphological analysis of this taxon and reviewed past taxonomic treatment. His proposed phylogeny supported the monophyly of the Anablepidae and Poeciliidae of Parenti (1981), but many changes are made to the classification of the Poeciliidae in order to present monophyletic groups as we now understand them. Although three subfamilies are recognized as previously in Nelson (1994), their composition is very different.

Family ANABLEPIDAE (323)—four-eyed fishes. Freshwater and brackish water, rarely coastal marine; southern Mexico to southern South America.

Epiotic and supraoccipital robust; pelvic fins distinctly behind tip of pectoral fin; pectoral girdle set low on side, radials situated ventrally or posteriorly; dorsal fin posteriorly placed, origin well behind anal fin. Maximum length 32 cm.

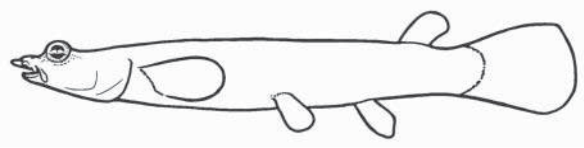
The recognition of the two subfamilies and their composition following Parenti (1981) has been supported by Ghedotti (1998, 2000). The Miocene fossil †*Carrionellus* of Ecuador may be an anablepid (Ghedotti 1998; Costa, 2011).

Three genera and 18 species (Ghedotti, 2003).

Subfamily Anablepinae. Tubular gonopodium formed from anal-fin rays and associated with sperm duct. In some males the gonopodium can move only to the left (sinistral); in others, only to the right (dextral). In females the genital aperture is open to the right or to the left. Perhaps, in mating, a left-handed (sinistral) male copulates only with a right-handed (dextral) female and vice versa. Dextral and sinistral mating types are known in both sexes of all species. Fertilization internal, bear young alive (viviparous).

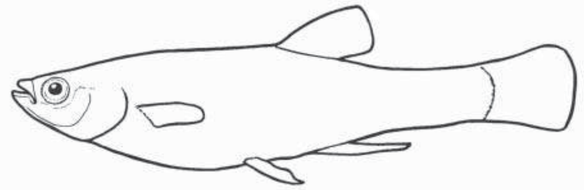
Two genera (*Anableps* and *Jenynsia*) and 17 species.

Anableps (four-eyed fishes). Freshwater and brackish water, rarely coastal marine; lowlands in southern Mexico to Honduras (Pacific slope) and northern South America (Atlantic slope). Eyes elevated above top of head and divided longitudinally (horizontally) into upper and lower portions giving two pupils on each side (water line in surface-swimming individuals in center of eye, and they can focus on images simultaneously from above and below water with their unusual double vision); gonopodium formed primarily from anal rays 3–6; first three anal-fin rays (excluding anteriormost, rudimentary ray of males) unbranched (as in Poeciliidae); dorsal fin with 7–10 rays and lying well behind anal fin; pectoral-fin rays 20–26; scales in lateral series 50–96; vertebrae 45–54 (more than in other Cyprinodontiformes). Maximum length up to 32 cm TL, usually somewhat less (females much larger than males), the largest of any cyprinodontiform.



Anableps has three species (Zahl et al., 1977; Miller, 1979; Ghedotti, 2003).

Jenynsia (one-sided livebearers)—Freshwater; southern South America in lowlands from Brazil, Paraguay, Uruguay, and Argentina. Eyes normal; gonopodium unscaled and formed primarily from anal rays 3, 6, and 7; pectoral-fin rays 15; scales in lateral series 25–28; vertebrae 29–31. Maximum length up to 12 cm in females, about 4 cm in males.



Jenynsia contains about 14 species (Ghedotti, 2003; Aguilera and Mirande, 2005; Lucinda et al., 2006; Koerber and Azpelicueta, 2009; Aguilera et al., 2013).

Subfamily Oxyzygonectinae. No gonopodium; inner jaw teeth tricuspidate; head in lateral view pointed anteriorly; dorsal and anal fins posteriorly placed, just before caudal peduncle and well behind midbody; scales in lateral series 29 or 30; vertebrae 28. Maximum length about 15 cm TL. Fertilization external. Pacific drainages in Nicaragua, Costa Rica, and Panama (occurs in estuaries but breeds in fresh water).

One species, *Oxyzygonectes dovii*, the White Eye (Ghedotti, 2003).

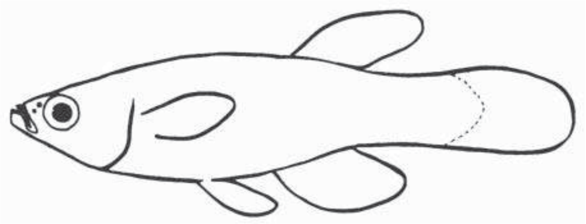
Family POECILIIDAE (324)—livebearers. Freshwater and brackish water; low elevations, eastern United States to South America and in Africa (including Madagascar).

Pectoral fins placed high on side of body due to radials placed in a dorsal position on the scapulocoracoid; anterior placement of pelvic fins; pleural ribs on the first several haemal arches; ventral hypohyal forms a bony cap over the anterior facet of the anterior ceratohyal; supraorbital pores modified such that neuromasts are found embedded in fleshy grooves. Gonopodium present or absent. Maximum length 20 cm attained in *Belonesox belizanus*, most species much smaller.

The subfamily classification of this family has been changed based on the work of Ghedotti (2000). Previously, in Nelson (1994) the three subfamilies recognized after Parenti (1981) were i) Poeciliinae with the same composition as here but with differing tribes recognized, ii) Fluviphylacinae with the one species of *Fluviphylax* then recognized, and iii) Aplocheilichthyinae with the present members of Aplocheilichthyinae and Procatopodinae.

Forty-two genera with about 353 species.

SUBFAMILY APLOCHEILICHTHYINAE (BANDED LAMPEYES). Western coastal Africa from mouth of the Senegal River to the mouth of the Congo River. This sub-family was previously recognized with six genera, including a non-monophyletic *Aplocheilichthys* (some earlier works also recognized that a larger *Aplocheilichthys* was not monophyletic, and Huber, 1999, reviewed the African members). Now, following Ghedotti (2000), all but *Aplocheilichthys spilauchen* are placed in the tribe Procatopodini. The one included species is regarded by Ghedotti (2000) as sister to all remaining poeciliids.



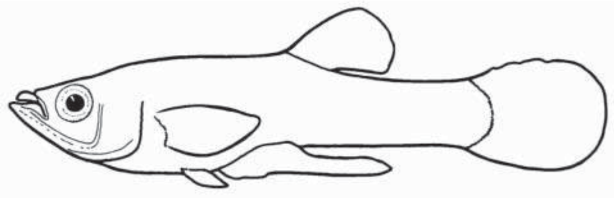
One genus *Aplocheilichthys* and about 24 species.

SUBFAMILY PROCATOPODINAE (LAMPEYES). Slender, usually shiny bluish or greenish in color, large eyes reflect the light. They are 2 to 15 centimeters long. Contains about 56 species.

Tribe fluviphylacini. South America (Brazil, Colombia, and Venezuela). *Fluviphylax* (5) (Lucinda, 2003). Maximum length 2 cm SL; these are the smallest of the cyprinodontiforms. Considered a subfamily in Nelson (1994).

Tribe procatopodini. Africa. Eleven genera, *Micropanchax* (9), *Lacustricola* (6), *Poropanchax* (5), *Platypanchax* (1), *Lamprichthys* (1), *Pantanodon* (2), *Hypsopanchax* (5), *Procatopus* (4, possible synonym *Hylopanchax* (6), *Plataplochilus* (8), *Rhexipanchax* (4) with 51 species (Huber, 1999; Wildekamp and Malumbres, 2004; Van Der Zee et al., 2013).

Subfamily Poeciliinae (livebearers). Male with elongated anterior anal-fin rays (gonopodium, primarily formed from the third, fourth, and fifth rays) with internal fertilization; eggs with large yolks, have live birth (ovovipiparous) (except in *Tomeurus*, which is egg-laying); exoccipital condyles absent; neural arches of the first vertebra open, not meeting to form a neural spine; metapterygoid absent; parietals present or absent; dorsal-fin rays 4–14; first three anal-fin rays unbranched; scales in lateral series 30–34; vertebrae usually 37. North, Central, and South America from southeastern Canada through to northeastern Argentina and Uruguay, including the Caribbean. This group includes many popular aquarium fishes such as the guppy, livebearers, mollies (molly in singular when used as the suffix in the common name), mosquitofishes, platyfishes (or the platys), and the swordtails. Several species, such as the Western Mosquitofish *Gambusia affinis* and the Sailfin Molly *Poecilia latipinna*, in addition to occurring in fresh water, can occur in brackish water and coastal marine waters. The many species of limias (*Limia*) are limited in their distribution to freshwater and coastal brackish water of several Caribbean islands, comprising a significant part of the freshwater fishes of these islands.



Nine tribes (following Ghedotti, 2000), 29 genera, and 273 species. Six of the tribes with 93 species occur in North America, ranging north from Mexico to southeastern Canada. Genera are largely recognized after Lucinda (2003). Lucinda and Reis (2005) revised this subfamily but changes could not be incorporated here; they resurrected the tribe Tomeurini and described the new tribes Brachyrhaphini and Priapichthyini as well as the supertribe Poeciliini. Phylogenetic relationships within this subfamily were investigated by Hrbek et al. (2007).

Tribe alfarini. One genus, *Alfaro* (2).

Tribe priapellini. One genus, *Priapella* (6).

TRIBE GAMBUSIINI. Four genera, *Belonesox* (1), *Brachyrhaphis* (12), and *Gambusia* (45), *Heterophallus* (2) with 60 species.

TRIBE HETERANDRINI. Seven genera, *Heterandria* (9)–Ghedotti, 2000, recognized *Pseudoxiphophorus* (1) as a valid genus), *Neoheterandria* (3), *Poeciliopsis* (24), *Priapichthys* (7), *Pseudopoecilia* (3), and *Xenophallus* (1), with 48 species (Agoretta et al., 2013).

TRIBE GIRARDINI. Three genera, *Carlhubbsia* (2), *Girardinus* (7), and *Quintana* (1), with 10 species (Doadrio et al., 2009).

TRIBE POECILIINI. Six genera, *Limia* (21), *Micropoecilia* (considered a synonym of *Poecilia* by some, e.g., Rodriguez 1997) (4), *Pamphorichthys* (6), *Phallichthys* (4), *Poecilia* (40), and *Xiphophorus* (28), with 103 species (e.g., Gutiérrez-Rodríguez et al., 2007; Figueredo, 2008; Schories et al., 2009; Bragança and Costa, 2010; Bragança et al., 2011; Poeser, 2011).

TRIBE CNESTERODONTINI. Five genera, *Cnesterodon* (10), *Phalloceros* (22), *Phalloptychus* (2), *Phallotorynus* (6), and *Tomeurus* (1), with 41 species (Aguilera et al., 2009). *Tomeurus* was placed alone in the tribe Tomeurini in Nelson (1994). Lucinda et al. (2005) studied relationships within *Phallotorynus.*

TRIBE SCOLICHTHYINI. One genus, *Scolichthys* (2).

TRIBE XENODEXINI. One genus, *Xenodexia* (1).

THE FOLLOWING ORDERS ARE PROPOSED TO BE IN A CLADE THAT IS SISTER TO OVALENTARIA (Little et al., 2010; Wainwright et al., 2012; Betancur-R. et al., 2013a, b). The proposed clade includes the orders Synbranchiformes, Anabantiformes (anabantoids), Carangiformes ("carangimorphs" or Carangoidei), Istiophoriformes (Sphyraenidae, Xiphiidae, and Istiophoridae), and Pleuronectiformes. The clade was labeled the "Carangimorpharia" by Betancur-R. et al. (2013a), but is unnamed and unranked in the present classification.

In addition to these orders, the suggested clade is thought to include also some families usually classified in Perciformes: Centropomidae, Leptobramidae, Nandidae, Polynemidae, and Toxotidae. Given the preliminary nature of the evidence, we have not moved most of these families from their previous orders at this time. We do consider these proposals very interesting and potentially transformative, pointing the way to future research including tests of their monophyly.

Order SYNBRANCHIFORMES (66)—swamp eels. Body elongate; pelvic fins absent; gill openings confined to lower half of body; ectopterygoid enlarged; endopterygoid reduced or absent; premaxillae nonprotrusible and without ascending process; extension of dentary posteroventrally along the ventral margin of the anguloarticular; palatine sutured along the posteroventral face the vomerine shaft; expansion of the hyohyoidei adductors dorsolaterally, thus sealing the operculum to the body wall restricting the opercular opening; distinctive morphology of the anterior vertebrae.

The molecular study of Betancur-R. et al. (2013a) surprisingly placed the Indostomidae (armored sticklebacks, usually placed in Gasterosteoidei) within the synbranchiform clade. That suggestion requires further testing; indostomids are retained in Gasterosteoidei herein.

The family composition of this order follows Johnson and Patterson (1993), Britz et al. (2003), and work by Gosline (1983) and Travers (1984b).

Three families, 13 genera, and about 117 species. All except a few species occur in fresh water.

Suborder Synbranchoidei. One family.

Family SYNBRANCHIDAE (325)—swamp eels. Tropical and subtropical freshwater, some species occasionally in brackish water (rarely marine); western Africa, Liberia, Asia, Indo-Australian Archipelago, Mexico, and Central and South America.

Body eel-like; pectoral and pelvic fins absent (pectorals present in early development of some species); dorsal and anal fins vestigial (reduced to a rayless ridge); caudal fin small (in *Macrotrema caligans*) or vestigial to absent; scales absent except in the species of the subgenus *Amphipnous* of *Monopterus*; eyes small (some species functionally blind with eyes sunken below skin); anterior and posterior nostrils widely separated; first vertebra with an articular plug and lateral flanges; basihyal ankylosed with the first basibranchial; first pharyngobranchial absent; second pharyngobranchial reduced to a tiny ossicle; fourth aortic arch complete; palatoquadrate articulating in two places, making these the only teleosts with an "amphistylic" jaw suspension; gill membranes united; small gill opening as slit or pore under head or throat (*Macrotrema* has normal size gill openings continuous with each other under throat); branchiostegal rays 4–6; swimbladder absent; ribs absent; vertebrae 98–188 (51–135 abdominal). Most species are protogynous hermaphrodites. As noted by Lauder and Liem (1983), these are among the most highly specialized teleosts in a large number of features (Rosen and Greenwood, 1976; Wiley and Johnson, 2010).

Most species are capable of air breathing. The cuchias of the genus *Monopterus* have paired lung-like suprabranchial pouches (with respiratory function) and the partially scaled body. These species are highly evolved as airbreathing fishes. Many have burrowing habits, while some live in caves. *Ophisternon*, as studied by Rosen (1975), has a highly disjunct distribution in the pantropics (e.g., one species is found in isolated centers in northern South America, northern Central America and southern Mexico, and Cuba). Maximum length almost 1 m, attained in *Ophisternon aenigmaticum* of the New World.

The major revision of this family by Rosen and Greenwood (1976) forms the basis for much the information here. They recognized two subfamilies of synbranchids—Macrotreminae (for *Macrotrema caligans*) and Synbranchinae (for the other species).

Four genera, *Macrotrema* (1, fresh and brackish water, in Thailand and Malay Peninsula), *Ophisternon* (6, two Americas and four Eurasia), *Synbranchus* (3, Mexico and Central and South America), *Monopterus* (13, Liberia and Pakistan to Japan), with 23 species (e.g., Bailey and Gans, 1998; Perdices et al., 2005; Britz et al., 2011).

Suborder Mastacembeloidei. Body elongate (eel-like); no pelvic fins; dorsal and anal fins continuous to or continuous with the small caudal fin; toothplate fused to hypobranchial three; interarcular cartilage absent; anterior nostrils found at tip of tube-like extensions; posttemporal absent, pectoral girdle (supracleithrum) attached to the vertebral column by a ligament; no air duct to swimbladder (physoclistic) (Britz and Kottelat, 2003).

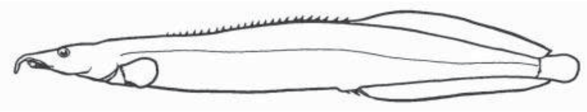
Family CHAUDHURIIDAE (326)—earthworm eels. Freshwater; northeastern India through Thailand to Korea (including parts of Malaysia and Borneo).

No dorsal or anal fin spines; body naked (*Chendol* has scales); no lateral line (except in *Chendol*); rostral appendage lost and dorsal, anal, and caudal fins fused in *Nagaichthys* (pectoral fin with only one ray) and *Pillaia*; endopterygoid and epineurals absent; basisphenoid present. Maximum length about 8 cm.

This family was not sampled by Betancur-R. et al. (2013a,b) but is included because of likely relationship to Mastacembelidae.

Six genera, *Bihunichthys* (1), *Chaudhuria* (3), *Chendol* (2), *Garo* (1), *Nagaichthys* (1), and *Pillaia* (2), with ten species (e.g., Kottelat and Lim, 1994; Kottelat, 2000a; Kullander et al., 2000; Britz and Kottelat, 2003; Britz 2010).

Family MASTACEMBELIDAE (327)—freshwater spiny eels. Freshwater; tropical Africa and through Syria to Malay Archipelago, China, and Korea.



Series of 9–42 isolated spines preceding the dorsal fin of 52–131 soft rays; anal fin usually with two or three spines and 30–130 soft rays; fleshy rostral appendage present; body covered with small scales (naked in about three species); no basisphenoid; vertebrae about 66–110. Maximum length up to

0.9 m. In some places mastacembelids are regarded as an excellent food fish; they are occasionally kept as an aquarium fish. They are found in a wide variety of habitats. Some species burrow in the substrate during the day or for certain months and have been found buried in soil in drying ponds.

Two subfamilies, not given here, were established by Travers in 1984 (see also Kottelat and Lim, 1994; Britz, 1996; Vreven and Teugels, 1996) as follows: Mastacembelinae (caudal fin distinct, rays either not confluent with dorsal and anal fin membranes or they extend posterior to and remain distinct from these fins, for *Macrognathus, Mastacembelus*, and *Sinobdella*) and Afromastacembelinae (caudal-fin rays confluent with posterior rays of dorsal and anal fins, for *Aethiomastacembelus* and *Caecomastacembelus*, in Africa).

Three genera, *Macrognathus* (22), *Mastacembelus* (61, synonyms *Aethiomastacembelus, Caecomastacembelus*), and *Sinobdella* (1, synonym *Rhynchobdella*) (Kottelat and Lim, 1994; Britz, 1996), with about 84 species (e.g., Britz, 1996; Arunkumar and Singh, 2000; Vreven, 2004; Vreven and Teugels, 1996, 1997; Britz, 2007, 2009, 2010b; Pethyagoda et al., 2008; Vreven and Stiassny, 2009; Brown et al., 2011).

Order CARANGIFORMES (67)—jacks. Marine; Atlantic, Pacific, Indian Oceans. One or two tubular ossifications (i.e., prenasals) around extension of nasal canal; presence of small, adherent cycloid scales (Smith-Vaniz, 1984; Johnson, 1984; Wiley and Johnson, 2010).

In the previous edition, a "carangoid lineage" of the next five families (Nematistiidae, Coryphaenidae, Rachycentridae, Echeneidae, and Carangidae) was suggested. Johnson (1984), Smith-Vaniz (1984), and O'Toole (2002) found Coryphaenidae, Rachycentridae, and Echeneidae to comprise a monophyletic group. For Johnson (1984) and Smith-Vaniz (1984), this clade is sister to Carangidae, while O'Toole (2002) recovered Coryphaenidae as sister to the clade of Rachycentridae + Echeneidae. Nematistiidae and Carangidae were also hypothesized by O'Toole (2002) to be related to these three families. These ideas have been corroborated by molecular studies (e.g., Gray et al., 2009; Betancur-R. et al., 2013a,b), and additional related families have been added.

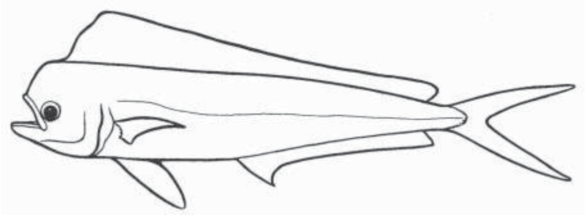
Six families, 37 genera, and 160 species.

Family NEMATISTIIDAE (328)—roosterfishes. Marine; tropical eastern Pacific.

Body compressed; small cycloid scales, about 120–130 in irregular series along lateral line (no scutes along lateral line); first dorsal with seven very elongate spines (which normally rest in a groove), second with one spine and 25–28 soft rays; anal fin with three spines (none detached from rest of fin) and about 15–17 soft rays; unique otophysic connection, swimbladder enters skull through large foramina in basioccipital and contacts inner ear (presumably increasing hearing sensitivity); 24 vertebrae (10 abdominal and 14 caudal).

One species, *Nematistius pectoralis* (Roosterfish), which is a popular gamefish ranging from southernmost California to Peru.

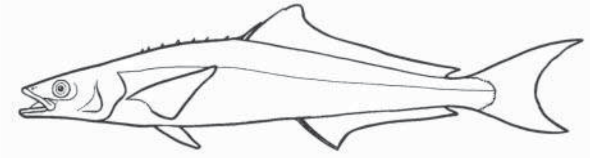
Family CORYPHAENIDAE (329)—dolphinfishes. Marine; Atlantic, Indian, and Pacific.



Dorsal fin originating on head, with 48–65 rays; no spines in dorsal and anal fins; caudal fin deeply forked; forehead prominent (steep and high) in adult males of the largest of the two species; color in life exceedingly beautiful; vertebrae 30–34. Maximum length 2.1 m, attained in *Coryphaena hippurus.* The term dolphinfish for the common name is preferred to the commonly used term dolphin to avoid confusion with the cetacean mammals known as dolphins. In parts of the Pacific, dolphinfishes are also known as mahimahi (and this is the name commonly used on restaurant menus). The common names for the two species are Pompano Dolphinfish (Spanish dorado enano) and Dolphinfish (Spanish dorado) (Nelson et al., 2004).

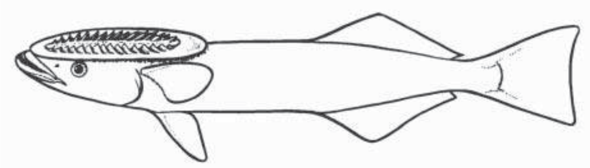
One genus, *Coryphaena*, with two species (e.g., Smith-Vaniz et al., 1999; Collette, 2003c).

Family RACHYCENTRIDAE (330)—cobias. Marine; Atlantic and Indo-Pacific. See note on sister-group relationships above under family Coryphaenidae.



Body elongate, head depressed; 6–9 short free spines ahead of the long dorsal fin (1–3 spines and 26–33 soft rays); anal fin long, with two or three spines and 22–28 soft rays; three dark stripes on side of body; 25 vertebrae. Maximum total length up to 2.0 m.One species, *Rachycentron canadum* (e.g., Smith-Vaniz et al., 1999; Collette. 2003c).

Family ECHENEIDAE (Echeneididae) (331)—remoras (sharksuckers). Marine; Atlantic, Indian, and Pacific.



Body elongate, head flattened, and lower jaw projecting past upper jaw; scales small, cycloid; dorsal and anal fins lacking spines, each with about 18–45 soft rays; swimbladder absent; branchiostegal rays 8–11; 26–41 vertebrae; sucking disc on head. The remora presses the disc against other fishes and creates a partial vacuum by operating the movable disc ridges like the slats in a Venetian blind, thereby causing the sucking action that permits it to obtain rides on larger animals. Remoras are found on sharks, bony fishes, sea turtles, and marine mammals; some species show considerable host specificity. A fully formed disc is present in specimens as small as 27 mm. Maximum length about 1.0 m, attained in *Echeneis naucrates.* The smallest species is 17 cm. See note on sister-group relationships above under family Coryphaenidae.

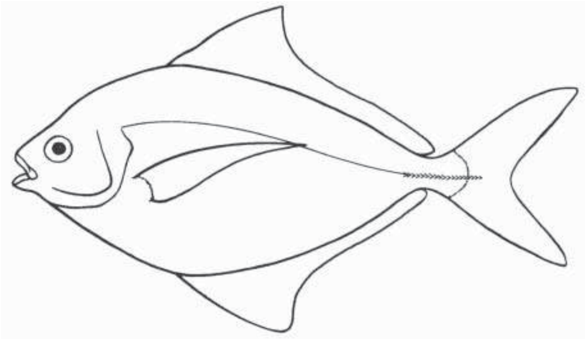
Gray et al. (2009) found molecular evidence that the monotypic *Phtheirichthys* is sister to the two species of *Echeneis,* with those together sister to the more diverse *Remora.* The nominal genus *Remorina* was nested within and synonymized with *Remora* on their evidence.

Britz and Johnson (2012), building on the century-earlier work of Houy (1910) and Gudger (1926), among others, made an elegant study of the ontogeny of the sucking disc, which develops from a transformed spinous dorsal fin, the spines of which are split to form 10–28 transverse movable laminae inside a fleshy margin.

Fossil echeneids are also of special interest because of the light they shed on the timing and evolution of the sucking disc. The early Oligocene remora †*Opisthomyzon glaronensis,* sometimes classified in the separate family †Opisthomyzonidae (e.g., Berg, 1940; Friedman, 2013) has a primitive disc with fewer, simpler lamellae than extant forms, and in a more posterior position (Gudger, 1926; Friedman et al., 2013, 2014; Britz and Johnson, 2012; Britz et al., 2014). An early Oligocene fossil was described by Micklich (1998).

Three genera, *Echeneis* (2), *Phtheirichthys* (1), and *Remora* (5), with eight widespread species (Smith-Vaniz et al., 1999; O'Toole, 2002; Collette, 2003c).

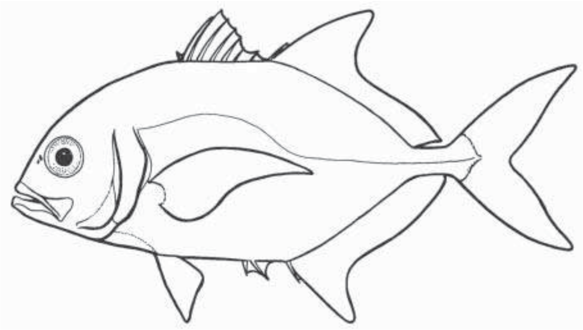
Family CARANGIDAE (332)—jacks and pompanos. Marine (rarely brackish); Atlantic, Indian, and Pacific.



Body generally compressed (but ranging from very deep to fusiform); only small cycloid scales in most species, ctenoid in a few (some scales on the lateral line are modified into spiny scutes in many species), naked areas variously developed; up to nine detached finlets sometimes present behind dorsal and anal fins (counts for these rays are included in following ray counts);

two dorsal fins in large juveniles and adults, the first with 4–8 spines (which in a few species are very short and lack a continuous membrane) and the second with one spine and 17–44 soft rays; usually three anal spines with the first two (rarely only one) detached from the rest of the anal fin and usually 15–39 soft rays; caudal fin widely forked; caudal peduncle slender; vertebrae 24–27 (usually 24).

Carangids are extremely variable in body shape, ranging from the shallow-bodied *Decapterus* and *Elagatis* to the extremely thin and deep-bodied *Selene*. The family contains some very important food species. The juveniles of some species extend into estuaries.



Two carangid species lack the pelvic fins, the surf inhabiting *Parona signata* from off southern Brazil and Argentina, and the epipelagic *Parastromateus niger* (in above figure), from the Indo-West Pacific. The latter species, which has a small pelvic fin in juveniles under 9 cm, was placed in its own family, Apolectidae (Formionidae), in Nelson (1984); placement in Carangidae follows the 1984 study of Smith-Vaniz. Both species have a deep and extremely compressed body, but what the selective forces are that are causing an independent loss of the pelvic fins in the only percoids to lack these fins is unknown; their ecology and swimming behavior are very dissimilar. Paleocene-Eocene species of the genus †*Trachicaranx*, which have the pelvic fins, may be relatively closely related to *Parastromateus*.

Some of the common names used for carangids are amberjacks, jacks, moonfishes, pilotfish, rudderfishes, pompanos, scads, and trevallies (singular trevally = crevally).

About 30 genera and 147 species (e.g., Smith-Vaniz et al., 1999; Smith-Vaniz, 2003; Kimura et al., 2013). Four subfamilies are provisionally recognized following Smith-Vaniz (1984) who ranked them as tribes. See also Gushiken (1988) for a published phylogenetic study.

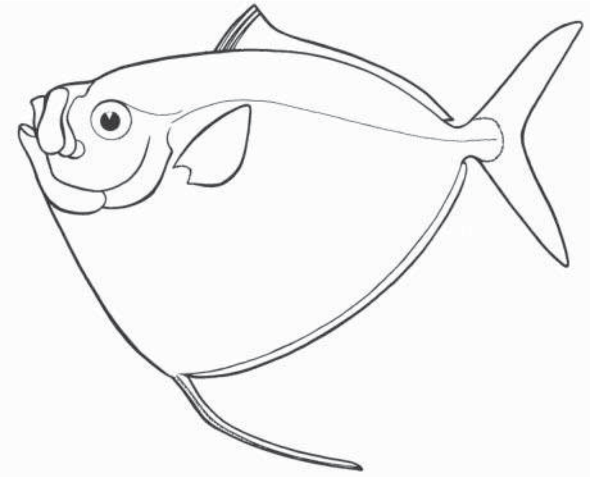
SUBFAMILY TRACHINOTINAE. Two genera, *Lichia* (1) and *Trachinotus* (20), with 21 species.

SUBFAMILY SCOMBEROIDINAE. Three genera, *Oligoplites* (5), *Parona* (1), and *Scomberoides* (4), with 10 species.

Subfamily Naucratinae. Five genera, *Campogramma* (1), *Elagatis* (1), *Naucrates* (1), *Seriola* (9), and *Seriolina* (1), with 13 species.

Subfamily Caranginae. The only subfamily with scutes present. Cárdenas et al. (2005) published on molecular phylogeny and historical biogeography of the genus *Trachurus*, but the postulated clades were not strongly supported, making the biogeographic interpretation speculative. Twenty genera, *Alectis* (3), *Alepes* (5), *Atropus* (1), *Atule* (1), *Carangoides* (20), *Caranx* (18), *Chloroscombrus* (2), *Decapterus* (11), *Gnathanodon* (1), *Hemicaranx* (4), *Megalaspis* (1), *Pantolabrus* (1), *Parastromateus* (1), *Pseudocaranx* (4), *Selar* (2), *Selaroides* (1), *Selene* (8), *Trachurus* (14), *Ulua* (2), and *Uraspis* (3) with 103 species (e.g., Kimura et al., 2013).

Family MENIDAE (333)—moonfishes. Marine; Indo-West Pacific.



Body compressed, disc-like, with sharp breast; dorsal contour nearly horizontal; mouth highly protrusible; dorsal fin with 43–45 soft rays, no spines; anal fin with 30–33 soft rays, no spines; first pelvic ray in adult prolonged.

Springer in Springer and Johnson (2004) placed Menidae in its own order, Meniformes, between Tetraodontiformes (which he regarded as preperciform) and Beryciformes, and suggested it might be more closely related to pre-percomorphs than to percomorphs. Coauthor Johnson strongly disagreed with this placement (personal communication, 2005), as detailed in a study by Friedman and Johnson (2005) on a Paleocene fossil from South America. *Mene* is included in the proposed sister-clade to Ovalentaria by Betancur-R. et al. (2013a,b), within a diverse Carangiformes.

One species, *Mene maculata.*

Order ISTIOPHORIFORMES (68)—barracudas and billfishes. The close relationship among Sphyraenidae, Xiphiidae, and Istiophoridae is suggested by several molecular studies including one of the alternative phylogenies of

Collette et al. (2006), and especially the results of Near et al. (2012a), and Betancur-R. et al. (2013a,b). Sphyraenidae had been placed in Scombroidei by Johnson (1986), who concluded that *Sphyraena* was the primitive sister group to other scombroids. The latter two families have long been considered close relatives; all three were placed in Scombriformes in Nelson (2006). Their present position is as possible members of a proposed sister-clade to Ovalentaria (Wainwright et al., 2012; Betancur-R. et al., 2013a,b).

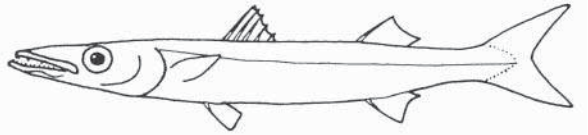
Santini and Sorenson (2013) published a molecular phylogeny with a presumed Late Cretaceous origin for istiophoriforms, and a proposed Miocene beginning for the diversification of the Istiophoridae. However, they did not sample sphyraenids, which are tentatively included here in the order Istiophoriformes.

Many istiophoriforms are exceptionally fast swimmers, like tunas with which they were formerly classified. The Blue Marlin *Machaira nigricans* was clocked, using acoustic telemetry, achieving burst speeds of up to 81 km/hr and sustained speeds after tagging of 29–43 km/hr (Block et al., 1992). At least some billfishes also have a form of cranial endothermy, maintaining high brain and retinal temperatures (Block et al., 1993; Little et al., 2010, 2012).

Fierstine (2006) summarized the fossil record of billfishes. The fossil family †Blochiidae (e.g., the Eocene †*Blochius* and possibly †*Aglyptorhynchus*) is related to the Xiphiidae, but the Cretaceous †*Cylindracanthus* may not belong to Istiophoriformes (Fierstine and Monsch, 2002). Other fossil billfishes include the extinct family †Palaeorhynchidae.

Three families, seven genera, and 39 species.

Family SPHYRAENIDAE (334)—barracudas. Marine (young occasionally in estuaries); tropical and subtropical Atlantic, Indian, and Pacific.

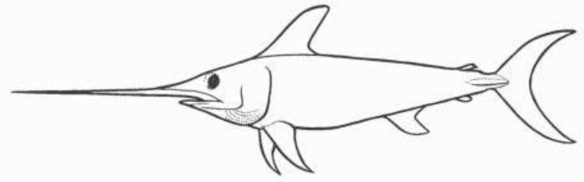


Body elongate; mouth large, jutting lower jaw with strong, large, ankylosed teeth; lateral line well developed; gill rakers absent to vestigial; pectoral fins relatively low; pelvic fins posterior to pectorals, approximately opposite first dorsal-fin origin two widely separated dorsal fins, the first with five spines and the second with one spine and nine soft rays; first dorsal fin often retraced in a groove; lateral-line scales 80–166; vertebrae 24 (11 + 13).

Barracudas are known to attack humans and are feared more than sharks in some areas (De Sylva, 1963). Maximum length normally to 1.8 m but said to reach somewhat longer lengths.

One genus, *Sphyraena*, with 27 species (e.g., H. Senou in Carpenter and Niem, 2001; Doiuchi and Nakabo, 2005; Pastore, 2009; Kadison et al., 2010).

Family XIPHIIDAE (335)—swordfishes. Marine; the single species is cosmopolitan in tropical, temperate, and cool areas of the Pacific, Indian, and Atlantic oceans (Nakamura, 1985).



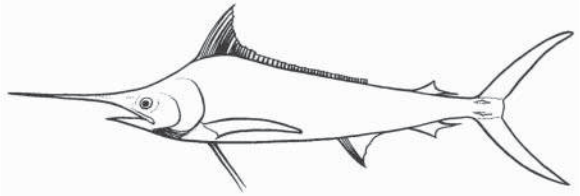
Bill depressed; scales absent in adult; pelvic fins and girdle absent; jaws toothless in adult; caudal peduncle in adult with single median keel on each side; 26 vertebrae. Length up to 4.5 m.

The Swordfish is a commercially valuable species. The sword is used to disable prey before ingestion (e.g., Scott and Tibbo, 1968).

There is abundant evidence that the Xiphiidae and Istiophoridae are sister groups (also see above under Istiophoriformes). In addition to less visible characters, both groups share the following features: elongate premaxillary bill (rostrum) in adults; mouth inferior; finlets absent behind dorsal and anal fins; dorsal-fin origin over back of head, first dorsal lacking true spines and with 37–55 rays; two anal fins; pectorals inserted low on body; pelvics reduced, with one spine and two rays, or absent; gill membranes free from isthmus; vertebrae 24 or 26.

One species, *Xiphias gladius* (Swordfish).

Family ISTIOPHORIDAE (336)—billfishes. Marine; most tropical and subtropical seas. Billfishes are extremely popular sportfishes.



Bill rounded; scales present in adults; pelvic fins elongate; jaws with teeth; caudal peduncle in adult with two keels on each side; dorsal fin with very long base, sometimes sail-like, depressible into groove; lateral line retained throughout life; 24 vertebrae. Length up to 4 m.

The bill is used to stun and disable prey fishes. Domenici et al. (2014) recorded an Atlantic Sailfish stealthily placing its bill within a school of prey sardines and then rapidly slashing from side to side.

Five genera: *Istiompax* (1), *Istiophorus* (1), *Kajikia* (2), *Makaira* (1), *Tetrapturus* (4), with about 11 species (e.g., Nakamura in Carpenter and Niem, 2001; Collette et al., 2006).

Istiophorus (sailfishes)—First dorsal fin sail shaped and distinctly taller than body depth; rays of pelvic fin very long. There has sometimes been only one worldwide species recognized, *Istiophorus platypterus* (e.g., Nelson et al., 2004), but Nakamura in Carpenter and Niem (2001) distinguished also *I. albicans* of the Atlantic. However, molecular evidence to date (summarized by Collette et al., 2006) does not support recognition of two species. There are two distinct mtDNA clades, with both present in the Atlantic but only one in the Indo-Pacific. However, there are no known morphological differences between the two clades, and a single species is recognized here.

Tetrapturus (spearfishes)—Forward portion of first dorsal fin about as high as body is deep.

Makaira, Kajikia, and *Istiompax* (*marlins*)—Forward portion of first dorsal fin not as high as body is deep in *Makaira* (shown in figure) and *Istiompax*; equal to or slightly greater than body depth in *Kajikia.*

Order ANABANTIFORMES (Labyrinthici) (69)—labyrinth fishes. Presence of a suprabranchial organ (also called a labyrinth organ; see below); distinctive afferent and efferent circulation to and from the suprabranchial organ; basioccipital with paired articular processes forming diarthrosis with the upper jaw; posterior extension of the swimbladder to the parhypural; larvae with a bilateral pair of oil vesicles used as floating devices (Britz, 1995, 2003; Wiley and Johnson, 2010).

The suprabranchial organ is an auxiliary breathing apparatus, allowing anabantoids to respire aerially as well as in water. Air taken in through the mouth passes through the labyrinth, usually with complex labyrinthine folding formed by expansion of first epibranchial, where capillaries absorb oxygen. As air is taken in at various intervals, old air is forced out of the labyrinth through the gill covers. This organ has enabled many species to occupy submarginal or even anoxic waters.

Unlike Nelson (2006), we here follow Britz (1995) as discussed by Wiley and Johnson (2010), who recognized two suborders with four families Anabantoidei (Anabantidae, Helostomatidae, and Osphronemidae) and Channoidei (Channidae). See below for potential close relatives of the Anabantiformes.

Two suborders 4 families, 21 genera, and about 207 species.

Suborder Anabantoidei. Suprabranchial air chamber separated from buccal cavity and respiratory air is confined to the suprabranchial cavity; foramen exoccipital that is covered by a tympanum-like membrane (Lauder and Liem, 1983); dorsal and anal fins with spines except in *Luciocephalus*; gill membranes scaly and broadly united; pelvic fins thoracic, usually with one spine and five soft rays; five or six branchiostegal rays; exoccipital bone usually with foramen covered by a membrane overlying the sacculus; swimbladder divided posteriorly, extending into caudal region; vertebrae 25–31 (see Wiley and Johnson, 2010).

Parental care has evolved in anabantoids and there is an exceptional wide diversity of behaviors. Only three of the 19 genera have species with free-spawning where parental care is absent. In species of the other 16 genera there may be substrate spawning with male parental care (*Sandelia*), nest building on submerged plants with male parental care (*Osphronemus*), bubble nesting with eggs deposited in the bubbles and either male parental or biparental care (species of most genera), and mouthbrooding with either male or female parental care (Rüber et al., 2006).

Recognition of this suborder as being monophyletic is based on Lauder and Liem (1983) finding four morphological derived characters and on Rüber et al. (2006) based on mitochondrial and nuclear DNA sequence data. Refinements to the classification of Nelson (2006) are based on references given below (the largest change is noted under Osphronemidae).

Fossils are scarce and the only known articulated anabantoid fossil is *Osphronemus* sp., possibly of Eocene age (Rüber et al., 2006). The disjunct African and Asian freshwater distribution of anabantoids raises interesting biogeographic questions explored by Rüber et al. (2006) but with firm conclusions relating to timing and dispersal versus vicariant explanations beyond our reach.

Three families, 19 genera, and about 170 species. All are freshwater and indigenous to Africa and southern Asia.

Family ANABANTIDAE (337)—climbing gouramies. Freshwater (rarely brackish); Africa and India to Philippines.

Jaws, prevomer, and parasphenoid with fixed conical teeth; mouth relatively large; upper jaw only weakly protrusile; one genus, *Sandelia*, only with cycloid scales, not ctenoid; gill rakers few and diet generally carnivorous. Monophyly of the anabantids and recognition of two subfamilies was supported by Rüber et al. (2006). Maximum length about 30 cm TL, attained in *Anabas cobojius* and *Sandelia bainsii.*

Four genera, *Anabas* (2), *Ctenopoma* (17), *Microctenopoma* (12), and *Sandelia* (2), with 33 species (e.g., Norris and Douglas, 1992). Most of the species, contained in the genera *Ctenopoma*, *Microctenopoma,* and *Sandelia*, occur in Africa; *Anabas* occurs in Asia.

Family HELOSTOMATIDAE (338)—kissing gouramies. Freshwater; Thailand to Malay Archipelago.

Premaxilla, dentaries, palatine, and pharynx devoid of teeth; two lateral lines, the lower commencing below the end of the upper; dorsal fin with 16–18 spines and 13–16 soft rays; anal fin with 13–15 spines and 17–19 soft rays; lateral-line scales 43–48; scales on top of head cycloid, others ctenoid. Numerous gill rakers form an elaborate filter apparatus on the gill arches which adapts the fish to filter feeding (horny teeth on the lips also enable the fish to scrape algae off surfaces). Parental care absent. Maximum length about 30 cm TL.

The sister group of this family is uncertain; it may be sister to Anabantidae or Osphronemidae, or form a trichotomy with both families (Rüber et al., 2006).

One species, *Helostoma temminckii* (Kissing Gourami).

Family OSPHRONEMIDAE (339)—gouramies and fighting fishes. Freshwater; Pakistan and India to Southeast Asia.

The classification of this family is based on Britz et al. (1995), Britz (2001) and Rüber et al. (2006), who supported its monophyly and found modest evidence that Belontiinae and Osphroneminae are sister taxa with the resulting clade sister to the remaining members. However, they did not confirm monophyly of the Luciocephalinae as recognized in Nelson (2006) with six genera (sharing, as noted in Britz, 2001, five branchiostegal rays rather than six as in most members of this family due to the loss of the first and secondly having a median process of the basioccipital that extends beneath the first vertebra and to which Baudelot's ligament is attached). Instead, they found support for a "spiral egg" clade of the four genera recognized here as the Luciocephalinae. The remaining two genera formerly placed in the Luciocephalinae are sister to the Macropodusinae (Rüber et al., 2006) and are placed in a separate subfamily here, the Trichogastrinae.

Maximum length about 70 cm SL, attained in *Osphronemus goramy*, which has been introduced around the world in the tropics.

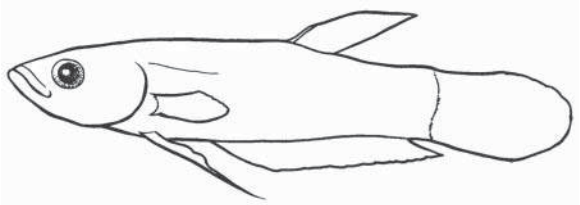
Four subfamilies, 14 genera, and about 136 species.

SUBFAMILY OSPHRONEMINAE (GIANT GOURAMIES). Freshwater; Southeast Asia. Prevomer and palatine devoid of teeth; one lateral line, complete and continuous; all scales ctenoid; dorsal fin with 11–16 spines and 10–14 soft rays; anal fin with 9–12 spines and 16–23 soft rays; 14–16 pectoral-fin rays; lateral scale rows 31–34; 30 or 31 vertebrae.

One genus, *Osphronemus*, with four species (Britz, 2001).

SUBFAMILY BELONTIINAE (COMBTAIL GOURAMIES). Southern Asia. One genus, *Belontia*, with two species.

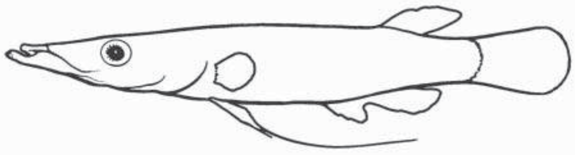
SUBFAMILY MACROPODUSINAE (SIAMESE FIGHTING FISHES, PARADISEFISHES). The formerly recognized subfamily name Macropodinae (preoccupied by a subfamily of kangaroos) was changed to Macropodusinae (*Bull. Zool. Nomencl.* 60(3):253–254, ICZN Opinion 2058 (Case 2661)).



Six genera, *Betta* (shown in figure) (73), *Macropodus* (9), *Malpulutta* (1), *Parosphromenus* (20), *Pseudosphromenus* (2), and *Trichopsis* (3), with 108 species (e.g., Britz, 2001; Freyhof and Herder, 2002; Rüber et al., 2004; Kottelat and Ng, 2005; Kowasupat, Panijpan, Ruenwongsa, and Jeenthong, 2012; Kowasupat, Panijpan, Ruenwongsa, and Sriwattanarothai, 2012; Schindler and Schmidt, 2004; Tan, 2009; Tan and Ng, 2005a,b, 2006;

Winstanley and Clements, 2008). *Trichopsis* is sister to the other five genera (Rüber et al., 2006). The genus *Betta*, with about 73 species, is the largest; some species are oral brooders and others are bubble nesters.

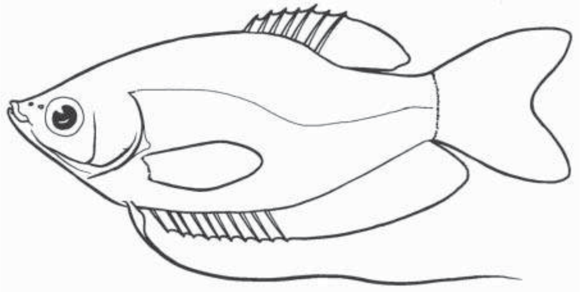
Subfamily Luciocephalinae. Freshwater; Malay Peninsula and Archipelago. Five branchiostegal rays (most members of this family have six, but the first has been lost in this clade; Britz, 2001). This is the "spiral egg" clade (Britz, 2001; Rüber et al., 2006).



In Nelson (1994), *Luciocephalus* (Pikehead) was recognized in its own family, and the others were placed in the subfamily Trichogastrinae (gouramies) of the family Belontiidae. *Luciocephalus* is quite distinctive in having the following characters: no dorsal or anal-fin spines; dorsal fin inserted posteriorly, with 9–12 rays; anal fin with a deep notch and 18 or 19 rays; pelvic fin with one spine and five soft rays (one of which is produced into a thread-like ray); caudal fin rounded; lateral-line scales about 40–42; mouth exceptionally protractile; gill membranes not united; median gular element present; no swimbladder; maximum length about 18 cm.

Five genera, *Ctenops* (1), *Luciocephalus* (in figure) (2), *Parasphaerichthys* (2), *Sphaerichthys* (4), and *Trichopodus* (4), with 13 species.

Subfamily Luciocephalinae. Freshwater; southern Asia. A clade distinct from Luciocephalinae with two monophyletic genera (Britz, 2001; Rüber et al., 2006).



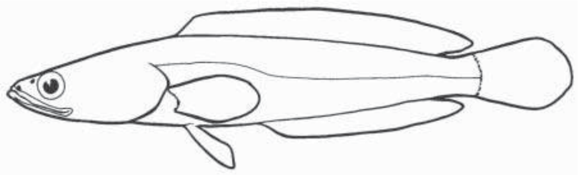
Two genera, Colisa (4) and Trichogaster (5; in figure), with 9 species.

Suborder Channoidei (Ophiocephaliformes). Saccular otic bulla mostly contained in prootic; metapterygoid with anterodorsal uncinate process either approaching or articulating with the neurocranium; accessory breathing organs with respiratory nodules on the first and second epibranchials parasphenoid and hyomandibula; (elongate autogenous bony element positioned between PU2 and PU3 of caudal fin skeleton; fin spines on all fins absent—see

Wiley and Johnson, 2010, who quote these two characters as Britz, personal communication) (Liem, 1980; Lauder and Liem, 1983).

One family, two genera (*Channa* and *Parachanna*), 37 species.

Family CHANNIDAE (340)—snakeheads. Freshwater; tropical Africa and southern Asia. Distribution maps and descriptive information for the species are given in Courtenay and Williams (2004).

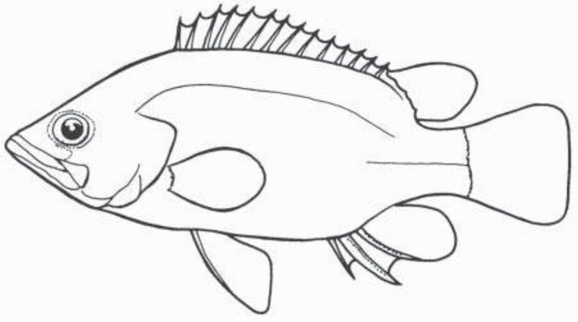


Body elongate; long dorsal and anal fins; pelvic fins usually present (some Asian species of *Channa* lack the pelvics), with six rays; no fin spines; cycloid or ctenoid scales; lower jaw protruding beyond upper; suprabranchial organ for air breathing present. Maximum length about 1.2 m.

Two genera, *Channa* (34, synonym *Ophicephalus*) and *Parachanna* (3), with 37 species (Courtenay and Williams, 2004; Courtenay et al., 2004; Adamson et al., 2010; Britz, 2007, 2013; Li et al., 2006; Zhang et al., 2002). The species of *Channa* are found in Asia and those of *Parachanna* in Africa. Murray (2006) described the fossil †*Parachanna fayumensis* from the Eocene and Oligocene of Egypt. *Channa* is an invasive species in North America that threatens many native species.

THE FOLLOWING THREE FAMILIES (Nandidae, Badidae, and Pristolepididae) form a monophyletic group with the Anabantiformes (the four families immediately above), characterized by possession of teeth on the parasphenoid, a unique feature among percomorphs according to Britz et al. (2012). Gosline (1971) had earlier recognized these three families and placed them at the start of his Percoidei. These families might prove to be members of the anabantiform clade, as has been suggested for one of them (Nandidae) by the molecular phylogeny of Betancur-R. et al. (2013a), who, however, did not sample the other two families.

Family NANDIDAE (341)—Asian leaffishes. Freshwater (occasionally brackish water); Africa, Pakistan, India, and southeastern Asia (to Sumatra). Anal fin with three spines. Maximum length 20 cm TL for *Nandus nandus*.



Head usually large; mouth usually large and highly protrusible; dorsal fin continuous; caudal fin rounded; lateral line incomplete or absent; pelvic fin usually scaly axillary process. Many are vicious predators. At rest, most look deceptively like drifting leaves.

Three genera, *Nandus* (7), *Polycentropsis* (1), and *Afronandus* (1), with nine species (Chakrabarty et al., 2006; Ng, 2008; Ng and Jaafar, 2008).

Family BADIDAE (342)—chameleonfishes. Pakistan and Burma.

Mouth relatively small and only slightly protrusible; no subocular shelf; dorsal fin with six or seven spines and 6–10 soft rays; anal fin with three spines and 6–8 soft rays; lateral-line scales 23–33.

These are colorful fishes that can change color very rapidly. Maximum length about 6.8 cm SL for *Badis assamensis.* This taxon was recognized with only one species in Nelson (1994), *Badis badis.*

Two genera, *Badis* (17) and *Dario* (5), with 22 species (Kullander and Britz, 2002; Britz et al., 2012; Britz and Kullander, 2013).

Family PRISTOLEPIDIDAE (343)—(Malayan) leaffishes. Small area of peninsular India and Sri Lanka, southeastern Asia, and parts of Malay Archipelago (e.g., Sumatra, Java, and Borneo).

Mouth relatively small and only slightly protrusible; subocular shelf present; parasphenoid tooth patch opposed by enlarged and toothed basibranchial toothplate. The most widespread species, *Pristolepis fasciata,* has: dorsal fin with 13–16 spines and 14–16 soft rays; anal fin with three spines and eight or nine soft rays; lateral-line scales 26–28; and maximum 20 cm TL.

One genus, *Pristolepis,* with about four species (Britz et al., 2012).

Order PLEURONECTIFORMES (Heterosomata) (70)—flatfishes. Adults not bilaterally symmetrical, with one eye migrating to the other side of the cranium; dorsal and anal fins with long bases; dorsal fin base overlapping at least the neurocranium except in *Psettodes*; body highly compressed, somewhat rounded on eyed side and flat on eyeless side; eyes can protrude above body surface, allowing fish to see when buried in the substrate; usually six or seven branchiostegal rays, rarely eight; body cavity small; adults almost always without swimbladder; scales cycloid, ctenoid, or tuberculate.

This is a very distinctive and economically important group. Young flatfishes are bilaterally symmetrical and swim upright, but early in their development, between 5–120 mm and usually 10–25 mm in length, one eye migrates across the top of the skull to lie adjacent to the eye on the other side. They then lie and swim on the eyeless side. The metamorphosis involves a complex modification of skull bones, nerves, and muscles, and it leaves one side of the fish eyeless (lower side) and the other side with two eyes (upper side). The upper side is pigmented, whereas the underside is usually light colored. Asymmetry may also be reflected in other characters such as dentition, squamation, and paired fins. Most species have both eyes on the right side and lie on the left side (dextral) or have both eyes on the left side and lie on the right side (sinistral). In some species both dextral (right-eyed) and sinistral (left-eyed) individuals may occur. Among the latter species, the pleuronectid *Platichthys stellatus* (the Starry Flounder) is especially interesting because of the varying frequency of dextral to sinistral individuals over its range in the North Pacific. Other members of the family are dextral, but almost all Starry Flounder from Japanese waters are sinistral, while off California the two types are about equal in frequency. As yet there appears to be no convincing argument for a direct adaptive advantage for being sinistral or dextral.

Flatfishes are benthic and carnivorous. Sexual maturity is attained from 1 to 15 years of age. Maximum length almost 3 m in the halibuts; much smaller in most groups.

Common names for flatfishes include flounder, halibut, sole, plaice, dab, sanddab, tonguefish, and turbot; some of these names apply to species in different families. Many species are important in commercial fisheries and are valued as a high-quality food source.

The classification of this order is based largely on Chapleau (1993), Cooper and Chapleau (1998a,b), and Hoshino (2001b). Much taxonomic information is in Desoutter et al. (2001).

Caudal-fin rays have been used in flatfish systematics. In an early study involving caudal fin-ray morphology, the “bothoid lineage” as comprising the Pleuronectidae herein, most Paralichthyidae, Scophthalmidae, and most Bothidae was recognized by Ahlstrom and Hensley (1984). Hoshino (2001a) established homologies among various rays and discussed the phylogenetic significance of the rays and associated structures. The highly modified scales and lateral-line tubes also differ in shape and fine sculpture among pleuronectiform taxa (e.g., Märss et al., 2015).

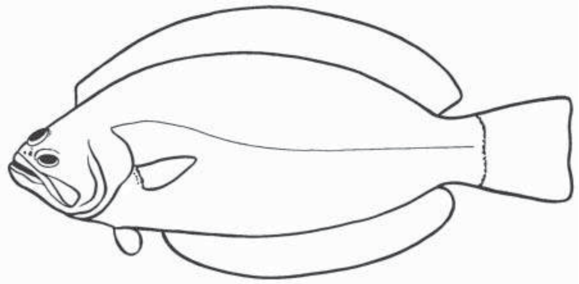
Schwarzhans (1999) documented the recent and fossil otoliths of the order, with much useful taxonomic information. Chanet (1997, 2003) summarized studies on the fossils of this order. Friedman (2008) named †*Heteronectes* and re-studied †*Amphistium*, both from the Eocene of Monte Bolca, Italy, concluding that they were successive stem-group pleuronectiforms, with asymmetric skulls but retaining an eye on each side of the head. Friedman (2008, 2012) also placed the Eocene crown-group flatfish †*Joleaudichthys* in Psettodoidei, and two other Eocene crown-group fossils, †*Numidopleura* and †*Eobothus*, within Pleuronectoidei. Many additional fossil genera and species are known.

The order has long been regarded as monophyletic (Chapleau, 1993; Berendzen and Dimmick, 2002). There is also general agreement that the Psettodidae are a distinct clade from the remainder of the pleuronectiforms, forming either the primitive sister group (Psettodoidei) to other pleuronectiforms (the Pleuronectoidei) (Cooper and Chapleau, 1998b; Hoshino, 2001b; Berendzen and Dimmick, 2002; Betancur-R. et al., 2013b) or else a separate clade convergent with pleuronectoids (e.g., Near et al., 2012a; Betancur-R. et al., 2013a) although within the latter two broad-scale molecular studies, support levels are weak for the alternative placement. Here we continue to include Psettodoidei within Pleuronectiformes as the primitive sister group to the rest.

About 772 extant species are recognized in approximately 129 genera and 14 families. About 10 species are thought to occur only in fresh water (six achirids, one soleid, and three cynoglossids); another few that are primarily freshwater enter estuaries or marine water, and another 20 species that are normally marine but occasionally enter freshwater. Munroe (2005a,b) discussed the taxonomic and geographic diversity of flatfishes.

Suborder Psettodoidei. Presence of a pseudomesial bar (i.e., an autogenous bone positioned between the blind-side lateral ethmoid and the blind-side frontal (Chapleau, 1993; Wiley and Johnson, 2010); dorsal fin not extending onto head (to or past eye); anterior dorsal and anal rays spinous; palatine with teeth; basisphenoid present; supramaxilla large; 24 or 25 vertebrae.

Family PSETTODIDAE (344)—spiny turbots. Marine; western Africa and Indo-West Pacific.



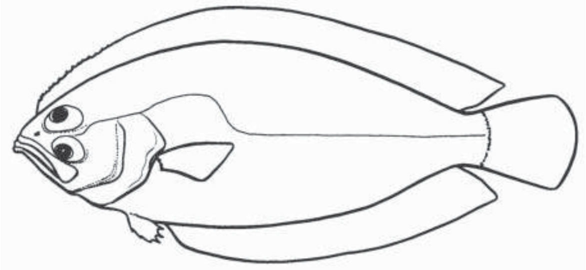
Pelvic fins nearly symmetrical, with one spine and five soft rays; mouth large; jaw teeth barbed; gill arches with groups of teeth; eyes sinistral or dextral; preopercular margin distinct, not covered with skin; 15 branched caudal-fin rays. Maximum length about 60 cm.

One genus, *Psettodes*, with three species: *P. belcheri* and *P. bennetti* from tropical western Africa (eastern Atlantic) and *P. erumei* from eastern Africa and the Red Sea to the western Pacific (e.g., Hensley in Carpenter and Niem, 2001).

Suborder Pleuronectoidei. Dorsal fin extending onto head at least to eyes; dorsal and anal fins without spines; palatine without teeth; no basisphenoid; supramaxilla vestigial (in some citharids) or absent; basihyal without tooth plates; uroneurals reduced or absent; vertebrae 26–70, 10 or more are abdominal.

Superfamily Citharoidea. One family.

Family CITHARIDAE (345)—largescale flounders. Marine; Mediterranean, Indo-West Pacific (Japan to Australia).



Pelvic fins with one spine and five soft rays; pelvic fin bases short; branchiostegal membranes basically separated from each other; posterior nostril on eyeless side enlarged.

The monophyly of this family has until recently been questioned. The cladistic analysis shown in Cooper and Chapleau (1998b) suggested that the dextral *Lepidoblepharon* is sister to all remaining pleuronectiforms, and the sinistral *Citharoides* is sister to the remaining pleuronectiforms. The sinistral *Citharus* was not shown on the cladogram, but the dextral *Brachypleura* was sister to a clade comprising the four families Scophthalmidae, Paralichthyidae, Bothidae, and Pleuronectidae; this clade along with *Brachypleura* (termed the bothoid lineage) was sister to all other pleuronectiforms, although Achiropsettidae was not placed in the Cooper and Chapleau (1998b) cladogram. Hoshino (2001b) established monophyly for the family based on six synapomorphies and showed that sinistral species and those that are dextral do not form monophyletic groups. Molecular studies (e.g., Betancur-R. et al., 2013b) support monophyly of at least *Lepidoblepharon*, *Citharoides*, and *Citharus*, although without sampling other genera.

Four genera, *Brachypleura* (1), *Citharoides* (3, synonym *Paracitharus*), *Citharus* (1, synonym *Eucitharus*), *Lepidoblepharon* (1), with about six species (e.g., D. A. Hensley in Carpenter and Niem, 2001; Hoshino, 2000, 2001b).

Superfamily Pleuronectoidea. Four families.

Family SCOPHTHALMIDAE (346)—turbots. Marine (occasionally in brackish water); northern Atlantic and Baltic, Mediterranean, Black seas.

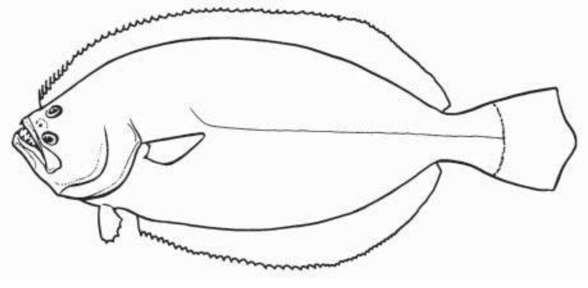
Eyes sinistral; both pelvic-fin bases elongate, mouth large and lower jaw prominent. Maximum length about 100 cm.

Monophyly of this family was confirmed by Chanet (2003), who recognized two subfamilies. The position of this family changed after Nelson (1994).

Common names for species include turbots, windowpanes, and brills. Only one species occurs in the Western Atlantic; the others occur in the northeastern Atlantic area.

Four genera, *Lepidorhombus* (2), *Phrynorhombus* (1), *Scophthalmus* (4, synonym *Psetta*; see Bailly and Chanet, 2010), and *Zeugopterus* (2), with about nine species (e.g., Chanet, 2003; Munroe, 2003b).

Family PARALICHTHYIDAE (347)—sand flounders. Marine, rarely freshwater; Atlantic, Indian, and Pacific. Also called largetooth flounders.



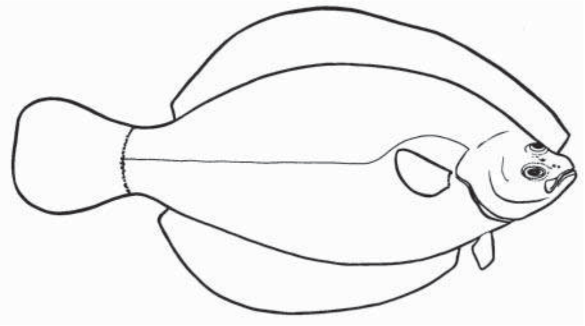
Eyes in most species sinistral; pelvic-fin bases short and nearly symmetrical (but position of bases variable between species); pectoral rays branched. Maximum length about 1.5 m.

A species of *Citharichthys* and of *Pseudorhombus* ascends rivers from the ocean in Africa. This family may not be monophyletic. The osteology of *Tephrinectes* was given by Hoshino and Amaoka (1998).

The position of this family is changed from Nelson (1994). Paralichthyidae and Pleuronectidae are sister taxa (Hoshino, 2001b; Betancur-R. et al., 2013b).

About 14 genera, *Ancylopsetta*, *Cephalopsetta*, *Citharichthys*, *Cyclopsetta*, *Etropus*, *Gastropsetta*, *Hippoglossina*, *Paralichthys*, *Pseudorhombus*, *Syacium*, *Tarphops*, *Tephrinectes*, *Thysanopsetta*, and *Xystreurys*, and about 111 species (e.g., van der Heiden and Mussot-Pérez, 1995; Hoshino and Amaoka, 1998, 1999; Amaoka and Hensley in Carpenter and Niem, 2001; Munroe, 2003b; Hoshino and Munro, 2004; Khidir et al., 2004; van der Heiden and González, 2005; Diaz de Astarloa et al., 2006; van der Heiden et al., 2009; Bailly and Chanet, 2010).

Family PLEURONECTIDAE (348)—righteye flounders. Marine (occasionally in brackish water, rarely in freshwater); Arctic, Atlantic, Indian, and Pacific.



Eyes almost always dextral; origin of dorsal fin above the eyes; lateral line well developed on both sides; pelvic fins symmetrical.

Nelson (1994) and Evseenko (2004) treated this family at the subfamily level, Pleuronectinae. The subfamilies Paralichthodinae, Poecilopsettinae, and Rhombosoleinae are now recognized as separate families.

Twenty-three genera with about 56 species. The following five subfamilies and the four tribes in the last subfamily are based on the cladistic analysis of Cooper and Chapleau (1998b). The commercially important and large halibuts belong to this family.

SUBFAMILY HIPPOGLOSSINAE. Five genera, *Atheresthes* (2), *Clidoderma* (1), *Hippoglossus* (2), *Reinhardtius* (1), and *Verasper* (2), with eight species (Cooper and Chapleau, 1998b; Nelson et al., 2004). Cooper and Chapleau (1998b) placed species of *Atheresthes* within *Reinhardtius*, but Nelson et al. (2004) recognized both genera, as did Orr and Matarese (2000); Nelson et al. (2004) also noted the 2001 molecular study of N. Suzuki, M. Nishida, and K. Amaoka finding that *A. evermanni* is not closely related to *Reinhardtius* and supporting the retention of *Atheresthes* as a valid genus.

SUBFAMILY EOPSETTINAE. One genus, *Eopsetta*, with two species (Cooper and Chapleau, 1998).

SUBFAMILY LYOPSETTINAE. One monotypic genus, *Lyopsetta* (Cooper and Chapleau, 1998).

SUBFAMILY HIPPOGLOSSOIDINAE. Three genera, *Acanthopsetta* (1), *Cleisthenes* (2), and *Hippoglossoides* (4), with seven species (Cooper and Chapleau, 1998b).

SUBFAMILY PLEURONECTINAE. Thirteen genera and 38 species.

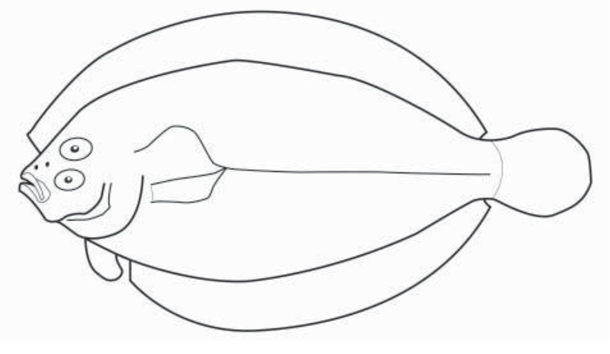
TRIBE PSETTICHTHYINI. One monotypic genus, *Psettichthys*.

TRIBE ISOPSETTINI. One monotypic genus, *Isopsetta*. Garrett (2005) reported hybrids between *Isopsetta* and *Parophrys* (in tribe Pleuronectini, below).

TRIBE MICROSTOMINI. Six genera, *Dexistes* (1), *Embassichthys* (1), *Glyptocephalus* (3, synonyms *Errex* and *Tanakius*), *Lepidopsetta* (3), *Microstomus* (4), and *Pleuronichthys* (7), with 19 species (Cooper and Chapleau, 1998b; Orr and Matarese, 2000; Suzuki et al., 2009). Cooper and Chapleau (1998b) placed *Embassichthys bathybius* within *Microstomus*, but Nelson et al. (2004) recognized both genera, as did Orr and Matarese (2000); however, the phylogenetic conclusions of Cooper and Chapleau (1998b) in recognizing monophyly of this clade are not in question.

TRIBE PLEURONECTINI. Five genera, *Limanda* (6), *Parophrys* (1), *Platichthys* (2), *Pleuronectes* (3), and *Pseudopleuronectes* (5), with 17 species (Cooper and Chapleau, 1998b; Suzuki et al., 2009).

Family BOTHIDAE (349)—lefteye flounders. Marine; Atlantic, Indian, and Pacific.



Eyes sinistral; pelvic-fin base on eyed side longer than on eyeless side, on midventral line and origin anterior to base on eyeless side; pectoral and pelvic-fin rays not branched; pelvic fins without a spine; at least two series of intermuscular bones (termed myorhabdoi); branchiostegal membranes connected; egg with a single oil globule in the yolk (true also of scophthalmids and paralichthyids). Chanet et al. (2004) demonstrated that the similarity in the ossification of ligaments in bothids and samarids is the result of convergence, not common ancestry.

Twenty genera, *Arnoglossus*, *Asterorhombus*, *Bothus*, *Chascanopsetta* (synonym *Pelecanichthys*), *Crossorhombus*, *Engyprosopon*, *Engyophrys*, *Grammatobothus*, *Japonolaeops*, *Kamoharaia*, *Laeops*, *Lophonectes*, *Monolene*, *Neolaeops*, *Parabothus*, *Perissias*, *Psettina*, *Taeniopsetta*, *Tosarhombus*, and *Trichopsetta*, with about 163 species (e.g., Hensley and Smale, 1997; Amaoka, Arai, et al., 1997; Amaoka, Mihara, et al., 1997; Amaoka and Imamura, 2000; D. A. Hensley and K. Amaoka in Carpenter and Niem, 2001; Munroe, 2003b; Hensley and Randall, 2003; Amaoka and Séret, 2005, 2010).

Superfamily Soleoidea. Eight families.

Family PARALICHTHODIDAE (350)—measles or peppered flounders. Marine; southern Africa.

Origin of dorsal fin before the eyes; lateral line with prominent curve over pectoral fin; vertebrae 30–31; eyed side brownish gray with small dark spots.

Considered a subfamily of Pleuronectidae in Nelson (1994) and Evseenko (2004).

One species, *Paralichthodes algoensis* of southern Africa (Heemstra in Smith and Heemstra, 1986:864; Evseenko, 2004).

Family POECILOPSETTIDAE (351)—bigeye flounders. Marine: Atlantic, Indian, and Pacific, primarily in deep water.

Origin of dorsal fin above the eyes; lateral line rudimentary on eyeless side; pelvic fins symmetrical; vertebrae 36–43.

Considered a subfamily of Pleuronectidae in Nelson (1994) and Evseenko (2004).

Three genera, *Marleyella* (2), *Nematops* (4), and *Poecilopsetta* (14), with 20 species (e.g., Guibord and Chapleau, 2001; Hoshino et al., 2001; Munroe, 2003b; Evseenko, 2004; Guibord and Chapleau, 2004; Amaoka et al., 2006; Kawai and Amaoka, 2006; Kawai et al., 2010).

Family RHOMBOSOLEIDAE (352)—rhombosoleids. Marine; primarily a South Pacific group, occurring mostly around Australia and New Zealand, with one species in the southwestern Atlantic.

Pelvic fins asymmetrical (one on the eyed side may be joined to anal fin); lateral line equally developed on both sides; pectoral radials absent; vertebrae 30–46.

Only *Oncopterus darwini* occurs in the southwestern Atlantic. Two species of *Rhombosolea* enter fresh water in New Zealand (McDowall, 1990). Some of the species resemble the Soleidae.

Considered a subfamily of Pleuronectidae in Nelson (1994) and Evseenko (2004).

Nine genera, *Ammotretis*, *Azygopus*, *Colistium*, *Oncopterus*, *Pelotretis*, *Peltorhamphus*, *Psammodiscus*, *Rhombosolea*, and *Taratretis*, with 19 species (e.g., Evseenko, 2004; Munroe, 2012).

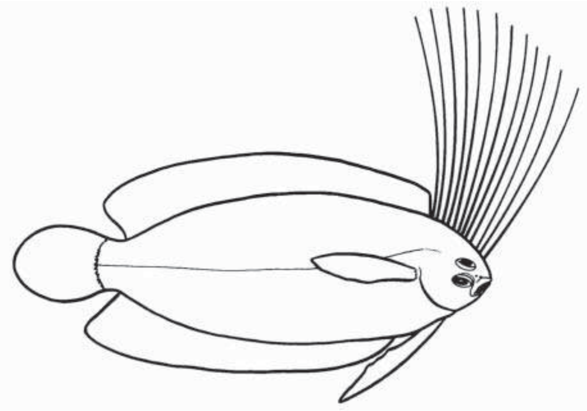
Family ACHIROPSETTIDAE (353)—southern flounders. Marine; Southern Hemisphere, Antarctic and subantarctic.

Eyes sinistral; body extremely compressed; pectoral fins rudimentary (juveniles) or absent; no fin spines; lateral line straight; branchiostegal membranes separate. Its relationships are uncertain, but it probably belongs in the clade of the following families.

This family was established by Evseenko (1984). For placement in classification, see above under the order.

Four genera, *Achiropsetta* (1), *Mancopsetta* (1), *Neoachiropsetta* (1), and *Pseudomancopsetta* (1), with four species (Heemstra in Gon and Heemstra, 1990; Miller, 1993; Evseenko, 1997).

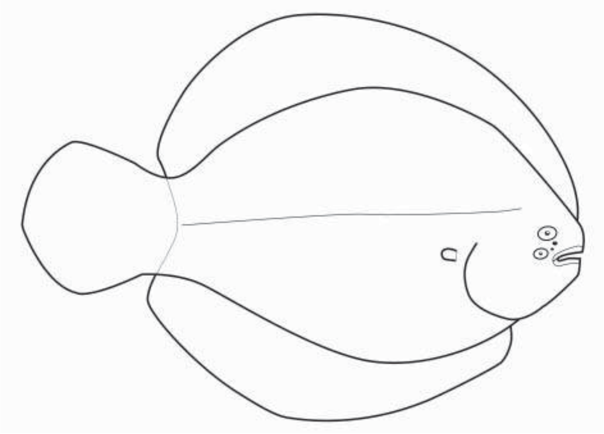
Family SAMARIDAE (354)—crested flounders. Marine, tropical and subtropical; Indo-Pacific, primarily in deep water.



Origin of dorsal fin in front of eyes; lateral line well developed or rudimentary; pelvic fins symmetrical; postcleithra absent (as is also true for the Achiridae, Soleidae, and Cynoglossidae).

Three genera, *Plagiopsetta* (3), *Samaris* (5), and *Samariscus* (19), with about 27 species (Quéro et al., 1989; Kawai et al., 2008, 2011).

Family ACHIRIDAE (355)—American soles. Marine and freshwater; Amphi-American (United States to Argentina).

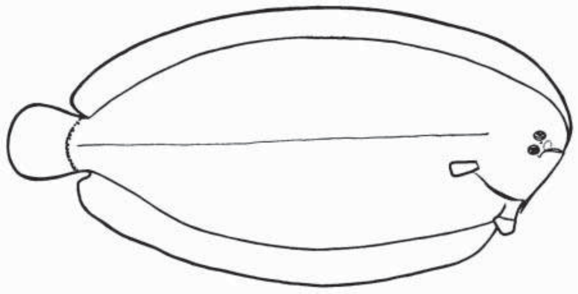


Eyes dextral; margin of preoperculum represented by a superficial groove; dorsal and anal fins free from caudal fin; right pelvic fin joined to anal fin.

The families Achiridae, Soleidae, and Cynoglossidae form a monophyletic group, with the Achiridae being the primitive sister group to the families Soleidae and Cynoglossidae. These three families have the skin of the lower jaw and interopercle continuous ventrally and covering the isthmus and branchiostegals.

About seven genera, *Achirus* (9), *Apionichthys* (7, synonyms *Achiropsis, Pnictes,* and *Soleonasus*), *Baiostoma* (1), *Catathyridium* (4), *Gymnachirus* (3), *Hypoclinemus (1),* and *Trinectes* (10), with about 35 species (Walker and Bollinger, 2001; Munroe, 2003b; Ramos, 2003a,b; Ramos et al., 2009; Duplain et al., 2012).

Family SOLEIDAE (356)—soles. Marine, tropical to temperate seas, primarily Europe to Australia and Japan, entering rivers in Africa (one species in freshwater), Asia, and Australia.



Eyes dextral; margin of preoperculum completely concealed; dorsal and anal fins free from caudal fin or united with caudal; pelvics free from anal fin. The Moses Sole or Speckled Sole, *Pardachirus marmoratus*, of the Indian Ocean, has a chemical defense against predation. Chapleau and Desoutter (1996) noted that *Dagetichthys lakdoensis* occurs 1,300 km inland from the Atlantic Ocean in Cameroon.

About 32 genera (e.g., *Achiroides, Aesopia, Aseraggodes, Austroglossus, Bathysolea, Brachirus, Dagetichthys, Dicologlossa, Heteromycteris, Leptachirus, Liachirus, Microchirus, Monochirus, Pardachirus, Pegusa, Solea, Soleichthys, Synaptura, Typhlachirus, Vanstraelenia,* and *Zebrias*) with about 175 species (Chapleau and Desoutter, 1996; Desoutter and Chapleau, 1997; Quéro, 1997; Desoutter, Chapleau, et al., 2001; Desoutter, Munroe et al., 2001; Munroe in Carpenter and Niem, 2001; Randall, 2002; Muchhala and Munroe, 2004; Vachon et al., 2005, 2007, 2008; Randall and Desoutter-Meninger, 2007). *Euryglossa,* formerly recognized in this family, is a synonym of *Brachyrus* (Desoutter et al., 2001).

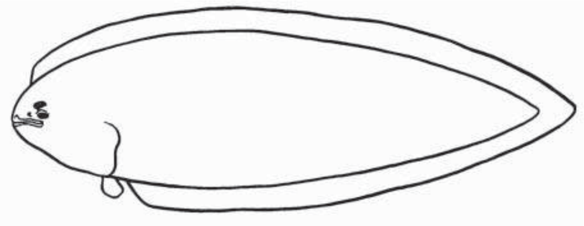
Family CYNOGLOSSIDAE (357)—tonguefishes. Marine (some entering freshwater); tropical and subtropical seas.

Eyes sinistral; margin of preoperculum concealed by skin and scales; dorsal and anal fins confluent with the pointed caudal fin; pelvic fin of eyeless side of four rays along midventral line, linked to anal fin in some, and pelvic girdle and fin on eyed side absent in some; pectoral fins absent (a fine membrane in *Symphurus*); eyes very small and usually close together; mouth asymmetrical; vertebrae 42–78 (usually 9 or 10 abdominal and 33–66 caudal). Maximum length for most species is less than 30 cm, rarely over 40 cm (up to about 48 cm).

Monophyly for this family and its two subfamilies was established by F. Chapleau in 1988.

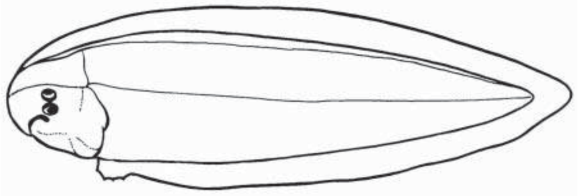
Three genera with about 143 species (e.g., Munroe, 1998).

SUBFAMILY SYMPHURINAE. Snout not hooked; mouth terminal and almost straight; lateral line absent on both sides; pelvic fin free from anal fin. Most are in deep water, occurring about 300–1,900 m.



One genus, *Symphurus,* with about 75 species, found on both sides of the Americas and in the eastern Atlantic and Indo-West Pacific (including Hawaii) (e.g., Munroe, 1998, 2003b; Munroe et al., 2000, 2011; T. A. Munroe in Carpenter and Niem, 2001; Krabbenhoft and Munroe, 2003; Munroe, 2006; Munroe and Hashimoto, 2008; Lee et al., 2009a,b, 2013).

SUBFAMILY CYNOGLOSSINAE. Snout hooked; mouth inferior and contorted; lateral line(s) well developed, at least on eyed side; pelvic fin confluent with anal fin. Most are shallow-water burrowing forms; about five species are known primarily from rivers, and three may occur in only freshwater, as noted by T. R. Roberts in 1989.



Two genera, *Cynoglossus* (lips without fringes) with about 62 species and *Paraplagusia* (lips on eyed side with fringes) with six species, found in the Old World from the eastern Atlantic to the western Pacific (e.g., Munroe in Carpenter and Niem, 2001).

THE FOLLOWING ORDERS ARE PROPOSED TO FORM A CLADE that is sister to all percomorpha except the subseries Ophidiida, Batrachoidida, and Gobiida. The suggested clade was called the "Scombrimorpharia" by Betancur-R. et al. (2013a) but is unnamed and unranked in the present classification. Orders that are suggested to be members include the Syngnathiformes and Scombriformes, as well as the Callionymiformes, Icosteiformes, and Scombrolabraciformes. Song et al. (2014) placed Callionymiformes within Syngnathiformes as the Callionymoidei, but we continue to recognize a separate order for Callionymiformes pending additional research.

In addition to these orders, the suggested clade is proposed to include several families usually classified in Perciformes: the Bramidae, Caristiidae, Mullidae, and Pomatomidae. Given the preliminary nature of the evidence for the contents of the clade, we have not removed these families from their previous orders at this time, though their listings are annotated to indicate their proposed revised placements. We consider the proposed revisions interesting and potentially transformative; future research is needed to further test them and to more deeply evaluate these and other potential members.

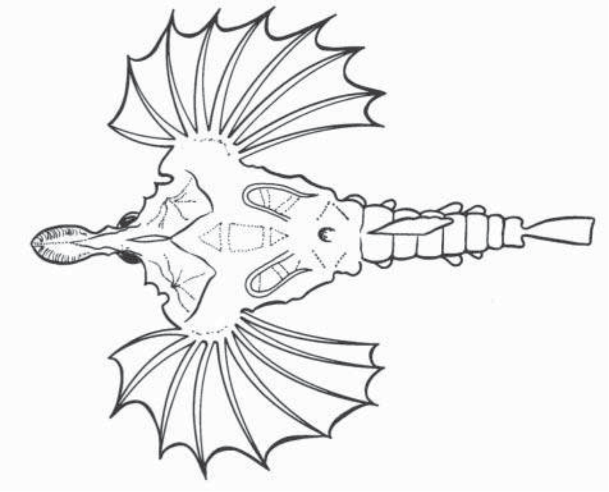
Order SYNGNATHIFORMES (71)—pipefishes and seahorses. Marine, temperate to tropical. Mouth small, at end of tube-shaped snout (except in the "finless" pipefish *Bulbonaricus*, whose adults lack even a short tubiform snout); pelvic fins, when present, abdominal; upper jaw not protractile; lachrymal usually present, other circumorbital bones usually absent; ribs absent; anterior 3–6 vertebrae elongate; aglomerular kidney in at least some. Members of the first suborder, the Syngnathoidei—the pegasids, syngnathids, and solenostomids—share a similar-shaped gill filament, a unique lobate gill filament termed the lopho-branch pattern (described by Johnson and Patterson, 1993). These three families, which share a complete body armor of bony plates, may form a monophyletic group (see Johnson and Patterson, 1993, and modifications by Britz and Johnson, 2002, for a description of various characters shared in these groups). In these taxa and in *Indostomus*, the gill filaments have fewer lamellae than in other teleosts, such as members of the suborder Aulostomoidei with the normal elongate gill filaments (described as comb-like).

Eight families with 69 genera and about 338 species.

Suborder Syngnathoidei. Head and trunk encased in bony plates and tail encircled by bony rings; metapterygoid and postcleithrum absent; gill openings each a small hole on dorsolateral surface behind head; lachrymal large; gill filaments tufted or lobate; posttemporal co-ossified with cranium; hyoid apparatus short, with elongate branchiostegal rays; common feeding mechanism (with interopercle widely separated from reduced subopercle); articular processes of mobile vertebral centra absent (Pietsch, 1978c). In addition, all members have a small toothless mouth.

Superfamily Pegasoidea. Pietsch (1978c) concluded that pegasids are most closely related to the solenostomid-syngnathid lineage. He also believed them to be closely related to the lower Eocene †*Ramphosus* of Italy and Denmark (and recognized the fossil family †Ramphosidae in the same superfamily).

Family PEGASIDAE (358)—seamoths. Marine, rarely brackish water; tropical to temperate, Indo-West Pacific.

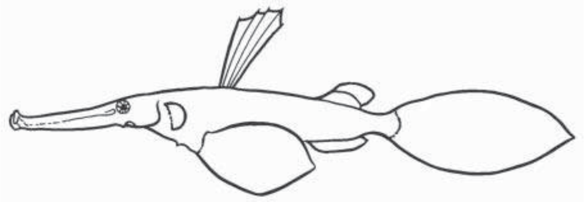


Body oddly shaped (broad and depressed), encased in bony plates; mouth beneath a long flattened rostrum (formed by fused elongate nasals), with an unusual mechanism for protrusion of the jaws; opercle and subopercle minute (widely separated from the interopercle), preopercle greatly enlarged; dorsal and anal fins short, opposite one another, each with five unbranched soft rays (spinous dorsal fin represented only by a horizontal pterygiophore); pectoral fins relatively large, horizontal, with 9–19 unbranched rays; pelvics abdominal, with one spine and two or three soft rays; caudal fin with eight unbranched rays; caudal peduncle quadrangular; five filamentous branchiostegal rays; supracleithrum absent; three circumorbital bones, lachrymal largest; no swimbladder; 19–22 vertebrae (anterior six of the seven abdominal ones elongate). Maximum length 14 cm, perhaps up to 18 cm, attained in *Pegasus volitans.* Seamoths occur in coastal waters, up to 150 m in depth.

Two genera, *Eurypegasus* (two species, with eight or nine tail rings and eyes visible in ventral view) and *Pegasus* (three species, with 11 or more tail rings and eyes not visible in ventral view), with five species (documented in a 1989 study by Palsson and Pietsch).

Superfamily Syngnathoidea. Branchiostegal rays 1–3; no lateral line; anterior three vertebrae elongate.

Family SOLENOSTOMIDAE (359)—ghost pipefishes. Marine; tropical Indo-West Pacific (from South Africa and the Red Sea to Fiji).



Body short, compressed and with large stellate bony plates; two separate dorsal fins, the first with five long feeble spines and the second with 17–22 unbranched soft rays on an elevated base; anal fin with 17–22 unbranched rays; pelvic fins relatively large, with one spine and six soft rays, opposite spinous dorsal; gill openings moderately large; females with brood pouch formed by the pelvics (the females brood the eggs, not the males as in syngnathids); circumorbital bones absent; vertebrae 32–34. Maximum length up to 16 cm.

One genus, *Solenostomus*, with six species (Orr et al., 2002).

Family SYNGNATHIDAE (360)—pipefishes and seahorses. Marine and brackish water, some species in fresh water; Atlantic, Indian, and Pacific.

Body elongate and encased in a series of bony rings; one dorsal fin, usually with 15–60 soft rays, anal fin very small and usually with 2–6 rays, and pectoral fin usually with 10–23 rays (the dorsal, anal, and pectoral fins may be absent in adults of some species, and all three are absent in adults of *Bulbonaricus*); no pelvic fins; caudal fin absent in some; tail (caudal peduncle) may be prehensile and employed for holding on to objects when caudal fin is absent; gill openings very small; supracleithrum absent; kidney present only on right side, aglomerular. Some species are very colorful. Maximum length about 65 cm. Lees et al. (2011) investigated the sculpture and morphology of dermal plates in two syngnathid genera.

Syngnathids are usually confined to shallow water. Most species occur in warm temperate to tropical waters but some pipefishes range into relatively cool water, occurring from southwestern Alaska to Tierra del Fuego in the Americas. At least 18 species are known only from fresh water (streams and lakes, most in the genus *Microphis*), about 37 are euryhaline (entering brackish water from either the oceans or rivers or both), and the rest are marine.

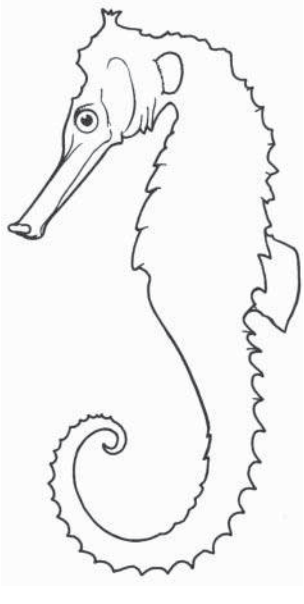
Males care for the eggs, which are attached to them by the female in a special area in the undersurface of the trunk or tail, which may or may not be developed into a pouch. Two groups, once given taxonomic rank, may be recognized based on whether the brood organ is on the tail (the Urophori or syngnathines), as in most genera and including seahorses and the ghost pipefishes, or on the trunk (the Gastrophori or doryrhamphines). Some genera such as *Acentronura* are, to a certain extent, morphological intermediates, if not evolutionary links, between pipefishes and seahorses. The intermediate forms and the various genera of seadragons of Australia, which resemble seahorses but reach a larger size and have leaf-like appendages, are placed in the pipefish subfamily.

Two subfamilies with 57 genera and about 298 species.

SUBFAMILY SYNGNATHINAE (PIPEFISHES). Marine and brackish water, some in freshwater.

Fifty-six genera, e.g., *Acentronura, Anarchopterus, Bhanotia, Bryx, Bulbonaricus, Campichthys, Choeroichthys, Corythoichthys, Cosmocampus, Dunckerocampus, Doryichthys, Doryrhamphus, Enneacampus, Festucalex, Halicampus, Heraldia, Hippichthys, Ichthyocampus, Leptonotus, Lissocampus, Micrognathus, Microphis, Nerophis, Nannocampus, Penetopteryx, Phyllopteryx, Siokunichthys, Solegnathus, Syngnathoides, Syngnathus, Vanacampus,* with about 244 species (Fritzsche, 2003; Fritzsche and Vincent, 2003; Kottelat, 2000a).

SUBFAMILY HIPPOCAMPINAE (SEAHORSES). Marine. Teske et al. (2004) proposed a molecular phylogeny and biogeographic scenario for the only genus.

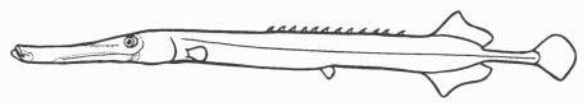


One genus, *Hippocampus*, with about 54 species (e.g., Kuiter, 2001, 2003; Lourie et al., 1999; Lourie and Randall, 2003; Casey et al., 2004; Lourie and Kuiter, 2008; Foster and Gomon, 2010).

Suborder Aulostomoidei. Teeth small or absent; lateral line well developed to absent; usually four or five (rarely three) branchiostegal rays; gills comb-like (not lobate); postcleithrum present. Two superfamilies.

Superfamily Aulostomoidea. Anterior four vertebrae elongate; three median, well-developed bones dorsally behind head (nuchal plates); usually six (rarely five) soft pelvic rays. Two families.

Family AULOSTOMIDAE (361)—trumpetfishes. Tropical marine; Atlantic and Indo-Pacific.

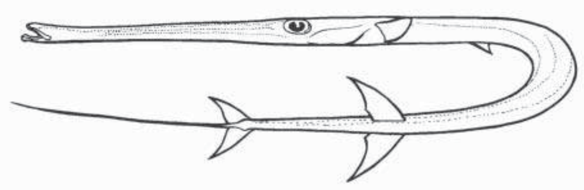


Body compressed, elongate, and scaly; fleshy barbel at tip of lower jaw; series of 8–12 isolated dorsal spines followed by a normal dorsal fin of 22–27 soft rays; anal rays 23–28; caudal fin rounded; anus far behind pelvics; lateral line well developed; abdominal vertebrae with two transverse processes of equal size (or a divided process); body musculature with a network of bony struts that forms an interwoven pattern (observed in *Aulostomus chinensis*); vertebrae 59–64 (24–26 + 35–38).

Trumpetfishes are predators and are usually seen on reefs. They often swim alongside larger fish or lie with their bodies at odd angles such as vertical with the head downward. Maximum length up to 80 cm.

One genus, *Aulostomus*, probably with three species (e.g., Fritzsche, 2003).

Family FISTULARIIDAE (362)—cornetfishes. Tropical marine; Atlantic, Indian, and Pacific.



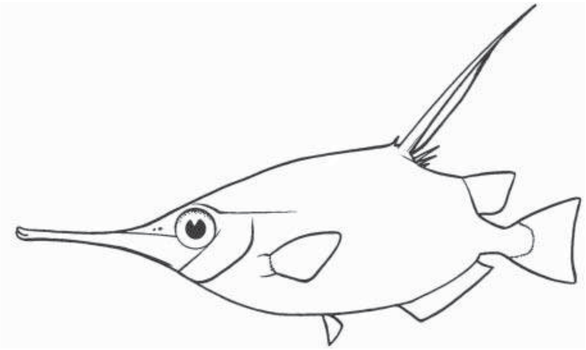
Body depressed, elongate, and naked or with minute prickles, and linear series of scutes (no scales); no barbel on jaw; no dorsal spines; anal and dorsal fins each with 13–20 soft rays; caudal fin forked with elongate filament produced by middle two caudal rays; anus short distance behind pelvic fins; lateral line well developed, arched anteriorly almost to middle of back and continuing onto caudal filament; abdominal vertebrae with two transverse processes but the posterior ones reduced; vertebrae 76–87.

Cornetfishes usually inhabit shallow waters of tropical and subtropical seas. They are predatory on other fishes, feeding both in open water and in coral reefs. Their long tubular snout, which functions as a pipette, is an excellent adaptation for feeding among reefs. Maximum length up to 1.8 m, attained in *Fistularia tabacaria*, usually less than 1 m.

One genus, *Fistularia*, with four species (e.g., Fritzsche, 2003).

Superfamily Centriscoidea. Anterior five or six vertebrae elongate; pelvic fins with one spine and four soft rays. The two included families are recognized as subfamilies of Centriscidae by some (e.g., Eschmeyer, 1998).

Family MACRORAMPHOSIDAE (363)—snipefishes. Tropical and subtropical marine; Atlantic, Indian, and Pacific.

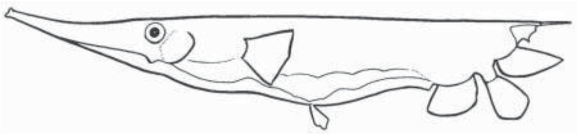


Body compressed, deep, and usually with bony plates on each side of back; no barbel on jaw; 4–8 dorsal spines, second spine very long, all joined by a membrane; second dorsal fin has about 11–19 soft rays; lateral line present or absent. Maximum length up to 30 cm.

First known in the fossil record from the Late Cretaceous, the earliest record of any syngnathiform. The species involved, †*Gasterorhamphosus zuppichinii*, resembles *Macroramphosus* in body shape but, among various differences, has some characters suggesting an affinity with the Gasterosteoidei.

Three genera, *Centriscops* (1), *Macroramphosus* (about 2), and *Notopogon* (5), with about 8 species (e.g., Duhamel, 1995; Fritzsche, 2003; Bilecenoglu, 2006).

Family CENTRISCIDAE (364)—shrimpfishes. Marine; Indo-Pacific.



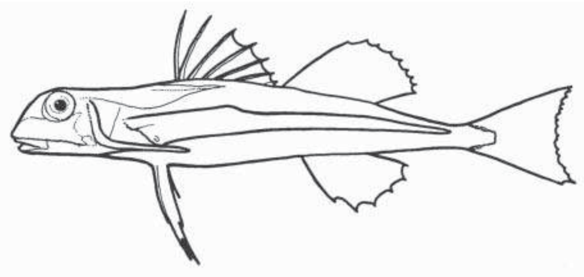
Extremely compressed, razor-like body with sharp ventral edge; body almost entirely encased by thin bony plates that are expansions of the vertebral column; first dorsal spine long and sharp at extreme end of body, followed by two shorter spines; soft dorsal fin and caudal fin displaced ventrally; no lateral line; mouth toothless. Swimming is in a vertical position, snout down. Maximum length up to 15 cm.

As with many of the other gasterosteiform families, there are many Tertiary fossils known. Fossil centriscids are known from the Eocene to Pliocene and fossil *Aeoliscus* are known from Oligocene-Miocene deposits of Europe (Parin and Micklich, 1996).

Two genera, *Aeoliscus* and *Centriscus*, with about four species.

Suborder Dactylopteroidei. Formerly with Scorpaeniformes, the placement of this group is controversial. Johnson and Patterson (1993), in not finding any evidence of scorpaeniform relationship, placed it in its own order next to the Scorpaeniformes. See also the detailed study of Imamura (2000), who found 20 synapomorphies showing a monophyletic relationship with the perciform family Malacanthidae (the subsequently redefined percoid family Dactylopteridae was divided into four subfamilies, of which the dactylopterids were one). However, this realignment was not supported by the molecular study of Smith and Wheeler (2004). We place the group with syngnathiforms, based on the molecular evidence (e.g., Betancur-R. et al., 2013a), because morphological evidence to the contrary is not strong. See also Shinohara and Imamura (2007).

Family DACTYLOPTERIDAE (Cephalacanthidae) (365)—flying gurnards. Marine tropical; Indo-Pacific and Atlantic.



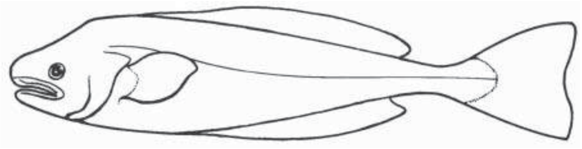
Large, blunt, bony head (with spines and keels); body covered with scute-like scales; tremendously enlarged and colorful pectoral fins with inner rays free, total of 28–37 rays; two free spines (the first may be on the nape) before the two dorsal fins; pelvic fins thoracic, each with one spine and four soft rays; no lateral line; 22 vertebrae. Maximum length about 50 cm.

These benthic fishes, which superficially resemble triglids, produce sounds by stridulation by using the hyomandibular bone and "walk" on the sea floor by alternately moving the pelvic fins. The common name arose in the belief that because of their large pectoral fin they could fly or at least glide for short distances. However, they seldom, if ever, leave the substrate and there is no evidence that they ever leave the water and glide.

Two genera, *Dactyloptena* (Indian and western and central Pacific) and *Dactylopterus* (Atlantic), with about seven species (e.g., Eschmeyer in Smith and Heemstra, 1986; Eschmeyer, 1997).

Order ICOSTEIFORMES (Malacichthyes) (72)—ragfishes. The one included family and species was placed in its own order, Icosteiformes, by Berg (1940) and Gosline (1971). More recently, Springer and Johnson (2004) presented a detailed analysis on its systematic relationships and presented evidence that it is probably not associated with the stromateoids, as suggested by some earlier authors. Here we tentatively align the order with the proposed syngnathiform/scombriform clade (see above).

Family ICOSTEIDAE (366)—ragfishes. Marine; Pacific coast of North America.



Body elliptical, highly compressed, and limp; skeleton largely cartilaginous; no spines in fins; minute prickles on fin rays; dorsal-fin rays 52–58; scales imbedded or absent in adult; pelvic fins loosely attached in young, lost in adults; five hypurals; 66–72 vertebrae. Maximum length 2 m. As noted in Springer and Johnson (2004), Allen in 2001[2003] presented information on records of the one species.

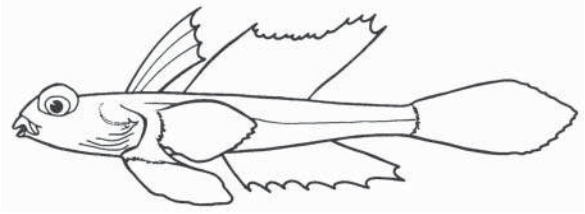
One species, *Icosteus aenigmaticus* (Mecklenburg, 2003).

Order CALLIONYMIFORMES (73). Head usually broad and depressed; body scaleless; mouth small; usually two dorsal fins present and first with 1–4 flexible spines (spinous fin absent in *Draculo*); pelvic fin with one spine and five soft rays; basibranchials present; vertebrae 21–23.

See the preceding section on gobiesocoids for comments on a possible affinity between that group and the callionymoids. Much work on this family has been done by Fricke (e.g., 2002a) and by Nakabo (e.g., 1987); they gave differing opinions on some generic compositions.

Two families, 22 genera, and 202 species (Fricke 2002a).

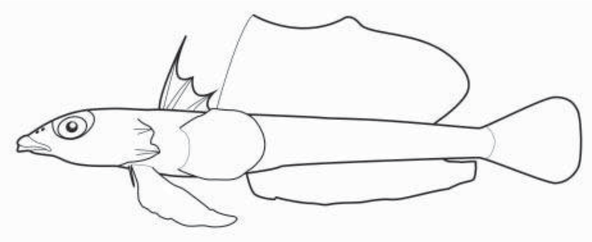
Family CALLIONYMIDAE (367)—dragonets. Marine (two species enter rivers), benthic; all warm seas, primarily Indo-West Pacific.



Gill opening reduced to a small opening on upper side of head; preopercle with a strong spine, opercle and subopercle spineless; lateral line continued on body; three radials in pectoral skeleton; usually no basisphenoid or post-temporal; paired nasal bones; two postcleithra; hypurals fused into a single plate; dorsal-fin spines usually four and soft rays 6–11; anal fin with 4–10 soft rays. Maximum length about 25 cm. Dragonets can be very colorful; sexual dimorphism is common.

Twenty genera, *Anaora* (1), *Bathycallionymus* (1), *Callionymus* (synonym *Calliurichthys*) (104), *Dactylopus* (2), *Diplogrammus* (7), *Draculo* (*Pogonymus*) (5), *Eocallionymus* (1), *Eleutherochir* (synonym *Bathycallionymus*) (1), *Foetorepus* (10), *Neosynchiropus* (2), *Paracallionymus* (1), *Protogrammus* (2), *Repomucenus* (5), *Pseudocalliurichthys* (1), *Spinicapitichthys* (1), with 188 species (e.g., Fricke, 2002a; Motomura and Mukai, 2006; Ng and Rainboth, 2011).

Family DRACONETTIDAE (368)—slope dragonets. Marine; Japan to Hawaii, Atlantic, and Indian.



Gill opening comparatively broad; opercle and subopercle each with a strong straight spine; preopercle spineless; lateral line developed on head but degenerate on body (in a groove); four radials in pectoral skeleton; basisphenoid and posttemporal present; no nasal bone; one postcleithrum; two separate hypurals; three dorsal-fin spines and 12–15 soft rays; anal fin with 12 or 13 soft rays; two nostrils on each side.

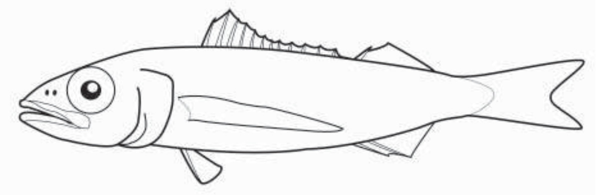
Draconettids are relatively rare. They occur primarily in tropical to warm temperate waters along the edge of the continental shelf or on seamounts in widely scattered areas.

This family was not sampled by Betancur-R. et al. (2013a), but they suggested it to be part of their syngnathiform/scombriform clade based on its close relationship to Callionymidae.

Two genera, *Centrodraco* (13) and *Draconetta* (1), with 14 species (e.g., Fricke, 2002a,b, 2010).

Order SCOMBROLABRACIFORMES (74)—longfin escolars. One family, genus, and species.

Family SCOMBROLABRACIDAE (369)—longfin escolars. Marine; deepwater Atlantic, Indian, and Pacific.



Premaxillae protractile; preopercle and opercle serrated; swimbladder with thin, elastic walls and, in adult, with bubble-like evaginations fitting into vertebral bullae; 30 vertebrae, fifth through twelfth of adults with expanded parapophyses, called the bullae, that bulge dorsolaterally and with ventral opening. Maximum length about 30 cm. The study of Johnson (1986) suggested, in cladistic terms, that it may be the primitive sister group of *Pomatomus* and the scombroids.

This monotypic family is among those postulated to be part of a basal percomorph syngnathiform/scombriform clade by Betancur-R. et al. (2013a) and others.

One species, *Scombrolabrax heterolepis* (Nakamura and Parin, 2003).

Order SCOMBRIFORMES (Pelagia) (75)—mackerels. Two suborders (Scombroidei and Stromateoidei). Membership of this order (or suborder) formerly included Sphyraenidae, Xiphiidae, and Istiophoridae, which are not included here. Orrell et al. (2006) supported separating scombroids from xiphioids on molecular evidence. Little et al. (2010), using phylogenetic analysis of nine mitochondrial and three nuclear loci, found strong evolutionary affinities of billfishes (Xiphiidae and Istiophoridae) with flatfishes (Pleuronectiformes) and jacks (Carangidae), but did not resolve the position of sphyraenids. Some broad-scale molecular studies (e.g., Near et al., 2012a; Betancur-R. et al. 2013a; Miya et al., 2013) supported inclusion of sphyraenids with xiphiids and istiophorids as they are in the present work, while placing the remaining scombriformes in another putative clade discussed above, sister to all Percomorpha except Ophidiida, Batrachoidida, and Gobiida, and within a subclade called the Pelagia by Miya et al. (2013).

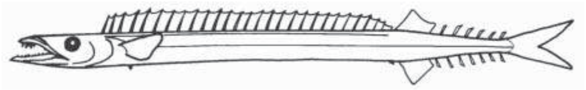
Two suborders (Scombroidei, Stromateoidei), nine families, 57 genera and 192 species.

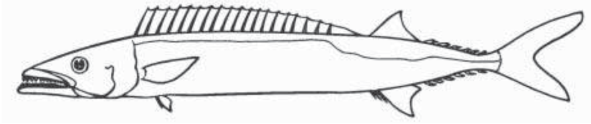
Suborder Scombroidei. Upper jaw not protrusible (premaxilla fixed); teeth ankylosed.

This suborder includes species that are among the world's fastest-swimming fishes. Bluefin Tuna have been recorded in captivity with sustained swimming speeds of up to 10.2 km per hour and short bursts of speeds estimated at about 54 km per hour (Wardle et al., 1989); Walters and Fierstine (1964) estimated yellowfin tuna to reach burst swimming speeds of more than 70 km per hour. Endothermy, the ability to maintain elevated body temperature by metabolic means, is achieved in tunas (subfamily Scombrinae, tribe Thunnini) in a manner similar to that in birds and mammals, whereas cranial endothermy, in which only the brain and eyes are warmed, occurs in *Gasterochisma* (subfamily Gasterochismatinae) (and also in the putatively unrelated billfishes; see above).

Three families with 41 genera and 199 species.

Family GEMPYLIDAE (370)—snake mackerels. Marine, tropical and subtropical seas, often in very deep water.





Body oblong or elongate and compressed; protruding lower jaw; teeth very long; maxilla exposed; isolated finlets usually present behind dorsal and anal fins; anal fin with one to three spines and 8–35 soft rays; caudal fin present; pectoral fin low on body; pelvic fin with one spine and five soft rays or reduced to one spine; vertebrae 32–58. Several genera, such as *Tongaichthys*, have many scombrid characters. *Diplospinus*, with its unusual lateral line and which is intermediate between the gempylids and trichiurids in many characters, is placed in the Gempylidae following Parin and Bekker (1979). According to Johnson (1986), *Lepidocybium* forms the sister group to the other gempylids.

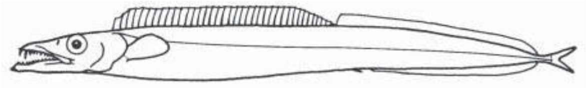
Sixteen genera, *Diplospinus* (1), *Epinnula* (1), *Gempylus* (upper figure) (1), *Lepidocybium* (1), *Nealotus* (1), *Neoepinnula* (2), *Nesiarchus* (synonym *Escolar*) (1), *Paradiplospinus* (2), *Promethichthys* (1), *Rexea* (7), *Rexichthys* (1), *Ruvettus* (1), *Thyrsites* (lower figure) (1), *Thyrsitoides* (1), *Thyrsitops* (1), and *Tongaichthys* (1), with 24 species (e.g., Nelson, 1994; Roberts and Stewart, 1997; Nakamura and Parin in Carpenter and Niem, 2001). Fossils include the Oligocene †*Abadzekhia* (Bannikov, 2005).

Family TRICHIURIDAE (371)—cutlassfishes. Marine: Atlantic, Indian, and Pacific.

Body very elongate and strongly compressed; protruding lower jaw; teeth very long; maxilla concealed by lacrymal; fang-like teeth usually present; single nostril on each side; gill cover splintered; dorsal fin extremely long based, with spines and soft rays (spinous portion usually shorter than soft rayed portion, notch between two portions in some species); anal fin with two spines and 56–121 soft rays; caudal fin small or absent; pectoral fin low on body; pelvic fin reduced (with a scale-like spine and one rudimentary soft ray) or absent; vertebrae 98–192 (34–53 + 55–151).

Ten genera with 44 species (e.g., Nelson, 1994; Parin, 1995; Nakamura and Parin in Carpenter and Niem, 2001).

SUBFAMILY APHANOPODINAE. Caudal fin small, forked; pelvic fin present, with scale-like spine and one rudimentary soft ray (external fin may be present only in juvenile); spinous dorsal fin with 38–46 rays, slight notch at division of spinous and soft portions.



Two genera, *Aphanopus* (7) and *Benthodesmus* (11), with 18 species (e.g., Parin, 1995; Stefanni and Knutsen, 2007).

SUBFAMILY LEPIDOPODINAE. Caudal fin present (small and forked) or absent; pelvic fin present, rudimentary; spinous dorsal fin usually with 3–10 rays, spinous and soft portions continuous; lateral line descending gradually behind the pectoral fin.

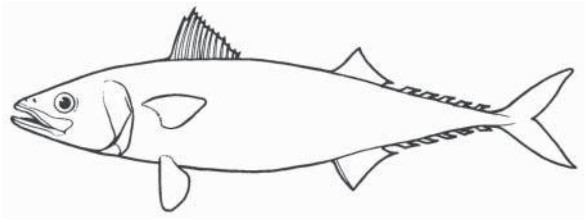
Four genera, *Assurger* (1), *Eupleurogrammus* (2), *Evoxymetopon* (3), and *Lepidopus* (6), with 12 species (e.g., Chakraborty et al., 2006).

SUBFAMILY TRICHIURINAE (HAIRTAILS). Caudal fin and hypurals absent; pelvic fin and skeleton absent; spinous dorsal fin with three or four rays, spinous and soft portions continuous; lateral line descending steeply from the pectorals and running near ventral profile of body.

Four genera, *Demissolinea* (1), *Lepturacanthus* (3), *Tentoriceps* (1), and *Trichiurus* (9), with 14 species (e.g., Burhanuddin and Iwatsuki, 2003; Chakraborty et al., 2005).

Family SCOMBRIDAE (372)—mackerels and tunas. Marine (rarely freshwater); tropical and subtropical seas.

Two dorsal fins (depressible into grooves) with 5–12 finlets behind second dorsal and anal fins; first dorsal fin with 9–27 rays, origin well behind head; pectoral fins inserted high on body; pelvic fins with one spine and five soft rays, placed beneath the pectorals; gill membranes free from isthmus; scales cycloid and usually small; slender caudal peduncle with two keels; specialized subcutaneous vascular system in *Thunnus* and its close relatives; vertebrae 31–64.



Some members are endothermic (see under suborder Scombroidei). These fast-swimming fish are exploited as popular sport and valuable commercial fisheries. Length up to 4.2 m, attained by Atlantic Bluefin Tuna, *Thunnus thynnus*, which migrates large distances and shows little evidence of geographically or genetically distinct populations in the Atlantic and Mediterranean. The Pacific Bluefin Tuna migrates across its ocean, and the Southern Bluefin Tuna migrates below about 40°S to reach a region between Australia and Indonesia (Alvarado Bremer et al., 2005). In contrast, other tunas do not migrate such great distances. The Bigeye Tuna, *T. obesus*, appears to maintain genetic distinctiveness of two haplotype groups, one almost exclusively in the Atlantic Ocean and the other in the Atlantic but also in the Indo-Pacific (Martínez et al., 2006).

This family was recovered as non-monophyletic by Betancur-R. et al. (2013a) but most other molecular and morphological research finds it to be monophyletic.

Fifteen genera with 51 species (about half the species belong to *Scomberomorus* and *Thunnus*) (e.g., Collette et al., 2001; Collette, 2003c,d; Miya et al., 2013). The following classification is based on Collette et al. (2001). An immense literature exists on this family with B. B. Collette giving us our present understanding of the diversity and systematics of this commercially important group.

SUBFAMILY GASTEROCHISMATINAE (BUTTERFLY KINGFISHES). Scales large, much larger than in other scombrids, about 80 in lateral series; pelvic fins longer than head length in juveniles, fitting into a deep, ventral groove; two anterior projections from the swimbladder extend into the back of the skull.

One species, the Butterfly Kingfish *Gasterochisma melampus*, primarily of the Southern Ocean.

SUBFAMILY SCOMBRINAE. Scales minute or absent.

TRIBE SCOMBRINI (MACKERELS). Two genera, *Rastrelliger* (3), and *Scomber* (4), with seven species. As with many common names, the name “mackerel” is used for species in many different families (e.g., Nelson et al., 2004).

TRIBE SCOMBEROMORINI (SPANISH MACKERELS). Three genera, *Acanthocybium* (1), *Grammatorcynus* (2), and *Scomberomorus* (18), with 21 species. *S. sinensis*, although normally marine, occurs in estuaries and is known from 300 km up the Mekong River. Collette and Russo (1985) defined the tribe and all the component species.

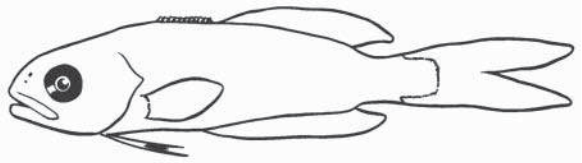
TRIBE SARDINI (BONITOS). Four genera, *Cybiosarda* (1), *Gymnosarda* (1), *Orcynopsis* (1), and *Sarda* (4), with seven species (e.g., Viñas et al., 2004, 2010). Collette and Chao (1975) defined the tribe and its species.

TRIBE THUNNINI (TUNAS). Five genera, *Allothunnus* (1), *Auxis* (2), *Euthynnus* (3), *Katsuwonus* (1), and *Thunnus* (8), with 15 species (e.g., Collette and Aadland, 1996; Bremer et al., 2005; Martínez et al., 2006; Qiu et al., 2013).

Suborder Stromateoidei. Toothed saccular outgrowths in gullet behind last gill arch (except in amarsipids); lachrymal bone covering most of maxilla; scales usually cycloid, weakly ctenoid in some; branchiostegal rays 5–7; hypural plates 2–6; caudal fin with 15 branched rays; vertebrae 24–61. Length up to 1.2 m.

Six families, 16 genera, and 73 species. All are marine. The classification is based primarily on the studies of R. L. Haedrich and M. H. Horn (Nelson, 1994). Doiuchi et al. (2003) provided a needed cladistic study based on morphological characters of the stromateoids employing all genera, finding Centrolophidae to be paraphyletic with the inclusion of *Psenopsis.* Doiuchi and Nakabo (2006), using phylogenetic analysis of mitochondrial DNA sequences, determined a monophyletic Centrolophidae.

Family AMARSIPIDAE (373)—amarsipas. Marine; tropical Indian and Pacific, close to the equator.

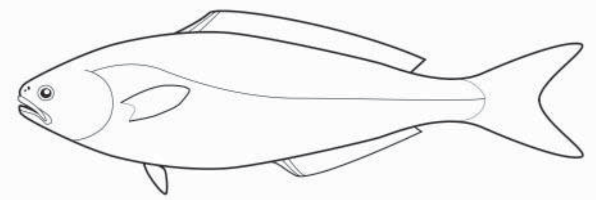


Pelvic fins present, jugular, their origin well before the pectoral fins; body translucent, no color pattern; pharyngeal sacs absent; dorsal fin with 10–12 short spines and 22–27 longer soft rays; anal fin with 28–32 soft rays, no spines; pectoral fin with 17–19 rays; vertebrae 45–47.

These were not sampled by Betancur-R. et al. (2013a) but are included here based on presumed relationship to Stomateidae.

One species, *Amarsipus carlsbergi,* described in 1969 (e.g., P. R. Last in Carpenter and Niem, 2001).

Family CENTROLOPHIDAE (374)—medusafishes. Marine; tropical to temperate, all seas except most of mid-Indian and mid-Pacific.

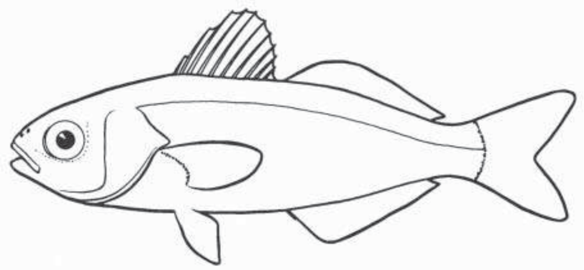


Dorsal fin continuous, spines either 0–5, weakly developed and graduating into the soft rays (as in figure and in the first three genera listed) or 5–9, stout, and considerably shorter than and generally not graduating into the soft rays (in the last three genera listed); total anal-fin rays 15–41 (usually three spines).

Centrolophus is the only stromateoid in the far North Atlantic (to Iceland), whereas *Icichthys* is the only stromateoid in the far North Pacific (to Alaska). Both genera are also in southern oceans.

Seven genera, *Centrolophus* (1), *Hyperoglyphe* (6), *Icichthys* (2), *Psenopsis* (6), *Schedophilus* (8), *Seriolella* (6), and *Tubbia* (2), with 31 species (McDowall in Carpenter and Niem, 2001; Haedrich, 2003; Last et al. 2013). *Schedophilus* and *Seriolella* were hypothesized to be sister taxa by Doiuchi et al. (2003).

Family NOMEIDAE (375)—driftfishes. Marine; tropical and subtropical seas.

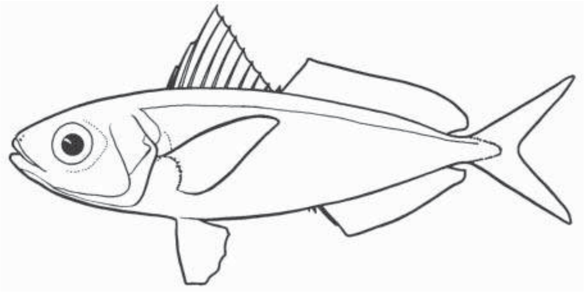


Two dorsal fins, the first with 9–12 slender spines and the second with 0–3 spines and 15–32 soft rays; anal fin with 1–3 spines and 14–30 soft rays. Maximum length about 1 m.

The 10-cm *Nomeus gronovii* (Man-of-War Fish) is circumtropical and usually found with the Portuguese Man-of-War (*Physalia*). The fish swims unharmed among the stinging tentacles.

Three genera, *Cubiceps* (10), *Nomeus* (1), and *Psenes* (5), with about 16 species (Last in Carpenter and Niem, 2001; Haedrich, 2003).

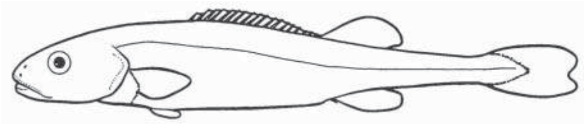
Family ARIOMMATIDAE (376)—ariommatids. Marine; deep water, tropical and subtropical coastlines of eastern North and South America, Africa, Asia, Kermadec Islands, and Hawaii.



Two dorsal fins, the first with 10–12 slender spines and the second with 14–18 soft rays; anal fin with three short spines and 13–16 soft rays; pectoral fin with 20–24 rays; caudal peduncle with two low, fleshy, lateral keels on each side; vertebrae 30–32.

One genus, *Ariomma,* with about seven species (P. R. Last in Carpenter and Niem, 2001; Haedrich, 2003).

Family TETRAGONURIDAE (377)—squaretails. Marine; tropical and subtropical seas.

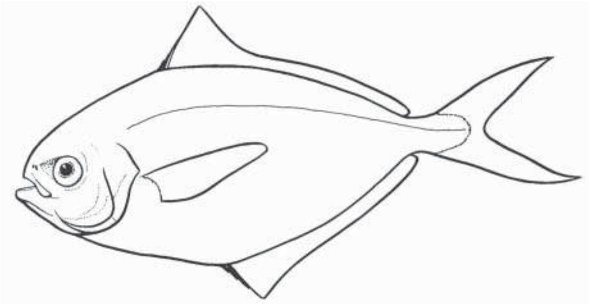


Body elongate; two dorsal fins, the first with 10–20 short spines and the second with 10–17 soft rays; anal fin with one spine and 10–16 soft rays; caudal peduncle with a single keel on each side; lateral-line scales 73–114; vertebrae 40–58. Individuals are thought to feed almost exclusively on coelenterates and ctenophores.

These were not sampled by Betancur-R. et al. (2013a) but included here based on presumed relationship to Stomateidae.

One genus, *Tetragonurus*, with three species. This is the most widely distributed of all the stromateoid genera (P. R. Last in Carpenter and Niem 2001; Haedrich, 2003).

Family STROMATEIDAE (378)—butterfishes. Marine; coastal North and South America, western Africa, and southern Asia (Indo-Pacific).



Body usually very deep; pelvic fins absent in adult (pelvic bones present in some young); dorsal fin continuous; anal fin usually with 2–6 spines and 30–50 soft rays.

Three genera, *Pampus* (5), *Peprilus* (7), and *Stromateus* (3), with 15 species (Liu and Li 1998; P. R. Last in Carpenter and Niem, 2001; Haedrich, 2003; Doiuchi et al., 2004; Cui et al. 2010).

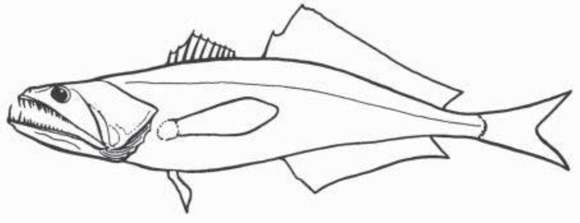
THE REMAINING TEN ORDERS OF PERCOMORPHA—Trachiniformes, Labriformes, Perciformes, Scorpaeniformes, Moroniformes, Acanthuriformes, Spariformes, Caproiformes, Lophiiformes, and Tetraodontiformes—have been suggested to constitute a clade of higher percomorphs by various broad-scale molecular studies (e.g., Near et al., 2012a; Betancur-R. et al., 2013a). In the previous edition (Nelson, 2006), many of these were classified as suborders of Perciformes. This unnamed clade is presented here to reflect recent phylogenetic proposals but recognizing that there is still a need for morphological and other character support.

Order TRACHINIFORMES (Uranoscopiformes in part) (76). According to Betancur-R. et al., 2013a, three trachinoid families, Ammodytidae, Pinguipedidae and Uranoscopidae form a clade (Uranoscopiformes) related to Labriformes. The trachinoid families Chiasmodontidae and Creediidae were putatively placed near syngnathiforms, but with weak nodal support. Most trachinoids, however, have not been sampled by them or other comparable molecular analyses, making a definitive composition of the group based on molecular evidence unknown. The evidence for dismantling the Trachiniformes (Trachinoidei of Nelson, 2006) is at present not very strong. We thus retain the group with the same membership as Nelson (2006) except for Trichodontidae (now in Cottoidei). We annotate specific families to indicate proposed alternative placements.

Imamura and Odani (2013) reviewed the history of classification of trachinoids, discussed the numerous points of disagreement, and recognized 11 families (listed alphabetically): Ammodytidae, Champsodontidae, Cheimarrichthyidae, Chiasmodontidae, Creediidae, Leptoscopidae, Percophidae, Pinguipedidae, Trachinidae, Trichonotidae, and Uranoscopidae.

Eleven families with a total of 53 genera and 301 species, the majority of which are tropical marine fishes, are recognized in this order.

Family CHIASMODONTIDAE (379)—swallowers. Marine; oceanic.

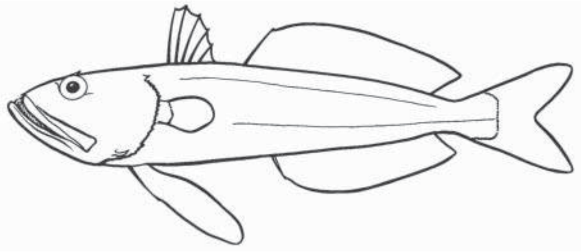


Premaxilla and maxilla long and slender, firmly united posteriorly; anterior tip of premaxilla expanded dorsally and diverging laterally; highly distensible mouth and stomach; first dorsal fin short with 7–8 flexible spines, second long with 18 to 29 segmented rays; anal fin with 1 spine and 17-29 segmented rays; 33–48 vertebrae. Placed in the Percoidei in Gosline (1971).

This family is among those postulated to be part of a basal percomorph syngnathiform/scombriform clade by Betancur-R. et al. (2013a) and others.

Four genera, *Chiasmodon* (7), *Dysalotus* (2), *Kali* (7, synonym *Gargaropteron*), and *Pseudoscopelus* (16), with 32 species (e.g., Johnson and Cohen, 1974; McEachran and Sutton, 2003; Melo et al., 2007; Spitz et al., 2007; Melo, 2008, 2009, 2010a,b). *Pseudoscopelus* bears photophores.

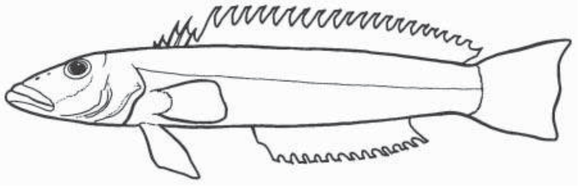
Family CHAMPSODONTIDAE (380)—gapers. Marine; Indo-Pacific.



Pelvic fins elongate, in front of pectorals; pectoral fins small, base oblique; spinous dorsal short, with five spines, soft dorsal, with 17–20 rays; anal fin with one spine and 17–20 soft rays. There is no evidence that *Champsodon* is related to chiasmodontids or to other trachinoids, and Johnson (1993) and Mooi and Johnson (1997) noted that it may be related to the scorpaeniforms. Eocene fossils of †*Eochampsodon* are known from the Northern Caucasus (Bannikov, 2004c).

One genus, *Champsodon*, with 13 species (Nemeth, 1994).

Family PINGUIPEDIDAE (381)—sandperches. Marine; Atlantic coast of South America and Africa, Indo-Pacific (to New Zealand and Hawaii), and off Chile.

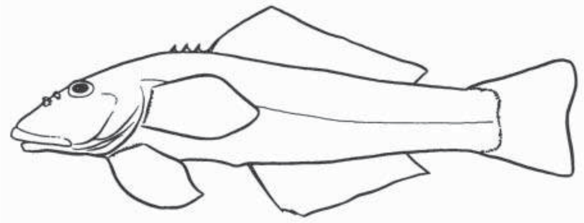


Pelvic fins below or slightly in front of pectorals, with one spine and five soft rays; mouth protractile and terminal; caudal fin truncate to deeply crescentic, with 13 or 15 branched rays; dorsal fin continuous, with 4–7 short spines and 19–27 soft rays; anal fin with 17–25 rays, first one or two may be spine-like; lateral line continuous; gill membranes united, free from isthmus, vertebrae 30–37.

The genera *Pinguipes*, *Prolatilus*, and *Pseudopercis*, with five species, are endemic to South America (one species of *Parapercis* occurs in South America) (Rosa and Rosa, 1998). See comments below under Cheimarrhichthyidae.

Seven genera, *Kochichthys* (1), *Parapercis* (74), *Pinguipes* (2), *Prolatilus* (1), *Pseudopercis* (2), *Ryukyupercis* (1), and *Simipercis* (1), with about 82 species (Rosa and Rosa, 1998; Randall and McCosker, 2002; Imamura and Matsuura, 2003; Ho and Shao, 2010; Liao et al., 2011; Yamanaka et al., 2011; Ho and Causs, 2012; Johnson and White, 2012; Sparks and Baldwin, 2012; Ho, 2013; Ho and Johnson, 2013).

Family CHEIMARRHICHTHYIDAE (382)—New Zealand torrentfishes. Freshwater (young are known from the sea); rivers of New Zealand.



Pelvic fins well in front of pectorals, wide apart, mouth nonprotractile and inferior; caudal fin with 13–15 branched rays; dorsal fin has three to five spines and 18–21 soft rays, the anterior three or four spines are short and stout and separated from the remainder of the continuous fin; anal fin with one or two spines and 15 soft rays; 15 pectoral rays; about 50 scales along lateral line; vertebrae 31–33. Maximum length about 15 cm.

The one species was placed its own family in previous editions (Nelson, 1976, 1984, 1994, and 2006); this placement, as opposed to recognition in the Pinguipedidae, was supported by Pietsch (1989), and by the systematic studies of Rosa and Rosa (1998) and Imamura and Matsuura (2003); the latter argued against a close relationship with *Parapercis*. However, a cladistic analysis involving all trachinoid genera is desirable to demonstrate whether or not *Cheimarrichthys* and the Pinguipedidae together form a monophyletic taxon. McDowall (2000) gave life history, ecological, and biogeographic information.

One species, *Cheimarrichthys fosteri* (McDowall 1990).

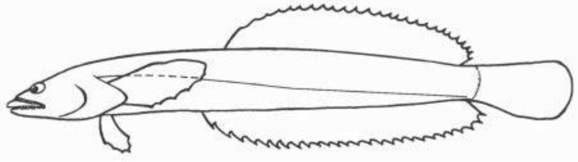
Family TRICHONOTIDAE (383)—sanddivers. Marine; Indo-West Pacific.

Eye with dorsal iris flap consisting of numerous elongate strands extending over lens; lower jaw projecting beyond upper jaw; anterior rays of dorsal fin in males of at least some species elongated; pelvic fin with one spine and five soft rays; lateral line on midside of body; predorsal bone between first two neural spines; postcleithrum present; lateral-line scales with a deep V-shaped notch in the posterior margin.

The families Trichonotidae, Creediidae, and Percophidae may form a monophyletic assemblage.

One genus, *Trichonotus*, and ten species (Randall and Tarr, 1994; Clark and Pohle, 1996; Nelson, 2001; Smith and Johnson, 2007; Katayama et al., 2012).

Family CREEDIIDAE (384)—sandburrowers. Marine; Indo-West Pacific (South Africa to Hawaii and Easter Island).



Row of cirri bordering lower jaw; dorsally projecting knob at symphysis of lower jaw; snout fleshy, projecting beyond lower jaw; lateral line descending abruptly or gradually to ventral surface; lateral-line scales, except for anteriormost ones, with posterior extension, often trilobed; body largely scaleless in a few species (lateral-line scales always present); dorsal fin continuous, with 12–43 unbranched soft rays; pelvis uniquely shaped, like an inverted bowl; pelvic fin with one spine and 3–5 soft rays (fins absent in the one species of *Apodocreedia*), interpelvic space very small; eye with infolding of the cornea at cornea-skin junction, and eyes slightly protruding. Bone of operculum highly splintered or fimbriated (can be revealed by passing light through the gill cover, this condition is present in some species of several other families). Maximum length about 8 cm.

Rosa (1995) published on the comparative osteology and monophyly of this family.

Eight genera, *Apodocreedia* (1), *Chalixodytes* (2), *Creedia* (4), *Crystallodytes* (2), *Limnichthys* (6), *Myopsaron* (1), *Schizochirus* (1), and *Tewara* (1), with about 18 species (Yoshino et al., 1999; Nelson, 2001; Shibukawa, 2010).

Family PERCOPHIDAE (385)—duckbills. Marine; Atlantic, Indo-West Pacific, and southeast Pacific.

Head depressed; eyes usually large and interorbital space narrow; spinous dorsal, if present, separate from soft dorsal; anal fin with or without a single spine; pelvic fin with one spine and five soft rays, interpelvic space wide.

There is some evidence (reviewed by Imamura and Odani, 2013) that Percophidae are polyphyletic, with Bembropinae belonging in Perciformes near Percidae (e.g., Betancur-R. et al., 2013a) or near Notothenioidei (Smith and Craig, 2007) (and perhaps Percophinae, which was not included in the two molecular studies), whereas Hemerocoetinae belong here in Trachinoidei near Creediidae, Leptoscopidae, and Trichonotidae (Odani and Imamura, 2011).

Three subfamilies, eleven genera and about 50 species.

SUBFAMILY PERCOPHINAE. Tropical western Atlantic. Dorsal fins with eight or nine spines and about 31 soft rays; anal fin with one weak spine and about 38–42 soft rays; lower jaw projecting past upper; caudal fin with 13 branched rays; dorsal iris flap absent; distinct flap above pectoral-fin base; scales above lateral line ctenoid but lateral-line scales not serrated, trilobed, or with keel; minute scales extending along rays of caudal fin.

One species, *Percophis brasiliensis*.

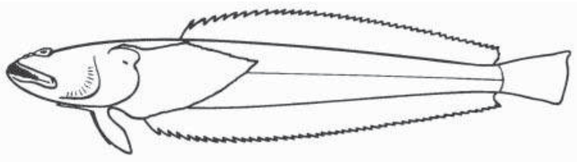
SUBFAMILY BEMBROPINAE. Dorsal fins with six spines (only first two crowded) and 13–18 soft rays; anal fin with 15–20 soft rays; lower jaw projecting past upper; caudal fin with 10 or 11 branched rays; maxillary tentacle present in *Bembrops*; scales ctenoid, with prominent keel on anterior few lateral-line scales.

Two genera, *Bembrops* (17), and *Chrionema* (6), with 23 species (e.g., Nelson, 1994; Das and Nelson, 1996; Thompson and Suttkus, 2002; Thompson, 2003b).

Subfamily Hemerocoetinae. Spines in dorsal fin, if present, 2–6 and usually very crowded at base; jaws about equal or upper jaw slightly longer than lower; caudal fin with seven or eight branched rays; dorsal iris flap present in most species; lateral-line scales trilobed or serrated on posterior margin; medial barbel at tip of snout in males of some species of *Hemerocoetes.*

Eight genera and 26 species *Dactylopsaron* (1), *Enigmapercis* (2), *Matsubaraea* (1), and *Squamicreedia* (1) lack protruding maxillary spines. *Acanthaphritis* (4, synonyms *Branchiopsaron* and *Spinapsaron*), *Hemerocoetes* (5, a New Zealand endemic lacking the spinous dorsal fin), *Osopsaron* (3), and *Pteropsaron* (9), (the latter two may be congeneric) have a spine protruding from the anterior face of the maxilla. (Nelson, 1994; Suzuki and Nakabo, 1996; Allen and Erdmann, 2012; Iwamoto, 2014).

Family LEPTOSCOPIDAE (386)—southern sandfishes. Marine, occasionally in estuaries; Australia and New Zealand.

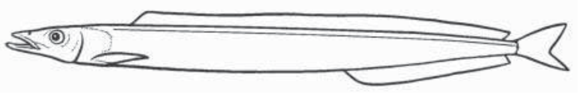


Mouth moderately oblique; lips fringed; eyes dorsal or nearly so; lateral line on middle of side; body with scales; pelvic fins widely separated; dorsal and anal fins long.

In New Zealand, *Leptoscopus macropygus* is known to occur also in the lower reaches of slow rivers (McDowall, 1990).

Three genera, *Crapatulus* (3), *Leptoscopus* (1), and *Lesueurina* (1), with five species (Nelson, 1994; Last et al. in Carpenter and Niem, 2001).

Family AMMODYTIDAE (387)—sand lances. Marine; cold to tropical, Arctic, Atlantic, Indian, and Pacific.

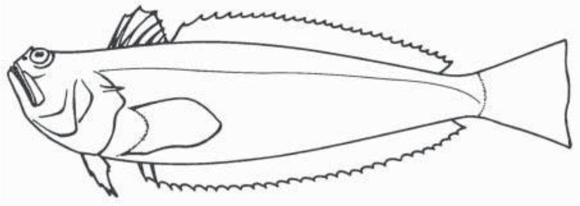


Body elongate; premaxilla protractile (except in *Hyperoplus*); caudal fin forked; dorsal and anal-fin spines absent; lower jaw projecting forward beyond upper jaw with symphysial process; scales cycloid, minute, arranged in oblique rows; pelvic fins usually absent (jugular and with one spine and four or five soft rays in *Embolichthys*); lateral line high, close to dorsal fin; no teeth; single long dorsal fin usually with 40–69 soft rays; anal-fin rays 14–36; seven branchiostegal rays; gill membranes separate; no swimbladder; vertebrae 52–78. Length up to 30 cm.

Pietsch and Zabetian (1990) regarded ammodytids as a possible sister group to Trachinidae plus Uranoscopidae, and gave a summary of meristic characters for many taxa of the suborder.

Seven genera, *Ammodytes* (6), *Ammodytoides* (10), *Bleekeria* (4), *Gymnammodytes* (3), *Hyperoplus* (2), *Lepidammodytes* (1), and *Protammodytes* (2), and 28 species (Collette and Randall, 2000; Ida et al., 1994).

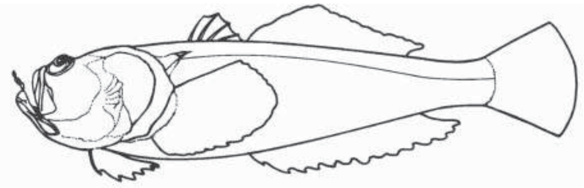
Family TRACHINIDAE (388)—weeverfishes. Marine; eastern Atlantic (most common in Mediterranean) and Black Sea.



Body elongate; dorsal fin with 5–7 spines and 21–32 soft rays; anal fin with two spines and 24–34 soft rays; pectoral fin with 15 rays; pelvic fins in front of pectorals, with 1 spine and 5 soft rays; poisonous glands associated with gill-cover spine and first dorsal spines; six infraorbitals; 34–43 vertebrae. These fish have a habit of burying in sand. They are able to inflict painful stings with their spines.

Two genera (as determined by Bentivegna and Fiorito, 1983), the monotypic *Echiichthys* (1) and *Trachinus* (8), with about nine species.

Family URANOSCOPIDAE (389)—stargazers. Marine, occasionally in estuaries; Atlantic, Indian, and Pacific.



Head large and cuboid; body naked or covered with small smooth scales; mouth extremely oblique; lips fringed; eyes dorsal or nearly so; lateral line on upper part of side; pelvic fins narrowly separated, with 1 spine and 5 soft rays, located under the throat; dorsal and anal fins moderately long, spinous dorsal absent in many; anal fin with 12–18 soft rays; some with a small worm-like filament extending from floor of mouth used to lure prey fish; two large double-grooved poison spines, with a venom gland at each base, just above the pectoral fin and behind the opercle; four infraorbitals; 24–29 vertebrae. Maximum length 70 cm.

One genus, *Astroscopus*, has internal nares used during inspiration and electric organs derived from portions of eye muscle.

Xenocephalus armatus (the Armored Blenny) from New Ireland, for which the family Xenocephalidae was recognized, once thought to be a trachinoid or blennioid and based on the missing holotype, was provisionally placed in the Dactylopteridae in Nelson (1994). Springer and Bauchot (1994) concluded that *Xenocephalus* is a senior synonym of the uranoscopid genus *Gnathagnus* Gill, 1861, the type species of which is *G. elongatus* (Temminck and Schlegel, 1843).

Eight genera, *Astroscopus* (4), *Genyagnus* (1), *Ichthyscopus* (8), *Kathetostoma* (9), *Pleuroscopus* (1), *Selenoscopus* (1), *Uranoscopus* (23), and *Xenocephalus* (6, synonym *Gnathagnus*), and 53 species (e.g., Springer and Bauchot, 1994; Kishimoto in Carpenter and Niem, 2001; Carpenter, 2003; Gomon and Roberts, 2011).

Order LABRIFORMES (77)—wrasses and relatives. The recognition of monophyly for this clade is based on characters in the pharyngeal region, particularly in the pharyngeal jaws, which are specialized for food processing. For example, i) the fifth ceratobranchials are united or fused to form a single lower pharyngeal jaw, suspended in a muscle sling (single or double), and ii) the upper pharyngeal jaw articulates by means of a diarthroses with the basicranium (see Stiassny and Jensen, 1987, for a detailed and critical discussion). However, as noted by Stiassny and Jensen (1987) and Johnson (1993), there is a high degree of homoplasy involved, and corroborative evidence from characters independent of the pharyngeal area is wanting.

Contrary to Nelson (2006) and Wiley and Johnson (2010), who recognized a Labriformes consisting of the six families Labridae, Scaridae, Odacidae, Embiotocidae, Cichlidae, and Pomacentridae, we recognize here a more restricted assemblage of the following three families: Labridae, Scaridae, and Odacidae. The Embiotocidae, Cichlidae, and Pomacentridae, considered by Wiley and Johnson (2010) to be part of Labriformes, have been moved to the Ovalentaria (Wainwright et al. 2012). Two other families, Gerreidae and Centrogenyidae, were tentatively grouped with or near the Labriformes by Betancur-R. et al. (2013a); the evidence for moving these is weak, and they remain in the Perciformes herein, although with their listings annotated to indicate their possible revised position.

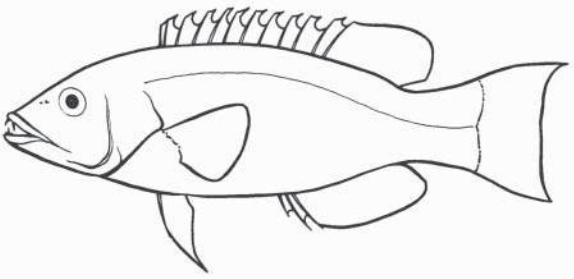
Most species of labrids and scarids are protogynous, that is, they can change their sex from female to male; there is a wide diversity of color patterns associated with sex and size. Males may be primary (not capable of sex change) or secondary (resulting from a sex change of a female). Various populations may consist of only secondary males (monandry) or primary and secondary males (diandry). In coloration, individuals with a color pattern characteristic of small adults are said to be in the initial phase, while those having a color pattern characteristic of the largest males are in the terminal phase. Sexual dichromatism is common and refers to the situation where terminal-phase males have a different color pattern from females.

Three families with about 87 genera and roughly 630 species.

Eocene fossil labriforms that can be assigned to the family Labridae include †*Bellwoodilabrus*, †*Eocoris*, and †*Phyllopharyngodon*, all known from Monte Bolca, Italy (Bannikov and Sorbini, 1990; Bellwood, 1991; Bannikov and Bellwood, 2014). Miocene fossils (Carnevale, 2014) include †*Symphodus westneati* and the extinct genus †*Wainwrightilabrus*.

Two Eocene labriforms of uncertain family position according to Bannikov and Bellwood (2014), also from Monte Bolca, are †*Tortonesia* (Tortonesidae), with 25 or 26 vertebrae and the uppermost branched principal ray of the caudal fin greatly elongated, and †*Sorbinia*, named by Bellwood (1995).

Family LABRIDAE (390)—wrasses. Marine; Atlantic, Indian, and Pacific.



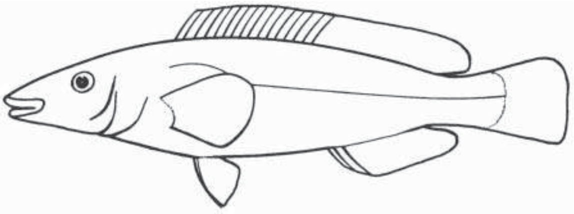
Mouth protractile; jaw teeth mostly separate, usually projecting outward; dorsal fin with 8–21 spines (usually fewer than 15) and 6–21 soft rays; anal fin with 2–6 spines (usually three) and 7–18 soft rays; scales cycloid, generally large to moderate with 25–80 along side (but may be small and exceed 100); lateral line continuous or interrupted; vertebrae usually 23–42. *Gomphosus* has an elongate snout.

This family is one of the most diversified of all fish families in shape, color, and size. Many species are highly colorful, and several color patterns may exist within a species. Most species bury themselves in sand at night. Some small species clean larger fishes of their ectoparasites. Wrasses are popular aquarium fishes, particularly species of the genus *Coris*. Maximum length about 2.3 m (e.g., *Cheilinus undulatus*), although many species are under 15 cm, and the shortest may be the 4.5 cm (*Minilabrus striatus* of the Red Sea). One labrid, *Conniella apterygia*, lacks the pelvic fins and supporting skeleton; it is part of the *Cirrhilabrus* group. Randall and Kuiter (1989) noted examples of partially piscivorous wrasses mimicking harmless fishes and in turn a harmless wrasse being mimicked by a piscivorous grouper. Many systematic works have been done recently (e.g., Gomon, 1997; Randall, 1999a,b, 2000; Rocha, 2004; Barber and Bellwood, 2005; Westneat and Alfaro, 2005; Read et al., 2006; Robertson et al., 2006; Yaakub et al., 2006; Randall, 2007; Weaver and Rocha, 2007; Carlson et al., 2008; Cowman et al., 2009; Luiz et al., 2009; Haney et al., 2010; Pinheiro et al., 2010; Rocha et al., 2010, 2012; Parenti and Randall, 2011; Russell, 2011; Hodge et al., 2012; Russell and Caig, 2013; Russell and Westneat, 2013; Victor et al., 2013; Westneat personal communication, 2015).

Some 71 genera: *Acantholabrus* (1), *Achoerodus* (2), *Ammolabrus* (1), *Anampses* (12), *Anchichoerops* (1), *Austrolabrus* (1), *Bodianus* (43) (one of the genera of hogfishes), *Centrolabrus* (3), *Cheilinus* (7), *Cheilio* (1), *Choerodon* (24) (synonym *Hypsigenys*), *Cirrhilabrus* (48), *Clepticus* (3), *Conniella* (1), *Coris* (27), *Ctenolabrus* (1), *Cymolutes* (3), *Decodon* (4), *Diproctacanthus* (1), *Doratonotus* (1), *Dotalabrus* (2), *Epibulus* (2), *Eupetrichthys* (1), *Frontilabrus* (1), *Gomphosus* (2), *Halichoeres* (79) (the most species-rich genus), *Hemigymnus* (3), *Hologymnosus* (4), *Iniistius*

(21), *Labrichthys* (1), *Labroides* (5), *Labropsis* (6), *Labrus* (4), *Lachnolaimus* (1), *Lappanella* (2), *Larabicus* (1), *Leptojulis* (5), *Macropharyngodon* (12), *Malapterus* (1), *Minilabrus* (1), *Notolabrus* (7), *Novaculichthys* (1), *Novaculoides* (1), *Novaculops* (6), *Ophthalmolepis* (1), *Oxycheilinus* (9), *Oxyjulis* (1), *Paracheilinus* (17), *Parajulis* (1), *Pictilabrus* (3), *Polylepion* (2), *Pseudocheilinops* (1), *Pseudocheilinus* (7), *Pseudocoris* (7), *Pseudodax* (1), *Pseudojuloides* (10), *Pseudolabrus* (12), *Pteragogus* (10), *Sagittalarva* (1), *Semicossyphus* (3), *Stethojulis* (10), *Suezichthys* (12), *Symphodus* (10), *Tautoga* (1), *Tautogolabrus* (1), *Terelabrus* (1), *Thalassoma* (28), *Wetmorella* (3), *Xenojulis* (1), *Xiphocheilus* (1), and *Xyrichtys* (11) (one of the genera of razorfishes), with about 519 species (Parenti and Randall, 2000; Westneat, 2003; Westneat and Alfaro, 2005). Fossil labrids are discussed above under Labriformes.

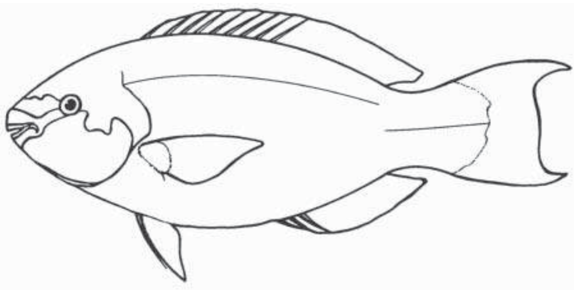
Family ODACIDAE (391)—cales. Coastal temperate marine; Australia and New Zealand.



Mouth nonprotractile; jaw teeth coalesced (parrot-like teeth); dorsal fin with 14–27 spines and 9–22 soft rays; pelvic fins each with one spine and four soft rays (pelvic fins absent in *Siphonognathus argyrophanes*, an extremely elongate odacid that is unique in several other features such as not exhibiting sexual dichromatism and having high meristic values); scales cycloid, usually small to moderate in size (about 30–108 in lateral line); vertebrae 31–54. Maximum length about 40 cm. The body shape is variable, some species are similar to scarids, and others are elongate with an elongated snout. Also known as weed-whitings.

Six genera, *Haletta* (1), *Heteroscarus* (1), *Neoodax* (1), *Odax* (2), *Olisthops* (1), and *Siphonognathus* (6), with a total of 12 species (Gomon and Paxton, 1985). Two of the four species of *Odax* are endemic to New Zealand, while the other odacids are confined to southern Australia.

Family SCARIDAE (Callyodontidae) (392)—parrotfishes. Marine (mainly tropical); Atlantic, Indian, and Pacific.



Mouth nonprotractile; jaw teeth usually coalesced (parrot-like teeth); dorsal fin with 9 spines and 10 soft rays; anal fin with 3 spines and 9 soft rays; pelvics each with 1 spine and 5 soft rays; branched caudal rays 11; scales large and cycloid, usually 22–24 in lateral line; 24–26 vertebrae.

Parrotfishes are herbivorous, usually grazing on dead coral substrates; they rarely feed on live coral (and rarely on seagrasses). Individuals of some species are known to secrete an envelope of mucus at night in which they rest. As with wrasses, sex change appears to be common in species of this family, and males in most species that have been studied may be either primary or secondary. Unlike the wrasses, parrotfishes are remarkably uniform in most meristic characters. The living color pattern, of which there is a wide diversity, is important in identifying many species; however, in addition to fading quickly in preservation, the color pattern can vary greatly with growth and sex change.

Previously the subfamilies Scarinae and Sparisomatinae were recognized, but Bellwood (1994) showed in a cladistic analysis that they were not justified.

Ten genera, *Bolbometopon* (1), *Calotomus* (5), *Cetoscarus* (2), *Chlorurus* (18), *Cryptotomus* (1), *Hipposcarus* (2), *Leptoscarus* (1), *Nicholsina* (2), *Scarus* (synonym *Callyodon*) (52), and *Sparisoma* (15), with 99 species (Westneat, 2003; Bellwood, 2004; Parenti and Randall, 2000, 2011; Robertson et al., 2006; Westneat et al., 2007; Smith et al., 2008; Bariche and Bernardi, 2009).

THE PERCIFORMES, including percids, centrarchids, percichthyids, serranids, and notothenioids, are likely still paraphyletic (e.g., with respect to the Scorpaeniformes); both are tentatively placed by some broad-scale molecular studies (e.g., Betancur-R. et al., 2013a) as the sister group to the last remaining major clade of Teleostei (see below), which putatively includes such groups as Moroniformes, Acanthuriformes, Spariformes, Caproiformes, Lophiiformes, and Tetraodontiformes. These studies are considered important, but still preliminary, because of issues such as incomplete taxon sampling and weak nodal support for many clades. Formal taxonomic groupings are not recognized here pending corroborating studies.

Order PERCIFORMES (78)—perches. The order Perciformes is the most diversified of all fish orders. Indeed, it is the largest order of vertebrates. Perciforms dominate in vertebrate ocean life and are the dominant fish group in many tropical and subtropical fresh waters.

In recent years, some families of perciforms have been removed and placed elsewhere in the Percomorpha. Nevertheless, Perciformes are still among the most diverse orders of fishes, and are the largest order of Percomorpha in numbers of families, genera, and species. Families that have tentatively been placed elsewhere by recent preliminary studies are retained here, but we note their proposed new positions.

Perciformes as restricted here contain 2 suborders, 62 families, about 365 genera, and about 2,248 species.

Suborder Percoidei. This suborder is the larger of the two in Perciformes, containing 46 families, 319 genera, and about 2,095 species. Many of the species normally occur only in fresh water (e.g., the percids). This suborder contains many highly colorful fishes.

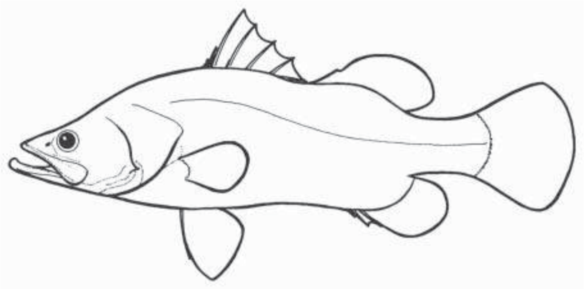
Even after removal of some of the families to other groups of percomorphs, other percoid families may follow. In the family treatments below, we indicate many of the proposed reassignments of percoid families, but we have not reclassified them because of the preliminary nature of the evidence.

	Lower teleosts	Percoidei
Spines in fins	Absent	Present in dorsal, anal, and pelvic fins
Dorsal fin number	One, adipose fin may also be present	Two, never an adipose fin
Scales	Cycloid	Ctenoid
Pelvic fin position	Abdominal	Thoracic
Pelvic-fin rays	Six or more soft rays	One spine and five soft rays
Pectoral-fin base	Ventral and horizontal	Lateral and vertical
Upper jaw bordered by	Short premaxilla and long maxilla	Premaxilla
Swimbladder	Duct present (physostomes)	Duct absent (physoclists)
Orbitosphenoid	Present	Absent
Mesocoracoid	Present	Absent
Epipleural and epicentral bones	Present	Absent
Bone cells in bone of adult	Present	Not apparent
Principal caudal fin ray number	Often 18 or 19	Never more than 17, often fewer

Although the Percoidei are a morphologically and ecologically diverse group, some comparisons to "typical" lower teleosts (e.g., Protacanthopterygii and Ostariophysi) can be informative. Many exceptions to these generalizations exist; for example, the bodies of many percoids are covered mainly by cycloid rather than the usual ctenoid scales. Many of the features of the Percoidei are also present in some other acanthomorphs; the table is not intended to show features originating in or restricted to the Percoidei, but merely serves to contrast percoids with lower teleosts.

Superfamily Percoidea. Some 46 families, 290 genera, and 1,964 species. Many of the families are very similar and poorly separated from one another; others are very distinctive and have been allied with other orders or placed in their own order.

Family CENTROPOMIDAE (393)—snooks. Marine (often brackish) and freshwater; tropical and subtropical waters North and Central America.



Lower jaw extending forward beyond upper jaw; lateral line extending onto tail, reaching posterior margin of fin; scaly process usually in pelvic axis; caudal fin deeply forked; dorsal fin in two portions (separated by a small gap), the first with eight spines and the second with 1 spine and 8–11 soft rays; anal fin with three spines and 5–8 soft rays; pelvic fin with 1 spine and 5 soft rays; seven branchiostegal rays; 24 vertebrae. Maximum length about 2.0 m.

In a cladistic analysis using 29 characters Otero (2004) demonstrated that the family Centropomidae, as previously defined, was paraphyletic, and the previously recognized subfamily Latinae is now recognized as a separate family (family Latidae, below).

This family is among those postulated to be part of the sister clade to the Ovalentaria, close to Pleuronectiformes, by Betancur-R. et al. (2013a).

One genus, *Centropomus*, with 12 species (e.g., Nelson et al., 2004).

Family LATIDAE (394)—lates perches. Marine, brackish, and freshwater; Indo-West Pacific and Africa.

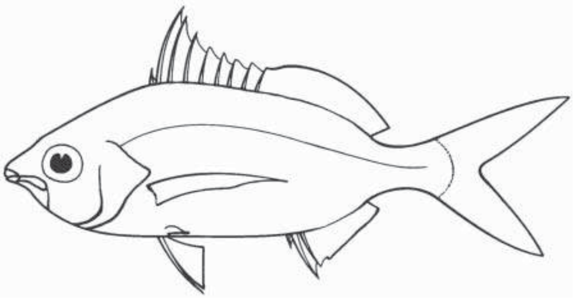
Dorsal fins not completely separated or, if separated, with one or two isolated spines between them; caudal fin usually rounded; 25 vertebrae. This family includes the large Nile Perch, *Lates niloticus.* The marginally catadromous Indo-West Pacific *Lates calcarifer* in Australia is known as the Barramundi, a term rarely also used for species of *Scleropages.*

Mooi and Gill (1995) gave family status to the former Latinae, previously a subfamily of Centropomidae. The new family Latidae is monophyletic and includes *Lates, Hypopterus, Psammoperca* and the fossil †*Eolates* (Eocene and Oligocene). Otero (2004) defined the family (then a subfamily) on the basis of six apomorphies.

This family is also among those postulated to be part of the sister clade to the Ovalentaria, with Centropomidae, close to Pleuronectiformes, by Betancur-R. et al. (2013a).

Three genera, *Hypopterus* (1) Eastern Indian Ocean, Western Australia, *Lates* (11, seven live in fresh water, four are endemic to Lake Tanganyika, others to brackish habitat of tropical Africa, and one is in the coastal marine and estuarine waters of the Indo-Pacific; fossils of *Lates* are well known in Africa and Europe) and *Psammoperca* (1, coastal Indo-Pacific waters), with 13 species (Otero, 2004; Li et al., 2011; Pethiyagoda and Gill, 2012).

Family GERREIDAE (395)—mojarras. Marine (occasionally brackish and rarely in fresh water); most warm seas.



Mouth highly protrusible; head scaly, upper surface smooth; scaly sheath along bases of dorsal and anal fins; dorsal fin with 9 or 10 spines and 9–17 soft rays; scales usually cycloid and often partially deciduous; gill membranes free from isthmus; tail deeply forked; 24 vertebrae. Maximum length 41 cm SL.

The Gerreidae are hypothesized to be the sister group of all higher Percomorpha including Labriformes and Perciformes by at least some molecular work (e.g., Betancur-R. et al., 2013a).

Eugerres mexicanus, of southern Mexico and northern Guatemala, is confined to fresh water. In addition, several species that are otherwise marine enter rivers (for example, *Eucinostomus melanopterus* and five species of *Gerres* in Africa, with *G. filamentosus* also in the Australian region, and species of *Diapterus*, *Eugerres*, and *Eucinostomus* in the New World).

Eight genera, *Deckertichthys* (1), *Diapterus* (4), *Eucinostomus* (10), *Eugerres* (7), *Gerres* (28), *Parequula* (2), *Pentaprion* (1), (with five or six spines in anal fin), and *Ulaema* (1), with 54 species (González-Acosta et al., 2007; Iwatsuki and Heemstra, 2007; Iwatsuki et al., 2007; Iwatsuki et al., 2012).

Family CENTROGENYIDAE (396)—false scorpionfishes. Marine (rarely brackish); east Indian and western Pacific.

Posterior rim of anterior nostril with large fringed flap; ventral margin of preopercle with three or four large forward pointing spines; dorsal fin with 13 or 14 spines and 9–11 branched soft rays, origin of fin over posterior margin of preopercle. Maximum length about 25 cm TL. This family was not classified in Nelson (1994), but mentioned under Percoidea.

This family was recovered, but with weak nodal support, as a basal member of the Labriformes clade (see above) by Betancur-R. et al. (2013a).

One species, *Centrogenys vaigiensis* (e.g., Gill, 1999; Leis and Trnski, 1999).

Family PERCILIIDAE (397)—southern basses. Freshwater; Chile.

Maximum total length 9.6 cm. This genus has been placed in the Percichthyidae. Arratia (2003) suggested that *Percilia* forms a clade with the Australian *Bostockia*, *Edelia*, and *Nannoperca*.

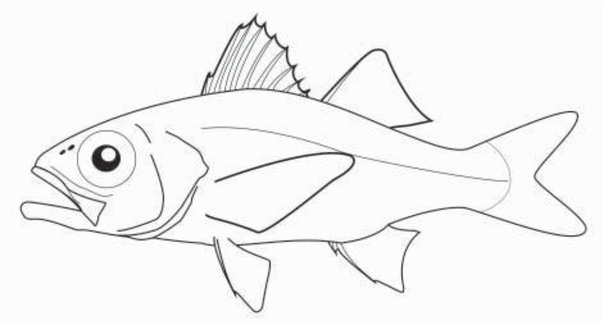
Two species, *Percilia gillissi* (Girard, 1855) and *P. irwini* (Eigenmann, 1928).

Family HOWELLIDAE (398)—oceanic basslets. Marine; Atlantic, Indian, and Pacific.

Eyes large; six infraorbital bones with smooth edges; lachrymal large, almost triangular, with strong dorsal process protruding outwards as spine in front of eye; infraorbital 2 small, rod-shaped; sensory canals of head open; hyomandibular process of metapterygoid absent; anterior plate of hyomandibular absent; contact pterygiophores of 1st and 2nd dorsal fins absent; free pterygiophore without distal element anterior to 2nd dorsal fin; 16 caudal vertebrae (Prokofiev, 2007). Maximum total length 10.9 cm reported for *Howella atlantica.*

Three genera: *Howella* (6), *Bathysphyraenops* (2), and *Pseudohowella* (1), with 9 species.

Family ACROPOMATIDAE (399)—lanternbellies. Marine; Atlantic, Indian, and Pacific.

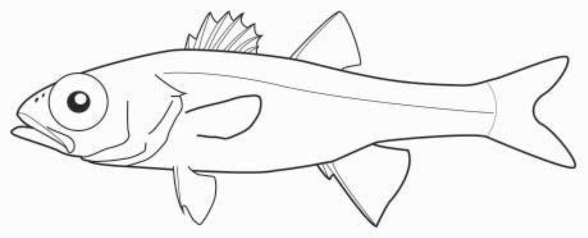


Two dorsal fins, the first with 7–10 spines and the second with or without a spine and 8–10 soft rays; anal fin with 2 or 3 spines and 7–9 soft rays; 7 branchiostegal rays; 25 vertebrae. The three species of *Acropoma* have light organs and the anus near the pelvic fin base—the only other perciforms with such an anterior anus is the serranid *Bullisichthys caribbaeus* and the apogonid *Apogon gularis.*

The family common name used in Nelson (1994) was "temperate ocean-basses."

Seven genera: *Acropoma* (6), *Apogonops* (1), *Doederleinia* (1), *Malakichthys* (7), *Neoscombrops* (3), *Synagrops* (12), and *Verilus* (1), with 31 species (e.g., Okamoto and Ida, 2002; Yamanoue and Matsuura, 2002, 2007; Heemstra, 2003a; Yamanoue et al. 2009). Several genera provisionally placed here in Nelson (1994) are now recognized in other families (Apogonidae, Howellidae, Polyprionidae, Symphysanodontidae). See Perciformes for possible fossils.

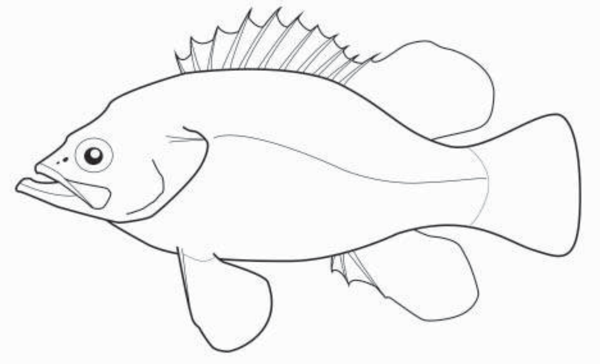
Family EPIGONIDAE (400)—deepwater cardinalfishes. Marine; Atlantic, Indian, and Pacific.



Differing from apogonids in having vertebrae usually 25; infraorbitals more than six; ascending processes of premaxillaries reduced or absent; rostral cartilage greatly enlarged; soft dorsal and anal fins covered with scales. *Sphyraenops* has three opercular spines as do serranids. Maximum length about 58 cm.

Seven genera: *Brepostoma* (1), *Brinkmannella* (1), *Epigonus* (36), *Florenciella* (1), *Microichthys* (2), *Rosenblattia* (1), and *Sphyraenops* (1), with 43 species (e.g., McCosker and Long, 1997; Gon, 2003; Ida et al., 2007; Okamoto, 2011, 2012; Okamoto and Motomura, 2011, 2012, 2013).

Family POLYPRIONIDAE (401)—wreckfishes. Marine; Atlantic, Indian, and Pacific.



Opercle with a horizontal ridge on dorsal aspect ending in a short spine; dorsal fin with 11 or 12 strong spines and 11 or 12 soft rays.

Two genera, *Polyprion* (2) and *Stereolepis* (2), with four species (e.g., Sedberry, 2003).

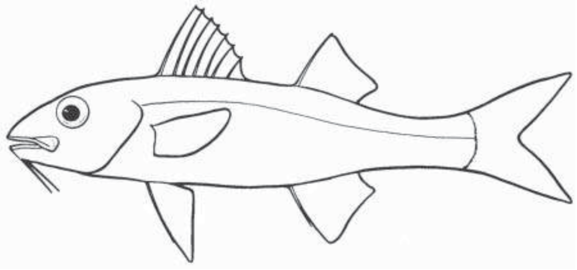
Family LATEOLABRACIDAE (402)—Asian seaperches. Western Pacific, inshore waters.

Dorsal spines 12–15; dorsal soft rays 12–16; anal spines 3; anal soft rays 7–9; protandrous, sex changing after maturation at age 2.

The sole genus was placed in its own family, Lateolabracidae, by Eschmeyer (1998) and Springer and Johnson (2004). Preliminary molecular studies suggest that *Lateolabrax* may be nested in Polyprionidae. The two species are commercially important.

One genus, *Lateolabrax*, with two species.

Family MULLIDAE (403)—goatfishes. Marine (rarely brackish water); Atlantic, Indian, and Pacific.



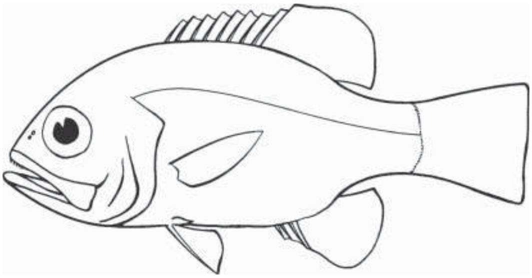
Two long independently movable hyoid barbels (used in detecting food); body elongate; two widely separated dorsal fins, the first with 6–8 spines and second with 1 spine and 8 or 9 soft rays; soft dorsal fin shorter than anal fin; anal fin with 1 or 2 small spines and 5–8 soft rays; caudal fin forked; 24 vertebrae.

Goatfishes are important as a food fish. Many are brightly colored. Maximum length up to 60 cm.

This family is among those postulated to be part of a basal percomorph syngnathiform/scombriform clade by Betancur-R. et al. (2013a) and others.

Six genera, *Mulloidichthys* (7), *Mullus* (5), *Parupeneus* (32), *Pseudupeneus* (3), *Upeneichthys* (3), and *Upeneus* (35), with 85 species (Golani, 2001; Kim and Nakaya, 2002; Randall and Myers, 2002; Randall, 2003; Uiblein, 2011; Uiblein and Causse, 2013; Uiblein and Lisher, 2013; Uiblein and McGrouther, 2012; Yamashita et al., 2011).

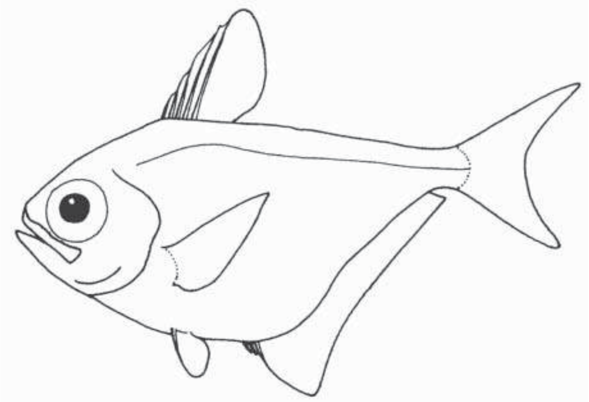
Family GLAUCOSOMATIDAE (404)—pearl perches. Marine; eastern Indian and western Pacific (Japan to Australia).



Dorsal fin with 8 graduated spines and 11–14 soft rays; anal fin with 3 spines and 12 soft rays; maxillae scaled; lateral line nearly straight and extending to tail; caudal fin lunate or truncate; vertebrae 25. Maximum length about 1.2 m. This taxon, which shares similarities in the complex swimbladder/vertebral association and dorsal gill-arch elements with *Pempheris*, is thought to be closely related to the pempherids.

One genus, *Glaucosoma*, with four species (McKay, 1997).

Family PEMPHERIDAE (405)—sweepers. Marine and brackish water; western Atlantic, Indian, and Pacific.



Body compressed and deep; maxillae not reaching beyond center of eye; preorbital smooth; eye large, without adipose lid; one short dorsal fin, originating before middle of body, with 4–7 graduated spines and 7–12 soft rays; anal fin with two (very rarely) or three spines and 17–45 soft rays; lateral-line scales usually 40–82; lateral line extending onto caudal fin; tubes of lateral line usually short and wide; gill rakers long and usually 25–31; luminescent organs in a few species; pyloric caeca 9 or 10; swimbladder absent in one species (*Pempheris poeyi*); 25 vertebrae (10 + 15). Maximum length about 30 cm.

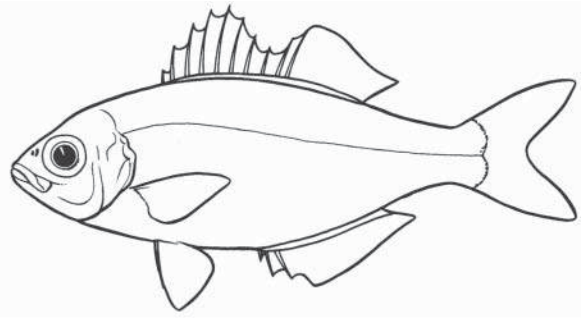
Two genera, *Parapriacanthus* (4), and *Pempheris* (28), with 32 species (e.g., Mooi, 1998). Osteology in the family was studied by Tominaga (1968).

Family OPLEGNATHIDAE (406)—knifejaws. Marine; Indo-Pacific (South Africa, Japan, southern half of Australia including Tasmania, Hawaiian archipelago, Galapagos, and Peru).

Teeth in adult united to form a parrot-like beak (as in Scaridae, but with usual percoid type of pharyngeal dentition, capable of crushing barnacle shells and sea urchins); spinous dorsal fin low in adults, basically as high as soft dorsal and continuous with it in juveniles; dorsal fin with 11 or 12 spines and 11–22 soft rays; anal fin with 3 spines and 11–16 soft rays; scales very small (unlike in scarids where they are large). Maximum length about 0.9 m.

One genus, *Oplegnathus*, with seven species.

Family KUHLIIDAE (407)—flagtails. Marine, brackish, and freshwater; Indo-Pacific.



Dorsal and anal fins each with a well-developed scaly sheath; dorsal fin deeply notched, with 10 spines and 9–13 soft rays; anal fin with three spines and 9–13 soft rays; no scaly pelvic axillary process; opercle with two spines; 25 vertebrae. Color generally silvery, often with dark markings on the caudal fin. Maximum length up to 45 cm TL for *Kuhlia rupestris*. The three nannopercine genera formerly placed in this family are now placed in the Percichthyidae. The most wide-ranging species and the only one to occur in the Americas is the coastal *Kuhlia mugil* (synonym *taeniura*), which extends from Africa to the tropical eastern Pacific, sometimes occurring in fresh water. The common name for the family in Hawaii, aholeholes, is also used elsewhere.

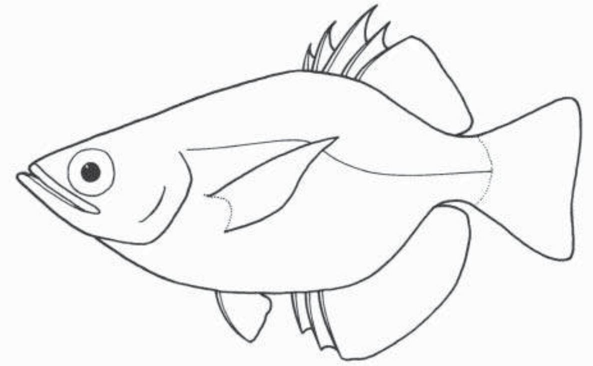
One genus, *Kuhlia*, with about 13 species; most of the species are marine and brackish but one, *K. rupestris*, occurs primarily in fresh water, and several others extend up rivers in continental areas and on oceanic islands (e.g., Tahiti) (e.g., Randall and Randall, 2001; Sato et al., 2004).

Family BATHYCLUPEIDAE (408)—bathyclupeids. Marine oceanic; Indian, western Pacific, and Gulf of Mexico.

One dorsal fin in posterior half of body, without spines; anal fin long, with one spine; dorsal and anal fins covered with scales; premaxillae and maxillae bordering mouth; usually 31 vertebrae (10 + 21).

One genus, *Bathyclupea*, with seven species.

Family TOXOTIDAE (409)—archerfishes. Marine coastal, brackish, and freshwater; from India to Philippines and Australia and Polynesia.



Body deep and compressed, greatest body depth 1.8–2.5 times in standard length; eye large; dorsal fin with 4–6 strong spines and 11–14 soft rays; anal fin with three spines and 15–18 soft rays; length of soft dorsal much shorter than soft portion of anal; mouth large, terminal (lower jaw protruding), and highly protractile; lateral-line scales about 25–47; seven branchiostegal rays; 24 vertebrae (10+14).

Archerfishes are capable of forcefully ejecting squirts of water from their mouths to down and eat insects. The widespread *Toxotes jaculator*, extending from India to New Hebrides, is normally found in brackish water near mangroves, while the others frequently occur in fresh water (often well inland). Maximum length 40 cm, attained in *T. chatereus*; usually under 16 cm.

This family is among those postulated to be part of the sister clade to the Ovalentaria near Istiophoriformes by Betancur-R. et al. (2013a).

One genus, *Toxotes*, with seven species (Allen, 1978; Allen, 2004).

Family ARRIPIDAE (410)—Australasian salmon (kahawai). Marine; South Pacific (southern Australia to New Zealand region).

Dorsal fin with 9 spines and 13–19 soft rays; anal fin with three spines and 9 or 10 soft rays; gill membranes free from isthmus; anal fin much shorter than the soft dorsal; caudal fin forked; 25 vertebrae. Maximum length about 90 cm.

One genus, *Arripis*, with four species (Paulin, 1993).

Family DICHISTIIDAE (Coracinidae) (411)—galjoen fishes. Marine coastal and brackish water; South Africa and Madagascar.

Body relatively deep; mouth small; dorsal fin with 10 spines and usually 18–23 soft rays; anal fin with three spines and usually 13 or 14 soft rays; gill membranes fused with isthmus; some teeth incisiform.

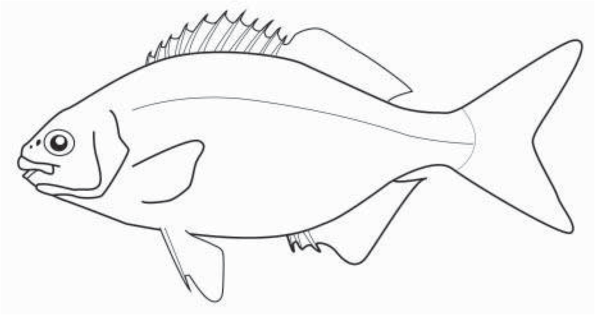
This inshore fish is a highly sought after sports fish in South Africa (Smith and Heemstra, 1986).

This family was recognized under the name Coracinidae in Nelson (1994), with the generic name *Coracinus*; Eschmeyer (1998) noted that *Coracinus* was published in a rejected work and is not available (the family name is formed from the next available synonym).

Although monophyly of this family could not be confirmed, Leis and van der Lingen (1997) found larval evidence to support the historical linking of species of Microcanthinae, Scorpidinae, Girellinae, and Kyphosinae (recognized by them at the family level; a grouping in the earlier study of Johnson, 1984) with possibly some affinity to the Arripidae (but not to the Ephippidae or Drepaneidae).

One genus, *Dichistius*, with two species (e.g., Leis and van der Lingen, 1997).

Family KYPHOSIDAE (412)—sea chubs. Marine; Atlantic, Indian, and Pacific.



Three spines and 10–28 soft rays; dorsal fin with 9–16 spines and 11–28 soft rays; 24–28 vertebrae (34 in *Graus*). Members of the first two subfamilies, except for *Graus*, are herbivorous, primarily consuming algae, while the others are primarily carnivorous. All are usually found near shore.

The following subfamilies, or combinations thereof, are often recognized as separate families. Johnson and Fritzsche (1989) provided evidence for the monophyly of a taxon including the first three subfamilies (which they rank as families, as did Johnson (1984). Yagishita et al. (2002) suggested that *Scorpis, Labracoglossa* (these two being sister taxa), *Girella, Microcanthus,* and *Kyphosus* are part of a monophyletic group but one shared with *Kuhlia* and *Oplegnathus.*

Fourteen genera with 53 species (e.g., Sakai and Nakabo, 2004, 2008; Knudsen and Clements, 2013a,b).

SUBFAMILY GIRELLINAE (NIBBLERS). Some incisiform teeth present; maxilla concealed beneath suborbital bone. Pacific (primarily Philippines to Australia but extending to California where the Opaleye, *Girella nigricans*, is a common inshore species) with *G. zonata* in the Atlantic. *Graus* occurs off Chile.

Two genera, *Girella* (18), and *Graus* (1), with about 19 species (e.g., Yagishita and Nakabo 2000).

SUBFAMILY KYPHOSINAE (RUDDERFISHES). Some incisiform teeth; maxilla exposed. Atlantic, Indian, and Pacific.

Three genera, *Hermosilla* (1), *Kyphosus* (15), and *Sectator* (1) (e.g., Sakai and Nakabo, 2004) with 17 species.

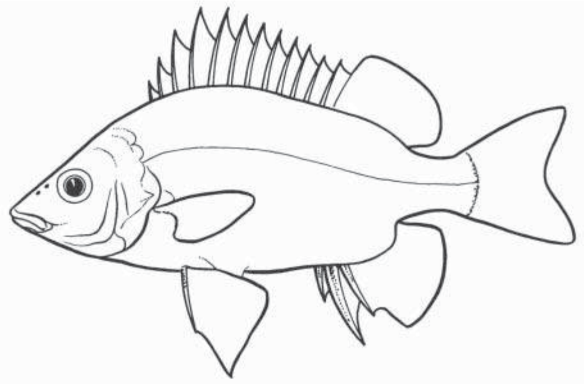
SUBFAMILY SCORPIDINAE (HALFMOONS). No incisiform teeth; pelvics well behind pectorals. Indo-Pacific (to California).

Five genera *Bathystethus* (2), *Labracoglossa* (2), *Medialuna* (2), *Neoscorpis* (1), and *Scorpis* (5), with 12 species.

SUBFAMILY MICROCANTHINAE (MICROCANTHINES). Recognized as a family by Johnson (1984).

Four genera, *Atypichthys* (2), *Microcanthus* (1), *Neatypus* (1), and *Tilodon* (1), with five species.

Family TERAPONTIDAE (Teraponidae, Theraponidae) (413)—grunters or tigerperches. Marine coastal, brackish, and freshwater, Indo-West Pacific (Africa to Japan, Fiji, and Samoa).



Body oblong to oblong-ovate, somewhat compressed; opercle with 2 spines, lower spine longer; dorsal fin with notch, 11–14 spines and 8–14 soft rays, spinous portion depressible into a groove formed by a sheath of scales; anal fin with three spines and 7–12 soft rays; pelvic fins inserted distinctly behind base of pectoral fins, with one spine and five soft rays; caudal fin rounded, truncate, or emarginate; lateral line continuous and extending onto caudal fin; vomer and palatines of most species lacking teeth; six branchiostegal rays; paired extrinsic swimbladder muscles arising from rear of skull or posttemporal and inserting on anterodorsal surface of the anterior chamber of the swimbladder (employed for sound production—a few other perciforms have sonic muscles, but they differ in position); swimbladder transversely divided (Vari, 1978, gives details on these features of the swimbladder which are unique within the perciforms); 25–27 vertebrae. Maximum length about 80 cm.

Most of the freshwater species occur in Australia and in New Guinea.

Sixteen genera (e.g., *Amniataba* (3), *Bidyanus* (2), *Hannia* (1), *Helotes* (1), *Hephaestus* (14), *Lagusia* (1), *Leiopotherapon* (4), *Mesopristes* (5), *Pelates* (3), *Pelsartia* (1), *Pingalla* (3), *Rhynchopelates* (1), *Scortum* (4), *Syncomistes* (4), *Terapon* (3), and *Variichthys* (2), with 52 species (e.g., Yoshino et al., 2002; Davis et al., 2013).

Family PERCICHTHYIDAE (433)—temperate perches. Freshwater (rarely brackish); Australia and South America (primarily Argentina and Chile).

Dorsal fins continuous, with or without a notch (may be deep); 7–12 spines (except 1–3 in *Gadopsis bispinosus*) and 8–38 soft rays; anal fin with three spines and 7–13 soft rays (16–20 in *Gadopsis*); scales ctenoid (with simple needle-like ctenii on posterior field) or secondarily cycloid, vertebrae 25–36 (40–50 in *Gadopsis*).

Nine genera with 24 species: in South America—*Percichthys* (5); in Australia—*Gadopsis* (2), *Guyu* (1), *Maccullochella* (4), *Macquaria* (2), *Percalates* (2), and the relatively derived *Bostockia* (1), *Nannatherina* (1), and *Nannoperca* (6) (Unmack et al., 2011; Morgan et al., 2013). *Percalates* was recently resurrected as distinct from *Macquaria* by Lavoué et al. (2014) based on mitogenomic evidence and may not belong in Percichthyidae but perhaps Cheilodactylidae.

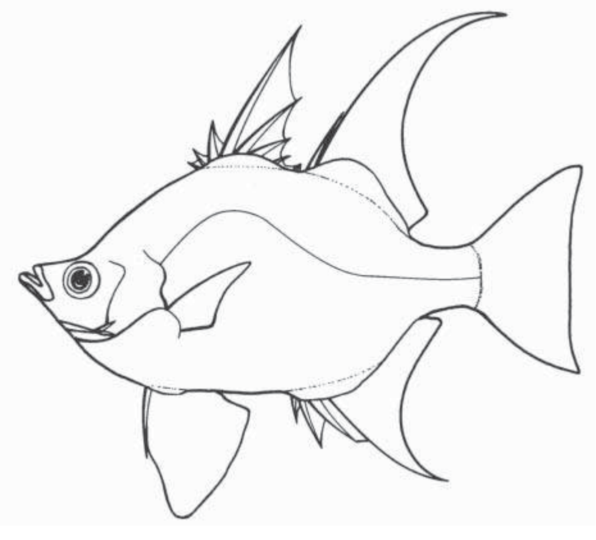
Family SINIPERCIDAE (415)—Chinese perches. Freshwater; eastern Asia.

Scales cycloid; star-shaped transverse section of first anal pterygiophore; roof of head naked; caudal fin rounded.

Siniperca is closely related to Centrarchidae according to Betancur-R. et al. (2013a) and Lavoué et al. (2014), though Chen et al. (2007) suggested that inclusion of *Coreoperca* could make the family as a whole paraphyletic or polyphyletic.

Two genera: *Siniperca* (9), *Coreoperca* (3), with 12 species (e.g. Zhao et al., 2008; Li et al., 2010; Lavoué et al., 2014). Fossils of both *Siniperca* and *Coreoperca* are known. One extinct genus, †*Inabaperca*, is based on fossils from shallow marine sediments in Japan (Yabumoto and Uyeno, 2000).

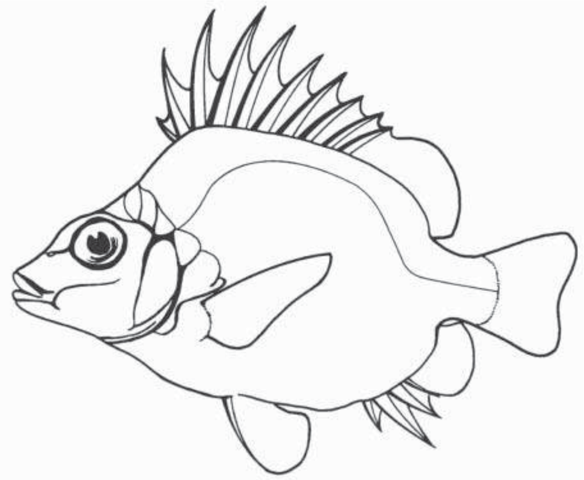
Family ENOPLOSIDAE (416)—oldwives. Marine; southern half of Australia.



Pelvic fins unusually large, each with a strong spine; external bones of head not rough; supramaxilla present; two sharp spines on lower angle of preoperculum. The fish has black vertical bands on a silvery body.

One species, *Enoplosus armatus* (Oldwife).

Family PENTACEROTIDAE (417)—armorheads. Marine; Indo-Pacific and southwestern Atlantic.



Body strongly compressed, ranging from very deep in *Pentaceros* (shown in figure) to only moderately deep in adult *Pentaceropsis*; head encased in exposed, rough, striated bone; no supramaxilla; single dorsal fin with 4–15 strong spines and 8–29 soft rays; anal fin with 2–5 strong spines and 6–17 soft rays; pelvic fins large, with one long, strong spine and five soft rays; scales small; 24–27 vertebrae. These fishes are commonly called boarfishes in Australia.

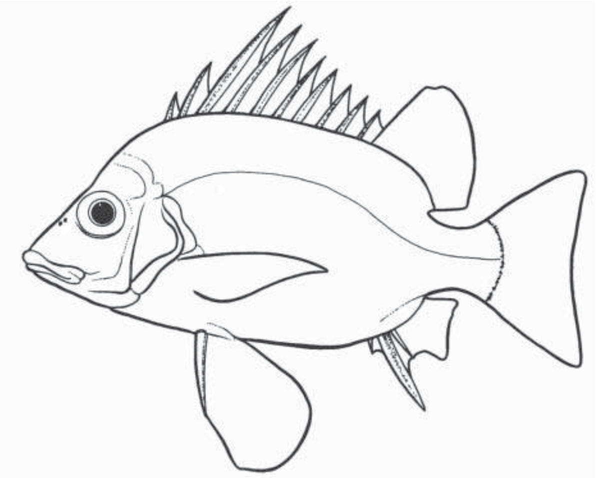
Seven genera in two subfamilies: Histiopterinae: *Histiopterus* (1), *Evistias* (1), *Zanclistius* (1), *Pentaceropsis* (1), *Paristiopterus* (2), and *Parazanclistius* (1); and Pentacerotinae: *Pentaceros* (1), with a total of about 13 species (Parin and Kotlyar, 1988; Humphreys et al., 1989; Kim, 2012).

Family DINOPERCIDAE (418)—cavebasses. Marine; Indian Ocean and eastern Atlantic Ocean off Angola.

Dorsal fin continuous but notched, with 9–11 spines and 18–20 soft rays; anal fin with 3 spines and 12–14 soft rays; caudal fin truncate; protruding lower jaw; exposed maxillae; large supramaxillae; preopercle serrate; frontal bones with high median crest; 2 opercular spines; 7 branchiostegal rays; large swimbladder with three pairs of intrinsic muscles; 26 vertebrae.

Two monotypic genera, *Centrarchops chapini* and *Dinoperca petersi* (Heemstra and Hecht, 1986).

Family BANJOSIDAE (419)—banjofishes. Marine; western Pacific, primarily coasts of China, southern Japan, and Korea.



Body deep, strongly compressed; head with steep, nearly straight profile; opercle spineless; dorsal fin with 10 flattened spines and 12 soft rays; anal fin with 3 spines, the second much longer than the other anal rays, and 7 soft rays; pelvics inserted behind base of pectorals; caudal fin slightly emarginate; lateral line continuous and complete; color brownish or olive with eight faint longitudinal darkish bands. This fish closely resembles the pomadasyids. Maximum length about 30 cm.

One species, *Banjos banjos* (e.g., Nakabo 2002).

Family CENTRARCHIDAE (420)—sunfishes. Freshwater; North America.

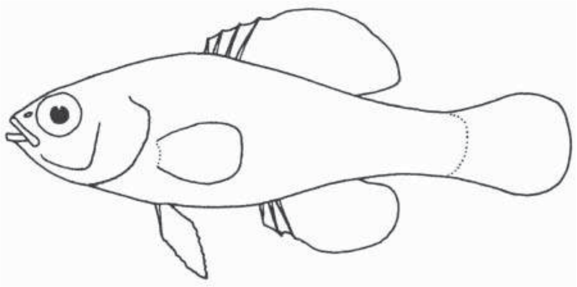
Infraorbital bones present in addition to the lachrymal (except in *Elassoma*); dentary and angular penetrated by lateral line; lateral line present on body, sometimes incomplete; anal fin spines usually three (or fewer, typically in species of *Enneacanthus*, *Lepomis*, and *Micropterus*) or five (or more, typically in species of *Acantharchus*, *Ambloplites*, *Archoplites*, *Centrarchus*, and *Pomoxis*); dorsal fin usually with 5–13 spines (most with 10–12); pseudobranch small and concealed; branchiostegal rays 6 or 7; gill membranes separate; vertebrae 28–33.

Most sunfishes are nest builders. The male hollows out a small depression with his tail and then guards the eggs. Centrarchids are an important sports fish and have been introduced into many areas beyond their native range. Some, such as *Lepomis macrochirus*, the Bluegill, have been used in physiological and ecological experimental work. Maximum length about 83 cm, attained in *Micropterus salmoides* (Largemouth Bass).

Centrarchids were widespread west of the Rocky Mountains by the Late Miocene; the fossil record includes †*Plioplarchus* and species of extant genera.

Nine genera with about 45 species. The classification with genera recognized is based on Roe et al. (2002), Near et al. (2004), and Near et al. (2012b). Gilbert (1998) gives a type catalogue of recent and fossil taxa.

Subfamily Elassomatinae (pygmy sunfishes). Freshwater; eastern United States (including the Mississippi River Valley). Infraorbitals (except lachrymal), basisphenoid, and endopterygoid absent; branchiostegal rays five; gill membranes broadly united across isthmus; dentary and angular not penetrated by lateral line; no lateral line on body; caudal fin rounded; cycloid scales; dorsal fin with 2–5 spines and 8–13 soft rays; anal fin with three spines and 4–8 soft rays. Maximum length 4.5 cm.

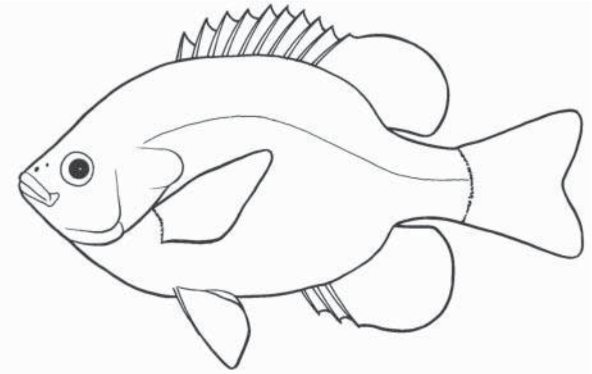


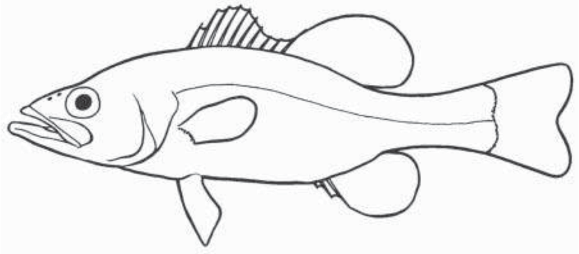
The relationships of *Elassoma* have been controversial, but convincing results from a number of different molecular studies now strongly suggest, in agreement with their classical taxonomic placement (e.g., Nelson, 1994, but not Nelson, 2006), that *Elassoma* belongs in the Centrarchidae and likely as the sister group to other centrarchids (Near et al., 2012b; Betancur-R. et al., 2013a; Lavoué et al., 2014).

One genus, *Elassoma* (7) (e.g., Gilbert, 1998, 2004; Nelson et al., 2004; Lavoué et al., 2014).

Subfamily Centrarchinae. Five genera, *Ambloplites* (4), *Archoplites* (1, the Sacramento Perch, is the only living centrarchid native west of the Rocky Mountains), *Centrarchus* (1), *Enneacanthus* (3), and *Pomoxis* (2, crappies), with 11 species (e.g., Darden, 2008; Roe et al., 2008; Near et al., 2012b; Lavoué et al., 2014).

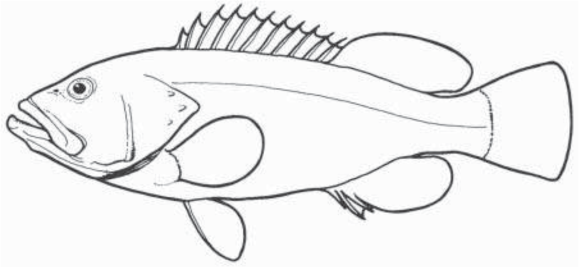
Subfamily Lepominae. *Acantharchus* and *Micropterus* are tentatively included here following the phylogenies of Near et al. (2004, 2012b).





Three genera, *Acantharchus* (1), *Lepomis* (13, figured previous page, synonym *Chaenobryttus*), and *Micropterus* (13, basses) (figured above) (e.g., Harris et al., 2005; Baker et al., 2013; Lavoué et al., 2014).

Family SERRANIDAE (421)—sea basses. Marine (a few freshwater); tropical and temperate seas.



Opercle with three spines—the main spine with one above it and one below it. Scales usually ctenoid, cycloid in some; lateral line complete and continuous (absent in one species), not extending onto caudal fin (running close to dorsal fin base in some Anthiinae); dorsal fin generally continuous, may be notched, with 7–13 spines—most have 10 or fewer and only *Acanthistius* and *Niphon* have 13; 3 anal fin spines; caudal fin usually rounded, truncate, or lunate (rarely forked); tip of maxilla exposed, not slipping beneath lachrymal when mouth closed; no scaly axillary pelvic process; pelvic fin with 1 spine and 5 soft rays; usually 7 branchiostegal rays; usually 24 vertebrae (25–28 in Anthiinae and some grammistins and 30 in *Niphon*); hermaphroditic, although the two sexes usually do not develop at the same time (most *Serranus* and their immediate relatives are functional hermaphrodites). Maximum length up to about 3 m (and weight up to about 400 kg); many species, however, grow no longer than 10 cm, and some anthiines such as *Plectranthias longimanus* reach only 3 cm.

The family in its present composition is thought to be monophyletic based on the apomorphic features of three opercular spines and the reductive absences of the posterior uroneural, procurrent spur, and third preural radial cartilages. The composition and recognition of monophyly is based on Johnson (1983, 1984). See also Randall and McCosker (1992) and Baldwin and Johnson (1993).

Three subfamilies are recognized (following Kendall, 1984), with about 75 genera and 538 species (e.g., Heemstra et al., 2003). Various other subfamily classifications have been proposed in the past, with up to 15 subfamilies given in some classifications employing noncladistic methods. Some workers have recognized the anthiine genus *Giganthias* in its own subfamily and epinepheline genus *Liopropoma* in the Liopropominae. *Caesioscorpis* is placed *incertae sedis.*

Subfamily Serraninae. Some 13 genera, 87 spp. (e.g., *Bullisichthys* (1), *Centropristis* (5), *Chelidoperca* (8), *Cratinus* (1), *Diplectrum* (12), *Dules* (1), *Hypoplectrus* (17) (the synchronous hermaphroditic hamlets), *Paralabrax* (9), *Parasphyraenops* (2), *Schultzea* (1), *Serraniculus* (1), *Serranus* (28)), and *Zalanthias* (1) (e.g., Lobel, 2011).

Subfamily Anthiinae. Some 30 genera, 217 species, most being Indo-West Pacific. *Acanthistius* (11), *Anatolanthias* (1), *Anthias* (9), *Baldwinella* (2), *Caesioperca* (2), *Caprodon* (3), *Choranthias* (1), *Dactylanthias* (2), perhaps *Epinephelides* (1), *Giganthias* (2), *Hemanthias* (3), *Holanthias* (2), *Hypoplectrodes* (8), *Lepidoperca* (10), *Luzonichthys* (6), *Meganthias* (4), *Nemanthias* (1), *Odontanthias* (15), *Othos* (1), *Plectranthias* (49), *Pronotogrammus* (3), *Pseudanthias* (64), *Rabaulichthys* (4), *Sacura* (4), *Selenanthias* (3), *Serranocirrhitus* (1), *Stigmatonotus* (1, of uncertain validity), *Tosana* (1), *Tosanoides* (2), and *Trachypoma* (1). (Smith et al., 2009; Heemstra, 2010; White, 2011; Williams et al., 2013).

Subfamily Epinephelinae. Some 32 genera with 234 species. Larvae with one or more elongate anterior dorsal fin spines (usually the second) and, in the tribe Epinephelini, an elongate pelvic fin spine. The five tribes recognized here for the subfamily Epinephelinae, defined on the basis of larval and adult characters, follow the studies of Baldwin, Johnson, and Kendall. However, Heemstra and Randall (1993) restrict the composition of the subfamily to the groupers (the tribe Epinephelini given here) as classically viewed. The species of "soapfishes" (with the skin toxin grammistin in four genera) are placed in the epinepheline tribes Diploprionini and Grammistini.

tribe niphonini. One species, *Niphon spinosus.*

tribe epinephelini (groupers). Fifteen genera, *Aethaloperca* (1), *Alphestes* (3), *Anyperodon* (1), *Cephalopholis* (24), *Cromileptes* (1), *Dermatolepis* (3), *Epinephelus* (87, some extending into estuaries), *Gonioplectrus* (1), *Gracilia* (1), *Hyporthodus* (13), *Mycteroperca* (15), *Paranthias* (2), *Plectropomus* (7), *Saloptia* (1), *Triso* (1), and *Variola* (2), with 163 species (e.g., Heemstra and Randall, 1993; van Herwerden et al., 2006; Craig and Hastings, 2007; Randall et al., 2013).

tribe diploprionini. Three genera, *Aulacocephalus* (1), *Belonoperca* (2), and *Diploprion* (2), with five species (Baldwin and Smith, 1998).

tribe liopropomini. Three genera, *Bathyanthias* (3), *Liopropoma* (30), and *Rainfordia* (1), with 34 species.

TRIBE GRAMMISTINI. Eight genera, *Aporops* (1), *Grammistes* (1), *Grammistops* (1), *Jeboehlkia* (1), *Pogonopera* (2), *Pseudogramma* (11), *Rypticus* (10), and *Suttonia* (2), with about 29 species (e.g., Randall and Baldwin, 1997; Baldwin and Weigt, 2012).

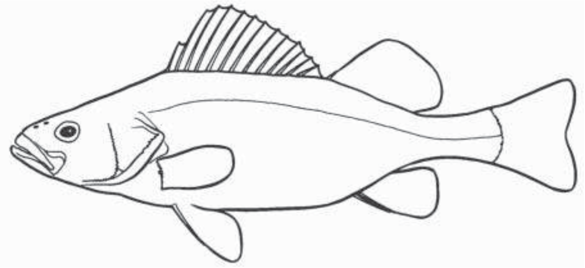
There are also two *incertae sedis* genera: *Caesioscorpis* (1), *Hemilutjanus* (1).

Family PERCIDAE (422)—perches. Freshwater; Northern Hemisphere.

Two dorsal fins, separate or narrowly joined (broadly joined in *Zingel*); 1 or, usually 2 anal spines (the second is usually weak); pelvic fins thoracic, with 1 spine and 5 soft rays; premaxilla protractile or nonprotractile; branchiostegal rays 5–8; branchiostegal membrane not joined to isthmus (may be united to each other or not); pseudobranchiae well developed to rudimentary; no subocular shelf; supramaxilla absent; one or no predorsal bones (never more than one; interneural before first pterygiophore); vertebrae 32–50. Maximum size up to 90 cm, attained in *Stizostedion vitreum* (Walleye); most species much smaller.

Nine genera with 236 species (220 in North America and 16 in Eurasia). The number of species in the genera endemic to North America is mainly from Page et al. (2013). The classification of Bruner (2011) is followed below where five monophyletic groups are recognized as subfamilies.

SUBFAMILY PERCINAE. Posterior edge of dorsal postcleithrum serrulate; moderate sized epioccipital process present; one predorsal bone; anteriormost interhaemal bone greatly enlarged; anal spines usually well developed; preopercle strongly serrate; usually seven or eight branchiostegal rays; body compressed; anal spines prominent; swimbladder well developed.

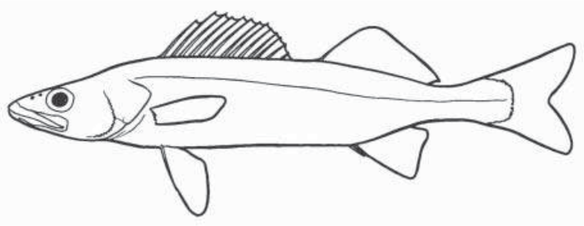


One genus with three species: the circumpolar *Perca* (3: the Eurasian *P. fluviatilis* which has been introduced into South Africa, Australia, and New Zealand, the almost identical North American *P. flavescens,* and *P. schrenki* of the Balkhash and Alakul' lakes area of Asia). The biology of various species, especially of *Perca,* is given by Craig (2000).

SUBFAMILY ACERINAE. Three extrascapular bones present; one predorsal bone. European and western Asian *Gymnocephalus* (5). *Gymnocephalus cernuus* has been introduced into North American Lakes Huron and Superior.

Subfamily Percarininae. Haemal funnel present on 1 to 3 precaudal vertebrae, epioccipital process absent. One genus *Percarina* (2) of the northern Black Sea area (Williams et al., 2007; Robins and Page, 2007).

Subfamily Luciopercinae. Size of first anal proximal pterygiophore weak and short, about the same length as the second anal proximal pterygiophore.



Three genera and ten species.

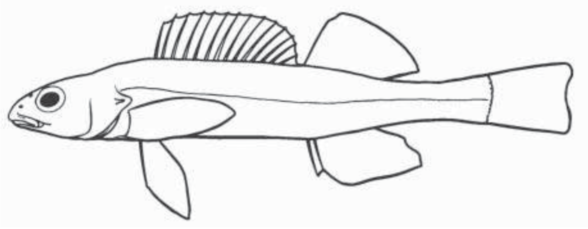
tribe luciopercini (pikeperches). One predorsal present, epioccipital process present, elongated and large, flange present on first infraorbital ventral to dermosphenotic present, 6 to 9 infraorbitals.

One genus, *Stizostedion* (5). The predaceous pikeperches, genus *Stizostedion,* with well-developed swimbladder, have three species in Europe (including the Caspian and Aral seas) and two species (Sauger and Walleye) in North America. Bruner (2011) made a convincing case that the Latvian common name Sander for the species *Stizostedion lucioperca* is not a valid generic name for walleyes, saugers, and pikeperches.

tribe romanichthyini. Basisphenoid absent, shape of supraoccipital crest is bilobed at posterior end; swimbladder absent.

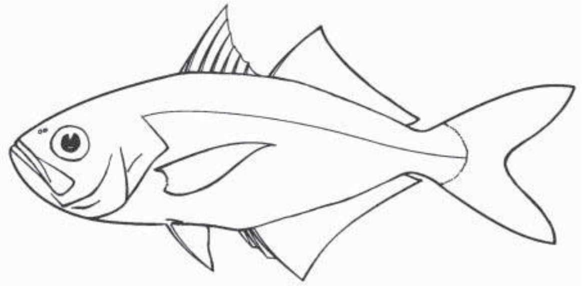
These are European darter-like fishes. *Zingel* (4) has 7 infraorbitals, tubercle-like gill rakers; *Romanichthys* (1) has 6 infraorbitals and slender, elongate gill rakers; *Zingel* is known from the Danube, Rhone, and Vardar systems and the very restricted *Romanichthys valsanicola* is native to Romania.

Subfamily Etheostomatinae. Caudal margin of posttemporal flange not serrulate, 2 proximal pterygiophores without spines between dorsal fins, vertical shaft of preopercle caudal margin smooth without spines, body slightly compressed or fusiform; anal spines moderately prominent; swimbladder reduced or absent. Seldom over 11 cm.



Three genera of North American darters: *Ammocrypta* (8) (*Crystallaria* is a subgenus of *Ammocrypta*; Bruner 2004, 2011), *Etheostoma* (156, *Nothonotus* is a subgenus of *Etheostoma*), and *Percina* (46), giving a total of 210 described species (species listed in Page et al., 2013; see also: Lang and Mayden, 2007; Pillar et al., 2008; Haponski and Stepien, 2008; Layman and Mayden, 2009; Keck and Near, 2009; Mayden, 2010; Near et al., 2011; Harrington and Near, 2012; Layman and Mayden, 2012; Suttkus et al., 2012).

Family LACTARIIDAE (423)—false trevallies. Marine; Indo-West Pacific.



Dorsal fins separate; soft-rayed portion of dorsal and anal fins covered with scales (all scales easily shed); each jaw with two small canine teeth at front; 24 vertebrae. Maximum length 40 cm TL.

One species, *Lactarius lactarius.*

Family DINOLESTIDAE (424)—long-finned pikes. Marine; southern Australia.

Body shape much like *Sphyraena*; lower jaw extending beyond upper jaw; vomer and palatine with teeth, some teeth in mouth canine-like; head, including maxilla, snout, and occiput covered with scales; axillary scale at pelvic base; dorsal fins widely separated, first with 4 or 5 visible spines, second with 1 short spine and 17–19 soft rays; anal fin with 1 short spine and 25–28 soft rays; lateral-line scales about 63–70, cycloid; lateral line continuing onto caudal fin; vertebrae 27 (10 + 17). Maximum length about 84 cm TL.

One species, *Dinolestes lewini* (e.g., Fraser, 1971; Paxton et al., 1989). The osteology was described by Starks (1899) and by Fraser (1971). This fish has a long and controversial taxonomic history, summarized by Fraser (1971), who favored placement in Dinolestidae as commonly followed since.

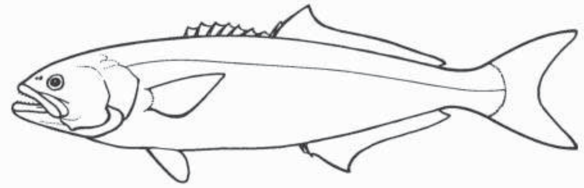
Family SCOMBROPIDAE (425)—gnomefishes. Marine; Indo-West Pacific and western Atlantic.

Eyes relatively large; two moderately high dorsal fins, the first with 7–10 spines.

Johnson (1986) (see also Johnson, 1993:12) suggested that *Scombrops* and *Pomatomus*, along with some acropomatids and *Scombrolabrax*, may be related to the scombroids. Heemstra (2003a) placed the genus in Acropomatidae. At least two species are Indo-West Pacific with *Scombrops oculatus* being widespread (it is the only one in the Atlantic, e.g., Bahamas and Caribbean area).

One genus, *Scombrops,* with three species (Smith-Vaniz et al., 1999; Heemstra, 2003a).

Family POMATOMIDAE (426)—bluefishes. Marine; Atlantic, Indian, and Pacific.



Dorsal fins separate, the first with 7 or 8 short spines and the second with 1 spine and 23–28 soft rays; anal fin with 2 or 3 spines and 23–27 soft rays; soft dorsal and anal fins covered with scales; jaw teeth prominent, ankylosed; preoperculum with a membrane flap over the suboperculum; black blotch at base of pectoral; 26 vertebrae. Maximum length 1.3 m.

The cosmopolitan *Pomatomus saltatrix* (Bluefish) is described as being a voracious predator, killing more fish than it can consume. See note above under family Scombropidae.

This family is among those postulated to be part of a basal percomorph syngnathiform/scombriform clade by Betancur-R. et al. (2013a) and others.

One species, *Pomatomus saltatrix* (e.g., Collette and Klein-MacPhee, 2002; Collette, 2003c).

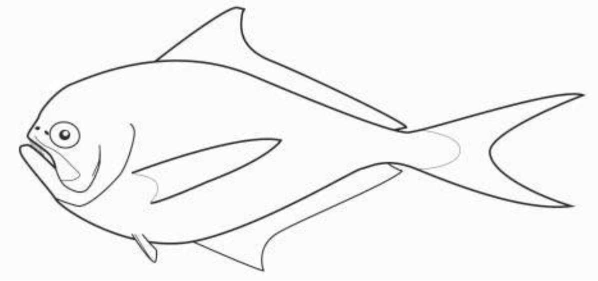
Family BRAMIDAE (427)—pomfrets. Marine; oceanic, Atlantic, Indian, and Pacific.

Single dorsal fin (extending length of body in some) with unbranched anterior spines; anal spines lost; 36–54 vertebrae. *Eumegistus* is thought to be the most primitive genus. Maximum length 85 cm, attained in *Taractichthys longipinnis.*

This family is among those postulated to be part of a basal percomorph syngnathiform/scombriform clade by Betancur et al. (2013a) and others.

Seven genera with about 20 species (Yatsu and Nakamura, 1989; Moteki et al., 1995; Thompson and Russell, 1996; Hartel and Triant, 1998; Thompson, 2003b).

SUBFAMILY BRAMINAE. Dorsal and anal fins of adults with scales and not wholly depressible; pelvic fins thoracic. Oligocene fossils of †*Paucaichthys* are known from Romania (Baciu and Bannikov, 2003).



Five genera, *Brama* (8), *Eumegistus* (2), *Taractes* (2), *Taractichthys* (2), and *Xenobrama* (1), with 15 species.

SUBFAMILY PTERACLINAE. Dorsal and anal fins high, scaleless, and completely depressible; pelvic fins often jugular or nearly so.

Two genera, *Pteraclis* (3), and *Pterycombus* (2), with five species.

Family CARISTIIDAE (428)—manefishes. Marine; oceanic.

Body deep; dorsal fin high and with long base (origin on head); anal spines lost; pelvic fins elongate, in advance or behind pectoral-fin base, with 1 spine and 5 soft rays; 15 branched caudal rays; seven branchiostegal rays; 35–40 vertebrae. These fishes have an association with siphonophores, including feeding on them.

This family is among those postulated to be part of a basal percomorph syngnathiform/scombriform clade by Betancur-R. et al. (2013a) and others.

Four genera, *Caristius* (8), *Paracaristius* (4), *Neocaristius* (1), and *Platyberyx* (6), with 19 species (e.g., Hartel and Triant, 1998; Britz and Hartel, 2012; Stevenson and Kenaley, 2011, 2013).

THE NEXT TWO FAMILIES were tentatively grouped with Acanthuriformes in the molecular study of Betancur-R. et al. (2013a), but the nodal support values were low and corroborating studies using other data are needed.

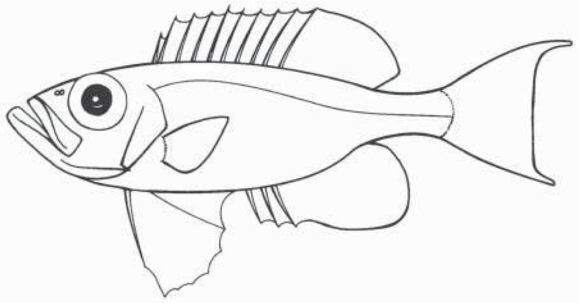
Family MONODACTYLIDAE (429)—moonfishes (fingerfishes). Marine and brackish water (sometimes entering freshwater); western Africa and Indo-Pacific.

Body strongly compressed and deep (deeper than long in some); pelvic fins present in juveniles but absent or reduced to spines in adults of *Monodactylus*; dorsal fin single and with a long base, covered with scales and 5–8 short graduated spines; anal fin with three spines, long base; mouth small; scales cycloid or ctenoid.

Moonfishes are occasionally sold as aquarium fishes. They are often of a silvery color. The four species of *Monodactylus* often ascend rivers, and some populations may live in fresh water.

Two genera, *Monodactylus* (4), and *Schuettea* (2, in New South Wales and Western Australia), with six species. Some authors place *Schuettea* in the Monodactylidae, but Tominaga (1968) in an osteological study of Pempheridae recommended placement of *Schuettea* in its own family. It differs from other monodactylids in a few characters (e.g., normally developed pelvic fins, cycloid scales, teeth absent from endopterygoid and ectopterygoid) but is provisionally retained in the family here.

Family PRIACANTHIDAE (430)—bigeyes (catalufas). Marine; tropical and subtropical, Atlantic, Indian, and Pacific.



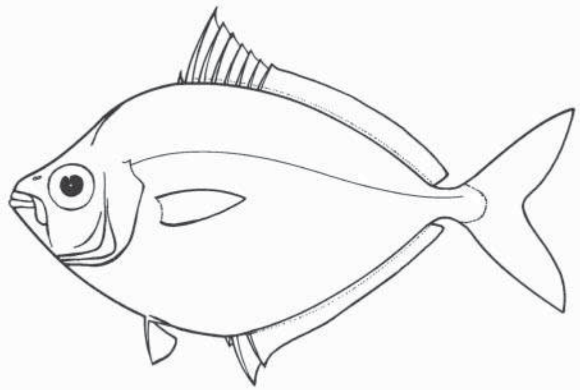
Eyes very large; mouth large, strongly oblique; dorsal fin continuous, usually with 10 spines and 11–15 soft rays; anal fin with 3 spines and 10–16 soft rays; caudal fin with 16 principal rays (14 branched), slightly emarginate to rounded; membrane present connecting the inner rays of the pelvic fin to the body; scales modified spinous cycloid (with strong spines but not ctenoid); scales on the branchiostegal membrane; color usually bright red; vertebrae 23 (very few other percoids have so few vertebrae).

Bigeyes are usually carnivorous and nocturnal. The tapetum lucidum, a brilliant reflective layer producing "eyeshine," may be of a unique form among teleosts. Maximum length about 69 cm TL for *Cookeolus japonicus.*

Four genera, *Cookeolus* (1), *Heteropriacanthus* (1), *Priacanthus* (12), and *Pristigenys* (5), with 19 species (e.g., Starnes, 2003; Iwatsuki et al., 2012). The fossil record was discussed in the revision of the family by Starnes (1988).

THE FOLLOWING SEVEN FAMILIES were suggested to be a clade related to Acanthuroidei, Monodactylidae, and Priacanthidae, although with somewhat weak evidence, by Betancur-R. et al. (2013a); some of the same families were also grouped in a similar position by Near et al. (2012a). They remain in Percoidei in this treatment pending further focused study.

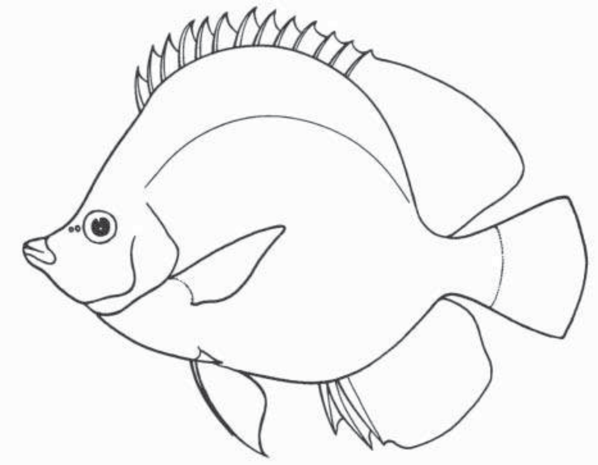
Family LEIOGNATHIDAE (431)—ponyfishes, slimys, or slipmouths. Marine and brackish water; Indo-West Pacific.



Body greatly compressed and slimy, with small scales; head usually naked, upper surface with bony ridges; gill membranes united with isthmus; mouth small and highly protrusible; teeth absent on palate; no pseudobranchiae; dorsal fin continuous, the anterior portion usually with 8 or 9 spines that are more or less elevated and the posterior portion with 14–16 soft rays; anal fin with 3 spines and 14 soft rays; both dorsal and anal fins fold into a basal scaly sheath; branchiostegal rays four or five; vertebrae 22–24. Ventral portion of body very silvery. The dorsal and anal fin spines have a locking mechanism. Leiognathids have a circumesophageal light organ with bacterial luminescence.

Nine genera, *Aurigequula* (1), *Equulites* (10), *Eubleekeria* (4), *Gazza* (5), *Karalla* (2), *Leiognathus* (8), *Nuchequula* (7), *Photopectoralis* (4), and *Secutor* (7), with about 48 species (e.g., Ikejima et al., 2004; Kimura et al., 2005, 2008a,b,c; Sparks et al., 2005; Sparks, 2006; Sparks and Chakrabarty, 2007; Chakrabarty et al., 2010; Abraham et al., 2011; Baldwin and Sparks, 2011).

Family CHAETODONTIDAE (432)—butterflyfishes. Marine; tropical to temperate Atlantic, Indian, and Pacific (primarily tropical Indo-West Pacific).



Body strongly compressed; no spine at angle of preopercle (small serrations may be present on the preopercle); well-developed pelvic axillary process; head region in larval (tholichthys) stage of most species covered with bony plates; dorsal fin continuous or with slight notch, with 6–16 spines and 15–30 soft rays, no procumbent spine; anal fin with 3–5 (usually 3) spines and 14–23 soft rays; caudal fin with 15 branched rays (17 principal), margin rounded to emarginate; scales extending onto the dorsal and anal fins; mouth small, terminal, protractile (the two species of the Indo-Pacific *Forcipiger* have a very elongate snout); gut coiled many times; swimbladder with two anteriorly directed processes; 24 vertebrae (11 + 13).

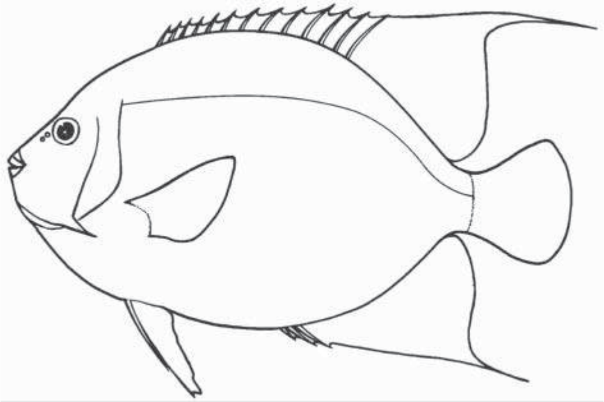
Most species of butterflyfish have brightly colored patterns. Also, most have a dark band running across the eye, and many have an "eyespot" on the dorsal or posterior part of the body—both patterns may serve to confuse predators.

Butterflyfishes generally occur near coral reefs and at depths of less than 20 m, but a few go to at least 200 m. A few species occur in brackish water. Most species are in the Australian to Taiwan region. Only 13 species occur in the Atlantic and 4 in the eastern Pacific. Butterflyfishes are known to feed on coral polyps (but are not known to break off coral) and on other invertebrates.

Butterflyfishes and angelfishes were, until the mid-1970s, combined in the same family; however, Burgess (1974) gave reasons for recognizing them in separate families (and noted many morphological differences, including those in osteology, between the two groups), and Bellwood et al. (2004) confirmed that the families are monophyletic (but not necessarily each other's closest relatives). Fessler and Westneat (2007) completed a molecular phylogeny of the family and recovered a monophyletic Chaetodontidae. Their study recovered a clade containing *Amphichaetodon*, *Coradion*, *Chelmonops*, *Chelmon*, *Forcipiger*, *Hemitaurichthys*, *Heniochus*, and *Johnrandallia*. *Prognathodes* was resolved as the sister to all *Chaetodon*. The topology of subgeneric clades differed significantly from hypotheses based on morphology in that the monophyly of the subgenera *Exornator* and *Chaetodon* was not supported.

Twelve genera (e.g., *Amphichaetodon* (2), *Chaetodon* (88), *Chelmon* (3), *Chelmonops* (2), *Coradion* (3), *Forcipiger* (3), *Hemitaurichthys* (4), *Heniochus* (8), *Johnrandallia* (1), *Parachaetodon* (1), *Prognathodes* (11), and *Roa* (3), with about 129 species (Allen et al., 1998; Kuiter and Debelius, 1999; Burgess, 2001; W. L. Smith et al., 2003; Burgess, 2003; Fessler and Westneat, 2007). The fossil record includes †*Chaetodon ficheuri* from the Miocene of Algeria (Carnevale, 2006).

Family POMACANTHIDAE (433)—angelfishes. Marine; tropical Atlantic, Indian, and Pacific (primarily in western Pacific).



Body strongly compressed; strong spine at angle of preopercle; no well-developed pelvic axillary process; larval stage lacking bony head plates but having spiny scales; dorsal fin continuous, with 9–15 spines and 15–37 soft rays, no procumbent spine; anal fin with 3 spines and 14–25 soft rays; dorsal and anal fins with elongate extension on hind margin in many species (shown in figure); caudal fin with 15 branched rays, margin rounded to lunate (strongly lunate, often with produced lobes, in some species of

Genicanthus); swimbladder lacking anteriorly directed processes; 24 vertebrae (10 + 14).

Angelfishes have striking color patterns and in many species the pattern in juveniles differs markedly from that of adults. They generally occur near coral reefs at depths of less than 20 m (very seldom below 50 m).

Eight genera, *Apolemichthys* (9), *Centropyge* (33), *Chaetodontoplus* (15), *Genicanthus* (10), *Holacanthus* (7), *Paracentropyge* (1), *Pomacanthus* (13), and *Pygoplites* (1), with 89 species (e.g., Pyle, 1997; Allen et al., 1998; Allen and Steene, 2004; Randall and Carlson, 2000; Burgess, 2003; Bellwood et al., 2004; Alva-Campbell et al., 2010; Di Battista et al., 2012).

Family MALACANTHIDAE (434)—tilefishes. Marine; Atlantic, Indian, and Pacific.

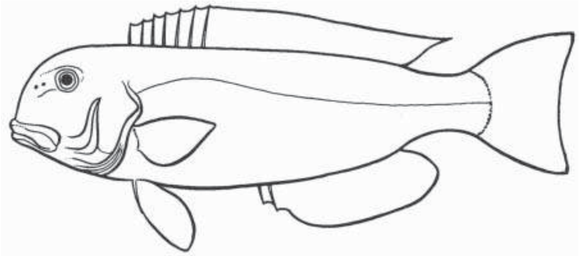
Dorsal fin relatively long, continuous, and with spines and soft rays (total of 22–84 elements); anal fin relatively long, with 1 or 2 weak spines and 11–55 soft rays; pelvic fin with 1 spine and 5 soft rays; single opercular spine, sharp and strong in Malacanthinae and *Caulolatilus*; 6 branchiostegal rays; caudal fin truncate to variously forked; 24, 25, or 27 vertebrae (10 or 11 precaudal vertebrae); larvae with elaborate head and scale spination.

Two subfamilies, five genera, and 45 species.

SUBFAMILY MALACANTHINAE (SAND TILEFISHES). Predorsal ridge absent; enlarged spine at angle of preoperculum in some; body usually more enlongate than in Latilinae, head rounded in profile; dorsal fin with 1–4 spines and 43–60 soft rays (*Malacanthus*) or 3–10 spines and 13–34 soft rays (*Hoplolatilus*); anal fin with 12–55 soft rays in addition to the spines. Sand tilefishes, unlike members of Latilinae, are known to construct or inhabit mounds or borrows. They are usually found in depths less than 50 m, whereas latilines are usually found at depths more than 50 m.

Two genera, *Malacanthus* (3) and *Hoplolatilus* (13), with 16 species (e.g., Earle and Pyle, 1997).

SUBFAMILY LATILINAE (= BRANCHIOSTEGINAE) (TILEFISHES). Predorsal ridge present; never an enlarged spine at angle of preopercle; body depth usually greater than in malacanthines; head rounded to squarish in profile; dorsal fin with 6–10 spines and 14–27 soft rays; anal fin with 11–26 soft rays in addition to the spines. Species are found at depths of 20–600 m.



Three genera, *Caulolatilus* (11), *Lopholatilus* (2), and *Branchiostegus* (16), with 29 species (e.g., Dooley, 2003; Dooley and Iwatsuki, 2012).

Family HAEMULIDAE (Pomadasyidae) (435)—grunts. Marine (many in brackish water, rarely in fresh water); Atlantic, Indian, and Pacific.

Dorsal fin continuous, with 9–14 spines and 11–26 soft rays; anal fin with three spines and 6–18 soft rays; mouth small; teeth on jaws usually cardiform, generally absent on vomer; enlarged chin pores usually present; seven branchiostegal rays; 26 or 27 vertebrae (10 or 11 + 16). Maximum length about 60 cm.

Johnson (1980) recognized two subfamilies: the Haemulinae, primarily of the New World with a short dorsal fin of 13–16 soft rays, and the Plectorhinchinae, of the Indo-West Pacific and eastern Atlantic with a long dorsal fin of 17–26 soft rays (comprises the last three genera listed below). Fishes in the last subfamily often have thick fleshy lips as adults (these are called the rubberlips or sweetlips) and are brightly colored.

Nineteen genera in two subfamilies, e.g., in Haemulinae: *Anisotremus* (8), *Boridia* (1), *Brachydeuterus* (1), *Conodon* (3), *Emmelichthyops* (1, Bonnetmouth), *Haemulon* (23), *Haemulopsis* (4), *Inermia* (1, Boga), *Isacia* (1), *Microlepidotus* (2), *Orthopristis* (7), *Parakuhlia* (1), *Pomadasys* (35), *Xenichthys* (3), and *Xenistius* (1), *Xenocys* (1), and in Plectorhinchinae: *Diagramma* (5), *Genyatremus* (4), *Parapristipoma* (4), and *Plectorhinchus* (28), with a total of about 133 species (e.g., Iwatsuki et al., 2000; Lindeman and Toxey, 2003; Bernardi et al., 2008; Rocha at al., 2008; Sanciangco et al., 2011; Tavera et al., 2012). The family Inermiidae recognized in Nelson (2006) is a junior synonym of Haemulidae (Tavera et al., 2012).

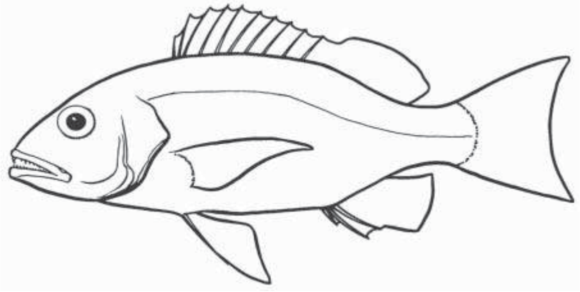
Family HAPALOGENIIDAE (436)—barbeled grunters. Marine, brackish, Pacific, Indian.

Body compressed; 10 pores on and behind chin including very small pair near symphysis; clusters of short, dense barbels on lower jaw and chin; teeth uniformly small, in bands on jaws, vomer, and palatines; 7 branchiostegals; head scaled dorsally and laterally; dorsal fin with 11 spines and 13–15 soft rays; anal fin with 3 spines and 8–9 soft rays; caudal fin rounded (Iwatsuki and Russell, 2006); Maximum length 40.0 cm SL in *Hapalogenys nigripinnis.*

Springer and Raasch (1995) established the family Hapalogeniidae (Haplogeniidae) for *Hapalogenys*, a genus of uncertain relationships.

One genus, *Hapalogenys* with 8 species (Iwatsuki and Nakabo, 2005).

Family LUTJANIDAE (437)—snappers. Marine (rarely in fresh water and estuaries); tropical and subtropical, Atlantic, Indian, and Pacific.



Dorsal fin continuous or with a shallow notch, with 9–12 spines and 9–18 soft rays; anal fin with 3 spines and 7–11 soft rays; pelvic fins inserted just behind pectoral base; mouth terminal, moderate to large; most with enlarged canine teeth on jaws, small teeth on palatines and usually on vomer; maxilla slips beneath preorbital when mouth closed; supramaxilla absent; seven branchiostegals caudal fin truncate to deeply forked; 24 vertebrae (10 + 14). Maximum length about 1.0 m.

Nelson (1994) gave reasons for treating the Caesionidae as a subfamily, but Nelson (2006) changed back to the classification followed in Nelson (1984) until there is more original research clearly showing the cladistic relationships of all taxa involved. Miller and Cribb (2007) explored the phylogenetic relationships of 27 species of common Indo-Pacific snappers using the 16S ribosomal RNA and cytochrome b mitochondrial genes and concluded Lutjanidae has four subfamilies: Caesioninae, Etelinae, Paradicichthyinae, and Lutjaninae. Holleman et al. (2013) continue to recognize Caesionidae. Until a phylogenetic analysis using morphology and/or nuclear DNA is completed, we continue to recognize Caesionidae.

Snappers are important food fishes but are sometimes responsible for ciguatera, the tropical fish-poisoning disease. They generally occur near the bottom in tropical and subtropical seas from shallow water to depths of about 550 m. Three species of *Lutjanus*, *L. fuscescens*, *L. goldiei*, and perhaps *L. maxweberi* of the Philippine–New Guinea region, are known only from fresh waters and estuaries (not from purely marine waters). The juveniles of several otherwise marine species of *Lutjanus* are known to enter brackish and fresh water.

Seventeen genera with 110 species recognized in four subfamilies (e.g., Anderson, 2003a; Moura and Lindeman, 2007; White and Last, 2012).

SUBFAMILY ETELINAE. Five genera, *Aphareus* (2), *Aprion* (1), *Etelis* (4), *Pristipomoides* (11), and *Randallichthys* (1), with 19 species.

SUBFAMILY APSILINAE. Four genera, *Apsilus* (2), *Lipocheilus* (1), *Paracaesio* (9), and *Parapristipomoides* (1), with 13 species.

SUBFAMILY PARADICICHTHYINAE. Two monotypic genera, *Symphorichthys* (1), and *Symphorus* (1).

SUBFAMILY LUTJANINAE. Six genera, *Hoplopagrus* (1), *Lutjanus* (70), *Macolor* (2), *Ocyurus* (1), *Pinjalo* (1), and *Rhomboplites* (1), with 76 species.

Family CAESIONIDAE (438)—fusiliers. Marine; Indo-West Pacific.

Ascending premaxillary process as a separate ossification from premaxilla; dorsal fin continuous with 10–15 slender spines and 8–22 soft rays; anal fin with 3 spines and 9–13 soft rays; mouth slightly upturned, small, and highly protrusible; jaw teeth small (absent in two species); caudal fin deeply forked; lateral-line scales 45–88; seven branchiostegal rays; 24 vertebrae. Fusiliers are planktivorous in contrast to the snappers, which tend to be benthic carnivores. Maximum length about 60 cm.

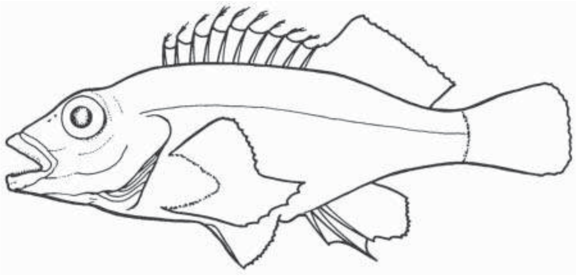
For comments on the change in family recognition, see above under Lutjanidae.

Four genera, *Caesio* (9), *Dipterygonotus* (1), *Gymnocaesio* (1), and *Pterocaesio* (12), with 23 species (Carpenter, 1990, 2001; Miller and Cribb, 2007; Holleman et al., 2013).

Superfamily Cirrhitoidea. Pelvics rather far behind pectorals; lower 5–8 rays of pectorals unbranched, usually thickened, and sometimes separate from one another; anal fin usually with three spines. In the provisional arrangement of cirrhitoid family relationships, Greenwood (1995) showed that the Cirrhitidae was most plesiomorphic, followed by the Chironemidae, with the Aplodactylidae, Cheilodactylidae, and Latridae forming an unresolved trichotomy. Changes in the family classification as shown here and the need for further study are also suggested in the molecular study of Burridge and Smolenski (2004), who suggested that the Latridae should be expanded to encompass some cheilodactylids, and further studies are desirable to understand the cladistic relationships of all genera in this superfamily.

Five families, 21 genera, and about 76 species.

Family CIRRHITIDAE (439)—hawkfishes. Marine; tropical western and eastern Atlantic, Indian, and Pacific (majority are Indo-Pacific).



Dorsal fin continuous with 10 spines and 11–17 soft rays; pectoral rays 14, the lower five to seven unbranched and membrane incised; cirri on interspinous membrane; anal-fin soft rays 5–7; scales cycloid or ctenoid; swimbladder absent; vertebrae 26. Maximum length about 55 cm.

Hawkfishes are usually small and richly colored fishes that live in rocky and coral habitats. They have many features in common with the scorpaenids.

Twelve genera (*Amblycirrhitus* (5), *Cirrhitichthys* (8), *Cirrhitops* (3), *Cirrhitus* (4), *Cristacirrhitus* (1), *Cyprinocirrhites* (1), *Isocirrhitus* (1), *Itycirrhitus* (1), *Neocirrhites* (1), *Notocirrhitus* (1), *Oxycirrhites* (1), and *Paracirrhites* (6)) with 33 species (Randall, 2001a; Gaither and Randall, 2013).

Family CHIRONEMIDAE (440)—kelpfishes. Marine; coastal Australia and New Zealand.

Dorsal fin with 14–16 spines and 15–21 soft rays; anal-fin soft rays 6–8; vomer with teeth, palatines without teeth; jaw teeth conical or villiform. Maximum length about 40 cm.

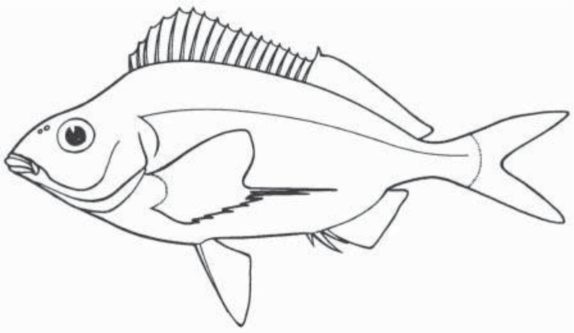
One genus, *Chironemus* (6), with six species (Burridge et al., 2006).

Family APLODACTYLIDAE (Haplodactylidae) (441)—marblefishes. Coastal marine; southern Australia, New Zealand, Peru, and Chile.

Dorsal fin with 14–23 spines and 16–21 soft rays; anal-fin soft rays 6–8; vomer with teeth; jaw teeth incisiform, lanceolate, or tricuspid.

One genus, *Aplodactylus* and five species (Russell, 2000; Burridge, 2000).

Family CHEILODACTYLIDAE (442)—morwongs. Marine; parts of the Southern Hemisphere in Atlantic, Indian, and Pacific, and in the Northern Hemisphere off coasts of China and Japan and the Hawaiian Islands.

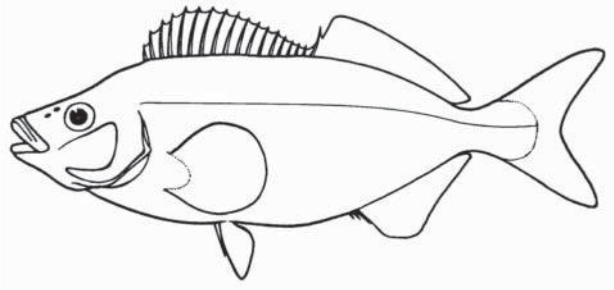


Dorsal fin continuous, may be almost separated, with 14–22 spines and 19–39 soft rays; anal fin with three spines (third may be difficult to detect) and 7–19 soft rays; vomer and palatines toothless; lower four to seven pectoral rays in adults usually thickened, elongated, and detached (free of rest of fin); usually 24 vertebrae. Maximum total length 1.2 m for *Dactylophora nigricans*.

The only species in the Northern Hemisphere belongs to the subgenus *Goniistius* of the genus *Cheilodactylus*, a taxon with an antitropical distribution. The last major revision was by Burridge and Smolenski (2004).

Four genera, *Cheilodactylus* (16), *Chirodactylus* (3), *Dactylophora* (1), and *Nemadactylus* (7), with 27 species (e.g., Burridge, 2004; Burridge and Smolenski, 2004).

Family LATRIDAE (443)—trumpeters. Marine; coastal southern Australia, New Zealand, Chile, and in the southern Atlantic.



Dorsal fin with 14–24 spines and 23–40 soft rays; anal fin with 18–35 soft rays; vomer with or without teeth. Trumpeters form an important sport fishery and are known for their fine taste.

Three genera, *Latridopsis* (2), *Latris* (2), and *Mendosoma* (1), with five species (Burridge and Smolenski, 2004).

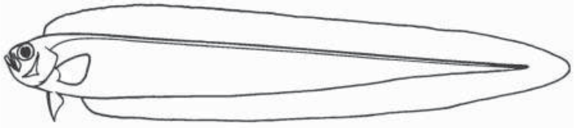
Superfamily Cepoloidea. One family with two subfamilies that were at one time (e.g., Nelson, 1984) treated as the separate families Cepolidae and Owstoniidae.

Family CEPOLIDAE (444)—bandfishes. Marine; eastern Atlantic (off Europe and in Mediterranean) and Indo-West Pacific (including New Zealand).

Dorsal fin continuous, with 0–4 spines (usually 3); anal fin with 0–2 spines; vomer and palatine toothless; single postcleithrum; six branchiostegal rays; lateral line along base of dorsal fin; epipleural ribs in some trunk vertebrae fused proximally to corresponding pleural ribs; body color generally red or pink. Maximum length 70 cm, attained in *Cepola rubescens* of the northeastern Atlantic and Mediterranean.

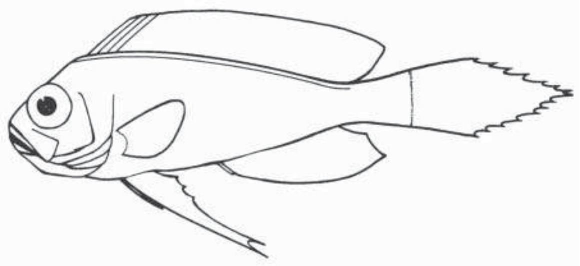
Five genera with 23 species (e.g., Smith-Vaniz in Smith and Heemstra, 1986; Bineesh et al., 2011). Two subfamilies are provisionally recognized.

SUBFAMILY CEPOLINAE. Highly compressed elongate body gradually tapering to the tail; dorsal and anal fins very long, each with over 65 rays, and connected with caudal fin; minute scales; about 65–80 vertebrae.



Two genera, *Acanthocepola* (4), and *Cepola* (5), with nine species. *Cepola haastii* is the only cepolid from New Zealand.

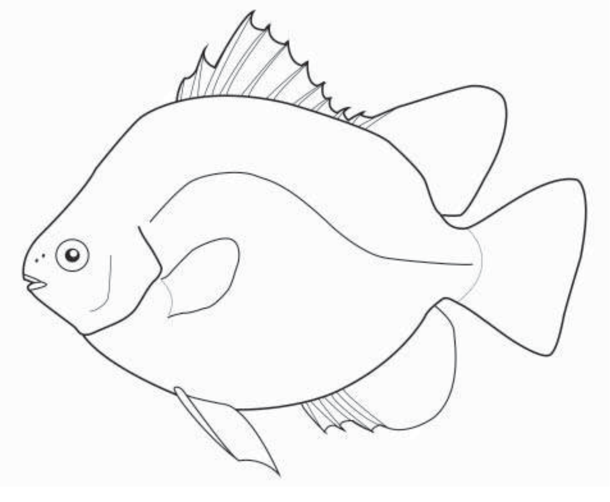
SUBFAMILY OWSTONIINAE. Elongate caudal fin; dorsal and anal fins each with fewer than 32 rays; 28–30 vertebrae. Deepwater.



Three genera, *Owstonia* (7), *Pseudocepola* (1), and *Sphenanthias* (6) with 14 species.

Superfamily Siganoidea. The next two families, Scatophagidae and Siganidae, have been suggested to be sister to Caproiformes, Lophiiformes, and Tetraodontiformes by both Betancur-R. et al. (2013a) and Near et al. (2012a). Although Holcroft and Wiley (2008) advocated placing them in an expanded Acanthuroidei, the molecular evidence is not yet strong enough and there is insufficient corroborating evidence to justify removing them from Percoidei at present.

Family SCATOPHAGIDAE (445)—scats. Marine and brackish water, occasionally entering fresh water; Indo-West Pacific (primarily southeastern Asia and Indo-Australian Archipelago but extending from South Africa to the Society Islands).



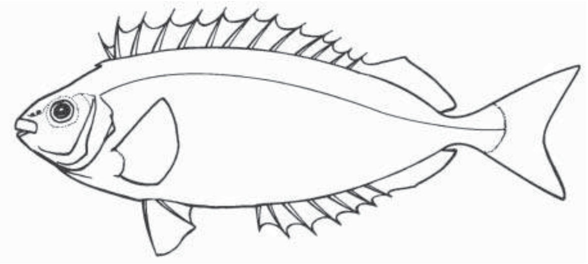
Body deep and compressed, resembling that of butterflyfishes; pelvic axillary process present; dorsal fin deeply notched, with 11 or 12 spines, first dorsal spine procumbent, and 15–18 soft rays; anal fin with four spines and 14–17 soft rays; caudal fin with 16 branched rays; mouth not protractile; 23 vertebrae

(11 + 12). Maximum length about 35 cm. At least one species, *Scatophagus tetracanthus*, can reproduce in fresh water.

As noted by Parenti (2004), the family gets its name from its members' habit of including human feces in the diet (which mainly includes algae). Tyler and Sorbini (1999) gave a phylogeny of the family, showing that the two fossil genera, the Eocene †*Eoscatophagus* and the Oligocene †*Oligoscatophagus* (both from Italy), form one clade and the extant species form another (the morphological differences are greater between the two fossil genera than between the two extant ones) and provided a key to all genera.

Two genera, *Scatophagus* (2) and *Selenotoca* (2), with four species (Parenti, 2004).

Family SIGANIDAE (446)—rabbitfishes. Marine (rarely in estuaries); tropical Indo-West Pacific and eastern Mediterranean.



Pelvic fins each with two strong spines and three soft rays between them; single dorsal fin with 13 strong spines and 10 soft rays; anal fin with 7 spines and 9 soft rays; spines venomous; a single row of compressed, asymmetrically bicuspid incisiform teeth in both jaws; vertebrae 23. Maximum length about 50 cm.

Most siganids are herbivorous. There is one species that is truly estuarine, *Siganus vermiculatus*; individuals of several other species may occur in estuaries for part of their life. Of the 28 species, 13 are schooling species while the remainder live among coral.

A molecular phylogeny was completed by Borsa et al. (2007). Four Eocene and Oligocene fossil genera are known, †*Archaeoteuthis*, †*Eosiganus*, †*Ruffoichthys* (which has only one spine and three soft rays in each pelvic fin), and †*Siganopygaeus* (Tyler and Bannikov, 1997).

One genus, *Siganus* (synonym *Teuthis*) with two subgenera, the subgenus *Siganus* with 23 species and the subgenus *Lo* with five species (established by D. J. Woodland in 1990; see also Tyler and Bannikov, 1997; Randall and Kulbicki, 2005; Borsa et al., 2007; Kuriiwa et al., 2007).

Suborder Notothenioidei (icefishes). Pelvic fins each with one spine and five (rarely four) branched rays, jugular; one nostril on each side; three plate-like pectoral fin radials (actinosts); dorsal fin spines usually nonpungent; principal caudal-fin rays 10–19, usually fewer than 15; usually two or three lateral lines, occasionally one (as in all bovichtids); body with ctenoid or cycloid scales or naked (except for lateral line scales); ribs poorly developed, floating or absent (the epineurals are usually well developed); palatine teeth absent and vomerine teeth usually absent except in bovichtids, which have both; branchiostegal rays 5–9; swimbladder absent; primarily Antarctic in distribution.

Most of the species of coastal fishes in the Antarctic region belong to this suborder. Some species live at an average temperature of –1.9 degrees C and have a glycoprotein in their blood that lowers the freezing point. Most of the species in subzero water are aglomerular. Some species lack red blood cells and hemoglobin. Most species are benthic; however, despite lacking a swimbladder, there are several species that have developed means of becoming buoyant, and some are pelagic.

Eight families with about 46 genera and 153 species. Eocene fossils are known (Balushkin, 1994; Bienkowska-Wasiluk et al., 2013). The Antarctic and subantarctic species were keyed and descriptive material given in Gon and Heemstra (1990) and Antarctic species given in Miller (1993). The interrelationships of the notothenoid families were discussed in Balushkin (1992, 2000), Lecointre et al. (1997), Eastman and Eakin (2000), Last et al. (2002), Near and Cheng (2008), Coscia et al. (2010), Janko et al. (2011), Lautrédou et al. (2012); Eastman et al. (2014); Near et al. (2012c), and the references therein. There is general agreement on the phylogenetic sequencing of the families (see references above). Notothenioids and zoarcoids may be closely related, with both having some affinity with the trachinoids, and all three being derived from some percoid group.

Family BOVICHTIDAE (Bovichthyidae) (447)—temperate icefishes. Marine; southern Australia, New Zealand, and southern South America regions.

Gill membranes free from isthmus, extending far forward; teeth on palatine and vomer; mouth protractile; spinous dorsal fin present (i.e., two dorsal fins present); one lateral line; snout not produced.

The spelling of the family name, changed from Bovichthyidae in Nelson (1994), follows Eschmeyer (1998). *Pseudaphritis urvilli*, formally recognized in this family, is now placed in its own family (see below). Also known as thornfishes.

Three genera, *Bovichtus* (8, synonym *Bovichthys*), *Cottoperca* (2), and *Halaphritis* (1), with 11 species (e.g., Eastman and Eakin, 2000; Last et al., 2002).

Family PSEUDAPHRITIDAE (448)—catadromous icefishes. Freshwater, brackish, and marine; southeastern Australia (including Tasmania) and southeastern Pacific off Chile.

Slender fishes with short 1st dorsal fin of about 8 spines; long 2nd dorsal of 25 soft rays; long anal fin with one spine and about 22 soft rays; caudal fin truncate or slightly emarginate; catadromous.

Pseudaphritis was formerly placed in the Bovichtidae. The genus is recognized in its own family following Balushkin (1992) and Lecointre et al. (1997), and this has also been accepted in Last et al. (2002) and Eastman and Eakin (2000). Last et al. (2002) summarized two opposing schools of thought on the relationships of *Pseudaphritis*: that it belongs to a monotypic family considered to be the sister group of other notothenioids including the bovichtid genera *Bovichtus* and *Cottoperca* (Balushkin), or that it is the sister group of the rest of the notothenioids excluding *Bovichtus* and *Cottoperca* (e.g., Lecointre et al., 1997; Betancur-R. et al., 2013a); either way, assigning family status is appropriate. The two species are widely disjunct in the southwest and southeast Pacific.

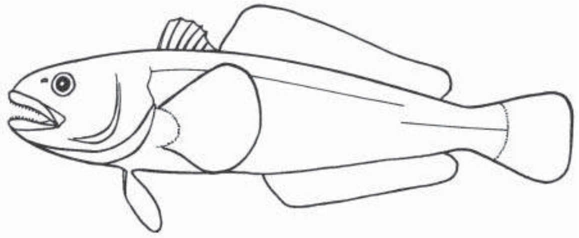
One genus with two species: *Pseudaphritis urvillii* occurs primarily in fresh water in coastal areas of southeast Australia and Tasmania with spawning appearing to occur in estuaries (e.g., Berra, 2001). *P. undulatus* occurs in the southeastern Pacific off Chile.

Family ELEGINOPSIDAE (449)—Patagonian blennies. Marine; off Chile and Argentina to Tierra del Fuego.

Dorsal fin with seven or eight spines and 23–27 soft rays. The one species was formerly placed in the Nototheniidae. It is recognized in its own family following Balushkin (1992) and this has also been accepted in Eastman and Eakin (2000).

One species, *Eleginops maclovinus.*

Family NOTOTHENIIDAE (450)—cod icefishes. Marine (rarely brackish); coastal Antarctica and southern Southern Hemisphere.



Body scaled; gill membranes forming a fold across the isthmus; mouth protractile; spinous dorsal fin present, with 3–11 spines (the second with 25–42 soft rays); one to three lateral lines; ribs present; three radials in pectoral skeleton, all with some connection to coracoid; 45–59 vertebrae. Nototheniids show a certain similarity to hexagrammids.

The majority of notothenioids are benthic. However, several species of this family, such as the abundant and circumpolar plankton feeder *Pleuragramma antarcticum,* are pelagic. They utilize lipid deposits and reduced skeletal mineralization to attain near neutral buoyancy in the absence of a swimbladder. Some species are cryopelagic, living beneath the sea ice.

Fourteen genera, *Aethotaxis* (2), *Cryothenia* (2), *Dissostichus* (2), *Gobionotothen* (5), *Gvozdarus* (2), *Lepidonotothen* (1), *Lindbergichthys* (2), *Nototheniops* (3), *Notothenia* (7, synonym *Indonotothenia*), *Pagothenia* (2), *Paranotothenia* (2), *Patagonotothen* (14), *Pleuragramma* (1), and *Trematomus* (11, synonym *Pseudotrematomus*), and about 56 species (e.g., Eastman and Eakin, 2000; Cziko and Cheng, 2006; Kunh and Near, 2009; Coscia et al., 2010). Some species range northward to such regions as New Zealand, Macquarie

Island, Chile, and Argentina. Most species of the family, however, occur in Antarctica.

Family HARPAGIFERIDAE (451)—spiny plunderfishes. Marine; littoral, extending north to subantarctic and to, for example, southern part of South America and Kerquelen and Macquarie islands.

Body naked; gill membranes broadly united to isthmus; spinous dorsal fin present, with 1–7 flexible spines; mouth protractile; chin barbel absent; strong spine on opercle and on subopercle; three hypurals; vertebrae 34–37.

The family content was changed after Nelson (1994); see below under Artedidraconidae.

One genus, *Harpagifer*, with about eleven species (Eastman and Eakin, 2000; Neyelov and Prirodina, 2006).

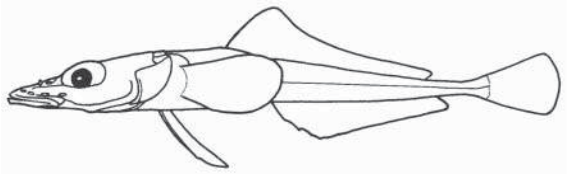
Family ARTEDIDRACONIDAE (452)—barbeled plunderfishes. Marine; deepwater Antarctic.

Body naked; gill membranes broadly united to isthmus; spinous dorsal fin present, with 1–7 flexible spines; mouth protractile; chin barbel present; opercle with hook-shaped spine; four or five hypurals; vertebrae 33–41.

Nelson (1994) recognized this as a subfamily of Harpagiferidae (although the two lineages are distinct, they also form a monophyletic group). It is recognized now following Hureau (1986); its recognition is generally accepted (e.g., Eastman and Eakin, 2000).

Four genera, *Artedidraco* (6), *Dolloidraco* (1), *Histiodraco* (1), and *Pogonophryne* (22), with 30 species (e.g., Eastman and Eakin, 2000; Eakin et al., 2009; Shandikov and Eakin, 2013; Shandikov et al., 2013).

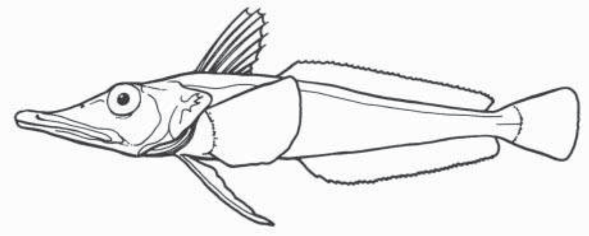
Family BATHYDRACONIDAE (453)—Antarctic dragonfishes. Marine; Antarctic.



Gill membranes united; mouth usually nonprotractile; no spinous dorsal fin; connection between nasal tube and buccal cavity (internal choana) in *Gymnodraco* and *Psilodraco* (Gon and Heemstra, 1990; Eastman 1991); one or more lateral lines; 45–79 vertebrae.

Eleven genera, *Acanthodraco* (1), *Akarotaxis* (1), *Bathydraco* (5), *Cygnodraco* (1), *Gerlachea* (1), *Gymnodraco* (1), *Parachaenichthys* (2), *Prionodraco* (1), *Psilodraco* (1), *Racovitzia* (2), and *Vomeridens* (1), with 17 species (Eastman and Eakin, 2000; Rey et al., 2011).

Family CHANNICHTHYIDAE (Chaenichthyidae) (454)—crocodile icefishes. Marine; Antarctic and southern South America.



Gill membranes united; mouth nonprotractile; snout produced and depressed; spinous dorsal fin present; pelvic fins broad or elongate; vertebrae 22–31. Maximum length 75 cm.

Most or all species are without red blood cells, and their blood is nearly colorless. The muscles lack myoglobin. Survival is probably permitted by the fish living in extremely cold, well-oxygenated water and having skin respiration and a large volume of blood that is efficiently circulated.

Eleven genera, *Chaenocephalus* (1), *Chaenodraco* (1), *Champsocephalus* (2), *Channichthys* (9), *Chionobathyscus* (1), *Chionodraco* (3), *Cryodraco* (3), *Dacodraco* (1), *Neopagetopsis* (1), *Pagetopsis* (2), and *Pseudochaenichthys* (1), with 25 species (Eastman and Eakin, 2000; Cocca et al., 2011).

Order SCORPAENIFORMES (79)—mail-cheeked fishes. This order contains the "mail-cheeked" fishes, distinguished by the suborbital stay, a posterior extension of the third infraorbital bone (counting the lachrymal), which extends across the cheek to the preoperculum and is usually firmly attached to that bone (it is absent in the Pataecidae—also not in zoracoids, trichodontids and some gasterosteoids). Head and body tending to be spiny or have bony plates; pectoral fin usually rounded, membranes between lower rays often incised; caudal fin usually rounded (occasionally truncate, rarely forked).

In regarding scorpaeniforms as perciform derivatives, Mooi and Gill (1995) and Mooi and Johnson (1997) gave them subordinal status within the order Perciformes. Imamura and Yabe (2002) also presented reasons for regarding this order as a suborder of perciforms.

In the present treatment, the Scorpaeniformes contain six suborders: Scorpaenoidei, Platycephaloidei, Normanichthyoidei, Zoarcoidei, Gasterosteoidei, and Cottoidei.

Some 41 families with 398 genera and about 2,092 species.

The arrangement of families and family boundaries is subject to much disagreement. Suggestions for some needed changes are given in Ishida (1994), Imamura and Shinohara (1998), Mandrytsa (2001), Imamura and Yabe (2002), Imamura (1996, 2004), and Smith and Wheeler (2004). Imamura and Yabe (2002) and Smith and Wheeler (2004) proposed major changes to a polyphyletic Scorpaeniformes. For example, Imamura and Yabe (2002) supported placing a new suborder Scorpaenoidei aligned with Serranidae in the Perciformes and aligning the suborder Cottoidei with the Zoarcoidei.

Mandrytsa (2001) added many new taxa and placed the family Pataecidae in the Perciformes, in its own suborder Pataecoidei. Mooi and Johnson (1997) suggested that the trachinoid family Champsodontidae is a scorpaeniform (which they ranked as the perciform suborder Scorpaenoidei); this was not supported in the molecular study of Smith and Wheeler (2004).

Suborder Scorpaenoidei. This suborder contains the world's most venomous fishes. They are usually brightly colored.

Fundamental work on Scorpaeniformes was by Matsubara (1943), who published the first comprehensive systematic treatment of the order, the position of Scorpaenoidei within it, and intergeneric relationships among its members. In later systematic work, Ishida (1994) split the family Scorpaenidae and recognized the following families in the suborder Scorpaenoidei (also listed in Imamura and Shinohara, 1998): Sebastidae, Setarchidae, Neosebastidae (the latter two being sister taxa), Scorpaenidae, Apistidae, Tetrarogidae (the latter two being sister taxa), Synanceiidae, Congiopodidae (the latter two being sister taxa), Gnathanacanthidae, Aploactinidae, and Pataecidae (the latter two being sister taxa), with the Caracanthidae, of unknown relationships, not being included. Imamura (2004), classifying the superfamily Scorpaenoidea, included 20 families: Sebastidae, Sebastolobidae, Scorpaenidae, Apistidae, Tetrarogidae, Synanceiidae, Aploactinidae, Congiopodidae, Gnathanacanthidae, Pataecidae, Caracanthidae, Eschmeyeridae, Neosebastidae, Plectrogeniidae, Parabembridae, Bembridae, Triglidae, Peristediidae, Hoplichthyidae, and Platycephalidae. He compared his cladistic results with those of others (e.g., Mandrytsa, 2001).

Six families with about 90 genera and 513 species.

Family SCORPAENIDAE (455)—scorpionfishes (rockfishes). Marine (rarely in fresh water); all tropical and temperate seas.

Body compressed; head usually with ridges and spines, one or 2 opercular spines (usually 2 divergent) and 3 to 5 preopercular spines (usually 5); suborbital stay usually securely fastened to preopercle (no attachment in some); scales, when present, usually ctenoid; dorsal fin usually single (often with a notch), usually with 11–17 spines and 8–17 soft rays; anal fin with 1–3 spines (usually 3) and 3–9 soft rays (usually 5); pelvic fin with 1 spine and 2–5 soft rays (usually 5); pectoral fin well developed (11–25 rays), rarely with 1 to 3 free lower rays; gill membranes free from isthmus; swimbladder absent in some (e.g., *Plectrogenium* and *Sebastolobus*); vertebrae 24–31. Venom gland in dorsal, anal, and pelvic spines in some species. Most have internal fertilization, and some give birth to live young (e.g., *Sebastes*). Some lay eggs in a gelatinous balloon, and *Scorpaena guttata* is reported to have an egg balloon that may be as much as 20 cm in diameter. Many species are commercially important.

Most species are in the Indian and Pacific oceans. For comments on the classification see above under suborder Scorpaenoidei. The sequencing of the following subfamilies, recognized as families by some workers as noted above, is based on conclusions in some of the listed works.

Here we retain the subfamily ranking as seen in Nelson (2006). We acknowledge that these subfamilies have been elevated to family status by some researchers. We consider Scorpaenidae a work in progress and anticipate revisionary studies including both molecular and morphological data in the near future.

Nine subfamilies, 65 genera with at least 454 species (e.g., Poss and Eschmeyer, 2003).

SUBFAMILY SEBASTINAE. Seven genera and about 131 species. Extensive information is given on the members of this subfamily, known as rockfishes, in the northeast Pacific by Love et al. (2002).

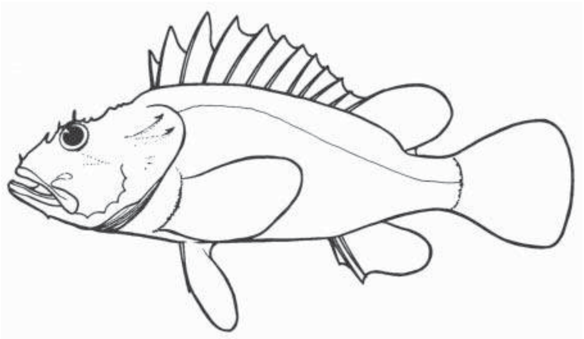
TRIBE SEBASTINI. Four genera, *Helicolenus* (8), *Hozukius* (2), *Sebastes* (107), and *Sebastiscus* (3), with about 120 species. *Helicolenus* and *Sebastes* occur in all oceans, whereas *Sebastiscus* and *Hozukius* occur only in the western Pacific. Kai et al. (2003) suggested that *Helicolenus*, and *Hozukius* are more closely related to *Sebastes* than to *Sebastiscus*. The live-bearing genus *Sebastes* is the largest in the family with about 110 species (almost all in the North Pacific) (Li et al., 2006; Hyde and Vetter, 2007; Kai and Nakabo, 2013).

TRIBE SEBASTOLOBINI. Three genera, *Adelosebastes* (1), *Sebastolobus* (3, with 15–17 dorsal spines, highest for the family), and *Trachyscorpia* (7), with 11 species (Motomura et al., 2007).

SUBFAMILY SETARCHINAE. Three genera, *Ectreposebastes* (2), *Lioscorpius* (2), and *Setarches* (3), with seven species (e.g., Imamura, 2004).

SUBFAMILY NEOSEBASTINAE. Two genera, *Maxillicosta* (6) and *Neosebastes* (12), with 18 species (Motomura, 2004a). As noted by Motomura (2004a), Ishida (1994) inferred that his families Neosebastidae and Setarchidae had a sister relationship and were secondarily divided from other scorpaenids. Imamura (1996), however, suggested that *Setarches* was more closely related to *Pontinus* and *Scorpaena* (tribe Scorpaenini herein), *Neosebastes* being sister to a clade comprising a species of Tetraroginae, two genera of Synanceiinae, an Aploactinidae, and an Apistinae. Smith and Wheeler (2004), in a molecular analysis, showed that *Maxillicosta* and *Congiopodus* had a sister relationship. As Motomura (2004a) concluded, the systematic position and relationships of the family Neosebastidae (as he recognized it) still lacks an established basis. Imamura (2004) regarded this subfamily (at the family level) as sister to the Platycephaloidei (as given here) (see also Motomura et al., 2006).

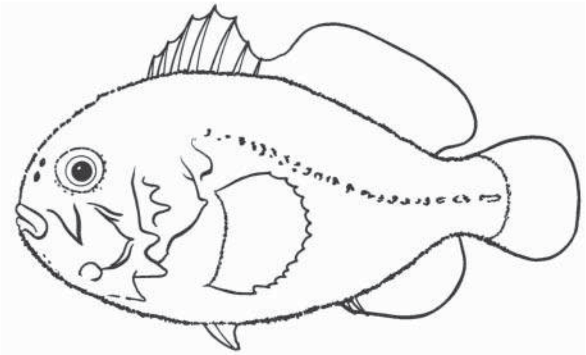
SUBFAMILY SCORPAENINAE. Twenty-two genera and about 211 species (Motomura et al., 2011).



TRIBE SCORPAENINI. At least 17 genera, *Hipposcorpaena* (1), *Hoplosebates* (1), *Idiastion* (3), *Iracundus* (1), *Neomerinthe* (14), *Neoscorpaena* (1), *Parascorpaena* (6), *Phenacoscorpius* (6), *Pogonoscorpius* (1), *Pontinus* (19), *Pteroidichthys* (3, synonym *Pteropelor), Rhinopias* (6), *Scorpaena* (61), *Scorpaenodes* (28), *Scorpaenopsis* (28), *Sebastapistes* (10), *Taenianotus* (1), *Thysanichthys* (1) with about 191 species (e.g., Randall and Eschmeyer, 2002; Randall and Greenfield, 2004; Motomura et al., 2006; Motomura and Last, 2009; Fricke et al., 2013).

TRIBE PTEROINI. Five genera, *Brachypterois* (1), *Dendrochirus* (5), *Ebosia* (2), *Parapterois* (2), and *Pterois* (10) (highly venomous lionfishes and turkeyfishes), with about 20 species (Matsunuma et al., 2013).

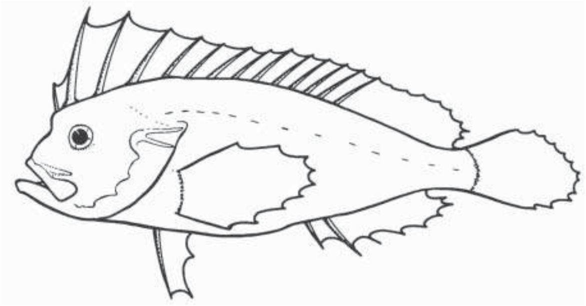
SUBFAMILY CARACANTHINAE (ORBICULAR VELVETFISHES OR CORAL CROUCHERS). Marine; Indian and Pacific, living among the branches of coral. Body oval, extremely compressed, and covered with small rough papillae; mouth small and terminal; one dorsal fin with a notch, origin on nape, with 6–8 spines and 11–14 soft rays; anal fin with 2 spines and 11–14 soft rays; pectoral fins with 12–15 rays; pelvic fins inconspicuous, with one spine and two or three small soft rays; gill openings restricted to sides; scales below the dorsal-fin base and on the dorsal surface of the head (the latter are minute and bear a single spine) and tube-like scales on the lateral line; vertebrae 24. Maximum length only 7 cm.



Classified as the family Caracanthidae by Nelson (1994, 2006), the small, distinctive, but rarely seen genus *Caracanthus* has been treated as a subfamily within Scorpaenidae by some (Shinohara and Imamura, 2005), as done here. There is some molecular evidence (e.g., Betancur-R. et al., 2013a) that it should be a tribe within Scorpaeninae, or even included within the tribe Scorpaenini. One genus, *Caracanthus*, with about four species.

SUBFAMILY APISTINAE. Three monotypic genera, *Apistops*, *Apistus*, and *Cheroscorpaena*. Members of this taxon have one or three free lower pectoral rays and a bilobed swimbladder.

SUBFAMILY TETRAROGINAE (SAILBACK SCORPIONFISHES OR WASP FISHES)

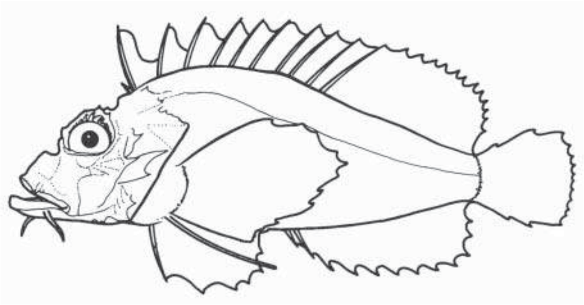


At least 17 genera, *Ablabys* (3, synonym *Amblyapistus*), *Centropogon* (3), *Gymnapistes* (1), *Coccotropsis* (1), *Cottapistus* (1), *Glyptauchen* (1), *Liocranium* (2), *Neocentropogon* (6), *Neovespicula* (1), *Notesthes* (1), *Ocosia* (7), *Paracentropogon* (4), *Pseudovespicula* (1), *Richardsonichthys* (1), *Snyderina* (2), *Tetraroge* (2), and *Vespicula* (3) with about 40 species. Tetrarogines are extremely venomous. They show some resemblance to the Aploactinidae. *Notesthes robusta* of coastal eastern Australia is primarily a freshwater fish (Motomura et al., 2008).

SUBFAMILY SYNANCEIINAE. Body scaleless (except for buried scales along the lateral line and other parts of the body), usually covered with skin glands; head large; swimbladder usually absent; venom glands present near base of hypodermic-like dorsal fin spines. The neurotoxin of these fishes is the most deadly of the fish venoms and can be fatal to humans. The fish is particularly dangerous because it usually rests in a half-buried position, looking much like a rock.

About nine genera and about 36 species.

TRIBE MINOINI. Lowermost ray of pectoral fin separated from the other 11 rays, fitted at its tip with a peculiar “cap”; body smooth; dorsal fin with 8–12 spines and 10–14 soft rays (4 spines and 18 soft rays in one species); anal fin with 2 spines and 7–11 soft rays; pelvic fin with 1 spine and 5 soft rays; soft fin rays unbranched; swimbladder present or absent; vertebrae 24–27. Maximum length usually 15 cm. Members of this group occur on mud and sand bottoms from about 10–420 m in the western Pacific and Indian oceans. They are thought to use the free pectoral ray for "walking" on the bottom.

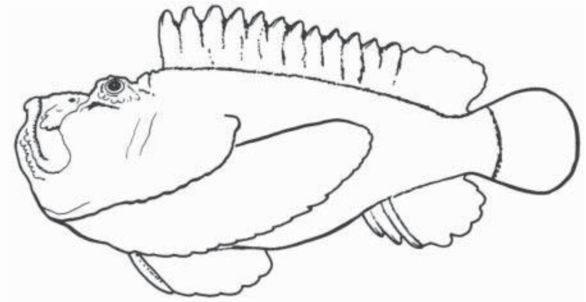


One genus, *Minous*, with 12 species.

TRIBE CHORIDACTYLINI. Two (*Inimicus*) or three (*Choridactylus*) lowermost pectoral rays separated from rest; body often with warts or lumps (caused by buried scales); dorsal fin with 12–18 spines and 5–10 soft rays; anal fin with two spines and 8–13 soft rays; pelvic fin with 1 spine and 5 soft rays; most soft fin rays branched; vertebrae 26–30. Members of this group occur on sand and silty bottoms from near shore to about 90 m in the western Pacific and Indian oceans. Imamura (2004) placed the two genera in separate subfamilies.

Two genera, *Inimicus* with 10 species and *Choridactylus* with four species (e.g., Poss and Mee, 1995).

TRIBE SYNANCEIINI *(*STONEFISHES*).* No free pectoral rays; skin glands present (appearing as "warts" in most species) and usually scattered over the body; dorsal fin with 11–17 spines and 4–14 soft rays; anal fin with 2–4 spines and 4–14 soft rays; pelvic fin with 1 spine and 3–5 soft rays; pectoral-fin rays 11–19; vertebrae 23–30.

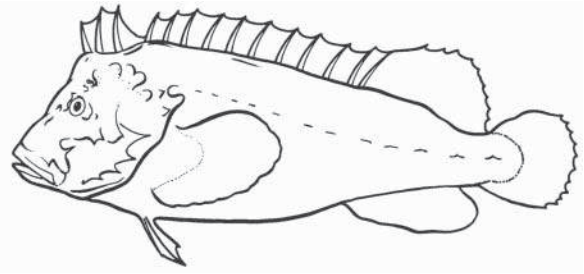


Two species, *Erosa erosa* (Japan to Australia) and *Dampierosa daruma* (north-western Australia), have a terminal mouth that is slightly oblique and lateral eyes that are directed outward. The remaining species have a vertical or superior mouth and dorsal eyes that are directed outward and upward or only upward. Some species are known from rivers.

Six genera, the monotypic *Erosa* (1), *Dampierosa* (1), *Pseudosynanceia* (1), *Leptosynanceia* (1), and *Trachicephalus* (1), and *Synanceia* (with five species), with a total of 10 species.

SUBFAMILY PLECTROGENIINAE. One genus, *Plectrogenium*, with two species. There is good evidence showing a relationship with the Platycephaloidei (Imamura, 1996, 2004).

Family APLOACTINIDAE (456)—velvetfishes. Marine; primarily coastal parts of western Pacific and Indian oceans.



Body usually covered with modified, prickly scales giving a velvety appearance (some species lack the prickles and have a smooth skin); head armed with knob-like lumps (rarely with pungent spines); all fin rays unbranched; anal-fin spines usually indistinct (rarely pungent) or absent; origin of dorsal fin far forward, above eye or almost so (except in *Adventor* and *Peristrominous*); anterior 3–5 dorsal-fin spines usually divergent, either elevated or largely devoid of connecting membrane; four species with three or four anterior spines forming a separate fin; pelvic fin with 1 spine and 2 or 3 soft rays; most species with fleshy extension on the anterior isthmus; palatine teeth absent; no gill slit behind the last arch; vertebrae 24–33. A species of the South China Sea, *Prosoproctus pataecus* is unique among scorpaenoid fishes in having the anus far forward, immediately behind the pelvic fin base. Most species occur in the Indonesian and Australian regions.

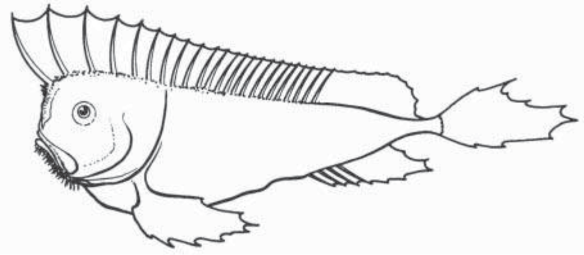
About 17 genera (e.g., *Acanthosphex* (1), *Adventor* (1), *Aploactis* (1), *Aploactisoma* (1), *Bathyaploactis* (2), *Cocotropus* (16), *Erisphex* (4), *Kanekonia* (3), *Matsubarichthys* (1), *Neoaploactis* (1), *Paraploactis* (7), *Peristrominous* (1), *Prosoproctus* (1), *Pseudopataecus* (2), *Ptarmus* (2), *Sthenopus* (1), and *Xenoploactis* (3) with about 48 species (e.g., Poss, 1999; Imamura and Shinohara, 2003). Three subfamilies are recognized by Mandrytsa (2001) and Imamura (2004), Aploactininae, Bathyaploactininae, and Matsubarichthyinae (Johnson, 2012).

Family ESCHMEYERIDAE (457)—cofishes. Marine; Fiji, Western Central Pacific.

Anterior end of isthmus without fleshy papillae; gill membranes not broadly united to isthmus; frontal and parietal bones strongly ossified; preorbital spines absent; anterior dorsal-fin spines short; scales absent except along lateral line; posteriomost base of caudal fin without spinous projections; pelvic fin membrane adnate to body, fused to membranes of opposite side; pectoral fin lacking a detached ray. Dorsal fin with 8 spines and 13 soft rays; 3 anal fins spines and 8 soft rays; 25 vertebrae (Poss and Springer, 1983).

Monotypic: *Eschmeyer nexus* Poss and Springer, 1983.

Family PATAECIDAE (458)—Australian prowfishes. Marine; Australia.

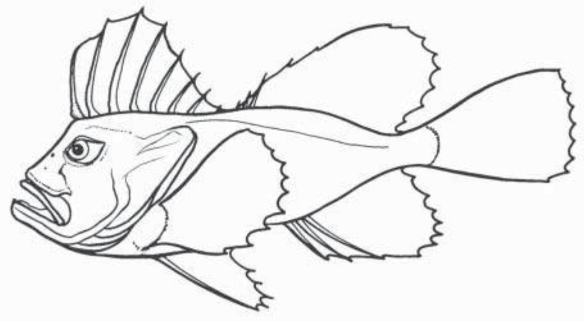


No pelvic fins; very long continuous dorsal fin extending from head to tail (connected with or free from caudal fin), with 19–25 spines and 7–17 soft rays; anal fin with 5–11 spines and 3–7 soft rays; pectoral fin with 8 rays; all fin rays unbranched; body scaleless (smooth or with tubercles or papillae); fleshy extension on the anterior isthmus; suborbital stay absent; vertebrae 34–44. Maximum length 30 cm. The modifier "Australian" has been added to the common name of the family in order to avoid confusion with the northern prowfish, a zaprorid.

Mandrytsa (2001) placed this family in the Perciformes, in its own suborder Pataecoidei.

Three genera, each probably monotypic, *Aetapcus*, *Neopataecus*, and *Pataecus*.

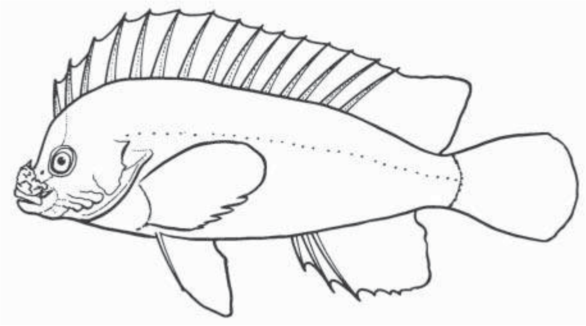
Family GNATHANACANTHIDAE (459)—red velvetfishes. Marine; southern Western Australia, South Australia, Victoria, and Tasmania.



Subrectangular fleshy pad in intermandibular area; pelvic fins present, with 1 spine and 5 soft rays; two separate dorsal fins of about equal length, the first with 7 spines, the second with 3 spines and 8–10 soft rays; anal fin with 3 spines and 8 or 9 soft rays; pectoral fin with 10–12 rays; body scaleless, with soft skin; 2 large spines on opercle, may be concealed by skin; vertebrae 28–30. The spines can inflict painful wounds. Maximum length 30 cm.

One species, *Gnathanacanthus goetzeei.*

Family CONGIOPODIDAE (460)—racehorses (pigfishes or horsefishes). Marine; Southern Hemisphere.



Snout relatively long; body without scales, skin sometimes granular; only one nostril on each side; gill opening reduced, above pectoral base; lateral line usually well developed; dorsal fins joined (separate in *Zanclorhynchus*), with 8–21 spines and 8–14 soft rays; anal fin with 0–3 spines and 5–10 soft rays; pectoral fin with 8–12 rays; vertebrae 28–39. Maximum length about 80 cm.

Species of this family tend to be benthic and occur up to 500 m in depth.

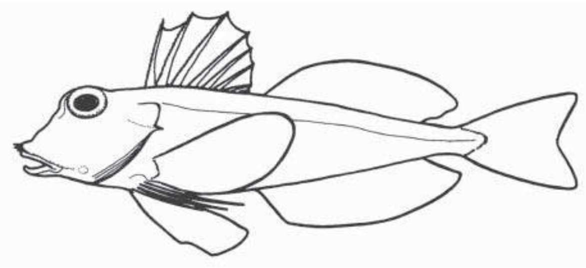
Mandrytsa (2001) placed *Alertichthys* and *Zanclorhynchus* in their own family, Zanclorhynchidae (placing Congiopodidae and Zanclorhynchidae in their own suborder Congiopodoidei). *Perryena* was placed in a new group (his Neocentropogoninae) in the Tetraroginae.

Four genera, *Congiopodus* with six species and the monotypic *Alertichthys*, *Perryena*, and *Zanclorhynchus*, with nine species (Ishii and Imamura, 2008).

Suborder Platycephaloidei. Body elongate; head depressed, usually with ridges and spines; two separate dorsal fins; pelvic fins widely separated, with 1 spine and usually 5 soft rays (as few as 3 in *Hoplichthys*); anal fin with 0, 1, or 3 spines and 5–18 soft rays; swimbladder present or absent; vertebrae 26 or 27. Imamura (1996) revised this taxon, but all suggestions have not yet been adopted.

Five families with 39 genera and about 273 species. The families Triglidae and Peristediidae are included in this lineage following Imamura (1996). See below under Bembridae for the possible recognition of two additional families, Parabembridae and Plectrogeniidae. This suborder is not recognized by Imurara (2004), and that study should be consulted for an alternative classification (see above under suborder Scorpaenoidei).

Family TRIGLIDAE (461)—searobins (gurnards). Marine; all tropical and temperate seas.



Mouth terminal or slightly inferior; head without barbels; preorbitals usually projecting forward; pectoral fin with lower three rays free and enlarged; barbels absent on lower jaw; two separate dorsal fins, the first with 7–11 spines and the second with 10–23 soft rays; anal fin with 0–1 spines and 11–23 soft rays; casque-like, bony head; lower two or three pectoral rays enlarged and free, used for detecting food; caudal fin with 9 or 10 branched rays; tip of snout usually with paired rostral (preorbital) projections, often bearing spines, giving the snout a bilobed appearance in dorsal view (especially pronounced in most peristediines); branchiostegal rays seven. Benthic habitat. Triglids are good sound producers. Maximum length up to 1 m.

Nine genera in three subfamilies with about 125 species (e.g., del Cerro and Lloris, 1997a, b; Richards and Jones, 2002; Richards and Miller, 2003; Richards et al., 2003).

SUBFAMILY PRIONOTINAE. Lateral line not bifurcate on caudal fin; Baudelot's ligament originates on skull; 26 vertebrae. Western Atlantic and eastern Pacific oceans (i.e., off Americas); most species in Atlantic.

Two genera, *Bellator* (8) and *Prionotus* (23), with 31 species.

SUBFAMILY PTERYGOTRIGLINAE. Two genera, *Pterygotrigla* (28, synonym *Parapterygotrigla*), *Bovitrigla* (1), with 29 species (Richards et al., 2003; Last and Richards, 2012).

SUBFAMILY TRIGLINAE. Five genera, *Chelidonichthys* (9, synonym *Aspitrigla) Eutrigla* (1), *Lepidotrigla* (53), *Trigla* (1), and *Trigloporus* (1) with about 65 species.

Family PERISTEDIIDAE (462)—armored searobins. Marine; found in deep water in the tropics of all oceans.

Body entirely encased by four rows of heavy spine-bearing plates on each side; mouth inferior; preorbitals each with a forward projection; pectoral fin with lower two rays free and enlarged; barbels on lower jaw.

Six genera, *Gargariscus (1)*, *Heminodus (1)*, *Paraheminodus* (4), *Peristedion* (23), *Satyrichthys* (7), and *Scalicus* (8) with about 44 species (e.g., Miller and Richards, 2003; Van Oijen et al. 2013).

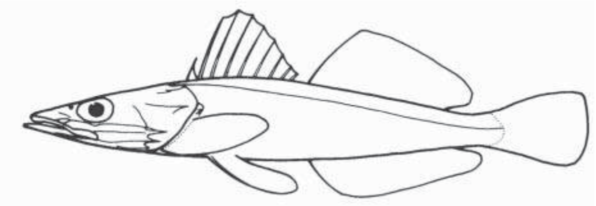
Family BEMBRIDAE (463)—deepwater flatheads. Marine; Indian and Pacific.

Head moderately to strongly depressed; pelvics below pectoral base; first dorsal fin with 6–12 spines and second dorsal fin with 8–12 soft rays; pectoral fin with 21–27 rays. Most are small, red, benthic fishes occurring from about 150–650 m.

The Indo-West Pacific *Parabembras,* with two species, is placed in its own family, Parabembridae, by Imamura (1996, 2004). *Bembradium* is aligned with *Plectrogenium* and placed in its own platycephaloid family Plectrogeniidae by Imamura (1996). Both *Parabembra* and *Bembradium* are provisionally retained here.

Five genera, *Bembradium* (2), *Bembradon* (1), *Bembras* (5), *Brachybembras* (1), and *Parabembras* (2, has been placed in its own family Parabembridae by some), with about 11 species (e.g., Imamura and Knapp, 1998).

Family PLATYCEPHALIDAE (464)—flatheads. Marine (some brackish); primarily Indo-Pacific.

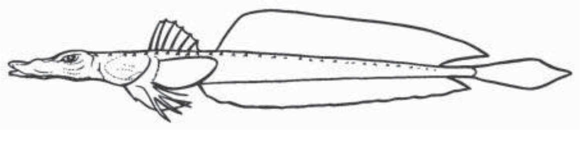


Head moderately to strongly depressed; pelvics behind pectoral base; first dorsal fin with 6–10 spines, first dorsal spine short and barely connected with rest of fin, and second dorsal fin with 11–15 soft rays; pectoral fin with 16–22 rays. Benthic habitat, often burying in the bottom, occurring from about 10–300 m. Maximum length about 1.1 m.

Solitas gruveli is the only species outside the Indo-Pacific, and it is in the eastern Atlantic off Africa. Two subfamilies are recognized by Imamura (1996), Platycephalalinae (for two genera) and Onigociinae.

About 18 genera (e.g., *Ambiserrula*, *Cociella*, *Elates*, *Grammoplites*, *Inegocia*, *Leviprora*, *Ratabulus*, *Papilloculiceps*, *Platycephalus*, *Rogadius*, *Solitas*, *Sorsogona*, *Suggrundus*, and *Thysanophrys*), with about 80 species (e.g., Knapp, 1996; Imamura 1996; Imamura and Knapp, 1999; Imamura 2012; Knapp, 2012).

Family HOPLICHTHYIDAE (465)—ghost flatheads. Marine; Indo-Pacific.



Body elongate; head extremely depressed and very wide, with spines and ridges; no scales, row of spiny scutes along side; lower pectoral rays (three or four) free; no anal spines; 26 vertebrae (8 + 18). Benthic, from about 10–1,500 m. Maximum length 43 cm. Winterbottom (1993) provided evidence of a possible (and unexpected) sister-group relationship of hoplichthyids to gobioids due to their sharing more apparently unique derived characters with that group than with any other taxon; this warrants further investigation.

One genus, *Hoplichthys*, with about 13 species (Nagano et al., 2012).

Suborder Normanichthyoidei. The relationships of the one included species, described by Clark (1937), are very uncertain. It was previously excluded from the Cottoidei, and this is supported by recent work (e.g., Yabe and Uyeno, 1996; Smith and Wheeler, 2004); but its relationships remain uncertain. Further comments are given in Nelson (1994).

Family NORMANICHTHYIDAE (466)—barehead scorpionfishes or mote sculpins. Marine; off Peru and Chile.

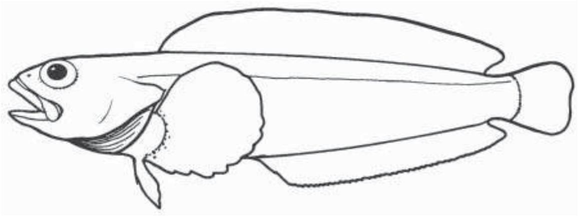
Body covered with ctenoid scales; head without armor; pelvic fin with one spine and five soft rays; ribs absent.

One species, *Normanichthys crockeri.*

Suborder Zoarcoidei. All have a single nostril, but there is no known diagnostic character or simple combination of characters that distinguishes this group from the other blenny-like perciforms. The monophyly of this taxon and most of its families is uncertain. The bathymasterids are still recognized as the most primitive family. Hilton (2009), Hilton and Kley (2005), Hilton and Stevenson (2013), and Schnell and Hilton (2015) have published on the osteology of various zoarcoid families.

The ten included families with 109 genera and 405 species occur primarily in the North Pacific. All species are marine.

Family BATHYMASTERIDAE (467)—ronquils. Marine coastal; North Pacific.



Dorsal fins continuous, usually with 41–48 rays, unbranched and branched; anal fin usually with 30–36 rays; pectoral-fin base vertical; lateral line high, ending near end of dorsal fin; palate with teeth; vertebrae 46–55. Maximum length for *Bathymaster signatus*˜about 38 cm TL.

Three genera, *Bathymaster* (4), *Rathbunella* (2), and *Ronquilus* (1), and seven species (Mecklenburg, 2003).

Family EULOPHIIDAE (468)—eulophiids. Marine coastal; North Pacific, off Korea and Japan.

Body very slender and very elongate; dorsal fin with many spines and few soft rays.

One genus *Eulophias* with three species (e.g. Kwun and Kim, 2012, 2013; Yamanaka et al., 2012).

Family ZOARCIDAE (469)—eelpouts. Marine, usually benthic; Arctic to Antarctic.

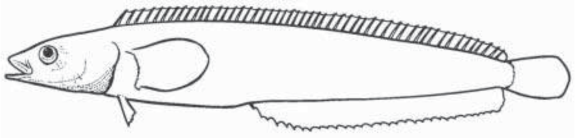
Body elongate; dorsal and anal fins long and confluent with caudal fin; mouth subterminal to terminal; pelvics, when present, small and in front of pectorals, jugular (in *Derepodichthys* the erectile pelvic fins are beneath the eyes); scales very small and embedded or absent; gill membranes joined to isthmus; swimbladder absent; vertebrae 58–150. The three species of *Zoarces* are ovoviviparous (not truly viviparous), and the other zoarcids are oviparous, some showing parental care. Length up to about 1.1 m, in *Macrozoarces americanus.*

The pelvic fins have been lost independently in many zoarcid genera. The genera *Parabrotula* and *Leucobrotula*, placed in this family in Nelson (1984) and thought by some workers to be at least related to the zoarcids (but in their own family, Parabrotulidae), are placed in the order Ophidiiformes. Extensive work on this family has been done by M. E. Anderson.

Four subfamilies are recognized in Anderson (1994) and Anderson and Fedorov (2004): Lycozoarcinae (with *Lycozoarces regaini,* western North Pacific), Zoarcinae (*Zoarces* with 4 species, 2 in North Atlantic and 2 in western North Pacific), Gymnelinae (12 genera and 35 species, most in the North Pacific), and Lycodinae (32 genera and 120 species, in all oceans).

About 59 genera (*Aiakas* (2), *Andriashevia* (1), *Argentinolycus* (1), *Austrolycus* (1), *Barbapellis* (1), *Bellingshausenia* (1), *Bentartia* (1), *Bilabria* (2), *Bothrocara* (8), *Bothrocarina* (2), *Crossostomus* (2), *Dadyanos* (1), *Davidijordania* (5), *Derepodichthys* (1), *Dieidolycus* (3), *Ericandersonia* (1), *Eucryphycus* (1), *Exechodontes* (1), *Gosztonyia* (1), *Gymnelopsis* (5), *Gymnelus* (12), *Hadropareia* (2), *Hadropogonichthys* (1), *Iluocoetes* (1), *Japonolycodes* (1), *Krusenterniella* (4), *Letholycus* (2), *Leucogrammolycus* (1), *Lycenchelys* (62), *Lycodapus* (13), *Lycodes* (64), *Lycodichthys* (2), *Lycodonus* (4), *Lycogrammoides* (1), *Lyconema* (1), *Lycozoarces* (1), *Magadanichthys* (1), *Maynea* (1), *Melanostigma* (7), *Nalbantichthys* (1), *Neozoarces* (2), *Notolycodes* (1), *Oidiphorus* (2), *Opaeophacus* (1), *Ophthalmolycus* (9), *Pachycara* (25), *Patagolycus* (1), *Phucocoetes* (1), *Piedrabuenia* (1), *Plesienchelys* (1), *Pogonolycus* (2), *Puzanovia* (2), *Pyrolycus* (2), *Santelmoa* (4), *Seleniolycus* (3), *Taranetzella* (1), *Thermarces* (3), and *Zoarces* (6), *Zoarchias* (6)), with about 294 species (Anderson, 1994; Anderson and Fedorov, 2004). The majority of species are in the North Pacific and North Atlantic; about 15 species are known from Arctic Canada, and at least 21 are known from the Antarctic and subantarctic. They are also known from temperate and tropical latitudes. (Biscoito and Almeida, 2004; Imamura et al., 2004; Shinohara et al., 2004; Stevenson and Anderson, 2005; Shinohara and Shirai, 2005; Anderson and Mincarone, 2006; Møller and Stewart, 2006; Shinohara and Sakurai, 2006; Stevenson and Orr, 2006; Møller and King, 2007; Stefanni et al., 2007; Kodama et al., 2008; Mincarone and Anderson, 2008; Matallanas, 2009, 2011; Anderson et al., 2009; Stevenson and Sheiko, 2009, Anderson, 2012; Matallanas and Corbella, 2012).

Family STICHAEIDAE (470)—pricklebacks. Marine, intertidal zone to 250 m; primarily North Pacific, a few in North Atlantic.



At least some spinous rays in long dorsal fin (entirely spinous in most species), 22–127 spines and 0–82 soft rays; anal fin with 1–5 spines at origin followed by 20–102 soft rays; pelvic fin absent or with up to 1 spine and 4 branched rays; pectoral fin small to large; ribs present; distance from snout to anal origin usually equal to or less than distance from anal origin to caudal fin; lateral line absent or up to four per side.

Mecklenburg and Sheiko (2004), based on several studies of others, recognized six subfamilies: Stichaeinae, Opisthocentrinae, Lumpeninae, Chirolophinae, Xiphisterinae, and Neozoarcinae.

Thirty-five genera, *Acantholumpenus* (1), *Alectrias* (6), *Alectridium* (1), *Anisarchus* (2), *Anoplarchus* (2), *Askoldia* (1, synonym *Ascoldia*), *Azygopterus* (1), *Bryozoichthys* (2), *Cebidichthys* (1), *Chirolophis* (8), *Dictyosoma* (3), *Ernogrammus* (3), *Esselenichthys* (2), *Eumesogrammus* (1), *Gymnoclinus* (1), *Kasatkia* (2), *Leptoclinus* (1), *Leptostichaeus* (1), *Lumpenella* (1), *Lumpenopsis* (4, synonym *Allolumpenus*), *Lumpenus* (3), *Neolumpenus* (1), *Opisthocentrus* (3), *Pholidapus* (1), *Phytichthys* (1), *Plagiogrammus* (1), *Plectobranchus* (1), *Poroclinus* (1), *Pseudalectrias* (1), *Soldatovia* (1), *Stichaeopsis* (2), *Stichaeus* (6), *Ulvaria* (1), *Xenolumpenus* (1), and *Xiphister* (2), with about 70 species (e.g., Mecklenburg and Sheiko, 2004; Shinohara and Yabe, 2009; Markevich and Kharin, 2011; Ji and Kim, 2012; Yamanaka et al., 2012)

Family CRYPTACANTHODIDAE (471)—wrymouths. Marine; northwest Atlantic and northern Pacific.

Pelvic fins absent (pelvic girdle present); mouth very oblique; dorsal and anal fins extending to caudal-fin base or confluent with caudal fin, dorsal fin with 60–80 spines and anal fin with 0–3 spines and 43–52 soft rays; lateral line obsolete; vertebrae 71–88.

One genus, *Cryptacanthodes* (synonyms *Cryptacanthoides*, *Delolepis*, and *Lyconectes*), with four species (Mecklenburg, 2003; Schnell and Hilton, 2014). The osteology of *Cryptacanthodes* was studied by Schnell and Hilton (2015).

Family PHOLIDAE (472)—gunnels. Marine; North Atlantic and North Pacific.

Dorsal fin with 75 to 100 spines, about twice as long as the anal fin; pectoral fins small or rudimentary, with 7–17 rays; pelvic fins rudimentary (1 spine and 1 soft ray) in most species or absent, along with pelvic girdle, in species of *Apodichthys* and some specimens of *Pholis fasciata*; vertebrae 80–107, centra asymmetrical;

ribs absent; distance from snout to anal origin usually more than distance from anal origin to caudal fin; lateral line short or absent.

Gunnels are small littoral fishes that, like some pricklebacks, are often found under rocks or in tide pools at low tide.

Four genera with about 15 species (Mecklenburg, 2003).

SUBFAMILY PHOLINAE. Body with pigmented patterns (bars, blotches, or spots). Most are North Pacific, a few North Atlantic.

One genus, *Pholis* (synonym *Allopholis*), with about 11 species.

SUBFAMILY APODICHTHYINAE. Body color relatively uniform (e.g., dark brown, green, or red). North Pacific.

Three genera, *Apodichthys* with two species off the North American coast, the monotypic *Rhodymenichthys* from Japan, and the monotypic *Ulvicola* from the Eastern Pacific from Central California to Baja California.

Family ANARHICHADIDAE (473)—wolffishes. Marine; North Atlantic and North Pacific.

Body naked or with minute cycloid scales; lateral line faint, with one or two branches anteriorly or absent; gill membranes attached to isthmus; dorsal fin with spines only; pectoral fins large; pelvic fins absent (rudiments of girdle retained); caudal fin small or pointed; jaws with strong conical canines anteriorly and with large molariform teeth laterally; vertebrae 72–89 to more than 250. Maximum length about 2.5 m.

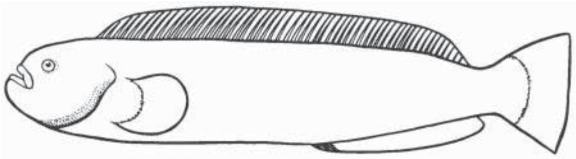
Two genera, *Anarhichas* with about four species (North Atlantic and Pacific) and *Anarrhichthys ocellatus* (Alaska to California) (Mecklenburg, 2003), with five species.

Family PTILICHTHYIDAE (474)—quillfishes. Marine; Pacific North America (Puget Sound to northwestern Alaska).

Body extremely elongate and slender; caudal fin absent; pelvics absent; body naked; dorsal fin with 90 isolated low spines and 137–145 high soft rays; anal fin with 185–196 high soft rays; no lateral line; vertebrae about 222–240. Maximum length 33 cm. The osteology of the sole species was studied by Hilton and Kley (2005).

One species, *Ptilichthys goodei* (e.g., Mecklenburg, 2003).

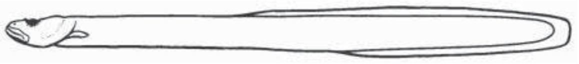
Family ZAPRORIDAE (475)—prowfishes. Marine; North Pacific (California to Alaska and Hokkaido).



No pelvic fins; gill membranes united; small cycloid scales on body; no lateral line; pectoral rays 24 or 25; dorsal fin long, with 54–57 spines; anal fin short, with three weak spines and 24–27 soft rays; large pores on head; vertebrae 61 or 62 (24–26 abdominal); pyloric caeca about 36—77; vertebrae 61–64. Maximum length 88 cm. The osteology of the sole species was studied by Hilton and Stevenson (2013).

One species, *Zaprora silenus* (e.g., Mecklenburg, 2003).

Family SCYTALINIDAE (476)—graveldivers. Marine; Pacific coast North America (southern California to northwestern Alaska).



No pelvic fins; gill membranes united; eyes very small and placed high on head; no scales; no lateral line; dorsal and anal fins on posterior half of back and confluent with caudal fin; vertebrae 69–71. Maximum length 15 cm. The osteology of this species was studied by Hilton (2009).

One species, *Scytalina cerdale* (e.g., Mecklenburg, 2003; Hilton, 2009).

Suborder Gasterosteoidei—sticklebacks. Upper jaw protractile, ascending process of premaxilla well developed; body often with armor of dermal plates; paired pelvic plates arising from a membranous outgrowth of the pelvic girdle; lateral body plates, when present, are represented by a single series of lateral and dermal ossifications; unpaired body plates in the dorsal and ventral series are formed from expanded proximal middle radials of dorsal and anal fin pterygiphores; during development, separate pectoral radials do not develop, and the pectoral radial plate fuses as a single unit to the scapulocoracoid; mouth usually small; branchiostegal rays 1–5; postcleithrum absent; pelvic girdle never attached directly to the cleithra; supramaxilla, orbitosphenoid, and basisphenoid absent; circumorbital bones, in addition to lachrymal, present; nasals and parietals present; anterior vertebrae not elongate; kidneys produce a glue-like substance used by males to construct a nest of plant material (condition in some species unknown); supracleithrum absent in *Aulorhynchus*, *Spinachia*, and *Gasterosteus wheatlandi.*

See Britz and Johnson (2002) for an in-depth study of the complex origin of the dermal plates of gasterosteoids and developmental characters listed above; see also Wiley and Johnson (2010). Lees et al. (2011) described the morphology and microstructure of dermal plates in several gasterosteids.

Many species are restricted to fresh water and many others are found in brackish water and able to enter either fresh or marine water.

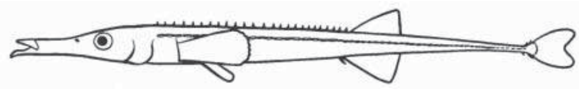
Four families, nine genera, and about 24 species (see comment on number of species under Gasterosteidae) (e.g., Bowne, 1994; Kawahara et al., 2008; Kawahara et al., 2009).

Family HYPOPTYCHIDAE (477)—sand eel. Marine; Japan and Korea to Sea of Okhotsk.

Body elongate, scutes and scales absent; spines absent; dorsal and anal fins posteriorly placed, each with about 20 soft rays; pelvic girdle and fins absent; pectoral-fin rays nine; caudal fin with 13 principal rays (11 branched); four branchiostegal rays; circumorbital ring incomplete; premaxillary teeth present in males but absent in females; about 29 pairs of pleural ribs, epipleurals absent; vertebrae about 55–57; hypural plate divided into upper and lower halves (all other gasterosteioids have a fused hypural plate except *Gasterosteus*, which also has a split hypural). Maximum length about 8.5 cm.

One genus and one species, *Hypoptychus dybowskii*.

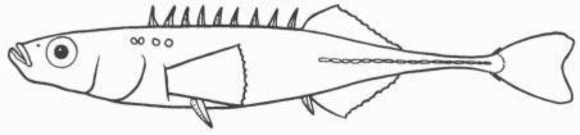
Family AULORHYNCHIDAE (478)—tubesnouts. Coastal marine; North Pacific.



Body elongate, with lateral bony scutes; series of 24–26 very short isolated dorsal spines, followed by a normal dorsal fin with about 10 soft rays; pelvic fin with 1 spine and 4 soft rays; caudal fin with 13 rays; 4 branchiostegal rays; circumorbital ring complete posteriorly; epineurals 0–3 (Johnson and Patterson, 1993, note that the epipleurals of acanthomorphs, except for *Polymixia*, are epineurals); vertebrae 52–56. Adult males of *Aulichthys* have a well-developed urogenital papilla. Maximum length 17 cm, attained in *Aulorhynchus flavidus*.

Two genera and two species, *Aulichthys japonicus* from Japan and Korea and *Aulorhynchus flavidus* from Alaska to California.

Family GASTEROSTEIDAE (479)—sticklebacks. Marine, brackish, and freshwater; Northern Hemisphere.



Body elongate or not, with lateral bony scutes (plates) or naked; series of 3–16 well-developed isolated dorsal spines (very rarely fewer than 3) followed by a normal dorsal fin with 6–14 rays; pelvic fin (rarely absent) with 1 spine and 1 or 2 soft rays; caudal fin usually with 12 rays; 3 branchiostegal rays; circumorbital ring incomplete posteriorly; epineurals present; vertebrae 28–42. Maximum length about 18 cm, attained in *Spinachia spinachia*. Parental care is given by the males of all species. A high proportion of individuals of three species in certain localities fail to develop the pelvic skeleton.

This family is famous for the numerous studies made of its species, especially in the fields of evolution, genetics, ethology, and physiology (e.g., Bell and Foster, 1994).

The recognition of 18 species in this family fails to account for the enormous diversity that exists. There are many taxonomic problems in the *Gasterosteus aculeatus* species complex and the *Pungitius pungitius* species complex.

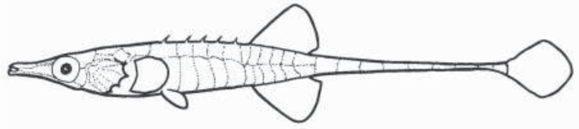
In the *Gasterosteus aculeatus* complex, the problems are partly because of extensive phenotypic variation. Some very exciting problems deal with sympatric pairs of *Gasterosteus* in British Columbia, studied in detail by McPhail, diversity in forms in nearby localities and evolutionary studies on plate variation (e.g., cyclical variation) over many years by Reimchen and Bell (see Nelson et al., 2004:220, for references). Three species have forms with and without the pelvic girdle occurring in sympatry (e.g., *Culaea* in Alberta documented by Nelson, 1969).

Five genera with, as a conservative figure (including species complexes), at least eighteen species: *Spinachia spinachia* (Fifteenspine Stickleback), marine, Atlantic of northern Europe; *Apeltes quadracus* (Fourspine Stickleback), usually marine and brackish water, Atlantic coast of central North America; *Gasterosteus wheatlandi* (Blackspotted Stickleback), usually marine, Atlantic coast of central North America; *Gasterosteus aculeatus* complex (Threespine Stickleback), marine, anadromous, and freshwater, Atlantic and Pacific coastal areas of North America (specimens have been taken in the open North Pacific) and Eurasia and part of Arctic, seldom above 100 m elevation; *Pungitius pungitius* complex (Ninespine Stickleback), diadromous and freshwater, Atlantic, Pacific, and Arctic coastal areas of North America and Eurasia and across much of above continental areas up to about 600 m; *Pungitius platygaster*, primarily in the Black Sea to Aral Sea area; *Pungitius hellenicus* in Greece; *Culaea inconstans* (Brook Stickleback), freshwater, North America.

Recent taxonomic studies include those by Keivany and Nelson (2000, 2004), McLennan and Mattern (2001), Mattern and McLennan (2004), Malhi et al. (2006), Kawahara et al. (2008), Mäkinen and Merila (2008), and Kawahara et al. (2009).

Miocene *Gasterosteus* fossils are known from eastern Siberia and California. †*Gasterosteus kamoensis* is a Miocene three-spined stickleback from central Japan described by Nazarkin et al. (2013). Bell et al. (2006) studied evolutionary change in the North American Miocene fossil stickleback †*G. doryssus*. Bell also described a Miocene fossil occurrence of the extant Threespine Stickleback, *G. aculeatus*.

Family INDOSTOMIDAE (480)—armored sticklebacks. Freshwater; parts of Southeast Asia.



Body slender and covered with bony scutes; upper jaw not protrusible; opercle with five to seven spines; dorsal and anal fins each with six rays, usually five isolated spines preceding the dorsal fin; three pectoral radials; 22–24 pectoral-fin rays; pelvic fin with four soft rays, no spine; gill filaments lobate; subopercle minute and interopercle present; parietals absent; six branchiostegal rays; no ribs; usually 21 vertebrae; swimbladder physoclistic. Maximum known length about 3.3 cm SL.

The systematic placement of the family in the Gasterosteoidei follows the conclusions of Britz and Johnson (2002) in their detailed anatomical study, although recent molecular studies place them with synbranchiforms (e.g., Kawahara et al., 2008; Betancur-R. et al., 2013a). Britz and Johnson (2002) reviewed other, earlier proposals of relationships.

The first species, *Indostomus paradoxus,* was described in 1929 from Lake Indawgyi in Upper Myanmar.

One genus, *Indostomus,* and three species (Britz and Kottelat, 1999b).

Suborder Cottoidei. Yabe (1985) recognized two monophyletic lineages, ranked as superfamilies. Bogutskaya and Naseka (2004) recognized the subfamilies Cottinae, Cottocomephorinae (with three species in *Cottocomephorus* and *Paracottus*), Comephorinae, and Abyssocottinae (including *Batrachocottus* and *Cyphocottus*) in Cottidae.

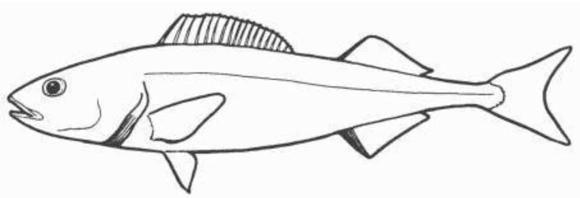
However, Smith and Wheeler (2004) in their molecular study, found that the Hexagrammidae, Liparidae, Cyclopteridae, and Psychrolutidae are monophyletic, but they did not corroborate the monophyly of the Cottidae, Hemitripteridae, or Agonidae as previously assumed. Based on the studies of Kontula et al. (2003), Sideleva (2003), Smith and Wheeler (2004), and Kinziger et al. (2005), all Lake Baikal sculpins are more closely related to some species of the Holarctic freshwater genus *Cottus* than to others. Kontula et al. (2003) also found strong support for the monophyly of the whole endemic Baikalian cottoid diversity.

Imamura et al. (2005) revised the classification of the Cottoidei and proposed recognition of six superfamilies. Smith and Busby (2014) analyzed molecular and morphological data to produce a phylogeny with six families in the Cottoidei: Agonidae, Cottidae, Jordaniidae, Psychrolutidae, Rhamphocottidae, and Scorpaenichthyidae. Close relatives of these, according to Smith and Busy (2014), are Liparidae, Cyclopteridae, Trichodontidae, Hexagrammidae, Zaniolepididae, and Anoplopomatidae. In the present work, cottoids and their close relatives are included as superfamilies within a more inclusive suborder Cottoidei.

Fifteen families with about 112 genera and 442 species.

Superfamily Anoplopomatoidea. One family (Imamura et al., 2005).

Family ANOPLOPOMATIDAE (481)—sablefishes. Marine; North Pacific.



Head without spines, ridges, or cirri; two dorsal fins, the second with 16–21 soft rays; anal fin with three weak spines and 11–19 soft rays; pelvic fins with

1 spine and 5 soft rays; two well-developed nostrils on each side; gill membranes attached to isthmus; lateral line single. Maximum length about 1.8 m, attained in *Erilepis zonifer* (the Skilfish).

Two genera and species (Mecklenburg, 2003), *Anoplopoma fimbria* (with well-separated dorsal fins and 17–30 spines in first dorsal) and *Erilepis zonifer* (with closely spaced dorsal fins and 12–14 spines in first dorsal). Both species range from Japan through the Bering Sea to California, although *E. zonifer* does not extend quite as far north or south as *A. fimbria.*

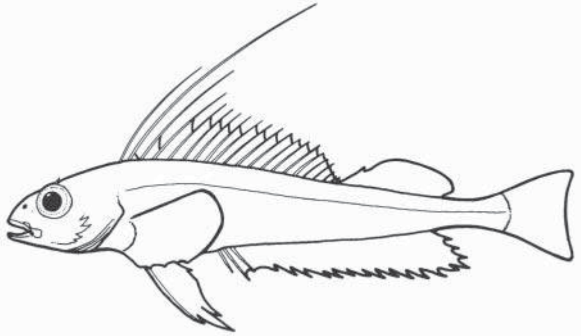
Superfamily Zaniolepidoidea. One family (Imamura et al., 2005), formerly a subfamily within Hexagrammidae (e.g., Nelson, 2006).

Family ZANIOLEPIDIDAE (482)—combfishes. Marine, eastern North Pacific from British Columbia to California.

Notch between 1st and 2nd dorsal fins; anal fin with 3–4 spines; caudal fin rounded or truncate; lateral line single, complete; scales ctenoid.

Following the phylogeny of Smith and Busby (2014), the Oxylebiinae are now a second subfamily in Zaniolepididae, as concluded on morphological grounds by Shinohara (1994).

SUBFAMILY ZANIOLEPIDINAE (COMBFISHES). Dorsal fin with deep notch in posterior third of fin; first three dorsal-fin spines very long, the second greatly prolonged in *Zaniolepis latipinnis*; anal fin with 3 spines; first two pelvic-fin rays thickened and long, extending past origin of anal fin; caudal fin truncated. Primarily benthic. Maximum length about 30 cm.



One genus with two species, *Zaniolepis frenata* and *Z. latipinnis.*

SUBFAMILY OXYLEBIINAE (PAINTED GREENLINGS). Body with 5–7 reddish vertical bars extending onto the fins; throat usually dark spotted; snout pointed; 2 pairs of cirri, one above eye and one midway between eye and origin of dorsal fin; dorsal fin divided by a shallow notch; anal fin usually with 3–4 large spines, of which the second is longest; caudal fin rounded; scales covering the head; one lateral line. Length up to 15 cm.

One species, *Oxylebius pictus*, of eastern Pacific from Alaska and British Columbia to Baja California.

Superfamily Hexagrammoidea. One family (Imamura et al., 2005).

Family HEXAGRAMMIDAE (483)—greenlings. Marine; North Pacific.

Head with cirri but without ridges or spines; lateral lines one or five; scales cycloid or ctenoid; one dorsal fin (but with a notch) with 16–28 spines and 11–30 soft rays; pelvic fin with 1 spine and 5 soft rays; well-developed anterior nostril on each side, posterior nostril (if present) reduced to a small pore; anal fin with 0–3 spines followed by soft rays; 6 or 7 branchiostegal rays; swimbladder absent; vertebrae 36–63. Maximum length up to 1.5 m, attained in *Ophiodon elongatus*; most other species less than 45 cm.

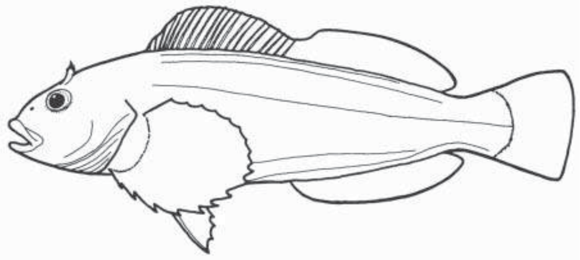
Although small, this is the most speciose family endemic to the North Pacific. Most species are primarily littoral.

Three subfamilies, three genera, and 9 species (Mecklenburg and Eschmeyer, 2003). Nelson (1994) gave references for the basis of this classification. Shinohara (1994) should be consulted for its study of comparative morphology and phylogeny. Smith and Busby (2014) gave evidence for removal of *Oxylebias* to Zaniolepididae.

Subfamily Ophiodontinae (lingcods). Dorsal fin divided into two parts by a deep notch, first portion with 24–28 spines and second portion with 20–24 soft rays; anal fin with 3 nonsegmented rays and 21–25 soft rays; head not covered with scales; only member with cycloid scales on body, others may have cycloid scales on head; caudal fin truncate or slightly emarginate; single lateral line; mouth large; jaws with small teeth interspersed with large fang-like teeth; feeds primarily on fishes, crustaceans, and squids and is extremely voracious; 57–59 vertebrae.

One species, *Ophiodon elongatus* (Lingcod), of eastern Pacific from southern Alaska to northern Mexico.

Subfamily Hexagramminae (greenlings). Dorsal fin divided approximately in the middle by a notch into an anterior spinous portion and a posterior soft portion; anal fin without spines; head covered with scales; caudal fin rounded, truncate, or slightly emarginate; no large ridges on skull; single lateral line (in the one species of the subgenus *Agrammus*, *H. agrammus* of Japan, Korea, and North China) or five (some may be short); vertebrae 47–57.



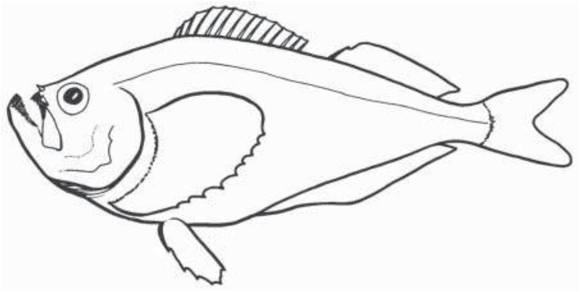
One genus, *Hexagrammos*, with six species, from western and eastern coasts of the North Pacific (south to Japan and northern Mexico).

Subfamily Pleurogramminae (atka mackerels). Dorsal fin without a notch but with 21–24 spines and 24–30 soft rays; anal fin usually without a spine and with 23–32 soft rays; scales partly covering head; caudal fin forked; strongly developed ridges on upper surface of skull; five lateral lines on body; vertebrae 59–62. Primarily pelagic.

Two species of *Pleurogrammus* (Atka mackerels) in the northern Pacific from northern Japan to Alaska (rarely south to California).

Superfamily Trichodontoidea. This superfamily was named by Imamura et al. (2005) to contain the Trichodontidae, formerly classified within Trachinoidei (e.g., Nelson, 2006).

Family TRICHODONTIDAE (484)—sandfishes. Marine; North Pacific.



Mouth nearly vertical, with fringed lips; suborbital stay lost; lachrymal-palatine articulation lost; pharyngobranchial one present; preopercle with five sharp spines; body scaleless; two dorsal fins, separated, the first with 8–16 spines and the second with 0–1 spine and 12–20 soft rays; anal fin with 0–1 spine and 28–32 soft rays; vertebrae 44–52. Normal habitat is lying partly buried in the bottom. Maximum length about 30.5 cm TL.

Evidence of monophyly with character support was provided by Smith and Busby (2014). Two genera with two species, *Arctoscopus japonicus* (Alaska to Korea) and *Trichodon trichodon* (northern California to Alaska) (Mecklenburg, 2003).

Superfamily Cottoidea. Basisphenoid absent; intercalar present, small and not contacting the prootic; scapula not attached to coracoid; hypurapophysis absent.

This superfamily is equivalent to the suborder Cottoidei of Smith and Busby (2014).

Seven families, 94 genera and about 387 species.

Family JORDANIIDAE (485)—longfin sculpin. Marine; Eastern Pacific, Canada to Southern California.

Pharyngobranchial one present; pelvic rays five; body and anal fin long; dorsal fins separated; gills reduced (Smith and Busby, 2014).

Monophyly and placement of this family are somewhat uncertain, though a position near the base of the cottoid radiation seems certain (Smith and Busby, 2014).

Perhaps two monotypic genera, *Paricelinus hopliticus*, maximum 20 cm TL, and *Jordania zonope*, maximum 15 cm TL.

Family RHAMPHOCOTTIDAE (EREUNIIDAE) (486)—grunt sculpins. Marine; North Pacific, Japan through Alaska to southern California.

Pharyngobranchial one present; several lower pectoral rays separated from upper pectoral-fin lobe and free of pectoral-fin membrane; dorsal and anal-fin stays present; caudal skeleton with all hypural and parhypural elements fused into a single complex element (Smith and Busby, 2014).

Ereunidae, previously a separate family (Nelson, 2006) are synonymized here with Rhamphocottidae following Smith and Busby (2014).

Rhamphocottus. Basioccipital-parasphenoid fossa present; pelvis highly modified, with an elongate subpelvic keel projecting forward and an anterodorsally projecting suprapelvic keel; four infraorbitals; palatine without teeth; six branchiostegal rays; all fin rays unbranched; first dorsal fin with 7–9 spines and second with 12–14 soft rays; anal fin with 6–8 soft rays; vertebrae 26–28. This is a very distinctive sculpin with its long head (head length is about half the standard length) and its elongate snout. Maximum length about 8 cm. One species, *Rhamphocottus richardsonii* (Mecklenburg, 2003).

Ereunias. Without the pelvic fin but with underlying pelvis and one vestigial spine present or absent; five rows of bony scales on body. Off south Japan. Monotypic.

Marukawichthys. With two species (pelvic fin present and with one spine and four soft rays; six rows on bony scales on body) from the Japan Sea and the Emperor Seamount Chain.

Family SCORPAENICHTHYIDAE (487)—Cabezon. Marine; off Western North America, northern British Columbia to southern California. Maximum length about 99 cm, weight up to 14 kg.

Head large; mouth broad; scales absent; caudal fin slightly rounded; dorsal spines 8–12; dorsal soft rays 15–18; anal spines 0; anal soft rays 11–13; vertebrae 35; color sexually dimorphic (females usually green, males usually red).

Placement as a near-basal cottoid lineage follows Smith and Busby (2014).

One monotypic genus: *Scorpaenichthys marmoratus.*

Family AGONIDAE (HEMITRIPTERIDAE) (488)—poachers and searavens. Marine; Arctic, northern North Atlantic, northwest Atlantic, North Pacific, and southern South America.

Body covered with bony plates and usually elongate; scales of larvae or pelagic juveniles modified into dermal spines; pelvic fins thoracic, with one spine and two soft rays; all fin rays unbranched; one or (usually) two dorsal fins, the first, when present, with 2–21 spines and second with 4–14 soft rays; anal fin with 4–28 soft rays; principal caudal-fin rays 10–12; 5 or 6 branchiostegal rays; basihyal rudimentary or absent; one or no tabular bones; predorsal bone absent; swimbladder absent; vertebrae 34–47. Maximum length about 30 cm.

Agonids range in depth from inshore shallow water to over 1,000 m. Most species occur in the North Pacific (extending south to Japan and northern Mexico). The following five species occur elsewhere: *Agonopsis chiloensis*—southern Chile and Argentina, including the Straits of Magellan and the Falkland Islands (the closest congeneric member of this remarkably disjunct species is in northern Mexico); *Agonus cataphractus*—Iceland, northeastern Atlantic, and adjacent Arctic; *Aspidophoroides monopterygius*—Arctic, northwestern Atlantic south to New York, and North Pacific south to Japan; *Leptagonus decagonus*—Arctic, northern Bering Sea, and northeastern and northwestern Atlantic; and *Ulcina olriki*—Arctic, northern Bering Sea, and northern northwestern Atlantic.

Eight subfamilies, 25 genera with 59 species (Sheiko and Mecklenburg, 2004, modified to include results of Smith and Busby, 2014).

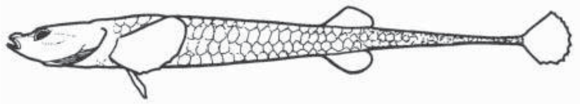
SUBFAMILY HEMILEPIDOTINAE. One genus, *Hemilepidotus* (6). Placement in Agonidae follows Smith and Busby (2014).

SUBFAMILY HEMITRIPTERIDAE. Three genera, *Blepsias* (2), *Hemitripterus* (3, with 1, the Sea Raven, in the Atlantic), and *Nautichthys* (3), with eight species (Mecklenburg, 2003).

SUBFAMILY BOTHRAGONINAE. One genus, *Bothragonus,* with two species.

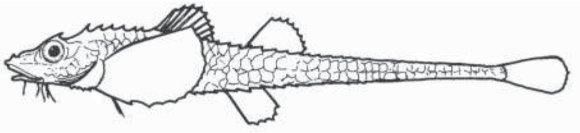
SUBFAMILY HYPSAGONINAE. Three genera, *Agonomalus* (3), *Hypsagonus* (2), and *Percis* (2), with seven species.

SUBFAMILY ANOPLAGONINAE. Two genera, *Anoplagonus* (2, in figure), and *Aspidophoroides* (1), with three species.



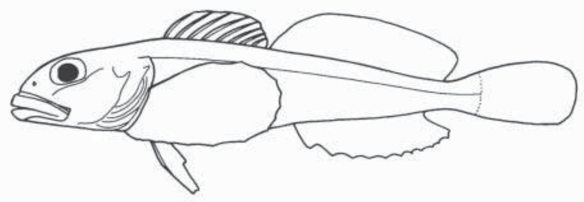
SUBFAMILY BRACHYOPSINAE. Six genera, *Brachyopsis* (1), *Chesnonia* (1), *Occella* (4), *Pallasina* (1), *Stellerina* (1), and *Tilesina* (1), with nine species.

Subfamily Agoninae. Six genera, *Agonopsis* (4), *Agonus* (1, in figure), *Freemanichthys* (1), *Leptagonus* (1), *Podothecus* (5), and *Sarritor* (3), with 15 species.



Subfamily Bathyagoninae. Three genera, *Bathyagonus* (4), *Odontopyxis* (1), and *Xeneretmus* (4), with nine species.

Family COTTIDAE (489)—sculpins. Marine and freshwater; Northern Hemisphere and eastern Australia, near New Guinea, and New Zealand.



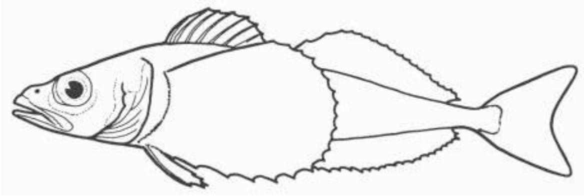
Body scales absent; branchiostegal membranes fused to isthmus; first proximal dorsal pterygiophores simple and slender in larvae; post-flexion larval body depth at pectoral-fin insertion moderate (Smith and Busby, 2014). The highly modified ctenoid scales and denticulated dermal bones of several cottids were studied by Märss et al. (2010b).

Most species are marine with the greatest diversity occurring along the North Pacific coastline. The only Southern Hemisphere cottids are four deep-water species of the genus *Antipodocottus* known from Australia, Kai Islands west of New Guinea, and New Zealand.

For comments on the placement of all Lake Baikal sculpins in Cottidae see above under suborder Cottoidei. We here recognize most of the Baikal sculpins in two subfamilies, with the remainder of the Baikal sculpins in the Cottinae.

Three subfamilies, 70 genera and about 282 species.

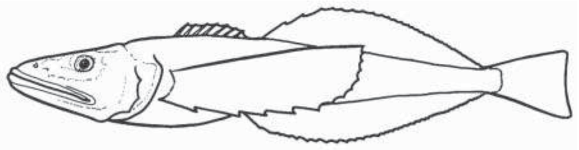
Subfamily Cottinae (sculpins). Body often appearing naked, commonly with scales or prickles (never completely encased in heavy bony armor); eye usually large and placed high on the head; lateral line present, single; pelvic fins (absent in one species) with 1 spine and 2–5 soft rays (usually 2 or 3 soft rays); no spines in anal fin; adults without swimbladder.



Many of the cottid nominal genera have been treated as subgenera of *Cottus*, and many of the genera are suggested to belong with Psychrolutidae (Smith and Busby, 2014), but we await a taxonomic revision of the two families including examination of types and formal synonymies.

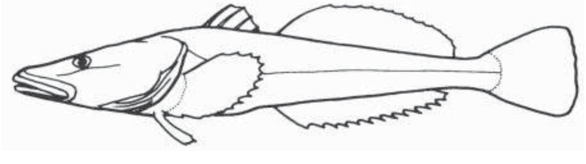
About 62 genera (e.g., *Alcichthys*, *Artediellus*, *Artedius*, *Ascelichthys* (lacks pelvics), *Asemichthys*, *Bero*, *Chitonotus*, *Clinocottus*, *Cottocomephorus* (lower figure, Lake Baikal, sometimes in family Cottocomephoridae), *Cottus*, *Enophrys*, *Furcina*, *Gymnocanthus*, *Icelinus*, *Icelus*, *Leptocottus*, *Micrenophrys*, *Myoxocephalus*, *Oligocottus*, *Pseudoblennius*, *Radulinus*, *Radulinopsis*, *Rastrinus*, *Ruscarius*, *Sigmistes*, *Synchirus*, *Taurulus*, *Trachidermis*, *Trichocottus*, *Triglops*, and *Vellitor*) with about 256 species (Kinziger et al., 2000; Yabe and Pietsch, 2003; Sideleva, 2003; Freyhof et al., 2005; Kinziger et al., 2005; Yokoyama and Goto, 2005; Ramon and Knope, 2008; Kai and Nakabl, 2009; Baumsteiger et al., 2012).

Subfamily Comephorinae (Baikal oilfishes). Freshwater pelagic; Lake Baikal, Siberia. Body naked; pectoral fins very long; no pelvic fins (pelvic bones present); postcleithra absent; body glassy-dull and translucent in living fish; body usually high in fat content; vertebrae 48–50; ovoviviparous. The lateral-line system on the head on these pelagic fishes consists of large cavities linked by narrow bony bridges with small external pores; the bone is porous. These adaptations that reduce the weight of the skeleton seem similar to that found in some psychrolutids. Maximum length about 20 cm.



One genus, *Comephorus*, with two species (Sideleva, 2003).

Subfamily Abyssocottinae (deepwater Baikal sculpins). Freshwater; primarily Lake Baikal, Siberia, generally below 170 m. Formerly a family in Nelson (2006). Postcleithra reduced or absent; dorsal fin with 3–10 spines and 10–21 soft rays; anal fin with 8–16 soft rays; pelvic fin with 1 spine and 2–4 soft rays; vertebrae 30–37 (see Sideleva, 1982:52–55, for a description of this family).



The sculpins in Lake Baikal are placed in three subfamilies: this subfamily, in the Comephorinae, and in the Cottinae.

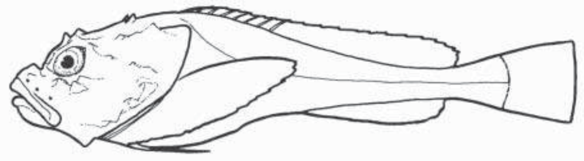
Seven genera, *Abyssocottus* (3), *Asprocottus* (8), *Cyphocottus* (2), *Cottinella* (1), *Limnocottus* (4), *Neocottus* (2), and *Procottus* (4), with about 24 species (Sideleva, 2003).

Family PSYCHROLUTIDAE (490)—fathead sculpins. Marine; Atlantic, Indian, and Pacific.

Body naked or with plates bearing prickles; interorbital space usually greater than exposed eye diameter (much smaller in *Malacocottus*); lateral line reduced, with 20 or fewer pores; pelvic fin with one spine and three soft rays; dorsal fins usually continuous with spinous dorsal, often partially hidden by skin (bases separate or nearly so in *Malacocottus* and *Dasycottus*); branchiostegal rays seven; prevomerine teeth present or absent, palatine teeth always absent; one or two postorbitals (if two, they are usually ring-like; cottids have two or three elongate postorbitals); system of well-developed bony arches, which may bear spines, on the cranium over the lateral-line system with wide intervening space; vertebrae 28–38. Maximum length about 65 cm, attained in *Psychrolutes paradoxus*. Psychrolutids range in depth from inshore shallow water (*P. sigalutes*) to up to about 2,800 m (*P. phrictus*).

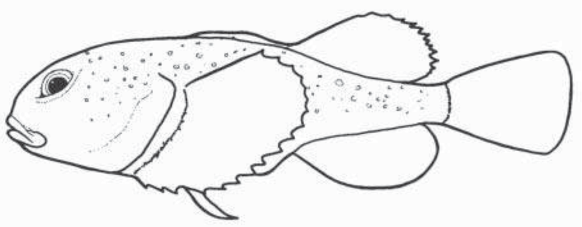
Two subfamilies (paraphyletic according to Jackson and Nelson, 1998) with eight genera and about 38 species (e.g., Nelson 1995; Jackson and Nelson, 1998, 1999, 2000). Both subfamilies have members in the Northern and Southern Hemispheres. Smith and Busby (2014) advocated transferring many marine members of the Cottidae to the Psychrolutidae.

SUBFAMILY COTTUNCULINAE. Head well ossified, interorbital margins hard, and head spines often present; relatively narrow interorbital area, width less than two times diameter of exposed eye; body and fins usually not of uniform color.



Five genera, *Ambophthalmos* (3), *Cottunculus* (8), *Dasycottus* (1), *Eurymen* (2), and *Malacocottus* (4) (Byrkjedal and Orlov, 2007).

SUBFAMILY PSYCHROLUTINAE. Head poorly ossified, interorbital margins soft, and head spines absent; wide interorbital area, width more than two times diameter of exposed eye; body and fins usually of uniform color.



Three genera, *Ebinania* (7), *Neophrynichthys* (2), and *Psychrolutes* (11, synonym *Gilbertidia*).

Family BATHYLUTICHTHYIDAE (491)—Antarctic sculpins. Marine; Antarctic Ocean (south Georgia Island).

Body naked; wide interorbital; one pair of long barbels on lower jaw at corner of mouth; single dorsal with anterior portion submerged under the skin, with 13 spines and 28 soft rays; anal fin with 36 rays; pelvic fin with 3 soft rays; all fin rays unbranched; teeth absent on vomer and palatines; branchiostegal rays seven; radials two; postcleithrum and pleural ribs absent; vertebrae 49.

Except for the elongate barbels and the caudal fin being joined with the dorsal and anal fins, the one known specimen (from 1,650 m) superficially looks like a *Psychrolutes*. The family was established with the description of the one species. Its phylogenetic position within the Cottoidei is uncertain.

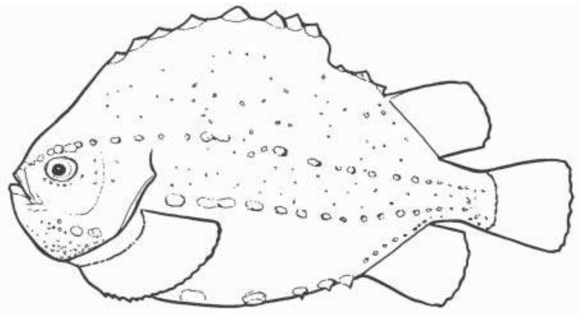
One species, *Bathylutichthys taranetzi*.

Superfamily Cyclopteroidea. Pelvic fins, when present, modified into a sucking disc, thoracic; vomerine teeth absent; lateral line usually absent; gill opening small. Able et al. (1984) described larval characters and presented comparative information on the two included taxa, the lumpfishes and the snailfishes. Märss et al. (2010a) compared the morphology and ultrastructure of the distinctive scales and other dermal ossicles in *Cyclopterus lumpus* and *Liparis liparis*.

Lumpfishes and snailfishes are thought to form a monophyletic group. However, most workers have recognized snailfishes in their own family, and this is followed here with monophyly of the group being expressed by the recognition of the superfamily Cyclopteroidea. Monophyly of the two families and their sister-group relationship were supported by Smith and Busby (2014).

Two families, 38 genera, and 434 species.

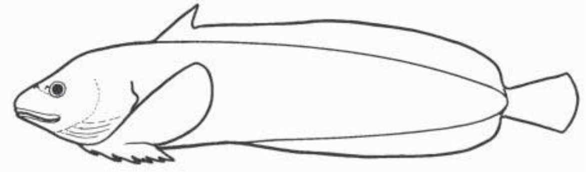
Family CYCLOPTERIDAE (492)—lumpfishes (lumpsuckers). Marine; cooler regions of the Northern Hemisphere.



Body globose, usually covered with tubercles; usually 2 short dorsal fins, the first with 4–8 spines (the spinous fin is beneath the skin in some species and not externally visible), the second with 8–13 soft rays, never confluent with caudal; anal fin short, with 7–13 soft rays; vertebrae about 23–29. Maximum length up to 60 cm.

About six genera, *Aptocyclus* (1, synonym *Pelagocyclus*), *Cyclopterus* (1), *Cyclopteropsis* (7), *Cyclopsis* (1), *Eumicrotremus* (15), and *Lethotremus* (2), and 27 species (Mecklenburg and Sheiko, 2003).

Family LIPARIDAE (Liparididae) (493)—snailfishes. Marine; Arctic to Antarctic.



Body elongate, scaleless (small prickles in some) and skin jelly-like; pharyngobranchial two lost; caudal-fin rays unbranched; dorsal fin (28–82 soft rays) and anal fin (24–76 soft rays) long, confluent, or nearly so, with caudal fin; pelvic fin (disc) absent in the 45 or more species of *Paraliparis* and in the monotypic *Nectoliparis*; nostrils single or paired (usually in *Liparis*); vertebrae 38–86. Maximum length about 80 cm.

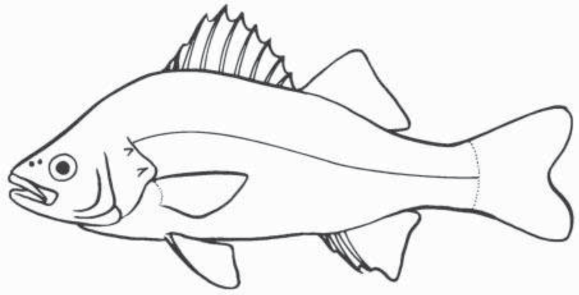
Snailfishes have an unusually wide geographic and habitat range. They occur from tide pools to depths of over 7,000 m. They are one of the most species-rich families of fishes in the Southern Ocean, the North Pacific, and the Arctic: they occur in the deep Indian Ocean, but only a few species are known from there (Chernova et al. 2004). They have also been found in the Galapagos Islands (Stein and Chernova 2002). As noted by Chernova et al. (2004), various subfamilies have been proposed (Paraliparidinae, Careproctinae, Rhodichthyinae, and Nectoliparidinae); they believe there is not enough information to support their use.

About 32 genera (e.g., *Acantholiparis*, *Careproctus*, *Crystallichthys*, *Elassodiscus*, *Eknomoliparis*, *Liparis*, *Lopholiparis*, *Nectoliparis*, *Notoliparis*, *Osteodiscus*, *Paraliparis*, *Polypera*, *Psednos*, *Rhodichthys*, *Temnocora*) with about 407 species (Andriashev, 2003; Stein and Chernova, 2002; Stein et al., 2001, 2003; Chernova et al., 2004; Orr, 2004; Stein, 2005; Orr and Busby, 2006; Knudsen et al., 2007; Baldwin and Orr, 2010; Stein, 2012a,b).

THE REMAINING SIX ORDERS OF TELEOSTS (Moroniformes, Acanthuriformes, Spariformes, Caproiformes, Lophiiformes, and Tetraodontiformes) are suggested to be part of a monophyletic group by Near et al. (2012a) and Betancur-R. et al. (2013a). The monophyly and relationships of all of these orders must be considered tentative because of low nodal support values for many subgroups and the need for increased taxon sampling, more focused analyses, and corroboration for many of the relationships from other data sources including morphology and paleontology. Additional families, linked with the above usually also with very low nodal support values, remain in the Perciformes in the present work, but their listings are annotated to indicate their putative new relationships.

Order MORONIFORMES (80)—temperate basses. This group of three families (Moronidae, Drepaneidae, and Ephippidae) has been suggested (e.g., Betancur-R. et al., 2013a) to be sister to all five of the remaining orders of teleosts. Smith and Craig (2007) had earlier recognized a suborder Moronoidei for a much broader assemblage of families.

Family MORONIDAE (494)—temperate basses. Brackish and freshwater and marine coastal areas; North America (Atlantic and Gulf of Mexico drainages, introduced elsewhere), Europe, and northern Africa.



Two dorsal fins, the first with 8–10 spines and the second with 1 spine and 10–13 soft rays; anal fin with 3 spines and 9–12 soft rays; opercle with 2 spines; lateral line extends almost to posterior margin of caudal fin; auxiliary row of lateral-line scales on the caudal fin above and below the main row; 7 branchiostegals; 25 vertebrae.

Williams et al. (2012) found a translocation in the mitochondrial *nd*6 gene that distinguishes *Morone* and *Dicentrarchus* from many other percomorphs, but they did not examine the other two families included here in Moroniformes.

Two genera, *Morone* (synonym *Roccus*) with four species from North America (two are confined to fresh water) (e.g., Heemstra, 2003a; Nelson et al., 2004; Liu et al., 2006; Williams et al., 2012), the closely related *Dicentrarchus* with two species from off Europe and North Africa, including the Mediterranean and Black seas and in coastal rivers. *Lateolabrax* is now in Polyprionidae.

Family DREPANEIDAE (495)—sicklefishes. Marine; Indo-West Pacific and West Africa.

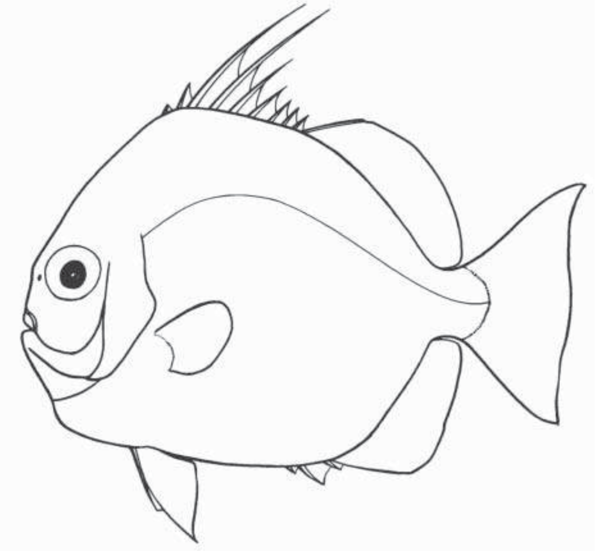
Dorsal fin with 13 or 14 spines and 19–22 soft rays; anal fin with 3 spines and 17–19 soft rays; mouth markedly protractile; pectoral fins longer than head, falcate; maxilla distally exposed; subocular shelf absent; 24 vertebrae. The recognition of this family for *Drepane* follows Johnson (1984), who placed it next to the Dichistiidae (= Coracinidae).

The spelling of this family name in previous editions was Drepanidae. As noted b Eschmeyer, 1998, Vol. 3:2889, Opinion 1046 of the ICZN required that it be Drepaneidae.

The Drepaneidae were suggested to belong to a clade with Moronidae and Ephippidae by Betancur-R. et al. (2013a), but see below for an earlier proposal by Tang et al. (1999) that it instead belongs within the suborder Acanthuroidei.

One genus, *Drepane*, with three species.

Family EPHIPPIDAE (496)—spadefishes. Marine (rarely in brackish water); Atlantic, Indian, and Pacific.



Comb-like series of large blunt gill rakers on first epibranchial; basihyal reduced or absent; interarcual cartilage absent; dorsal fin with 5 or 9 spines and 18–40 soft rays; 3 anal-fin spines and 15–28 soft rays; gill membranes united to isthmus; body deep and laterally compressed; mouth small; no teeth on vomer or palatines; spinous portion of dorsal fin distinct from soft-rayed portion (except in *Platax*, in which the young have very elongate dorsal and anal fins); 6 branchiostegals; 24 vertebrae. Young individuals may have black bands extending around the body that are lost with growth.

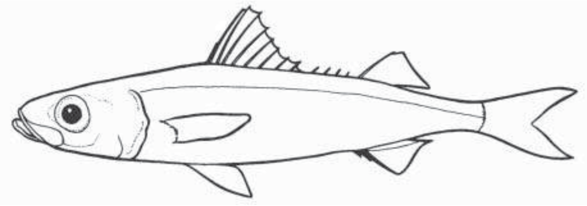
Johnson (1993) recognized seven genera in the family, which now includes eight with recognition of *Zabidius* as valid.

Eight genera, *Chaetodipterus* (3), *Ephippus* (2), *Parapsettus* (1), *Platax* (5), *Proteracanthus* (1), *Rhinoprenes* (1), *Tripterodon* (1), and *Zabidius* (1), with 15 species (e.g., Heemstra in Carpenter and Niem, 2001; Burgess, 2003).

Order ACANTHURIFORMES—(81) surgeonfishes and relatives. Eighteen families. This large and very diverse clade was recovered by Betancur-R. et al. (2013a) and by Near et al. (2012a) in their broad-scale molecular studies, with substantially similar internal relationships, although the latter study did not sample as many taxa as the former. Several of the families were in Percoidei (Nelson, 2006), although that position was often recognized as a default one owing to lack of evidence to the contrary. Additionally, several percoid families are putatively related to Acanthuriformes but remain in Percoidei in this edition with annotations about their putative relationships. Two suborders, Sciaenoidei and Acanthuroidei, are recognized.

Suborder Sciaenoidei. The following two families very tentatively form a clade separate from the Acanthuroidei according to Betancur-R. et al. (2013a).

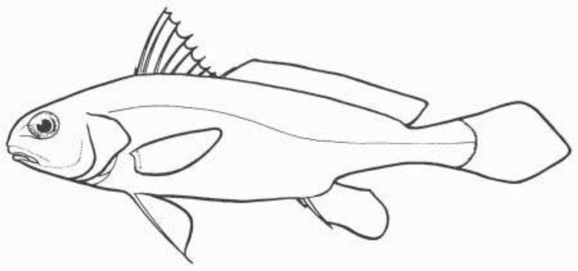
Family EMMELICHTHYIDAE (497)—rovers. Marine; primarily tropical to warm temperate regions of Indo-Pacific, southern Pacific, eastern Atlantic, and Caribbean Sea.



Jaws toothless or nearly so, very protractile; maxilla expanded distally, scaled, and not covered by preorbital bone when mouth closed; supramaxilla well developed; rostral cartilage large; dorsal fin continuous but with slight notch (*Plagiogeneion*), divided to base (*Erythrocles*), or with an apparent gap with intervening isolated short spines visible or not (*Emmelichthys*, as shown in figure); dorsal fin with 11–14 spines and 9–12 soft rays; anal fin with 3 spines and 9–11 soft rays; caudal fin forked with the two lobes folding in scissor-like fashion; seven branchiostegals; 24 vertebrae (10 + 14). Maximum length up to 50 cm. Adults are usually near the bottom in depths of 100–400 m.

Three genera, *Plagiogeneion* (5), *Emmelichthys* (6), and *Erythrocles* (6), with 17 species (Miyahara and Okamura, 1998; Heemstra, 2003b).

Family SCIAENIDAE (498)—drums (croakers). Marine, brackish, and freshwater (particularly in South America); Atlantic, Indian, and Pacific.



Dorsal fin long, with a deep notch separating spinous from soft portion (rarely separate), first with 6–13 spines and second with 1 spine and usually 20–35 soft rays; anal fin with 1 or 2 spines (both are usually weak but the second may be large) and 6–13 soft rays; lateral-line scales extending to the end of caudal fin; caudal fin slightly emarginate to rounded; upper bony edge of opercle forked, bony flap present above gill opening; single barbel or a patch of small barbels on chin of some species; head with large cavernous canals (part of the lateral-line system); conspicuous pores on snout and lower jaw; vomer and palatine without teeth; swimbladder (rarely rudimentary in adults) usually with many branches; otoliths (sagitta at least) exceptionally large; vertebrae 24–30.

Sciaenids can produce sound by using the swimbladder as a resonating chamber. Some are important food fishes. They occur in shallow water, usually near continental regions, and are absent from islands in the mid-Indian and Pacific oceans. Several marine species enter estuaries, and about 28 species are restricted to fresh water (Atlantic drainages) in the Americas. The freshwater members are *Aplodinotus grunniens*, extending from southern Saskatchewan and Quebec to Guatemala, and species of *Pachypops*, *Pachyurus*, and *Plagioscion* (enters estuaries), in South America. This very large family was revised by Sasaki (1989), based on morphology, to include 10 subfamilies.

About 67 genera (e.g., *Aplodinotus* (1), *Argyrosomus* (9), *Aspericorvina* (1), *Atractoscion* (2), *Atrobucca* (10), *Austronibea* (1), *Bahaba* (3), *Bairdiella* (5), *Boesemania* (1), *Cheilotrema* (2), *Chrysochir* (1), *Cilus* (1), *Collichthys* (2), *Corvula* (3), *Ctenosciaena* (2), *Cynoscion* (25), *Daysciaena* (1), *Dendrophysa* (1), *Elattarchus* (1), *Equetus* (2), *Genyonemus* (1), *Isopisthus* (2), *Johnius* (34), *Kathala* (1), *Larimichthys* (3), *Larimus* (6), *Leiostomus* (1), *Lonchurus* (2), *Macrodon* (3), *Macrospinosa* (1), *Megalonibea* (1), *Menticirrhus* (9), *Micropogonias* (6), *Miichthys* (1), *Miracorvina* (1), *Nebris* (2), *Nibea* (10), *Odontoscion* (3), *Ophioscion* (10), *Otolithes* (2), *Otolithoides* (2), *Pachypops* (3), *Pachyurus* (10), *Panna* (1), *Paralonchurus* (6), *Paranibea* (1), *Paranebris* (1), *Pareques* (7), *Pennahia* (5), *Pentheroscion* (1), *Petilipinnis* (1), *Plagioscion* (7), *Pogonias* (1), *Protonibea* (1), *Protosciaena* (2), *Pseudotolithus* (6), *Pteroscion* (1), *Pterotolithus* (2), *Robaloscion* (2), *Roncador* (1), *Sciaena* (2), *Sciaenops* (1), *Seriphus* (1), *Sonorolux* (1), *Stellifer* (24), *Totoaba* (1), and *Umbrina* (17)) with 283 species (e.g., Sasaki, 1989; Schwarzhans, 1993; Chao et al., 2001; Bortone, 2002; Chao, 2003; Casatti, 2005; Vergara-Chen et al., 2009; Iwatsuki et al., 2012; Béarez and Schwarzhans, 2013; Santos et al., 2013;).

Suborder Acanthuroidei. Gill membranes broadly united at the isthmus, restricting the branchial aperture ventrally; premaxillae nonprotrusible or only slightly so; frontal and supraoccipital bones cancellous in most; interarcual cartilage absent; body deeply compressed; mouth small.

Monophyly of the suborder Acanthuroidei and sequencing of the families were recognized in Nelson (2006) following the classical works of Tyler et al. (1989) and Winterbottom (1993), subsequently supported by Tyler and Sorbini (1999). Tang et al. (1999) largely agreed although there was some disparity between the molecular and morphological evidence. Tyler et al. (1989) demonstrated, based largely on larval characters, that the single living species of the very different appearing *Luvarus* (family Luvaridae) was a member of this suborder; this species, *L. imperialis,* had previously been placed among the carangoids or scombroids, the latter as in Nelson (1984). Tang et al. (1999) concluded that *Drepane* belongs within this suborder, but it is recognized here in the Moroniformes (see above), in the family Drepaneidae. They further suggested *Zanclus* to be nested within the acanthurids, but that was not supported by Betancur-R. et al. (2013a).

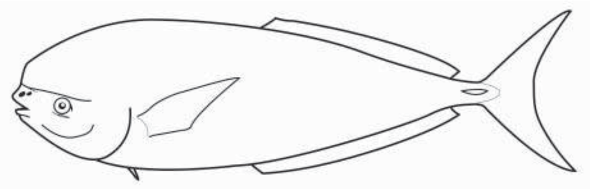
Based on the results of Holcroft and Wiley (2008) and Betancur-R. et al. (2013a), we recognize only a core group of three families in the order: Luvaridae, Zanclidae, and Acanthuridae. Drepaneidae, Siganidae, Ephippidae, and

Scatophagidae have been included at times, but molecular evidence puts them elsewhere.

Almost all species are herbivorous, feeding mostly on algae. The Acanthuridae pass through a planktonic larval stage, termed the acronurus stage, in which their bodies are transparent and have vertically elongate scales. Acanthuroids usually also have a large swimbladder, lunate caudal fin, five branchiostegals, and 22 or 23 vertebrae.

Three families, 8 genera, and 84 species (e.g., Holcroft and Wiley, 2008; Hubert et al., 2010).

Family LUVARIDAE (499)—louvar. Marine, tropical to warm temperate, pelagic; world-wide.



Body strongly compressed with slender keeled caudal peduncle; upper jaw not protrusible and mouth very small; groove running above eye; anus well forward, approximately beneath pectoral-fin base. Adults with dorsal and anal fins each with about 14 rays, in posterior half of body, 22 vertebrae. Juveniles with dorsal-fin origin well forward, fin initially with 2 spines and 20–22 soft rays, anterior ones lost with growth; anal fin with about 22 rays, lacking spines. Maximum length about 1.8 m TL.

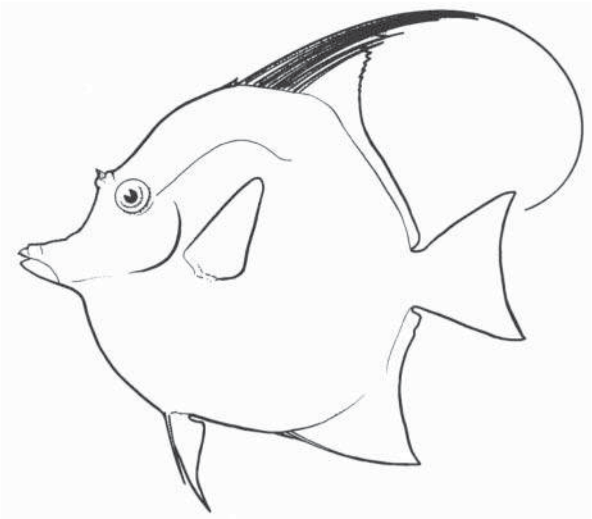
The osteology and metamorphosis of this species is described by Tyler et al. (1989); as noted above, the fin morphology of juveniles (up to about 20 cm) is very different from that of adults. They are reported to feed on jellyfishes, ctenophores, etc. These fish have an enormous egg production; a 1.7 m individual had an estimated 47.5 million eggs, characteristic of non-schooling oceanic fish. *Luvarus imperialis* is the only pelagic member of an otherwise shorefish group (Tyler et al., 1989).

Bannikov and Tyler (1995) revised the families Luvaridae (and described new Eocene fossils including the genus †*Avitoluvarus*; see also Bannikov and Tyler, 2001) and †Kushlukiidae (with the Eocene †*Kushlukia*) and found 10 synapomorphies showing that the two families are sister taxa (at the node between the siganid and zanclid + acanthurid clades).

One species, *Luvarus imperialis* (e.g., Bannikov and Tyler, 1995).

Family ZANCLIDAE (500)—Moorish Idols. Marine; tropical Indo-Pacific.

Tubular snout with a small mouth containing many elongate bristle-like teeth; dorsal-fin spines (6 or 7) elongated into a whip-like filament; caudal peduncle unarmed; spine at corner of mouth in juveniles and protuberances in front of eyes in adults.



The Moorish Idol is most commonly found in coral-reef areas. The extended snout in the adult is well suited for foraging for invertebrates and algae in small crevices. The broad vertical black bars on a largely whitish background and elongated dorsal fin filament make it a very attractive fish. The butterfly-fish, *Heniochus acuminatus*, another popular aquarium fish, and the Moorish Idol bear a marked resemblance to each other.

One species, *Zanclus cornutus* (synonym *Z. canescens*).

†Family MASSALONGIIDAE. Eocene of Monte Bolca, Italy. Tenth interneural space with one basal pterygiophore. This family was named by Tyler and Bannikov (2005) based on one fossil genus, †*Massalongius*. According to Tyler and Micklich (2011), Massalongiidae are the immediate outgroup of the Acanthuridae.

Family ACANTHURIDAE (501)—surgeonfishes. Marine; all tropical and subtropical seas (absent in Mediterranean).

Pelvic fins with one spine and three (*Naso* and *Paracanthus*) or (usually) 5 soft rays; dorsal and anal fins with elaborate spine-locking mechanism; dorsal fin usually with 4–9 spines and 19–31 soft rays; anal fin with 2 or 3 spines and usually 19–36 soft rays; tenth interneural space with 2–3 basal pterygiophores. Their name derives from scalpel-sharp spines on either side of the tail.

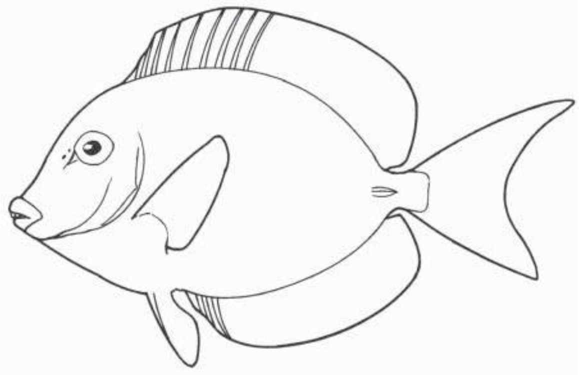
Six genera and 73 species. The subfamilies and tribes are recognized after Winterbottom (1993). From the rich Eocene and Oligocene fossil record, acanthurids were much more diverse at the generic level than they are now (e.g., Tyler, 2000; Tyler and Micklich 2011). An important morphological study is that of Tyler (1970) on the spine-locking mechanism. Sorenson et al. (2013) presented a time-tree analysis of the family.

Fossils include †*Glarithurus* from the Oligocene of Switzerland (Tyler and Micklich, 2011), unique among acanthurids in having a single anal-fin basal pterygiophore in the first interhaemal space, as opposed to two or more in other acanthurids.

Subfamily Nasinae (unicornfishes). Two anal spines, three soft pelvic rays rather than five in addition to the spine, one or two fixed dermal plates on the caudal peduncle, and some species with a protuberance on the frontal region developing with age; four branchiostegals. Indo-Pacific.

One genus, *Naso* (including the subgenus *Axinurus*), and 20 species (Borden, 1998; Randall, 2001b, c; Horne et al., 2008).

Subfamily Acanthurinae. Three anal spines; one or more movable flexible dermal spines (fixed in *Prionurus*) on the caudal peduncle, which, when extended, can form a formidable weapon (in a deep groove in the Acanthurini); five branchiostegals; jaw teeth spatulate. Maximum length about 66 cm.



There are three recognized tribes with five genera and 53 species (e.g., Randall and Earle, 1999; Randall, 2001c,d; Randall and Clements, 2001; Hubert et al., 2010; Bernal and Rocha, 2011).

tribe prionurini. (Primarily Pacific, with *Prionurus* (7) (three anal spines and 3–10 fixed bony plates on the caudal peduncle).

tribe zebrasomini. Two genera, *Paracanthus* (1), and *Zebrasoma* (tangs) (7).

tribe acanthurini. Two genera, *Acanthurus* (38), and *Ctenochaetus* (9), but Sorenson et al. (2013) suggest these two genera should be combined into one genus. Recent studies include Bernal and Rocha (2011).

Order SPARIFORMES (82)—breams and porgies. The six families placed here include three of originally four families previously identified on morphological evidence as the “Sparoid lineage” (e.g., Nelson 2006), together with three families (Callanthiidae, Sillaginidae, and Lobotidae) provisionally grouped with them on molecular evidence (Near et al. 2012a, 2013; Betancur-R. et al. 2013a).

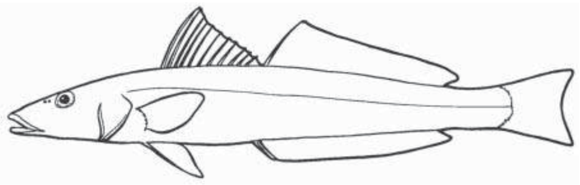
Family CALLANTHIIDAE (502)—splendid perches or groppos. Marine; eastern Atlantic (including the Mediterranean), Indian, and Pacific.

Flat nasal organ devoid of lamellae; lateral line running along base of dorsal fin and terminating near end of dorsal fin or on caudal peduncle; dorsal fin with 11 spines and 9–11 soft rays; midlateral row of modified scales with series of pits and/or grooves; well-developed median frontal crest with associated elongation of ossified sensory canal; supraneural bones oblique, not interdigitating with first two neural spines; vertebrae 24. Maximum length about 25 cm. Magnificently colored.

The position of this family is very uncertain. Morphological evidence is equivocal for placement within Percoidei (reviewed by Anderson et al., 2015). One broad-scale molecular study (Near et al., 2013) groups them with the Sillaginidae, which in turn have been grouped with Spariformes (Betancur-R. et al., 2013a).

Two genera, *Callanthias* (7) and *Grammatonotus* (6), with about 13 species (Anderson et al., 2015) (see also Gill and Mooi 1993; Anderson 1999; Mundy and Parrish 2004).

Family SILLAGINIDAE (503)—sillagos (whitings, smelt-whitings). Marine (coastal) and brackish water, rarely into fresh water; Indo-West Pacific.

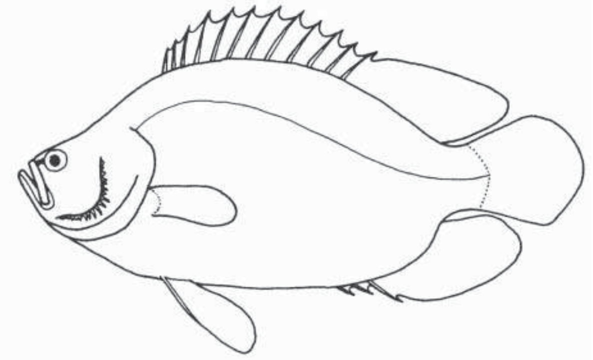


Body elongate; mouth small; two dorsal fins (little or no interspace), first with 10–13 spines (second spine elongate in *Sillaginopsis*) and second with 1 slender spine and 16–27 soft rays; anal fin with 2 small spines and 14–26 soft rays; three predorsal bones; swimbladder absent or vestigial (in *Sillaginopsis*) to highly complex with various extensions; vertebrae 32–44 (their number is highly variable for a small percoid family). Maximum length usually about 45 cm, up to about 70 cm.

The juveniles of several species commonly enter estuaries; a few species extend into fresh water, and then only rarely. Members occur in relatively shallow water and extend from South Africa to Japan and Australia. The common name “whitings” is used in Australia, but it is used elsewhere for some gadiforms. Kaga (2013) completed a morphological phylogenetic study of the family, containing much new anatomical information.

Five genera *Sillaginodes* (1, King George Whiting), *Sillaginops* (1), *Sillaginopoides* (1), *Sillaginopsis* (1), and *Sillago* (30), with a total of 34 species (McKay, 1992; Kaga et al., 2010; Kaga and Ho, 2012; Kaga, 2013).

Family LOBOTIDAE (504)—tripletails. Marine, brackish, and freshwater; most warm seas.



Palatine and vomer toothless; caudal fin rounded, profile similar to centrarchids; rounded lobes on anal and second dorsal fins giving fish the appearance of having three tails; dorsal fin with 12 spines and 15 or 16 soft rays; 24 vertebrae.

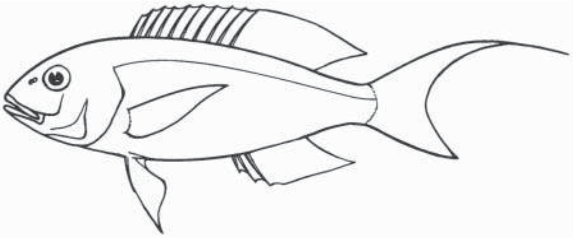
The very young can camouflage themselves by turning sideways and floating like leaves. Maximum length about 1.0 m.

The inclusion of the species of *Datnioides* (tigerperches) in this family is provisional; some works place it in its own family or have aligned it with other families. If recognized in its own family, Kottelat (2000b) argued that the valid family-group name is Datnioididae. Species of *Datnioides* have been recognized under the generic name *Coius* (family Coiidae) (e.g., Kottelat, 1998:111), but Kottelat (2000b) regarded *Coius* as a synonym of *Anabas*, and thus Datnioididae can no longer be considered a synonym of Coiidae. Hilton and Bemis (2005) concluded there was a possibility of relationship between *Lobotes* and *Datnionoides* based on their grouped tooth replacement and caudal fin morphology.

Two genera, *Datnioides* (with five species that are freshwater and brackish from India to Borneo and New Guinea) and *Lobotes* (2, marine), with about seven species.

THE NEXT THREE FAMILIES had been called the "sparoid lineage" on morphological grounds (e.g., Johnson, 1980; Carpenter and Johnson, 2002; Nelson, 2006): Nemipteridae, Lethrinidae, and Sparidae (with junior synonym Centracanthidae that was listed as a fourth "sparoid" family in Nelson, 2006). There are now also molecular phylogenetic results suggestive of this clade (Betancur-R. et al., 2013a).

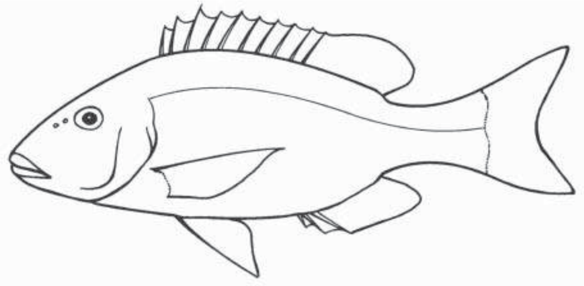
Family NEMIPTERIDAE (505)—threadfin breams. Marine; tropical and subtropical, Indo-West Pacific.



Dorsal fin continuous, with 10 spines and nine soft rays; anal fin with 3 spines and seven or eight soft rays; caudal fin in some with filament off upper lobe; six branchiostegals; gill membranes free from isthmus; subocular shelf and accessory subpelvic keel well developed; opisthotic (= intercalar) well developed (lost or fused in the three related families); 24 vertebrae. Nemipterids, part of the sparoid assemblage, appear to be most closely related to lethrinids.

Five genera, *Nemipterus* (25), *Parascolopsis* (12), *Pentapodus* (12), *Scaevius* (1), and *Scolopsis* (17), with 67 species (e.g., Russell, 2001; Mishra et al., 2013).

Family LETHRINIDAE (506)—emperors or emperor breams. Marine coastal; tropical, west Africa and Indo-West Pacific.

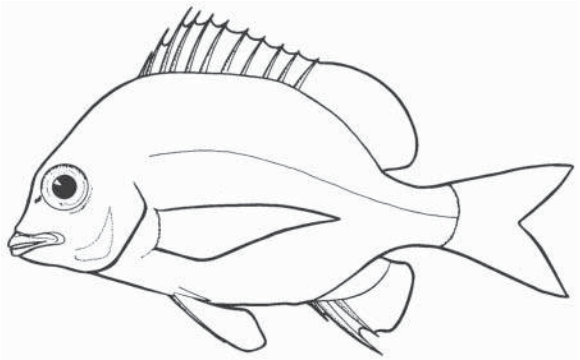


Dorsal fin continuous, with 10 spines and 9 or 10 soft rays; anal fin with 3 spines and 8–10 soft rays; 6 branchiostegals; no accessory subpelvic keel; reduced subocular shelf; 24 vertebrae.

Only one species occurs in the Atlantic Ocean—*Lethrinus atlanticus.* Some authors recognize the subfamily Lethrininae (the emperors—cheek scaleless, nine soft dorsal-fin rays, subocular shelf absent) for *Lethrinus* and the subfamily Monotaxinae (the large-eye breams—cheeks each with at least three transverse rows of scales, 10 soft dorsal-fin rays, subocular shelf present) for the other four genera; the phylogenetic validity of this arrangement, however, is uncertain. See above under family Nemipteridae, for comment on phylogenetic relationships of this family.

Five genera, *Gnathodentex* (1), *Gymnocranius* (8), *Lethrinus* (27), *Monotaxis* (1), and *Wattsia* (1), with about 38 species (e.g., Carpenter and Randall, 2003).

Family SPARIDAE (507)—porgies. Marine (very rarely brackish and freshwater); Atlantic, Indian, and Pacific.



Dorsal fin continuous, usually with 10–13 spines and 10–15 soft rays; anal fin with 3 spines and 8–14 soft rays; maxilla covered by a sheath when mouth closed; 6 branchiostegals; 24 vertebrae (10 + 14). Maximum length about 1.2 m.

The continental western Atlantic Sheepshead, *Archosargus probatocephalus*, which occasionally occurs in brackish water, is known to enter fresh water rarely in Florida. Four species of sparids occur in brackish water in Australia and one species of *Acanthopagrus*, which enters fresh water, is known to spawn in brackish water.

As noted in Orrell et al. (2002), six sparid subfamilies have been recognized (Boopsinae, Denticinae, Diplodinae, Pagellinae, Pagrinae, and Sparinae); they were not monophyletic in all their analyses. Their analysis supported a monophyletic Sparidae only with the inclusion of *Spicara* (formerly in Centracanthidae); the latter genus and *Centracanthus* are both now in Sparidae, rendering the Centracanthidae a junior synonym. Fossils now classified as centracanthids include †*Nasloavcea* from the Miocene of Modova, Eastern Europe, and two species of *Spicara* from Azerbaijan and Algeria (Bannikov, 2006).

Thirty-seven genera (e.g., *Acanthopagrus* (20), *Archosargus* (3), *Argyrops* (4), *Argyrozona* (1), *Boops* (2), *Boopsoidea* (1), *Calamus* (13), *Centracanthus* (1), *Cheimerius* (2), *Chrysoblephus* (6), *Crenidens* (1), *Cymatoceps* (1), *Dentex* (13), *Diplodus* (15), *Evynnis* (3), *Gymnocrotaphus* (1), *Lagodon* (1), *Lithognathus* (4), *Oblada* (1), *Pachymetopon* (3), *Pagellus* (6), *Pagrus* (6), *Parargyrops* (1), *Petrus* (1), *Polyamblyodon* (2), *Polysteganus* (5), *Porcostoma* (1), *Pterogymnus* (1), *Rhabdosargus* (6), *Sarpa* (1), *Sparidentex* (1), *Sparodon* (1), *Sparus* (1), *Spicara* (8), *Spondyliosoma* (2), *Stenotomus* (2), and *Virididentex* (1)) with 148 species (e.g., Orrell et al., 2002; Carpenter, 2003; Bargelloni et al., 2005; Iwatsuki, et al., 2006; Iwatsuki and Carpenter, 2006, 2009; Chiba et al., 2009; Iwatsuki and Heemstra, 2010, 2011a,b; Iwatsuki and Maclaine, 2013; Santini et al., 2014; Tanaka and Iwatsuki, 2013).

THE NEXT THREE ORDERS form a clade in several recent molecular phylogenies (e.g., Near et al., 2012a; Betancur-R. et al., 2013a). The Caproiformes, with one family Caproidae, were classified in the previous edition as suborder Caproidei within Perciformes, but were included with Zeiformes in earlier editions (e.g., Nelson, 1994). The resemblances to Zeiformes are now regarded as convergent. The exact relationships among these three orders (Caproiformes, Tetraodontiformes, and Lophiiformes) remain uncertain.

Order CAPROIFORMES (83)—boarfishes. One family. Rosen (1973a) observed that the caproid caudal skeleton is of percoid type in having three epurals and the parhypural plus five hypurals articulating with a terminal half-centrum, whereas the zeiforms have only one or two epurals and the hypurals fused together into large plates. Subsequently, Rosen (1984) suggested that caproids, zeiforms, and tetraodontiforms form a clade. However, Tyler et al. (2003) were not convinced. Johnson and Patterson (1993) also made a case for caproids being perciforms. The present position as sister to Lophiiformes and/or to Tetraodontiformes, based on recent morphological evidence (Chanet et al.,

2013) and several molecular studies (e.g., Yamanoue et al., 2007; Near et al., 2012a; Betancur-R. et al., 2013a; Santini et al., 2013) is broadly consistent with the Johnson and Patterson (1993) proposal.

Tyler and Santini (2005), in a morphological analysis, placed the fossil taxa †Sorbinipercidae, containing †*Sorbinicapros* and †*Sorbiniperca*, together with †Zorzinichthyidae containing †*Zorzinichthys*, all from the Eocene of Monte Bolca, Italy, in a single clade related to the caproids (see also Bannikov and Tyler, 1999; Tyler and Bannikov, 2002).

Family CAPROIDAE (508)—boarfishes. Marine; Atlantic, Indian, and Pacific.

Body covered with small ctenoid scales; dorsal-fin spines 7–9; anal-fin spines two or three; pelvic fin with one spine and five soft rays; caudal fin rounded; distinct sagittal crest; pleural ribs present; vertebrae 21–23. Monophyly of this family is uncertain.

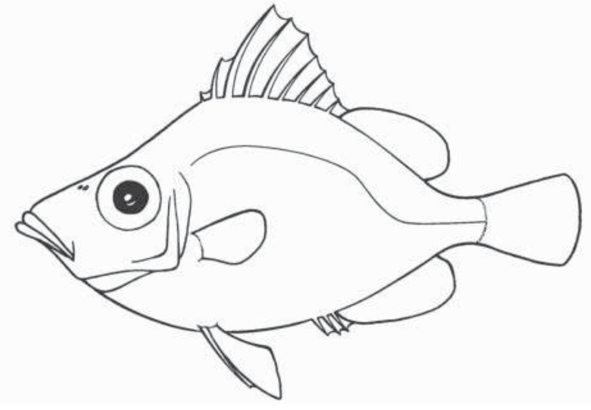
Two subfamilies, two genera, and 18 species.

Subfamily Antigoniinae. Red-colored fishes with extremely deep and slim bodies (rhomboid shape); most body scales with large elevated ridge, curved posteriorly; dorsal fin with eight or nine spines and 26–38 soft rays; three anal spines, separate from the anal soft rays; 10 branched caudal rays (12 principal rays and total of 7 or 8 procurrent rays); maxillary process of palatine articulates with anterior end of nasal.

Most species occur between approximately 50–600 m.

One genus, *Antigonia*, with about 17 species. In addition, fossil species of *Antigonia* including †*A. veronensis* are known from the Eocene and Miocene. See Nelson (1994), Parin (2003), and Parin and Borodulina (2005, 2006) for references.

Subfamily Caproinae. Caudal fin with 12 branched rays (14 principal rays and total of two procurrent rays); five distinct hypurals (not fused). Differing from Zeidae, with which they have a superficial external similarity, in lacking abdominal spinous plates.



One species, *Capros aper*, occurring in the Mediterranean Sea and eastern North Atlantic.

Order LOPHIIFORMES (84)—anglerfishes. First spine of spinous dorsal, if present, on head and transformed into illicium (line) and esca (bait), a device for attracting prey to mouth; epiotics separated from parietals, meeting on the midline posterior to the supraoccipital; gill openings reduced to small tube-like openings positioned at or behind the pectoral-fin base; first and second ural centra fused to the first preural centrum to form a plate; pectoral radials 2–5, elongate and narrow, the ventral-most radial expanded distally; eggs spawned in a gelatinous sheath; pelvic fins, if present, in front of pectorals, with one spine and four (rarely) or five soft rays; five or six branchiostegals; no ribs; first vertebra fused to skull; swimbladder, when present, physoclistous (Pietsch and Grobecker, 1987).

The following classification is based on the phylogenetic conclusions of Pietsch and Grobecker (1987) as followed by Wiley and Johnson (2010). We recognize five suborders with the following phylogenetic relationships:

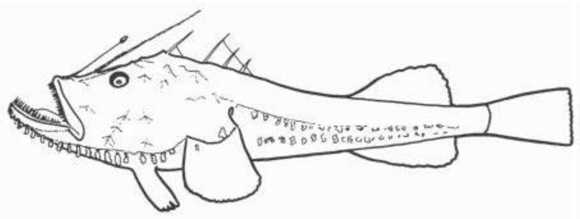
Lophioidei {Antennarioidei [Chaunacoidei (Ogcocephaloidei + Ceratioidei)]}

The Lophioidei are considered primitive sister group of the other suborders. The Antennarioidei share with Chaunacoidei, Ogocephaloidei, and Ceratioidei a reduction in egg and larval size, and a reduction in dorsal fin spines to three or fewer. Chaunacoidei, Ogocephaloidei, and Ceratioidei share a second dorsal spine that is embedded beneath the skin of the head and the absence of gill filaments on the first gill arch. Ogocephaloidei and Ceratioidei share a reduction of the second dorsal spine, the absence of the third dorsal spine and pterygiogore, and posttemporals that are fused to the cranium.

Eighteen families with about 72 genera and 358 species. All are marine. Most species occur in deep water.

Suborder Lophioidei. Pelvic fins present; spinous dorsal fin behind head with one to three spines; fourth pharyngobranchial present and toothed; pseudobranch large; body scaleless; frontals united. One family.

Family LOPHIIDAE (509)—goosefishes. Marine; Arctic, Atlantic (including the Mediterranean Sea), Indian, and Pacific.



Huge, wide, flattened head (head rounded in *Sladenia*); teeth well developed; fringe of small flaps extending around lower jaw and along sides of head onto body; pectoral-fin rays 13–28; second dorsal fin with 8–12 soft rays; anal fin with 6–10 rays; vertebrae 18 or 19 and, in *Lophius*, 26–31.

The mobile fishing apparatus has a flap of flesh at its tip that acts like a lure, attracting prey within reach of its large mouth. Size up to 1.2 m.

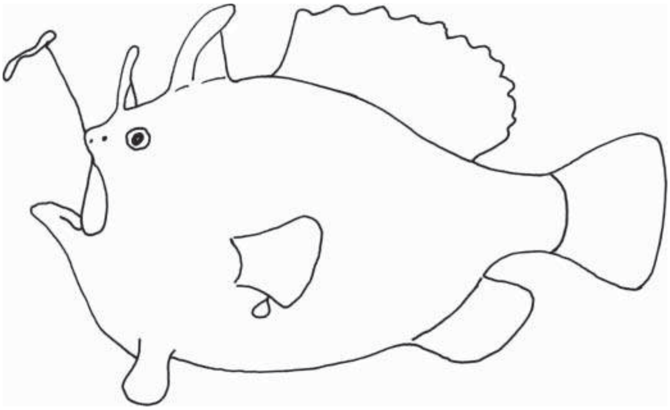
Four genera, *Lophiodes* (17), *Lophiomus* (1), *Lophius* (7), and *Sladenia* (3), with 28 species (Caruso, 1985; Charrier et al., 2006; Ho et al., 2008).

Fossil taxa include †*Eosladenia caucasica* from the Eocene of the northern Caucasus (Bannikov, 2004a), and †*Sharfia mirabilis* from the Eocene of Monte Bolca, Italy (Pietsch and Carnevale, 2011).

Suborder Antennarioidei. Spinous dorsal fin consisting of three separate cephalic spines (the first is the modified illicium; the second dorsal spine may be short, but it is never embedded beneath the skin); pterygiophores of illicium and third spine of dorsal fin with highly compressed dorsal expansions; interhyal with medial posteriorly directed process that makes contact with the preopercle (Pietsch 1981; Wiley and Johnson, 2010).

Four families with 21 genera and 64 species.

Family ANTENNARIIDAE (510)—frogfishes. Marine; all tropical and subtropical seas (absent from the Mediterranean), occasionally temperate (e.g., western Atlantic and southern Australia).



Deep-bodied (globose); nape not conspicuously humped; mouth large; eyes lateral; body covered with loose skin, naked or with denticles; gill opening below or behind base of pectoral fin; pelvic fin of one spine and 5 soft rays; parietals separated by supraoccipital; pectoral radials 3; swimbladder usually present (absent in *Kuiterichthys* and *Tathicarpus*); soft dorsal-fin rays 10–16; soft anal-fin rays 6–10; pectoral-fin rays 6–14; vertebrae 18–23; palatine teeth present. The fishing pole (illicium) of frogfishes, a modification of the first dorsal spine, is pronounced and highly variable among species. Maximum length 36 cm, some only 3 cm.

Frogfishes are benthic except for the widespread and pelagic *Histrio histrio,* which uses its prehensile pectoral fin for "clasping" or moving on floating sargassum. The Indo-Australian species *Antennarius biocellatus* is the only frogfish known to occur in brackish and fresh water. Pietsch and Grobecker (1987) give distributional information on the various species. The feeding dynamics of frogfishes are described by Pietsch and Grobecker (1987); they note cases of aggressive mimicry in which the lures of different species resemble a polychaete, an amphipod, and a small fish. In addition, there are a few species with parental care in which the eggs may also be acting as a lure.

Thirteen genera, *Allenichthys* (1), *Antennarius* (11), *Antennatus* (12), *Echinophryne* (3), *Fowlerichthys* (5), *Histiophryne* (5), *Histrio* (1), *Kuiterichthys* (1), *Lophiocharon* (3), *Nudiantennarius* (1), *Phyllophryne* (1), *Rhycherus* (2), and *Tathicarpus* (1), with 47 species (e.g., Pietsch and Grobecker 1987; Ohnishi et al., 1997; Randall and Holcom, 2001; Pietsch et al., 2009; Arnold, 2012, 2013; Arnold and Pietsch, 2011, 2012).

Family TETRABRACHIIDAE (511)—tetrabrachiid frogfishes. Marine; western and northern coasts of Australia, southern coast of New Guinea, and the south Molucca Islands of Indonesia.

Body elongate and strongly compressed; mouth small; eyes small and dorsal; swimbladder absent; nape humped; soft dorsal-fin rays 16 or 17; anal-fin rays 11 or 12; pectoral-fin rays 9, fin divided into two portions; palatine teeth absent. Maximum length about 7 cm.

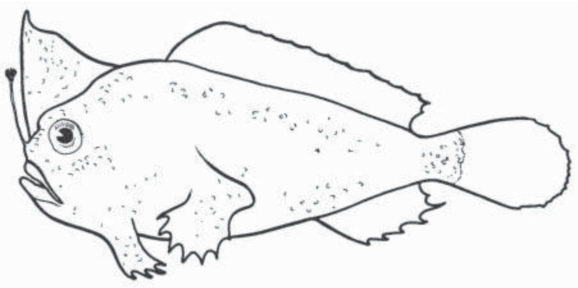
Two monotypic genera, *Tetrabrachium ocellatum* and *Dibrachichthys melanurus* (Pietsch and Grobecker, 1987; Pietsch et al., 2009).

Family LOPHICHTHYIDAE (512)—lophichthyid frogfishes. Marine; Arafura Sea, western New Guinea.

Nape not humped; soft dorsal-fin rays 12 or 13; anal-fin rays 9; pectoral-fin rays 7; palatine teeth present.

One species, *Lophichthys boschmai* (Pietsch and Grobecker, 1987).

Family BRACHIONICHTHYIDAE (513)—handfishes (warty anglers). Marine; southern Australia, primarily off Tasmania.



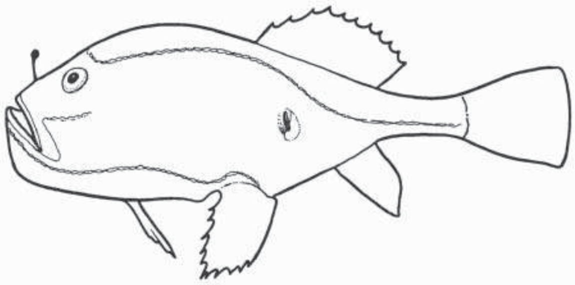
Body deep; skin naked or covered with denticles; second and third dorsal spines united by a membrane; gill opening small, behind base of pectoral fin; soft dorsal-fin rays 15–18, unbranched; anal-fin rays 7–10; pelvic fin with 1 spine and 4 soft rays; parietals meeting on midline; pectoral radials 2.

Maximum length 15 cm. They are benthic, occurring in inshore waters at depths up to 60 m.

Five genera, *Brachionichthys* (2), *Brachiopsilus* (3), *Pezichthys* (5), *Sympterichthys* (3), *Thymichthys* (1) with 14 species (e.g., Paxton et al., 1989; Last et al., 2007; Last and Gledhill, 2009). The fossil taxa †*Histionotophorus bassani* and †*Orrichthys longimanus*, are known from the Eocene of Monte Bolca, Italy (Carnevale and Pietsch, 2010).

Suborder Chaunacoidei. One family.

Family CHAUNACIDAE (514)—coffinfishes or sea toads. Marine; Atlantic, Indian, and Pacific.

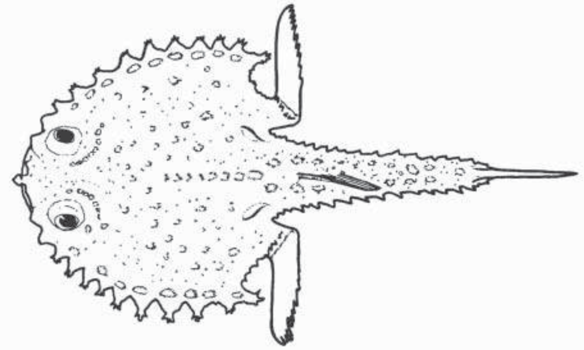


Body globose; skin covered with denticles; illicium, but no other spinous dorsal rays; mouth oblique; gill opening behind base of pectoral fin; anal-fin rays 5–7; body color pink to deep reddish-orange. Maximum size about 35 cm.

Two genera, *Chaunacops* (3, synonym *Bathychaunax*) and *Chaunax* (19), with 22 species (Caruso, 1989; Caruso et al., 2006; Ho and Shao, 2010a; Ho and Last, 2013; Ho et al., 2013). The species occur between depths of 90 m to more than 2,000 m.

Suborder Ogcocephaloidei. One family.

Family OGCOCEPHALIDAE (515)—batfishes. Marine; all tropical and many subtropical seas (absent from the Mediterranean Sea).



Body usually much depressed and flattened ventrally (somewhat box shaped in *Coelophrys* of the Indo-West Pacific); illicium relatively short (composed primarily of the modified pterygiophore of the first fin spine) but remnant of second dorsal spine present; illicial cavity, opening anteriorly, housing the esca when illicium is retracted; mouth nearly horizontal; gill opening in or above pectoral-fin base; two or two and one-half gills (first arch reduced and lacking filaments); soft dorsal fin small, usually present, 1–6 rays; anal fin short, with 3 or 4 rays; pectoral fin with 10-19 soft rays; pelvic fin with one spine and 5 soft rays; vertebrae 16-12; well-developed tubercle-like scales. Species have either conical tubercles or multispined structures called "bucklers" (spines arranged in a radiating pattern) in addition to having very small tubercles. All have a modified type of scale associated with the lateral line organs.

Batfishes walk about on the bottom on their large arm-like pectoral fins and smaller pelvic fins. They are awkward swimmers. Size normally 20 cm; up to 40 cm in *Ogcocephalus nasutus*. They are known primarily from outer continental shelves and continental slopes to 1,500–3,000 m with one species known from 4,000 m; a few species occur inshore, and rarely known upstream in rivers.

Ten genera, *Coelophrys*, *Halieutopsis*, *Dibranchus*, *Halieutaea*, *Halicmetus*, *Malthopsis*, *Halieutichthys*, *Ogcocephalus*, *Solocisquama*, and *Zalieutes*, with 78 species (Bradbury, 1999, 2003; Ho et al., 2013).

Suborder Ceratioidei. Pelvic fins absent; pseudobranch absent; usually scaleless (prickles, spines, or plates may be present); supraoccipitals immediately behind frontals and between the parietals; frontals not united; palatine reduced or absent; denticular bones in dwarf males; basihyal absent; lower pharyngeals reduced and toothless; pectoral-fin rays 12–28 (except *Ctenochirichthys* with 28–30); 8 or 9 caudal-fin rays; only females with illicium, the tip of which usually has a light organ (undoubtedly increasing its function in attracting prey; light organs may also be present elsewhere); vertebrae 19–24. (Pietsch 2009; Pietsch and Orr, 2007; Wiley and Johnson, 2010).

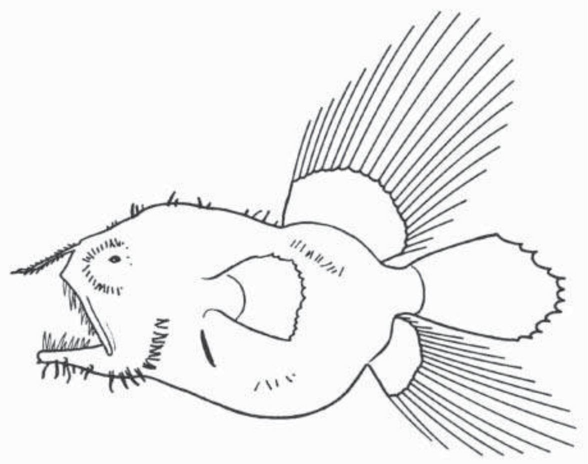
Marked sexual dimorphism is characteristic of the ceratioids. The longest female known in each family is 3 to 13 times longer than the longest male known (within species the difference can be much greater). The adult males of all species in at least four families feed in a parasitic fashion on the larger females. After metamorphosis into the parasitic-like stage, these males actively seek out females (probably through a female-emitted, species-specific pheromone), attach to their bodies, and feed on their blood (a vascular connection may exist in all such parasitic-like relationships). Males are generally different in appearance from females (females are pictured and used for the family descriptions herein), although dorsal and anal fin-ray counts are the same. The sexually mature males of the Ceratiidae, Linophrynidae, and perhaps the Neoceratiidae are obligatory sexual parasites (nonparasitized females never have developed ovaries, and free-living males never have developed testes or undergo postmetamorphic growth), while parasitism in the Caulophrynidae and one oneirodid genus may be facultative (most other taxa are thought to be nonparasitic). In some families the males are nonparasitic; in these cases it appears that they do not feed after metamorphosis and survive until spawning on nutrients stored during larval life. In the past, males, females, and larva of the same species have been described as different species. Some species are still known only from males, females, or larva and often from only a few specimens. About one-third of the number of recognized species are known only from a single female specimen.

Larval life is spent in the upper, food-rich oceanic layer; most adults are meso- or bathypelagic (usually occurring between 1,500 and 2,500 m; adult thaumatichthyids are benthic between 1,000 and 3,600 m). Ceratioids extend from the subarctic to the subantarctic but are absent from the Mediterranean Sea.

Maximum size in most species is seldom longer than 8 cm; however, *Ceratias holboelli* reaches at least 1.2 m.

Eleven families, 35 genera, and about 166 species.

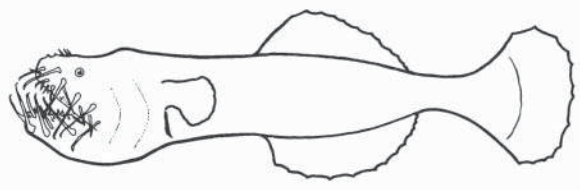
Family CAULOPHRYNIDAE (516)—fanfins. Marine; Atlantic, Indian, and Pacific.



No distal bulb with light organ on illicium; mature males feed in parasitic fashion on females; pelvic fins in larvae (only ceratioid with pelvics at some stage); two pectoral radials (all other ceratioids have 3–5); dorsal fin with six (in *Robia*) or 14–22 normal rays, and anal fin with 5 (in *Robia*) or 12–19 rays (other ceratioids have 13 or fewer anal-fin rays); extremely elongate dorsal and anal rays; eight caudal-fin rays.

Two genera, *Robia* (*R. legula*), monotypic, and *Caulophryne* (4), with five species (e.g., Pietsch, 1979; Balushkin and Fedorov, 1986).

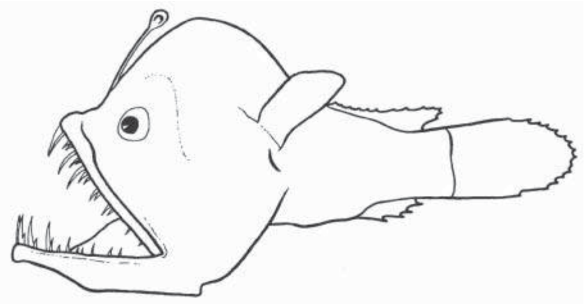
Family NEOCERATIIDAE (517)—spiny seadevils. Marine; Atlantic, Indian, and Pacific.



Illicium absent; long movable teeth outside jaws in females; mature males feed in parasitic fashion on females; dorsal fin with 11–13 rays and anal fin with 10–13 rays; pectoral-fin rays 12-15; pelvic fins absent.

One species, *Neoceratias spinifer*.

Family MELANOCETIDAE (518)—black seadevils. Marine; Atlantic, Indian, and Pacific.



Blackish in color with gelatinous, mostly scaleless, globose body; fang-like teeth lining jaws; teeth depressible only in females. Dorsal fin with 12–17 rays; anal fin with 3 or 4 rays; pectoral fin with15-23 rays. Males free-living, never parasitic; females possess a small club-shaped illicial rudiment projecting from the head.

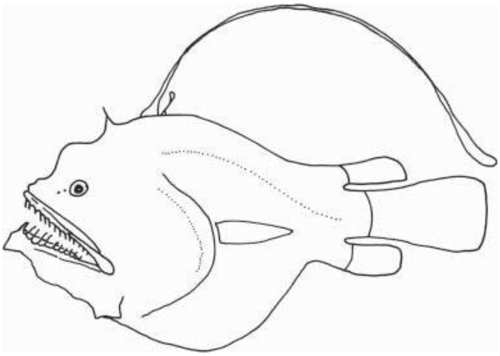
One genus, *Melanocetus*, with six species. (Pietsch and Van Duzer, 1980).

Family HIMANTOLOPHIDAE (519)—footballfishes. Marine; Atlantic, Indian, and Pacific.

Both sexes lack parietals throughout life (present in other ceratioids except lost in adult females of *Rhynchactis*); tri-radiate pelvic bone; six branchiostegal rays; no epurals; bony plates, each with a median spine, over body; dorsal fin with five or six rays and anal fin with four rays; caudal fin with nine rays; pectoral-fin rays 14–18; vertebrae about 19. Females differ from other ceratioids in having a blunt and short snout; papillae on snout and chin. Maximum length 46 cm (maximum length of males 3.9 cm, the largest of free-living ceratioid males) (Bertelsen and Krefft, 1988).

One genus, *Himantolophus*, with 21 species (Bertelsen and Krefft, 1988; Pietsch 2009; Stewart and Pietsch, 2010; Pietsch and Kenaley, 2011).

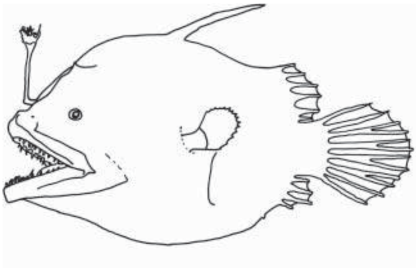
Family DICERATIIDAE (520)—double anglers. Marine; continental shelf or slope of tropical and subtropical seas, Atlantic and Indo-West Pacific.



Females distinguished from all other ceratioids in having second cephalic ray externally exposed in young specimens, club-shaped, with distal light organ, and emerging from head directly behind base of illicium; skin spines present; dorsal fin with five to seven rays and anal fin with four rays; small pelvic bone present, connected with cleithrum.

Two genera, *Diceratias* (3) and *Bufoceratias* (3, synonym *Phrynichthys*), with six species (Pietsch et al. 2004).

Family ONEIROIDIDAE (521)—dreamers. Marine; Atlantic, Indian, and Pacific.



Skin naked or with short spines in some females; dorsal fin with 4–8 rays; 4–7 anal-fin rays; and pectoral fin with 13-30 rays; Metamorphosed females posess an anteriorly directed narrow, spatulate process that extends over the posterolateral surface of the retspective sphenotic; jaws equal anteriorly. With the exception of *Bertella idiomorpha* and *Leptacanthichthys gracilispinis*, males are free-living and non-parasitic

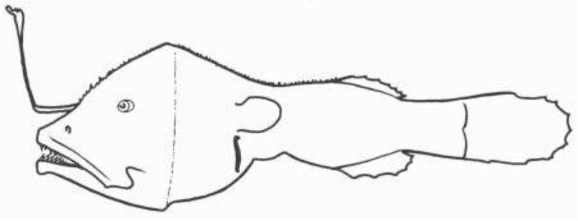
Sixteen genera, *Bertella* (1), *Chaenophryne* (5), *Chirophryne* (1), *Ctenochirichthys* (1), *Danaphryne* (1), *Dermatias* (1) *Dolopichthys* (7), *Leptacanthichthys* (1), *Lophodolos* (2), *Microlophichthys* (2), *Oneirodes* (35), *Pentherichthys* (1), *Phyllorhinichthys* (2), *Puck* (1), *Spiniphyne* (2), and *Tyrannophryne* (1), with about 64 species (e.g., Ho and Shao, 2004; Pietsch and Kharin, 2004; Pietsch and Baldwin, 2006; Pietsch 2009).

Family THAUMATICHTHYIDAE (522)—wolftrap anglers. Marine; Atlantic and Pacific.

Similar to Oneirodidae, but differing from it and all other ceratioid families in having upper jaw (i.e., the premaxillaries) extending far beyond lower jaw and upper arm of operculum divided into two or more branches.

Two genera, *Lasiognathus* (5) and *Thaumatichthys* (3), with eight species (Bertelsen and Pietsch, 1996, Pietsch, 2005; Pietsch and Sutton 2015).

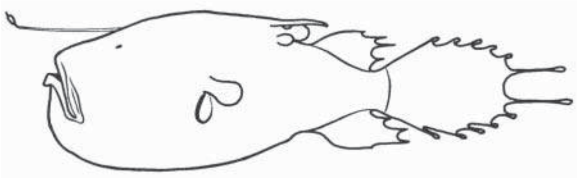
Family CENTROPHRYNIDAE (523)—prickly seadevils. Marine; Atlantic, Indian, and Pacific.



Teeth numerous but small is size; small hyoid barbel present in young of both sexes; anterior spine on subopercular; skin with numerous small spines; dorsal fin with 5–7 rays; 15 or 16 pectoral-fin rays; 3–4 pectoral radials; and 5 or 6 anal-fin rays. Mature males feed in parasitic fashion on females (Vieira et al., 2013).

One species, *Centrophryne spinulosa.*

Family CERATIIDAE (524)—warty seadevils. Marine; Atlantic, Indian, and Pacific.

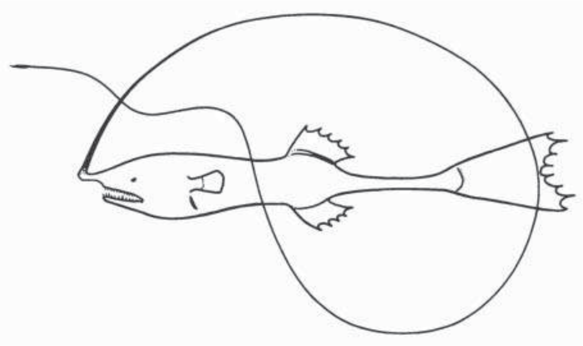


Females with two or three rays modified into caruncles (low fleshy appendages) in front of soft dorsal fin; cleft of mouth vertical to strongly oblique; parietals large; mature males feed in parasitic fashion on females; dorsal fin soft rays usually 4, rarely 5; anal-fin rays 4; pectoral-fin rays 15-19; larvae “humpbacked.”

Maximum length at least 77 cm, up to 1.2 m (*Ceratias holboelli*).

Two genera, *Ceratias* (3) and the monotypic *Cryptopsaras*, with a total of four species. (Pietsch, 1986).

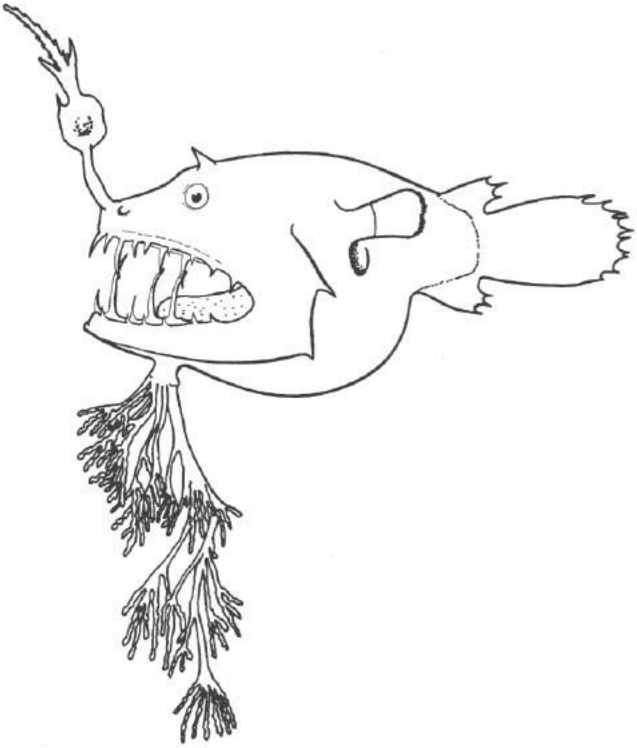
Family GIGANTACTINIDAE (525)—whipnose anglers. Marine; Atlantic, Indian, and Pacific.



Body elongate in females; illicium almost as long as or longer than body; upper jaw extending slightly beyond lower jaw; five pectoral radials; dorsal fin with 3–10 rays and anal fin with 3–8 rays; nine caudal-fin rays.

Two genera, *Gigantactis* (20) and *Rhynchactis* (3), with 23 species (Bertelsen et al., 1981; Bertelsen and Pietsch, 1998, 2002).

Family LINOPHRYNIDAE (526)—leftvents. Marine; Atlantic, Indian, and Gulf of Panama.



Mature males feed in parasitic fashion on females; dorsal and anal-fin soft rays usually three; anus sinistral; hyoid barbel in female *Linophryne*.

Five genera, *Linophryne* (22), *Acentrophryne* (2), *Borophryne* (1), *Haplophryne* (1), and *Photocorynus* (1), with 27 species (e.g., Gon, 1992; Pietsch and Shimazaki, 2005; Pietsch, 2009).

Order TETRAODONTIFORMES (Plectognathi) (85)—plectognaths. No parietals, nasals, or infraorbitals, and ribs usually absent; posttemporal, if present, simple and fused with pterotic of skull; extrascapulars absent; hyomandibula and palatine firmly attached to skull; gill openings restricted and positioned anterior to the pectoral-fin base; maxilla usually firmly united or fused with premaxilla; scales usually modified as spines, shields, or plates; lateral line present or absent, sometimes multiple; swimbladder present except in molids; anal-fin spines absent; pelvic fin with at most one spine and two soft rays; caudal fin with 12 or fewer principal rays; vertebrae usually 21 or fewer (exceptions being some of the Monacanthidae, Tetraodontidae, and Diodontidae).

Tetraodontiformes can produce sounds by grinding the jaw teeth or the pharyngeal teeth or by vibrating the swimbladder. The stomach of some tetraodontiforms is highly modified to allow inflation to an enormous size. Fishes with this ability belong to the families Tetraodontidae, Diodontidae, and, where it is less well developed, the monotypic Triodontidae; they are popularly called "puffers." Inflation is caused by gulping water into a ventral diverticulum of the stomach when the fish is frightened or annoyed. Deflation occurs by expelling the water. If the fish is removed from the water, inflation can occur with air. The triodontid and most balistids and monacanthids have another mechanism for slightly enlarging their bodies, by expanding a ventral flap supported by a large movable pelvic bone.

The present classification, changed above the family level from Nelson (1994), owes a great deal to the cladistic morphological study of both fossil and extant taxa by Santini and Tyler (2003). Recent morphological and molecular evidence unites Caproiformes, Lophiiformes, and Tetraodontiformes.

Extensive information on the finely preserved Monte Bolca fossils of Eocene age from Italy was given by Tyler and Santini (2002) and Santini and Tyler (2004). Recent morphological and developmental studies include those by Konstantinidis and Johnson (2012a,b) on ontogeny of the caudal skeleton and jaws. Uehara et al. (2014) examined in detail the presumably synapomorphous phenomenon of extreme shortening of the spinal nerve cord in certain tetraodontiforms (Aracanidae, Ostraciidae, Monacanthidae, Balistidae, Molidae, Tetraodontidae, and Diodontidae), a feature they did not find in the remaining three families (Triodontidae, Triacanthidae, and Triacanthodidae).

Molecular phylogenies have been produced by Holcroft (2005), Yamanoue et al. (2007, 2008, 2009, 2011) and Santini et al. (2013). Neither the morphological studies nor the molecular studies agree on all points, though as Matsuura (2015) stated in a recent review of the situation, there is substantial support for several groupings of the 10 recognized families. The present treatment is slightly modified from that in Nelson (2006) to take into account some of the molecular hypotheses, but without adopting any particular study's phylogeny completely.

Five suborders, ten families with approximately 106 genera and 435 extant species. At least 14 species occur only in fresh water, and another eight or so may be found in fresh water.

†***Suborder Plectocretacicoidei.*** Three Late Cretaceous families, †Cretatriacanthidae, †Plectocretacicidae, and †Protriacanthidae, were recognized by Tyler and Sorbini (1996) and Santini and Tyler (2003).

Suborder Triodontoidei. One family. The phylogenetic position of the Triodontidae is extremely variable among the relevant studies. Assuming that the absence of dorsal nerve cord shortening is a primitive feature, this might be evidence against placement of the Triodontidae in the Tetraodontoidei, where it was in Nelson (2006).

Family TRIODONTIDAE (527)—threetooth puffers. Marine; Indo-West Pacific.

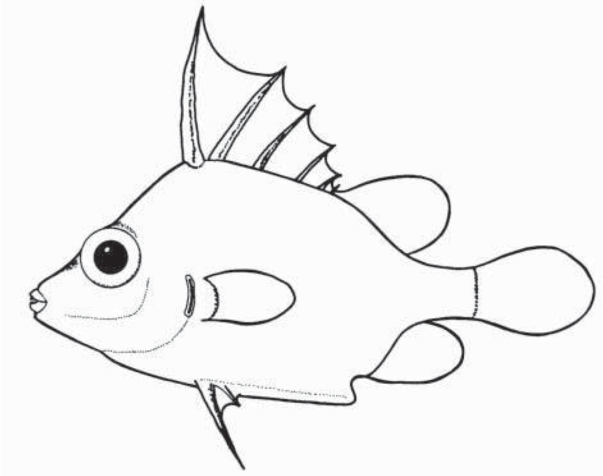
Three fused teeth in jaws (upper jaw with a median suture, the lower without); pelvis present; dorsal nerve cord not greatly shortened; dorsal and anal fins usually with 11 rays (a small spiny dorsal fin of 1 or 2 rays is present in most specimens from Indonesia to Japan); ribs and epipleurals present; caudal fin with 12 principal rays and numerous procurrent rays, deeply forked. Maximum length about 48 cm.

One species, *Triodon macropterus* (synonym *T. bursarius*) (e.g., Matsuura in Carpenter and Niem, 2001; Matsuura, 2015). An Eocene fossil, †*Triodon antiquus*, is very similar to the one extant species.

Suborder Triacanthoidei. Matsuura (2015) considered the monophyly of the Triacanthodidae and Triacanthidae to be well established by molecular studies (e.g., Santini et al., 2013). Although not synapomorphies, the two families share the following primitive features: dorsal nerve cord not greatly shortened; pelvic-fin spine large and able to be locked into position; upper jaw slightly protractile (ascending process of premaxilla well developed); pelvic fin with one large spine and up to two soft rays; dorsal fin usually with six spines; caudal fin with 12 principal rays; 2–6 separate hypurals; 20 vertebrae.

Some 15 genera and 30 species.

Family TRIACANTHODIDAE (528)—spikefishes. Marine; deepwater benthic; tropical and subtropical western Atlantic and Indo-Pacific.



Dorsal-fin rays 12–18 of which the first six are spines grading in size from anterior to posterior; anal-fin rays 11–16; caudal fin rounded to truncate.

Two subfamilies, 11 genera, and about 23 species (Tyler, 1997; Matsuura in Carpenter and Niem, 2001).

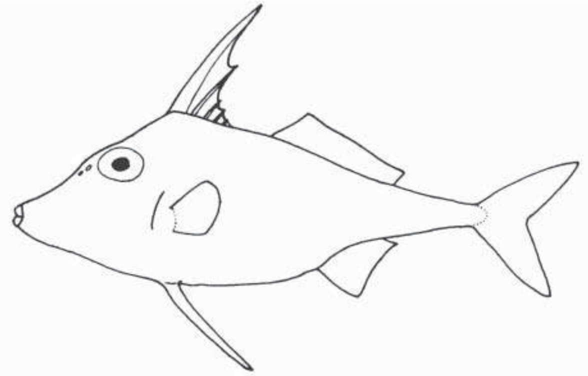
SUBFAMILY HOLLARDINAE. Western Atlantic, one species in Hawaii.

Two genera, *Hollardia* (3) and *Parahollardia* (2), with five species. The orthography of the subfamily name is changed from Nelson (1994) following Santini and Tyler (2003).

SUBFAMILY TRIACANTHODINAE. Indo-Pacific, one species in western Atlantic.

Nine genera, *Atrophacanthus* (1), *Bathyphylax* (3), *Halimochirurgus* (2), *Johnsonina* (1), *Macrorhamphosodes* (2), *Mephisto* (1), *Paratriacanthodes* (3), *Triacanthodes* (4), and *Tydemania* (1), with 18 species (Santini, 2006).

Family TRIACANTHIDAE (529)—triplespines. Marine; shallow benthic; Indo-Pacific.



Dorsal-fin rays 19–26; first ray is a long spine; pelvic fins formed from two spines respectively, and together with the dorsal spine give the fish a tripod-like appearance, and thus the common name of triplespines; anal-fin rays 13–22; caudal fin deeply forked. Maximum length about 28 cm.

Fossils include the Eocene †*Protacanthodes* (Tyler and Santini 2002).

Four genera, *Pseudotriacanthus* (1), *Triacanthus* (2), *Tripodichthys* (3), and *Trixiphichthys* (1), with seven species (e.g., K. Matsuura in Carpenter and Niem, 2001; Santini and Tyler, 2002a).

Suborder Ostracioidea (Ostracodermi). Santini et al. (2013) and Matsuura (2015) placed the following two families as sisters. In addition, two fossil families were recognized by Santini and Tyler (2003): †Spinacanthidae, and †Protobalistidae. Fourteen genera and 37 species.

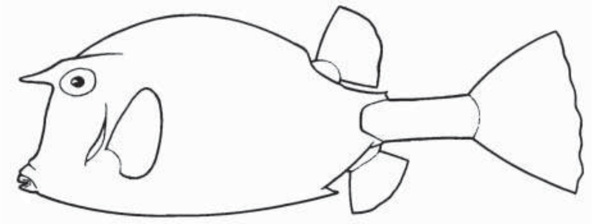
Family ARACANIDAE (530)—deepwater boxfishes. Marine; relatively deep water in the Indo-West Pacific from Hawaii to South Africa; most abundant around Australia.

Carapace open behind the dorsal and anal fins; ventral ridge more or less developed; caudal fin usually with 11 principal rays.

Sometimes considered a subfamily, many authors recognize Aracanidae as a family (e.g., Santini and Tyler, 2003; Matsuura, 2015).

Six genera, *Anoplocapros* (3, *Strophiurichthys*), *Aracana* (2), *Caprichthys* (1), *Capropygia* (1), *Kentrocapros* (4), *Polyplacapros* (1), with 12 species. Fossils include †*Proaracana* from the middle Eocene of Monte Bolca (Santini and Tyler, 2003).

Family OSTRACIIDAE (Ostraciontidae) (531)—boxfishes (cowfishes and trunkfishes). Marine, tropical; Atlantic, Indian, and Pacific.



Body encased in a bony carapace; carapace closed, at least behind the anal fin; no ventral ridge; no pelvic skeleton; no spinous dorsal; dorsal and anal fins each with 9–13 rays; upper jaw not protractile; usually 18 vertebrae; caudal fin with 10 principal rays. Maximum length about 60 cm.

Some trunkfishes are known to discharge a toxic substance, termed "ostracitoxin," which will kill other fishes in confined quarters. The substance is also toxic to the trunkfish, but less so than to most other fishes. Fossils include the Eocene †*Eolactoria* and the Oligocene †*Oligolactoria* (Tyler and Santini, 2002).

Leis (1984), in an article based on early life history characters, placed Ostraciidae in a clade with the Diodontidae and Molidae (i.e., it would be placed in the present suborder Tetraodontoidei), in contrast with earlier works using adult specimens aligning it with the Balistidae and Monacanthidae.

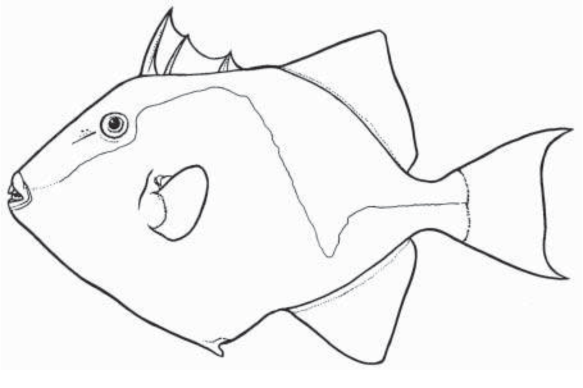
Eight genera, *Acanthostracion* (4), *Lactophrys* (2), *Lactoria* (4), *Ostracion* (8), *Paracanthostracion* (1), *Rhinesomus* (1), *Rhynchostracion* (1), and *Tetrosomus* (4), with about 25 species (e.g., Matsuura in Carpenter and Niem, 2001; Matsuura, 2015).

Suborder Balistoidei (Sclerodermi). Body usually compressed; frontals extending far anterior to articulation between lateral ethmoid and ethmoid; head and body covered with scales (scales may be highly modified and hidden by tissue); no pelvic fins (pelvic spine or tubercle present in balistines and some monacanthines, underlying pelvis present); first dorsal spine with locking mechanism (the small second spine, when present, forms the locking mechanism); upper jaw not protractile; upper jaw with two rows of protruding incisor-like teeth; soft dorsal fin with 23–52 rays and anal fin with 20–66 rays; caudal fin with 12 principal rays; the eyes can be rotated independently. Maximum length about 1.0 m, attained in *Aluterus scriptus.*

Three fossil families were recognized by Santini and Tyler (2003): †Moclaybalistidae, †Bolcabalistidae, and †Eospinidae.

About 40 genera and 149 species.

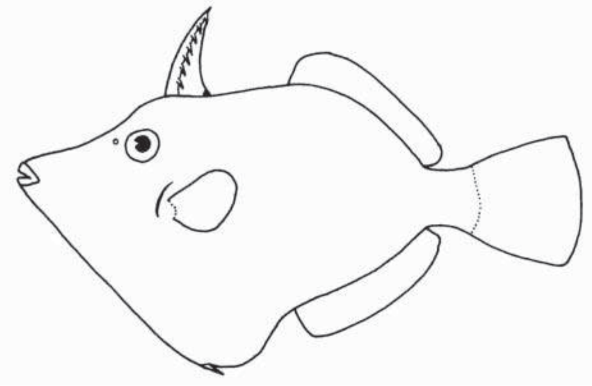
Family BALISTIDAE (532)—triggerfishes. Marine; Atlantic, Indian, and Pacific.



Three dorsal spines (third can be minute); all soft fins with branched rays; scales in regular series, plate-like; upper jaw usually with four teeth in outer and three in the inner series on each premaxillary, developed more for crushing than for nibbling; 18 vertebrae.

Twelve genera, *Abalistes* (3), *Balistapus* (1), *Balistes* (7), *Balistoides* (2), *Canthidermis* (3), *Melichthys* (3), *Odonus* (1), *Pseudobalistes* (3), *Rhinecanthus* (7), *Sufflamen* (5), *Xanthichthys* (1), and *Xenobalistes* (6), with 42 species (e.g., Matsuura in Carpenter and Niem, 2001; Matsuura, 2015).

Family MONACANTHIDAE (533)—filefishes. Marine; Atlantic, Indian, and Pacific.



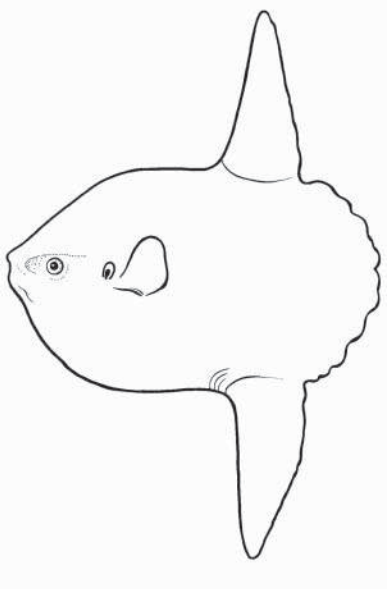
Usually two dorsal spines—the second is usually much smaller and it may be absent; soft dorsal, anal, and pectoral rays simple; scales small, in regular series; body prickly or furry to touch; upper jaw usually with three teeth in outer and two in the inner series on each premaxillary, developed for nibbling; 19–31 vertebrae. The greatest number of filefishes, some 54 species, occur in Australia (Hutchins, 1997). Miyajima et al. (2014) described a Miocene filefish in an extant genus (†*Aleuterus shigensis*) from Japan. Pliocene and Pleistocene fossils (the genus †*Frigocanthus* and two new species related to the Recent *Aluterus*) are known from Italy and Greece (Sorbini, 1988; Sorbini and Tyler, 2004).

About 28 genera (e.g., *Aluterus*, *Amanses*, *Anacanthus*, *Brachaluteres*, *Cantherhines*, *Chaetoderma*, *Enigmacanthus*, *Monacanthus*, *Navodon*, *Oxymonacanthus*, *Paraluteres*, *Paramonacanthus*, *Pervagor*, *Pseudalutarius*, *Rudarius*, *Stephanolepis*, and *Thamnaconus*) with about 107 species (e.g., Hutchins, 1997, 2002; Hutchins in Carpenter and Niem, 2001; Matsuura, 2015).

Suborder Tetraodontoidei (Gymnodontes). Jaw "teeth" fused (true teeth are absent in adults—the upper and lower jaws have cutting edges; a similar looking beak is found in the Scaridae); depending on the presence or absence of sutures, there may be two, three, or four such "teeth"; upper jaw not protractile; posttemporal absent; urohyal absent except in *Triodon*; pelvis absent except in *Triodon* and pelvic fin (spine and rays) absent.

Three families, 36 genera, and 218 species. Fossils include the Eocene †*Eoplectus* and †*Zignoichthys* (Tyler and Santini, 2002).

Family MOLIDAE (534)—molas (ocean sunfishes). Marine; tropical and subtropical; Atlantic, Indian, and Pacific.



Two fused structures in jaws; no spines in dorsal or anal fins; no caudal peduncle; caudal fin lost, posterior end of body reduced to a leathery flap or pseudo-caudal (clavus); two minute nostrils on each side; lateral line absent; no swimbladder; 16–18 vertebrae.

Johnson and Britz (2005) tested the hypothesis that the clavus is 1) a highly modified caudal fin, or 2) formed by highly modified elements of the dorsal and anal fins. Based on ontogenetic evidence, they concluded that the latter is correct, that it is formed by modified elements of the dorsal and anal fin, and that the caudal fin is lost in molids (see also Britz and Johnson, 2005).

The major locomotory thrust is provided by the powerful dorsal and anal fins. It has been estimated that up to 300 million eggs can be produced by one *Mola mola* (the ocean sunfish), probably making it the most fecund fish species. Molas feed extensively on jellyfishes. Maximum length over 2 m with weights up to 1,000 kg. Fossils include the Eocene †*Eomola* and the Miocene †*Austromola*. Santini and Tyler (2002b) gave a phylogeny of this family.

Three genera and four species: *Masturus lanceolatus* (recognized in *Mola* by some), *Mola mola, Mola ramsayi,* and *Ranzania laevis* (P. Parenti, 2003).

Family TETRAODONTIDAE (535)—puffers. Marine, with several entering and occurring in brackish and fresh water; tropical and subtropical; Atlantic, Indian, and Pacific.

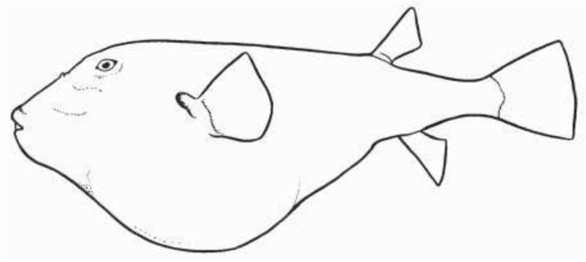
Body inflatable; body naked or with only short prickles (often confined to belly); four fused teeth in jaws (teeth in each jaw fused but separated by a median suture); premaxillae and dentaries not fused to opposite member at midline; dorsal and anal fins usually each with 7–18 soft rays (many more in *Chonerhinos* and *Xenopterus*); epineurals absent; caudal fin with 10 principal rays and no procurrent rays, moderately forked to rounded.

The "flesh" (especially the viscera) of some puffers contains the alkaloid poison tetraodotoxin, produced by the fish, which can be fatal. In at least some species, the gonads at spawning time contain the highest concentration of this poison; none occurs in the muscle.

About 12 species of *Carinotetraodon*, *Chonerhinos*, and *Tetraodon* occur only in fresh water, primarily in the Congo River and in southern Asia. Maximum length 90 cm; most much less.

Some 26 genera with about 196 species (e.g., Matsuura in Carpenter and Niem, 2001; Matsuura, 2015).

SUBFAMILY TETRAODONTINAE. Body broadly rounded in cross section; one or two conspicuous nostrils on each side; lateral line usually conspicuous; gill opening usually extending below midportion of pectoral fin; erectable ridge of skin on dorsal and ventral midline only in *Carinotetraodon* (which may be related to *Canthigaster*, placed in the next subfamily; Tyler, 1980); vertebrae 17–29.



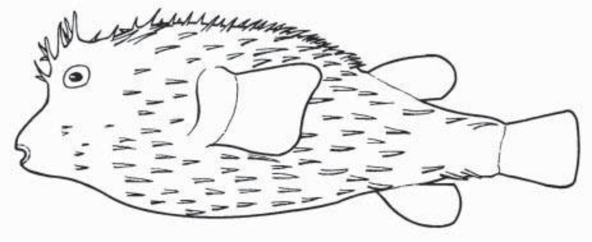
About 25 genera (e.g., *Amblyrhynchotes*, *Arothron*, *Auriglobus*, *Carinotetraodon*, *Chelonodon*, *Chonerhinos*, *Colomesus*, *Contusus*, *Ephippion*, *Feroxodon*, *Guentheridia*, *Javichthys*, *Lagocephalus*, *Marilyna*, *Omegophora*, *Pao*, *Pelagocephalus*, *Polyspina*, *Reicheltia*, *Sphoeroides*, *Takifugu* (synonym *Fugu*), *Tetraodon* (see Eschmeyer, 1998, for discussion of orthography of possible synonym *Monotretus*, *Monotreta*, or *Monotrete*), *Tetractenos*, *Torquigener*, and *Tylerius* with about 159 species (e.g., Roberts, 1998b; Britz and Kottelat, 1999c; Saenjundaeng et al., 2013).

SUBFAMILY CANTHIGASTRINAE (SHARPNOSE PUFFERFISHES). Body laterally compressed (deeper than broad) in uninflated condition; single inconspicuous nostril on each side; lateral line inconspicuous; gill opening restricted, ending ventrally about level of midportion of pectoral fin; snout elongate and relatively pointed; erectable ridge of skin on dorsal and ventral midline; vertebrae usually 17 (8 + 9). Maximum length usually less than 12 cm. Most species of sharpnose puffers occur in shallow water, usually near coral reefs, and feed on benthic organisms. All but one species (which occurs in the Atlantic) occur in tropical Indo-Pacific waters (from the Red Sea and South Africa to Central America).

Tyler (1980) suggested that *Carinotetraodon* (in Tetraodontinae, above) is the closest relative of *Canthigaster*, based on sharing traits such as distinct (not meeting in the midline) parapophyses on the first few abdominal vertebrae, and the ability to erect mid-dorsal and mid-ventral keels during courtship (Tyler, 1980; Britz and Kottelat, 1999). Depending on the relationships of *Carinotetraodon* within Tetraodontidae, it is possible that separating the subfamilies Canthigastrinae and Tetraodontinae is incorrect.

One genus, *Canthigaster*, with 37 species (e.g., Moura and Castro, 2002).

Family DIODONTIDAE (536)—porcupinefishes (burrfishes). Marine; Atlantic, Indian, and Pacific.



Body inflatable; body covered with well-developed sharp spines (in some species the spines erect only when body is inflated); two fused structures in jaws (parrot-like); premaxillae and dentaries completely fused to opposite member at midline.

Adults inhabit inshore waters while the young are pelagic.

Seven genera, *Allomycterus* (1), *Chilomycterus* (6), *Cyclichthys* (3), *Dicotylichthys* (1), *Diodon* (5), *Lophodiodon* (1), and *Tragulichthys* (1), with 18 species (Leis in Carpenter and Niem, 2001; Matsuura, 2015).

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Index

Aaptosyax, 183
Abactochromis, 344
Abadzekhia, 415
Abalistes, 523
abas, 160
Abisaadia, 139
Abisaadichthys, 132
Ablabys, 471
Ablennes, 368
Aboma, 332
Aborichthys, 192
Abramis, 184
Abramites, 200
Abudefduf, 339
Abyssoberyx, 310
Abyssobrotula, 318
Abyssocottinae, 485, 492
Abyssocottus, 492
Acanthanectes, 347
Acanthaphritis, 425
Acantharchus, 444, 445, 446
Acanthemblemaria, 351
Acanthistius, 446, 447
Acanthobrama, 184
Acanthobunocephalus, 233
Acanthocepola, 461
Acanthochaenus, 310
Acanthocharax, 205
Acanthochromis, 338
Acanthocleithron, 227
Acanthoclininae, 336
Acanthoclinus, 336, 337
Acanthocobitis, 192
Acanthocybium, 417
Acanthodes, 97, 100, 101
acanthodians, 43, 44, 96
ACANTHODIDAE, 101
ACANTHODIFORMES, 97, 100
Acanthodii, 36, 40, 95, 96, 98
Acanthodopsis, 101
Acanthodoras, 234
Acanthodraco, 466
Acanthogobius, 330
Acantholabrus, 428
Acantholingua, 247
Acantholiparis, 495
Acantholumpenus, 480
Acanthomorpha, 276, 278, 279, 280, 307
acanthomorphs, 278
Acanthonus, 318
Acanthopagrus, 506
Acanthophthalmus, 190
Acanthoplesiops, 337
Acanthopoma, 213
Acanthopsetta, 400
Acanthopsoides, 190
acanthopterygian, 280
Acanthopterygii, 264, 265, 279, 280, 284, 286, 302, 303, 353
Acanthorhina, 51
Acanthoscyllium, 62
Acanthosphex, 473
Acanthostega, 111
Acanthostracion, 522
ACANTHOTHORACIFORMES, 37
Acanthuridae, 499, 500, 501
ACANTHURIFORMES, 420, 430, 452, 495, 497
Acanthurinae, 502
Acanthurini, 502
Acanthuroidei, 453, 462, 496, 497, 498, 499
Acanthurus, 502
Acantopsis, 190
Acarobythites, 319
Acaronia, 344
Acentrogobius, 332
Acentronichthys, 236
Acentronura, 408
Acentrophorus, 121
Acentrophryne, 518
Acerinae, 448
Acestridium, 217

Acestrocephalus, 205
ACESTRORHYNCHIDAE, 198, 203
acestrorhynchids, 203
Acestrorhynchinae, 203
Acestrorhynchus, 203
Acheilognathinae, 184
Acheilognathus, 184
ACHIRIDAE, 402, 403
Achiroides, 404
Achiropsetta, 402
ACHIROPSETTIDAE, 398, 402
Achiropsis, 403
Achirus, 403
Achoania, 103
Achoerodus, 428
Achondrostoma, 184
Acidorhynchus, 115
Acipenser, 120
ACIPENSERIDAE, 119
ACIPENSERIFORMES, 118
Acipenserinae, 120
Acipenseroidei, 118
Acnodon, 199
Acrania, 16
Acritolepis, 98
Acrocheilus, 184
Acrochordonichthys, 224
ACRODONTIDAE, 56
Acrodus, 56
Acrolamna, 64
ACROLEPIDAE, 113
Acrolepis, 113
Acromycter, 148
Acronemus, 55
Acropoma, 434
ACROPOMATIDAE, 434, 450
Acrorhizodus, 56
Acrosqualiodus, 77
Acrossocheilus, 183
Acroteriobatus, 86
ACTINISTIA, 103
ACTINOLEPIDIDAE, 39
Actinolepidoidei, 39
Actinolepis, 39
Actinopterygii, 95, 96, 97, 101, 111, 112, 115, 116, 117
  crown-group, 116
  stem-group, 112
Aculeola, 76
Acuticurimata, 201
Acyrtops, 352
Acyrtus, 352
Adamas, 371
Adelosebastes, 469
Adelotremus, 349
Adinia, 374
Adiposia, 192
Adontosternarchus, 241
ADRIANICHTHYIDAE, 363, 364, 370
adrianichthyids, 364
Adrianichthyinae, 365
Adrianichthyoidei, 354, 363
Adrianichthys, 365
Adventor, 473
AEDUELLIDAE, 113
Aegyptobatus, 56
Aeoliscus, 411
Aequidens, 344
Aesopia, 404
AESOPICHTHYIDAE, 114
Aesopichthys, 112
Aetapcus, 474
Aethalionopsis, 177
Aethaloperca, 447
Aethaspis, 39
Aetheodontus, 116
Aethiomastacembelus, 383
Aethotaxis, 465
Aetobatus, 93, 94
Aetomylaeus, 93, 94
African pikes, 196
African tetras, 196
Africentrum, 304
Afromastacembelinae, 383
Afronandus, 395
Agamyxis, 234
AGASSIZODONTIDAE, 50
AGENEIOSIDAE, 234
Ageneiosus, 234
Agkistracanthus, 51
Aglyptorhynchus, 388
Agnatha, 18
agnathans, 18, 19
Agoniates, 205
Agoniatinae, 205
AGONIDAE, 485, 490
Agoninae, 491
Agonomalus, 490
Agonopsis, 490, 491
Agonostomus, 342
Agonus, 490, 491
Agosia, 184
Agoultichthys, 124
Agrammus, 487
Agrostichthys, 284
Ahlia, 146
Ahliesaurus, 273
aholeholes, 438
Aiakas, 479
Aidablennius, 348
Ailia, 221, 228
Ailiichthys, 228
AILIIDAE, 221, 228
AIPICHTHYIDAE, 280
AIPICHTHYOIDIDAE, 280
Akarotaxis, 466
Akawaio, 240
Akihito, 330
Aktaua, 94
AKYSIDAE, 221, 223, 224, 228
Akysinae, 224
Akysis, 224
Alabes, 352, 353
ALABETIDAE, 353
Alaska Blackfish, 250
Albatrossia, 296
Albertonia, 125
Albula, 134, 136
ALBULIDAE, 136
ALBULIFORMES, 133, 136
Albulinae, 136
Alburninae, 183, 184
Alburnoides, 184
Alburnus, 184
Alcichthys, 492
Alcockia, 318
Alcoveria, 105
Aldrichetta, 342
Aldrovandia, 138
Alectis, 387
Alectrias, 480
Alectridium, 480
Alepes, 387
Alepidomus, 362, 363
ALEPISAURIDAE, 275
Alepisauroidea, 273
Alepisauroidei, 267, 270
Alepisaurus, 275, 276
Alepocephali, 161, 162, 172
ALEPOCEPHALIDAE, 173, 174
ALEPOCEPHALIFORMES, 161, 172
Alepocephaloidei, 161, 172, 252
Alepocephalus, 174
Alertichthys, 475
Alestes, 196
ALESTIDAE, 193, 196
ALESTIIDAE, 193, 196
Alestiinae, 204
Alestoidea, 196

Aleuterus, 523
Alfarini, 379
Alfaro, 379
alfonsinos, 313, 314
algae eaters, 187
Algansea, 184
Alionematichthys, 319
Allanetta, 363
Allenbatrachus, 323
Allenichthys, 510
Alloberyx, 304
Alloblennius, 348
Alloclinus, 351
Allocyttus, 291
Allodontichthys, 374
Allolumpenus, 480
Allomicrodesmus, 329
Allomogurnda, 329
Allomycterus, 526
Alloophorus, 374
Allopholis, 481
Allosmerus, 257
ALLOTHRISSOPIDAE, 131
Allothrissops, 131
Allothunnus, 417
Allotoca, 374
Allotriognathi, 280
Almascyllium, 62
Alopias, 66
ALOPIIDAE, 66
Alosa, 171
Alosinae, 170, 171, 172
Alphestes, 447
Alticorpus, 344
Alticus, 348
Altrichthys, 338
Aluterus, 522, 523
Amanses, 523
Amaralia, 233
Amarginops, 229
amarsipas, 418
AMARSIPIDAE, 418
Amarsipus, 418
Amatitlania, 344
Amazonsprattus, 168
AMBASSIDAE, 334, 335
Ambassis, 335
Ambastaia, 190
amberjacks, 386
Ambiserrula, 477
Ambloplites, 444, 445
Amblyapistus, 471
Amblyceps, 224
Amblychaeturichthys, 330
AMBLYCIPITIDAE, 221, 223, 224, 228
Amblycirrhitus, 459
Amblydoras, 234
Amblyeleotris, 332
Amblygaster, 171, 172
Amblyglyphidodon, 339
Amblyopinae, 330
AMBLYOPSIDAE, 284, 289
Amblyopsis, 289
Amblypharyngodon, 182
Amblypomacentrus, 339
AMBLYPTERIDAE, 113
Amblypterus, 113
Amblyraja, 85
Amblyrhynchotes, 525
Amblysemius, 125
Ambophthalmos, 493
Ameca, 374
AMEIURIDAE, 235
Ameiurus, 235, 236
American soles, 402
Amia, 122, 125, 126, 128
AMIIDAE, 124, 125, 126
AMIIFORMES, 121, 124, 125
Amioidei, 125
Amioides, 325
Amiopsis, 126
Amissidens, 232
Ammocrypta, 450
Ammocryptocharax, 196
Ammodytes, 426
Ammodytidae, 421, 425
Ammodytoides, 426
Ammoglanis, 214
Ammolabrus, 428
Ammotretis, 402
Amniataba, 441
Amoya, 332
Ampheristus, 317
Amphiarius, 232
AMPHIASPIDIDAE, 28
Amphichaetodon, 455
Amphichthys, 323
AMPHILIDAE, 226
AMPHILIIDAE, 226
Amphiliinae, 226
Amphilius, 226
Amphilophus, 344
AMPHIOXIFORMES, 16
amphioxus, 16
Amphiperca, 315
Amphiplaga, 288
Amphipnous, 381
Amphiprion, 337, 338
Amphiprioninae, 337, 338
Amphistichus, 335
Amphistium, 396
Amsichthys, 340
Amylodon, 52
Amyzon, 187
ANABANTIDAE, 390, 391
ANABANTIFORMES, 334, 380, 390, 394
Anabantoidei, 390
Anabas, 391, 504
ANABLEPIDAE, 370, 376
Anablepinae, 376
Anableps, 377
ANACANTHOBATIDAE, 84
Anacanthobatis, 84, 85
Anacanthobythites, 319
Anacanthus, 523
ANACORACIDAE, 64
Anadoras, 234
Anaecypris, 184
Anaethalion, 134
Analectis, 281
Anampses, 428
Anaora, 413
Anarchias, 143
Anarchopterus, 408
ANARHICHADIDAE, 481
Anarhichas, 481
Anarrhichthys, 481
Anaspida, 29, 30
ANASPIDIFORMES, 29
Anaspidoglanis, 228
Anaspidomorphi, 18, 26, 29
Anatirostrum, 332
Anatolanthias, 447
Anatolepis, 22
Anatolichthys, 375
ANCHARIIDAE, 231, 232
Ancharius, 231
Anchichoerops, 428
ANCHIPTERASPIDIDAE, 29
Anchoa, 168
Anchovia, 167, 168
Anchoviella, 168
anchovies, 167
Ancistrinae, 217
Ancistrogobius, 332
Ancistrus, 217
Ancylopsetta, 399
Andamia, 123, 348
Andersonia, 226
Andinaspis, 27
ANDINICHTHYIDAE, 210
Andinichthys, 210
Andinoacara, 344
Andreevichthys, 108
Andreolepis, 101, 111, 113

Andriashevia, 479
Anduzedoras, 234
Anematichthys, 183
anemonefishes, 338
angel sharks, 79
angelfishes, 343, 455, 456
Anglaspis, 29
anglerfishes, 508
anglers, 508
  double anglers, 515
  warty anglers, 510
  whipnose anglers, 517
  wolftrap anglers, 516
Angoumeius, 77
Anguilla, 139, 144, 152, 153
Anguillavus, 139
ANGUILLIDAE, 152
ANGUILLIFORMES, 133, 134, 139, 140, 142
Anguilloidei, 149, 151
Anisarchus, 480
Anisochrominae, 340
Anisochromis, 340
Anisotremus, 457
Ankistrorhynchus, 85
Annaichthys, 129
Annamia, 192
Annea, 60
Anodontiglanis, 221
Anodontinae, 199
Anodontostoma, 172
Anodus, 199, 201
ANOMALOPIDAE, 303, 306
Anomalops, 306
Anomotodon, 65
Anoplagoninae, 490
Anoplagonus, 490
Anoplarchus, 480
Anoplocapros, 521
Anoplogaster, 306
ANOPLOGASTRIDAE, 303, 305
Anoplogastroidei, 305
Anoplopoma, 486
ANOPLOPOMATIDAE, 485
Anoplopomatoidea, 485
Anoptichthys, 204
ANOSTOMIDAE, 197, 200
Anostomoidea, 198
Anostomoides, 200
Anostomus, 200
Anotodus, 66
Anotophysi, 174, 175
ANOTOPTERIDAE, 275
Anotopterus, 274, 275, 276
Anoxypristis, 87
Antarcilamna, 44
ANTARCTASPIDIDAE, 39
Antarctiberyx, 308
Antarctic dragonfishes, 466
Antarctic sculpins, 494
Antarctilamna, 44
ANTARCTILAMNIDAE, 44
ANTARCTILAMNIFORMES, 44
Antennablennius, 348
ANTENNARIIDAE, 509
Antennarioidei, 508, 509
Antennarius, 509, 510
Antennatus, 510
Anthias, 447
Anthiinae, 446, 447
ANTIARCHIFORMES, 37
antiarchs, 37
Antigonia, 507
Antigoniinae, 507
Antipodocottus, 491
Anyperodon, 447
Apagesoma, 318
APALOLEPIDIDAE, 31
Apalolepis, 31
Apareiodon, 198
Apateodus, 267
APATEOPHOLIDAE, 267
Apeltes, 484
Aphanius, 375
Aphanopodinae, 416
Aphanopus, 416
Aphareus, 458
Aphetohyoidea, 97
Aphos, 322
APHREDODERIDAE, 284, 288
Aphredoderus, 289
Aphyocharacidium, 206
Aphyocharacinae, 206
Aphyocharax, 206
Aphyocypris, 185
Aphyodite, 206
Aphyoditeinae, 206
Aphyolebias, 372
APHYONIDAE, 319
aphyonids, 319
Aphyonus, 320
Aphyoplatys, 371
Aphyosemion, 371
Apionichthys, 403
APISTIDAE, 468
Apistinae, 469, 471
Apistogramma, 344
Apistoloricaria, 217
Apistops, 471
Apistus, 471
Apletodon, 352
APLOACTINIDAE, 468, 469, 471, 473
Aploactininae, 473
Aploactis, 473
Aploactisoma, 473
Aplocheilichthyinae, 378
Aplocheilichthys, 378
APLOCHEILIDAE, 371
Aplocheiloidei, 370
Aplocheilus, 371
Aplochiton, 256
APLOCHITONIDAE, 242
Aplochitoninae, 255, 256
APLODACTYLIDAE, 459, 460
Aplodactylus, 460
Aplodinotus, 499
Apodes, 139
Apodichthyinae, 481
Apodichthys, 480, 481
Apodocreedia, 424
Apogon, 325, 434
Apogonichthyoides, 325
Apogonichthys, 325
APOGONIDAE, 324, 326, 434
Apogoninae, 325
Apogonops, 434
APOLECTIDAE, 386
Apolemichthys, 456
Apomatoceros, 213
Apopterygion, 347
Aporops, 448
Appendicularia, 15
Aprion, 458
Apristurus, 69
Apsilinae, 458
Apsilus, 458
Apsopelix, 130
Apterichtus, 146
APTERONOTIDAE, 241
Apteronotoidea, 240
Apteronotus, 241
Aptocyclus, 495
Aptychotrema, 86
Aquilopiscis, 130
Aracana, 521
ARACANIDAE, 518, 521
Araiophos, 260
Arandaspida, 18, 27
ARANDASPIDIFORMES, 27
Arandaspis, 27
Arapaima, 153, 157
Araripelepidotes, 122

ARARIPICHTHYIDAE, 132
ARARIPICHTHYIFORMES, 132
Araripichthys, 132
arawana, 158
ARCHAEOBATIDAE, 82
Archaeobatis, 50
Archaeolamna, 64
ARCHAEOLAMNIDAE, 64
Archaeomanta, 95
Archaeonectes, 108
Archaeoteuthis, 463
Archamia, 325
archerfishes, 438, 439
ARCHIPELEPIDIDAE, 31
ARCHIPELEPIDIFORMES, 31
Archipelepis, 31
Archolaemus, 241
Archoplites, 444, 445
Archosargus, 506
Arcos, 352
Arctogadus, 302
Arctolepis, 39
Arctoscopus, 488
Arctozenus, 275
ARGANODONTIDAE, 109
Arganodus, 109
Argentina, 253
argentines, 253
ARGENTINIDAE, 252, 253
ARGENTINIFORMES, 161, 172, 252
Argentinoidei, 252
Argentinolycus, 479
ARGIDAE, 216
Argonectes, 200
Argopleura, 206
Argyripnus, 260
Argyropelecus, 260
Argyrops, 506
Argyrosomus, 499
Argyrozona, 506
ARHYNCHOBATIDAE, 84
Arhynchobatinae, 84, 85
Arhynchobatis, 85
ARIIDAE, 209, 219, 231, 232
Ariinae, 232
Arioida, 210
Arioidea, 229, 231
Ariomma, 419
ARIOMMATIDAE, 419
ariommatids, 419
Ariopsis, 232
Ariosoma, 148
Aristichthys, 186
Aristostomias, 264
Arius, 232
ARMIGATIDAE, 163
Armigatoidei, 163
Armigatus, 163
Armored Blenny, 426
armored searobins, 476
armored sticklebacks, 484
armorheads, 443
Arnoglossus, 401
Arothron, 525
Arrhamphus, 367
ARRIPIDAE, 439, 440
Arripis, 439
Artedidraco, 466
ARTEDIDRACONIDAE, 466
Artediellus, 492
Artedius, 492
arthrodires, 39
ARTHRODIRIFORMES, 39
aruana, 158
Asarcenchelys, 146
Ascelichthys, 492
Ascidiacea, 15
ascidians, 15
Ascoldia, 480
Asemichthys, 492
Aseraggodes, 404
Aserotaspis, 28
Asian seaperches, 435
ASIANTHIDAE, 315
Asianthus, 315
Asiatic glassfishes, 334
ASIATOCERATODONTIDAE, 109
Asiatoceratodus, 109
ASINEOPIDAE, 279
Asineops, 279, 280
Askoldia, 480
Aspasma, 352
Aspasmichthyes, 352
Aspasmodes, 352
Aspasmogaster, 352
Aspericorvina, 499
Aspidontus, 349
Aspidoparia, 182
Aspidophoroides, 490
Aspidoras, 215
Aspidorhynchei, 127
ASPIDORHYNCHIDAE, 127
ASPIDORHYNCHIFORMES, 127
Aspidorhynchus, 127
Aspistor, 232
Aspitrigla, 476
Aspius, 184
Aspredinichthys, 233
ASPREDINIDAE, 221, 223, 232
Aspredininae, 233
Aspredo, 233
Asprocottus, 492
Asquamiceps, 174
Assessor, 336
Assiculoides, 340
Assiculus, 340
Assurger, 416
Astatotilapia, 344
Astephus, 235, 236
Asteracanthus, 56
Asterodermus, 82, 86
ASTEROLEPIDIDAE, 39
Asterolepis, 39
Asterophysus, 234
Asterorhombus, 401
ASTEROSTEIDAE, 37
Asterotrygon, 91
Asterropteryx, 332
Asthenocormus, 127
Astrapogon, 325
Astraspida, 27
ASTRASPIDIFORMES, 27
Astraspis, 18, 27, 28
ASTROBLEPIDAE, 196, 215, 216, 217
Astroblepus, 216
Astrodoras, 234
Astronesthes, 262
Astronesthinae, 262
Astronesthoidea, 261
Astronotus, 344
Astroscopus, 426, 427
Astyanax, 204
Asymbolus, 69
Asymmetron, 16
ASYMMETRONTIDAE, 16
Atacamaia, 104
Ataeniobius, 374
Ataxolepis, 313
Ateleaspis, 33, 34
ATELEOPODIDAE, 265
ATELEOPODIFORMES, 265
Ateleopodomorpha, 264, 265
Ateleopus, 265
Atelomycterus, 69
Athenaegis, 28
Atheresthes, 399
Atherina, 363
Atherinason, 363
Atherinella, 357

ATHERINIDAE, 341, 356, 357, 358, 360, 362
ATHERINIFORMES, 334, 354, 355, 362
Atherininae, 363
Atherinoida, 355, 357
Atherinoidei, 357
Atherinomorinae, 362, 363
Atherinomorpha, 302, 333, 334, 341, 342, 353, 354, 355
Atherinomorus, 363
Atherinops, 356
ATHERINOPSIDAE, 355, 356, 357, 358, 362
Atherinopsinae, 356
Atherinopsini, 356
Atherinopsis, 356
Atherinopsoidei, 355, 357
Atherinosoma, 363
Atherion, 360
ATHERIONIDAE, 357, 360
Atka mackerels, 488
Atlantic Sailfish, 389
Atlantic Sheepshead, 506
Atlantoraja, 85
Atomaster, 200
Atopacanthus, 100
Atopochilus, 227
Atopodontus, 227
Atractodenchelys, 142
Atractoscion, 499
Atractosteus, 123
Atrilinea, 184
Atrobucca, 499
Atrophacanthus, 520
Atropus, 387
Atrosalarias, 348
Atule, 387
Atypichthys, 441
Auchenionchus, 351
AUCHENIPTERIDAE, 232, 234
Auchenipterinae, 234
Auchenipterus, 234
Auchenoceros, 298
AUCHENOGLANIDAE, 228
AUCHENOGLANIDIDAE, 226, 228, 229
Auchenoglaninae, 222
Auchenoglanis, 228, 229
Aulacocephalus, 447
Aulastomatomorpha, 174
Aulichthys, 483
Aulohalaelurus, 69
Aulolepis, 280
Aulonocara, 344
Aulopareia, 332
AULOPIDAE, 266, 268
AULOPIFORMES, 265, 266, 276
AULOPODIDAE, 269
Aulopoidei, 266, 267, 269
Aulopus, 269
Aulopyge, 183
AULORHYNCHIDAE, 483
Aulorhynchus, 482, 483
AULOSTOMIDAE, 409
Aulostomoidea, 409
Aulostomoidei, 405, 409
Aulostomus, 409
Aulotrachichthys, 308
Aurigequula, 454
Auriglobus, 525
Australasian salmon, 439
Australian prowfishes, 474
Australoheros, 344
Australosomus, 116
Austrobatrachus, 323
Austrofundulus, 372
AUSTROGLANIDIDAE, 219, 222
Austroglanis, 219
Austroglossus, 404
Austrolabrus, 428
Austrolebias, 372
Austrolycus, 479
Austromallotus, 257
Austromola, 524
Austronibea, 499
Austrophyllolepis, 39
Auxis, 417
Avitoluvarus, 500
Avitosmerus, 241
Avocettina, 151
Awaous, 196, 330
Axelia, 104
Axelrodia, 206
Axelrodichthys, 105
Axinurus, 502
Axoclinus, 347
Ayarnangra, 225
Ayu, 257
AZTECODONTIDAE, 44
Aztecodus, 44
Aztecula, 184
Azurina, 338
Azygopterus, 480
Azygopus, 402

Bacchiaichthys, 320, 321
Bachmannia, 210
BACHMANNIIDAE, 210
Bachynectes, 347
BADIDAE, 394, 395
Badis, 395
BAGARIIDAE, 224
Bagarius, 225
Bagre, 232
Bagreinae, 232
Bagrichthys, 223
BAGRIDAE, 219, 220, 221, 222, 228, 229
Bagroidea, 232
Bagroides, 223
Bagrus, 222, 223
Bahaba, 499
Bahariyodon, 56
Baikal oilfishes, 492
Baileychromis, 344
Baione, 247
Baiostoma, 403
Bairdiella, 499
Bajacalifornia, 174
Bajaichthys, 281
Balantiocheilos, 183
Baldwinella, 447
Balistapus, 523
Balistes, 523
BALISTIDAE, 518, 522
Balistoidei, 522
Balistoides, 523
Balitora, 191
BALITORIDAE, 191, 192, 196
balitorines, 191
Balitoropsis, 191
Ballerus, 184
bamboo sharks, 61
BANANOGMIIDAE, 132
bandfishes, 461
Bandringa, 45
BANDRINGIDAE, 45
Bangana, 182
bangos, 177
bangus, 177
banjofishes, 444
Banjos, 444
BANJOSIDAE, 444
Barameda, 110
Barathrites, 318
Barathrodemus, 318
Barathronus, 320
Barbantus, 173
Barbapellis, 479
Barbatula, 192
barbel, 181
barbeled dragonfishes, 261

barbeled grunters, 457
barbeled hound sharks, 70
barbeled plunderfishes, 466
barbels, 183
Barbinae, 183
Barbourisia, 311
BARBOURISIIDAE, 311
Barbucca, 192
BARBUCCIDAE, 192
Barbulifer, 332
Barbuligobius, 332
Barbus, 181, 183
Barchatus, 323
barehead scorpionfishes, 478
Barilius, 182
BARLOWODIDAE, 31
Barlowodus, 31
barracudas, 387, 388
barracudinas, 274
  barracudinas, 274
  naked barracudinas, 276
  sudid barracudinas, 274
Barramundi, 432
barreleyes, 253
Barwickia, 108
Bascanichthys, 146
Basilichthys, 356
basking sharks, 67
Bassania, 315
basses, 446
  basses, 446
  sea basses, 446
  southern basses, 433
  temperate basses, 495, 496
basslets, 336
Bassogigas, 318
Bassozetus, 318
Batasio, 223
batfishes, 511, 512
Bathophilus, 261, 263
Bathyagoninae, 491
Bathyagonus, 491
Bathyanthias, 447
Bathyaploactininae, 473
Bathyaploactis, 473
Bathybagrus, 229
Bathybates, 344
Bathyblennius, 348
Bathycallionymus, 413
Bathycetopsis, 212
Bathychaunax, 511
Bathyclarias, 230
Bathyclupea, 438
BATHYCLUPEIDAE, 438
bathyclupeids, 438
Bathydraco, 466
BATHYDRACONIDAE, 466
BATHYGADIDAE, 296
Bathygadus, 296
Bathygobius, 332
Bathylaco, 173
BATHYLACONIDAE, 173, 174
bathylaconids, 173
Bathylagichthys, 254
BATHYLAGIDAE, 254
Bathylagoides, 254
Bathylagus, 254
Bathyleptus, 271
BATHYLUTICHTHYIDAE, 494
Bathylutichthys, 494
Bathylychnops, 253
Bathymaster, 478
BATHYMASTERIDAE, 478
Bathymicrops, 271
Bathymyrinae, 148
Bathymyrus, 148
Bathyonus, 318
Bathyphylax, 520
Bathyprion, 174
Bathypterois, 270, 271
Bathyraja, 85
BATHYSAURIDAE, 272
Bathysaurinae, 268
Bathysauroides, 266, 272
BATHYSAUROIDIDAE, 271
Bathysauropsinae, 271
bathysauropsines, 271
Bathysauropsis, 266, 271
Bathysaurus, 268, 272
Bathysolea, 404
Bathysomi, 281
Bathysphyraenops, 434
Bathystethus, 441
Bathytroctes, 174
Bathytyphlops, 271
Batidoidimorpha, 80
Batoidea, 56, 73, 80
Batomorphi, 37, 43, 56, 57, 73, 80, 81, 84, 95
batomorphs, 54
Batrachocephalus, 232
Batrachocottus, 485
Batrachoides, 323
Batrachoidida, 314, 320, 405, 414
BATRACHOIDIDAE, 321
BATRACHOIDIFORMES, 284, 320, 321, 323
Batrachoidinae, 321, 322, 323
Batrachomoeus, 323
Batrichthys, 323
Batrochoglanis, 238
Bdellodus, 56
Bdellostoma, 21
beaked sandfishes, 177
Bealbonn, 49
beardfishes, 285, 286
Beaufortia, 192
Bedotia, 358, 359
BEDOTIIDAE, 357
Bedotiinae, 358
Belantsea, 50
BELANTSEIDAE, 50
Belemnobatis, 82, 86
Belemnocerca, 104
Belgorodon, 53
Beliops, 337
Bellapiscis, 347
Bellator, 476
Bellingshausenia, 479
Bellocia, 174
Bellottia, 318, 319
Bellwoodilabrus, 427
Belobranchus, 329
Belodontichthys, 219
Belone, 368
Belonepterygion, 337
Belonesox, 378, 380
BELONIDAE, 368, 369
BELONIFORMES, 334, 354, 363, 364
Belonion, 368
Belonoglanis, 226
Belonoidei, 365
Belonoperca, 447
Belonophago, 195
Belonorhynchus, 115
Belonostomus, 127
BELONTIIDAE, 393
Belontiinae, 392
Beluga, 120
Bembradium, 476, 477
Bembradon, 477
Bembras, 477
BEMBRIDAE, 468, 475, 476
Bembropinae, 424
Bembrops, 424
Benitochromis, 344
BENNEVIASPIDAE, 34
Bentartia, 479
Benthalbella, 273, 274
Benthenchelys, 146
Benthesikyme, 267

Benthobatis, 83
Benthocometes, 318
Benthodesmus, 416
Benthophilus, 332
Benthosaurus, 271
Benthosema, 278
Bergiaria, 237
Bero, 492
Bertella, 515
Berybolcensis, 304
Berycida, 279, 303, 308
BERYCIDAE, 309, 314
BERYCIFORMES, 279, 285, 303, 308, 309, 387
beryciforms, 308
Berycoidei, 308, 313
Berycopsis, 286
Beryx, 314
Betta, 392
Bhanotia, 408
Bhavania, 191
Bibarba, 190
bichirs, 116, 117
Bidenichthys, 319
Bidyanus, 441
Bifax, 323
bigeye flounders, 401
Bigeye Tuna, 417
bignose fishes, 312
bigscale fishes, 313
Bihunichthys, 382
Bilabria, 479
billfishes, 387, 389, 414
Biotodoma, 344
Birgeria, 113
BIRGERIIDAE, 113
Birkenia, 30
Birkeniae, 29
Birkeniida, 29
Bivibranchia, 200
Bivibranchiini, 200
Black Arowana, 158
black seadevils, 514
blackchins, 277
Bleekeria, 426
Bleheratherina, 363
Bleheratherininae, 363
Blenniella, 348
blennies, 346, 352
    Armoured Blenny, 426
    combtooth blennies, 348
    kelp blennies, 349
    labrisomid blennies, 350
    Patagonian blennies, 465
    sand stargazers, 347
    triplefin blennies, 346
    tube blennies, 351
BLENNIIDAE, 333, 348
BLENNIIFORMES, 333, 341, 346
Blenniinae, 349
Blennioclinus, 350
Blennioidei, 334, 346, 352
Blennius, 349
Blennodesmus, 340
Blennodon, 347
Blennophis, 350
Blepsias, 490
Blicca, 181, 184
blind cusk-eels, 319
blind sharks, 60
BLOCHIIDAE, 388
Blochius, 388
blue eyes, 358, 359
Blue Marlin, 388
Blue Shark, 72
Bluefin Tuna, 414
Bluefish, 451
bluefishes, 451
Bluegill, 444
boarfishes, 443, 506, 507
Bobasatrania, 114
BOBASATRANIIDAE, 114
Bobbichthys, 130
Bobbodus, 50
Bodianus, 428
Boehlkenchelys, 144
Boesemania, 499
Boga, 457
BOGODIDAE, 335
Bolbocara, 296
Bolbometopon, 430
BOLCABALISTIDAE, 522
Boleophthalmus, 330
Bolinichthys, 278
Bollandaspis, 39
Boltyshia, 249
Bonapartia, 260
bonefishes, 133, 136
bonitos, 417
Bonnerichthys, 127
Bonnetmouth, 457
bony fishes, 44, 101
bonytongues, 155, 156
Boops, 506
Boopsinae, 506
Boopsoidea, 506
BOOTHIALEPIDIDAE, 31
Boothialepis, 31
Boraras, 182
Boreaspis, 33
Boreogadus, 302
Boreosomus, 113, 115
Boridia, 457
Borodinopristis, 85
Borophryne, 518
Borostomias, 262
Bostockia, 433, 442
Bostrychus, 329
BOTHIDAE, 166, 396, 398, 400
Bothragoninae, 490
Bothragonus, 490
BOTHRIOLEPIDIDAE, 38
Bothriolepidoidei, 38
Bothriolepis, 38
Bothrocara, 479
Bothrocarina, 479
Bothus, 401
Botia, 190
BOTIIDAE, 189
Botiinae, 189
Boulengerella, 203
Boulengerochromis, 343
BOVICHTHYIDAE, 464
Bovichthys, 464
BOVICHTIDAE, 464
Bovichtus, 464, 465
Bovitrigla, 476
Bowfin, 122, 125, 126
bowfins, 121, 122, 125, 126
bowmouth guitarfishes, 86
boxfishes, 521
    boxfishes, 521
    deepwater boxfishes, 521
BRACHAELURIDAE, 60
Brachaelurus, 60
Brachaluteres, 523
BRACHIONICHTHYIDAE, 510
Brachionichthys, 511
Brachiopsilus, 511
Brachiopterygii, 116
Brachirus, 404
Brachyamblyopus, 330
Brachybembras, 477
Brachycarcharias, 65
Brachychalcinus, 205
Brachydanio, 181, 182
Brachydeuterus, 457
Brachygalaxias, 256
Brachyglanis, 236
Brachygobius, 330
Brachyhypopomus, 240
Brachyistius, 335
Brachymylus, 52
Brachymystax, 246, 248
Brachyopsinae, 490

Brachyopsis, 490
Brachyplatystoma, 237
Brachypleura, 398
Brachypterois, 470
Brachyrhamdia, 236
Brachyrhaphini, 379
Brachyrhaphis, 380
Brachyrhizodus, 94
Brachyrus, 404
Brachythoracoidei, 40
Brama, 452
bramble sharks, 78
BRAMIDAE, 405, 451
Braminae, 451
Bramocharax, 204
Branchioica, 213
Branchiopsaron, 425
Branchiosteginae, 456
Branchiostegus, 456
Branchiostoma, 16
BRANCHIOSTOMATIDAE, 16
Brannerion, 135
Bransonella, 47
BRANSONELLIFORMES, 47
breams, 502
  emperor breams, 505
  large-eye breams, 505
  threadfin breams, 504
Bregmaceros, 300
BREGMACEROTIDAE, 294, 299, 300
Breitensteinia, 224
BREMBODONTIDAE, 121
Brepostoma, 435
Breviraja, 85
Brevoortia, 171
Brienomyrus, 160
Briggsia, 352
Brindabellaspis, 37
Brinkmannella, 435
bristlemouths, 259
Britobatis, 88
Brochiraja, 85
Brochis, 215
Brochoadmones, 99
BROCHOADMONIDAE, 99
Brook Trout, 247
Brookvalia, 115
Brosme, 302
Brosmodorsalis, 319
Brosmolus, 319
Brosmophycinae, 318, 319
Brosmophycinini, 319
Brosmophycis, 319
Brosmophysiops, 319
Brotula, 317
Brotulinae, 317
Brotulinella, 319
Brotulotaenia, 317
Brotulotaeniinae, 317
Brustiarius, 232
Bryaninops, 332
Brychaetus, 157
Brycinus, 196
Brycon, 193, 205
Bryconaethiops, 196
Bryconamericus, 206
Bryconexodon, 205
Bryconinae, 205, 206
Bryconops, 205
Bryozoichthys, 480
Bryx, 408
Buccochromis, 344
BUCHANOSTEIDAE, 40
Bucklandium, 210
Buenia, 332
buffaloes, 188
Bufoceratias, 515
Bujurquina, 344
Bulbonaricus, 405, 407, 408
Bull Shark, 72
bullhead sharks, 59
Bullisichthys, 434, 447
Bullockia, 213
Bunaka, 329
Bunocephalinae, 233
Bunocephalus, 233
Burbot, 301
Burnhamia, 95
burrfishes, 526
BUTIDAE, 326, 329
Butis, 329
butterfishes, 420
butterfly kingfishes, 417
butterfly rays, 92
butterflyfish, 501
butterflyfishes, 156, 454, 455, 462
Bythaelurus, 69
Bythites, 318, 319
BYTHITIDAE, 318
Bythitinae, 318
Bythitoidei, 315, 318

Cabezon, 489
Cabonnichthys, 110
Caecomastacembelus, 383
Caecorhamdella, 236
Caecula, 146
Caelatoglanis, 225
Caenotropus, 201
Caesio, 459
CAESIONIDAE, 458
Caesioninae, 458
Caesioperca, 447
Caesioscorpis, 447, 448
Cairnsichthys, 358, 359
Calamoichthys, 117
Calamopleurus, 126
Calamopteryx, 319
Calamus, 506
cales, 429
Callanthias, 503
CALLANTHIIDAE, 502, 503
Callechelys, 146
CALLICHTHYIDAE, 214, 215
Callichthyinae, 215
Callichthys, 215
Calliclinus, 351
CALLIONYMIDAE, 412, 413
CALLIONYMIFORMES, 405, 412
Callionymoidei, 352, 405
Callionymus, 413
Callipurbeckia, 124
CALLIPURBECKIDAE, 124
Calliurichthys, 413
Callogobius, 332
Callopanchax, 371
Calloplesiops, 336
CALLORHINCHIDAE, 51, 52
Callorhinchoidea, 52
Callorhinchus, 52
CALLORHYNCHIDAE, 52
Callorhynchoidea, 52
Callyodon, 430
CALLYODONTIDAE, 429
Calophysus, 237
Calotomus, 430
Calumia, 329
Campellolebias, 372
Campichthys, 408
Campogramma, 387
Campostoma, 184
Campylomormyrus, 160
CAMUROPISCIDAE, 40
Camuropiscis, 40
Cancelloxus, 350
Candidia, 185
candiru, 213
Canobius, 113
Canonia, 31
Canowindra, 110
CANOWINDRIDAE, 110

Cantherhines, 523
Canthidermis, 523
Canthigaster, 525, 526
Canthigastrinae, 525, 526
Canthophrys, 190
Cantioscyllium, 62
Capoeta, 183
Caprichthys, 521
Caproberyx, 304
Caprodon, 447
CAPROIDAE, 315, 506, 507
Caproidei, 506
CAPROIFORMES, 420, 430, 462, 495, 506, 518
Caproinae, 507
Capromimus, 292
Capropygia, 521
Capros, 507
Caquetaia, 344
CARACANTHIDAE, 468, 471
Caracanthinae, 470
Caracanthus, 471
CARANGIDAE, 383, 385, 386, 414
CARANGIFORMES, 334, 380, 383, 387
Carangimorpharia, 380
Caranginae, 387
carangoid lineage, 383
Carangoidei, 380
Carangoides, 387
Caranx, 143, 387
CARAPIDAE, 316
Carapinae, 316
Carapus, 317
Carassius, 181, 183
CARCHARHINIDAE, 55, 70, 71, 72
CARCHARHINIFORMES, 42, 57, 58, 68
carcharhiniforms, 42
Carcharhinus, 72
Carcharias, 42, 63, 65
Carchariolamna, 68
Carcharocles, 64
Carcharodon, 64, 68
Carcharoides, 68
Cardabiodon, 64
CARDABIODONTIDAE, 64
cardinalfishes, 324
  deepwater cardinalfishes, 434
CARDIPELTIDA, 28
Cardipeltis, 28
Careproctinae, 495
Careproctus, 495
Caridosuctor, 104
Carinacanthus, 46
Carinotetraodon, 525, 526
CARISTIIDAE, 405, 452
Caristius, 452
Carlana, 205
Carlarius, 232
Carlhubbsia, 380
Carnegiella, 207
carps, 181
  carps, 180, 183
  mountain carps, 186
carpet sharks, 59
Carpiodes, 188
Carrionellus, 376
Carycinacanthus, 100
CASEODONTIDAE, 50
Caseodus, 50
Caspiomyzon, 25
cat sharks, 69
Cataetyx, 319
Cataphractops, 215
Catathyridium, 403
Catesbya, 144
catfishes, 207, 208, 209, 210
  “talking catfishes”, 233
  airbreathing catfishes, 230
  airsac catfishes, 231
  angler catfishes, 220
  armorhead catfishes, 235
  Asian "schilbeids", 221
  auchenoglanidids, 228
  bagrid catfishes, 222
  banjo catfishes, 232
  barbelless catfishes, 234
  bottlenose catfishes, 234
  bullheads, 235
  bumblebee catfishes, 238
  butter catfishes, 228
  callichthyid armored catfishes, 214
  candiru, 213
  channel catfishes, 235
  Chiapas catfishes, 229
  claroteids, 229
  climbing catfishes, 216
  driftwood catfishes, 234
  eeltail catfishes, 220
  electric catfishes, 227
  erethistid catfishes, 225
  Flathead Catfish, 236
  frogmouth catfishes, 220
  glass catfishes, 219
  heptapterids, 236
  imperial catfishes, 222
  loach catfishes, 226
  long-whiskered catfishes, 236
  lookdown catfishes, 237
  loweye catfishes, 237
  madtoms, 236
  Malagasy catfishes, 231
  Mekong giant catfish, 219, 220
  mountain catfishes, 214
  nanobagrid catfishes, 221
  North American catfishes, 235
  parasitic catfishes, 212
  pencil catfishes, 212
  ritas, 221
  rock catfishes, 219
  schilbeid catfishes, 228
  sea catfishes, 231, 232
  shark catfishes, 219
  sheatfishes, 218
  sisorid catfishes, 224
  spiny dwarf catfishes, 215
  squarehead catfishes, 220
  squeakers, 227
  stonecat, 236
  stream catfishes, 223
  suckermouth armored catfishes, 216
  sun catfishes, 222
  thorny catfishes, 233
  torrent catfishes, 224
  upside-down catfishes, 227
  velvet catfishes, 210
  walking catfish, 230
  wels, 218
  whale catfishes, 211
Cathaymyrus, 16
Cathorops, 232
Catlocarpio, 181, 183
Catoprion, 199
CATOSTOMIDAE, 187
Catostominae, 188
Catostomini, 189
Catostomus, 187, 188, 189
CATURIDAE, 124, 125
Caturoidei, 125
  Caturus, 125
  Caulolatilus, 456
  Caulophryne, 513
CAULOPHRYNIDAE, 512, 513
cavebasses, 443
cavefishes, 289

Cavenderichthys, 131
Cazon, 71
Cebidichthys, 480
Cederstroemia, 61
Cenocarcharias, 65
CENTRACANTHIDAE, 504, 506
Centracanthus, 506
CENTRARCHIDAE, 442, 444, 445
Centrarchinae, 445
Centrarchops, 443
Centrarchus, 444, 445
CENTRISCIDAE, 410
Centriscoidea, 410
Centriscops, 410
Centriscus, 411
Centroberyx, 308, 314
Centrobranchus, 278
Centrochir, 234
Centrodoras, 234
Centrodraco, 413
CENTROGENYIDAE, 427, 433
Centrogenys, 433
Centrolabrus, 428
CENTROLOPHIDAE, 418
Centrolophus, 418, 419
Centromochlinae, 235
Centromochlus, 235
CENTROPHORIDAE, 75
Centrophorides, 78
Centrophorus, 75
Centrophryne, 516
CENTROPHRYNIDAE, 516
Centropogon, 471
CENTROPOMIDAE, 335, 380, 431, 432
Centropomus, 432
Centropristis, 447
Centropyge, 456
Centroscyllium, 76
Centroscymnus, 76
Centroselachus, 76
Centrosqualus, 78
CEPHALACANTHIDAE, 411
CEPHALASPIDAE, 34
CEPHALASPIDIFORMES, 32, 33
Cephalaspidomorphi, 23, 33
Cephalocassis, 232
Cephalochordata, 13, 16, 18
cephalochordates, 15, 17
Cephalopholis, 447
Cephalopsetta, 399
Cephaloscyllium, 69
Cephalosilurus, 238
CEPHALOXENIDAE, 116
Cephaloxenus, 116
Cephalurus, 69
Cepola, 461
CEPOLIDAE, 461
Cepolinae, 461
Cepoloidea, 461
Ceratias, 513, 516
CERATIIDAE, 512, 516
Ceratioidei, 508, 512
Ceratobregma, 347
CERATODONTIDAE, 109
CERATODONTIFORMES, 108
Ceratodus, 109
Ceratoglanis, 219
Ceratoscopelus, 278
Cercamia, 325
Cestraeus, 342
Cetengraulis, 168
Cetichthys, 312
CETOMIMIDAE, 309, 311, 312, 313
Cetomimoidea, 309, 310
Cetomimoides, 313
Cetomimus, 312, 313
Cetonurus, 296
Cetopangasius, 220
CETOPSIDAE, 211, 218
Cetopsidium, 212
Cetopsinae, 212
Cetopsis, 212
Cetopsogiton, 212
Cetopsoidei, 211
Cetopsorhambia, 236
CETORHINIDAE, 67
Cetorhinus, 67
Cetoscarus, 430
Cetostoma, 312
Chaca, 220
CHACIDAE, 220
CHAENICHTHYIDAE, 467
Chaenobryttus, 446
Chaenocephalus, 467
Chaenodraco, 467
Chaenogaleus, 71
Chaenomugil, 342
Chaenophryne, 515
CHAENOPSIDAE, 346, 351
Chaenopsis, 351
Chaetoderma, 523
Chaetodipterus, 497
Chaetodon, 455
CHAETODONTIDAE, 454, 455
Chaetodontoplus, 456
Chaetostoma, 217
Chalaroderma, 348
Chalcalburnus, 184
Chalixodytes, 424
chameleonfishes, 395
Champsocephalus, 467
Champsodon, 422
CHAMPSODONTIDAE, 421, 422, 468
Chanda, 335
CHANDIDAE, 334, 335
Chandramara, 223
CHANIDAE, 176
Chaninae, 177
Channa, 393, 394
Channallabes, 230
CHANNICHTHYIDAE, 467
  Channichthys, 467
CHANNIDAE, 390, 394
Channoidei, 390, 393
Channomuraena, 143
Chanodichthys, 186
Chanoides, 179
Chanos, 177
Chapalichthys, 374
char, 244
CHARACIDAE, 175, 195, 198, 203, 204, 206
Characidiinae, 195, 196, 204
Characidium, 196
CHARACIFORMES, 179, 180, 193, 207, 209
Characinae, 205
characins, 193, 203
Characiphysi, 179, 193, 207
Characodon, 374
Characoidea, 202
Characoidei, 195
Charax, 205
Charitopsis, 177
Charitosomus, 177
Charocoidei, 198
chars or charrs, 246
  Arctic Char, 247
  Brook Trout, 247
  Bull Trout, 247
  Dolly Varden, 247
  Lake Trout, 247
  Longfin Char, 247
Chascanopsetta, 401
Chasmistes, 189
Chasmoclupea, 170
Chasmocranus, 236

- *Chasmodes*, 348
- *Chatrabus*, 323
- *Chattertonodus*, 31
- *Chaudhuria*, 382
- CHAUDHURIIDAE, 382
- Chauliodontini, 262
- *Chauliodus*, 263
- CHAUNACIDAE, 511
- Chaunacoidei, 508, 511
- *Chaunacops*, 511
- *Chaunax*, 511
- *Cheilinus*, 428
- *Cheilio*, 428
- CHEILOBRANCHIDAE, 353
- Cheilobranchinae, 353
- *Cheilobranchus*, 353
- CHEILODACTYLIDAE, 442, 459, 460
- *Cheilodactylus*, 460
- *Cheilodipterus*, 325
- *Cheilopogon*, 366
- *Cheiloprion*, 339
- *Cheilotrema*, 499
- CHEIMARRHICHTHYIDAE, 421, 422
- *Cheimarrichthys*, 423
- *Cheimerius*, 506
- CHEIRACANTHIDAE, 100
  - *Cheiracanthus*, 100
  - *Cheirodon*, 206
- Cheirodontinae, 206
- Cheirodontini, 206
- CHEIROLEPIDIDAE, 113
- CHEIROLEPIDIFORMES, 113
- *Cheirolepis*, 111, 113
- CHEIROTRICIDAE, 266
- *Chela*, 182, 185
- *Chelidonichthys*, 476
- *Chelidoperca*, 447
- *Chelmon*, 455
- *Chelmonops*, 455
- *Chelon*, 342
- *Chelonodon*, 525
- *Chendol*, 382
- *Cheroscorpaena*, 471
- *Cherublemma*, 318
- *Chesnonia*, 490
- Chetia, 344
- Cheungkongella, 13, 15
- Chiasmodon, 421
- CHIASMODONTIDAE, 421
- Chilara, 318
- Chilatherina, 359
- *Chilobrycon*, 205
- *Chilochromis*, 344
- *Chiloconger*, 148
- CHILODONTIDAE, 197, 200
- *Chilodus*, 201
- *Chiloglanis*, 227
- *Chilomycterus*, 526
- *Chilorhinus*, 144
- *Chiloscyllium*, 61, 62
- *Chimaera*, 53
- chimaeras, 51
  - longnose chimaeras, 52
  - plownose chimaeras, 52
  - shortnose chimaeras, 53
- CHIMAERIDAE, 48, 53
- CHIMAERIFORMES, 49, 51
- chimaeriforms, 50
- Chimaeroidea, 52
- Chimaeroidei, 51
- chimaeroids, 41, 51, 57
- CHIMAEROPSIDAE, 51
- *Chimaeropsis*, 51
- *Chimarrichthys*, 225
- Chinese perches, 442
- *Chinlea*, 105
- *Chionobathyscus*, 467
- *Chionodraco*, 467
- CHIROCENTRIDAE, 166, 169
- *Chirocentrites*, 131
- *Chirocentrodon*, 166, 167
- *Chirocentrus*, 162, 169
- *Chirodactylus*, 460
- CHIRODIPTERIDAE, 107, 108
  - *Chirodipterus*, 107, 108
- CHIRODONTIDAE, 114
  - *Chirodus*, 114
- Chirolophinae, 480
  - *Chirolophis*, 480
  - *Chiromystus*, 131
- CHIRONEMIDAE, 459
- *Chironemus*, 460
- *Chirophryne*, 515
- *Chirostoma*, 356
- *Chirostomias*, 263
- *Chitala*, 158, 159
- *Chitonotus*, 492
- *Chlamydogobius*, 330
- CHLAMYDOSELACHIDAE, 74
- Chlamydoselachus, 74
- Chlidichthys, 340
- CHLOPSIDAE, 144
- *Chlopsis*, 144
- Chlopsoidei, 144
- CHLOROPHTHALMIDAE, 266, 272
- Chlorophthalmoidea, 272
- Chlorophthalmoidei, 266
- *Chlorophthalmus*, 266, 273
- *Chloroscombrus*, 387
- *Chlorurus*, 430
- *Choerodon*, 428
- *Choeroichthys*, 408
- *Chologaster*, 289
- CHONDRENCHELYIDAE, 49, 51
- CHONDRENCHELYIFORMES, 51
- *Chondrenchelys*, 51
- Chondrichthiomorphi, 35
- chondrichthyan, 43, 45
- chondrichthyans, 43, 44
- Chondrichthyes, 35, 36, 40, 41, 42, 43, 47, 48, 97
  - stem-group, 43
  - crown-group, 47
- CHONDRICHTHYOMORPHI, 40
- CHONDROSTEI, 118
- CHONDROSTEIDAE, 118
- CHONDROSTEIFORMES, 118
- *Chondrosteus*, 118
- *Chondrostoma*, 184
- *Chonerhinos*, 525
- *Choranthias*, 447
- Chordata, 13, 14, 17
- chordates, 13, 14
- Choridactylini, 472
- *Choridactylus*, 472
- *Chorisochismus*, 352
- *Chriodorus*, 367
- *Chrionema*, 424
- *Chromidotilapia*, 344
- Chrominae, 337, 338
- *Chromis*, 337, 338
- *Chromobotia*, 190
- *Chrosomis*, 183, 184
- *Chrysichthys*, 229
- *Chrysiptera*, 339
- *Chrysoblephus*, 506
- *Chrysochir*, 499
- CHUCHINOLEPIDIDAE, 38
- *Chuchinolepis*, 38

Cichla, 344
Cichlasoma, 343, 344
CICHLIDAE, 333, 342, 427
cichlids, 342
CICHLIFORMES, 334, 341, 342, 346
Ciliata, 301
Cilus, 499
CIMOLICHTHYIDAE, 267
Cimolichthyinae, 275
Cimolichthys, 275
Cinetodus, 232
Cirrhibarbis, 350
Cirrhigaleus, 78
Cirrhilabrus, 428
Cirrhimuraena, 146
Cirrhinus, 182
Cirrhitichthys, 459
CIRRHITIDAE, 459
Cirrhitoidea, 459
Cirrhitops, 459
Cirrhitus, 459
Cirrhoscyllium, 60
Cirricaecula, 146
Cirriemblemaria, 351
Cirrimaxilla, 143
Cirripectes, 348
Cirrisalarias, 348
Citharichthys, 399
CITHARIDAE, 397
Citharidium, 195
CITHARINIDAE, 195
citharinids, 195
Citharinoidei, 193, 194
Citharinops, 195
Citharinus, 194, 195
Citharoidea, 397
Citharoides, 398
Citharus, 398
Cladarosymblema, 110
Cladistia, 115, 116, 117
CLADOCYCLIDAE, 131
Cladocyclus, 131
Cladodoides, 47
CLADODONTIFORMES, 47
  Cladoselache, 46
CLADOSELACHIDAE, 46
CLADOSELACHIFORMES, 46
Cladoselachimorpha, 46
Clariallabes, 230
Clarias, 230
Clariger, 330
CLARIIDAE, 208, 230
Clarioidea, 229, 230
CLAROTEIDAE, 210, 219, 222, 226, 228, 229, 232
Claroteinae, 222
Clarotes, 229
Cleidopus, 307
Cleisthenes, 400
CLEITHROLEPIDAE, 116
CLEITHROLEPIDIDAE, 116
Cleithrolepis, 116
Clepticus, 428
Clevelandia, 330
Clidoderma, 399
Climacoporus, 350
CLIMATIIDAE, 99
CLIMATIIFORMES, 97, 98, 99
Climatius, 99
clingfishes, 351, 352
CLINIDAE, 346, 349
Clininae, 349
Clinitrachus, 350
Clinocottus, 492
Clinoporus, 349, 350
Clinostomus, 184
Clinus, 350
Clupanodon, 162, 171, 172
Clupea, 171
Clupeacharacinae, 205
Clupeacharax, 205
Clupeichthys, 170
CLUPEIDAE, 164, 166, 169, 257
CLUPEIFORMES, 163, 164, 165
Clupeinae, 170, 171, 172
Clupeocephala, 131, 160
Clupeocharax, 196
Clupeoidei, 166
Clupeoides, 170, 171
Clupeomorpha, 161, 162, 163, 165, 172
Clupeonella, 170, 171
Clupisoma, 221
Clypeobarbus, 183
Cnesterodon, 380
Cnesterodontini, 380
Cnidoglanis, 221
Cobelodus, 46
cobias, 384
COBITIDAE, 190
COBITIDIDAE, 190
Cobitis, 190
Cobitoidea, 186, 189
Coccoderma, 104
COCCODONTIDAE, 121
Coccodus, 121
Coccolepis, 113
Coccorella, 274
COCCOSTEIDAE, 40
Coccosteus, 40
Coccotropsis, 471
Cochlefelis, 232
Cochleoceps, 352
Cochliodon, 217
COCHLIODONTIDAE, 51
COCHLIODONTIFORMES, 49, 51
Cochliodontomorpha, 50
cochliodonts, 50
Cochliodus, 51
Cociella, 477
Cocotropus, 473
codlets, 300
codlings, 298
Codoma, 184
cods, 293, 302
  cods, 300
  deepsea cods, 298
  eel cods, 300
  eucla cod, 297
  moray cods, 300
  pelagic cods, 295
  tadpole cods, 299
Coelacanthida, 103
COELACANTHIDAE, 105, 106
COELACANTHIFORMES, 104
coelacanths, 103, 104, 105
Coelacanthus, 105
COELOLEPIDAE, 32
COELOLEPIDIFORMES, 31
Coelophrys, 512
Coelorhynchus, 296
Coelorinchus, 296
Coffin Ray, 83
coffinfishes, 511
cofishes, 473
COIIDAE, 504
Coilia, 167, 168
Coiliinae, 168
Coius, 504
Colisa, 393
Colistium, 402
collared carpet sharks, 60
Colletteichthys, 323
Collichthys, 499
COLOBODONTIDAE, 116
Colobodus, 116
Coloconger, 145

COLOCONGRIDAE, 145
Cologrammus, 350
Cololabis, 369
Colomesus, 525
Colossoma, 199
Colpichthys, 356
Columbia, 288
combfishes, 486
Comephorinae, 485, 492
Comephorus, 492
Cometicercus, 31
COMMENTRYIDAE, 113
Common Carp, 181
Compsaraia, 241
Compsura, 206
Compsurini, 206
Conger, 148
CONGIOPODIDAE, 468, 475
Congiopodoidei, 475
Congiopodus, 469, 475
Congocharax, 195
Congochromis, 344
Congoglanis, 226
Congolapia, 344
Congothrissa, 170, 171
CONGOTHRISSIDAE, 171
Congresox, 147
CONGRIDAE, 147
Congrinae, 148
Congrogadinae, 334, 340
Congrogadus, 340
Congroidei, 134, 141, 145
Conidens, 352
Conniella, 428
Conocara, 174
Conodon, 457
Conodonta, 17, 18
Conodontophorida, 13, 17
conodonts, 13, 17
Conorhynchos, 209, 236
Conta, 225
Continae, 225
Contusus, 525
convict blennies, 342, 345
Cookeolus, 453
cookiecutter sharks, 77
Cooyoo, 131
Copadichromis, 344
Copeina, 203
Copella, 203
Copionodon, 213
Copionodontinae, 213
COPODONTIDAE, 49, 50
COPODONTIFORMES, 50
Copodus, 50
Coptobrycon, 206
CORACINIDAE, 439, 440, 496
Coracinus, 440
Coradion, 455
Coraglanis, 225
coral crouchers, 470
Coralliozetus, 351
COREGONIDAE, 244
Coregoninae, 244, 245
Coregonus, 245
Coreius, 184
Coreobagrus, 223
Coreoperca, 315, 442
Corica, 170
Coris, 428
cornetfishes, 409, 410
Corniger, 305
Cornuata, 34
CORONODONTIDAE, 44, 46
Coronodus, 44, 46
CORVASPIDIDA, 28
Corvaspis, 28
Corvula, 499
Corydoradinae, 215
Corydoras, 215
Corynopoma, 206
Coryphaena, 384
CORYPHAENIDAE, 383, 384, 385
Coryphaenoides, 296
CORYPHAENOIDIDAE, 296
Coryphoblennius, 348
Corythoichthys, 408
Cosmocampus, 408
Cosmopolitodus, 68
Cottapistus, 471
COTTIDAE, 485, 491, 493
Cottinae, 485, 491, 492
Cottinella, 492
Cottoclinus, 351
COTTOCOMEPHORIDAE, 492
Cottocomephorinae, 485
Cottocomephorus, 485, 492
Cottoidea, 488
Cottoidei, 421, 467, 485, 488, 491, 494
Cottoperca, 464, 465
Cottunculinae, 493
Cottunculus, 493
Cottus, 485, 492
Cotylopus, 330
Couesius, 184
cow sharks, 74
cowfishes, 521
cownose rays, 94
Craniata, 13, 14, 17, 18
craniates, 13, 14, 17, 18, 19
  stem craniate, 14
CRANOGLANIDIDAE, 235
Cranoglanis, 235
Crapatulus, 425
Crassinarke, 84
Craterocephalinae, 363
Craterocephalus, 363
Cratinus, 447
Cratoamia, 126
Creagrutus, 206
Creedia, 424
CREEDIIDAE, 421, 423, 424
Cremnochorites, 347
Crenicara, 344
Crenichthys, 370, 373
Crenicichla, 343, 344
Crenicthys, 374
Crenidens, 506
Crenimugil, 342
CRENUCHIDAE, 195, 204
Crenuchinae, 195, 204
Crenuchoidea, 195
Crenuchus, 196
Creocele, 352
crested flounders, 402
crestfishes, 283
Cretalamna, 64
Cretascymnus, 76
CRETATRIACANTHIDAE, 519
CRETAZEIDAE, 290
Cretazeus, 290
Creteuchiloglanis, 225
Cretodus, 63
Cretomanta, 95
Cretorectolobus, 61
Cretoxyrhina, 64
CRETOXYRHINIDAE, 64
crevally, 386
Cristabatis, 82
Cristacirrhitus, 459
Cristatogobius, 332
Cristiceps, 350
Cristivomer, 247
croakers, 498
crocodile sharks, 65
Crocodilichthys, 347
Croilia, 332
Cromeria, 178
Cromileptes, 447
Crossocheilus, 182
CROSSOGNATHIDAE, 130

CROSSOGNATHIFORMES, 130
Crossognathus, 130
Crossoloricaria, 217
Crossopholis, 119
Crossorhinus, 61
Crossorhombus, 401
Crossosalarias, 349
Crossostomus, 479
Cruciglanis, 238
Cruriraja, 84, 85
Cruxentina, 201
Cryodraco, 467
Cryothenia, 465
Cryptacanthodes, 480
CRYPTACANTHODIDAE, 480
Cryptacanthoides, 480
Cryptarius, 232
Cryptichthys, 347
Cryptocentroides, 332
Cryptocentrus, 332
Cryptoheros, 344
Cryptolebias, 372
Cryptopsaras, 516
Cryptotomus, 430
Cryptotora, 191
Cryptotrema, 351
Crystallaria, 450
Crystallichthys, 495
Crystallodytes, 424
CTENACANTHIDAE, 47
CTENACANTHIFORMES, 46, 55
ctenacanthiforms, 55
CTENACANTHIMORPHA, 46
Ctenacanthus, 47
Ctenacis, 70
Ctenochaetus, 502
Ctenochirichthys, 512, 515
CTENODONTIDAE, 108
CTENODONTIFORMES, 108
Ctenodus, 108
Ctenogobius, 330
Ctenolabrus, 428
CTENOLUCIIDAE, 202, 203
Ctenolucius, 203
Ctenopharyngodon, 186
Ctenopoma, 391
Ctenops, 393
Ctenoptychius, 50
Ctenosciaena, 499
Ctenosquamata, 265, 276
Ctenothrissa, 280
CTENOTHRISSIFORMES, 280
Ctenurella, 39
Cualac, 376
Cubanichthyinae, 375
Cubanichthys, 375
Cubiceps, 419
cuchias, 381
cucumber fishes, 269
Culaea, 484
CULMACANTHIDAE, 100
Culmacanthus, 98, 100
Culter, 186
Cultrinae, 185
Cuneatus, 123
Curimata, 201
Curimatella, 201
CURIMATIDAE, 197, 201
Curimatopsis, 201
Curimatorbis, 201
Cusk, 301
cusk-eels, 315, 317
cutlassfishes, 415
CYATHASPIDIDAE, 29
CYATHASPIDIFORMES, 28
Cybiosarda, 417
Cycleptinae, 188
Cycleptus, 188
Cyclichthys, 526
CYCLOBATIDAE, 84
Cyclobatis, 84
Cyclocheilichthys, 183
Cyclomyaria, 15
Cyclopsetta, 399
Cyclopsis, 495
CYCLOPTERIDAE, 485, 494
Cyclopteroidea, 494
Cyclopteropsis, 495
Cyclopterus, 494, 495
Cyclosquamata, 264, 265, 266
cyclostome, 19
Cyclothone, 260, 261
Cyclurus, 126
Cyema, 149
CYEMATIDAE, 149
Cygnodraco, 466
Cylindracanthus, 388
Cymatoceps, 506
Cymatogaster, 335
Cymolutes, 428
Cynodon, 198
CYNODONTIDAE, 197, 198, 203
cynodontids, 198
Cynodontinae, 198
CYNOGLOSSIDAE, 402, 403, 404
Cynoglossinae, 404
Cynoglossus, 405
Cynolebias, 372
Cynopoecilus, 372
Cynoponticus, 147
Cynopotamus, 205
Cynoscion, 499
Cynothrissa, 171
Cypho, 340
Cyphocharax, 201
Cyphocottus, 485, 492
Cyprichromis, 344
Cyprinella, 184
CYPRINIDAE, 175, 181, 186, 330
CYPRINIFORMES, 179, 180
Cyprininae, 182, 183
Cyprinion, 183
Cypriniphysi, 179, 180
Cyprinocirrhites, 459
Cyprinodon, 376
CYPRINODONTIDAE, 370, 372, 375
CYPRINODONTIFORMES, 334, 354, 363, 364, 369, 377
Cyprinodontinae, 375
Cyprinodontini, 376
Cyprinodontoidea, 374
Cyprinodontoidei, 370, 372
Cyprinoidea, 181
Cyprinus, 181, 183
Cypselurinae, 366
Cypselurus, 366
Cyranichthys, 267
Cyranorhis, 112
Cyrtaspidichthys, 29
CYTTIDAE, 290
Cyttoidei, 290
Cyttomimus, 290, 292
Cyttopsinae, 291
Cyttopsis, 291
Cyttula, 292
Cyttus, 290

dab, 396
Dacodraco, 467
Dactylagnus, 347
Dactylanthias, 447
Dactylobatus, 85
Dactylophora, 460
Dactylopsaron, 425
Dactyloptena, 412
DACTYLOPTERIDAE, 411, 427

Dactylopteroidei, 411
Dactylopterus, 412
Dactylopus, 413
DACTYLOSCOPIDAE, 347, 348
Dactyloscopus, 347
Dactylosurculus, 319
Dadyanos, 479
Daector, 322
Dagetella, 117
Dagetichthys, 404
Daggertooth, 275
Dalatias, 77
DALATIIDAE, 75, 77
Dalgoichthys, 279, 307
Dallasiella, 64
Dallia, 248, 249, 250, 251
Dalmatichthys, 286
Dalophis, 146
Damocles, 46
Dampierosa, 472, 473
damselfishes, 337
  anemonefishes, 338
  chromines, 338
  damselfishes, 337
  lepidozygines, 338
  pomacentrines, 338
  sergeant-majors, 339
Danacetichthys, 312
Danakilia, 344
Danaphos, 260
Danaphryne, 515
Danatinia, 281
Danichthys, 366
Danio, 181, 182
Danionella, 182
Danioninae, 182, 185, 330
Dannevigia, 318
DAPEDIIDAE, 122
DAPEDIIFORMES, 122
Dapedium, 122
Daramattus, 292
Dario, 395
dartfishes, 331
DARTMUTHIIDAE, 34
Dascyllus, 337, 338
Dastilbe, 177
DASYATIDAE, 55, 88, 90, 91, 93
Dasyatis, 91
Dasyatoidea, 91
Dasycottus, 493
Dasyloricaria, 217
Datnioides, 504
DATNIOIDIDAE, 504
Datnionoides, 504
Davichthys, 135
Davidijordania, 479
Davodus, 50
Dayella, 170
Daysciaena, 499
Deania, 75
DEBEERIIDAE, 49, 50
debeeriids, 48
DEBEERIIFORMES, 48, 50
Debeerius, 50
Decapterus, 386, 387
Deckertichthys, 433
Decodon, 428
deepsea lizardfishes, 272
deepsea smelts, 254
deep-sea spiny eels, 133, 137, 138
deepsea tripod fishes, 270
deepwater Baikal sculpins, 492
deepwater boxfishes, 521
deepwater cardinalfishes, 434
deepwater flatheads, 476
Dellichthys, 352
Delminichthys, 184
Delolepis, 480
Delpitoscyllium, 62
Deltistes, 189
Deltodus, 51
DELTOPTYCHIIDAE, 51
Deltoptychius, 51
Delturinae, 218
Delturus, 218
Demissolinea, 416
Denaea, 46
Denariusa, 335
Dendrochirus, 470
Dendrodus, 43
Dendrophysa, 499
Dentatherina, 360, 361
DENTATHERINIDAE, 360
Dentex, 506
DENTICEPITIDAE, 166
Denticeps, 166
Denticetopsis, 212
Denticinae, 506
DENTICIPITIDAE, 165
Denticipitoidei, 165
Dentilepisosteus, 123
Dentiraja, 85
Deraniyagala, 170
DERCETIDAE, 267
Dercetis, 267
Dercetoides, 267
Derepodichthys, 479
Derhamia, 202
DERICHTHYIDAE, 145
Derichthys, 145
Derilissus, 352
Dermatias, 515
Dermatolepis, 447
Dermatopsis, 319
Dermatopsoides, 319
Dermogenys, 367
DESMIODONTIFORMES, 49
Desmiodus, 49
Desmodema, 284
deuterostome, 14
Deuterostomia, 13
devil rays, 94, 95
Dexistes, 400
DIABOLEPIDIDAE, 107
DIABOLEPIDIFORMES, 107
Diabolepis, 107
Diademichthys, 352
Diademodus, 45
Diagramma, 457
Dialipina, 102, 111, 113
DIALIPINIFORMES, 101
Dialommus, 351
Diancistrus, 319
Dianema, 215
Dianolepis, 38
Diaphenchelys, 144
Diaphus, 278
Diapoma, 206
Diapteron, 371
Diapterus, 433
Diastobranchus, 142
Dibrachichthys, 510
Dibranchus, 512
Dicentrarchus, 496
Diceratias, 515
DICERATIIDAE, 515
DICHISTIIDAE, 439, 496
Dichistius, 440
Dicologlossa, 404
Dicosternon, 260
Dicotylichthys, 526
Dicrolene, 318
Dicrossus, 344
Dictyopyge, 115
Dictyosoma, 480
Didogobius, 332
Didymothallus, 319
Dieidolycus, 479
Dinaspidella, 29
Dinematichthyini, 319
Dinematichthys, 319

DINICHTHYIDAE, 40
Dinolestes, 450
DINOLESTIDAE, 450
Dinoperca, 443
DINOPERCIDAE, 443
DINOPTERYGIIDAE, 280
Dinotopterus, 230
Diodon, 526
DIODONTIDAE, 518, 522, 526
Diogenichthys, 278
Dionda, 184
DIPLACANTHIDAE, 100
DIPLACANTHIFORMES, 99
Diplacanthopoma, 319
Diplacanthus, 100
Diplecogaster, 352
Diplectrum, 447
Diplobatis, 83
DIPLOCERCIDAE, 104
Diplocercides, 104
Diplocrepis, 353
Diplodinae, 506
Diplodoselache, 47
DIPLODOSELACHIDAE, 47
Diplodus, 506
Diplogrammus, 413
Diplolonchidion, 56
Diplomystes, 211
DIPLOMYSTIDAE, 208, 210, 211
Diplomystoidei, 210
Diplomystus, 162, 163
Diplophos, 260
Diploprion, 447
Diploprionini, 447
Diplorhina, 26
Diplospinus, 415
Diplospondichthys, 112
Diplotaxodon, 344
Diplurus, 105
Dipnoi, 107
DIPNOIFORMES, 107
Dipnomorpha, 106
DIPNORHYNCHIDAE, 107
DIPNORHYNCHIFORMES, 107
Dipnorhynchus, 107
Diproctacanthus, 428
DIPTERIDAE, 108
DIPTERIFORMES, 107
Dipterimorpha, 107
Dipteronotus, 116
Dipterus, 108
Dipterygonotus, 459
Dipturus, 85
Diptychus, 183
Dipulus, 319
Diretmichthys, 306
DIRETMIDAE, 303, 306
Diretmoides, 306
Diretmus, 306
Dischistodus, 339
Discopyge, 83
Discoserra, 112, 115
Discotrema, 353
Discoverichthys, 271
discus fish, 343
Disparichthys, 317
Dissostichus, 465
DISTICHODONTIDAE, 194
distichodontids, 194
Distichodus, 194, 195
DISTOBATIDAE, 56
Distobatus, 56
Distocyclus, 241
Ditrema, 335
Ditropichthys, 312
Dodekablennius, 349
Doederleinia, 434
dogfish sharks, 75, 77
dogfishes, 78
DOIICHTHYIDAE, 232
Doiichthys, 232
Dolichallabes, 230
Dolichamphilius, 226
Dolicholagus, 254
Dolichopteroides, 253
Dolichopteryx, 253
Dolichosudis, 275
Doliobatis, 82, 86
Doliodus, 44, 45
DOLIOLIDA, 15
Dolloidraco, 466
Dolopichthys, 515
dolphin, 384
dolphinfish, 384
    Pompano Dolphinfish, 384
dolphinfishes, 384
Domeykos, 130
DORADIDAE, 232, 233, 234
dorado, 384
dorado enano, 384
Doradoidea, 221, 229, 232
Doraops, 233, 234
Doras, 234
Doratonotus, 428
dories, 289
    armoreye dories, 291
    dories, 292
    lookdown dories, 290
    oreos, 290
    smooth dories, 291
    tinselfishes, 292
Dormitator, 328, 329
Dorosoma, 172
Dorosomatinae, 169, 170, 171, 172
DORSETICHTHYIDAE, 130
DORSETICHTHYIFORMES, 130
Dorsetichthys, 130
Dorsetoscyllium, 60
Doryichthys, 408
DORYPTERIDAE, 114
DORYPTERIFORMES, 114
Dorypterus, 114
doryrhamphines, 408
Doryrhamphus, 408
Dotalabrus, 428
dottybacks, 339
double anglers, 515
Doumea, 226
Doumeinae, 226
Draconetta, 413
DRACONETTIDAE, 413
Draculo, 412, 413
dragonets, 412
    slope dragonets, 413
dragonfishes, 259
    Antarctic dragonfishes, 466
    barbeled dragonfishes, 261
    black dragonfishes, 263
    loosejaws, 263
    scaleless black dragonfishes, 263
    scaly dragonfishes, 262
    snaggletooths, 262
    viperfishes, 262
dreamers, 515
Drepanaspis, 29
Drepane, 496, 499
DREPANEIDAE, 440, 496, 499
DREPANIDAE, 496
DREPANOLEPIDIDAE, 31
Drepanolepis, 31
driftfishes, 419
Drombus, 332
drums, 498
duckbilled fishes, 365
duckbills, 424
Dules, 447
Dunckerocampus, 408
Dundocharax, 195

DUNKLEOSTEIDAE, 40
Dunkleosteus, 40
Dupouyichthys, 233
Dussumieria, 162, 170
Dussumieriinae, 169, 170
Dussumieriini, 170
Duyunolepis, 34
Dwardius, 63
Dysalotus, 421
Dysomma, 141, 142
Dysommatinae, 141
Dysommina, 142

eagle rays, 93
Eaglesomia, 223, 229
earthworm eels, 382
Eastmanosteus, 40
Ebinania, 493
Ebosia, 470
Echelus, 146
ECHENEIDAE, 383, 384
ECHENEIDIDAE, 384
Echeneis, 385
Echidna, 144
Echidnocephalus, 138
Echiichthys, 426
Echinochimaera, 51
ECHINOCHIMAERIDAE, 51
Echinochimaeroidei, 51
echinoderms, 13
Echinophryne, 510
ECHINORHINIDAE, 75, 78
ECHINORHINIFORMES, 57, 78
Echinorhinus, 79
Echiodon, 317
Echiophis, 146
Echiostoma, 263
Ecklonaiichthys, 353
Eclectochromis, 344
Ecsenius, 349
Ectodus, 344
Ectosteorhachis, 110
Ectreposebastes, 469
Edaphodon, 52
Edaphodontinae, 52
Edelia, 433
EDESTIDAE, 50
Edestus, 50
eelblennies, 340
eelpouts, 479
eels, 133, 139–153
  Angler Snake Eel, 146
  arrowtooth eels, 141
  bobtail snipe eels, 149
  conger eels, 147
  cutthroat eels, 141, 142
  duckbill eels, 147
  duckbill oceanic eels, 145
  false moray eels, 144
  freshwater eels, 152
  garden eels, 148
  gulper eels, 150
  longneck eels, 145
  moray eels, 143
  mud eels, 142
  mustard eels, 141
  myroconger eels, 143
  narrowneck eels, 145
  onejaw gulper eels, 150
  pelican eels, 150
  pike conger eels, 147
  primitve cave eels, 140
  pugnose parasitic eel, 141
  sawtooth eels, 151
  shorttail eels, 145
  snake eels, 145, 146
  snipe eels, 151
  snubnose parasitic eel, 141
  spaghetti eels, 149
  swallower eels, 150
  worm eels, 145, 146
EESTILEPIDIDAE, 32
Eestilepis, 32
Eeyorius, 298
Egertonodus, 56
Egglestonichthys, 332
Eglonaspis, 28
Ego, 332
Ehirava, 170
Ehiravinae, 165, 170
Eichstaettia, 134
Eigenmannia, 240, 241
EIGENMANNIIDAE, 240
Eigenmannina, 199
Ekemblemaria, 351
Eknomoliparis, 495
Elacatinus, 332
Elachocharax, 196
Elagatis, 386, 387
Elasmobranchii, 45, 56, 57, 97
elasmobranchs, 41, 43, 45, 54, 55, 56, 57
Elasmodus, 52
Elassichthys, 369
Elassodiscus, 495
Elassoma, 444, 445
ELASSOMATIDAE, 303
Elassomatinae, 445
Elates, 477
Elattarchus, 499
electric eel, 239
electric rays, 82, 83
Electrolux, 84
Electrona, 278
ELECTROPHORIDAE, 239
Electrophorus, 238, 239
Eleginops, 465
ELEGINOPSIDAE, 465
Eleginus, 302
ELEOTRIDAE, 328, 329
ELEOTRIDIDAE, 326, 328
Eleotris, 329
elephantfishes, 159
Eleutherochir, 413
Ellimma, 164
ELLIMMICHTHYIDAE, 164
ELLIMMICHTHYIFORMES, 163
Ellimmichthyinae, 164
Ellimmichthyoidei, 163
Ellimmichthys, 162, 164
Ellimminae, 164
Ellisella, 240
Ellochelon, 342
Ellopostoma, 192
ELLOPOSTOMATIDAE, 192
ELONICHTHYIDAE, 113
Elopichthys, 181, 184
ELOPIDAE, 135
ELOPIFORMES, 133, 135
Elopomorpha, 128, 132, 133, 134
Elopopsis, 130
Elops, 128, 134, 135
Elopsomolos, 135
Elotrica, 332
Elpistostegalia, 110
ELPISTOSTEGALIDAE, 110
ELPISTOSTEGALIFORMES, 110
Elpistostege, 111
Ematops, 319
Embassichthys, 400
Embiotoca, 335
EMBIOTOCIDAE, 334, 335, 427
Emblemaria, 351
Emblemariopsis, 351
Embolichthys, 425
EMMELICHTHYIDAE, 498
Emmelichthyops, 457

Emmelichthys, 498
emperor breams, 505
emperors, 505
Empetrichthyinae, 372, 373
Empetrichthys, 370, 373, 374
Emsolepis, 45
Encheliophis, 316, 317
Encheloclarias, 230
Enchelybrotula, 318
Enchelycore, 144
Enchelynassa, 144
Enchelyolepis, 124
Enchelyopus, 301
Enchelyurus, 349
ENCHODONTIDAE, 267, 275
Enchodontinae, 275
Enchodontoidei, 267, 275
Enchodus, 275
Encrasicholina, 168
Endeiolepis, 29
Endennia, 116
Engraulicypris, 182
ENGRAULIDAE, 162, 166, 167
ENGRAULIDIDAE, 167
Engraulinae, 168
Engraulis, 168
Engraulisoma, 205
Engyophrys, 401
Engyprosopon, 401
Enigmacanthus, 523
Enigmapercis, 425
Enigmatochromis, 344
Enneacampus, 408
Enneacanthus, 444, 445
Enneanectes, 347
Enneapterygius, 347
Enophrys, 492
Enoplophthalmus, 257
ENOPLOSIDAE, 442
Enoplosus, 443
Entelognathus, 37
Entomacrodus, 349
Entomocorus, 234
Entosphenus, 25, 196
Eobothus, 396
Eocallionymus, 413
Eochampsodon, 422
Eocitharinus, 193
Eocoris, 427
EOCOTTIDAE, 315
Eocottus, 315
Eoetmopterus, 76
Eohiodon, 154, 155
Eoholocentrum, 304
Eolactoria, 521
Eolates, 432
Eomacronies, 223
Eomanodon, 52
Eometlaouia, 61
Eomobula, 95
Eomola, 524
Eonemachilus, 192
Eoplectus, 523
Eoplinthicus, 95
Eopsetta, 400
Eopsettinae, 400
Eosalmo, 248
Eosasia, 315
Eoscatophagus, 463
Eoserranus, 315
Eosiganus, 463
Eosladenia, 509
EOSPINIDAE, 522
Eosqualiolus, 77
Eostegostoma, 60
Eosternoptyx, 260
Eostriatolamia, 63
Eotorpedo, 83
Eoxenocypris, 186
Epalzeorhynchos, 182
Epapterus, 234
Epetriodus, 318
EPHIPPIDAE, 440, 496, 497, 499
Ephippion, 525
Ephippus, 497
Epibulus, 428
Epiceratodus, 109
EPIGONICHTHYIDAE, 16
Epigonichthys, 16
EPIGONIDAE, 434
Epigonus, 435
Epinephelides, 447
Epinephelinae, 447
Epinephelini, 447
Epinephelus, 447
Epinnula, 415
Epiplatina, 371
Epiplatys, 371
Eptatretinae, 21
Eptatretus, 20, 21
Equetus, 499
Equulites, 454
Eremichthys, 184
Eremophilus, 212, 213
Erepsilepis, 32
ERETHESTIIDAE, 228
Erethistes, 225
ERETHISTIDAE, 221, 223, 225
Erethistinae, 225
Erethistoides, 225
Eretmichthys, 318
Eretmophorus, 298
Ereunias, 489
EREUNIIDAE, 489
Ericandersonia, 479
Ericara, 174
Ericentrus, 350
Erichalcis, 163, 241
Ericymba, 184
Eridacnis, 70, 77
Erilepis, 486
Erimonax, 184
Erimystax, 184
Erimyzon, 189
Erimyzontini, 189
Eriptychiida, 27
Eriptychius, 18, 27
Erismatopterus, 288
Erisphex, 473
Ernogrammus, 480
Ernstichthys, 233
Erosa, 472, 473
Erotelis, 329
Erpetoichthys, 117
Errex, 400
Errivaspis, 29
Erromyzon, 192
Erymnacanthus, 100
ERYTHRINIDAE, 197
Erythrinoidea, 197
Erythrinus, 197
Erythrocles, 498
Erythroculter, 186
Eschmeyer, 474
ESCHMEYERIDAE, 468, 473
Escolar, 415
Escualosa, 171
Eskimaspis, 39
ESOCIDAE, 249, 251
ESOCIFORMES, 241, 243, 248, 249
Esomus, 182
Esox, 248, 249, 250, 251
Esselenichthys, 480
Estesox, 249
Etelinae, 458
Etelis, 458
Ethadophis, 146
Etheostoma, 450
Etheostomatinae, 449
Ethmalosa, 171, 172
Ethmidium, 162, 171
ETMOPTERIDAE, 75, 77
Etmopterus, 76

Etroplus, 343, 344
Etropus, 399
Etrumeus, 170
Euacanthomorpha, 278, 284
Euantiarcha, 38
Euantiarchi, 38
Eubiodectes, 131
Eubleekeria, 454
Eubrachythoraci, 40
Euchilichthys, 227
Euchiloglanis, 225
Euchondrocephali, 48, 49
Eucinostomus, 433
Eucitharus, 398
EUCLICHTHYIDAE, 297
Euclichthys, 297
Eucrossorhinus, 61
Eucryphycus, 479
Eudontomyzon, 25
Eugaleaspis, 34
EUGENEODONTIDAE, 50
EUGENEODONTIFORMES, 48, 50
eugeneodontiforms, 48
Eugeneodus, 50
Eugerres, 433
Eugnathichthys, 195
Eugnathogobius, 330
Eugnathostomata, 36, 40, 97, 98, 99
Eugomphodus, 65
Euleptorhamphus, 365, 367
Euleptorhampus, 367
Eulophias, 478
EULOPHIIDAE, 478
eulophiids, 478
Eumecichthys, 283
Eumegistus, 451, 452
Eumesogrammus, 480
Eumicrotremus, 495
Euosteichthyes, 101
Eupallasella, 184
Eupetrichthys, 428
Euphanerops, 30
Eupleurogrammus, 416
Eupogonesthes, 262
Eupomacentrus, 339
Euprotomicroides, 77
Euprotomicrus, 77
Euristhmus, 221
Euryacanthus, 100
Euryarthra, 86
Eurycaraspis, 39
Eurycheilichthys, 217
Euryglossa, 404
Eurymen, 493
Eurypegasus, 407
EURYPHARYNGIDAE, 150
Eurypharynx, 150
Eurypholis, 275
Eurypleuron, 316
Eurypterygii, 265, 266
Eusebichthys, 132
Euselachians, 53, 54
Euselachii, 43, 47, 53, 55, 56, 58, 73, 81, 95
Eusphyra, 73
Eusthenodon, 110
Eusthenopteron, 110
Eustomias, 263
Eusurculus, 319
Eutaeniichthys, 330
Eutaeniophorinae, 312, 313
Eutaeniophorus, 313
Euteleostei, 128, 160, 241, 242, 251
Euteleostomi, 101
EUTHACANTHIDAE, 99
Euthacanthus, 99
Euthynnus, 417
Euthynotus, 127
Eutrigla, 476
Eutropiichthys, 221
Evarra, 184
Evermannella, 274
EVERMANNELLIDAE, 274
Evermannia, 332
Evermannichthys, 332
Eviota, 332
Evistias, 443
Evorthodus, 330
Evoxymetopon, 416
Evynnis, 506
Exallias, 349
ex-Danioninae, 185
Exechodontes, 479
Exerpes, 351
EXOCOETIDAE, 365, 367
Exocoetinae, 366
Exocoetoidea, 365
Exocoetoidei, 365
Exocoetus, 366
Exodon, 204, 205
Exoglossum, 184
Exonautes, 366
Exornator, 455
Exostoma, 225

Facciolella, 147
Fadenia, 50
Fajumia, 210, 223
FALCATIDAE, 46
Falcatus, 46
false brotulas, 320
false cat sharks, 70
false scorpionfishes, 433
false trevallies, 450
Fanfangia, 182
fanfins, 513
fangtooths, 305
Farlowella, 217
fathead sculpins, 493
Fenestraja, 85
Feroxodon, 525
Festucalex, 408
FIERASFERIDAE, 316
fierasfers, 316
Figaro, 69
fighting fishes, 392
filefishes, 523
finback cat sharks, 70
fingerfishes, 452
Fiordichthys, 319
Fissodus, 50
Fistularia, 410
FISTULARIIDAE, 409
Flagellostomias, 263
flagfins, 268
flagtails, 438
Flammeo, 304
flannel-mouth characiforms, 201
flashlight fishes, 306
flatfishes, 395, 396, 414
flatheads, 475
  deepwater flatheads, 476
  flatheads, 477
  ghost flatheads, 477
Fleurantia, 108
FLEURANTIIDAE, 108
Florenciella, 435
Floridichthys, 376
flounder, 396
  bigeye flounders, 401
  crested flounders, 402
  largescale flounders, 397
  lefteye flounders, 400
  measles flounders, 401
  peppered flounders, 401
  righteye flounders, 399
  sand flounders, 398
  southern flounders, 402
Fluviphylacinae, 378
Fluviphylacini, 379
Fluviphylax, 378
flying gurnards, 411
flyingfishes, 365
Foa, 325

Fodiator, 366
Fodiatorinae, 366
Foerschichthys, 371
Foetorepus, 413
Folipistrix, 60
footballfishes, 514
Forbesichthys, 289
Forcipiger, 454, 455
FORMIONIDAE, 386
Formosania, 192
Forsterygion, 347
Fossorochromis, 344
four-eyed fishes, 376, 377
Fowleria, 325
Fowlerichthys, 510
Franciscodoras, 234
Fraudella, 336
Freemanichthys, 491
freshwater eels, 152
freshwater hatchetfishes, 206
freshwater sleepers, 327
freshwater smelts, 256
freshwater spiny eels, 382
Frigocanthus, 523
Frigorilepis, 45
Frilled Shark, 74
frilled sharks, 74
frogfishes, 509
  frogfishes, 509
  lophichthyid frogfishes, 510
Frontilabrus, 428
Fucomimus, 350
Fugu, 525
FUNDULIDAE, 370, 374
Funduloidea, 372
Fundulopanchax, 371
Fundulus, 374
Furcacauda, 31
FURCACAUDIDAE, 31
FURCACAUDIFORMES, 30, 31
Furcina, 492
Furgaleus, 71
fusiliers, 458

Gadella, 298
Gadiculus, 302
GADIDAE, 294, 299, 300, 301
GADIFORMES, 284, 285, 290, 293, 294, 302
Gadinae, 301, 302
Gadoidea, 299
Gadoidei, 294, 297
Gadomus, 296
Gadopsis, 442
Gadus, 300, 302
Gagata, 225
Gaidropsarinae, 301
Gaidropsarus, 294, 301
Galaxias, 196, 255, 256
Galaxiella, 256
GALAXIIDAE, 242, 254
galaxiids, 254
GALAXIIFORMES, 252, 254
galaxiiforms, 254
Galaxiinae, 255
Galaxioidei, 241
Galea, 58
Galeaspida, 18, 30
GALEASPIDIFORMES, 32, 34
Galeichthyinae, 232
Galeichthys, 232
Galeocerdo, 71, 72
Galeocharax, 205
Galeocorax, 64
Galeomorphi, 43, 56, 57, 58, 59
Galeorhininae, 71
Galeorhinus, 71
Galeus, 69
galjoen fishes, 439
Gambusia, 379, 380
Gambusiini, 380
Ganges Shark, 72
Ganntouria, 62
Ganodus, 52
Ganopristis, 85
gapers, 422
Gargariscus, 476
Gargaropteron, 421
Garmanella, 376
Garo, 382
Garra, 182
gars, 121, 122, 123
Gasterochisma, 415, 417
Gasterochismatinae, 415, 417
GASTEROPELECIDAE, 206
Gasteropelecus, 207
Gasterorhamphosus, 410
GASTEROSTEIDAE, 482, 483
GASTEROSTEIFORMES, 303
Gasterosteoidei, 381, 410, 467, 482, 485
Gasterosteus, 482, 483, 484
Gasterotomus, 201
Gastrocyathus, 353
Gastrocymba, 353
Gastromyzon, 192
GASTROMYZONTIDAE, 191, 192, 193
gastromyzontines, 191
Gastrophori, 408
Gastropsetta, 399
Gastroscyphus, 353
Gavialiceps, 147
Gazza, 454
Gelanoglanis, 235
GEMPYLIDAE, 415
Gempylus, 415
Gemuendina, 37
Genicanthus, 456
Genidens, 232
Genyagnus, 427
Genyatremus, 457
Genyonemus, 499
Genypterus, 317, 318
Geophagus, 344
Geotria, 25
GEOTRIIDAE, 23, 25
Gephyroberyx, 308
Gephyrocharax, 206
Gephyroglanis, 229
GERDALEPIDIDAE, 38
Gerdalepis, 38
Gerlachea, 466
GERREIDAE, 427, 433
Gerres, 433
Geryichthys, 196
ghost flatheads, 477
ghost pipefishes, 407, 408
Ghrisichthys, 131
Gibbechinorhinus, 79
gibberfishes, 310
GIBBERICHTHYIDAE, 309, 310
Gibberichthys, 310
GIBBODONTIDAE, 121
Gibbonsia, 350
GIGANTACTINIDAE, 517
Gigantactis, 517
Giganthias, 447
Gigantura, 271
GIGANTURIDAE, 271
Giganturoidei, 272
Gila, 184
Gilbertidia, 493
Gilbertolus, 198, 203
Gilchristella, 170
Gillellus, 347
Gillichthys, 330
Gillicus, 131
Gilliodus, 50

Gilloblennius, 347
Gilpichthys, 20, 24
GINGLYMODI, 122, 128
Ginglymostoma, 62
GINGLYMOSTOMATIDAE, 60, 61, 62
Girardinini, 380
Girardinichthys, 374
Girardinus, 380
Girella, 440
Girellinae, 440
Giuris, 329
Glacialepis, 32
GLADIOBRANCHIDAE, 100
Gladiobranchus, 100
Gladioglanis, 236
Gladiogobius, 332
Glanapteryginae, 212, 214
Glanapteryx, 214
Glandulocauda, 206
Glandulocaudinae, 206
Glanidium, 235
Glaniopsis, 192
Glaphyropoma, 213
Glaridoglanis, 225
Glarithurus, 501
Glaucosoma, 437
GLAUCOSOMATIDAE, 436
Glaucostegus, 86
Glenoglossa, 146
Glickmanodus, 56
Glossamia, 325
Glossanodon, 253
Glossogobius, 332
Glossolepis, 359
Glyphis, 72
Glyptauchen, 471
Glyptocephalus, 400
Glyptolepis, 107
Glyptoparus, 349
Glyptoperichthys, 218
Glyptophidium, 318
Glyptosterninae, 225
Glyptosternon, 225
Glyptothorax, 225
Gnathagnus, 427
GNATHANACANTHIDAE, 468, 474
Gnathanacanthus, 474
Gnathanodon, 387
Gnathocharax, 203
Gnathodentex, 505
Gnathodolus, 200
Gnatholebias, 372
Gnatholepis, 329, 330
Gnathonemus, 159, 160
Gnathophis, 148
Gnathopogon, 184
Gnathostomata, 31, 32, 34, 35, 95
gnathostomes, 18, 19, 45, 50
gnomefishes, 450
goatfishes, 436
Gobibagrus, 223
gobies, 326, 332
  blind cave gobies, 328
  butid sleepers, 329
  freshwater sleepers, 327
  gobies, 331
  Gobionellus-like gobies, 329
  loach gobies, 327
  mudskipper gobies, 329
  spinycheek sleepers, 328
GOBIESOCIDAE, 333, 334, 351, 352
GOBIESOCIFORMES, 284, 351
Gobiesocinae, 352
Gobiesox, 353
Gobiida, 314, 323, 326, 405, 414
GOBIIDAE, 181, 326, 329, 330, 331, 332, 333
GOBIIFORMES, 285, 323, 324, 326, 327, 333
Gobio, 184
Gobiobotia, 184
Gobiodon, 332
Gobioidei, 326, 327, 331
Gobiomorphus, 329
Gobiomorus, 329
GOBIONELLIDAE, 326, 329, 330
Gobionellinae, 330
Gobionellus, 329, 330
Gobioninae, 184
Gobionotothen, 465
Gobiopsis, 332
Gobiopterus, 330
Gobiosoma, 332
Gobitrichinotus, 332
Gobius, 332
goblin sharks, 64
Gobulus, 332
Goeldiella, 236
Gogangra, 225
Gogo, 231
Gogodipterus, 107, 108
Gogolia, 71
Gogonasus, 110
Gogoselachus, 45
goldfishes, 183
Gollum, 70
gombessas, 105
Gomphosus, 428
Gonialosa, 172
Gonichthys, 278
Goniistius, 460
Gonioplectrus, 447
Goniporus, 32
GONORYNCHIDAE, 176, 177
GONORYNCHIFORMES, 175, 176
Gonorynchus, 174, 177
Gonostoma, 260
GONOSTOMATIDAE, 259, 261
Gonostomatoidei, 259
Goodea, 374
GOODEIDAE, 370, 372, 373
goodeids, 372
Goodeinae, 373
Goodrichthys, 46, 47
goosefishes, 508
Gordichthys, 176
Gorgasia, 148
Gorgonichthys, 40
Gorogobius, 332
Gosiutichthys, 162, 171
Goslinia, 237
Gosztonyia, 479
Gouania, 353
Goulmimichthys, 130
gouramies, 392, 393
  climbing gouramies, 391
  combtail gouramies, 392
  giant gouramies, 392
  kissing gouramies, 391
Gracilia, 447
Grahamichthys, 329
Gramma, 336
GRAMMATIDAE, 333, 334, 336
Grammatobothus, 401
Grammatonotus, 503
Grammatorcynus, 417
Grammatostomias, 263
GRAMMICOLEPIDIDAE, 292
Grammicolepidinae, 292
Grammicolepis, 292
GRAMMIDAE, 336
Grammistes, 448
Grammistini, 447, 448
Grammistops, 448

Grammonus, 319
Grammoplites, 477
Grasseichthys, 178
Graus, 440
graveldivers, 482
graylings, 245
Great White Shark, 68
greeneyes, 272
greenlings, 487
  painted greenlings, 486
Greenwoodella, 130
Greenwoodochromis, 344
GREGORIIDAE, 49
gregoriids, 48
Gregorius, 49
grenadiers, 296
Grenfellaspi, 38
Griphognathus, 108
GROENLANDASPIDIDAE, 39
groppos, 503
Grossipterus, 108
Grossius, 106
groupers, 447
Grundulus, 206
grunters, 441
grunts, 457
Guavina, 329
gudgeons, 184
Gudusia, 171, 172
Guentheridia, 525
Guentherus, 265
Guianacara, 344
GUILDAYICHTHYIDAE, 115
GUILDAYICHTHYIFORMES, 115
Guildayichthys, 112, 115
guitarfishes, 85
Guiyu, 103
Gulaphallinae, 362
Gulaphallus, 361, 362
gulper sharks, 75
Gunnellichthys, 332
gunnels, 480, 481
Gunterichthys, 319
guppy, 379
Gurgesiella, 85
gurnards, 475
Guttigadus, 298
Guyu, 442
Gvozdarus, 465
Gymnachirus, 403
Gymnallabes, 230
Gymnammodytes, 426
Gymnapistes, 471
Gymnapogon, 325, 326
GYMNARCHIDAE, 156, 160
Gymnarchus, 153, 160
Gymnelinae, 479
Gymnelopsis, 479
Gymnelus, 479
Gymnocaesio, 459
Gymnocanthus, 492
Gymnocephalus, 448
Gymnochanda, 335
Gymnocharacinae, 206
Gymnocharacinus, 193, 204, 206
Gymnoclinus, 480
Gymnocorymbus, 204, 205
Gymnocranius, 505
Gymnocrotaphus, 506
Gymnocypris, 183
Gymnodontes, 523
Gymnodraco, 466
Gymnogeophagus, 344
Gymnogobius, 330
Gymnoichthys, 125
Gymnomuraena, 144
Gymnorhamphichthys, 240
Gymnosarda, 417
Gymnoscopelus, 278
Gymnoscyphus, 353
Gymnothorax, 143, 144
GYMNOTIDAE, 238
GYMNOTIFORMES, 174, 179, 180, 207, 209, 238
Gymnotoidei, 238
Gymnotus, 238, 239
Gymnoxenisthmus, 329
Gymnura, 92
GYMNURIDAE, 88, 91, 92
GYRACANTHIDAE, 99
Gyracanthides, 99
GYRINOCHEILIDAE, 187
Gyrinocheilus, 187
Gyrinomimus, 312, 313
GYRODONTIDAE, 121
Gyrodus, 121
Gyrosteus, 118

Habroichthys, 116
haddock, 302
HADRODONTIDAE, 121
Hadronector, 104
HADRONECTORIDAE, 104
Hadropareia, 479
Hadropogonichthys, 479
Hadrosteus, 40
Haemomaster, 213
HAEMULIDAE, 457
Haemulinae, 457
Haemulon, 457
Haemulopsis, 457
hagfishes, 14, 17, 19, 20, 21
Haikouella, 13, 14
Haikouichthys, 13, 14
hairtails, 416
hairyfish, 312
hakes, 293
  luminous hakes, 295
  merlucciid hakes, 298
  phycid hakes, 299, 301
  southern hakes, 295, 298
hakelings, 298
Halaelurus, 69
Halaphritis, 464
Halargyreus, 298
Halec, 267
HALECIDAE, 267
Halecoidei, 267
Halecomorphi, 122, 124, 128
Halecostomi, 121
Haletta, 429
halfbeaks, 366
  viviparous halfbeaks, 367
halfmoons, 441
halibut, 396
Halicampus, 408
Halichoeres, 428
Halicmetus, 512
Halidesmus, 340
Halieutaea, 512
Halieutichthys, 512
Halieutopsis, 512
Halimochirurgus, 520
Halimuraena, 340
Halimuraenoides, 340
Haliophis, 340
Halobatrachus, 323
Halonodon, 51
Halophryne, 323
Halophryninae, 321, 323
HALOSAURIDAE, 137
Halosauropsis, 138
halosaurs, 137
Halosaurus, 138
Haludaria, 183
hamlets, 447
hammerhead sharks, 72
Hampala, 183
handfishes, 510
Handuichthys, 279, 307
Hannia, 441

Hanyangaspis, 34
HAPALOGENIIDAE, 457
Hapalogenys, 457
Haploblepharus, 69
Haplochromis, 344
Haplocylix, 353
HAPLODACTYLIDAE, 460
Haplodoci, 320
HAPLOGENIIDAE, 457
HAPLOLEPIDAE, 113
Haplolepis, 113
Haplomi, 248
Haplophryne, 518
Haplotaxodon, 344
Haptenchelys, 142
Haptoclinus, 351
Haptogenys, 349
Hara, 225
Hardistiella, 24
hardnose skates, 85
Harengula, 167, 171, 172
HARPACANTHIDAE, 49
Harpadon, 268
Harpadontinae, 268
Harpagifer, 466
HARPAGIFERIDAE, 466
Harpagofututor, 51
Harriotta, 53
Harriottinae, 53
Harttia, 217
Hassar, 234
Hastatobythites, 319
Hastichthys, 267
Hatcheria, 213
hatchetfishes, 206, 260
  freshwater hatchetfishes, 206
  marine hatchetfishes, 260
hawkfishes, 459
Hayenchelys, 139
Hazeus, 332
headstanders, 200
  headstanders, 200
  toothed headstanders, 200
Heckelichthys, 131
Heightingtonaspis, 39
Helcogramma, 347
Helcogrammoides, 347
HELENOLEPIDIDAE, 32
Helenolepis, 32
Helichthys, 115
Helicolenus, 469
Helicophagus, 220
HELICOPRIONIDAE, 50
Heliobatis, 91
Heliotrygon, 91
Helmolepis, 116
HELODONTIDAE, 49, 50
HELODONTIFORMES, 48, 50
Helodus, 48, 49, 50
HELOGENEIDAE, 211
Helogeneinae, 211
Helogenes, 212
Helostoma, 391
HELOSTOMATIDAE, 390, 391
Helotes, 441
Hemanthias, 447
Hemerocoetes, 425
Hemerocoetinae, 424, 425
Hemiancistrus, 217
Hemiarus, 232
Hemibagrus, 223
Hemibrycon, 206
Hemicalypterus, 122
Hemicaranx, 387
Hemicetopsis, 212
hemichordates, 13
Hemichromis, 344
Hemiculter, 186
Hemicyclaspis, 34
Hemidoras, 234
Hemieleotris, 329
Hemiemblemaria, 351
HEMIGALEIDAE, 71
Hemigaleus, 71
Hemiglyphidodon, 339
Hemigobius, 330
Hemigrammocharax, 195
Hemigrammopetersius, 196
Hemigrammus, 204
Hemigymnus, 428
Hemileiocassis, 223
Hemilepidotinae, 490
Hemilepidotus, 490
Hemilutjanus, 448
Hemimyaria, 15
Hemimyzon, 191
Heminodus, 476
Heminoemacheilus, 192
HEMIODONTIDAE, 197, 198, 199
hemiodontids, 199
Hemiodontinae, 199
Hemiodontini, 199
Hemiodopsis, 199
Hemiodus, 199
Hemipristis, 71
Hemipsilichthys, 218
HEMIRAMPHIDAE, 365, 366, 367
Hemiramphus, 367
Hemirhamphodon, 367
Hemisalanx, 258
Hemisaurida, 267
HEMISCYLLIIDAE, 61
Hemiscyllioidea, 61
Hemiscyllium, 61, 62
Hemisilurus, 219
Hemistichodus, 195
Hemitaurichthys, 455
Hemitremia, 184
Hemitriakis, 71
HEMITRIPTERIDAE, 485, 490
Hemitripterus, 490
Heniochus, 455, 501
Henochilus, 205
Henonemus, 213
Hephaestus, 441
Hephthocara, 318, 319
HEPSETIDAE, 196
Hepsetus, 193, 197
HEPTAPTERIDAE, 209, 236
Heptapterinae, 236
Heptapterus, 236
Heptranchias, 75
HEPTRANCHIIDAE, 75
Heraldia, 408
Hercynolepis, 49
Herichthys, 344
Herklotsichthys, 171
Hermosilla, 441
Heros, 344
herring smelts, 253
herrings, 164
  anchovies, 167
  denticle herrings, 165
  freshwater herrings, 171
  herrings, 169
  longfin herrings, 166
  menhadens, 169
  pilchards, 169
  round herrings, 169, 170
  sardines, 169
  shads, 169, 171
  sprats, 169
  wolf herrings, 169
Herwigia, 173, 174
Hesperoleucus, 184
Heterandria, 380
Heterandriini, 380
Heterelotris, 332

HETERENCHELYIDAE, 139, 142
Heterenchelys, 142
Heteristius, 347
Heterobranchus, 230
Heterocharacinae, 203
Heterocharax, 203
Heteroclinus, 350
Heteroconger, 148
Heterocongrinae, 148
HETERODONTIDAE, 59
HETERODONTIFORMES, 42, 57, 58, 59
Heterodontus, 59
Heteromycteris, 404
HETEROMYRIDAE, 143
Heteronarce, 84
Heteronectes, 396
Heteropetalus, 50
Heterophallus, 380
Heterophorcynus, 60
Heterophotus, 261, 262
Heteropleuron, 16
Heteroplopomus, 332
Heteropneustes, 208, 231
HETEROPNEUSTIDAE, 208, 230, 231
Heteropriacanthus, 453
Heteroptychodus, 56
Heteroscarus, 429
Heteroscyllium, 60
Heteroscymnoides, 77
Heterosomata, 395
Heterostichus, 349, 350
Heterostraci, 18, 27, 28
Heterostrophus, 122
Heterotidinae, 157
Heterotis, 153, 157
Heteroyunnanolepis, 38
HEXAGRAMMIDAE, 485, 486, 487
Hexagramminae, 487
Hexagrammoidea, 487
Hexagrammos, 488
Hexanchida, 57, 73
HEXANCHIDAE, 73, 74
HEXANCHIFORMES, 57, 58, 73, 74
Hexanchus, 74, 75
Hexanematichthys, 232
Hexatrygon, 88, 90
HEXATRYGONIDAE, 88, 89
Hierops, 276
Hildebrandia, 148
Hilsa, 171
HIMANTOLOPHIDAE, 514
Himantolophus, 515
Himantura, 91
Hime, 269
Hintonia, 278
Hiodon, 153, 154, 155
HIODONTIDAE, 155
HIODONTIFORMES, 153, 155
Hippichthys, 408
Hippocampinae, 408
Hippocampus, 409
Hippoglossina, 399
Hippoglossinae, 399
Hippoglossoides, 400
Hippoglossoidinae, 400
Hippoglossus, 399
Hippopotamyrus, 160
Hipposcarus, 430
Hipposcorpaena, 470
Hirculops, 349
Hirella, 34
Hirundichthys, 366
Hisonotus, 217
HISPIDOBERYCIDAE, 310
hispidoberycids, 310
Hispidoberyx, 308, 310
Histiobranchus, 142
Histiodraco, 466
Histionotophorus, 511
Histionotus, 124
Histiophryne, 510
Histiopterinae, 443
Histiopterus, 443
Histrio, 509, 510
Hito, 219
Hoffstetterichthys, 210
hogfishes, 428
Holacanthomorpha, 284
Holacanthopterygii, 278
Holacanthus, 456
Holanthias, 447
Holapogon, 325
Holcomycteronus, 318
Hollardia, 520
Hollardinae, 520
HOLOCENTRIDAE, 303, 304, 309
HOLOCENTRIFORMES, 303, 304, 308
Holocentrinae, 304
Holocentrites, 304
Holocentrus, 304
holocephalans, 42, 43
Holocephali, 37, 43, 47, 48, 49, 50, 51, 95
Holocephalimorpha, 48, 49, 50
Hologinglymostoma, 62
Hologymnosus, 428
Holohalaelurus, 69
Holophagus, 106
HOLOPTYCHIIDAE, 107
HOLOPTYCHIIFORMES, 106
Holoptychius, 107
Holostei, 121, 122
Holtbyrnia, 173
Homalacanthus, 100
HOMALODONTIDAE, 56
Homalodontus, 56
Homaloptera, 191
HOMALOPTERIDAE, 191
homalopterines, 191
Homalopteroides, 191
Homalopterula, 191
Homodiaetus, 213
Homostolus, 318
Hongeo, 85
Hongshuia, 182
Hoplarchus, 344
Hoplerythrinus, 197
Hoplias, 197
HOPLICHTHYIDAE, 468, 477
Hoplichthys, 475, 477
Hoplobrotula, 317, 318
Hoplocharax, 203
Hoplolatilus, 456
Hoplomyzontinae, 233
Hoplopagrus, 458
Hoplopteryx, 308
Hoplosebates, 470
Hoplosternum, 215
Hoplostethus, 308
Hoplunnis, 147
HORABAGRIDAE, 222, 228
Horabagrus, 222, 228
Horadandia, 182
Horaglanis, 230
HORAICHTHYIDAE, 364, 370
Horaichthyinae, 365
Horaichthys, 364, 365
Horbatshia, 260
horsefishes, 475
Horseshoeichthys, 163
hound sharks, 70
Howella, 434
HOWELLIDAE, 434
Howittacanthus, 101
Howqualepis, 111

Hozukius, 469
Huananaspis, 34
Hubbsina, 374
huchen, 246
Hucho, 246
Humboldtichthys, 240
Husinae, 121
Huso, 120, 121
Hyalobagrus, 223
Hybodonta, 55, 56
HYBODONTIDAE, 56
HYBODONTIFORMES, 55
hybodontiforms, 55, 56
hybodonts, 55
Hybodus, 56
Hybognathus, 184
Hybopsis, 184
Hydrocynus, 193, 196
Hydrolagus, 53
Hydrolycus, 198
Hygophum, 278
Hylaeobatis, 56
Hylopanchax, 379
Hymenocephalus, 296
Hymenogadus, 296
Hypancistrus, 217
Hypentelium, 189
Hypergastromyzon, 192
Hyperlophus, 162, 171
Hyperoartii, 23
Hyperoglyphe, 419
Hyperopisus, 160
Hyperoplus, 425, 426
Hyperotreti, 20
Hyperprosopon, 335
Hyphessobrycon, 204
Hypleurochilus, 349
Hypnos, 83
Hypnosqualea, 54, 78
hypnosqualean, 79
Hypoatherina, 363
Hypoclinemus, 403
Hypodoras, 234
Hypogaleus, 71
Hypolophites, 91
Hypolophus, 91
Hypomasticus, 200
Hypomesus, 257
Hypophthalmichthys, 184, 186
HYPOPHTHALMIDAE, 237
Hypophthalmus, 237
Hypoplectrodes, 447
Hypoplectrus, 447
Hypopleuron, 318
HYPOPOMIDAE, 240
Hypopomus, 240
Hypopterus, 432
Hypoptopoma, 217
Hypoptopomatinae, 217
HYPOPTYCHIDAE, 482
Hypoptychus, 483
Hypopygus, 240
Hyporhamphus, 366, 367
Hyporthodus, 447
Hypostominae, 217, 218
Hypostomus, 217
Hypotodus, 65
Hypotremata, 80
Hypsagoninae, 490
Hypsagonus, 490
Hypseleotris, 329
HYPSIDORIDAE, 208, 211
Hypsidoris, 211
Hypsidoroidei, 210, 211
Hypsigenys, 428
Hypsoblennius, 349
Hypsocormus, 127
Hypsopanchax, 379
Hypsophrys, 344
Hypsurus, 335
Hypsypops, 339
Hysterocarpus, 335

Iago, 71
Iansan, 86
Iberochondrostoma, 184
Iberocypris, 184
icefishes, 258, 463
  catadromous icefishes, 464
  cod icefishes, 465
  crocodile icefishes, 467
  temperate icefishes, 464
Icelinus, 492
Icelus, 492
Ichthyapus, 146
ICHTHYBORIDAE, 194
Ichthyborus, 195
Ichthyocampus, 408
Ichthyococcus, 261
Ichthyodectes, 131
ICHTHYODECTIDAE, 131
ICHTHYODECTIFORMES, 131
Ichthyoelephas, 202
Ichthyomyzon, 24
Ichthyostega, 111
Ichthyotringa, 267
ICHTHYOTRINGIDAE, 267
Ichthyotringoidei, 267
Ichthyscopus, 427
Icichthys, 418, 419
ICOSTEIDAE, 412
ICOSTEIFORMES, 405, 412
Icosteus, 412
ICTALURIDAE, 235
Ictaluroidea, 229, 235
Ictalurus, 235, 236
Ictiobinae, 188
Ictiobus, 188
Idiacanthinae, 263
Idiacanthus, 261, 263
Idiastion, 470
Idiolophorhynchus, 297
Idiolychnus, 278
Idus, 184
Igdabatis, 94
Iguanodectes, 205
Iguanodectinae, 205
Ijimaia, 265
Ikechaoamia, 125
Iksookimia, 190
Ilisha, 166, 167
Iluocoetes, 479
Ilyodon, 374
Ilyophinae, 141
Ilyophis, 141, 142
Ilypnus, 330
Imparfinis, 236
Inabaperca, 315, 442
Incaichthys, 210
Incara, 329
Indiaichthys, 315
Indonotothenia, 465
INDOSTOMIDAE, 285, 484
Indostomus, 405, 485
Inegocia, 477
Inermia, 457
INERMIIDAE, 457
infantfishes, 331
Iniistius, 428
Inimicus, 472
Iniopterygia, 48, 49
INIOPTERYGIDAE, 49
INIOPTERYGIFORMES, 48, 49
Iniopterygii, 48
Iniopteryx, 49
Inpaichthys, 206
Insentiraja, 85
Iodotropheus, 344
Ioichthys, 253
IONOSCOPIDAE, 124
IONOSCOPIFORMES, 124, 125
Iotichthys, 184
IPNOPIDAE, 266, 270, 271

Ipnopinae, 270
Ipnops, 270, 271
Iracema, 240
Iracundus, 470
Iranocichla, 344
Iriatherina, 359
Irolita, 85
Irregulareaspis, 29
Irvineia, 228
Isacia, 457
Isanichthys, 122
Isanodus, 56
Isbrueckerichthys, 217
ISCHNACANTHIDAE, 100
ISCHNACANTHIFORMES, 97, 98, 100
Ischnacanthus, 100
Ischyodus, 52
Ischyrhiza, 85
Isidobatus, 86
Isistius, 67, 77, 79
Isocirrhitus, 459
Isogomphodon, 72
ISONIDAE, 341, 357
Isopisthus, 499
Isopsetta, 400
Isopsettini, 400
Istiblennius, 349
Istieus, 137
Istigobius, 332
Istiompax, 389, 390
ISTIOPHORIDAE, 380, 387, 388, 389, 414
ISTIOPHORIFORMES, 334, 380, 387, 388, 389, 439
Istiophorus, 389, 390
Isurolamna, 68
Isurus, 64, 68
Ituglanis, 213
Itycirrhitus, 459
Ivindomyrus, 160

Jackquhermania, 92
jacks, 383, 385, 386, 414
Jaekelotodus, 65
Jagorina, 37
JALODONTIDAE, 45
Jalodus, 45
Jamoytius, 23, 30
Janassa, 50
JANASSIDAE, 50
Japigny, 241
Japonolaeops, 401
Japonolycodes, 479
Jarvikia, 108
Javichthys, 525
jawed vertebrates, 34
jawfishes, 341
jawless craniates, 13
Jaydia, 325
Jeboehlkia, 448
jellynose fishes, 265
Jenkinsia, 170
Jenynsia, 377
JENYNSIIDAE, 370
JIANGHANICHTHYIDAE, 186
Jianghanichthys, 187
Jinshaia, 191
Jiuquanichthys, 154
Joffrichthys, 157
Johnius, 499
Johnlongia, 65
Johnrandallia, 455
Johnsonina, 520
Joleaudichthys, 396
Jonoichthys, 127
Jordanella, 376
Jordania, 489
JORDANIIDAE, 485, 488
Joturus, 342
Judeichthys, 177
Julidochromis, 344
Jupiaba, 204
Jurengraulis, 168

kahawai, 439
Kajikia, 389, 390
Kali, 421
Kalops, 112
Kaluga, 120
Kalyptatherina, 360
Kalyptodoras, 234
Kamoharaia, 401
Kanekonia, 473
KANNATHALEPIDIDAE, 45
Kannathalepis, 45
Karaisurus, 68
Karalepis, 347
Karalla, 454
Karsten, 330
Kasatkia, 480
KASIDORIDAE, 310
Kasidoron, 310
Kathala, 499
KATHEMACANTHIDAE, 43
kathemacanthids, 44
Kathemacanthus, 44
Kathetostoma, 427
Katibasia, 192
KATOPORODIDAE, 32
Katoporodus, 32
Katsuwonus, 417
Kaupichthys, 144
Kelloggella, 332
kelpfishes, 459
Kenoza, 249, 250, 251
Kentrocapros, 521
Kenyaconger, 148
Kermichthys, 244
Kestratherina, 363
Ketengus, 232
Khouribgaleus, 71
KIAERASPIDAE, 34
Kichulchoia, 190
killifishes, 369, 374
  Middle American killifishes, 372
Kimberleyeleotris, 329
King-of-the-Salmon, 284
kitefin sharks, 77
Kiunga, 359
Klausewitzia, 196
Kneria, 178
knerias, 178
Knerichthys, 129
KNERIIDAE, 176, 178
Kneriinae, 176, 178
Kneriini, 178
knifefishes
  banded knifefishes, 239
  bluntnose knifefishes, 240
  electric eel, 239
  electric knifefish, 239
  featherfin knifefishes, 158
  ghost knifefishes, 241
  glass knifefishes, 240
  nakedback knifefishes, 238
  Neotropical knifefishes, 238
  Old World knifefishes, 158
  ratttail knifefishes, 240
  sand knifefishes, 239
knifejaws, 437
Knightia, 162, 171
Knipowitschia, 332
Knodus, 206
Kochichthys, 422
koi, 181
Komoceraspis, 34
Konosirus, 172
Kopua, 353
Koreocobitis, 190

Kosswigichthys, 375
Kottelatia, 184
Kottelatlimia, 190
Koumansetta, 332
Kraemeria, 332
KRAEMERIIDAE, 331
Kreffichthys, 278
Kribia, 329
Krobia, 344
Kronichthys, 217
Krusenterniella, 479
KRYPTOGLANIDAE, 216, 219
Kryptoglanis, 210, 219
Kryptolebias, 372
Kryptolebiatinae, 372
Kryptophanaron, 306
Kryptopterus, 219
Kuhlia, 438, 440
KUHLIIDAE, 438
Kuiterichthys, 509, 510
Kujdanowiaspis, 39
Kumba, 296
Kureykaspis, 28
KURTIDAE, 324, 326
KURTIFORMES, 323, 324, 326, 333
Kurtus, 324
Kushlukia, 500
KUSHLUKIIDAE, 500
Kuyangichthys, 154
Kwangoclupea, 164
KYPHOSIDAE, 440
Kyphosinae, 440
Kyphosus, 440, 441

Labeo, 182, 202
Labeoninae, 182
labeos, 182
Labichthys, 151
Labidesthes, 356, 357
Labidochromis, 344
Labracinus, 339, 340
Labracoglossa, 440, 441
Labrichthys, 429
LABRIDAE, 427, 428
LABRIFORMES, 420, 421, 427, 429, 433
LABRISOMIDAE, 346, 350
Labrisomus, 351
Labroides, 429
Labropsis, 429
Labrus, 429
labyrinth fishes, 390
Labyrinthici, 390
Lacantunia, 210, 229
LACANTUNIIDAE, 209, 216, 226, 229
Laccognathus, 107
Lachneratus, 325
Lachnolaimus, 429
LACTARIIDAE, 450
Lactarius, 450
Lactophrys, 522
Lactoria, 522
Lacustricola, 379
Ladibesocypris, 184
Ladigesia, 196
Laemolyta, 200
Laemonema, 298
Laeops, 401
Laetacara, 344
Lagarodus, 50
Lagiacrusichthys, 273, 274
Lagocephalus, 525
Lagochila, 189
Lagodon, 506
Lagusia, 441
Laides, 221, 228
Laiphognathus, 349
Lake Baikal sculpins, 491
Lake Trout, 247
Lalaelurus, 69
Lamiopsis, 72
Lamna, 68
LAMNIDAE, 64, 67
LAMNIFORMES, 42, 57, 58, 63
Lamnostoma, 146
Lampadena, 278
Lampanyctinae, 278
Lampanyctodes, 278
Lampanyctus, 278
Lampetra, 24, 25
Lampetrinae, 25
lampeyes, 378
  banded lampeyes, 378
Lampichthys, 278
lampreys, 14, 19, 23
  northern lampreys, 24
  southern lampreys, 25
  southern topeyed lampreys, 26
Lamprichthys, 379
LAMPRIDAE, 281, 282
LAMPRIDIDAE, 282
LAMPRIDIFORMES, 278, 280, 282
Lampridomorpha, 280
LAMPRIFORMES, 265, 280, 282, 284, 302
Lamprimorpha, 264, 265, 279, 280
Lampriomorpha, 280
Lampris, 282
Lamprogrammus, 317, 318
Lamprologus, 344
Lampromorpha, 280
Lanarkia, 30, 31
LANARKIIDAE, 31
lancelets, 13, 16
lancetfishes, 275
lantern sharks, 75
lanternbellies, 434
lanterneye fishes, 306
lanternfishes, 276, 277
Lapitaichthys, 319
Lappanella, 429
Larabicus, 429
large-eye breams, 505
Largemouth Bass, 444
largescale deep-sea lizardfish, 271
largescale flounders, 397
Larimichthys, 499
Larimus, 499
Larvacea, 15
Lasanius, 29, 30
Lasiancistrus, 217
Lasiognathus, 516
LATEOLABRACIDAE, 435
Lateolabrax, 435, 496
Lateopisciculus, 288
Lates, 432
lates perches, 432
LATIDAE, 432
Latilinae, 456
Latimeria, 95, 105, 106
LATIMERIIDAE, 105, 106
Latinae, 432
Latinopollis, 117
LATRIDAE, 459, 460
Latridopsis, 461
Latris, 461
Latropiscis, 269
Laugia, 104
LAUGIIDAE, 104
Lavinia, 184
leaffishes, 337, 394, 395
  (Malayan) leaffishes, 395
  Asian leaffishes, 394
  South American leaffishes, 337
Lebacacanthus, 47
Lebiasina, 202
LEBIASINIDAE, 202
Lebiasininae, 202

Lebonichthys, 135
Lecanogaster, 353
Leedsichthys, 127
lefteye flounders, 400
leftvents, 517
Lefua, 192
Legnonotus, 124
legskates, 85
Leiarius, 237
Leidybatis, 94
Leiocassis, 223
LEIODONTIDAE, 49
Leiodus, 49
LEIOGNATHIDAE, 453
Leiognathus, 454
Leiopotherapon, 441
Leiostomus, 499
Leiuranus, 147
lemon sharks, 72
lenok, 246
Lepadichthys, 353
Lepadicyathus, 353
Lepadogaster, 353
Lepidamia, 325
Lepidammodytes, 426
LEPIDASPIDIDA, 28
Lepidaspis, 28
Lepidiolamprologus, 344
Lepidion, 298
Lepidoblennius, 347
Lepidoblepharon, 398
Lepidocephalichthys, 190
Lepidocephalus, 190
Lepidocybium, 415
Lepidogalaxias, 241, 242, 243, 251
LEPIDOGALAXIIDAE, 242
LEPIDOGALAXIIFORMES, 242, 251
Lepidogobius, 330
Lepidomeda, 184
Lepidonectes, 347
Lepidonotothen, 465
Lepidoperca, 447
Lepidophanes, 278
Lepidopodinae, 416
Lepidopsetta, 400
Lepidopus, 416
Lepidorhombus, 398
Lepidorhynchus, 296
Lepidosiren, 109
LEPIDOSIRENIDAE, 109
Lepidotes, 122
LEPIDOTIDAE, 124
Lepidotrigla, 476
Lepidozyginae, 338
Lepidozygus, 338
LEPISOSTEIDAE, 123
LEPISOSTEIFORMES, 121, 122, 123
Lepisosteus, 123, 128, 368
Lepominae, 445
Lepomis, 444, 446
Lepophidiini, 318
Lepophidium, 318
Leporellus, 200
Leporinus, 200
Leptacanthichthys, 515
Leptachirus, 404
Leptagoniates, 206
Leptagonus, 490, 491
Leptatherina, 363
Leptaulopus, 269
Lepthoplosternum, 215
Leptobotia, 190
LEPTOBRAMIDAE, 380
Leptobrotula, 318
Leptobrycon, 206
leptocephalus, 133, 134, 137, 139, 148, 149
Leptocharacidium, 196
Leptocharias, 70
LEPTOCHARIIDAE, 70
LEPTOCHILICHTHYIDAE, 174
Leptochilichthys, 172, 174
Leptoclinus, 480
Leptocottus, 492
Leptocypris, 182
Leptoderma, 174
Leptodoras, 234
Leptoglaninae, 226
Leptoglanis, 226
Leptojulis, 429
Leptolebias, 372
Leptolepides, 241
LEPTOLEPIDIDAE, 130
LEPTOLEPIDIFORMES, 130
Leptolepis, 130
Leptolucania, 374
Leptonotus, 408
Leptophilypnus, 329
Leptorhamdia, 236
Leptoscarus, 430
LEPTOSCOPIDAE, 421, 424, 425
Leptoscopus, 425
Leptostichaeus, 480
Leptostomias, 263
Leptostyrax, 64
Leptosynanceia, 473
Lepturacanthus, 416
Lepturichthys, 191
Lermichthys, 374
LESTIDIIDAE, 275, 276
Lestidiops, 275, 276
Lestidium, 275, 276
Lestradea, 344
Lestrodus, 50
Lestrolepis, 275, 276
Lesueurina, 425
Letharchus, 147
Lethenia, 68
Lethenteron, 25
Letholycus, 479
Lethotremus, 495
LETHRINIDAE, 504, 505
Lethrininae, 505
Lethrinops, 344
Lethrinus, 505
Leucaspius, 184
Leucicorus, 318
Leuciobrotula, 318
Leuciscinae, 182, 183
Leuciscus, 245
Leucobrotula, 320, 479
Leucogrammolycus, 479
Leucoraja, 85
Leucos, 184
Leucosoma, 258
Leuresthes, 356
Leurochilus, 347
Leuroglossus, 254
Leviprora, 477
Leyvaichthys, 212
Liachirus, 404
Liauchenoglanis, 228
Libanechelys, 139
LIBOTONIIDAE, 288
Libotonius, 288
Libys, 106
Lichia, 386
lightfishes, 261
Lignobrycon, 205
Ligulalepis, 111
Lile, 171
Limanda, 400
Limia, 379, 380
limias, 379
Limnichthys, 424
Limnocottus, 492
Limnomis, 111
Limnothrissa, 171
Lindbergichthys, 465
Lingcod, 487
lings, 301
Liniparhomaloptera, 192

Linkenchelys, 142
Linophryne, 518
LINOPHRYNIDAE, 512, 517
Liobagrus, 224
Liobranchia, 353
Liocranium, 471
LIODESMIDAE, 124, 125
Liodesmus, 125
lionfishes, 470
Liopogramma, 336
Liopropoma, 336, 447
Liopropominae, 447
Liopropomini, 447
Lioscorpius, 469
Liosomadoras, 233, 234
LIPARIDAE, 485, 495
LIPARIDIDAE, 495
Liparis, 494, 495
Lipocheilus, 458
Lipogenys, 138
Lipolagus, 254
Lipophrys, 349
Lipopterichthys, 217
Liposarcus, 218
Lissoberyx, 308
Lissocampus, 408
Lissodus, 56
Lissonanchus, 353
Listrura, 214
Lithodoras, 234
Lithogeneinae, 217
Lithogenes, 217
Lithognathus, 506
Lithopoecilus, 364
Lithoxus, 217
Litobranchus, 349
livebearers, 378, 379
  one-sided livebearers, 377
Liza, 342
lizardfishes, 266, 268
  Bombay ducks, 268
  deepsea lizardfishes, 272
  largescale deep-sea lizardfish, 271
  sand-diving lizardfishes, 269
Lo, 463
loaches, 180, 181, 189, 190
  botiid loaches, 189
  coolie loaches, 190
  fire-eyed loaches, 192
  gastromyzontid loaches, 191
  golden dojo, 190
  hillstream loaches, 191
  horse-face loach, 190
  kuhli loaches, 190
  longfin loaches, 190
  river loaches, 191
  serpent loaches, 193
  stone loaches, 192
  sturgeon-mouthed loaches, 192
  sucker loaches, 191
  weatherfishes, 190
lobe-finned fishes, 102
Lobianchia, 278
Lobotes, 504
LOBOTIDAE, 502, 503
Loganellia, 18, 31, 32
LOGANELLIIDAE, 32
LONCHIDIIDAE, 56
Lonchidion, 56
Lonchogenys, 203
Lonchopisthus, 341
Lonchurus, 499
longfin escolars, 413
Longfin Mako, 68
long-finned pikes, 450
LONGODIDAE, 32
Longodus, 32
lophichthyid frogfishes, 510
LOPHICHTHYIDAE, 510
Lophichthys, 510
LOPHIIDAE, 508
LOPHIIFORMES, 284, 420, 430, 462, 495, 506, 508, 518
Lophiobagrus, 229
Lophiocharon, 510
Lophiodes, 509
Lophioidei, 508
Lophiomus, 509
Lophionotus, 124
Lophiosilurus, 238
Lophius, 508, 509
Lophodiodon, 526
Lophodolos, 516
Lophogobius, 332
Lopholatilus, 456
Lopholiparis, 495
Lophonectes, 401
Lophosteus, 101, 111, 113
LOPHOTIDAE, 283
Lophotus, 283
Lorenzichthys, 338
Loricaria, 217
Loricariichthys, 217
LORICARIIDAE, 174, 175, 215, 216
Loricariinae, 217
Loricarioidei, 210, 212, 214, 215
Lota, 295, 302
Lotella, 298
Lotilia, 332
Lotinae, 301
louvar, 500
Lovettia, 256
Lovettiinae, 255, 256
Loweina, 278
Loxodon, 72
Lubbockichthys, 340
Lucania, 374
Lucayablennius, 351
Lucifuga, 318, 319
Lucigadus, 296
Luciobarbus, 183
Luciobrama, 184
Luciocephalinae, 392, 393
Luciocephalus, 393
Luciocyprinus, 183
Luciopercinae, 449
Luciopercini, 449
Luciopimelodus, 237
Luciosudis, 273
Luckius, 106
Luenchelys, 139
Luganoia, 116
LUGANOIDAE, 116
LUGANOIFORMES, 116
Luisichthys, 130
Luisiella, 131
Lumiconger, 148
Lumpenella, 480
Lumpeninae, 480
Lumpenopsis, 480
Lumpenus, 480
lumpfishes, 494
lumpsuckers, 494
Lunaspis, 39
lungfishes, 107, 108
  African lungfishes, 109
  Australian lungfishes, 109
  South American lungfishes, 109
Lupinoblennius, 349
Lupopsyroides, 97, 98
Lupopsyrus, 98
Luposicya, 332
Lusitanichthys, 179
LUTJANIDAE, 457, 458, 459
Lutjaninae, 458
Lutjanus, 143, 458
LUVARIDAE, 499, 500
Luvarus, 499, 500

Luxilus, 184
Luzonichthys, 447
Lycenchelys, 479
Lycengraulis, 168
Lycodapus, 479
Lycodes, 479
Lycodichthys, 479
Lycodinae, 479
Lycodontis, 144
Lycodonus, 479
Lycogrammoides, 479
Lyconectes, 480
Lyconema, 479
LYCONIDAE, 298
Lyconodes, 298
Lyconus, 298
Lycoptera, 154
LYCOPTERIDAE, 154
LYCOPTERIFORMES, 154
Lycothrissa, 168
Lycozoarces, 479
Lycozoarcinae, 479
Lyomeri, 149
Lyopsetta, 400
Lyopsettinae, 400
Lythrurus, 184
Lythrypnus, 332

Maccullochella, 442
Machaira, 388
mackerel sharks, 63, 67
mackerels, 414, 416, 417
  snake mackerels, 415
  Spanish mackerels, 417
Macolor, 458
Macquaria, 442
Macrhybopsis, 184
Macristiella, 271
Macristium, 272
Macrocephenchelys, 148
Macrochirichthys, 185
Macrodon, 499
Macrognathus, 383
Macroparalepis, 275, 276
Macropetalichthys, 39
Macropharyngodon, 429
Macropinna, 253
Macropodinae, 392
Macropodus, 392
Macropodusinae, 392
Macropoma, 106
MACRORAMPHOSIDAE, 410
Macroramphosus, 410
Macrorhamphosodes, 520
Macrorhizodus, 68
MACROSEMIIDAE, 124
MACROSEMIIFORMES, 122, 124
Macrosemimimus, 124
Macrosemiocotzus, 124
Macrosemius, 124
Macrospinosa, 499
Macrostomias, 262
Macrothyraspis, 34
Macrotrema, 381, 382
Macrotreminae, 382
MACROURIDAE, 294, 296
Macrouroidei, 294, 295
Macrouroides, 297
MACROUROIDIDAE, 294
Macrouroidinae, 297
Macrourus, 296
Macrozoarces, 479
MACRUROCYTTIDAE, 292
Macrurocyttinae, 292
Macrurocyttus, 292
MACRURONIDAE, 297, 298
Macruronus, 298
Mafdetia, 84
Magadanichthys, 479
Magnisudis, 276
Magosternarchus, 241
Magrebichthys, 286
Mahengecharax, 193
Mahengichthys, 178
mahimahi, 384
mail-cheeked fishes, 467
Majungaichthys, 319
Makaira, 389, 390
Makararaja, 91
MALACANTHIDAE, 411, 456
Malacanthinae, 456
Malacanthus, 456
Malacichthyes, 412
Malacocephalus, 296
Malacocottus, 493
Malacoctenus, 351
Malacoglanis, 214
Malacoraja, 85
Malacosarcus, 310
Malacosteinae, 263
Malacosteus, 264
Malakichthys, 434
MALAPTERURIDAE, 226, 227
Malapterurus, 227
Malapterus, 429
Mallotus, 257
Malpulutta, 392
Malthopsis, 512
Manberodus, 44
Mancopsetta, 402
Manducus, 260
manefishes, 452
Man-of-War Fish, 419
Manonichthys, 340
Manta, 95
manta rays, 95
Maratecoara, 372
marblefishes, 460
Marcusenius, 159, 160
Margariscus, 184
Margrethia, 260
Marilyna, 525
marine hatchetfishes, 260
marine smelts, 252
Marleyella, 401
marlins, 390
Marosatherina, 360
Marsdenichthys, 110
Marsdenius, 100
Marukawichthys, 489
Mascarenichthys, 319
Masillosteus, 123
MASSALONGIIDAE, 501
Massalongius, 501
Massamorichthys, 288
MASTACEMBELIDAE, 138, 382
Mastacembelinae, 383
Mastacembeloidei, 382
Mastacembelus, 383
Mastiglanis, 236
Mastigopterus, 318
Masturus, 524
Mataeocephalus, 296
Matanul, 347
Matsubaraea, 425
Matsubarichthyinae, 473
Matsubarichthys, 473
Maulisia, 173
Maurolicinae, 260
Maurolicus, 260
Mawsonia, 105
MAWSONIIDAE, 105
Maxillicosta, 469
Maylandia, 344
Maynea, 479
Mayomyzon, 24
MAYOMYZONTIDAE, 20, 24
MCCONICHTHYIDAE, 288
Mcconichthys, 288
Mccoskerichthys, 351
Meadia, 142
Mecaenichthys, 339

Meda, 184
medakas, 364
Medialuna, 441
Medusablennius, 349
medusafishes, 418
Megachasma, 67
MEGACHASMIDAE, 66
Megadontognathus, 241
Megalamphodus, 204
Megalancistrus, 217
Megalaspis, 387
Megalebias, 372
Megalechis, 215
MEGALICHTHYIDAE, 110
Megalichthys, 110
Megalocenter, 213
Megalocoelacanthus, 106
Megalodon, 68
Megalodoras, 234
Megalomycter, 313
MEGALOMYCTERIDAE, 309, 311, 312, 313
Megalonema, 237
Megalonibea, 499
MEGALOPIDAE, 135
Megalops, 133, 134, 136
megamouth sharks, 66
Meganthias, 447
Megapiranha, 199
Megaselachus, 64
Megasqualus, 78
Megatooth Shark, 68
Megupsilon, 376
Meiacanthus, 349
Melamphaes, 314
MELAMPHAIDAE, 309, 313
Melanecta, 112
Melanoacanthus, 100
MELANOCETIDAE, 514
Melanocetus, 514
Melanocharacidium, 196
Melanochromis, 344
Melanogrammus, 302
Melanolagus, 254
MELANONIDAE, 294, 295
Melanonoidei, 294, 295
Melanonus, 294, 295
Melanorhinus, 357
Melanostigma, 479
Melanostomias, 263
Melanostomiinae, 263
Melanotaenia, 359
MELANOTAENIIDAE, 341, 357, 358, 359
Melanotaeniinae, 358
Melanotaenioidei, 357
Melapedalion, 367
Melichthys, 523
Melodichthys, 319
Melvius, 126
Membradini, 357
Membras, 357
MENASPIDAE, 51
MENASPIFORMES, 49, 51
Menaspis, 49, 51
Mendosoma, 461
Mene, 387
menhadens, 169
MENIDAE, 387
Menidia, 354, 356, 357
Menidiinae, 356
Menidiini, 356
MENIFORMES, 387
Menticirrhus, 499
Mephisto, 520
Meridensia, 116
Meristodondoides, 56
Merlangius, 302
MERLUCCIIDAE, 297, 298
Merluccius, 294, 299
Merodoras, 234
MESACANTHIDAE, 100
Mesacanthus, 100
Mesiteia, 62
Mesobius, 296
Mesobola, 182
Mesoborus, 195
Mesopoma, 112
Mesopristes, 441
MESTURIDAE, 121
Metahomaloptera, 191
Metavelifer, 281, 282
Metelectrona, 278
Meteoria, 320
Metriaclima, 344
Metynnis, 199
Michin, 130
Micralestes, 196
Micrenophrys, 492
MICROBRACHIIDAE, 38
Microbrachius, 38
Microbrotula, 319
Microcambeva, 214
Microcanthinae, 440, 441
microcanthines, 441
Microcanthus, 440, 441
Microcharacidium, 196
Microchirus, 404
Microcobitis, 190
Microctenopoma, 391
Microcyprini, 369
MICRODESMIDAE, 331
Microdesminae, 331
Microdesmus, 332
Microetmopterus, 76
Microgadus, 295, 302
Microglanis, 238
Micrognathus, 408
Microgobius, 332
Microichthys, 435
Microlepidogaster, 217
Microlepidotus, 457
Microlipophrys, 349
Microlophichthys, 516
Micromesistius, 302
Micrometrus, 335
Micromischodus, 199
Micromoema, 372
Micromyzon, 233
Micronema, 219
Micropanchax, 379
Micropercops, 328
Microphilypnus, 329
Microphis, 407, 408
Microphysogobio, 184
Micropoecilia, 380
Micropogonias, 499
Micropterus, 444, 445, 446
Microschemobrycon, 206
Microspathodon, 339
Microsternarchus, 240
Microstoma, 254
Microstomatichthyoborus, 195
MICROSTOMATIDAE, 253
Microstomini, 400
Microstomus, 400
Microsynodontis, 227
Microthrissa, 171, 172
midshipmen, 322
Miguashaia, 104
MIGUASHAIIDAE, 104
Miichthys, 499
Mikrogeophagus, 344
milkfishes, 175, 176
Millerichthys, 372
Millerigobius, 332
Milyeringa, 328
MILYERINGIDAE, 326, 328
Mimagoniates, 206
Mimia, 112
Mimoblennius, 349
Minicrania, 38
Minilabrus, 428, 429
minnow(s), 181, 183
Minoini, 471
Minous, 472
Minyclupeoides, 171
Minysicya, 332

Minytrema, 189
Mioplosus, 314
Miracorvina, 499
Mirapinna, 312
MIRAPINNIDAE, 309, 311, 312, 313
Mirapinninae, 312
Mirorictus, 173
Miroscyllium, 76
Misgurnus, 190
Mistichthys, 330
Mitsukurina, 65
MITSUKURINIDAE, 64
Miuroglanis, 212, 214
Mixomyrophis, 146
Moapa, 184
Mobula, 95
Mobulinae, 94, 95
MOCHOKIDAE, 226, 227
Mochokus, 227
MOCLAYBALISTIDAE, 522
Modicus, 353
Moema, 372
Moenkhausia, 204
Mogurnda, 329
mojarras, 433
Mola, 524
molas, 524
MOLIDAE, 518, 522, 524
mollies, 379
Mollisquama, 77
Molva, 302
MONACANTHIDAE, 518, 522, 523
Monacanthus, 523
Mongolepidida, 28, 45
Mongolepis, 45
MONOCENTRIDAE, 303, 307
Monocentris, 307
Monochirus, 404
Monocirrhus, 337
MONODACTYLIDAE, 452, 453
Monodactylus, 452
MONOGNATHIDAE, 150
Monognathus, 150
Monolene, 401
Monomitopus, 318
Monopenchelys, 144
Monopterus, 381, 382
Monorhina, 33
Monotaxinae, 505
Monotaxis, 505
Monothrix, 319
Monotreta, 525
Monotrete, 525
Monotretus, 525
Moolgarda, 342
mooneyes, 155
moonfishes, 386, 387, 452
Mooredontus, 47
Moorish Idol, 500, 501
Mora, 298
Mordacia, 23, 26
MORDACIIDAE, 23, 26
MORIDAE, 294, 297, 298
Moringua, 149
MORINGUIDAE, 149
Moringuoidei, 148
MORMYRIDAE, 156, 159, 160
Mormyrops, 160
Mormyrus, 160
Morone, 496
MORONIDAE, 496
MORONIFORMES, 420, 430, 495, 496, 499
Moronoidei, 496
morwongs, 460
Moses Sole, 403
mosquitofishes, 379
mote sculpins, 478
mountain carps, 186
Moxostoma, 187, 189
Moxostomatini, 189
Moythomasia, 111
mudminnows, 179, 251
  African Mudminnow, 179
  mudminnows, 251
mudskippers, 330
Mugil, 342
MUGILIDAE, 341, 342, 354
MUGILIFORMES, 334, 341, 342
Mugilogobius, 330
Mugiloidei, 333, 341
Mugiloides, 342
Mugilomorpha, 303, 334
mullets, 341, 342
MULLIDAE, 405, 436
Mulloidichthys, 436
Mullus, 436
Mummichog, 374
Muraena, 144
MURAENESOCIDAE, 147
Muraenesox, 147
Muraenichthys, 146
MURAENIDAE, 143
Muraeninae, 143
Muraenoclinus, 350
Muraenoidei, 142, 144
MURAENOLEPIDIDAE, 294, 300
Muraenolepidoidei, 294
Muraenolepis, 300
Murrindalaspis, 37
Muskellunge, 250
Mustelus, 71
Myaka, 345
Mycteroperca, 143, 447
MYCTOPHIDAE, 277
MYCTOPHIFORMES, 276, 285
Myctophinae, 278
Myctophum, 278
Myersglanis, 225
Myersina, 332
Mylesinus, 199
Myleus, 199
MYLIOBATIDAE, 88, 91, 93
MYLIOBATIFORMES, 57, 86, 87, 88
myliobatiforms, 42
Myliobatinae, 93
Myliobatis, 93, 94
Myliobatoidei, 57, 88
Myllokunmingia, 13, 14
Mylocheilus, 184
Mylochromis, 345
Mylopharodon, 184
Mylopharyngodon, 186
Myloplus, 199
MYLOSTOMATIDAE, 40
Myoglanis, 236
Myopsaron, 424
Myoxocephalus, 492
MYRIACANTHIDAE, 51
Myriacanthoidei, 51
Myriacanthus, 51
Myrichthys, 147
Myripristinae, 305
Myripristis, 305
Myroconger, 143
MYROCONGRIDAE, 143
Myrophinae, 146
Myrophis, 146
Mystriophis, 147
Mystus, 223
Myxine, 20, 22
MYXINI, 20
MYXINIDAE, 20
MYXINIFORMES, 14, 20
Myxinikela, 20, 24
Myxininae, 21, 22
Myxinomorphi, 18, 19
Myxocyprininae, 187
Myxocyprinus, 188

Myxodagnus, 347
Myxodes, 350
Myxodinae, 350
Myxus, 342

Nagaichthys, 382
Nahangbagrus, 224
Nahanniaspi, 29
Nahanniaspis, 29
naked barracudinas, 276
Nalbantichthys, 479
Nanaichthys, 176
NANDIDAE, 337, 380, 394
Nandus, 394, 395
Nangra, 225
Nanichthys, 369
Nannacara, 345
Nannaethiops, 195
Nannatherina, 442
Nannobrachium, 278
Nannocampus, 408
Nannocharax, 195
Nannoperca, 433, 442
Nannopetersius, 196
Nannoplecostomus, 218
Nannosalarias, 349
Nannostomini, 203
Nannostomus, 203
Nanobagrus, 221, 222
Nanochromis, 345
Nanocorax, 64
Nansenia, 253
Narcetes, 174
Narcine, 83
NARCINIDAE, 83
Narcininae, 83
Nardoichthys, 315
Nardonoides, 179
Nardopiscis, 130
Nardorex, 267
Narke, 84
Narkinae, 83
Nasinae, 502
Nasloavcea, 506
Naso, 501, 502
Nasolamia, 72
Natalichthys, 340
Naucrates, 387
Naucratinae, 387
Nautichthys, 490
Navodon, 523
Naxilepis, 111
Nealotus, 415
Neamia, 325
Neatypus, 441
Nebris, 499
Nebrius, 59, 62
Nectamia, 325
Nectoliparidinae, 495
Nectoliparis, 495
Nedystoma, 232
needlefishes, 363, 368
Neenchelys, 146
Neeyambaspis, 34
Negaprion, 72
NEMACHEILIDAE, 186, 192
Nemacheilus, 192
Nemaclinus, 351
Nemadactylus, 460
Nemadoras, 234
Nemamyxine, 22
Nemanthias, 447
Nemapteryx, 232
Nematalosa, 172
NEMATISTIIDAE, 383
Nematistius, 383
Nematobrycon, 206
Nematocharax, 205
NEMATOGENYIDAE, 213, 214
Nematogenys, 214
Nematognathi, 207
Nematolebias, 372
Nematops, 401
NEMICHTHYIDAE, 145, 151
Nemichthys, 151
NEMIPTERIDAE, 504, 505
Nemipterus, 505
Nemophini, 348
Nemuroglanis, 236
Neoachiropsetta, 402
Neoanguilla, 153
Neoaploactis, 473
Neobola, 182
Neobythites, 318
Neobythitinae, 317, 318
Neobythitoides, 318
Neocaristius, 452
Neocentropogon, 471
Neocentropogoninae, 475
Neoceratias, 514
NEOCERATIIDAE, 512, 513
NEOCERATODONTIDAE, 108, 109
Neoceratodus, 109
Neochanna, 255, 256
Neocirrhites, 459
Neoclinus, 350, 351
Neoconger, 149
Neocottus, 492
Neocyttus, 291
Neoditrema, 335
Neodontobutis, 328
Neoepinnula, 415
Neoeucirrhichthys, 190
Neofundulus, 372
Neogastromyzon, 192
Neoglyphidodon, 339
Neogobius, 332
Neoharriotta, 52, 53
Neoheterandria, 380
Neolaeops, 401
Neolamprologus, 345
Neolebias, 195
Neolumpenus, 480
Neomerinthe, 470
Neomyxine, 22
Neomyxus, 342
Neonesthes, 262
Neoniphon, 304
Neonoemacheilus, 192
Neoodax, 429
Neoophorus, 374
Neoopisthopterus, 167
Neopagetopsis, 467
Neopataecus, 474
Neophos, 260
Neophrynichthys, 493
Neoplecostominae, 217
Neoplecostomus, 217
Neopomacentrus, 339
Neopterygii, 116, 121
Neoraja, 85
Neosalangichthys, 258
Neosalanx, 258
Neoscombrops, 434
NEOSCOPELIDAE, 277
Neoscopelus, 277
Neoscorpaena, 470
Neoscorpis, 441
Neosebastes, 469
NEOSEBASTIDAE, 468, 469
Neosebastinae, 469
neoselachians, 54
Neoselachii, 56, 57
Neosiluroides, 221
Neosilurus, 221
NEOSTETHIDAE, 341
Neostethus, 361, 362
Neosynchiropus, 413
Neoteleostei, 241, 243, 252, 264, 265
Neotoca, 374
Neotropius, 222
Neotrygon, 91
Neovespicula, 471
Neozoarces, 479

Neozoarcinae, 480
Nerophis, 408
Nes, 332
Nesiarchus, 415
Nesides, 104
Nesogalaxias, 255, 256
Nesogobius, 332
Nessorhamphus, 145
Nettastoma, 147
NETTASTOMATIDAE, 147
Nettenchelys, 147
Netuma, 232
New Zealand torrentfishes, 422
Nexilosus, 339
Nezumia, 296
nibblers, 440
Nibea, 499
Nicholsicypris, 185
Nicholsina, 430
Nielsenichthys, 319
Nigerium, 223
Nikolivia, 31
NIKOLIVIIDAE, 31
Nile Perch, 432
Niphon, 446, 447
Niphonini, 447
Nipponocypris, 185
Niwaella, 190
Nkondobagrus, 223
Nocomis, 184
NOMEIDAE, 419
Nomeus, 419
Nomorhamphus, 367
noodlefishes, 258
Norfolkia, 347
NORMANICHTHYIDAE, 478
Normanichthyoidei, 467, 478
Normanichthys, 478
Normichthys, 173
Northern Hemisphere smelts, 257
Nostolepis, 98
NOTACANTHIDAE, 138
NOTACANTHIFORMES, 133, 137
Notacanthus, 134, 138
Notagogus, 124
Notarius, 232
NOTELOPIDAE, 130
Notelops, 130
Notemigonus, 184
Notesthes, 471
NOTHOBRANCHIIDAE, 371
Nothobranchius, 371
Nothonotus, 450
Notidanodon, 75
Notidanoidei, 73
Notidanoides, 75
Notidanus, 75
Notocetichthys, 312
NOTOCHEIRIDAE, 355, 356, 357, 358
Notocheirus, 356, 357, 358
Notocirrhitus, 459
Notoclinops, 347
Notoclinus, 347
Notodectes, 127
Notoglanidium, 228
Notogoneus, 177
Notograptus, 337
Notolabrus, 429
Notolepis, 275
Notoliparis, 495
Notolychnus, 278
Notolycodes, 479
Notomuraenobathys, 300
Notomyxine, 22
Notophycis, 298
Notopogon, 410
NOTOPTERIDAE, 156, 158
Notopteridarum, 158
Notopterinae, 158
Notopteroidei, 155, 156
Notopterus, 158, 159
Notoraja, 85
Notorhizodon, 110
NOTORYNCHIDAE, 75
Notorynchus, 74, 75
Notoscopelus, 278
NOTOSUDIDAE, 273
Notosudis, 273
Notosudoidea, 273
Notothenia, 465
NOTOTHENIIDAE, 465
Notothenioidei, 424, 463
Nototheniops, 465
Notropis, 184
Noturus, 208, 235
Novaculichthys, 429
Novaculoides, 429
Novaculops, 429
Novumbra, 248, 249, 251
Nuchequula, 454
Nudiantennarius, 510
numbfishes, 83
Numidopleura, 396
Nursalliinae, 121
nurse sharks, 62
nurseryfishes, 324
Nyassachromis, 345
Nybelinella, 320
Nybelinoides, 252

oarfishes, 284
OBAICHTHYIDAE, 123
Obaichthys, 123
Oblada, 506
Obliquogobius, 332
Obtusacanthus, 43, 97
Occella, 490
Occidentarius, 232
Occithrissops, 131
Ocean Sunfish, 524
ocean sunfishes, 524
oceanic basslets, 434
Ochetobius, 184
Ochmacanthus, 213
Ocosia, 471
Ocyurus, 458
ODACIDAE, 427, 429
Odax, 429
Odaxothrissa, 171
Odontamblyopus, 330
Odontanthias, 447
ODONTASPIDIDAE, 65
Odontaspis, 65
Odonteleotris, 329
Odontesthes, 353, 355, 356
ODONTOBUTIDAE, 326, 327, 328
Odontobutis, 328
Odontocharacidium, 196
Odontognathus, 167
Odontomacrurus, 296
Odontopyxis, 491
Odontoscion, 499
Odontostilbe, 206
Odontostomias, 263
Odontostomops, 274
Odonus, 523
Oedalechilus, 342
OGCOCEPHALIDAE, 511
Ogcocephaloidei, 508, 511
Ogcocephalus, 512
Ogilbia, 319
Ogilbyina, 340
Oidiphorus, 479
Okamejei, 85
Okkelbergia, 24, 25
Oldmanesox, 249
oldwives, 442
Olgibichthys, 319
Oligocottus, 492

Oligolactoria, 521
Oligolepis, 330
Oligoplites, 386
Oligosarcus, 204
Oligoscatophagus, 463
Olisthops, 429
Olivaichthys, 211
Ollentodon, 374
Oloplotosus, 221
Olympic Mudminnow, 249
Olyra, 222, 223
OLYRIDAE, 222
OMALODONTIDAE, 44
OMALODONTIFORMES, 44
Omalodus, 44
Oman, 349
Omegophora, 525
Omobranchus, 349
Omosoma, 286
Omosomopsis, 286
OMOSUDIDAE, 276
Omosudis, 275, 276
Omox, 348, 349
Ompok, 219
Onchopristis, 85
Onchystoma, 183
Oncopterus, 401, 402
Oncorhynchus, 246, 247, 248
Oncorynchus, 247
Onefin Cat Shark, 68
Oneirodes, 516
ONEIRODIDAE, 312, 515, 516
Onigociinae, 477
Oniichthys, 123
Onuxodon, 317
ONYCHODONTIDA, 106
ONYCHODONTIDAE, 106
ONYCHODONTIFORMES, 106
Onychodus, 106
Opaeophacus, 479
opahs, 280
Opeatogenyus, 353
Ophicephalus, 394
OPHICHTHIDAE, 145
Ophichthinae, 146
Ophichthus, 147
Ophiclininae, 349
Ophiclinops, 349
Ophiclinus, 349
Ophidiida, 314, 315, 320, 405, 414
OPHIDIIDAE, 317
OPHIDIIFORMES, 284, 294, 315, 479
Ophidiinae, 317
Ophidiini, 318
Ophidioidei, 284, 294, 315
Ophidion, 318
Ophioblennius, 349
Ophiocara, 329
OPHIOCEPHALIFORMES, 393
Ophiodon, 487
Ophiodontinae, 487
OPHIOPSIDAE, 124
Ophiopsis, 125
Ophioscion, 499
Ophisternon, 381, 382
Ophisurus, 147
Ophthalmolepis, 429
Ophthalmolycus, 479
Opisthocentrinae, 480
Opisthocentrus, 480
Opisthomyzon, 385
OPISTHOMYZONIDAE, 385
Opisthonema, 171
OPISTHOPROCTIDAE, 253
Opisthoproctus, 253
Opisthopterus, 167
OPISTOGNATHIDAE, 333, 334, 341
Opistognathus, 341
OPLEGNATHIDAE, 437
Oplegnathus, 437, 440
Opostomias, 263
Opsanus, 322, 323
Opsaridium, 182
Opsariichthyinae, 185
Opsariichthys, 185
Opsarius, 182
Opsodoras, 234
Opsopoeodus, 184
Optivus, 308
Opua, 332
Orange Roughy, 308
orbicular velvetfishes, 470
Orcynopsis, 417
ORECTOLOBIDAE, 60, 61
ORECTOLOBIFORMES, 57, 58, 59, 60
Orectoloboidea, 60
Orectoloboidei, 57, 60
Orectoloboides, 61
Orectolobus, 61
Oregonichthys, 184
Oreichthys, 183
Oreochromis, 343, 344, 345
Oreoglanis, 225
Oreoleuciscus, 184
Oreonectes, 192
Oreosoma, 291
OREOSOMATIDAE, 290
Oreosomatinae, 291
Orestiacanthus, 46
Orestias, 375
Orestiini, 375
Orinocodoras, 234
Ornategulum, 163
Ornatoscyllium, 60
Ornithoprion, 50
ORODONTIDAE, 49, 55
ORODONTIFORMES, 48, 49
orodonts, 48
Orodus, 49
Orpodon, 65
Orrichthys, 511
Orthacanthus, 47
ORTHACODONTIDAE, 74
Orthacodus, 74
Orthechinorhinus, 79
Orthochromis, 345
Orthocormus, 127
Orthodon, 184
Orthopristis, 457
Orthospinus, 205
Orthosternarchus, 241
Orthrias, 192
Orvikuina, 111
Oryzias, 364, 365
ORYZIATIDAE, 370
ORYZIIDAE, 364
Oryziinae, 364
OSHUNIIDAE, 124
OSMERIDAE, 256, 257
OSMERIFORMES, 170, 241, 252, 256
Osmeroidei, 256, 257
Osmeroides, 135
OSMEROMORPHA, 252, 264
Osmeromorphi, 241
Osmerus, 256, 257
Osopsaron, 425
Osorioichthys, 114
OSPHRONEMIDAE, 390, 391, 392
Osphroneminae, 392
Osphronemus, 391, 392
Ospia, 125
Ossancora, 234
Ostarioclupeomorpha, 128, 160, 161

Ostariophysan, 344
Ostariophysi, 161, 172, 174, 175, 431
Ostariostoma, 155
OSTARIOSTOMIDAE, 155
Osteichthyes, 36, 37, 40, 95, 96, 97, 101
  stem-group, 101
  crown-group, 102
Osteochilus, 182
Osteodiscus, 495
Osteogeneiosus, 232
OSTEOGLOSSIDAE, 156
OSTEOGLOSSIFORMES, 153, 155
Osteoglossinae, 157
OSTEOGLOSSOCEPHALA, 153
Osteoglossoidei, 156
Osteoglossomorpha, 128, 133, 153, 154
Osteoglossum, 153, 157, 158, 163
Osteolepidida, 110
OSTEOLEPIDIDAE, 110
OSTEOLEPIDIFORMES, 110
Osteolepis, 110
Osteostraci, 18, 30, 33
Osteostracomorphi, 18, 26, 31, 32
Ostichthys, 305
Ostorhinchus, 325
OSTRACIIDAE, 518, 521, 522
Ostracioidea, 521
Ostracion, 522
OSTRACIONTIDAE, 521
Ostracodermi, 521
ostracoderms, 18, 26
Othos, 447
Otocephala, 128, 160, 161, 162, 172, 252
Otocinclus, 217
OTODONTIDAE, 64, 68
Otodus, 64
Otolithes, 499
Otolithoides, 499
Otomorpha, 161, 162
Otopharynx, 345
Otophidium, 318
Otophysi, 174, 179, 180, 207, 209, 238
Otothyris, 217
Ouledia, 92
Ovalentaria, 314, 326, 333, 334, 335, 342, 380, 387, 388, 427, 432, 439
Overia, 32
Owstonia, 462
OWSTONIIDAE, 461
Owstoniinae, 462
Oxuderces, 330
OXUDERCIDAE, 329, 330, 331, 332
Oxudercinae, 330
Oxybrycon, 206
Oxycercichthys, 340
Oxycheilinus, 429
Oxycirrhites, 459
Oxyconger, 147
Oxydoras, 234
Oxyeleotris, 329
Oxygaster, 185
Oxygastri, 185
Oxygastrinae, 185
Oxyjulis, 429
Oxylapia, 345
Oxylebias, 487
Oxylebiinae, 486
Oxylebius, 487
Oxymetopon, 332
Oxymonacanthus, 523
OXYNOTIDAE, 76, 77
Oxynotus, 77
Oxyporhamphinae, 366
Oxyporhamphus, 366, 367
Oxyropsis, 217
Oxyzygonectes, 378
Oxyzygonectinae, 377

Paarecbasis, 206
Pachyamia, 126
Pachycara, 479
Pachychilon, 184
PACHYCORMIDAE, 127
PACHYCORMIFORMES, 127
Pachycormus, 127
Pachygaleus, 71
Pachyhexanchus, 75
Pachymetopon, 506
Pachymylus, 52
Pachypanchax, 371
Pachypops, 499
Pachypterus, 222
PACHYRHIZODONTIDAE, 130
Pachyrhizodus, 130
Pachystomias, 263, 264
Pachyurus, 499
Pacific salmon, 247
  Amago, 248
  Cherry Salmon, 248
  Chinook Salmon, 248
  Chum Salmon, 248
  Coho Salmon, 248
  kokanee, 248
  Masu Salmon, 248
  Pink Salmon, 248
  Rainbow Trout, 246
  Sockeye Salmon, 248
Pacific trouts, 246, 247
pacus, 198
paddlefishes, 118
  Chinese Paddlefish, 119
  North American Paddlefish, 119
Padogobius, 332
Paedocypris, 182, 330
Paedogobius, 330
Pagellinae, 506
Pagellus, 506
Pagetopsis, 467
Pagothenia, 465
Pagrinae, 506
Pagrus, 506
painted greenlings, 486
Palaeacanthaspis, 37
Palaeobates, 56
Palaeobathygadus, 296
Palaeobrachaelurus, 60
Palaeocarcharias, 63
Palaeocarcharodon, 63
PALAEOCENTROTIDAE, 281
Palaeocentrotus, 281
Palaeodenticeps, 166
PALAEOESOCIDAE, 249
Palaeoesox, 249
Palaeogobio, 181
Palaeolycus, 275
PALAEONISCIDAE, 113
PALAEONISCIFORMES, 113
Palaeonotopterus, 156, 158
Palaeoperca, 315
Palaeophichthys, 115
Palaeopomacentris, 338
Palaeorhincodon, 63
PALAEORHYNCHIDAE, 388
PALAEOSPINACIDAE, 59
Palaeospondylus, 108
Paleogaleus, 71
Paleohoplias, 193

Paleopsephurus, 119
Palidiplospinax, 59
Pallasina, 490
Pamphorichthys, 380
Pampus, 420
Panaque, 217
Pandaka, 330
PANDERICHTHYIDAE, 110
Panderichthys, 111
Pangasianodon, 219, 220
PANGASIIDAE, 219, 220, 228
Pangasius, 220
Pangio, 190
Panna, 499
Pantanodon, 379
Pantodon, 153, 155, 156
PANTODONTIDAE, 156
Pantolabrus, 387
Pantosteus, 189
Panturichthys, 142
Panxianichthys, 125
PANXIOSTEIDAE, 40
Pao, 525
Papiliolebias, 372
Papilloculiceps, 477
Papuengraulis, 168
Papuligobius, 330
Papyrocranus, 158, 159
Parabarbus, 181
Parabathymyrus, 148
Parabatrachus, 323
Parabembra, 477
Parabembras, 476, 477
PARABEMBRIDAE, 468, 475, 476, 477
Parablenniini, 348
Parablennius, 349
Parabothus, 401
Parabotia, 190
Parabramis, 186
Parabrotula, 320, 479
PARABROTULIDAE, 315, 320, 479
Paracaesio, 458
Paracallionymus, 413
Paracanthopoma, 213
Paracanthopterygii, 264, 265, 278, 279, 280, 284, 285, 286, 287, 288, 290, 315, 320, 351
Paracanthostracion, 522
Paracanthus, 501, 502
Paracaristius, 452
Paracentropogon, 471
Paracentropyge, 456
Paracentrus, 304
Paraceratodus, 109
Paracestracion, 59
Paracetonurus, 296
Paracetopsis, 212
Parachaenichthys, 466
Parachaetodon, 455
Parachanna, 393, 394
Parachanos, 177
Paracheilinus, 429
Paracheirodon, 204
Parachela, 185
Parachiloglanis, 225
Parachondrostoma, 184
Paracirrhites, 459
Paracitharus, 398
Paraclinus, 351
Paraclupea, 162, 164
PARACLUPEIDAE, 163, 164
Paraclupeinae, 164
Paraclupeini, 164
Paracobitis, 192
Paraconger, 148
Paracottus, 485
Paradapedium, 122
Paradiancistrus, 319
Paradicichthyinae, 458
Paradiglanis, 229
Paradiplospinus, 415
paradisefishes, 392
Paradistichodus, 195
Paradoxodacna, 335
Paradoxoglanis, 227
Paraechinorhinus, 79
Paraetmopterus, 76
Paragalaxias, 255, 256
Paragaleus, 71
Paraginglymostoma, 60
Paragobiodon, 332
Paragoniates, 206
Paragunnellichthys, 332
Paraheminodus, 476
Paraheptranchias, 75
Parahollardia, 520
Paraholtbyrnia, 173
Parahucho, 247
Parahypsos, 349
Parailia, 228
Parajulis, 429
Parakneria, 178
Parakuhlia, 457
Parakysinae, 224
Parakysis, 224
Paralabrax, 447
Paralaemonema, 298
PARALEPIDIDAE, 274, 275
Paralepidocephalus, 190
Paralepidotus, 124
Paralepis, 275
Paralichthodes, 401
PARALICHTHODIDAE, 401
Paralichthodinae, 399
PARALICHTHYIDAE, 396, 398, 399
Paralichthys, 399
Paraliparidinae, 495
Paraliparis, 495
Paralogania, 32
Paralonchurus, 499
Paralticus, 349
Paraluteres, 523
Parambassis, 335
Paramblypterus, 113
Paramisgurnus, 190
Paramonacanthus, 523
Paramormyrops, 159
Paramphilius, 226
Paramugil, 342
Paramyxine, 21
Paramyxininae, 21
Paranaichthys, 114
Parancistrus, 217
Paranebris, 499
Paraneetroplus, 345
Paranibea, 499
Paranomotodon, 63
Paranotothenia, 465
Paranthias, 447
PARAORTHACODONTIDAE, 74
Parapercis, 422, 423
Paraphago, 195
Parapholidophorus, 129
Paraphorosoides, 77
Parapimelodus, 237
Paraplagusia, 405
PARAPLESIOBATIDAE, 37
Paraplesiobatis, 37
Paraplesiops, 336
Paraploactis, 473
Paraplotosus, 221
Parapocryptes, 330
Parapriacanthus, 437
Parapristipoma, 457
Parapristipomoides, 458
Paraprotomyzon, 192
Parapsettus, 497
Parapterois, 470
Parapteronotus, 241
Parapterygotrigla, 476
Pararasbora, 185

Parargyrops, 506
Pararhincodon, 60
Pararhinichthys, 184
Parasaccogaster, 319
Parasciadonus, 320
Parascolopsis, 505
Parascorpaena, 470
PARASCYLLIIDAE, 60
Parascyllioidei, 57, 60
Parascyllium, 60
Paraselachii, 48, 49
Paraselachimorpha, 48, 49
PARASEMIONOTIDAE, 124
PARASEMIONOTIFORMES, 124, 125
Parasemionotus, 124, 125
Parasilurus, 219
Parasphaerichthys, 393
Parasphyraenops, 447
Parastegophilus, 213
Parastremma, 205
Parastromateus, 386, 387
Parasudis, 273
Parataeniophorus, 312, 313
Parateleopus, 265
Paratherina, 360
Paratilapia, 345
Paratrachichthys, 308
Paratriacanthodes, 520
Paratriakis, 71
Paratrimma, 332
Paratrygon, 91
Paratrygonorrhina, 86
Parauchenoglanis, 228
PARAULOPIDAE, 266, 267, 269
Paraulopoidei, 267, 269
Paraulopus, 266, 270
Paravandellia, 213
Paravinciguerria, 244
Paraxenisthmus, 329
Parazacco, 185
Parazanclistius, 443
Parazen, 291
PARAZENIDAE, 291
Parazeninae, 291
Pardachirus, 403, 404
Pareiodon, 213
Pareiorhaphis, 217
Pareiorhina, 217
Parenchelyurus, 349
Parenchodus, 275
Pareques, 499
Parequula, 433
Paretroplus, 345
Pareuchiloglanis, 225
Pareutropius, 228
Parexocoetinae, 366
Parexocoetus, 366
Parexus, 99
Parhomaloptera, 192
Pariah, 332
Paricelinus, 489
Parinoberyx, 308
Pariosternarchus, 241
Paristiopterus, 443
Parkraemeria, 332
Parma, 339
Parmaturus, 69
Parmops, 306
Parodon, 198
PARODONTIDAE, 197
parodontids, 197
Parona, 386
Parophidion, 318
Parophrys, 400
Parosphromenus, 392
Parotocinclus, 217
Parotodus, 64
Parrella, 332
parrotfishes, 429, 430
Parupeneus, 436
Parupygus, 240
Parvicrepis, 353
Parvilux, 278
Parviparma, 329
Parvodus, 56
Pastinachus, 91
PATAECIDAE, 467, 468, 474
Pataecoidei, 468, 474
Pataecus, 474
Patagolycus, 479
Patagonian blennies, 465
Patagonotothen, 465
Pattersonella, 252
Pattersonichthys, 280
Paucaichthys, 451
Paucicanthus, 98
Paulicea, 237
Pauranthus, 315
Pavoclinus, 350
Pavoraja, 85
Paxton, 325, 326
pearl perches, 436
pearleyes, 273
pearlfishes, 316
Peckoltia, 217
Pectenocypris, 181
Pectinochromis, 340
PEGASIDAE, 406
Pegasoidea, 406
Pegasus, 406, 407
Pegusa, 404
PEIPIAOSTEIDAE, 118
PEIPIAOSTEIFORMES, 118
Peipiaosteus, 118
Pelagia, 414
Pelagocephalus, 525
Pelagocyclus, 495
Pelangia, 359
Pelargorhynchus, 267
Pelasgus, 184
Pelates, 441
Pelecanichthys, 401
Pelecus, 184
Pellisolus, 173
Pellona, 166, 167
Pelloninae, 167
Pellonula, 171, 172
Pellonulinae, 170, 171, 172
Pelotius, 304
Pelotretis, 402
Pelsartia, 441
Pelteobagrus, 223
PELTOPLEURIDAE, 116
PELTOPLEURIFORMES, 116
Peltopleurus, 116
Peltorhamphus, 402
Pelvicachromis, 345
PEMPHERIDAE, 437, 452
Pempheris, 437
pencilfishes, 202, 203
pencilsmelts, 253
Penetopteryx, 408
Pennahia, 499
Penopus, 318
Pentaceropsis, 443
Pentaceros, 443
PENTACEROTIDAE, 443
Pentacerotinae, 443
PENTANCHIDAE, 69
Pentanchus, 68, 69
Pentapodus, 505
Pentaprion, 433
Pentathyraspis, 34
Pentherichthys, 516
Pentheroscion, 499
Pentlandia, 108
Peprilus, 420
Perca, 448
Percalates, 442
Percarina, 449
Percarininae, 449
Perccottus, 328
PERCICHTHYIDAE, 442
Percichthys, 442

perches, 430
  Chinese perches, 442
  lates perches, 432
  pearl perches, 436
  perches, 448
  splendid perches, 503
  temperate perches, 442
PERCIDAE, 424, 448
PERCIFORMES, 326, 341, 380, 405, 420, 424, 427, 430, 433, 434, 467, 468, 474, 495, 506
Percilia, 433
PERCILIIDAE, 433
Percina, 450
Percinae, 448
Percis, 490
Percoidea, 431, 433
Percoidei, 394, 421, 431, 453, 462, 497
Percomorpha, 279, 285, 303, 314, 315, 414, 420, 430, 433
Percomorphacea, 314, 315
PERCOPHIDAE, 421, 423, 424
Percophinae, 424
Percophis, 424
PERCOPSIDAE, 284, 287, 288
PERCOPSIFORMES, 284, 285, 287, 288
Percopsis, 288
Pereulixia, 349
Periophthalmodon, 330
Periophthalmus, 330
Perissias, 401
PERISTEDIIDAE, 468, 475, 476
Peristedion, 476
Peristrominous, 473
PERLEIDIDAE, 116
PERLEIDIFORMES, 116
Perleidus, 116
Peronedys, 349
Perryena, 475
Persparsia, 173
Perulibatrachus, 323
Pervagor, 523
PETALICHTHYIFORMES, 39
Petalichthys, 368
PETALODONTIDAE, 50
PETALODONTIFORMES, 48, 50
petalodontiforms, 49
petalodonts, 48
Petersius, 196
Petilipinnis, 499
Petrocephalus, 160
Petrochromis, 345
Petroleuciscus, 184
Petromyzon, 24
Petromyzontida, 23
PETROMYZONTIDAE, 23, 24
PETROMYZONTIFORMES, 14, 23
Petromyzontinae, 24
Petromyzontomorphi, 18, 23
Petroscirtes, 349
Petrotilapia, 345
Petrotyx, 318
Petrus, 506
Petulanos, 200
Pezichthys, 511
PEZOPALLICHTHYIDAE, 31
Pezopallichthys, 31
Phaenomonas, 147
Phaeoptyx, 325
Phago, 195
Phalacronotus, 219
Phallichthys, 380
Phalloceros, 380
Phalloptychus, 380
PHALLOSTETHIDAE, 341, 357, 360, 361
Phallostethinae, 361
Phallostethus, 362
Phallotorynus, 380
Phanerodon, 335
PHANEROPLEURIDAE, 108
Phaneropleuron, 108
PHANERORHYNCHIDAE, 115
PHANERORHYNCHIFORMES, 115
Phanerorhynchus, 115
Phareodus, 154, 157
PHARMACICHTHYIDAE, 280
Pharyngolepis, 30
Phenablennius, 348, 349
Phenacobius, 184
Phenacogaster, 205
Phenacogrammus, 196
Phenacoscorpius, 470
Phenacostethus, 362
Phenagoniates, 206
Pherallodichthys, 353
Pherallodiscus, 353
Pherallodus, 353
Phialaspis, 28
Phillipsilepis, 31
Philypnodon, 329
PHLEBOLEPIDIDAE, 32
Phlebolepis, 32
PHLYCTAENIIDAE, 39
Phlyctaenioidei, 39
PHOEBODONTIDAE, 45
PHOEBODONTIFORMES, 45
Phoebodus, 45
PHOLIDAE, 480
Pholidapus, 480
PHOLIDICHTHYIDAE, 334, 341, 345, 346
Pholidichthys, 346
Pholidochromis, 340
Pholidoctenus, 129
Pholidophoretes, 129
PHOLIDOPHORIDAE, 128, 129
PHOLIDOPHORIFORMES, 129, 130
Pholidophorus, 129, 130
PHOLIDOPLEURIDAE, 116
PHOLIDOPLEURIFORMES, 116
Pholidopleurus, 116
Pholidorhynchodon, 129
Pholinae, 481
Pholis, 480, 481
Phorcynis, 60
PHOSICHTHYIDAE, 261
Phosichthyoidei, 261
Phosichthys, 261
PHOTICHTHYIDAE, 261
Photichthys, 261
Photoblepharon, 306
Photocorynus, 518
Photonectes, 263
Photopectoralis, 454
Photostomias, 261, 264
Photostylus, 174
Phoxinellus, 184
Phoxinus, 183, 184
Phractocephalus, 237
Phractolaeminae, 176, 178
Phractolaemus, 179
Phractura, 226
Phreatobius, 209, 236
Phrynichthys, 515
Phrynorhombus, 398
Phthanophaneron, 307

Phtheirichthys, 385
Phucocoetes, 479
Phycinae, 301
Phycis, 301
Phylactocephalus, 267
Phyllogobius, 332
PHYLLOLEPIDIDAE, 39
Phyllolepidoidei, 39
Phyllolepis, 39
Phyllonemus, 229
Phyllopharyngodon, 427
Phyllophryne, 510
Phyllopteryx, 408
Phyllorhinichthys, 516
Phymolepis, 38
Physiculus, 298
Physopyxis, 234
Phytichthys, 480
Piabucina, 202
Piabucus, 205
Piaractus, 199
pickerels, 250, 251
  Chain Pickerel, 250
  Grass Pickerel, 250
  Redfin Pickerel, 250
Pictichromis, 340
Pictilabrus, 429
Piedrabuenia, 479
pigfishes, 475
Pikaia, 16
pike-characids, 203
Pikehead, 393
pikeperches, 449
pikes, 248, 249, 250, 251
  Amur Pike, 250
  longfinned pikes, 450
  Muskellunge, 250
  Northern Pike, 250
  Southern Pike, 250
pilchards, 169
Pillaia, 382
pilotfish, 386
Pimelodella, 236
PIMELODIDAE, 209, 236, 237, 238
Pimelodina, 237
Pimelodinae, 236, 237
Pimelodoidea, 229, 236
Pimelodus, 237
Pimephales, 184
pinecone fishes, 307
Pingalla, 441
PINGUIPEDIDAE, 421, 422, 423
Pinguipes, 422
Pinjalo, 458
Pinniwallago, 219
pipefishes, 405, 408
  ghost pipefishes, 407
  pipefishes, 407
Pipiscius, 24
piranhas, 198
Pirarucú, 157
pirate perches, 288
Pirskenius, 329
Pisces, 35, 97
Pisodonophis, 147
Pituana, 372
Pituriaspida, 18, 34
PITURIASPIDIFORMES, 32, 34
Pituriaspis, 34
Piveteauia, 104
Placidichthys, 125
Placidochromis, 345
PLACODERMI, 36, 37, 97
Placodermiomorphi, 35, 36
Placolepis, 39
Plagiogeneion, 498
Plagiogrammus, 480
Plagiopsetta, 402
Plagioscion, 499
Plagiotremus, 346, 349
Plagopterus, 184
plaice, 396
Plancterus, 374
Planonasus, 70
Platanichthys, 171
Plataplochilus, 379
Platax, 497
Platichthys, 396, 400
Platinx, 130
Platyallabes, 230
Platybelone, 368
Platyberyx, 452
Platycephalalinae, 477
PLATYCEPHALIDAE, 468, 477
Platycephaloidei, 467, 469, 473, 475
Platycephalus, 477
Platyclarias, 230
Platydoras, 234
platyfishes, 379
Platygillellus, 347
Platyglanis, 229
Platygobio, 184
Platypanchax, 379
Platyrhina, 88
PLATYRHINIDAE, 87, 88
Platyrhinoidei, 57, 87
Platyrhinoidis, 88
Platysalmo, 247
PLATYSIAGIDAE, 116
PLATYSOMIDAE, 114
PLATYSOMIFORMES, 114
Platysomus, 114
Platystacus, 233
Platytroctes, 173
PLATYTROCTIDAE, 172
Platytropius, 222
Platyurosternarchus, 241
Platyxystrodus, 51
Plecodus, 345
PLECOGLOSSIDAE, 256, 257
Plecoglossus, 257, 258
Plecostomus, 217
Plectobranchus, 480
PLECTOCRETACICIDAE, 519
Plectocretacicoidei, 519
Plectognathi, 518
plectognaths, 518
Plectorhinchinae, 457
Plectorhinchus, 457
Plectranthias, 446, 447
Plectrochilus, 213
PLECTROGENIIDAE, 468, 475, 476
Plectrogeniinae, 473
Plectrogenium, 468, 473, 476
Plectroglyphidodon, 339
Plectropomus, 447
Plectrypops, 305
Plesienchelys, 479
PLESIOBATIDAE, 88
PLESIOBATIDIDAE, 88
Plesiobatis, 88, 89, 90
Plesiofuro, 116
Plesiolebias, 372
Plesiolycoptera, 155
Plesiomyxocyprinus, 187
Plesiomyzon, 192
PLESIOPIDAE, 333, 334, 336
Plesiopinae, 336
Plesiops, 336
Plesioselachus, 45
Plesiotrygon, 91
PLETHODIDAE, 132
Plethodus, 132
Pleuracanthodii, 47
Pleuracanthus, 47
Pleuragramma, 465
Pleurodus, 50
Pleurogramminae, 488
Pleurogrammus, 488

Pleuronectes, 400
PLEURONECTIDAE, 396, 398, 399, 401
PLEURONECTIFORMES, 334, 380, 395, 396, 414, 432
Pleuronectinae, 399, 400
Pleuronectini, 400
Pleuronectoidea, 398
Pleuronectoidei, 396, 397
Pleuronichthys, 400
Pleurophysus, 213
Pleuroscopus, 427
Pleurosicya, 332
Pleurotremata, 58
Plicatodus, 47
Plicatoscyllium, 62
Plicofollis, 232
Plinthicus, 95
Pliodetes, 122
Plioplarchus, 444
Pliosteostoma, 167
Pliotrema, 80
PLOTOSIDAE, 209, 220, 221
Plotosus, 208, 221
plunderfishes, 466
  barbeled plunderfishes, 466
  spiny plunderfishes, 466
Pnictes, 403
poachers, 490
Poblana, 356
Podothecus, 491
Poecilia, 354, 379, 380
POECILIIDAE, 370, 376, 377, 378
Poeciliinae, 378, 379
Poeciliini, 379, 380
Poecilioidea, 374, 376
Poeciliopsis, 354, 380
Poecilobrycon, 203
Poecilocharax, 196
Poecilodus, 51
Poecilopsetta, 401
POECILOPSETTIDAE, 401
Poecilopsettinae, 399
Pogoneleotris, 329
Pogonias, 499
Pogonichthys, 184
Pogonolycus, 479
Pogonopera, 448
Pogonophryne, 466
Pogonopoma, 217
Pogonoscorpius, 470
Pogonymus, 413
Polistotrema, 21
Pollachius, 302
Pollia, 117
Pollichthys, 261
Pollimyrus, 160
Polyacanthonotus, 138
POLYACRODONTIDAE, 56
Polyacrodus, 56
Polyamblyodon, 506
Polybranchiaspis, 34
POLYCENTRIDAE, 334, 337
Polycentropsis, 337, 395
Polycentrus, 337
Polyipnoides, 260
Polyipnus, 260
Polylepion, 429
POLYMEROLEPIDIFORMES, 44
Polymetme, 261
Polymixia, 285, 286, 287, 294, 483
POLYMIXIIDAE, 286
POLYMIXIIFORMES, 278, 285, 286, 287
POLYNEMIDAE, 341, 380
Polyodon, 119
POLYODONTIDAE, 118, 119
Polyodontinae, 119
Polyosteorhynchus, 104
Polypera, 495
Polyplacapros, 521
Polyprion, 435
POLYPRIONIDAE, 434, 435, 496
POLYPTERIDAE, 117
POLYPTERIFORMES, 111, 116
Polypterus, 111, 115, 117
Polyrhizodus, 50
Polyspina, 525
Polysteganus, 506
POMACANTHIDAE, 455
Pomacanthus, 456
POMACENTRIDAE, 334, 337, 427
Pomacentrinae, 337, 338
Pomacentrus, 339
Pomachromis, 339
POMADASYIDAE, 457
Pomadasys, 457
POMATOMIDAE, 405, 451
Pomatomus, 414, 450, 451
pomfrets, 451
Pomoxis, 444, 445
pompanos, 385, 386
Ponticola, 332
Pontinus, 469, 470
Pontosudis, 275
ponyfishes, 453
poolfishes, 373
Poptella, 205
Poracanthodes, 100
PORACANTHODIDAE, 100
Poraspis, 29
Porbeagle, 68
Porcostoma, 506
porcupinefishes, 526
porgies, 502, 505
Porichthyinae, 321
Porichthys, 322
Porocephalichthys, 319
Porochilus, 221
Poroclinus, 480
Poroderma, 69
Porogadus, 318
Porogobius, 332
POROLEPIDAE, 107
POROLEPIFORMES, 106
Porolepimorpha, 106
Porolepis, 107
Poromitra, 314
Poropanchax, 379
Porophoraspis, 27
Poropuntius, 183
Pororhiza, 56
Porotergus, 241
Posidonichthys, 353
Potamalosa, 162, 171
Potamarius, 232
Potamobatrachus, 323
Potamorhina, 201
Potamorrhaphis, 368
Potamosilurus, 232
Potamothrissa, 171
Potamotrygon, 91, 92
POTAMOTRYGONIDAE, 91
Powellichthys, 144
Powichthys, 107
Praealticus, 349
Praeproscyllium, 70
Premnas, 337, 338
PRIACANTHIDAE, 315, 453
Priacanthus, 453
Priapella, 379
Priapellini, 379
Priapichthyini, 379
Priapichthys, 380
priapiumfishes, 361
pricklebacks, 480, 481
prickle-fishes, 308

pricklefishes, 310
prickly seadevils, 516
Prietella, 235, 236
Priocharax, 205
Priohybodus, 56
Priolepis, 332
Prionace, 72
Prionobrama, 206
Prionobutis, 329
Prionodraco, 466
PRIONOLEPIDIDAE, 267
Prionolepis, 267
Prionotinae, 476
Prionotus, 476
Prionurini, 502
Prionurus, 502
Priscacara, 314
PRISCACARIDAE, 314
Priscosturion, 120
Priscusurus, 63
Pristella, 204
Pristiapogon, 325
Pristicon, 325
PRISTIDAE, 87
PRISTIFORMES, 57, 85
Pristigaster, 167
PRISTIGASTERIDAE, 162, 166
Pristigasterinae, 167
Pristigenys, 453
Pristilepis, 305
PRISTIOPHORIDAE, 78, 80
PRISTIOPHORIFORMES, 54, 57, 75, 78, 80, 81
pristiophoriforms, 54
Pristiophorus, 80
Pristiorajea, 54
Pristipomoides, 458
Pristis, 87
Pristobrycon, 199
PRISTODONTIDAE, 50
Pristodus, 50
PRISTOLEPIDIDAE, 394, 395
Pristolepis, 395
Pristotis, 339
Proaracana, 521
Probathygadus, 296
Probolodus, 204
Procatopodinae, 378
Procatopodini, 378, 379
Procatopus, 379
Proceramala, 112
Procerusternarchus, 240
Procetichthys, 312
Procheirichthys, 116
PROCHILODONTIDAE, 197, 201
Prochilodus, 202
Procottus, 492
Proetmopterus, 76
Proeutropiichthys, 221
PROFUNDULIDAE, 370, 372
Profundulus, 372
Prognathodes, 455
Prognathoglossum, 156
Prognichthys, 366
Prohalecites, 126
Proheterodontus, 59
Prolatilus, 422
Promesacanthus, 100
Promethichthys, 415
Promyxele, 49
Pronothobranchius, 371
Pronotogrammus, 447
Propherallodus, 353
Propristis, 87
Propterus, 124
Propycnoctenion, 110
Prosarctaspis, 28
Prosaurodon, 131
Prosauropsis, 127
Proscinetinae, 121
Proscosturion, 120
PROSCYLLIIDAE, 70
Proscyllium, 70
Proscymnodon, 76
Prosopium, 243, 245
Prosoproctus, 473
Protacanthodes, 521
Protacanthopterygii, 241, 243, 251, 252, 431
PROTACRODONTIDAE, 55
PROTACRODONTIFORMES, 55
Protammodytes, 426
Protanguilla, 139, 140, 141, 145, 150
PROTANGUILLIDAE, 140
Protanguilloidei, 140
PROTASPIDIDAE, 29
Protemblemaria, 351
Proteothrinax, 74
Proteracanthus, 497
PROTOBALISTIDAE, 521
Protoblepharon, 307
Protobrama, 132
PROTOBRAMIDAE, 132
Protochondrostoma, 184
Protoclupea, 130
Protocobitis, 190
PROTODONTIDAE, 43, 44
Protodus, 43
Protoginglymostoma, 62
Protogobius, 327
Protogrammus, 413
Protolamna, 64
Protolophotus, 283
Protomelas, 345
Protomyctophum, 278
Protomyzon, 192
Protonibea, 499
Protopsephurus, 119
PROTOPTERASPIDIDAE, 29
Protopteraspis, 29
PROTOPTERIDAE, 109
Protopterus, 109
Protosalanx, 258
Protoscaphirhynchus, 120
Protosciaena, 499
Protosephurinae, 119
Protosphyraena, 127
PROTOSPINACIDAE, 78
PROTOSPINACIFORMES, 57, 78
Protospinax, 78
Protosqualus, 78
Prototroctes, 258
PROTOTROCTIDAE, 256, 258
Protoxynotus, 77
PROTRIACANTHIDAE, 519
prowfishes, 481
  Australian prowfishes, 474
Psammobatis, 85
Psammodiscus, 402
PSAMMODONTIDAE, 49, 50
PSAMMODONTIFORMES, 50
Psammodus, 50
Psammolepis, 29
Psammoperca, 432
Psammorhynchus, 120
PSAMMOSTEIDAE, 29
Psammphiletria, 226
Psarolepis, 103, 106, 112
Psectrogaster, 201
Psednos, 495
Psenes, 419
Psenopsis, 418, 419
PSEPHODONTIDAE, 51
Psephodus, 51
Psephurus, 119
Psettichthyini, 400

Psettichthys, 400
Psettina, 401
Psettodes, 395, 397
PSETTODIDAE, 396, 397
Psettodoidei, 396, 397
Pseudacanthicus, 217
Pseudalectrias, 480
Pseudalutarius, 523
Pseudamia, 326
Pseudamiinae, 326
Pseudamiops, 326
Pseudancistrus, 217
Pseudanos, 200
Pseudanthias, 447
PSEUDAPHRITIDAE, 464
Pseudaphritis, 464, 465
Pseudapocryptes, 330
Pseudaspius, 184
Pseudauchenipterus, 234
Pseudecheneis, 225
Pseudechidna, 144
Pseudechinorhinus, 79
Pseudeutropius, 222, 228
Pseudexostoma, 225
Pseudobagarius, 224
Pseudobagrus, 223, 235
Pseudobalistes, 523
Pseudobarbus, 183
Pseudobathylagus, 254
Pseudoblennius, 492
Pseudobunocephalus, 233
Pseudocalliurichthys, 413
Pseudocaranx, 387
Pseudocarcharias, 66
PSEUDOCARCHARIIDAE, 65
Pseudocepola, 462
Pseudocetopsis, 212
Pseudochaenichthys, 467
Pseudocheilinops, 429
Pseudocheilinus, 429
Pseudochondrostoma, 184
PSEUDOCHROMIDAE, 334, 339
Pseudochrominae, 339
Pseudochromis, 336, 339, 340
PSEUDOCORACIDAE, 64
Pseudocorax, 64
Pseudocoris, 429
Pseudocorynopoma, 206
Pseudocurimata, 201
Pseudocyttinae, 291
Pseudocyttus, 291
Pseudodalatias, 56
PSEUDODALATIIDAE, 56
Pseudodax, 429
Pseudodoras, 234
Pseudogastromyzon, 192
Pseudogilbia, 319
Pseudoginglymostoma, 62
Pseudogobio, 184
Pseudogobius, 330
Pseudogramma, 448
Pseudohemiodon, 217
Pseudohowella, 434
Pseudojuloides, 429
Pseudolabrus, 429
Pseudolaguvia, 225
Pseudolais, 220
Pseudomancopsetta, 402
Pseudomegachasma, 65
PSEUDOMONOCENTRIDAE, 307
PSEUDOMONOCENTRIDIDAE, 307
Pseudomonocentris, 279, 307
Pseudomugil, 359, 360
PSEUDOMUGILIDAE, 357
Pseudomugilinae, 358, 359
Pseudomugilini, 359
Pseudomyrophis, 146
Pseudomystus, 223
Pseudonezumia, 296
PSEUDONOTIDANIDAE, 74
Pseudonus, 319
Pseudopataecus, 473
Pseudopercis, 422
PSEUDOPETALICHTHYIFORMES, 37
Pseudopetalichthys, 37
Pseudophoxinus, 184
Pseudophycis, 298
PSEUDOPIMELODIDAE, 209, 238
Pseudopimelodinae, 236, 237
Pseudopimelodoidea, 237
Pseudopimelodus, 238
Pseudoplesiopinae, 340
Pseudoplesiops, 340
Pseudopleuronectes, 400
Pseudopoecilia, 380
Pseudoraja, 85
Pseudorasbora, 184
Pseudorhinogobius, 330
Pseudorhombus, 399
PSEUDOSCAPANORHYNCHIDAE, 64
Pseudoscapanorhynchus, 64
PSEUDOSCAPHIRHYNCHINAE, 120
Pseudoscaphirhynchus, 120
Pseudoscopelus, 421
Pseudosetipinna, 168
Pseudosphromenus, 392
Pseudostegophilus, 213
Pseudosynanceia, 473
Pseudotocinclus, 217
Pseudotolithus, 499
Pseudotrematomus, 465
Pseudotriacanthus, 521
PSEUDOTRIAKIDAE, 70
Pseudotriakis, 70
PSEUDOTRICHONOTIDAE, 266, 269
Pseudotrichonotus, 269
Pseudotropheus, 345
Pseudotylosurus, 368
Pseudovespicula, 471
Pseudoxiphophorus, 380
Pseudupeneus, 436
Psilodraco, 466
PSILORHYNCHIDAE, 181, 186
Psilorhynchoides, 186
Psilorhynchus, 186
Psilotris, 332
Psuedomugilinae, 359, 360
Psychrolutes, 493, 494
PSYCHROLUTIDAE, 485, 492, 493
Psychrolutinae, 493
Ptarmus, 473
Pteraclinae, 452
Pteraclis, 452
Pteragogus, 429
Pterapogon, 325
PTERASPIDIDAE, 29
PTERASPIDIFORMES, 29
Pteraspidomorpha, 26
Pteraspidomorphi, 18, 26
Pteraspis, 29
Ptereleotrinae, 331
Ptereleotris, 332
Pterengraulis, 168
PTERICHTHYIDAE, 39
Pterichthyodes, 38
Pterobunocephalus, 233
Pterocaesio, 459
Pterocryptis, 219
Pterodoras, 234
Pterogobius, 330
Pterogymnus, 506
Pterohemiodus, 199
Pteroidichthys, 470
Pteroini, 470
Pterois, 470

Pterolebias, 372
Pteromylaeus, 93, 94
Pteronemacheilus, 192
Pteronisculus, 113
Pteronotropis, 184
Pteropelor, 470
Pterophyllum, 343, 345
Pteroplatytrygon, 91
Pteropsaron, 425
Pteroscion, 499
Pterothrissinae, 137
Pterothrissus, 137
Pterotolithus, 499
Pterycombus, 452
Pterygoplichthys, 218
Pterygotrigla, 476
Pterygotriglinae, 476
PTILICHTHYIDAE, 481
Ptilichthys, 481
Ptomacanthus, 98
Ptychocheilus, 181, 184
Ptychochromis, 345
Ptychochromoides, 345
Ptychocorax, 64
PTYCHODONTIDAE, 56
Ptychodus, 56
PTYCHOLEPIDIDAE, 115
PTYCHOLEPIDIFORMES, 115
Ptycholepis, 115
Ptychotrygon, 85
PTYCHOTRYGONIDAE, 85
Ptychotrygonoides, 85
PTYCTODONTIDAE, 39
PTYCTODONTIFORMES, 39
Pucapampella, 41, 45
Puck, 516
pufferfishes, 254
    sharpnose pufferfishes, 525
puffers, 518
    threetooth puffers, 519
Pungitius, 483, 484
Pungu, 345
Puntius, 183
pupfishes, 375
Puzanovia, 479
Pycnaspis, 27
Pycnocraspedum, 318
Pycnoctenion, 110
PYCNODONTIDAE, 121
PYCNODONTIFORMES, 121
PYCNOSTEROIDIDAE, 280
Pycnosteus, 29
Pygidianops, 214
PYGIDIIDAE, 212
Pygocentrus, 199
Pygoplites, 456
PYGOPTERIDAE, 113
Pylodictis, 235, 236
Pylorobranchus, 146
Pyramodon, 316
Pyramodontinae, 316
Pyritocephalus, 113
Pyrolycus, 479
PYROSOMIDA, 15
Pyrrhulina, 203
Pyrrhulininae, 203
Pyrrhulinini, 202, 203
Pythonichthys, 142

Qingmenodus, 106
Quadratinae, 21
Quadratus, 21
Quebecius, 107
Quetzalichthys, 125
Quietula, 330
Quijinolepis, 38
quillback, 188
quillfishes, 481
Quintana, 380
Quirichthys, 358, 363

Rabaulichthys, 447
rabbitfishes, 463
racehorses, 475
Racenisia, 240
Rachovia, 372
Rachoviscus, 204
RACHYCENTRIDAE, 383, 384
Rachycentron, 384
Raconda, 166, 167
Racovitzia, 466
RADIICEPHALIDAE, 283
Radiicephalus, 283
Radotina, 37
Radulinopsis, 492
Radulinus, 492
ragfishes, 412
Raiamas, 182
rainbowfishes, 358
    blue eyes, 359
    Celebes rainbowfishes, 359
    Madabascar rainbowfishes, 358
rainbowfishes, 358
Rainfordia, 447
Raja, 85
Rajella, 85
RAJIDAE, 42, 55, 84
RAJIFORMES, 42, 57, 80, 82, 84
Rajimorphi, 80
Rajinae, 85
Rajoidei, 84
Rajorhina, 85
Rama, 223
Ramallichthys, 177
Ramnogaster, 171
RAMPHOSIDAE, 406
Ramphosus, 406
Randallichthys, 458
Raneya, 318
Raniceps, 299
RANICIPITIDAE, 299
Ranulfoichthys, 163
Ranzania, 524
Rasbora, 182
Rasborinae, 185
Rasboroides, 182
Rasbosoma, 184
Rastrelliger, 417
Rastrineobola, 182
Rastrinus, 492
Ratabulus, 477
ratfishes, 53
Rathbunella, 478
Ratsirakia, 329
rattails, 296
ray-finned fishes, 111
Raynerius, 112
rays, 54, 80
razorfishes, 429
REBELLATRICIDAE, 104
Rebellatrix, 104
Rectoris, 182
red hake, 316
red velvetfishes, 474
REDFIELDIIDAE, 115
REDFIELDIIFORMES, 115
Redfieldius, 115
Redigobius, 330
reedfish, 117
REGALECIDAE, 284
Regalecus, 284
Reganella, 217
Reicheltia, 525
Reinhardtius, 399
Relictus, 184
Remigolepis, 39
Remora, 385
remoras, 384, 385
Remorina, 385
Renova, 372

Repomucenus, 413
Reporhamphus, 367
requiem sharks, 71
Reticulodus, 56
Retroculus, 345
Retropinna, 259
RETROPINNIDAE, 256, 258
Retropinnoidei, 256, 258
Rexea, 415
Rexichthys, 415
Rhabdalestes, 196
Rhabdamia, 325
Rhabdoblennius, 349
Rhabdoderma, 104
RHABDODERMATIDAE, 104
Rhabdofario, 247
RHABDOLEPIDAE, 113
Rhabdolichops, 241
Rhabdosargus, 506
Rhachiaspis, 29
Rhacochilus, 335
Rhacolepis, 130
Rhacoviscus, 206
Rhadinesthes, 262
RHADINICHTHYIDAE, 114
Rhadinocentrus, 359
Rhamdella, 236
Rhamdia, 236
Rhamdiinae, 236, 237
RHAMPHICHTHYIDAE, 239
Rhamphichthyoidea, 239
Rhamphichthys, 240
Rhamphocetichthys, 312
Rhamphochromis, 345
RHAMPHOCOTTIDAE, 485, 489
Rhamphocottus, 489
Rhamphodopsis, 39
Rhaphiodon, 198
Rharbichthys, 275
Rhechias, 148
RHENANIFORMES, 37
Rhenanoperca, 315
Rheocles, 359
Rhexipanchax, 379
Rhina, 86
Rhincodon, 59, 62, 63
RHINCODONTIDAE, 60, 61, 63
Rhinecanthus, 523
Rhinelepis, 218
Rhinesomus, 522
Rhinichthys, 184
RHINIDAE, 84, 86, 87
RHINIFORMES, 86
Rhiniodon, 63
RHINIODONTIDAE, 63
RHINOBATIDAE, 84, 85, 86
RHINOBATIFORMES, 86
Rhinobatos, 86
Rhinocephalus, 299
Rhinochimaera, 53
RHINOCHIMAERIDAE, 48, 52
Rhinochimaerinae, 53
Rhinodoras, 234
Rhinogobius, 330, 332
Rhinolekos, 217
Rhinomugil, 342
Rhinomuraena, 144
Rhinopias, 470
Rhinoprenes, 497
Rhinoptera, 94
Rhinopteraspis, 29
Rhinopterinae, 94
Rhinoraja, 85
Rhinosardinia, 172
Rhinoscymnus, 76
Rhizodontida, 110
RHIZODONTIDAE, 110
RHIZODONTIFORMES, 110
Rhizodontimorpha, 110
RHIZODOPSIDAE, 110
Rhizodopsis, 110
Rhizodus, 110
Rhizoprionodon, 72
Rhizosomichthys, 213
Rhoadsia, 205
Rhoadsiinae, 205
Rhodeus, 184
Rhodichthyinae, 495
Rhodichthys, 495
Rhodymenichthys, 481
Rhombichthys, 164
Rhomboplites, 458
Rhombopterygia, 86
Rhombosolea, 401, 402
RHOMBOSOLEIDAE, 401
rhombosoleids, 401
Rhombosoleinae, 399
RHONDELETIIDAE, 309
RHYACICHTHYIDAE, 326, 327, 328
Rhyacichthys, 326, 327
Rhycherus, 510
Rhynchactis, 514, 517
RHYNCHOBATIDAE, 87
Rhynchobatus, 86, 87
Rhynchobdella, 383
Rhynchoconger, 148
Rhynchocypris, 184
Rhynchodercetis, 267
RHYNCHODIPTERIDAE, 108
Rhynchodipterus, 108
Rhynchodoras, 234
Rhynchogadus, 298
Rhynchohyalus, 253
Rhyncholepis, 30
Rhynchopelates, 441
Rhynchorhamphus, 367
Rhynchostracion, 522
Rhytiodus, 200
ribbonfishes, 283
Ribeiroclinus, 350
ricefishes, 364
Richardsonichthys, 471
Richardsonius, 184
Riekertia, 323
righteye flounders, 399
Rimicola, 353
Rineloricaria, 217
Rinoctes, 174
Rioraja, 85
Risor, 332
Rita, 221, 222
RITIDAE, 220, 221, 222, 228
Ritinae, 222
river sharks, 72
river stingrays, 91
RIVULIDAE, 196, 371
Rivulinae, 372
rivulines, 370
    African rivulines, 371
    Asian rivulines, 371
    New World rivulines, 371
Rivulus, 371, 372
Roa, 455
Robaloscion, 499
Robia, 513
Robinsia, 144
Robinsichthys, 332
Robustichthys, 125
Roccus, 496
rockfishes, 468
rocklings, 301
Roeboexodon, 205
Roeboides, 205
Roestes, 198, 203
Roestinae, 198, 203
Rogadius, 477
Rohtee, 183
Romanichthyini, 449
Romanichthys, 449
Romanogobio, 184

Romerodus, 50
Romundina, 37
Roncador, 499
Rondeletia, 311
RONDELETIIDAE, 311
ronquils, 478
Ronquilus, 478
Roosterfish, 383
roosterfishes, 383
ropefish, 117
Rosaura, 271
Rosenblattia, 435
Rosenblattichthys, 274
Rostroraja, 85
Rotuma, 329
rough sharks, 76
roughies, 305, 308
Rouleina, 174
Roulletia, 65
round stingrays, 89, 92
rovers, 498
Ruanoho, 347
Rubicundinae, 21
Rubicundus, 21
Rubiesichthyinae, 176
Rubiesichthys, 176
Rudarius, 523
rudderfishes, 386, 440
Ruffoichthys, 463
Ruscarius, 492
Rusichthys, 340
Rutilus, 184
Ruvettus, 415
Rypticus, 448
Ryukyupercis, 422

sabalo, 177
Sabanejewia, 190
sabertooth fishes, 274
sablefishes, 485
Sacabambaspis, 27
SACCOBRANCHIDAE, 231
Saccodon, 198
Saccogaster, 319
SACCOPHARYNGIDAE, 150
SACCOPHARYNGIFORMES, 133, 134
Saccopharyngoidei, 133, 149
Saccopharynx, 150
Sacramento Perch, 445
Sacura, 447
Sagamichthys, 173
Sagittalarva, 429
sailback scorpionfishes, 471
Sailfin Molly, 379
sailfishes, 389
Sainthilairia, 117
Salamanderfish, 243
salamanderfishes, 242
Salangichthys, 258
SALANGIDAE, 256, 258
Salanx, 258
Salaria, 349
Salarias, 349
Salariinae, 348
Salariini, 348
Saldenioichthys, 315
Salilota, 298
Salmininae, 206
Salminops, 179
Salminus, 205
Salmo, 246, 247
salmon, 244, 246
  Atlantic salmon, 246, 247
  Australasian salmon, 439
  Brown Trout, 247
  Pacific salmon, 246–248
Salmon Shark, 68
SALMONIDAE, 244, 246
SALMONIFORMES, 241, 243, 244
Salmoninae, 244, 246, 248
Salmostoma, 182
Salmothymus, 247
Saloptia, 447
Salpida, 15
salps, 15
Salvelinus, 246, 247
Salvethymus, 246, 247
SAMARIDAE, 402
Samaris, 402
Samariscus, 402
sanddivers, 331, 423
  kraemeriid sanddivers, 331
  trichonotid sanddivers, 423
sand eel, 482
sandfishes, 177, 425, 488
  beaked sandfishes, 177
  sandfishes, 488
  southern sandfishes, 425
sand flounders, 398
sand lances, 425
sand stargazers, 347
sand tiger sharks, 65
sand tilefishes, 456
Sandalodus, 51
sandburrowers, 423
sanddab, 396
sand-diving lizardfishes, 269
Sandelia, 390, 391
Sander, 449
Sandivia, 30
sandperches, 422
Sangiorgioichthys, 124
Sanopus, 323
Santanaclupea, 163
Santanichthys, 179
Santelmoa, 479
Sapperichthys, 177
Sarcocheilichthyinae, 185
Sarcocheilichthys, 184
Sarcoglanidinae, 214
Sarcoglanis, 214
Sarcopterygii, 95, 96, 97, 101, 102, 103, 112, 116
  crown-group, 103
Sarda, 417
Sardina, 171
Sardinella, 171
sardines, 169
Sardini, 417
Sardinops, 171
Sargocentron, 304
Sargochromis, 345
Sargodon, 122
Sarmarutilus, 184
Sarotherodon, 344, 345
Sarpa, 506
Sarritor, 491
Sartor, 200
Sashatherina, 363
Satan, 235, 236
Satanoperca, 345
Satyrichthys, 476
Saurenchelys, 147
SAURICHTHYIDAE, 115
SAURICHTHYIFORMES, 115
Saurichthys, 115
Saurida, 268
sauries, 369
Sauripterus, 110
Saurocephalus, 131
Saurodon, 131
SAURODONTIDAE, 131
Saurogobio, 185
Sauromuraenesox, 147
Sauropsis, 127
Saurorhamphus, 275
Saurorhynchus, 115
Sauvagella, 170
saw sharks, 80
sawfishes, 85
scads, 386

Scaevius, 505
Scalicus, 476
Scapanorhynchus, 65
Scaphirhynchinae, 120
Scaphirhynchus, 120
Scardinius, 184
SCARIDAE, 427, 429, 437, 523
Scarinae, 430
Scartella, 349
Scartichthys, 349
Scartomyzon, 189
Scarus, 430
SCATOPHAGIDAE, 462, 500
Scatophagus, 463
scats, 462
Scaturiginichthys, 359
Scaumenacia, 108
Schedophilus, 419
Schilbe, 228
SCHILBEIDAE, 220, 222, 226, 228
SCHILBIDAE, 228
Schindleria, 331, 332
SCHINDLERIIDAE, 331
Schismorhynchus, 146
Schistura, 192
Schizochirus, 424
Schizodon, 200
Schizothorax, 183
Schizurichthys, 115
Schroederichthys, 69
Schuettea, 452
Schultzea, 447
Schultzichthys, 213
Schultzidia, 146
Sciadeops, 232
Sciades, 232
Sciadonus, 320
Sciaena, 499
SCIAENIDAE, 498
Sciaenoidei, 497, 498
Sciaenops, 499
Scizolecis, 217
Sclerodermi, 522
SCLERODIDAE, 34
SCLERODONTIDAE, 34
Scleromystax, 215
Scleronema, 213
Scleropages, 153, 157, 158, 432
SCLERORHYNCHIDAE, 85
Sclerorhynchus, 85
Scolecenchelys, 146
Scolichthyini, 380
Scolichthys, 380
Scoliodon, 72
SCOLOPLACIDAE, 215
SCOLOPLAGIDAE, 215
Scoloplax, 216
Scolopsis, 505
Scomber, 417
SCOMBERESOCIDAE, 368, 369
Scomberesocoidea, 367
Scomberesox, 369
Scomberoides, 386
Scomberoidinae, 386
Scomberomorini, 417
Scomberomorus, 417
SCOMBRIDAE, 416
SCOMBRIFORMES, 334, 388, 405, 414
Scombrimorpharia, 405
Scombrinae, 417
Scombrini, 417
Scombroidei, 388, 414, 417
SCOMBROLABRACIDAE, 413
SCOMBROLABRACIFORMES, 405, 413
Scombrolabrax, 414, 450
SCOMBROPIDAE, 450, 451
Scombrops, 450, 451
SCOPELARCHIDAE, 273
Scopelarchoides, 274
Scopelarchus, 274
Scopelengys, 277
Scopeloberyx, 314
Scopelogadus, 314
Scopelomorpha, 264, 265, 276
Scopelopsis, 278
SCOPELOSAURIDAE, 273
Scopelosaurus, 273
SCOPHTHALMIDAE, 396, 398
Scophthalmus, 398
Scorpaena, 468, 469, 470
SCORPAENICHTHYIDAE, 485, 489
Scorpaenichthys, 489
SCORPAENIDAE, 468, 469, 471
SCORPAENIFORMES, 303, 411, 420, 467, 468
Scorpaeninae, 469, 471
Scorpaenini, 470, 471
Scorpaenodes, 470
Scorpaenoidea, 468
Scorpaenoidei, 467, 468, 475
Scorpaenopsis, 470
Scorpidinae, 440, 441
Scorpiodoras, 234
scorpionfishes, 468
    barehead scorpionfishes, 478
    false scorpionfishes, 433
Scorpis, 440, 441
Scortum, 441
Screbinodus, 110
Scriptaphyosemion, 371
sculpins, 485, 491
    Antarctic sculpins, 494
    Baikal oilfishes, 492
    deepwater Baikal sculpins, 492
    fathead sculpins, 493
    grunt sculpins, 489
    longfin sculpins, 488
    mote sculpins, 478
Scutatospinosa, 164
Scutatospinosinae, 164
Scuticaria, 143
SCYLIORHINIDAE, 55, 69
Scyliorhinus, 69
Scylliogaleus, 71
Scymnodalatias, 76
Scymnodon, 76
Scytalina, 482
SCYTALINIDAE, 482
sea basses, 446
sea chubs, 440
seadevils, 513, 514, 516
    black seadevils, 514
    prickly seadevils, 516
    spiny seadevils, 513
    warty seadevils, 516
seadragons, 408
seahorses, 405, 407, 408
seamoths, 406
searavens, 490
    Sea Raven, 490
searobins, 475
    armored searobins, 476
sea toads, 511
Searsia, 173
SEARSIIDAE, 172
Searsioides, 173
sea-squirts, 13
Sebastapistes, 470
Sebastes, 468, 469
SEBASTIDAE, 468
Sebastinae, 469
Sebastini, 469
Sebastiscus, 469
SEBASTOLOBIDAE, 468
Sebastolobus, 468, 469

Sectator, 441
Secutor, 454
selachians, 42, 50, 56
Selachii, 43, 56, 57, 58, 81, 95
Selachimorpha, 58
Selachophidium, 318
Selar, 387
Selaroides, 387
Selenanthias, 447
Selene, 386, 387
Seleniolycus, 479
Selenoscopus, 427
SELENOSTEIDAE, 40
Selenotoca, 463
Semaprochilodus, 202
Semicossyphus, 429
Semiolepis, 124
SEMIONOTIDAE, 123, 124
SEMIONOTIFORMES, 122, 123, 124
Semionotus, 124
Semiplotus, 183
Semlikiichthys, 315
Semotilus, 184
Serenichthys, 104
Serenoichthys, 117
Seretolepis, 44
Seriola, 387
Seriolella, 419
Seriolina, 387
Seriphus, 499
SERPENTICOBITIDAE, 192, 193
Serpenticobitis, 193
Serraniculus, 447
SERRANIDAE, 446, 467
Serraninae, 447
Serranocirrhitus, 447
Serranus, 446, 447
Serrapinnus, 206
SERRASALMIDAE, 197, 198
Serrasalminae, 174
Serrasalmus, 199
Serrilepis, 267
Serrivomer, 152
SERRIVOMERIDAE, 151
Setarches, 469
SETARCHIDAE, 468, 469
Setarchinae, 469
Setipinna, 168
Sewellia, 192
shads, 169, 171
  gizzard shads, 171
Shankouclavis, 15
Sharfia, 509
sharks, 54
sharksuckers, 384
sharpnose pufferfishes, 525
sheatfishes, 218
Sheenstia, 122
Shielia, 30, 32
SHIELIIDAE, 32
Shimenolepis, 38
Shortfin Mako, 68
shrimpfishes, 410
Siamese fighting fishes, 392
SIBYRHYNCHIDAE, 49
Sicamugil, 342
sicklefishes, 496
Sicyases, 353
Sicydiinae, 330
Sicyopterus, 330
Sicyopus, 330
SIGANIDAE, 462, 463, 499
Siganoidea, 462
Siganopygaeus, 463
Siganus, 463
Sigmistes, 492
Sigmops, 260
Signigobius, 332
Silhouettea, 332
SILLAGINIDAE, 502, 503
Sillaginodes, 503
Sillaginopoides, 503
Sillaginops, 503
Sillaginopsis, 503
Sillago, 503
sillagos, 503
Silonia, 221
Siluranodon, 228
Silurichthys, 219
SILURIDAE, 216, 218, 219
SILURIFORMES, 179, 180, 207, 209
Siluriphysi, 179, 193, 207, 209
Siluroidei, 209, 210, 211, 218, 219, 220, 229, 232
Silurolepis, 38
Silurus, 208, 218, 219
Silver Arowana, 158
silver dollar tetras, 205
silver dollars, 198
silversides, 354
  Mercer's tusked silverside, 360
  New World silversides, 355
  Old-World silversides, 362
  priapiumfishes, 361
  pricklenose silversides, 360
  rainbowfishes, 358
  surf sardines, 357
  surf silversides, 357
Silvinichthys, 213
Simenchelyinae, 141
Simenchelys, 141
Similiparma, 339
Simipercis, 422
Simpsonichthys, 371, 372
Sinamia, 125
SINAMIIDAE, 124, 125
Sindoscopus, 347
Sineleotris, 328
Sinibotia, 190
Sinigarra, 182
Siniperca, 315, 442
SINIPERCIDAE, 315, 442
Sinobatis, 85
Sinobdella, 383
Sinocyclocheilus, 183
Sinogastromyzon, 191
SINOLEPIDAE, 38
Sinolepidida, 38
Sinolepis, 38
Sinusoidea, 240
Sio, 314
Siokunichthys, 408
Siphamia, 325
Siphateles, 184
Siphonognathus, 429
Sirembo, 318
Sisor, 225
SISORIDAE, 221, 223, 224, 225, 228
Sisorinae, 225
Sisoroidea, 221, 223, 225
six-gill sharks, 73
sixgill stingrays, 89
skates, 80, 84
Skiffia, 374
Skilfish, 486
Skiotocharax, 196
Skythrenchelys, 146
Sladenia, 508, 509
sleeper rays, 83
sleeper sharks, 76
sleepers, 327, 328, 329
  butid sleepers, 329
  freshwater sleepers, 327
  ocean sleepers, 329
  spinycheek sleepers, 328
slickheads, 172, 173, 252
slimeheads, 308

slimys, 453
slipmouths, 453
slope dragonets, 413
Smegmamorpha, 303, 314
smelts, 252, 256, 258
  Capelin, 257
  deepsea smelts, 254
  Eulachon, 257
  freshwater smelts, 256
  herring smelts, 253
  marine smelts, 252
  Northern Hemisphere smelts, 257
  pencilsmelts, 253
  southern smelts, 258
smelt-whitings, 503
Smilosicyopus, 330
Smithichthys, 350
snaggletooths, 262
snailfishes, 495
snake mackerels, 415
snake mudheads, 178
snakeheads, 394
snappers, 457
snipe eels, 151
snipefishes, 410
snooks, 431
Snyderichthys, 184
Snyderidia, 316
Snyderina, 471
soapfishes, 447
Socnopaea, 223
Sodolepis, 45
Soederberghia, 108
softnose skates, 84, 85
Soldatovia, 480
soldierfishes, 305
soles, 396, 403
  American soles, 402
Solea, 404
Solegnathus, 408
Soleichthys, 404
SOLEIDAE, 402, 403
SOLENOSTOMIDAE, 407
Solenostomus, 407
Soleoidea, 401
Soleonasus, 403
Solitas, 477
Solivomer, 277
Solnhofenamia, 126
Solocisquama, 512
Somileptus, 190
SOMNIOSIDAE, 76, 77
Somniosus, 76
Sonoda, 260
Sonorolux, 499
Sophialepis, 31
Sorbinia, 428
Sorbinicapros, 507
SORBINICHARACIDAE, 193
Sorbinicharax, 193
Sorbinichromis, 338
SORBINICHTHYIDAE, 163, 164
Sorbinichthys, 164
Sorbiniperca, 315, 507
SORBINIPERCIDAE, 315, 507
Sorgentinini, 356
Sorosichthys, 308
Sorsogona, 477
Sorubim, 237
Sorubimichthys, 237
South American darters, 195
southern basses, 433
southern flounders, 402
Southern Frilled Shark, 74
southern graylings, 258
spadefishes, 497
Spaniblennius, 349
Spaniodon, 256
Spanish mackerels, 417
SPARIDAE, 504, 505, 506
Sparidentex, 506
SPARIFORMES, 420, 430, 495, 502, 503
Sparinae, 506
Sparisoma, 430
Sparisomatinae, 430
Sparodon, 506
Sparus, 506
Spathobatis, 82, 86
Spatuloricaria, 217
spearfishes, 390
Speckled Sole, 403
Spectrolebias, 372
Spectrunculus, 318
Speirsaenigma, 257, 258
Speonesydrion, 107
Speoplatyrhinus, 289
Sperata, 223
Sphaeramia, 325
Sphaerichthys, 393
Sphagemacrurus, 296
Sphenanthias, 462
SPHENOCEPHALIDAE, 279, 287
SPHENOCEPHALIFORMES, 279, 286
Sphenocephaloidei, 286
Sphenocephalus, 279, 287
Sphenodus, 74
Sphenonectris, 31
Spherosteus, 118
Sphoeroides, 525
Sphyraena, 143, 388, 450
SPHYRAENIDAE, 341, 380, 387, 388, 414
Sphyraenops, 435
Sphyrna, 73
SPHYRNIDAE, 72
Spicara, 506
spikefishes, 520
SPINACANTHIDAE, 521
Spinachia, 482, 483, 484
Spinapsaron, 425
Spinibarbus, 183
Spinicapitichthys, 413
Spiniphyne, 516
Spinipterus, 234
Spinocaudichthys, 112, 279
Spintherobolus, 206
Spiny Basslets, 336
Spiny Dogfish, 78
spiny plunderfishes, 466
spiny seadevils, 513
spiny turbots, 397
spinyfins, 306
Spirinchus, 257
splendid perches, 503
Spondyliosoma, 506
spookfishes, 253
Spottobrotula, 318
Spratelloides, 170
Spratelloidinae, 170
Spratelloidini, 170
Spratellomorpha, 170, 171
sprats, 169
Spratticeps, 163
Sprattus, 171
Springeratus, 350
Springerichthys, 347
springfishes, 373
spurdogs, 78
Squalea, 73
Squalicorax, 64
Squalida, 57, 73, 75
SQUALIDAE, 77
Squalidus, 185
Squaliforma, 218
SQUALIFORMES, 54, 57, 75, 78
squaliforms, 42
Squaliobarbinae, 186
Squaliobarbus, 186
Squaliodalatias, 77
Squaliodus, 77

Squaliolus, 77
Squalius, 184
Squalogadus, 294, 297
Squalomorphi, 43, 56, 57, 58, 73
Squaloraja, 49, 51
SQUALORAJIDAE, 51
SQUALORAJIFORMES, 51
Squalorajoidei, 51
Squalus, 78
Squamicreedia, 425
squaretails, 420
Squatigaleus, 71
Squatina, 47, 79, 80
SQUATINACTIDAE, 47
SQUATINACTIFORMES, 46, 47
Squatinactis, 47
Squatinida, 57, 73, 75, 78
SQUATINIDAE, 78, 79
SQUATINIFORMES, 54, 57, 75, 78, 79, 81
Squatiscyllium, 61
squirrelfishes, 304
Stalix, 341
Stanulus, 349
stargazers, 426
Starksia, 350, 351
Stathmonotus, 350, 351
Stauroglanis, 214
Steatogenys, 240
Steeneichthys, 336
Stegastes, 339
Stegolepis, 39
Stegophilinae, 213
Stegophilus, 213
Stegostenopos, 240
Stegostoma, 59, 62
STEGOSTOMATIDAE, 60, 61, 62
STEGOTRACHELIDAE, 114
Stegotrachelus, 114
STEINBACHODONTIDAE, 56
Steinbachodus, 56
Steindachneria, 295, 296
Steindachneridion, 238
STEINDACHNERIIDAE, 295
Steindachnerina, 201
Stellerina, 490
Stellifer, 499
Stemonidium, 152
Stemonosudis, 275
Stenatherina, 363
Stenobrachius, 278
Stenodus, 245
Stenogobius, 330
Stenolebias, 372
Stenolicmus, 214
Stenotomus, 506
STENSIOELLIFORMES, 37
STEPHANOBERYCIDAE, 310
STEPHANOBERYCIFORMES, 303, 309
Stephanoberycoidea, 309
Stephanoberycoidei, 308
Stephanoberyx, 310
Stephanolepis, 523
Stereolepis, 435
Sternarchella, 241
Sternarchogiton, 241
Sternarchorhamphus, 241
Sternarchorhynchus, 241
STERNOPTYCHIDAE, 260
Sternoptychinae, 260
Sternoptyx, 260
STERNOPYGIDAE, 238, 240
Sternopygoidei, 239
Sternopygus, 239, 240, 241
STETHACANTHIDAE, 46
Stethacanthus, 46
Stethaprion, 205
Stethaprioninae, 205
Stethojulis, 429
Stethopristes, 291
Stevardiinae, 206
Sthenopus, 473
STIASSNYIFORMES, 333
STICHAEIDAE, 480
Stichaeinae, 480
Stichaeopsis, 480
Stichaeus, 480
Sticharium, 349
STICHOCENTRIDAE, 280
Stichonodon, 205
Stichopterus, 118
sticklebacks, 483
    armored sticklebacks, 484
    Blackspotted Stickleback, 484
    Brook Stickleback, 484
    Fifteenspine Stickleback, 484
    Fourspine Stickleback, 484
    Ninespine Stickleback, 484
    Threespine Stickleback, 484
Stigmatochromis, 345
Stigmatogobius, 330
Stigmatonotus, 447
Stigmodus, 43
stingrays, 87
Stiphodon, 330
Stizostedion, 448, 449
Stokellia, 259
STOLEPHORIDAE, 167
Stolephorus, 168
Stolothrissa, 171
STOMATEIDAE, 418, 420
Stomatorhinus, 160
STOMIAHYKIDAE, 108
Stomiahykus, 108
Stomias, 262
STOMIATIFORMES, 259
Stomiatii, 252
STOMIIDAE, 259, 261, 263
STOMIIFORMES, 252, 256, 259, 264, 265
Stomiinae, 262
Stomiini, 262
Stomioidea, 261
Stompooria, 255
stonefishes, 472
Stonogobiops, 332
Storrsia, 348
Strangomera, 171
Stratodus, 267
Strepsodus, 110
Strianta, 49
Striatolamia, 65
Stroinolepis, 30, 32
STROMATEIDAE, 420
Stromateoidei, 414, 418
Stromateus, 420
Strongylosteus, 118
Strongylura, 368
Strophidon, 144
Strophiurichthys, 521
STRUNIIFORMES, 106
Strunius, 106
sturgeons, 118, 119
Sturisoma, 217
Stygichthys, 204
Stygnobrotula, 319
STYLEPHORIDAE, 285, 293
STYLEPHORIFORMES, 284, 285, 290, 293
Stylephorus, 285, 293
Styloichthys, 102
Stypodon, 184
subholosteans, 115
Subterbranchialia, 48, 49

Suckers, 187
  blue suckers, 188
  buffaloes, 188
  carpsuckers, 188
  chubsuckers, 189
  Harelip Sucker, 189
  hog suckers, 189
  jumprocks, 189
  lake suckers, 189
  Longnose Sucker, 189
  quillback, 188
  redhorses, 189
  White Sucker, 189
sudid barracudinas, 274
SUDIDAE, 274
Sudis, 274
Sueviota, 332
Suezichthys, 429
Sufflamen, 523
Suggrundus, 477
Sundadanio, 182
SUNDASALANGIDAE, 165, 170, 257
Sundasalanx, 165, 170
Sundolyra, 223
sunfishes, 444
  Ocean Sunfish, 524
  sunfishes, 444
SUPERCILIASPIDIDAE, 34
Superciliaspis, 33
Suprasinelepichthys, 201
surfperches, 335
surgeonfishes, 497, 501
Sutorectus, 61
Suttonia, 448
Svetovidovia, 298
swallowers, 421
swamp eels, 380
sweepers, 437
sweetfish, 257
Swenzia, 106
Swordfish, 389
swordfishes, 389
swordtails, 379
Syacium, 399
Sylvestrilamia, 65
Symbolophorus, 278
SYMMORIIDAE, 46
SYMMORIIFORMES, 46
Symmorium, 46
Symphodus, 427, 429
Symphorichthys, 458
Symphorus, 458
Symphurinae, 404
Symphurus, 404
SYMPHYSANODONTIDAE, 434
Symphysodon, 343, 345
Sympterichthys, 511
Sympterygia, 85
Synagropoides, 315
Synagrops, 434
Synanceia, 473
SYNANCEIIDAE, 468
Synanceiinae, 469, 471
Synanceiini, 472
SYNAPHOBRANCHIDAE, 139, 141
Synaphobranchinae, 142
Synaphobranchoidei, 140, 141
Synaphobranchus, 142
Synaptolaemus, 200
Synaptura, 404
SYNBRANCHIDAE, 381
SYNBRANCHIFORMES, 138, 303, 334, 380
Synbranchinae, 382
Synbranchoidei, 381
Synbranchus, 382
Synchirus, 492
Syncomistes, 441
Syncrossus, 190
SYNECHODONTIFORMES, 57, 59
Synechodus, 59
SYNGNATHIDAE, 407
SYNGNATHIFORMES, 334, 405
Syngnathinae, 408
Syngnathoidea, 407
Syngnathoidei, 405, 406
Syngnathoides, 408
Syngnathus, 408
Synodontaspis, 65
SYNODONTIDAE, 266, 268, 272
Synodontinae, 268
Synodontis, 227
Synodontoidei, 266, 267, 272
Synodus, 268

Taaningichthys, 278
Tachydoras, 234
TACHYSURIDAE, 231
Tachysurus, 223, 232
Tactostoma, 261, 263
Taeniacara, 345
Taeniamia, 325
Taenianotus, 470
Taenioides, 330
Taeniopsetta, 401
Taeniosomi, 281
Taeniura, 91
Taeniurops, 91
taimen, 246
Takifugu, 525
Talismania, 174
Talivalia, 32
TALIVALIIDAE, 32
Tamanka, 330
Tampichthys, 184
Tanakia, 184
Tanakius, 400
Tandanus, 221
Tanganikallabes, 230
Tanichthys, 182, 185
Tanyemblemaria, 351
tapertails, 283
tapetails, 312
Taractes, 452
Taractichthys, 451, 452
Taranetzella, 479
Taratretis, 402
Tarletonbeania, 278
Tarphops, 399
Tarpon, 136
TARRASIIDAE, 115
TARRASIIFORMES, 115
Tarrasius, 115
Tarsistes, 86
Tasmanogobius, 332
Tateurndina, 329
Tathicarpus, 509, 510
Tatia, 235
Taubateia, 217
Taunayia, 236
Tauredophidium, 318
Taurulus, 492
Tautoga, 429
Tautogolabrus, 429
Tegeolepis, 114
Teixeirichthys, 339
Teleocephala, 126, 128, 132, 133
Teleocichla, 345
teleostean fishes, 126
Teleostei, 121, 126, 127, 128, 129, 130, 131, 132, 179, 430
  total-group, 126
  crown-group, 132
Teleosteomorpha, 126
Teleostomi, 35, 40, 44, 95, 96
teleosts, 128, 129
telescopefishes, 271

Telestes, 184
Telmatherina, 360
Telmatherininae, 359
Telmatochromis, 345
Tembeassu, 241
Temnocora, 495
temperate basses, 495, 496
temperate ocean-basses, 434
temperate perches, 442
tenpounders, 133, 135
Tentoriceps, 416
Tenualosa, 169, 171
Tenuicentrum, 304
Teoichthys, 125
Tephrinectes, 399
Teramulus, 363
Terapon, 441
TERAPONIDAE, 441
TERAPONTIDAE, 441
Terateleotris, 328
Terelabrus, 429
Terranatos, 372
Tesakoviaspidida, 28
TESAKOVIASPIDIDAE, 28
Tesakoviaspis, 28
Teslepis, 45
TESSERASPIDIDA, 28
Tesseraspis, 28
Tetanopsyrus, 100
Tethybatis, 88
tetrabrachiid frogfishes, 510
TETRABRACHIIDAE, 510
Tetrabrachium, 510
Tetracamphilius, 226
Tetracentrum, 335
Tetractenos, 525
Tetragondacninae, 317
Tetragondacnus, 317
Tetragonolepis, 122
Tetragonopterinae, 206
Tetragonopterus, 206
TETRAGONURIDAE, 420
Tetragonurus, 420
Tetranematichthys, 234
Tetraodon, 525
TETRAODONTIDAE, 518, 524, 526
TETRAODONTIFORMES, 387, 420, 430, 462, 495, 506, 518
Tetraodontinae, 525, 526
Tetraodontoidei, 519, 522, 523
Tetrapleurodon, 25
Tetrapoda, 35, 111
tetrapods, 101, 102, 111
Tetrapturus, 389, 390
Tetraroge, 471
TETRAROGIDAE, 468
Tetraroginae, 469, 471, 475
tetras, 193
Tetronarce, 83
Tetrosomus, 522
Teuthis, 463
Tewara, 424
Texatrygon, 85
Tigrigobius, 332
Thaiodus, 56
THALASSELEOTRIDAE, 326
THALASSELEOTRIDIDAE, 326, 329
Thalasseleotris, 329
Thalassenchelys, 145
Thalassobathia, 319
Thalassoma, 429
Thalassophryne, 322
Thalassophryninae, 322
Thaleichthys, 257
Thaliacea, 15
Thamnaconus, 523
Tharbacus, 323
Tharrhias, 177
THAUMATICHTHYIDAE, 516
Thaumatichthys, 516
Thaumaturus, 155
Thelodonti, 30
THELODONTIFORMES, 31
Thelodontomorphi, 18, 26, 30
thelodonts, 30
  fork-tailed thelodonts, 31
  thelodontiform thelodonts, 31
Thelodus, 32
Theragra, 302
THERAPONIDAE, 441
Theraps, 345
Theriodes, 190
Thermarces, 479
Thermichthys, 319
Thermobiotes, 141, 142
Thoburnia, 189
Thoburniini, 189
Thoracocharax, 207
Thoracochromis, 345
THORACOPTERIDAE, 116
Thoracopterus, 116
Thorectichthyinae, 164
Thorectichthys, 164
Thorichthys, 345
thornbacks, 87, 88
thornfishes, 464
Thorophos, 260
threadfin breams, 504
thread-tails, 293
threetooth puffers, 519
thresher sharks, 66
Thrinax, 74
Thrissina, 168
Thrissops, 131
Thryssa, 168
Thryssocypris, 182
Thunnini, 417
Thunnus, 416, 417
Thursius, 110
THYESTIIDAE, 34
Thymallinae, 244, 245, 248
Thymallus, 244, 245, 246
Thymichthys, 511
Thyrsites, 415
Thyrsitoides, 415
Thyrsitops, 415
Thysanactis, 263
Thysanichthys, 470
Thysanophrys, 477
Thysanopsetta, 399
Tiger Shark, 72
tigerperches, 441, 504
Tiktaalik, 111
tilapia, 343, 344, 345
tilefishes, 456
  sand tilefishes, 456
Tilesina, 490
Tilodon, 441
Tiluropsis, 137
Tilurus, 137
Timorichthys, 319
Tinca, 185
Tincinae, 185
Tingitanichthys, 130
Tingitanius, 88
Tischlingerichthys, 175
TITANICHTHYIDAE, 40
Tiupampichthys, 193
Tlayuamichin, 124
toadfishes, 320, 321
Toarcibatis, 82
TOLYPELEPIDIDA, 28
Tolypelepis, 28
Tometes, 199
Tomeurini, 379, 380
Tomeurus, 379, 380
Tomicodon, 353
Tominanga, 360
Tomocichla, 345
Tondanichthys, 367

Tongaichthys, 415
tonguefish, 396
tonguefishes, 404
Toombsaspis, 28
toothless characiforms, 201
topminnow, 374
topminnows, 374
Tor, 181, 183
Torpedaspis, 29
TORPEDINIDAE, 82
TORPEDINIFORMES, 57, 82, 87
Torpedo, 83
torpedo electric rays, 82
Torquigener, 525
Tortonesia, 428
TORTONESIDAE, 428
Tosana, 447
Tosanoides, 447
Tosarhombus, 401
Totoaba, 499
Toxotes, 439
TOXOTIDAE, 380, 438
Traccatichthys, 192
Trachelochismus, 353
Trachelyichthys, 234
Trachelyopterus, 234
Trachicaranx, 386
Trachicephalus, 473
TRACHICHTHYIDAE, 303, 307, 308
TRACHICHTHYIFORMES, 303, 305, 308, 309
Trachichthyoidei, 305, 306, 309
Trachichthyoides, 304
Trachichthys, 308
Trachidermis, 492
TRACHINIDAE, 421, 425, 426
TRACHINIFORMES, 420, 421
Trachinocephalus, 268
Trachinoidei, 421, 424, 488
Trachinops, 336
Trachinotinae, 386
Trachinotus, 386
Trachinus, 426
TRACHIPTERIDAE, 283
Trachipterus, 284
Trachonurus, 296
Trachurus, 387
Trachycorystes, 234
Trachyglanis, 226
Trachypoma, 447
Trachyrinchus, 297
TRACHYRINCIDAE, 296
Trachyrincinae, 297
trachyrincines, 296, 297
Trachyrincus, 297
Trachyscorpia, 469
Trachystoma, 342
Tragularius, 173
Tragulichthys, 526
trahiras, 197
Tranodis, 108
TRAQUAIRASPIDIFORMES, 28
Traquairaspis, 28
Traquairichthys, 101
TRAQUAIRIIDAE, 51
Traquairius, 51
Travancoria, 191
TREMATASPIDAE, 34
Tremataspis, 34
Trematocara, 345
Trematomus, 465
trevallies, 386
  false trevallies, 450
TREWAVASIIDAE, 121
TRIACANTHIDAE, 518, 519, 520
Triacanthodes, 520
TRIACANTHODIDAE, 518, 519, 520
Triacanthodinae, 520
Triacanthoidei, 519
Triacanthus, 521
Triaenodon, 72
TRIAKIDAE, 70, 72
Triakinae, 71
Triakis, 71
Trianectes, 347
Triathalassothia, 323
Tribodus, 56
Tribolodon, 184
TRICHIURIDAE, 415
Trichiurinae, 416
Trichiurus, 416
Trichocottus, 492
Trichodon, 488
TRICHODONTIDAE, 421, 485, 488
Trichodontoidea, 488
Trichogaster, 393
Trichogastrinae, 392, 393
Trichogenes, 213
Trichogeninae, 213
TRICHOMYCTERIDAE, 196, 212, 214
Trichomycterinae, 213
Trichomycterus, 213
TRICHONOTIDAE, 421, 423, 424
Trichonotus, 423
Trichopodus, 393
Trichopsetta, 401
Trichopsis, 392, 393
Tricuspicanthus, 100
Tricuspidalestes, 196
Tridens, 214
Tridensimilis, 214
Tridentiger, 330
Tridentinae, 214
Tridentopsis, 214
triggerfishes, 522
Trigla, 476
TRIGLIDAE, 468, 475
Triglinae, 476
Trigloporus, 476
Triglops, 492
Trigonectes, 372
Trigonognathus, 76
Trigonolampa, 263
Trigonotodus, 63
Trimerolepis, 32
Trimma, 332
Trimmatom, 332
Trinectes, 403
Trinorfolkia, 347
Triodon, 519, 523
TRIODONTIDAE, 518, 519
Triodontoidei, 519
Triodus, 47
Triphoturus, 278
triplespines, 520
tripletails, 503
Triplomystini, 164
Triplomystus, 164
Triplophos, 260
Triplophysa, 192
Tripodichthys, 521
Triportheus, 205
Tripterodon, 497
Tripterophycis, 298
TRIPTERYGIIDAE, 346
Tripterygion, 347
Triso, 447
Trisopterus, 302
TRISTICHOPTERIDAE, 110
Tristichopterus, 110
TRISTYCHIIDAE, 56
Tristychius, 56
Trixiphichthys, 521
Troglichthys, 289
Trogloglanis, 235, 236
Tropidophoxinellus, 184
trout, 244, 246

trout-perches, 287
trouts, 246
trumpeters, 460
trumpetfishes, 409
trunkfishes, 521
Trygon, 91
TRYGONIDAE, 90
Trygonoptera, 89, 90
Trygonorrhina, 86
Trypauchen, 330
Tselfatia, 132
TSELFATIIDAE, 132
TSELFATIIFORMES, 131
Tuamotuichthys, 319
Tubbia, 419
tube-eyes, 293
tubeshoulders, 172
tubesnouts, 483
tunas, 416, 417
  Atlantic Bluefin Tuna, 414, 417
  Bigeye Tuna, 417
  Pacific Bluefin Tuna, 417
  Southern Bluefin Tuna, 417
  Yellowfin Tuna, 414
Tungtingichthys, 315
Tunicata, 15
tunicates, 13, 15
Turania, 65
turbots, 396, 398
  spiny turbots, 397
Turinia, 30, 32
TURINIIDAE, 32
turkeyfishes, 470
Turkmene, 281
TURKMENIDAE, 281
Tycheroichthys, 164
Tydemania, 520
Tylerius, 525
Tylochromis, 345
Tylosurus, 368
Typhlachirus, 404
Typhleotris, 328
Typhliasina, 319
Typhlichthys, 289
Typhlobagrus, 236
Typhlobelus, 214
Typhlogobius, 330
Typhlonarke, 84
Typhlonus, 318
Tyrannochromis, 345
Tyrannophryne, 516
Tyson, 329
Tyttobrycon, 206
Tyttocharax, 206
Uaru, 345
Ubidia, 241
Ucla, 347
Udalepis, 45
UEGITGLANIDIDAE, 230
Uegitglanis, 230
Ulaema, 433
Ulcina, 490
Ultimostomias, 264
Ulua, 387
Ulutitaspis, 29
Ulvaria, 480
Ulvicola, 481
Umbra, 248, 249, 251, 375
UMBRIDAE, 249, 251
Umbrina, 499
Unamichthys, 131
Unarkaspis, 29
Uncisudis, 275
Undina, 106
Ungusurculus, 319
unicornfishes, 502
Upeneichthys, 436
Upeneus, 436
Uraniacanthus, 100
URANOLOPHIDAE, 107
Uranolophus, 107
URANOSCOPIDAE, 421, 425, 426
URANOSCOPIFORMES, 421
Uranoscopus, 427
Uraspis, 387
Urenchelys, 139
Urobatis, 89, 93
Urochordata, 13, 15
urochordates, 13, 15, 16
  ascidian urochordates, 13, 15
  larvacean urochordates, 15
  thaliacean urochordates, 15
Uroconger, 147, 148
Urogymnus, 91
UROLOPHIDAE, 89, 93
Urolophoides, 91
Urolophus, 89, 90
Uronema, 108
URONEMIDAE, 108
Urophori, 408
Urophycis, 299, 301, 316
Uropterygiinae, 143
Uropterygius, 143
Urotrygon, 88, 89, 93
UROTRYGONIDAE, 89, 92
Usakias, 66

Vaillantella, 190
VAILLANTELLIDAE, 189, 190
Vaillantellinae, 192
Valamugil, 342
Valencia, 374
Valencia toothcarps, 374
Valenciennea, 332
Valenciennellus, 260
VALENCIIDAE, 374
Valencioidea, 374
Valiukia, 32
Vallecillichthys, 131
Vanacampus, 408
Vandellia, 213
Vandelliinae, 212, 213
Vanderhorstia, 332
Vanmanenia, 192
Vanstraelenia, 404
VARASICHTHYIDAE, 130
Varasichthys, 130
Variabilichromis, 345
Varicorhinus, 183
Varicus, 332
Variichthys, 441
Variola, 447
Vasnetzovia, 187
Vectiselachos, 56
Velifer, 282
VELIFERIDAE, 281
velifers, 281
Vellitor, 492
velvetfishes, 473
  orbicular velvetfishes, 470
  red velvetfishes, 474
Venefica, 147
Ventichthys, 318
Ventrifossa, 296
Verasper, 399
Verilus, 434
Verma, 146
Vernicomacanthus, 99
Veronavelifer, 281
Vertebrata, 19, 22
vertebrates, 17, 19, 22
Vespicula, 471
Vetulicolia, 14
Vidalamia, 126
Vidalamiinae, 126
Vimba, 184
Vincentia, 325
Vinciguerria, 261
Vinctifer, 127

viperfishes, 262
Virididentex, 506
Vitiaziella, 313
viviparous brotulas, 318
viviparous halfbeaks, 367
Vladichthys, 323
Voelklichthys, 124
Vomeridens, 466
Vomerogobius, 332

Waengsjoeaspis, 33
Wainwrightilabrus, 427
Wallago, 219
Walleye, 448
Wardigneria, 47
warty anglers, 510
warty seadevils, 516
waryfishes, 273
wasp fishes, 471
Watsonulus, 124, 125
Wattsia, 505
weasel sharks, 71
weatherfishes, 190
wedgefishes, 87
weed-whitings, 429
weeverfishes, 426
WELLINGTONELLIDAE, 45
Weltonia, 75
Wendyichthys, 112
Wertheimeria, 234
Western Mosquitofish, 379
Wetmorella, 429
whalefishes, 310
  flabby whalefishes, 312
  red (redvelvet) whalefishes, 311
  redmouth whalefishes, 311
whale sharks, 63
Wheelerigobius, 332
whipnose anglers, 517
whiptail stingrays, 90
whiptails, 296, 297
whitebait, 255, 256
whitefishes, 244, 245
  ciscoes, 245
  Inconnu, 245
  lake whitefishes, 245
  round whitefishes, 245
Whiteia, 104
WHITEIIDAE, 104
White Shark, 68
whitings, 299, 503
  hake whitings, 299
  smelt-whitings, 503
Wimania, 104
Winteria, 253
wobbegongs, 61
Woellsteinia, 65
wolffishes, 481
wolftrap anglers, 516
Woodichthys, 112
Woodsia, 261
wormfishes, 331
wrasses, 427, 428, 430
wreckfishes, 435
wrymouths, 480
Wuhanlinigobius, 330
WUTTAGOONASPIDIDAE, 40

Xanthichthys, 523
XENACANTHIDAE, 47
XENACANTHIFORMES, 47
Xenacanthimorpha, 47
Xenacanthus, 47
Xenagoniates, 206
Xenentodon, 368
Xeneretmus, 491
Xenichthys, 457
Xenisma, 374
XENISTHMIDAE, 329
Xenisthmus, 329
Xenistius, 457
Xenobalistes, 523
Xenobrama, 452
Xenocara, 217
XENOCEPHALIDAE, 426
Xenocephalus, 426, 427
Xenocharax, 194, 195
Xenochromis, 345
Xenoclarias, 230
Xenoconger, 144
XENOCONGRIDAE, 144
Xenocyprinae, 185, 186
Xenocypris, 186
Xenocyproides, 186
Xenocys, 457
Xenodermichthys, 174
Xenodexia, 380
Xenodexini, 380
Xenojulis, 429
Xenolepidichthys, 292
Xenolumpenus, 480
Xenomedea, 350, 351
Xenomugil, 342
Xenomystax, 148
Xenomystinae, 159
Xenomystus, 158, 159
Xenoophorus, 374
Xenophallus, 380
Xenophthalmichthys, 254
Xenoploactis, 473
Xenopoclinus, 350
Xenopoecilus, 365
Xenopterus, 525
Xenotaenia, 374
Xenotilapia, 345
Xenotoca, 374
Xenoturbella, 13
Xenurobrycon, 206
Xenyllion, 279, 287
Xiphactinus, 131
Xiphasia, 348, 349
Xiphias, 389
XIPHIIDAE, 380, 387, 388, 389, 414
Xiphister, 480
Xiphisterinae, 480
Xiphocheilus, 429
Xiphodolamia, 64
XIPHODOLAMIIDAE, 64
Xiphophorus, 380
Xiurenbagrus, 224
Xixiaichthys, 156
Xyelacyba, 318
Xylacanthus, 100
Xyliphius, 233
Xyrauchen, 189
Xyrichtys, 429
Xystodus, 268
Xystreurys, 399
Xystrogaleus, 71

Yabrudichthys, 267
Yanbiania, 155
Yanosteus, 118
Yaoshania, 192
Yaoshanicus, 185
Yarrella, 261
Yasuhikotakia, 190
Yellowfin Tuna, 414
Yirrkala, 147
Yoga, 332
Yongeichthys, 332
Youngolepis, 107
Yunnanilus, 192
Yunnanolepida, 38
YUNNANOLEPIDIDAE, 38
Yunnanolepidoidei, 38
Yunnanolepis, 38
Yunnanozoa, 14
YUNNANOZOIDAE, 14
Yunnanozoon, 13, 14
YUNNANOZOONIDAE, 14
yunnozoans, 14
Yuriria, 184

Zabidius, 497
Zacco, 185
Zaireichthys, 226
Zalanthias, 447
Zalembius, 335
Zalieutes, 512
Zameus, 76
ZANCLIDAE, 499, 500
Zanclistius, 443
ZANCLORHYNCHIDAE, 475
Zanclorhynchus, 475
Zanclus, 499, 501
ZANIOLEPIDIDAE, 485, 486, 487
Zaniolepidinae, 486
Zaniolepidoidea, 486
Zaniolepis, 486
ZANOBATIDAE, 88
Zanobatus, 87, 88
Zapogon, 325
Zappa, 330
Zappaichthys, 323
Zaprora, 482
ZAPRORIDAE, 481
Zapteryx, 86
Zearaja, 85
zebra sharks, 62
zebrafish, 181
Zebrasoma, 502
Zebrasomini, 502
Zebrias, 404
Zebrus, 332
ZEIDAE, 292, 507
ZEIFORMES, 284, 285, 289, 290, 303, 506
Zeioidei, 290
ZENARCHOPTERIDAE, 365, 367
Zenarchopterus, 367
ZENASPIDAE, 34
Zenion, 292
ZENIONIDAE, 291
ZENIONTIDAE, 291
Zenopsis, 290, 293
Zeoidei, 290
Zephyrichthys, 319
Zeus, 290, 293
Zhanjilepis, 38
Zignoichthys, 523
Zingel, 448, 449
Zoarces, 479
Zoarchias, 479
ZOARCIDAE, 479
Zoarcinae, 479
Zoarcoidei, 284, 294, 467, 478
Zoogoneticus, 374
Zoramia, 325
Zoroteleostei, 241, 242, 251, 252
zoroteleosts, 251
ZORZINICHTHYIDAE, 507
Zorzinichthys, 507
Zosterisessor, 332
Zu, 284
Zuegelepis, 32
Zungaro, 237

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