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# Comparative anatomy and phylogenetic systematics of the family Uranoscopidae (Actinopterygii: Perciformes)

Veera VILASRI<sup>1), 2)</sup>

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## Contents

I. Introduction	1
II. Materials and methods	3
III. Phylogenetic methodology	4
IV. Anatomy of Uranoscopidae	4
1. Osteology	4
1-1. Circumorbital bones	4
1-2. Cranium	11
1-3. Jaws	22
1-4. Hyoid arch	25
1-5. Suspensorium and opercular bones	28
1-6. Branchial complex	34
1-7. Pectoral and pelvic girdles	38
1-8. Axial skeleton and median fin supports	43
1-9. Caudal skeleton	51
2. Myology	54
2-1. Cheek muscle	54
2-2. Cephalic muscles between cranium and suspensorium-operculum	56
2-3. Ventral muscles of head	56
2-4. Branchial muscles	59
2-5. Pectoral and pelvic muscles	62
2-6. Muscles associated with median fins	66
2-7. Caudal fin muscles	68
2-8. Body muscles	69
3. Other morphology	70
V. Monophyly of family Uranoscopidae	77
VI. Phylogenetic relationships of Uranoscopidae	77
VII. Comparison with previous study	83
VIII. Sister group of Uranoscopidae	83
IX. Classification	84
1. Family Uranoscopidae	84
2. Genera in the family Uranoscopidae	85
2-1. Key to the genera of Uranoscopidae	86
2-2. Genus <i>Astroscopus</i> Brevoort, 1860	87
2-3. Genus <i>Genyagnus</i> Gill, 1861	88
2-4. Genus <i>Ichthyoscopus</i> Swainson, 1839	88
2-5. Genus <i>Kathetostoma</i> Günther, 1860	89
2-6. Genus <i>Pleuroscopus</i> Barnard, 1927	89
2-7. Genus <i>Uranoscopus</i> Linnaeus, 1758	90
2-8. Genus <i>Xenocephalus</i> Kaup, 1858	90
X. General discussion	91
1. Characters modified for a benthic existence present in all uranoscopids	91
2. Benthic adaptations varying among the Uranoscopidae	94
2-1. Feeding mechanism	94

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2-2. Pectoral-fin mechanism .....	97
2-3. Respiratory mechanism .....	99
2-4. Sensory system mechanism .....	100
2-5. Lingual lure organ mechanism .....	101
2-6. Orbital electric organ mechanism .....	101
3. Conclusion .....	101
XI. Summary .....	102
XII. Acknowledgments .....	102
XIII. Literature cited .....	103

### Abstract

The anatomy of the family Uranoscopidae including osteological and mycological features is examined and described in details based on eight genera and 32 uranoscopid species. As results of anatomy and phylogenetic analysis, the monophyly of the family is reconfirmed to be strongly supported by 59 synapomorphies (plus 11 according to ACCTRAN). The phylogenetic relationships of uranoscopids were inferred from the morphological characters in 113 transformation series. *Pleuroscopus* and *Xenocephalus*, having a sister relationship, are branched off initially from remaining members, and monophyletic *Kathetostoma* is branched off. *Kathetostoma* has a sister relationship with a monophyletic group comprising *Uranoscopus*, *Genyagnus*, *Ichthyscopus* and *Astroscopus*. *Selenoscopus* is inferred as nesting deeply phylogenetically within *Uranoscopus*. In addition, a sister relationship of the Uranoscopidae and Trachinidae is examined to be supported by 22 synapomorphies (plus two according to ACCTRAN). The newly defined family Uranoscopidae comprises seven genera: *Pleuroscopus*, *Xenocephalus*, *Kathetostoma*, *Uranoscopus*, *Genyagnus*, *Ichthyscopus* and *Astroscopus*. The monotypic genus *Selenoscopus* is synonymized with *Uranoscopus*. The benthic life style of Uranoscopidae is described and discussed.

**Key words:** Comparative anatomy, Phylogenetic systematics, Uranoscopidae

## I. Introduction

The family Uranoscopidae (sensu Nelson, 2006), of the perciform suborder Trachinoidei, includes eight genera and about 50 species (Nelson, 2006). Species inhabit bottoms from nearshore to the deep sea in tropical and temperate waters of the world at depths ranging from the littoral zone to 900 m (Nakabo, 2002; Carpenter, 2002; Gomon, 2008). Members of the family are characterized morphologically by a large and cuboid head, extremely oblique mouth, large pectoral fin, pelvic fins located under the throat, four infraorbitals, and 24–29 vertebrae (see Nelson, 2006). Uranoscopids have unique life style, burying them into sand or mud, with only their eyes and mouth cleft protruding from the substrate (Kishimoto, 2001).

The Uranoscopidae has been variously classified. Günther (1860) recognized four genera, *Uranoscopus*, *Agnus*, *Anema* and *Kathetostoma*, while Mees (1960) recognized 10 genera, *Uranoscopus*, *Ichthyscopus*, *Astroscopus*, *Kathetostoma*, *Nematagnus*, *Genyagnus*, *Gnathagnus*, *Ariscopus*, *Excectides* and *Pleuroscopus*. More recently, Okamura and Kishimoto (1993) established the new genus, *Selenoscopus* and Springer and Bauchot (1994) concluded that *Xenocephalus* is a senior synonym of *Gnathagnus*. Nelson (2006) regards the family as comprising eight genera, *Astroscopus*, *Genyagnus*, *Ichthyscopus*, *Kathetostoma*, *Pleuroscopus*, *Selenoscopus*, *Uranoscopus* and *Xenocephalus*. The systematic disagreement of previous studies is attributable to the lack of comprehensive phylogenetic analyses of the family.

In 1989, Pietsch inferred the phylogenetic relationships of

the Uranoscopidae cladistically for the first time and recognized the seven genera in the family based mainly on osteological characters: *Astroscopus*, *Gnathagnus*, *Genyagnus*, *Ichthyscopus*, *Kathetostoma*, *Pleuroscopus* and *Uranoscopus*. In addition, he inferred the phylogenetic position of the family among the Trachinoidei and showed 12 synapomorphies for the family. However, Pietsch's (1989) relationships are questionable. He overlooked many derived characters and his evaluation of several characters have been disputed by a number of authors (Johnson and Patterson, 1993; Mooi and Johnson, 1997; Imamura and Matsuura, 2003; Imamura and Odani, 2013). Therefore, a reevaluation of relationships and a resultant classification for the family, as well as stronger evidence to support the monophyly of the family, are needed, as no one has attempted to seriously reconstruct the uranoscopid relationships since Pietsch (1989).

The sister relationship of the Uranoscopidae and Trachinidae has been previously proposed by several authors (Pietsch, 1989; Imamura and matsuura, 2003). Although this relationship seems to have been accepted, synapomorphies cited in these studies were based on an examination of few species and the cladistic outcome may be erroneous. These synapomorphies require evaluation.

The goals of this study are: 1) to describe the osteological and mycological anatomy of Uranoscopidae; 2) to reconstruct the phylogenetic relationships of the family at the species level based on morphological characters; 3) to evaluate the monophyly of the family and identify its sister group; and 4) to revise the classification of the family based on the outcomes. Adaptations and evolutionary processes for a

benthic life style in the Uranoscopidae are also discussed.

## II. Materials and Methods

Osteological and myological examinations were made on specimens stained with Alizarin Red-S and Alcian Blue, and dissected under the microscopes MZ 8 and MZ 12 equipped with a camera lucida. Neither *Selenoscopus turbisquamatus* (BSKU 30740) nor *Uranoscopus filibarbis* (MNHN 3098) were examined myologically due to the absence of specimens for preparation. Terminology follows Pietsch (1989), Imamura (2004), Imamura and Matsuura (2003) and Imamura and Yabe (2002) for osteology, and Winterbottom (1974) for myology. Prior to taxonomic reassessment the classification of uranoscopid genera and their species followed Pietsch (1989), except for the recognition of *Xenocephalus* as a senior synonym of *Gnathagnus* (see Springer and Bauchot, 1994), and the most recently described *Selenoscopus* Okamura and Kishimoto, 1993. Methods of measurements and counts follow Hubbs and Lagler (1958), except for the number of caudal fin rays, which follows Arratia (2008). The institutional codes follow Eschmeyer (1998), except for the Hokkaido University Museum (HUMZ) and Thailand Natural History Museum (THNHM). Specimen lengths are expressed as millimeters standard length (SL). Measurements were made with calipers to the nearest 0.1 mm.

**Materials used for dissection.** Family Uranoscopidae: 8 genera and 32 species. *Astroscopus guttatus*, USNM 406518 (92 mm SL); *A. sexspinosus*, HUMZ 91661 (248 mm SL); *A. y-graecum*, NCSM 46108 (142 mm SL); *A. zephyreus*, LACM 35736-40 (106 mm SL); *Genyagnus monopterygius*, NMNZ P.032749 (97 mm SL); *Ichthyscopus barbatus*, AMS I.25863-001 (186 mm SL); *I. lebeck*, HUMZ 190039 (205 mm SL); *I. sannio*, AMS I.15672-001 (217 mm SL); *Kathetostoma albigutta*, USNM 406517 (1 of 5 specimens, 96 mm SL); *K. averruncus*, HUMZ 173617 (101 mm SL); *K. canaster*, NMV A21575 (160 mm SL); *K. cubana*, USNM 406519 (81 mm SL); *K. giganteum*, HUMZ 66567 (167 mm SL); *K. laeve*, AMS I.17806-007 (224 mm SL); *K. nigrofasciatum*, NMV A9599 (145 mm SL); *Pleuroscopus pseudodorsalis*, AMS I.26926-003 (251 mm SL); *Selenoscopus turbisquamatus*, BSKU 30740 (270 mm SL); *Uranoscopus albesca*, USNM 406520 (120 mm SL); *U. archionema*, HUMZ 81513 (142 mm SL); *U. bicinctus*, HUMZ 80657 (122 mm SL); *U. cognatus*, THNHM F00665 (1 of 5 specimens, 112 mm SL); *U. crassiceps*, HUMZ 190016 (161 mm SL); *U. filibarbis*, MNHN 3098 (134 mm SL); *U. japonicus*, HUMZ 94987 (163 mm SL); *U. oligolepis*, HUMZ 190042 (161 mm SL); *U. polli*, USNM 406521 (95 mm SL); *U. scaber*, USNM 406522 (130 mm SL); *U. tosae*, HUMZ 105814 (148 mm SL); *Xenocephalus armatus*, AMS I.31441-005 (95 mm SL); *X. australiensis*, HUMZ 193986 (186 mm SL); *X. egregius*,

USNM 406516 (1 of 3 specimens, 129 mm SL); *X. elongatus*, HUMZ 63654 (167 mm SL).

**Comparative materials.** Suborder Percoidei: 17 families and 28 species. Acropomatidae: *Acropoma japonicum*, HUMZ 106188 (83 mm SL); *Doederleinia berycoides*, HUMZ 135105 (110 mm SL); *Malakichthys wakiyae*, HUMZ 79411 (114 mm SL); *Synagrops japonicus*, HUMZ 79447 (105 mm SL). Ambassidae: *Ambassis vachellii*, HUMZ 198820 (47 mm SL). Apogonidae: *Apogon semi-lineatus*, HUMZ 175499 (79 mm SL); *Cheilodipterus subulatus*, HUMZ 112063 (81 mm SL). Banjosidae: *Banjos banjos*, HUMZ 37284 (120 mm SL). Caesionidae: *Pterocaesio digramma*, HUMZ 39826 (111 mm SL). Cheilodactylidae: *Cheilodactylus zebra*, HUMZ 36355 (114 mm SL). Howellidae: *Howella zina*, HUMZ 130513 (75 mm SL). Latesidae: *Lates mariae*, HUMZ 125944 (98 mm SL); *Lates microlepis*, HUMZ 138721 (121 mm SL); *Psammoperca waigiensis*, HUMZ 170713 (107 mm SL). Lutjanidae: *Lutjanus fulvus*, HUMZ 80518 (102 mm SL); *L. ophuysenii*, HUMZ 107051 (82 mm SL); *Macolor macularis*, HUMZ 63074 (123 mm SL). Pempheridae: *Pempheris schwenkii*, HUMZ 62960 (103 mm SL). Percichthyidae: *Macquaria colonorum*, HUMZ 198428 (117 mm SL); *Siniperca scherzeri*, HUMZ 170715 (124 mm SL). Polynemidae: *Polynemus plebeius*, HUMZ 48733 (108 mm SL). Polyprionidae: *Stereolepis doederleini*, HUMZ 71230 (102 mm SL). Pomatomidae: *Pomatomus saltatrix*, HUMZ 146032 (146 mm SL). Sciaenidae: *Johnius belangerii*, HUMZ 37859 (116 mm SL). Scombroptidae: *Scombrops boops*, HUMZ 39620 (118 mm SL). Sparidae: *Polysteganus coeruleopunctatus*, HUMZ 73314 (133 mm SL); *Acanthopagrus schlegelii*, HUMZ 103537 (78 mm SL). Terapontidae: *Terapon theraps*, HUMZ 105799 (116 mm SL). Suborder Trachinoidei: 1 family and 2 species. Trachinidae: *Trachinus draco*, USNM 198840 (114 mm SL); *Echiichthys vipera*, MNHN-IC-1999-1120 (1 of 2 specimens, 111 mm SL).

**Materials used for counts and examination of external morphology (Uranoscopidae only).** *Astroscopus y-graecum*, NCSM 46103 (156 mm SL), 46106 (169 mm SL), 46107 (143 mm SL); *Kathetostoma albigutta*, USNM 358238 (4 specimens, 116-117 mm SL); *K. giganteum*, HUMZ 66563 (184 mm SL), 66564 (217 mm SL), 66565 (147 mm SL), 66566 (213 mm SL), 91491 (131 mm SL); *Pleuroscopus pseudodorsalis*, AMS I.26823-001 (246 mm SL), I.27466-001 (265 mm SL); *Selenoscopus turbisquamatus*, BSKU 30738-30740 (3 specimens, 189-207 mm SL); *Uranoscopus cognatus*, THNHM F00665 (4 specimens, 96-116 mm SL); *U. japonicus*, HUMZ 35166 (140 mm SL), 39516 (150 mm SL), 61966 (163 mm SL), 62018 (138 mm SL), 62023 (154 mm SL), 62024 (164 mm SL), 62025 (146 mm SL), 62029 (141 mm SL), 65244 (177 mm SL), 94905 (134 mm SL); *U. tosae*, HUMZ 35723



(111 mm SL), 35762 (94 mm SL), 36063 (135 mm SL), 36720 (84 mm SL), 37111 (96 mm SL), 149978 (120 mm SL), 157877 (100 mm SL); *Xenocephalus egregius*, USNM 186218 (200 mm SL), 187900-2 (3 specimens, 116-194 mm SL); UAIC 4278.03 (2 specimens, 184-219 mm SL), 4282.07 (197 mm SL), 6716.02 (177 mm SL); *X. elongatus*, HUMZ 49868 (227 mm SL), 51965 (191 mm SL), 52590 (222 mm SL), 52595 (209 mm SL), 65957 (222 mm SL), 90595 (193 mm SL), 90620 (169 mm SL), 94859 (255 mm SL), 200392 (200 mm SL).

### III. Phylogenetic Methodology

The methods of phylogenetic analysis follow the cladistic approach by Hennig (1966). Outgroup comparisons were used to determine character polarity (Watrous and Wheeler, 1981; Wiley, 1981).

Several authors have regarded the Trachinidae as the sister group of the Uranoscopidae (Pietsch, 1989; Imamura and Matsuura, 2003). However, the Trachinidae is not an adequate outgroup on its own as it has many derived characters (e.g., Pietsch, 1989; Pietsch and Zabetian, 1990; Imamura and Matsuura, 2003; this study), whose plesiomorphic conditions are present in the Uranoscopidae. Because of the hypothesized close relationship between the two, character polarities in these families were determined by using another perciform suborder, the Percoidei, which has been considered to retain many primitive characters among the Perciformes, as additional outgroup (e.g., Greenwood et al., 1966; Johnson, 1984, Nelson, 1994; Imamura, 2000). In this study, "typical percoid" conditions were inferred from the literature including percoid description and from the specimens examined this study. The typical percoid condition was also used to evaluate the monophyly of the Uranoscopidae and Trachinidae.

The character data set was analyzed using PAUP\*4.0b10 (Swofford, 2002), including ACCTRAN and DELTRAN optimizations and heuristic algorithms. The character evolutions were mostly inferred as "ordered" (Wagner parsimony; Farris, 1970), except for transformation series with considerable character loss or difficulties in ordering characters because of considerable modifications, for which characters were treated as "unordered" (Fitch parsimony; Fitch, 1971). Character evolutions employed with the cladogram were estimated by using MacClade ver. 4.0 (Maddison and Maddison, 2000). All autapomorphic characters and characters commonly recognized in Uranoscopidae were excluded from the phylogenetic analysis, because they have no effect to infer relationships. In addition, some characters of *Selenoscopus turbisquamatus* and *Uranoscopus filibarbis*, that could not be examined, were coded as "?".

## IV. Anatomy of Uranoscopidae

### 1. Osteology

#### 1-1. Circumorbital bones (Figs. 1-9, Table 1)

**Description.** The circumorbital bones or the infraorbitals, are plate-like. They possess a tubular structure for the infraorbital sensory canal in all uranoscopids, except for the largest element of the second infraorbital (see also section Homology of infraorbitals discussed below) on the left side of a specimen of *Astroscopus y-graecum* (NCSM 46108, 142 mm SL) that lacked this structure (Figs. 4C, 6D). These bones are situated on the lateral surface of the head and arranged in a semicircle, surrounding the ventral and posterior parts of the eye. Four infraorbitals are present in most uranoscopids, while the infraorbitals on the left side of a specimen of *A. y-graecum* (NCSM 46108, 142 mm SL) and the right side of a specimen of *A. zephyreus* (LACM 35736-40, 106 mm SL) are comprised of seven and five infraorbitals, respectively (Figs. 4B-C, 6C-D). The lateral aspect of each infraorbital is rugose and partially covered with small pits. They also have many small tubercles laterally in *Pleuroscopus pseudodorsalis* and *Xenocephalus* spp. (Figs. 1, 3B, 5E).

The sensory canal of the infraorbitals is completely roofed and ossified, each possessing a large sensory pore on either end (Figs. 1, 6-7). The sensory canal at the posterior end of the fourth infraorbital is mesially continuous with the canal on the lateral end of the frontal and that on the anterior end of the pterotic. The canal of each infraorbital has branches to innervate all parts of the bone (Fig. 7B). These branches open on the lateral, dorsal and mesial surfaces of the infraorbitals with additional large pores and numerous minute pores (Fig. 7A). The numbers of the additional large pores on the lateral surface of the first to third infraorbitals and the dorsal surface of the fourth infraorbital in Uranoscopidae are summarized in Table 1.

The first infraorbital (= lachrymal), the anteriormost element of the infraorbitals, is rhomboid and expanded ventrally (Figs. 1-4, 6, 8). The anterodorsal and posterodorsal portions of this bone each have a facet; the anterior facet is articulated with the tip of the anterior process of the palatine mesially and the posterodorsal facet with the lateral ethmoid mesially. These facets are separated by a dorsomesial ridge. A process below the posterodorsal facet connects with the lateral surface of the palatine median plate. The first infraorbital also contacts with the maxilla anteromesially and is attached to the second infraorbital posteriorly with connective tissue. The bone possesses a subocular shelf on the posteromesial region, which is attached to the anterior margin of the shelf of the second infraorbital with connective tissue. Two and three well developed anterior spines are present on the anterior portion of the bone in *Astroscopus* spp. and *Genyagnus monopterygius*, respectively (Figs. 2B, 4), but poorly developed or absent in the others (Figs. 1, 2A, C, 3).

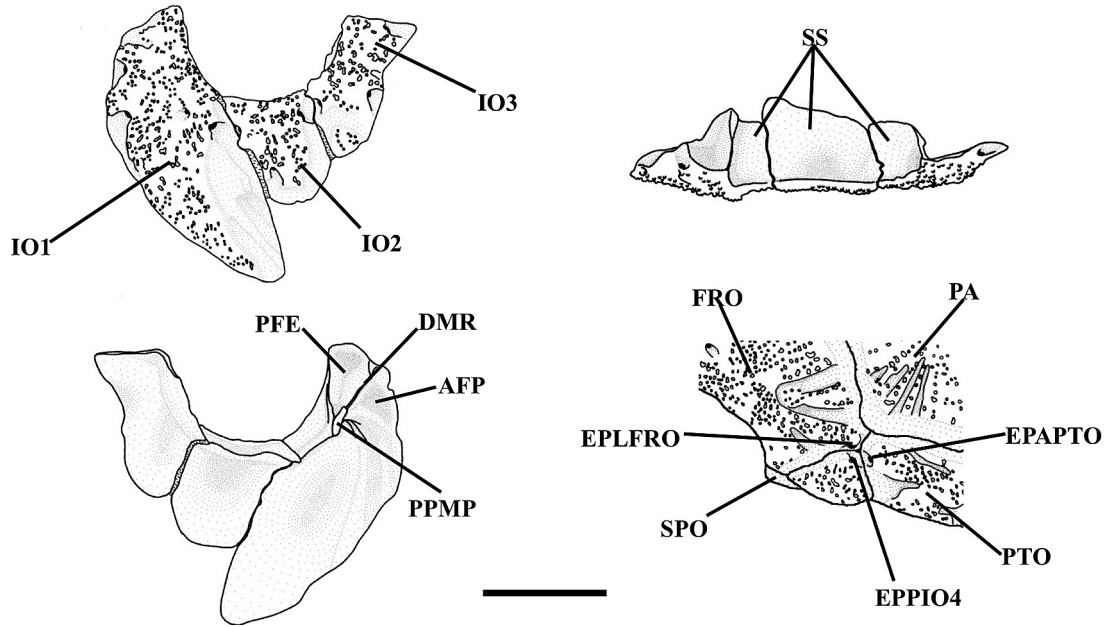


Fig. 1. Lateral (upper left), mesial (lower left) and dorsal (upper right) views of first to third infraorbitals of left side and dorsal view of lateral portion of left side of cranium (lower right) in *Xenocephalus armatus*. AFP, anterior facet for articulation with palatine; DMR, dorsomesial ridge; FRO, frontal; IO1-3, first to third infraorbitals; PA, parietal; PFE, posterodorsal facet for articulation with lateral ethmoid; PPMP, process for connection with palatine median plate; PTO, pterotic; SPO, sphenotic; SS, subocular shelf. Sensory pores: EPPIO4, pore at posterior end of fourth infraorbital; EPLFRO, pore at lateral end of frontal; EPAPTO, pore at anterior end of pterotic. Bar indicates 5 mm.

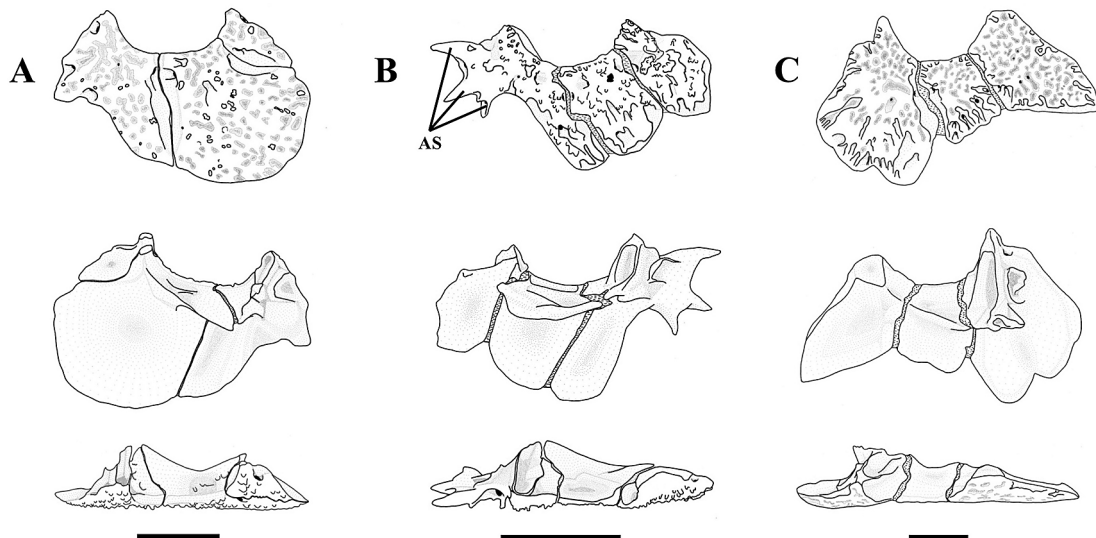


Fig. 2. Lateral (upper), mesial (middle) and dorsal (lower) views of first to third infraorbitals of left side. A, *Uranoscopus scaber*; B, *Genyagnus monopterygius*; C, *Ichthyoscopus sannio*. AS, anterior spines of first infraorbital. Bars indicate 5 mm.

An anteriormost, additional large sensory pore on the first infraorbital is sandwiched by the two spines in *Astroscopus* spp. (Figs. 4, 6B-D), and by the anterior two of the three spines in *G. monopterygius* (Fig. 2B).

The second infraorbital is rather square, situated between the first and third infraorbitals and forms the ventral portion of the orbit (Figs. 1-4, 6, 8). This bone has a well developed subocular shelf dorsally. The anterior tip of the shelf bonds

with the palatine by a ligament (Fig. 8A). The second infraorbital is attached mesially with the sphenotic in *Astroscopus guttatus*, *A. y-graecum*, *A. zephyreus*, *Kathetostoma laeve*, *K. nigrofasciatum*, *Uranoscopus bicinctus* and *U. oligolepis*, and with the sphenotic and frontal in *U. scaber*; but is separated from the cranium in *A. sexspinosus*, *Genyagnus monopterygius*, *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus*, *Ichthyoscopus* spp., *Xenocephalus* spp., and remaining

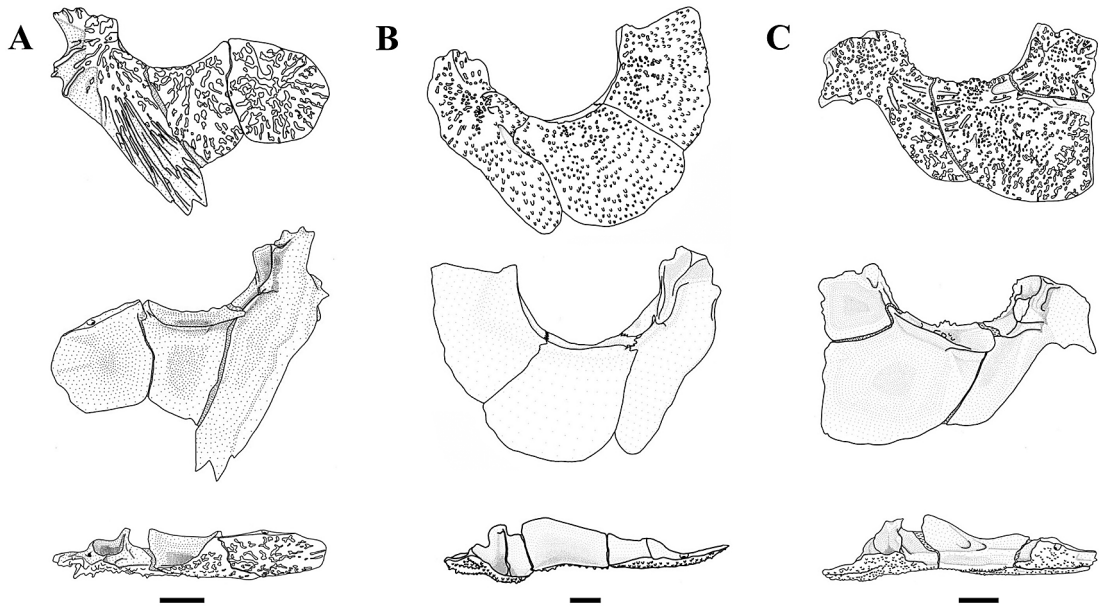


Fig. 3. Lateral (upper), mesial (middle) and dorsal (lower) views of first to third infraorbitals of left side. A, *Kathetostoma laeve*; B, *Pleuroscopus pseudodorsalis*; C, *Selenoscopus turbisquamatus*. Bars indicate 5 mm.

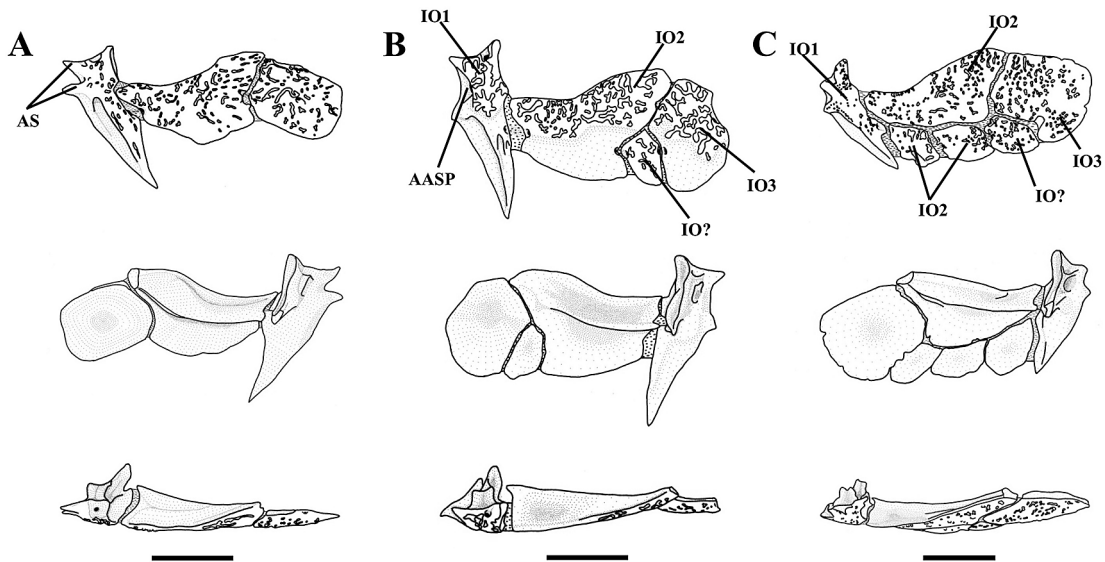


Fig. 4. Lateral (upper), mesial (middle) and dorsal (lower) views of first to third infraorbitals on left side. A, *Astroscopus guttatus*; B, *Astroscopus zephyreus*; C, *A. y-graecum*. AASP, anteriormost additional large sensory pore; AS, anterior spines of first infraorbital; IO1-3, first to third infraorbitals; IO?, unidentified infraorbital element. Bars indicate 5 mm.

species of *Kathetostoma* and *Uranoscopus*. On the left side of a specimen of *A. y-graecum* (NCSM 46108, 142 mm SL), the second infraorbital is divided into three elements: the largest element is plate-like, bears the subocular shelf and lacks a sensory canal; and the remaining two elements, situated below the largest element, both have a sensory canal.

The third infraorbital is well developed and broad (Figs. 1-4, 6-9). It possesses a subocular shelf in *Kenocephalus* spp., *Ichthyoscopus* spp., *Genyagnus monopterygius*, *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus*, *Kathetostoma averruncus*, *K. cubana*, *Uranoscopus albesca*, *U.*

*cognatus*, *U. crassiceps*, *U. japonicus*, *U. tosae* and *U. polli* (Figs. 1, 2B-C, 3B-C), but lacks the shelf in others. In most uranoscopids, this bone is separated from the hyomandibula (Fig. 9A), while the posterior margin of this bone contacts the exposed part of the hyomandibula in *K. nigrofasciatum*, *K. albigutta*, *K. averruncus* and *K. cubana* (Fig. 9B). The third infraorbital forms the posteroventral portion of the orbit in most uranoscopids (Figs. 1-3), but does not in *Astroscopus guttatus*, *A. y-graecum* and *A. zephyreus* (Fig. 4). The third infraorbital is connected with the second infraorbital anteriorly by connective tissue and is tightly attached with the



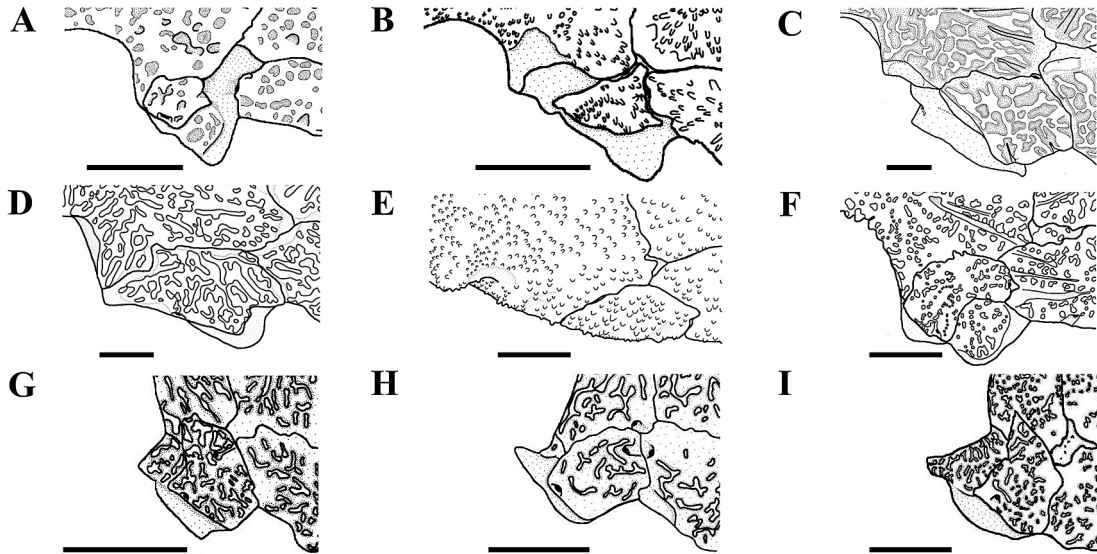


Fig. 5. Dorsal view of lateral portion of cranium on left side. A, *Uranoscopus scaber*; B, *Genyagnus monopterygius*; C, *Ichthyoscopus sannio*; D, *Kathetostoma laeve*; E, *Pleuroscopus pseudodorsalis*; F, *Selenoscopus turbisquamatus*; G, *Astroscopus guttatus*; H, *A. zephyreus*; I, *A. y-graecum*. Bars indicate 5 mm.

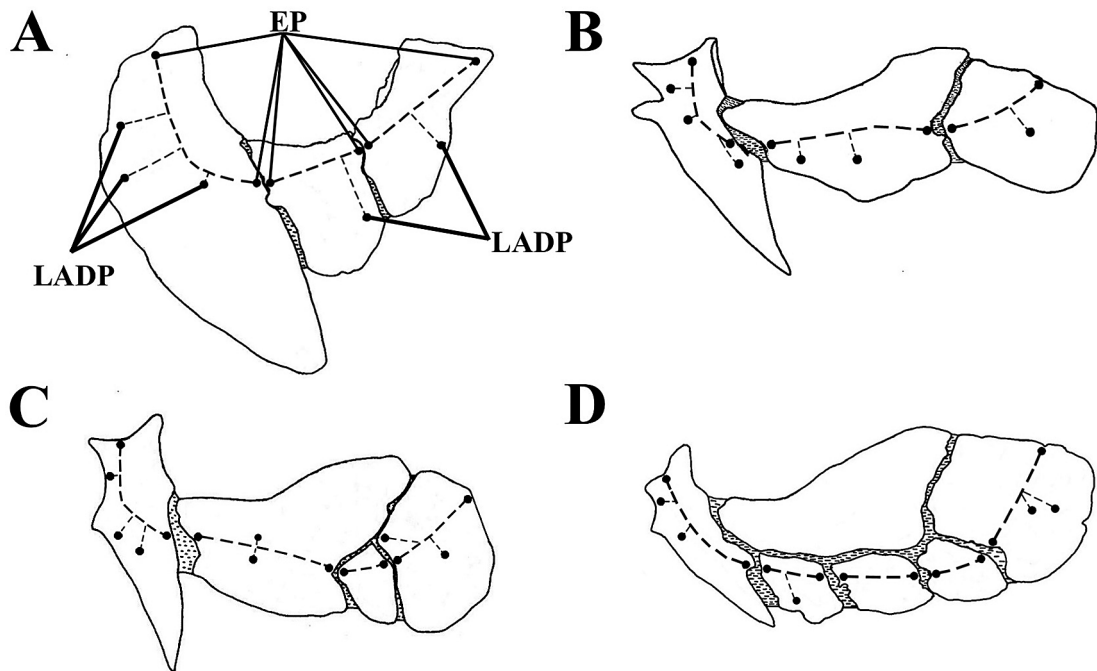


Fig. 6. Position of sensory canal (dashed line) and large sensory pores (solid black circles) in first to third infraorbitals of left side. A, *Xenocephalus armatus*; B, *Astroscopus guttatus*; C, *A. zephyreus*; D, *A. y-graecum*. EP, sensory pore at ends of infraorbital; LADP, additional large sensory pore.

fourth infraorbital and sphenotic posteriorly. The posterior region of this bone also contacts the frontal in *Ichthyoscopus* spp., *G. monopterygius*, *U. scaber* and *U. tosaе*.

The fourth infraorbital (= dermosphenotic) is situated on the dorsal surface of the sphenotic (Figs. 1, 5, 8A). This bone forms the posterior part of the orbit in *Kathetostoma* spp., *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. bicinctus*, *U. cognatus* and *U.*

*polli*, but does not in the others. The fourth infraorbital is firmly attached to the sphenotic ventrally.

An unidentified element with a sensory canal is present below the connection of the second and third infraorbitals on the left side of a specimen of *Astroscopus y-graecum* (NCSM 46108, 142 mm SL) and the right side of a specimen of *A. zephyreus* (LACM 35736-40, 106 mm SL) (Figs. 4B-C, 6C-D).

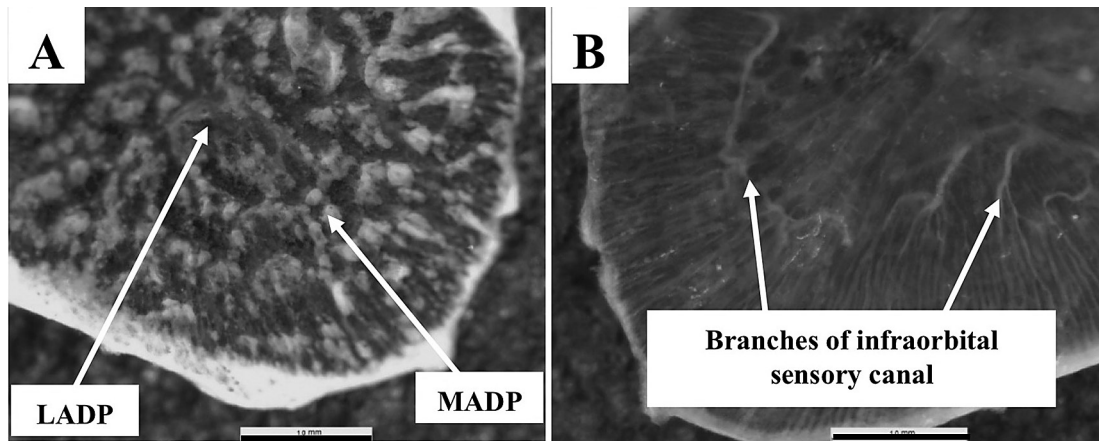


Fig. 7. Lateral (A) and mesial (B) surfaces of third infraorbital of left side after removing skin in *Astroscopus guttatus*. LADP, additional large sensory pore; MADP, additional minute sensory pore. Bars indicate 1 mm.

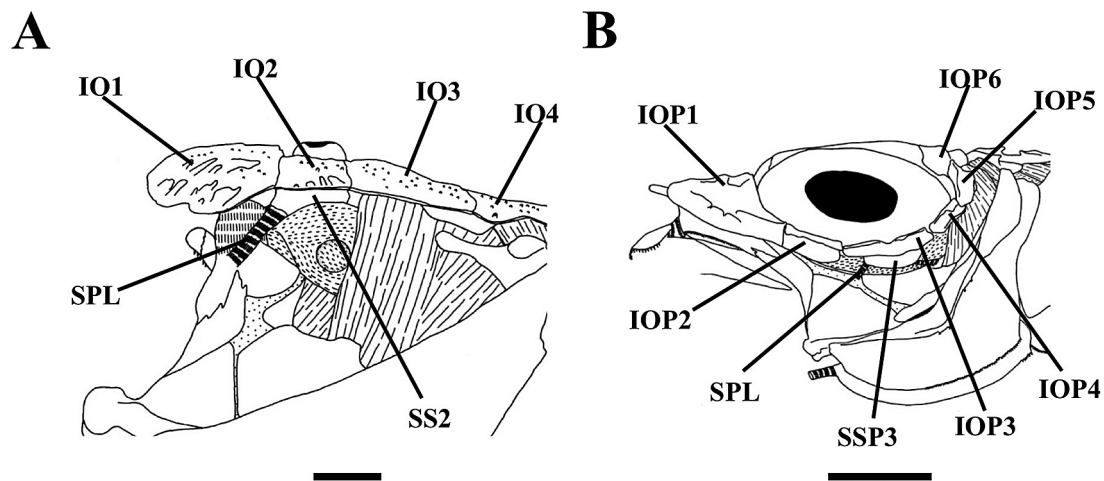


Fig. 8. Ventrolateral view of left side of head after removing jaws and adductor mandibulae. A, *Ichthyscopus sannio* (Uranoscopidae); B, *Acropoma japonicum* (Percoidae). IO1-4, first to fourth uranoscopid infraorbitals; IOP1-6, first to sixth percoid infraorbitals; SPL suspensorium ligament; SS2 subocular shelf of uranoscopid second infraorbital; SSP3 subocular shelf of third percoid infraorbital. Bars indicate 5 mm.

**Homology of infraorbitals.** Uranoscopids fundamentally possess four infraorbitals (Fig. 8A), while percoids have six (Fig. 8B). Therefore, two autogenous elements are absent in the family. The first and fourth infraorbitals of uranoscopids are apparently homologous with the first infraorbital and sixth infraorbital (= dermosphenotic) of percoids, respectively, as the uranoscopid first infraorbital articulates with the lateral ethmoid and the fourth infraorbital is firmly attached to the sphenotic with its sensory canal continuous with that of the frontal and pterotic, as are the first and sixth infraorbitals in typical percoids.

Smith and Bailey (1962) showed that the subocular shelf is present only on the third infraorbital in most percoid taxa. In addition, the third infraorbital forms the lower orbit in percoids (e.g., Tominaga, 1968; Fraser, 1972; Sasaki, 1989; Otero, 2004; this study). Waldman (1986) examined the subocular shelf on the third infraorbital in numerous berycoid and perciform families, and found that it is strongly

bonded to the suspensorium by connective tissue or ligaments (Fig. 8B). In uranoscopids, the second infraorbital usually has a subocular shelf and the shelf is bonded with the palatine by a ligament (Fig. 8A). Accordingly, the uranoscopid second infraorbital is considered to be homologous with the percoid third infraorbital. Other infraorbitals do not have a ligamentous attachment in the family. Accepting this hypothesis, it is recognized that the autogenous element being homologous with the percoid second infraorbital is absent in uranoscopids.

One large plate-like bone with a subocular shelf but lacking a sensory canal, and three small bones with a sensory canal below the larger bone are present between the first and third infraorbitals on the left side of a specimen of *Astroscopus y-graecum* (Figs. 4C, 6D), while one small bone having a sensory canal is present below the junction of the second and third infraorbitals on the right side of a specimen of *A. zephyreus* (Figs. 4B, 6C). Of these, the shelf on the plate-like



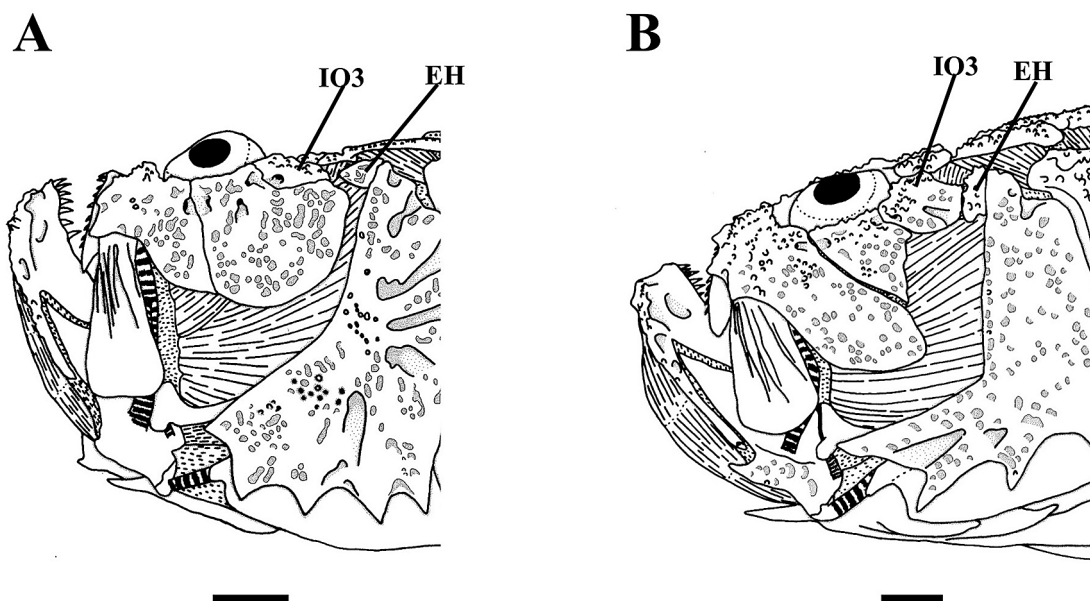


Fig. 9. Left side of head after removing skin. A, *Uranoscopus scaber*; B, *Kathetostoma averruncus*. EH, exposed part of hyomandibula; IO3, third infraorbital. Bars indicate 5 mm.

Table 1. Number of additional large sensory pores on lateral surface of first to third infraorbitals and dorsal surface of fourth infraorbital in Uranoscopidae

Taxa	Number of additional large sensory pores			
	Lateral surfaces			Dorsal surface
	First infraorbital	Second infraorbital	Third infraorbital	Fourth infraorbital
<i>Pleuroscopus</i>	4	2	2	0
<i>Xenocephalus</i>	3	1	1-2	0
<i>Uranoscopus</i>	3	1-2	0-1	0
<i>Kathetostoma</i>	3-6	1-7	1-10	0-1
<i>Genyagnus</i>	8	7	8	0
<i>Ichthyoscopus</i>	4-6	1	1-2	0-3
<i>Astroscopus</i>	2-3	1-4	1-5	0-3
<i>Selenoscopus</i>	3	5	3	0

bone is bonded with the palatine by a ligament. Therefore, this bone is regarded as being homologous with the uranoscopid second infraorbital (= third percoid infraorbital). The small bones in *A. zephyreus* and *A. y-graecum* are identifiable as infraorbitals, because they have a sensory canal like the infraorbitals of percoids. However, the one element in *A. zephyreus* and the last one of the three bones in *A. y-graecum* can not be identified, because they are situated below connection of the second and third infraorbitals, and they can be derived from the uranoscopid second and third infraorbitals. The anterior two small bones in *A. y-graecum* are considered to be derived from the uranoscopid second infraorbital, because they are situated posterior to the ventral expansion of the first infraorbital and below the plate-like second infraorbital. Therefore, in the right side of a specimen of *A. y-graecum*, the second infraorbital is considered to be

divided into three elements in total.

The identity for the remaining element, the third infraorbital in uranoscopids is unclear. This bone is situated between two elements homologous with the percoid third infraorbital and sixth infraorbitals. Three hypotheses are equally possible: the third infraorbital of uranoscopids is homologous with (1) the percoid fourth infraorbital (thus the infraorbital homologous with the percoid fifth infraorbital is absent), (2) the percoid fifth infraorbital (the infraorbital homologous with the percoid fourth infraorbital is absent), and (3) the fused percoid fourth and fifth infraorbitals.

#### Characters variable among Uranoscopidae

##### *TS 1. Spines on anterior portion of first infraorbital.*

0: spines poorly developed or absent; 1: two spines present; 2: three spines present (unordered).

**Ingroup.** Two and three spines are present on the anterior portion of the first infraorbital in *Astroscopus* spp. (character 1-1) and *Genyagnus monopterygius* (character 1-2), respectively, whereas spines are poorly developed or absent at this position in other uranoscopids (character 1-0).

**Outgroup.** The prominent spine is poorly developed or absent on the anterior portion of the first infraorbital in percoids (character 1-0) (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study).

**TS 2. Second infraorbital and cranium.** 0: separated; 1: attached to sphenotic; 2: attached to sphenotic and frontal (ordered as 0-1-2).

**Ingroup.** The second infraorbital is attached to the sphenotic in *Astroscopus guttatus*, *A. y-graecum*, *A. zephyreus*, *Kathetostoma laeve*, *K. nigrofasciatus*, *U. bicinctus* and *U. oligolepis* (character 2-1), and to the sphenotic and frontal in *U. scaber* (character 2-2). The bone is not attached to the cranium in other uranoscopids (character 2-0).

**Outgroup.** In percoids, the third infraorbital, homologous with the uranoscopid second infraorbital, is not attached to the cranium (character 2-0) (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study).

**TS 3. Subocular shelf on third infraorbital.** 0: absent; 1: present.

**Ingroup.** The subocular shelf is present on the third infraorbital in *Ichthyoscopus* spp., *Xenocephalus* spp., *Genyagnus monopterygius*, *Selenoscopus turbisquamatus*, *Pleuroscopus pseudodorsalis*, *Kathetostoma averruncus*, *K. cubana*, *Uranoscopus japonicus*, *U. tosae*, *U. albesca*, *U. cognatus*, *U. crassiceps* and *U. polli* (character 3-1), but absent in other uranoscopids (character 3-0).

**Outgroup.** As discussed above, the third infraorbital of uranoscopids is considered to be homologous with the fourth and/or fifth infraorbitals of percoids. The subocular shelf is absent on the fourth and fifth infraorbitals in percoids (character 3-0) (Smith and Bailey, 1962; Tominaga, 1968; this study).

**TS 4. Third infraorbital and hyomandibula.** 0: separated; 1: in contact.

**Ingroup.** The posterior margin of the third infraorbital contacts the exposed part of the hyomandibula in *Kathetostoma nigrofasciatum*, *K. albigutta*, *K. averruncus* and *K. cubana* (character 4-1), but is separated from the hyomandibula in other uranoscopids (character 4-0).

**Outgroup.** The fourth and fifth infraorbitals are separated from the hyomandibula in percoids (character 4-0) (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study).

**TS 5. Third infraorbital and orbit.** 0: third infraorbital forming part of the orbit; 1: third infraorbital not forming part of the orbit.

**Ingroup.** The third infraorbital forms part of the orbit in all uranoscopids (character 5-0), except for *Astroscopus guttatus*, *A. y-graecum* and *A. zephyreus* that have the bone sepa-

rated from the orbit (character 5-1).

**Outgroup.** The fourth and fifth infraorbitals form the orbit in percoids (character 5-0) (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study).

**TS 6. Third infraorbital and frontal.** 0: separated; 1: in contact.

**Ingroup.** The third infraorbital contacts the frontal in *Ichthyoscopus* spp., *Genyagnus monopterygius*, *Uranoscopus scaber* and *U. tosae* (character 6-1), whereas the two are separated in other uranoscopids (character 6-0).

**Outgroup.** The fourth and fifth infraorbitals, one or both of which are homologous with the uranoscopid third infraorbital, are separated from the frontal (character 6-0) in percoids (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study).

**TS 7. Fourth infraorbital and orbit.** 0: fourth infraorbital forming part of the orbit; 1: fourth not forming part of the orbit.

**Ingroup.** The fourth infraorbital forms part of the orbit in *Kathetostoma* spp., *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. bicinctus*, *U. cognatus* and *U. polli* (character 7-0), but not in other uranoscopids (character 7-1).

**Outgroup.** The uranoscopid fourth infraorbital is homologous with the percoid sixth infraorbital. In most percoids, the sixth infraorbital usually forms part of the orbit (character 7-0) (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study).

**TS 8. Unidentified infraorbital element.** 0: absent; 1: present.

**Ingroup.** An unidentified element in the infraorbital series is present below the junction of the second and third infraorbitals on the left side of a specimen of *Astroscopus y-graecum* (NCSM 46108, 142 mm SL) and the right side of a specimen of *A. zephyreus* (LACM 35736-40, 106 mm SL) (character 8-1), but absent in other uranoscopids (character 8-0).

**Outgroup.** In percoids, no bony elements have been reported below the junction of the third to fifth infraorbitals, which are homologous with the second and third uranoscopid infraorbitals (character 8-0) (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study).

#### Characters synapomorphic for Uranoscopidae

*Two facets of the first infraorbital separated by a dorsomesial ridge.* Two facets of the first infraorbital articulating with the tip of the anterior process of the palatine mesially and the lateral ethmoid mesially are separated by a dorsomesial ridge in all uranoscopids. This ridge is absent in percoids (Tominaga, 1968; Otero, 2004; this study).

*Presence of subocular shelf on the first infraorbital.* The first infraorbital possesses a subocular shelf posteromesially in all uranoscopids. In contrast, the first infraorbital lacks a shelf in most percoids (Smith and Bailey, 1962; this study).

*Absence of an infraorbital homologous with the percoid*

*second infraorbital.* An infraorbital, homologous with the second infraorbital typically present in percoids, is absent in all uranoscopids (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; Imamura, 2000; this study).

#### Autapomorphies for terminal taxa

*None.*

#### Other observed variations

*Sensory pores of infraorbitals.* The sensory pores of infraorbitals are highly variable with regard to the number of large and minute pores in uranoscopids (Table 1), as they are percoid fishes. For example, the infraorbital sensory canal running through all six infraorbitals has few or no branches and 8–11 sensory pores in two percids *Etheostoma edwini* (see Hubbs and Cannon, 1935) and *Perca fluviatilis* (see Disler, 1971), and an apogonid *Gymapogon japonicus* (see Takagi, 1988), but has many branches and numerous minute pores in an apogonid *Rhabdamia cypselurus* (see Hayashi, 1991) and a lactarid *Lactarius lactarius* (see Deng and Zhan, 1986). Accordingly, the number of sensory pores cannot be polarized, and are not used for the phylogenetic analysis.

*Second infraorbital divided into three elements.* The second infraorbital in the right side of a specimen of *Astroscopus y-graecum* (NCSM 46108, 142 mm SL) is divided into three elements: the largest element having a subocular shelf but lacking a sensory canal and the remaining two, situated below to the largest element, possessing a sensory canal. The second infraorbital in other uranoscopids and the percoid third infraorbital, regarded as homologous with the uranoscopid second infraorbital, are not divided in this fashion (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study). Because this character was found only in the right side of a specimen of *A. y-graecum* and is thought to be an aberration.

### 1–2. Cranium (Figs. 10–17)

**Description.** The cranium comprises six unpaired elements, the prevomer, ethmoid, parasphenoid, basisphenoid, supraoccipital and basioccipital, and eleven paired elements, the nasals, lateral ethmoids, frontals, pterosphenoids, sphenotics, prootics, parietals, pterotics, epiotics, intercalars and exoccipitals. The extrascapulae, associated with the posterior portion of the cranium, are also described in this section. The cranium occupies the dorsal portion of the head and its dorsal surface is broad, flat, strongly rugose and pitted. The anterodorsal portion of the cranium has a deep fossa, the interorbital fossa, extending posteriorly beyond the interorbital space and accommodating the long ascending process of the premaxillae. The pterotic, parietal and epiotic lack a posttemporal fossa.

The prevomer is a flat, broadly triangular bone situated on the anteriormost portion of the cranium. It is connected with the lateral ethmoid posterodorsally and posterolaterally, and

the parasphenoid posteroventrally. The prevomer is in contact with the ethmoid posterodorsally in *Astroscopus* spp. (Fig. 11D) and connected by the ethmoid cartilage to it in other uranoscopids (Figs. 10, 11A–C). The prevomer possesses one vomerine tooth plate anteroventrally in *Ichthyoscopus* spp. and *Xenocephalus australiensis* (Fig. 12D), but two tooth plates in other uranoscopids (Figs. 12A–C, 13). Teeth on the tooth plates are small and conical in all uranoscopids, except for *Ichthyoscopus* spp., which has small conical teeth laterally and villiform teeth medially (Fig. 12D).

The nasal is a small flat bone connected with the frontal posteriorly. The dorsal surface of this bone is both covered by skin and smooth in all uranoscopids (Figs. 10, 11A), except for *Xenocephalus* spp., *Astroscopus y-graecum*, *A. sexspinosus*, *A. zephyreus* and *Pleuroscopus pseudodorsalis* (Fig. 11B–D), which have the surface exposed and sculptured. The nasal has a supraorbital sensory canal continuous with the canal of the frontal.

The ethmoid is a thin, flat bone, when present, situated on the anterior region of the cranium and connected with the lateral ethmoid laterally and the frontal posteriorly. Anteriorly, it is connected directly with the prevomer in *Astroscopus* spp. and via the ethmoid cartilage in other uranoscopids. The ethmoid is present in *Astroscopus* spp., *Uranoscopus* spp., *Genyagnus monopterygius* and *Selenoscopus turbisquamatus* (Figs. 10A–C, 11D), but absent in other uranoscopids (Figs. 10D, 11A–C).

The lateral ethmoid, forming the anterior border of the orbit, is a short, thick bone situated on the anterolateral portion of the cranium. The bones on either side mostly are separated by the frontal. The lateral ethmoid connected with the prevomer anteroventrally, the ethmoid mesially, the frontal posterodorsally, and the parasphenoid posteroventrally. The lateral expansion of the lateral ethmoid has a facet for articulation with the first infraorbital laterally. The ventral region of the bone has two facets, the anterior and posterior facets, for articulations with the palatine. The anterior facet is directed ventrally in *Kathetostoma* spp., *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis* (Figs. 11A–C, 13A–C, 14E–G), but is directed anteriorly in other uranoscopids (Figs. 10, 11D, 12, 13D, 14A–D, H). The lateral ethmoid is also connected to the maxilla anteriorly via a maxillo-lateral ethmoid ligament and to the palatine via a palato-lateral ethmoid ligament.

The frontal is a large bone, forming the anterior half of the cranial roof. It is connected with the supraoccipital, parietal and pterotic posteriorly, the ethmoid and lateral ethmoid anteriorly, the sphenotic posterolaterally, and the prootic posteroventrally. The frontal is also in contact with the second infraorbital in *Uranoscopus scaber* and the third infraorbital in *Ichthyoscopus* spp., *Genyagnus monopterygius*, *U. scaber* and *U. tosae*. The anteroventral region of the frontal is connected with the parasphenoid in *G. monopterygius*



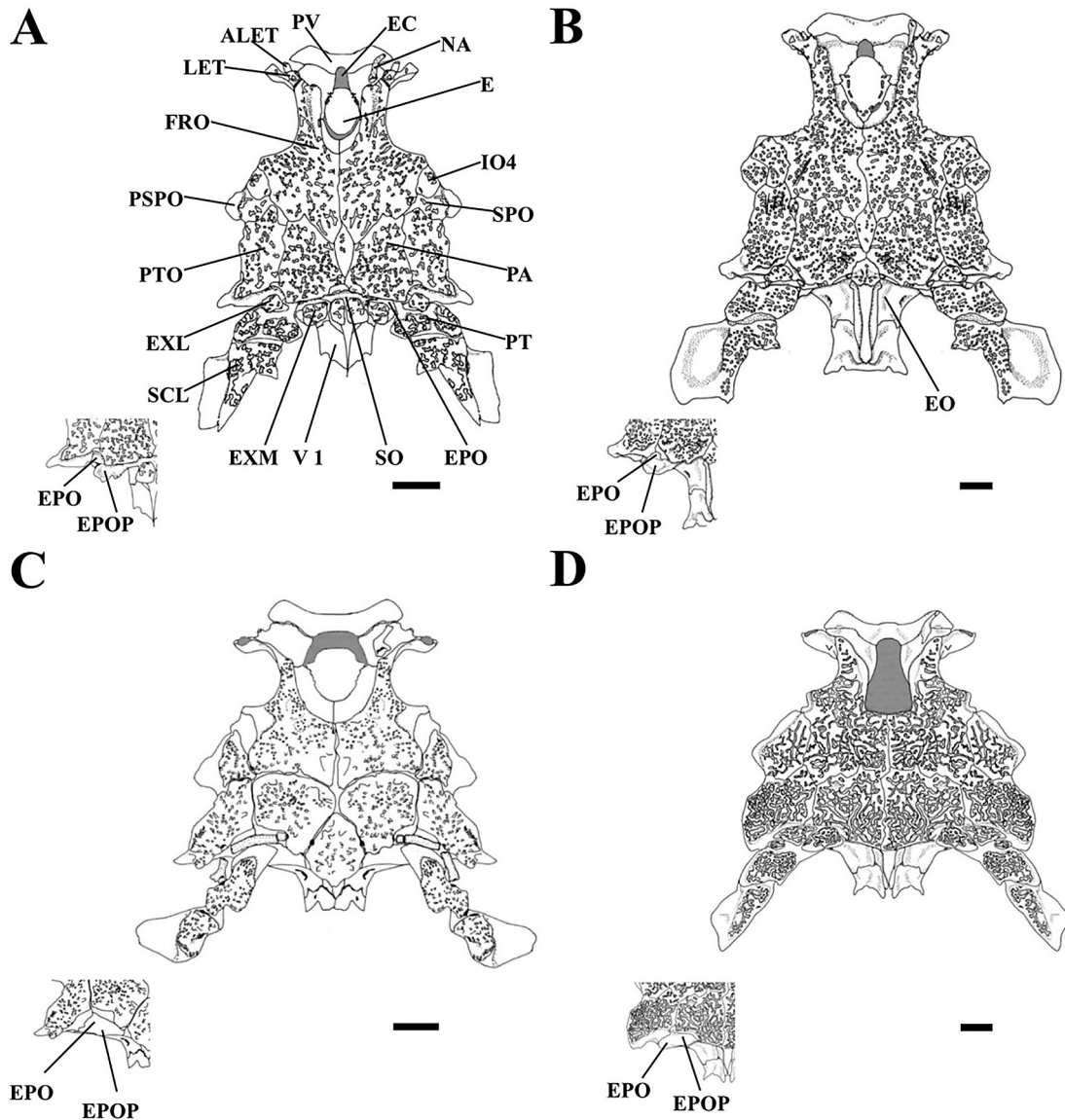


Fig. 10. Dorsal views of cranium (right) and epiotic region of left side with posttemporal removed (left). A, *Uranoscopus tosaе*; B, *Selenoscopus turbisquamatus*; C, *Genyagnus monopterygius*; D, *Ichthyscopus barbatus*. ALET, anterior facet of lateral ethmoid; E, ethmoid; EC, ethmoid cartilage; EO, exoccipital; EPO, epiotic; EPOP, epiotic process; EXL, lateral extrascapula; EXM, medial extrascapula; FRO, frontal; IO4, fourth infraorbital; LET, lateral ethmoid; NA, nasal; PA, parietal; PSPO, posterolateral process of sphenotic; PT, posttemporal; PTO, pterotic; PV, prevomer; SCL, supracleithrum; SO, supraoccipital; SPO, sphenotic; V1, first vertebra. Bars indicate 5 mm.

(Fig. 14C), but is separated it in other uranoscopids (Fig. 14A-B, D-H). The ventral region of the frontal expands ventrally and is connected with the parasphenoid in *U. albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. japonicus*, *U. oligolepis* and *U. tosaе* (Fig. 15D), but is separated it in other uranoscopids (Fig. 15A-C). The anterior portions of the paired frontal are well separated by the ethmoid cartilage, if the ethmoid is absent. A frontal spine is present on the dorsal surface of this bone in *Pleuroscopus pseudodorsalis* (Fig. 14F), but is absent in other uranoscopids (Fig. 14A-E, G-H). The frontal possesses a supraorbital sensory canal, which is continuous with the canal of the nasal

anteriorly, and those of the fourth infraorbital (= dermosphenotic) and pterotic laterally.

The parietal is a broad, slightly flat bone, forming the posterior half of the dorsal cranium roof. It is connected with the frontal anteriorly, the sphenotic and pterotic laterally, the supraoccipital mesially and the epiotic posteriorly. The parietal is also connected with its antimere mesially in all uranoscopids (Figs. 10A-B, D, 11), except for *Genyagnus monopterygius* (Fig. 10C). A parietal spine is present on the dorsal surface of this bone in *Pleuroscopus pseudodorsalis* (Fig. 14F), but is absent in other uranoscopids (Fig. 14A-E, G-H). The parietal has a roofed sensory canal in *Ichthysco-*

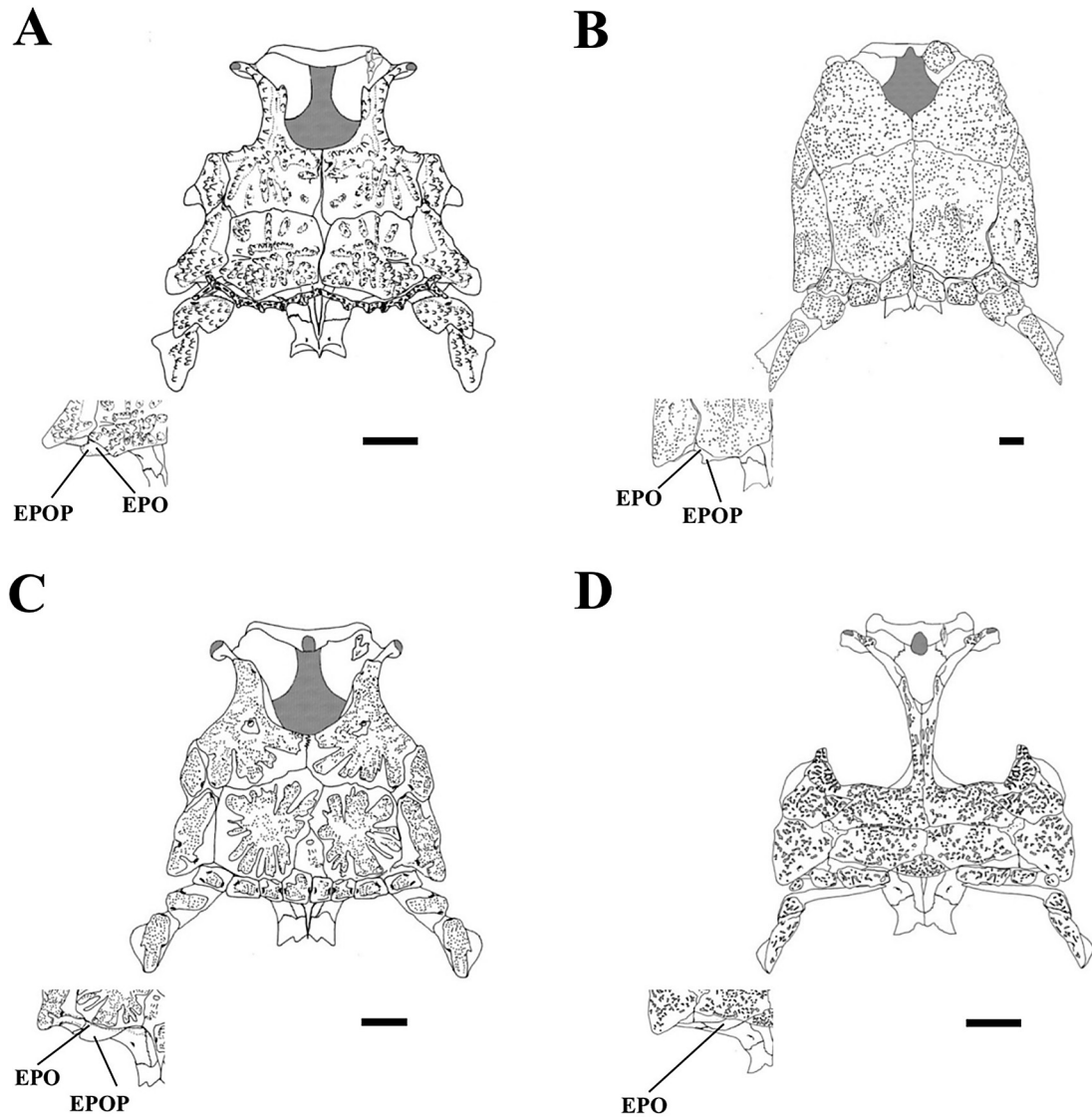


Fig. 11. Dorsal views of cranium (right) and epiotic region with posttemporal removed (left). A, *Kathetostoma giganteum*; B, *Pleuroscopus pseudodorsalis*; C, *Xenocephalus elongatus*; D, *Astroscopus y-graecum*. Abbreviations are as in Fig. 10. Bars indicate 5 mm.

*pus* spp. and *G. monopterygius* (Fig. 16F, H), and an unroofed canal in *Astroscopus guttatus* and *A. zephyreus* (Fig. 16E, G). In *Ichthyoscopus* spp., These canals are continuous with the canals of the innermost medial extrascapula laterally and the parietal on the opposite side mesially (Fig. 16H). In *G. monopterygius*, *A. guttatus* and *A. zephyreus*, the canal is continuous with the canal of the innermost medial extrascapula laterally and that of the supraoccipital mesially (Fig. 16E–G). The parietal lacks a sensory canal in the remaining uranoscopids (Fig. 16A–D).

The sphenotic, a stout bone, forming the posterodorsal wall of the orbit. It is connected with the frontal mesially, the pterotic posteriorly, the pterosphenoid anteroventrally, the prootic ventrally, and the fourth infraorbital (= dermosphenotic) dorsally, and contacting the third infraorbital laterally. The sphenotic also contacts the second infraorbital in

*Astroscopus guttatus*, *A. y-graecum*, *A. zephyreus*, *Kathetostoma laeve*, *K. nigrofasciatum*, *Uranoscopus bicinctus*, *U. oligolepis* and *U. scaber*. The posterolateral process serving as the origin of the levator arcus palatini and dilatator operculi is present in all uranoscopids (Figs. 10, 11A, D), except for *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis* (Fig. 11B, C). A socket for the articulation with the anterior condyle of the hyomandibula is present on the posterolateral corner of the sphenotic.

The pterosphenoid forms the posterior wall of the orbit and is connected with the frontal anterodorsally, the prootic ventrally and the sphenotic posteriorly. It is connected with the parasphenoid anteroventrally in all uranoscopids (Fig. 15B, D), except for *Astroscopus* spp., *Pleuroscopus pseudodorsalis*, *Xenocephalus armatus* and *X. australiensis* (Fig. 15A, C).

The basisphenoid is absent in all uranoscopids (Fig. 14A–



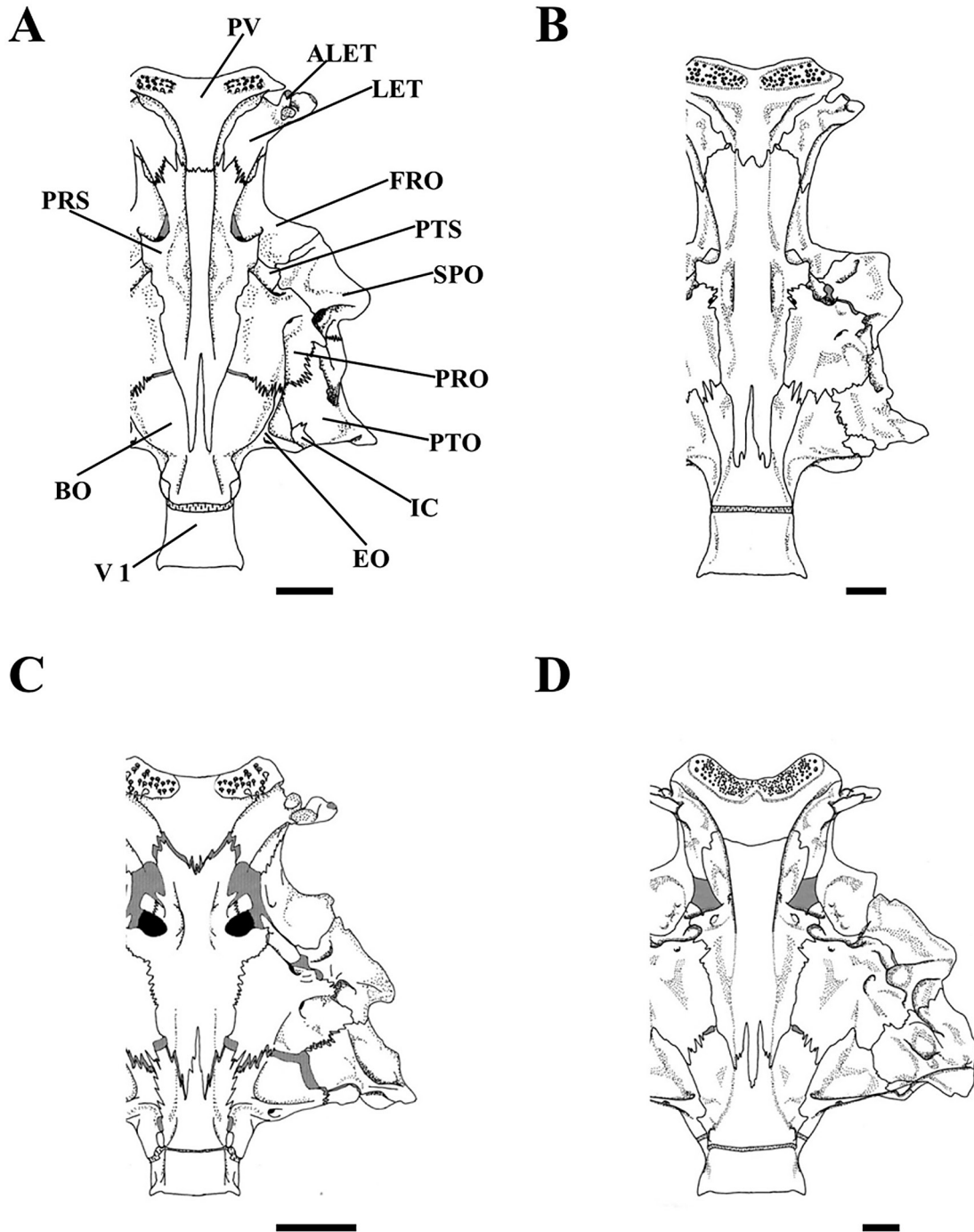


Fig. 12. Ventral view of left side of cranium. A, *Uranoscopus tosae*; B, *Selenoscopus turbisquamatus*; C, *Genyagnus monoptyerygius*; D, *Ichthyscopus barbatus*. ALET, anterior facet of lateral ethmoid; BO, basioccipital; EO, exoccipital; FRO, frontal; IC, intercalar; LET, lateral ethmoid; PRO, prootic; PRS, parasphenoid; PTO, pterotic; PTS, pterosphenoid; PV, prevomer; SO, supraoccipital; SPO, sphenotic; V1, first vertebra. Bars indicate 5 mm.

G), except for *Astroscopus y-graecum*, *A. guttatus* and *A. sex-spinosus*, which have a small basisphenoid in connective tissue separated from the prootic, pterosphenoid and parasphenoid (Fig. 14H).

The parasphenoid, situated on the ventral part of the cranium, is short and shaft like. It is connected with the prevomer and lateral ethmoid anteriorly, the prootic posterolaterally,

and the basioccipital posteriorly. The parasphenoid is connected with the pterosphenoid posterodorsally in *Ichthyscopus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Genyagnus monoptyerygius*, *Selenoscopus turbisquamatus*, *Xenocephalus egregius* and *X. elongatus* (Fig. 15B, D), the frontal anterodorsally in *G. monoptyerygius* (Fig. 14C) and posterodorsally in *U. albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassi-*

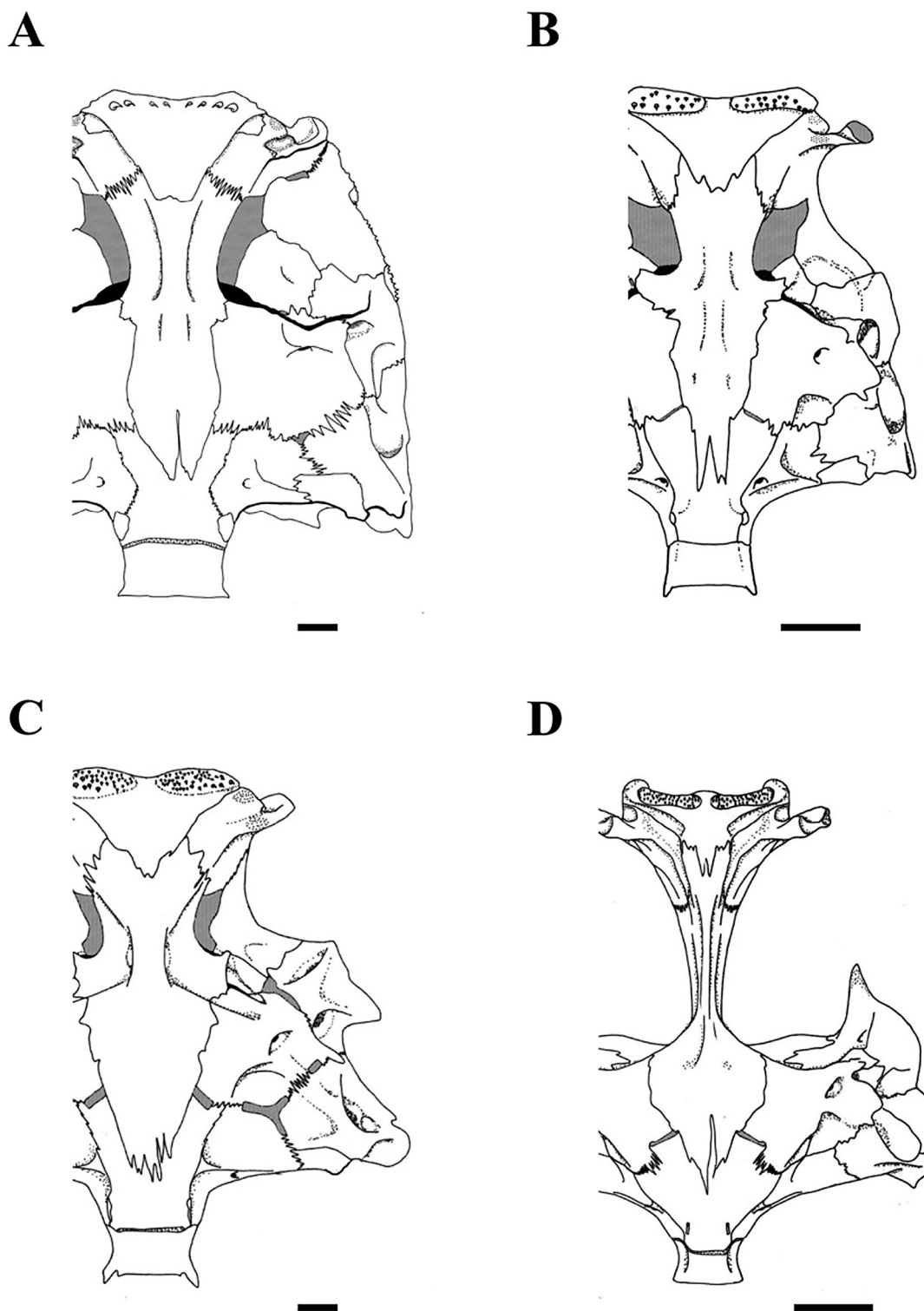


Fig. 13. Ventral view of left side of cranium. A, *Pleuroscopus pseudodorsalis*; B, *Xenocephalus elongatus*; C, *Kathetostoma giganteum*; D, *Astroscopus y-graecum*. Bars indicate 5 mm.

*ceps*, *U. japonicus*, *U. oligolepis* and *U. tosae* (Fig. 15D).

The prootic is a broad, plate-like bone, occupying most of the posteroventral region of the orbit and the anteroventral portion of the auditory bulla. It is connected with the pterosphenoid anteriorly, the basioccipital and exoccipital posteri-

orly, the sphenotic and pterotic dorsally, and the parasphenoid ventrally. The prootic and sphenotic forms a socket for articulating with the anterior condyle of the hyomandibula. The prootic possesses the trigeminofacialis chamber anteroventral to the socket for articulation with the hyomandibula.

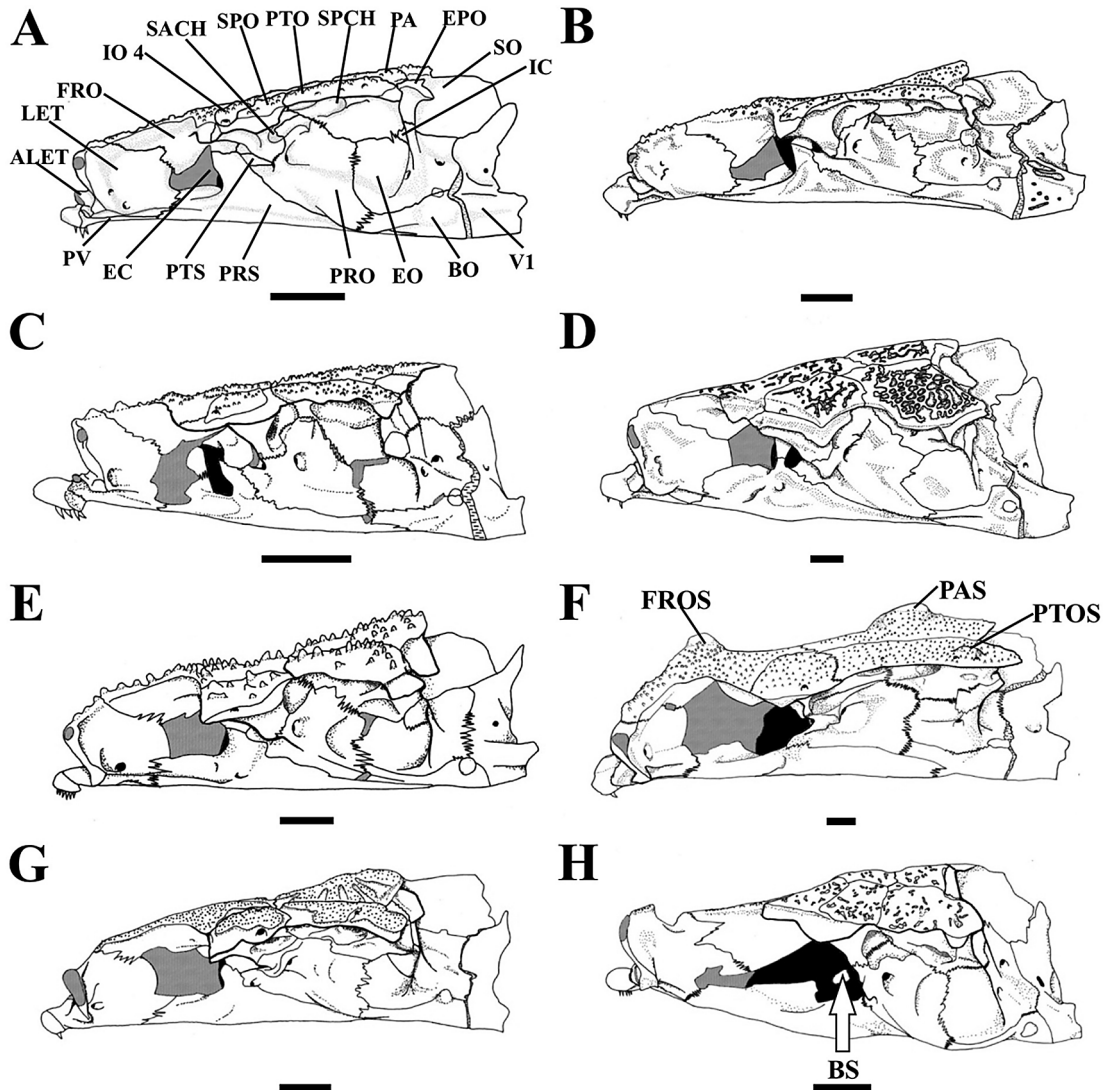


Fig. 14. Lateral view of left side of cranium. A, *Uranoscopus tosaе*; B, *Selenoscopus turbisquamatus*; C, *Genyagnus monopterygius*; D, *Ichthyoscopus barbatus*; E, *Kathetostoma giganteum*; F, *Pleuroscopus pseudodorsalis*; G, *Xenocephalus elongatus*; H, *Astroscopus y-graecum*. BS, basisphenoid; FROS, frontal spine; PAS, parietal spine; PTOS, pterotic spine; SACH, socket for articulation with anterior condyle of hyomandibula; SPCH, socket for articulation with posterodorsal condyle of hyomandibula; other abbreviations are as in Figs. 10 and 12. Bars indicate 5 mm.

The pterotic is plane dorsally, and occupies the dorsolateral portion of the cranium. It is connected with the frontal and sphenotic anteriorly, the prootic, exoccipital and intercalary ventrally, the parietal medially, and the epiotic posteriorly. The ventromedial region of the pterotic has a socket for articulation with the posterodorsal condyle of the hyomandibula. The pterotic has a cephalic sensory canal that is continuous with the canal of the lateral extrascapula posteriorly and the canals of the fourth infraorbital and frontal anteriorly. The lateral portion of the pterotic has lateral openings of the cephalic sensory canal, one of which is continuous with the preoperculo-mandibular sensory canal ventrolaterally. A spine is present on the dorsal surface of the pterotic in *Pleuroscopus pseudodorsalis* and *Xenocephalus egregius* (Fig. 14F), but is absent in other uranoscopids (Fig. 14A-E,

G-H).

The epiotic has a narrow dorsal surface and is situated on the posterior part of the cranium. It is connected with the parietal anterodorsally, the supraoccipital mesially, the pterotic dorsolaterally and the exoccipital posteriorly. An epiotic process projects posteriorly and supports the dorsal arm of the posttemporal in all uranoscopids (Figs. 10, 11A-C), except for *Astroscopus* spp., which lacks the process (Fig. 11D).

The intercalary is a small bone forming the posteroventral portion of the cranium. It is connected with the pterotic dorsolaterally and the exoccipital ventromedially, but is separated from the prootic. The posterior portion of the intercalary is attached to the lower limb of the posttemporal by a ligament. The bone is present in all uranoscopids (Figs. 12, 13A-C, 14A-G) except *Astroscopus y-graecum* and *A. sexspinosus*

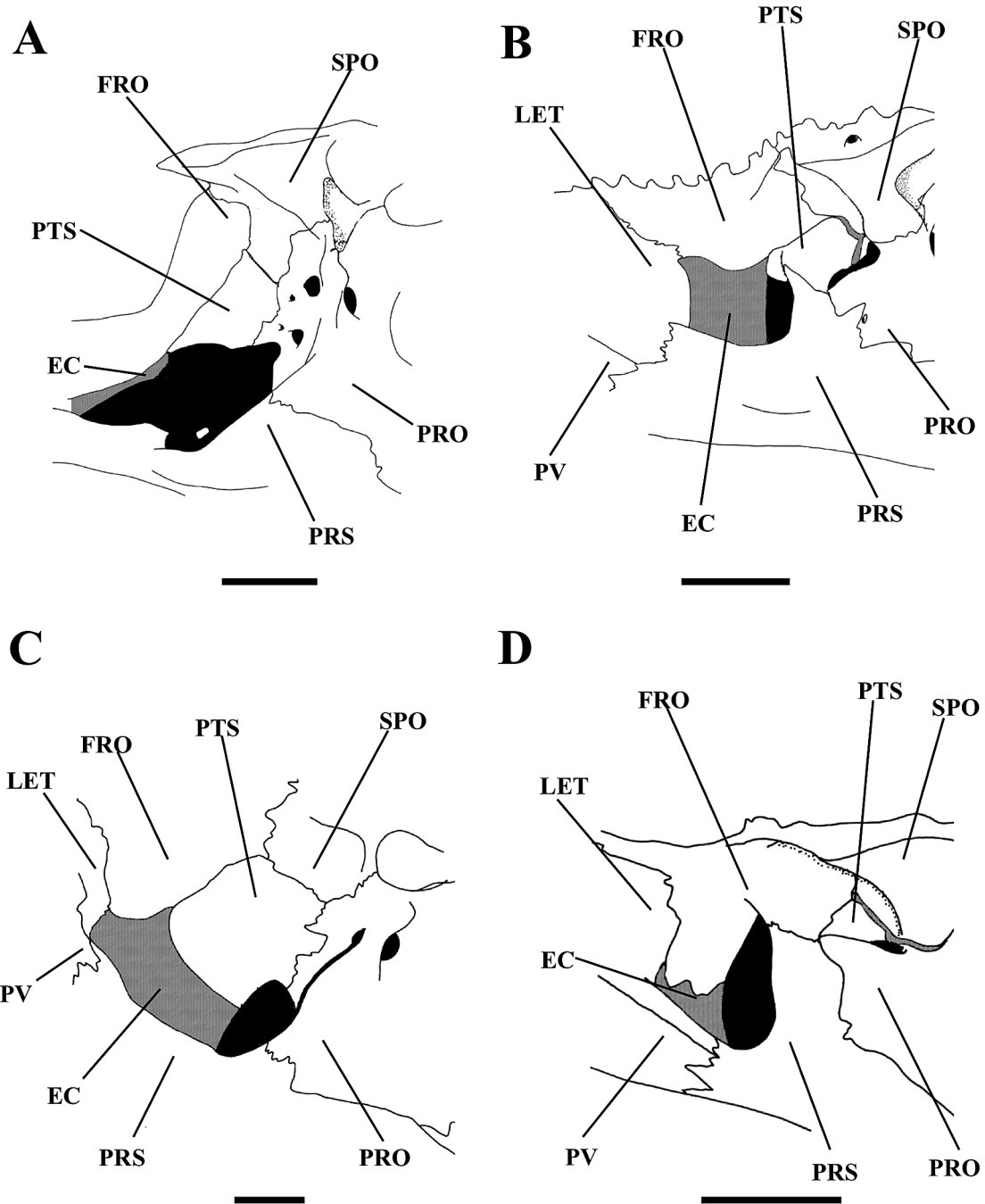


Fig. 15. Anteroventral view of postorbital region on left side. A, *Astroscopus y-graecum*; B, *Kathetostoma giganteum*; C, *Pleuroscopus pseudodorsalis*; D, *Uranoscopus cognatus*. Abbreviations are as in Figs. 10 and 12. Bars indicate 5 mm.

(Figs. 13D, 14H).

The supraoccipital occupies the posteromedial roof of the cranium. It has a narrow anterodorsal region and is connected to the frontal anteriorly, the parietal and epiotic laterally, and the exoccipital and first neural spine posteriorly. A supraoccipital crest on the posterior portion of this bone projects posteriorly beyond the posterior margin of the basioccipital in *Kathetostoma* spp., *Uranoscopus* spp., *Xenocephalus* spp., *Pleuroscopus pseudodorsalis* and *Selenoscopus turbisquamatus* (Fig. 14A-B, E-G), but does not reach as far

*Astroscopus* spp., *Ichthyoscopus* spp. and *Genyagnus monoptygius* (Fig. 14C-D, H). A sensory canal, crosses the dorsal surface of the supraoccipital in *Astroscopus* spp., *Uranoscopus* spp., *S. turbisquamatus* and *G. monoptygius*. The canal is unroofed in *Uranoscopus* spp. and *A. zephyreus* (Fig. 16B, G), but roofed in *S. turbisquamatus*, *G. monoptygius*, *A. guttatus*, *A. y-graecum* and *A. sexspinosus* (Fig. 16C-F). The sensory canal is continuous with the canal of the innermost medial extrascapula laterally in *Uranoscopus* spp., *S. turbisquamatus*, *A. sexspinosus* and *A.*



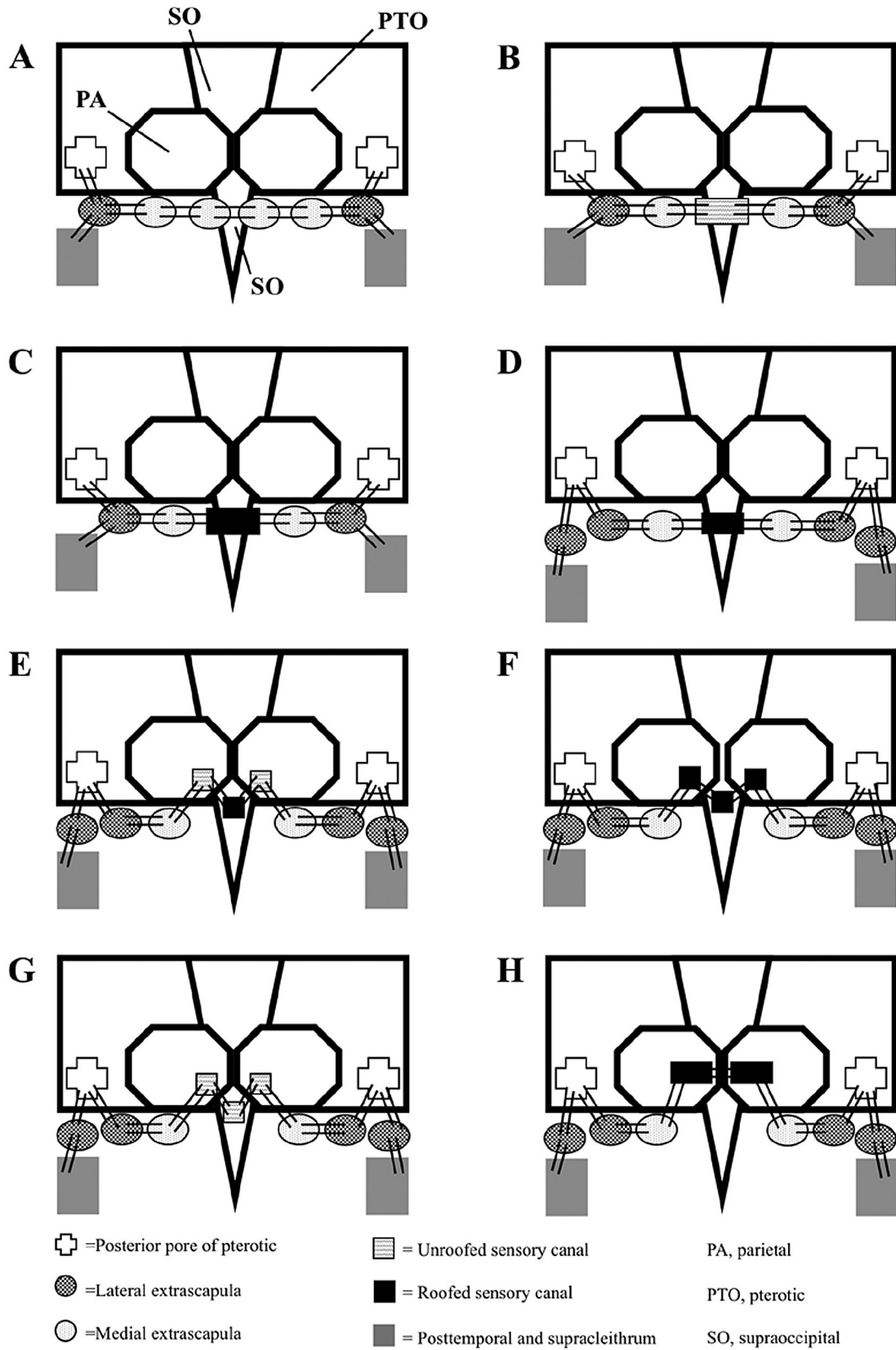


Fig. 16. Diagrammatic representations of sensory canal systems. A, *Pleuroscopus pseudodorsalis*; B, *Uranoscopus tosa*; C, *Selenoscopus turbisquamatus*; D, *Astroscopus y-graecum*; E, *A. guttatus*; F, *Genyagnus monopterygius*; G, *A. zephyreus*; H, *Ichthyoscopus barbatus*.



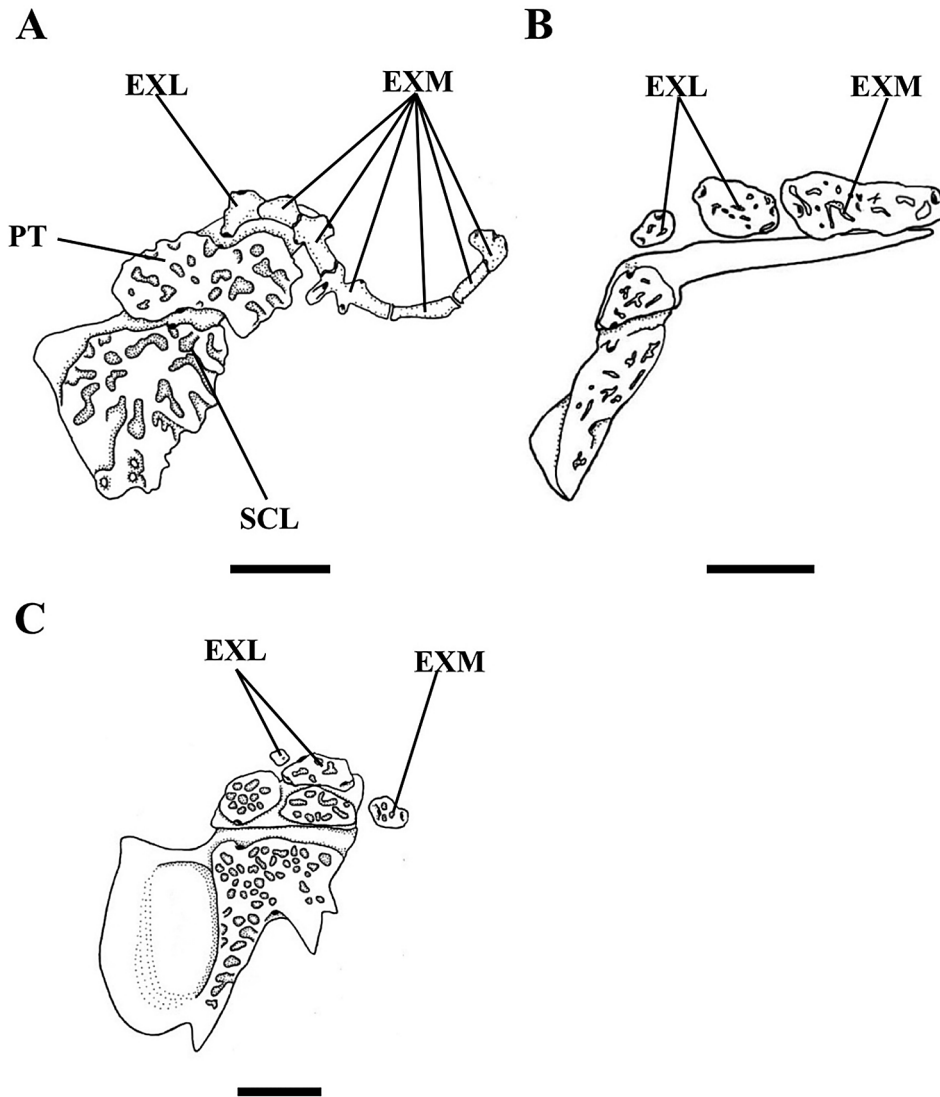


Fig. 17. Dorsal view of extrascapulae, posttemporal and supracleithrum on left side. A, *Kathetostoma nigrofasciatum*; B, *Astroscopus y-graecum*; C, *Uranoscopus oligolepis*. EXL, lateral extrascapula; EXM, medial extrascapula; PT, posttemporal; SCL, supracleithrum. Bars indicate 5 mm.

*y-graecum* (Fig. 16B-D), whereas it is continuous with the canal of the parietal laterally in *G. monopterygius*, *A. zephyreus* and *A. guttatus* (Fig. 16E-G). The supraoccipital lacks the sensory canal in other uranoscopids (Fig. 16A, H).

The exoccipital forms the posteromesial wall of the cranium and surrounds the posterodorsal region of the auditory bulla. It is connected with the supraoccipital dorsomesially, the prootic anteriorly, the intercalar and pterotic dorsolaterally and the basioccipital ventrally. The exoccipital condyles on the two sides are separated from each other above the basioccipital, while the dorsal portions of the bones are attached to each other to form the foramen magnum. The bone is firmly attached with the first neural spine along its posterodorsal border.

The basioccipital is situated on the posteroventral portion of the cranium and forms a major condyle for firm attachment

to the first vertebral centrum. It is connected with the exoccipital dorsally, the prootic anterolaterally and the parasphenoid anteriorly.

The extrascapula situated dorsally behind the posterior edge of the cranium, comprises the lateral and medial extrascapulae. The lateral extrascapula is a single bone with a sensory canal having two lateral and one medial pores in *Kathetostoma* spp., *Xenocephalus* spp., *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. polli* and *U. tosae*; the two lateral pores are continuous with the canals of the pterotic anteriorly and the posttemporal posteriorly, while the medial pore is continuous with the canal of the medial extrascapula mesially (Fig. 17A). The lateral extrascapula has two elements, the horizontal and longitudinal elements, each having a sensory canal and two

pores, in *Astroscopus* spp., *Ichthyoscopus* spp., *Genyagnus monopterygius*, *U. scaber* and *U. archionema*; the pores of the horizontal element are continuous with the sensory canals of the pterotic dorsolaterally and the medial extrascapula mesially, and the pores of the longitudinal element with the canals of the pterotic anteriorly and the posttemporal posteriorly (Fig. 17B). In *U. oligolepis*, the lateral extrascapula also comprises two elements with the horizontal element having a sensory canal and three pores, but the longitudinal element lacks a sensory canal and pores; the three pores of the horizontal element are continuous with the sensory canals of the pterotic dorsolaterally, the posttemporal posteriorly and the medial extrascapula mesially (Fig. 17C). The medial extrascapulae are zero in *I. sannio* and the right side of a specimen of *I. lebeck*, one in *Astroscopus* spp., *Uranoscopus* spp., *S. turbisquamatus*, *I. barbatus* and the left side of a specimen of *I. lebeck*, two in *K. albigutta*, *K. cubana*, *P. pseudodorsalis*, *X. armatus*, *X. australiensis* and *X. egregius*, three in *K. averuncus* and *X. elongatus*, four in *K. canaster*, *K. giganteum* and *K. laeve*, and six in *K. nigrofasciatum*. The medial extrascapulae on the two sides are separated by the supraoccipital in *Uranoscopus* spp., *S. turbisquamatus*, *A. y-graecum* and *A. sexspinosus* (Fig. 16B-D), and by the supraoccipital and parietal in *Ichthyoscopus* spp., *G. monopterygius*, *A. guttatus* and *A. zephyreus* (Fig. 16E-H), while they are connected in *Kathetostoma* spp., *Xenocephalus* spp. and *P. pseudodorsalis* (Fig. 16A). The medial extrascapula is attached to the supraoccipital mesially in *U. crassiceps* and *U. tosaе* (Fig. 10A), but are separated in other uranoscopids (Figs. 10B-D, 11). The sensory canal of the medial extrascapula is continuous with that of the lateral extrascapula laterally. The canal is also continuous mesially with that of the parietal in *Ichthyoscopus* spp., *G. monopterygius*, *A. guttatus* and *A. zephyreus* (Fig. 16E-H), and with that of the supraoccipital in *Uranoscopus* spp., *S. turbisquamatus*, *A. y-graecum* and *A. sexspinosus* (Fig. 16B-D); the canals of both sides are continuous in the others (Fig. 16A).

**Identification of sensory canals of supraoccipital and parietal.** A sensory canal is present on the dorsal surface of the supraoccipital in *Uranoscopus* spp., *Astroscopus* spp., *Selenoscopus turbisquamatus* and *Genyagnus monopterygius*, and the dorsal surface of the parietal in *Ichthyoscopus* spp., *G. monopterygius*, *A. guttatus* and *A. zephyreus*, but are absent from these surfaces in other uranoscopids and percoids that have the sensory canal only passing through extrascapulae. Consequently, presence of the sensory canals on the surface of these bones is regarded as a derived character.

Pietsch (1989) suggested that a sensory canal on the supraoccipital in *Astroscopus* spp., *Ichthyoscopus* spp. and *G. monopterygius*, and the parietal in *Ichthyoscopus* spp. and *G. monopterygius* represent the canal of medial extrascapulae fused to those bones. The hypothesis is not accepted here as the alternative hypothesis that a canal is formed on the bone

directly cannot be discounted. Therefore, the homology between medial extrascapulae, sensory canals on the parietal and the supraoccipital remains unclear. To overcome this, only absence and presence of canals associated with the supraoccipital and parietal are used for the phylogenetic analysis. These characters can be polarized based on a comparison with percoids, having the supraoccipital and parietal without a canal, even if the homology of the canals is unclear. In addition, other characters associated with the medial extrascapulae (e.g., connection of medial extrascapula on both sides; contact between medial extrascapula and sensory canal of supraoccipital; and number of medial extrascapulae) were also omitted from the phylogenetic analysis.

#### Characters variable among Uranoscopidae

**TS 9.** *Number of vomerine tooth plates.* 0: one; 1: two.

*Ingroup.* The prevomer possesses one tooth plate anteroventrally in *Ichthyoscopus* spp. and *Xenocephalus australiensis* (character 9-0), but has two tooth plates in the other uranoscopids (character 9-1).

*Outgroup.* The prevomer has one tooth plate in percoids (character 9-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 10.** *Nasal.* 0: covered by skin and smooth; 1: exposed and sculptured.

*Ingroup.* The nasal is covered by skin and has a smooth surface in all uranoscopids (character 10-0), except for *Xenocephalus* spp., *Astroscopus y-graecum*, *A. sexspinosus*, *A. zephyreus* and *Pleuroscopus pseudodorsalis*, which have an exposed nasal with a sculptured surface (character 10-1).

*Outgroup.* The nasal is embedded under skin and smooth in percoids (character 10-0) (this study).

**TS 11.** *Ethmoid.* 0: present; 1: absent.

*Ingroup.* The ethmoid is present in *Astroscopus* spp., *Uranoscopus* spp., *Genyagnus monopterygius* and *Selenoscopus turbisquamatus* (character 11-0), while it is absent in other uranoscopids (character 11-1).

*Outgroup.* The ethmoid is present in percoids (character 11-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; Otero, 2004; this study).

**TS 12.** *Anterior facet of lateral ethmoid.* 0: directed ventrally; 1: directed anteriorly.

*Ingroup.* The anterior facet of the lateral ethmoid for articulation with the palatine is directed ventrally in *Xenocephalus* spp., *Kathetostoma* spp. and *Pleuroscopus pseudodorsalis* (character 12-0), while it is directed anteriorly in other uranoscopids (character 12-1).

*Outgroup.* The anterior facet is directed ventrally in percoids (character 12-0) (Johnson, 1980; this study).

**TS 13.** *Sensory canal of parietal.* 0: canal absent; 1: roofed canal present; 2: unroofed canal present (unordered).

*Ingroup.* The parietal lacks a sensory canal in all uranoscopids (character 13-0), except for *Ichthyoscopus* spp.,

*Astroscopus guttatus*, *A. zephyreus* and *Genyagnus monopterygius*. A roofed canal is present on the parietal in *Ichthyoscopus* spp. and *G. monopterygius* (character 13-1), and an unroofed canal is present in *A. guttatus* and *A. zephyreus* (character 13-2).

*Outgroup.* The parietal lacks a sensory canal in percoids (character 13-0) (Shinohara, 1994; Imamura and Yabe, 2002; this study).

**TS 14.** *Posterolateral process of sphenotic.* 0: present; 1: absent.

*Ingroup.* A posterolateral process of the sphenotic that serves as the origin of the levator arcus palatini and dilatator operculi is present in all uranoscopids (character 14-0), except for *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis*, which lack the process (character 14-1).

*Outgroup.* A posterolateral process of the sphenotic is present in percoids (character 14-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; Otero, 2004; this study).

**TS 15.** *Basisphenoid.* 0: present and attaching to prootic, pterosphenoid and parasphenoid; 1: present, but separated from these elements; 2: absent (unordered).

*Ingroup.* The basisphenoid is absent in all uranoscopids (character 15-2), except for *Astroscopus y-graecum*, *A. guttatus* and *A. sexspinosus*, which have a small basisphenoid separated from the prootic, pterosphenoid, and parasphenoid (character 15-1).

*Outgroup.* This bone is present and attached to the prootic, pterosphenoid and parasphenoid in percoids (character 15-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 16.** *Posterodorsal portion of parasphenoid.* 0: separated from pterosphenoid and frontal; 1: connected to pterosphenoid, but not frontal; 2: connected to pterosphenoid and frontal (ordered as 0-1-2).

*Ingroup.* The posterodorsal portion of the parasphenoid is separated from the pterosphenoid and frontal in *Astroscopus* spp., *Pleuroscopus pseudodorsalis*, *Xenocephalus armatus* and *X. australiensis* (character 16-0). This portion of the parasphenoid is connected to the pterosphenoid in *Ichthyoscopus* spp., *Kathetostoma* spp., *Genyagnus monopterygius*, *Selenoscopus turbisquamatus*, *Uranoscopus polli*, *U. scaber*, *X. egregius* and *X. elongatus* (character 16-1), and to the pterosphenoid and frontal in *U. albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. japonicus*, *U. oligolepis* and *U. tosaе* (character 16-2).

*Outgroup.* The posterodorsal portion of the parasphenoid is separated from the pterosphenoid and frontal in percoids (character 16-0) (Shinohara, 1994; Imamura and Yabe, 2002; this study).

**TS 17.** *Pterotic spine.* 0: absent; 1: present.

*Ingroup.* A pterotic spine is absent in all uranoscopids (character 17-0), except for *Pleuroscopus pseudodorsalis* and *Xenocephalus egregius*, which have a spine (character 17-1).

*Outgroup.* A pterotic spine is absent in percoids (character 17-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 18.** *Epiotic process.* 0: present; 1: absent.

*Ingroup.* An epiotic process is present in all uranoscopids (character 18-0), except for *Astroscopus* spp., which lack a process on the epiotic (character 18-1).

*Outgroup.* In percoids, an epiotic process is present (character 18-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 19.** *Intercalar.* 0: large, in contact with prootic; 1: small, separated from prootic; 2: absent (unordered).

*Ingroup.* The intercalar is small and separated from the prootic in all uranoscopids (character 19-1), except *Astroscopus y-graecum* and *A. sexspinosus*, which lack the bone (character 19-2).

*Outgroup.* The intercalar is large and contacts the prootic in percoids (character 19-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 20.** *Posterior portion of supraoccipital crest.* 0: extending posteriorly beyond posterior margin of basioccipital; 1: not reaching posteriorly to posterior margin of the basioccipital.

*Ingroup.* The posterior portion of the supraoccipital crest extends posteriorly beyond the posterior margin of the basioccipital in *Uranoscopus* spp., *Kathetostoma* spp., *Xenocephalus* spp., *Pleuroscopus pseudodorsalis* and *Selenoscopus turbisquamatus* (character 20-0), while it does not reach the level in *Astroscopus* spp., *Ichthyoscopus* spp. and *Genyagnus monopterygius* (character 20-1).

*Outgroup.* The posterior portion of the supraoccipital crest extends posteriorly beyond the posterior margin of the basioccipital in percoids (character 20-0) (this study).

**TS 21.** *Sensory canal of supraoccipital.* 0: canal absent; 1: roofed canal present; 2: unroofed canal present (unordered).

*Ingroup.* The supraoccipital lacks a sensory canal in most uranoscopids (character 21-0). A roofed canal is present on the supraoccipital in *Selenoscopus turbisquamatus*, *Genyagnus monopterygius*, *Astroscopus y-graecum*, *A. sexspinosus* and *A. guttatus* (character 21-1), and an unroofed canal is present in *Uranoscopus* spp. and *A. zephyreus* (character 21-2).

*Outgroup.* The supraoccipital lacks a sensory canal in percoids (character 21-0) (this study).

**TS 22.** *Lateral extrascapula.* 0: single element with canal and three pores; 1: two elements, each with canal and two pores; 2: two elements, horizontal element with canal and three pores, and longitudinal element without canal and pores (unordered).

*Ingroup.* The lateral extrascapula is composed of two elements, the horizontal and longitudinal elements, each having a canal and two pores, in *Astroscopus* spp., *Ichthyoscopus* spp.,

*Genyagnus monopterygius*, *Uranoscopus scaber* and *U. archionema* (character 22-1), but comprises two elements, a horizontal element having a canal and three pores, and a longitudinal element lacking a canal and pores, in *U. oligolepis* (character 22-2). The lateral extrascapula comprises a single element with a canal and three pores in other uranoscopids (character 22-0).

*Outgroup.* The lateral extrascapula is comprised with a single element with three pores in percoids (character 22-0) (Imamura and Yabe, 2002; this study).

#### Characters synapomorphic for Uranoscopidae

*Dorsal surface of cranium broad and flat.* The dorsal surface of the cranium is broad and flat in uranoscopids. In contrast, the surface is typically narrow and convex in percoids (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; Otero, 2004; this study).

*Presence of interorbital fossa.* Uranoscopids have an interorbital fossa, extending posteriorly beyond the interorbital space and engulfing a long ascending process of the premaxilla, which is absent in typical percoids (Tominaga, 1968; Sasaki, 1989; this study).

*Absence of posttemporal fossa.* A posttemporal fossa, formed by the pterotic, parietal and epiotic that is well developed in percoids, is absent in uranoscopids (Yabe, 1985; this study).

*Presence of maxillo-lateral ethmoid ligament.* The cranium and upper jaw of uranoscopids are usually connected by a single ligament, that extends from the lateral ethmoid to the lateral process of maxilla. In contrast, percoids have a ligament connecting the ethmoid and lateral process of the maxilla (Johnson, 1980; Sasaki, 1989). Because no other ligaments connect the cranium and upper jaw in uranoscopids and percoids, the ligament in uranoscopids is considered to be homologous with the ligament of percoids and the position of the attachment has changed in uranoscopids.

*Anterior socket for articulation with anterior condyle of hyomandibula present on posterolateral corner of sphenotic.* An anterior socket for articulation with the anterior condyle of the hyomandibula is present on the posterolateral corner of the sphenotic in uranoscopids. In contrast, an anterior socket is present on the anteromesial corner of the sphenotic in percoids (Tominaga, 1968; Sasaki, 1989; Otero, 2004).

*Supraoccipital crest formed on posterior portion of supraoccipital.* A supraoccipital crest is formed on the posterior portion of the supraoccipital in all uranoscopids. In contrast, a crest is formed on the anterior portion of this bone in typical percoids (Tominaga, 1968; this study).

#### Autapomorphies for terminal taxa

*Anteroventral region of frontal connected with parasphenoid.* The anteroventral region of the frontal is connected with the parasphenoid in *Genyagnus monopterygius*, but sep-

arated from the parasphenoid in other uranoscopids, as well as in percoids (Sasaki, 1989). This character is considered to be an autapomorphy of the species.

*Presence of parietal spine.* A parietal spine is present on the dorsal surface of the parietal in *Pleuroscopus pseudodorsalis*, but absent in other uranoscopids and percoids (Shinohara, 1994; Imamura and Yabe, 2002; this study). Therefore, the character is regarded as an autapomorphy of this species.

*Presence of frontal spine.* A frontal spine is present on the dorsal surface of the frontal in *Pleuroscopus pseudodorsalis* but absent in other uranoscopids and percoids (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study). Accordingly, the character is considered to be autapomorphic for the species.

#### Other observed variations

*Shape of prevomerine teeth.* The prevomerine teeth are small conical and villiform in *Ichthyoscopus* spp., but small and conical in other uranoscopids. Prevomerine teeth are small conical and/or villiform in percoids (Imamura, 1996; this study). Therefore, the polarity of the two conditions in uranoscopids cannot be determined and the characters are not used for the phylogenetic analysis.

#### 1-3. Jaws (Figs. 18-19)

**Description.** The jaws consist of the premaxilla and maxilla in the upper jaw, and the dentary, anguloarticular, retroarticular and coronomackelian in the lower jaw. The supramaxillae are absent. Single rostral and Meckelian cartilages are present in the jaws.

The premaxilla is a toothed, L-shaped bone with four processes: the ascending process, articular process, alveolar process and postmaxillary process. The long, sharp ascending process, is attached to the rostral cartilage posteriorly. The articular process is situated posterolateral to the ascending process with a deep notch between them. The alveolar process has conical teeth along its ventral margin and almost the same length as the ascending process. The postmaxillary process is well developed and situated on the posterior portion of the alveolar process.

The maxilla comprises two parts, the head and shaft. The head has the lateral process, premaxillary condyle and cranial condyle. The lateral process and premaxillary condyle sandwich the articular process of the premaxilla anteriorly. A thick ligament connects the lateral process and anterior surface of the lateral ethmoid. The cranial condyle articulates with the anterior surface of the lateral ethmoid mesially, its basal portion articulating with the prevomer and lateral ethmoid ventrally. The ligament primordium inserts on the anterolateral surface of the maxillary shaft and a tendon from the adductor mandibulae section 1 inserts on the mesial surface of the maxilla posterior to the premaxillary condyle. A



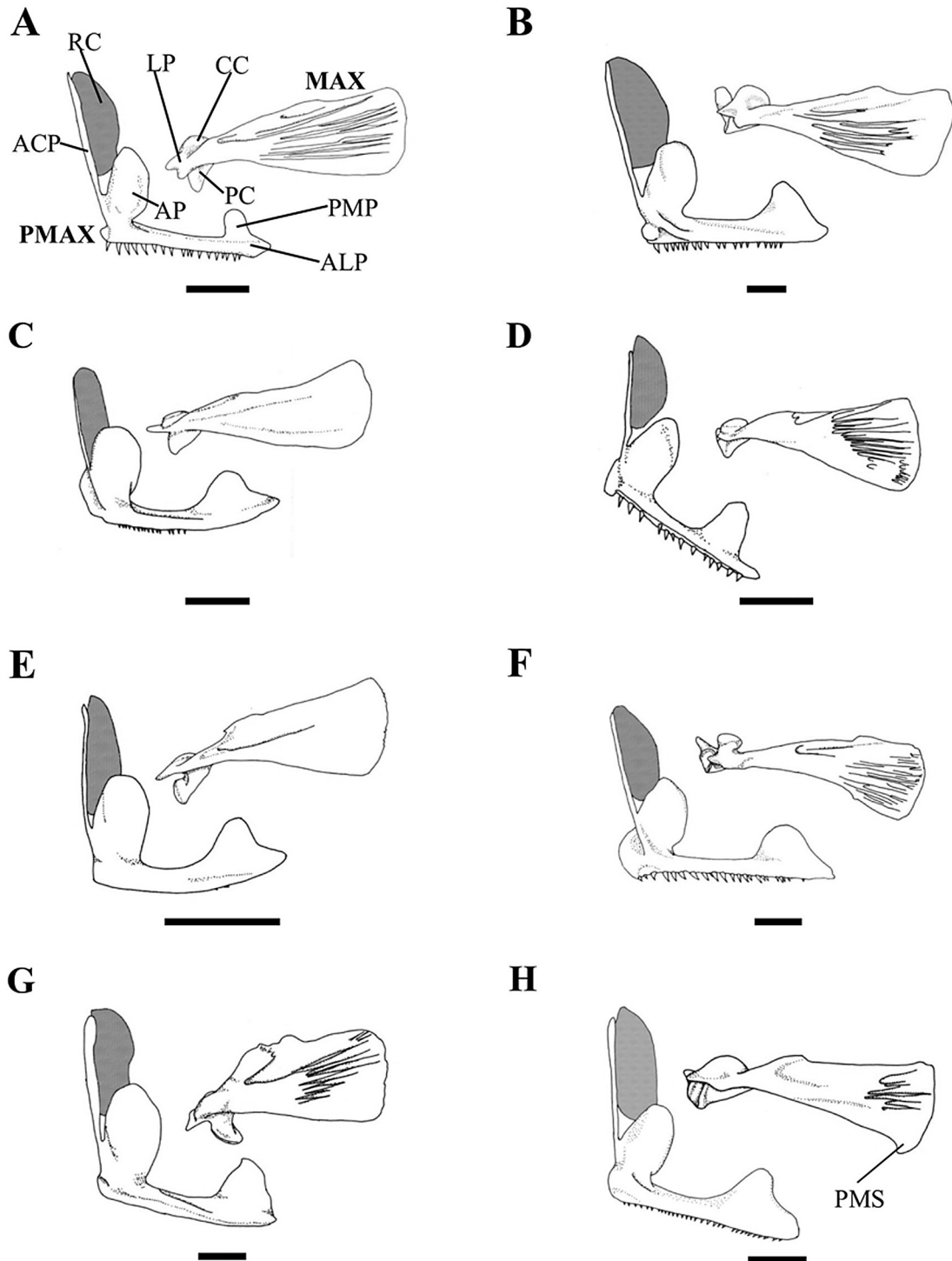


Fig. 18. Lateral view of upper jaw on left side. A, *Uranoscopus tosaе*; B, *Selenoscopus turbisquamatus*; C, *Astroscopus y-graecum*; D, *Xenocephalus egregius*; E, *Genyagnus monopterygius*; F, *Pleuroscopus pseudodorsalis*; G, *Ichthyoscopus lebecki*; H, *Kathetostoma nigrofasciatum*. ACP, ascending process; ALP, alveolar process; AP, articular process; CC, cranial condyle; LP, lateral process; MAX, maxilla; PC, premaxillary condyle; PMAX, premaxilla; PMP, postmaxillary process; PMS, process on posteroventral margin of maxillary shaft; RC, rostral cartilage. Bars indicate 5 mm.

process on the posteroventral margin of the maxillary shaft is present in *Kathetostoma canaster*, *K. laeve* and *K. nigrofasciatum* (Fig. 18H), but is absent in other uranoscopids (Fig. 18A-G).

The dentary possesses conical teeth dorsally and a tubular structure forming the anterior portion of the preoperculo-mandibular sensory canal of the lateral line system laterally. The dentary is connected to the anguloarticular posteriorly



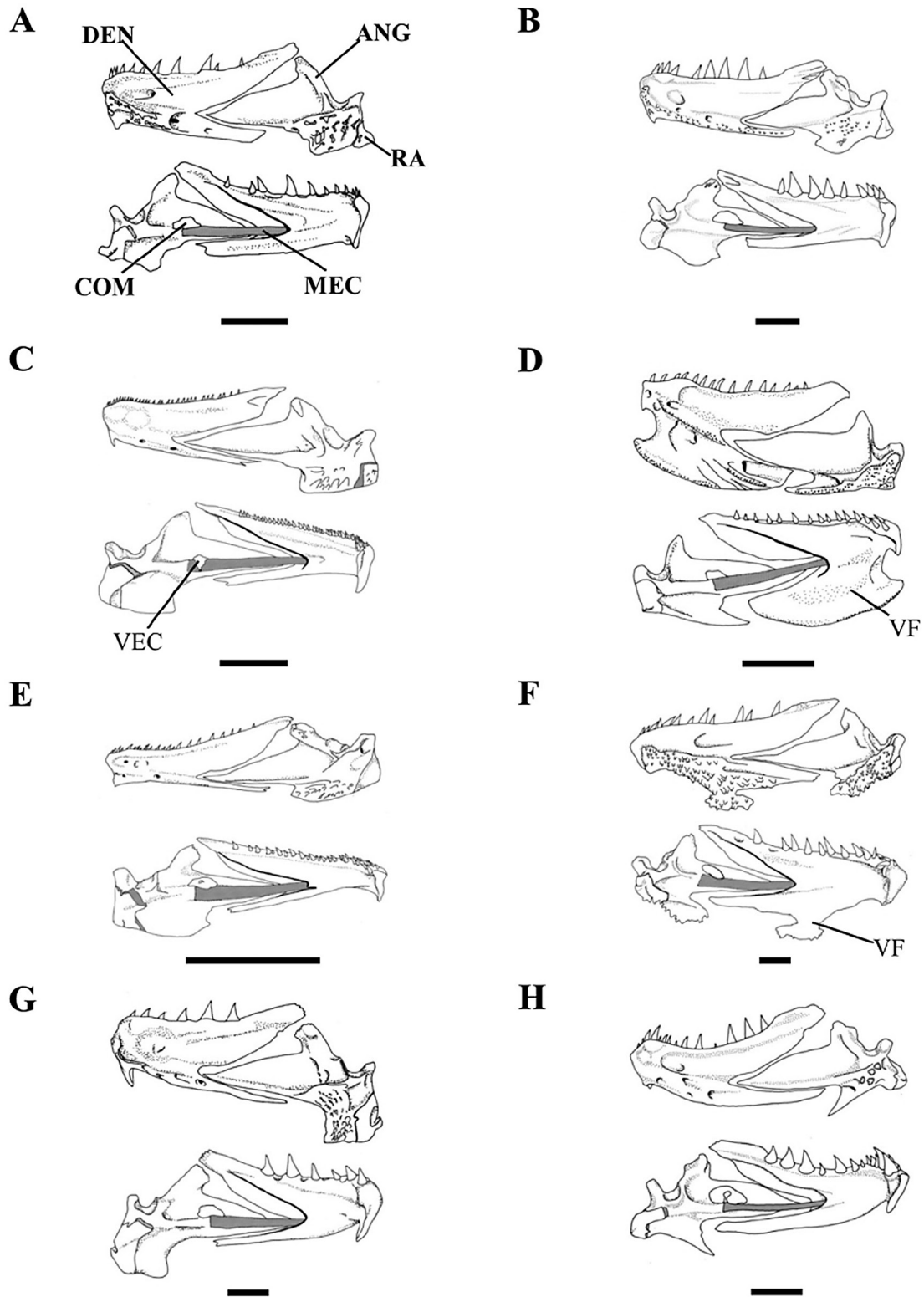


Fig. 19. Lateral (upper) and mesial (lower) views of lower jaw of left side. A, *Uranoscopus tosaе*; B, *Selenoscopus turbisquamatus*; C, *Astroscopus y-graecum*; D, *Xenocephalus egregius*; E, *Genyagnus monopterygius*; F, *Pleuroscopus pseudodorsalis*; G, *Ichthyscopus lebecki*; H, *Kathetostoma nigrofasciatum*. ANG, anguloarticular; COM, coronomeckelian; DEN, dentary; MEC, Meckelian cartilage; RA, retroarticular; VEC, ventral expansion of coronomeckelian; VF, ventral flange of dentary. Bars indicate 5 mm.

and the Meckelian cartilage mesially. This bone has a ventral flange in *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis* (Fig. 19D, F), which is absent in other uranoscopids (Fig. 19A-C, E, G-H).

The anguloarticular occupies the posterior part of the lower jaw and has an anterior projection, that is inserted into a deep notch of the dentary. It articulates with the condyle of the quadrate posterodorsally and is connected to the retroarticular posteroventrally. The anguloarticular is attached to the Meckelian cartilage and coronomeckelian mesially. The sensory canal of this bone is continuous with those of the preopercle posteriorly and dentary anteriorly.

The retroarticular is a small bone, situated on the posteroventral corner of the anguloarticular. It is bonded to the preopercle by a strong ligament.

The coronomeckelian is a tiny bone connected to the mesial surface of the anguloarticular and the posterior end of the Meckelian cartilage. It is confined within the dorsal surface of the Meckelian cartilage in all uranoscopids (Fig. 19A-B, D-H), except for *Astroscopus* spp. and *Uranoscopus bicinctus*, in which the bone is expanded ventrally and almost attaches to the ventral edge of the Meckelian cartilage (Fig. 19C).

#### Characters variable among Uranoscopidae

**TS 23.** *Process on posteroventral margin of maxillary shaft.* 0: absent; 1: present.

*Ingroup.* A process is present on the posteroventral margin of the maxillary shaft is present in *Kathetostoma canaster*, *K. laeve* and *K. nigrofasciatum* (character 23-1), while this process is absent in other uranoscopids (character 23-0).

*Outgroup.* Most percoids lack a process on the posteroventral margin of the maxillary shaft (character 23-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 24.** *Ventral flange of dentary.* 0: absent; 1: present.

*Ingroup.* A ventral flange on the dentary is absent in all uranoscopids (character 24-0), except for *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis*, which have one (character 24-1).

*Outgroup.* In most percoids, a flange ventrally on the dentary is absent (character 24-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 25.** *Coronomeckelian.* 0: confined within dorsal surface of Meckelian cartilage; 1: expanded ventrally, almost attached to ventral edge of Meckelian cartilage.

*Ingroup.* The coronomeckelian is confined within the dorsal surface of Meckelian cartilage in all uranoscopids (character 25-0), except for *Astroscopus* spp. and *Uranoscopus bicinctus*, in which the bone is expanded ventrally, and almost attaches to the ventral edge of the Meckelian cartilage (character 25-1).

*Outgroup.* The coronomeckelian is confined within the dorsal surface of the Meckelian cartilage in percoids (charac-

ter 25-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

#### Characters synapomorphic for Uranoscopidae

None.

#### Autapomorphies for terminal taxa

None.

#### Other observed variations

None.

#### 1-4. Hyoid arch (Figs. 20-23)

**Description.** The hyoid arch is situated on the lateral side of the head and includes the hypohyals, ceratohyal, epihyal, interhyal, branchiostegal rays, basihyal and urohyal.

The hypohyals are large, broad bones situated on the anteriormost part of the hyoid arch. They comprise two bones, the dorsal and ventral hypohyals. The dorsal hypohyal is connected with the ventral hypohyal ventrally and the ceratohyal posteriorly. It is also firmly attached to the lateral surface of a bony complex formed by the first basibranchial and urohyal. The ventral hypohyal is connected to the dorsal hypohyal dorsally and the ceratohyal posteriorly, and is bonded by a strong ligament to the urohyal mesially.

The ceratohyal is a large, flattened bone, with deep anterior and posterior portions, and a narrow middle. It is connected to the hypohyals anteriorly and the epihyal posteriorly, and ventrally suspends all branchiostegal rays, except the posteriormost. A beryciform foramen is present in *Kathetostoma* spp. and *Ichthyoscopus lebeck* (Fig. 20E, G-H), but is absent in other uranoscopids (Fig. 20A-D, F). A bridge above the foramen is ossified in *Kathetostoma giganteum*, *K. laeve*, *K. canaster*, *K. cubana*, *K. albigutta* and *K. averruncus*, but is cartilaginous in *K. nigrofasciatum* and *I. lebeck*.

The epihyal is a flattened, triangular bone connected to the ceratohyal anteriorly. It has a cavity for articulating with the ventral end of the interhyal posteriorly and suspends the posteriormost branchiostegal ray anteroventrally.

The interhyal is a rod-like bone with cartilaginous caps on both ends. It articulates with the posterior portion of the epihyal ventrally and is tightly attached to a cartilaginous socket surrounded by the hyomandibula, preopercle and symplectic dorsally.

The dorsal tips of the branchiostegal rays are attached to the ceratohyal and epihyal. These rays are rod-like in uranoscopids (Fig. 20A-D, G), except for *Astroscopus* spp., *Ichthyoscopus* spp., *Kathetostoma canaster*, *K. giganteum*, *K. laeve* and *K. nigrofasciatum*, which have the posteriormost leaf-like (Fig. 20E-F, H). All uranoscopids have six branchiostegal rays (Fig. 20B-H), except for *Uranoscopus tosae* and *K. cubana* which have seven (Fig. 20A).

The unpaired urohyal is short, nodular, and lacks the poste-

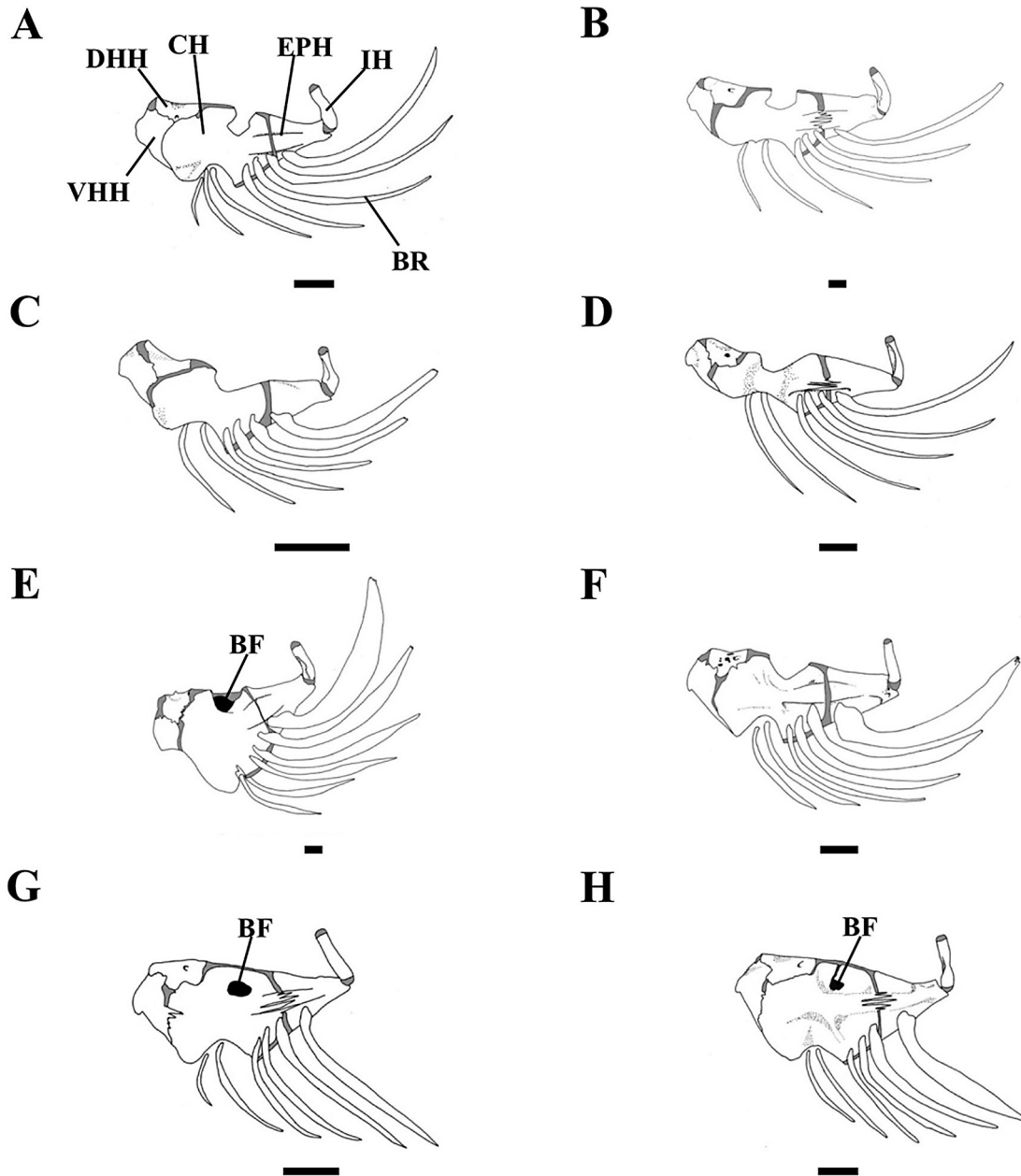


Fig. 20. Lateral view of left hyoid arch. A, *Uranoscopus tosaе*; B, *Pleuroscopus pseudodorsalis*; C, *Genyagnus monopterygius*; D, *Xenocephalus egregius*; E, *Ichthyscopus lebeck*; F, *Astroscopus y-graecum*; G, *Kathetostoma albigutta*; H, *K. nigrofasciatum*. BF, beryciform foramen; BR, branchiostegal ray; CH, ceratohyal; DHH, dorsal hypohyal; EPH, epihyal; IH, interhyal; VHH, ventral hypohyal. Bars indicate 5 mm.

rior projection. It is firmly sutured with the first basibranchial dorsally and attached with the second basibranchial dorsally in *Ichthyscopus* spp., *Xenocephalus* spp. and *Genyagnus monopterygius* (Fig. 23B), but separated from the second basibranchial in other uranoscopids (Fig. 23A).

The basihyal, also unpaired, is plate-like and articulates with the first basibranchial posteriorly. It is rod-like in *Xenocephalus* spp., but fan-like in other uranoscopids. A single narrow cartilage is present at the anterior edge of the basihyal in all uranoscopids (Fig. 22A-D, F-G), except *Genyagnus monopterygius* and *Ichthyscopus barbatus*, which

have two cartilaginous caps (Fig. 22E). Three free cartilages are situated anterior to the basihyal in *Astroscopus guttatus* (Fig. 22G), but are missing in other uranoscopids (Fig. 22A-F).

**Characters variable among Uranoscopidae**

**TS 26.** *Beryciform foramen of ceratohyal.* 0: present, bridge above it ossified; 1: present, bridge above it cartilaginous; 2: absent (unordered).

*Ingroup.* A beryciform foramen is present in *Kathetostoma* spp. and *Ichthyscopus lebeck*. A bridge above the

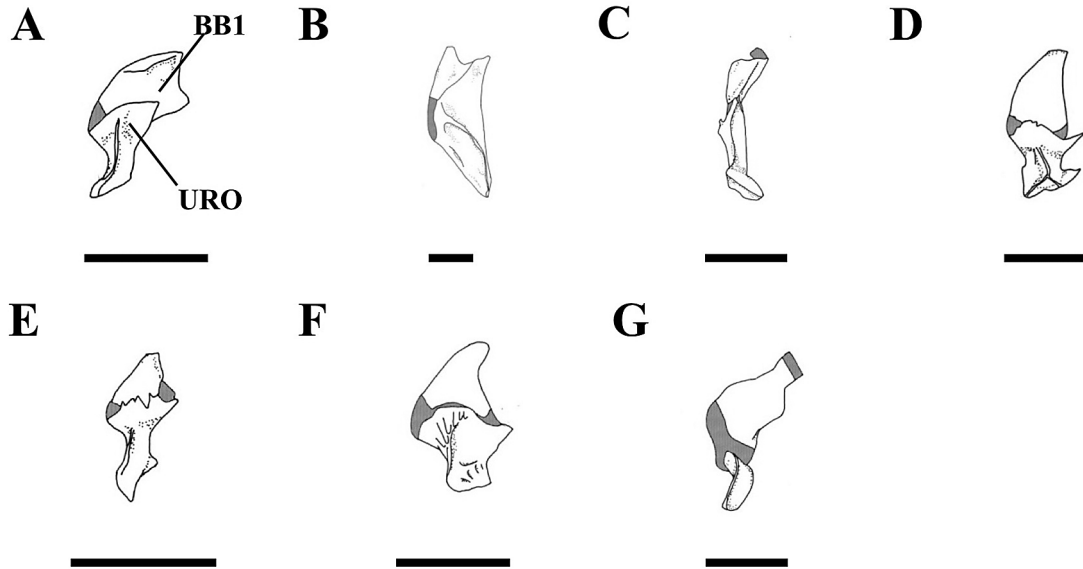


Fig. 21. Left lateral view of first basibranchial and urohyal. A, *Uranoscopus cognatus*; B, *Ichthyscopus lebeck*; C, *Kathetostoma giganteum*; D, *Pleuroscopus pseudodorsalis*; E, *Genyagnus monopterygius*; F, *Xenocephalus elongatus*; G, *Astroscopus y-graecum*. BB1, first basibranchial; URO, urohyal. Bars indicate 5 mm.

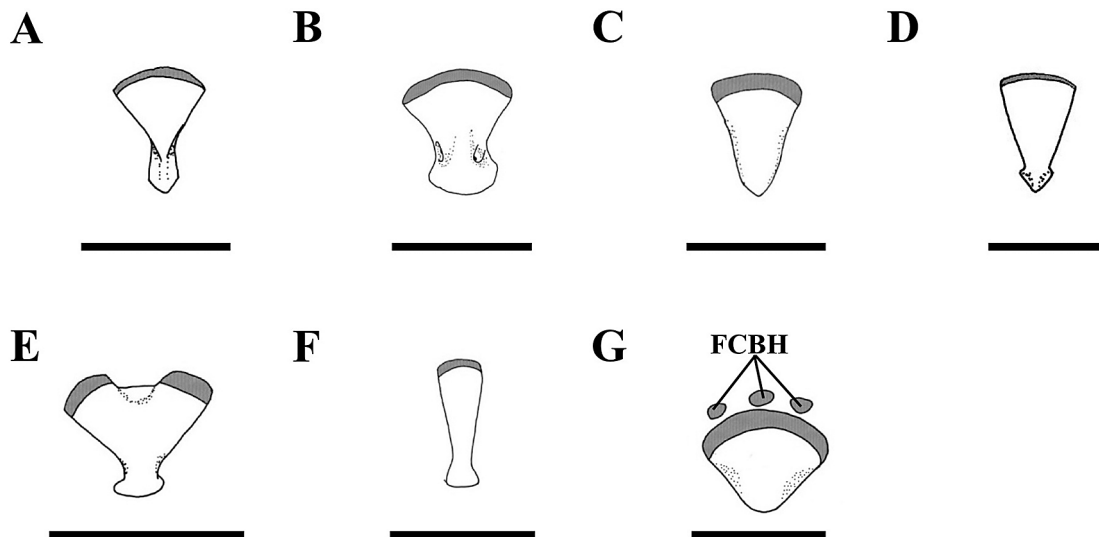


Fig. 22. Dorsal view of basihyal (anterior end at top). A, *Uranoscopus cognatus*; B, *Ichthyscopus lebeck*; C, *Kathetostoma giganteum*; D, *Pleuroscopus pseudodorsalis*; E, *Genyagnus monopterygius*; F, *Xenocephalus elongatus*; G, *Astroscopus guttatus*. FCBH, free cartilages of basihyal. Bars indicate 5 mm.

foramen is ossified in *K. giganteum*, *K. laeve*, *K. canaster*, *K. cubana*, *K. albigutta* and *K. averruncus* (character 26-0), but cartilaginous in *K. nigrofasciatum* and *Ichthyscopus lebeck* (character 26-1). The foramen is absent in other uranoscopids (character 26-2).

*Outgroup.* In percoids, a berciform foramen is usually present and the bridge above it ossified (character 26-0) (Tominaga, 1968; Shinohara, 1994; this study).

**TS 27.** *Posteriormost branchiostegal ray.* 0: leaf-like; 1: rod-like.

*Ingroup.* The posteriormost branchiostegal ray is leaf-like in *Astroscopus* spp., *Ichthyscopus* spp., *Kathetostoma*

*canaster*, *K. giganteum*, *K. laeve* and *K. nigrofasciatum* (character 27-0), but is rod-like in other uranoscopids (character 27-1).

*Outgroup.* The posteriormost branchiostegal ray is leaf-like in most percoids (character 27-0) (Tominaga, 1968; Sasaki, 1989; this study).

**TS 28.** *Number of branchiostegal rays.* 0: seven; 1: six.

*Ingroup.* *Uranoscopus tosae* and *Kathetostoma cubana* have seven branchiostegal rays (character 28-0), while other uranoscopids have six (character 28-1).

*Outgroup.* The number of branchiostegal rays in most percoids is seven (character 28-0) (Fraser, 1968; Tominaga,



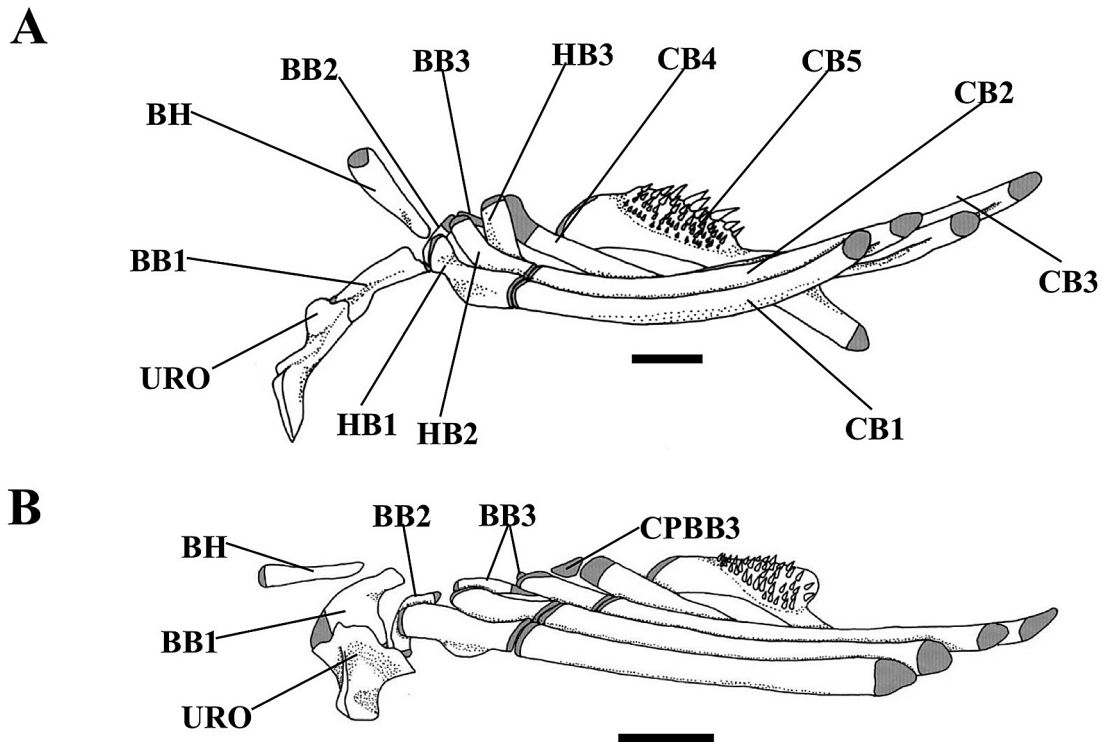


Fig. 23. Left lateral view of urohyal and branchial elements. A, *Kathetostoma nigrofasciatum*; B, *Xenocephalus australiensis*. BB1-3, first to third basibranchials; BH, basihyal; CB1-5, first to fifth ceratobranchials; CPBB3, cartilage situated posterior to third basibranchials; HB1-3, first to third hypobranchials; URO, urohyal. Bars indicate 5 mm.

1968; Sasaki, 1989; this study).

**TS 29. Urohyal and second basibranchial.** 0: separated; 1: attached.

*Ingroup.* The urohyal is attached to the second basibranchial in *Ichthyoscopus* spp., *Xenocephalus* spp. and *Genyagnus monopterygius* (character 29-1), but separated from each other in other uranoscopids (character 29-0).

*Outgroup.* The urohyal is typically separated from the second basibranchial in percoids (character 29-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 30. Anterior edge of basihyal.** 0: single narrow cartilage present; 1: two cartilaginous caps present.

*Ingroup.* A single narrow cartilage is present at the anterior margin of the basihyal in all uranoscopids (character 30-0), except *Genyagnus monopterygius* and *Ichthyoscopus barbatus*, which have two cartilages at the margin (character 30-1).

*Outgroup.* A single narrow cartilage is present on the anterior margin of the basihyal in most percoids (character 30-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

#### Characters synapomorphic for the Uranoscopidae

*Urohyal sutured with first basibranchial.* The urohyal is sutured with the first basibranchial in all uranoscopids examined, while it is usually attached to the ventral surface of the

first basibranchial via connective tissue in percoids (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

*Posterior projection of urohyal absent.* A posterior projection of the urohyal is absent in uranoscopids, but generally present and well developed in typical percoids (Fraser 1968; Tominaga 1968; Sasaki 1989; this study).

#### Autapomorphies for terminal taxa

*Presence of three free cartilages anterior to basihyal.* Three free cartilages are situated anterior to the basihyal in *Astroscopus guttatus*. The character is considered to be autapomorphic for this species, as other uranoscopids and percoids lack them (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

#### Other observed variations

None.

#### 1-5. Suspensorium and opercular bones (Figs. 24-26)

**Description.** The suspensorium is located on the lateral side of the head and articulates with the lower jaw anteriorly and cranium dorsally. It consists of the hyomandibula, metapterygoid, quadrate, symplectic, endopterygoid, ectopterygoid and palatine. The operculum comprises the preopercle, opercle, interopercle and subopercle.

The hyomandibula is a large bone situated dorsally in the

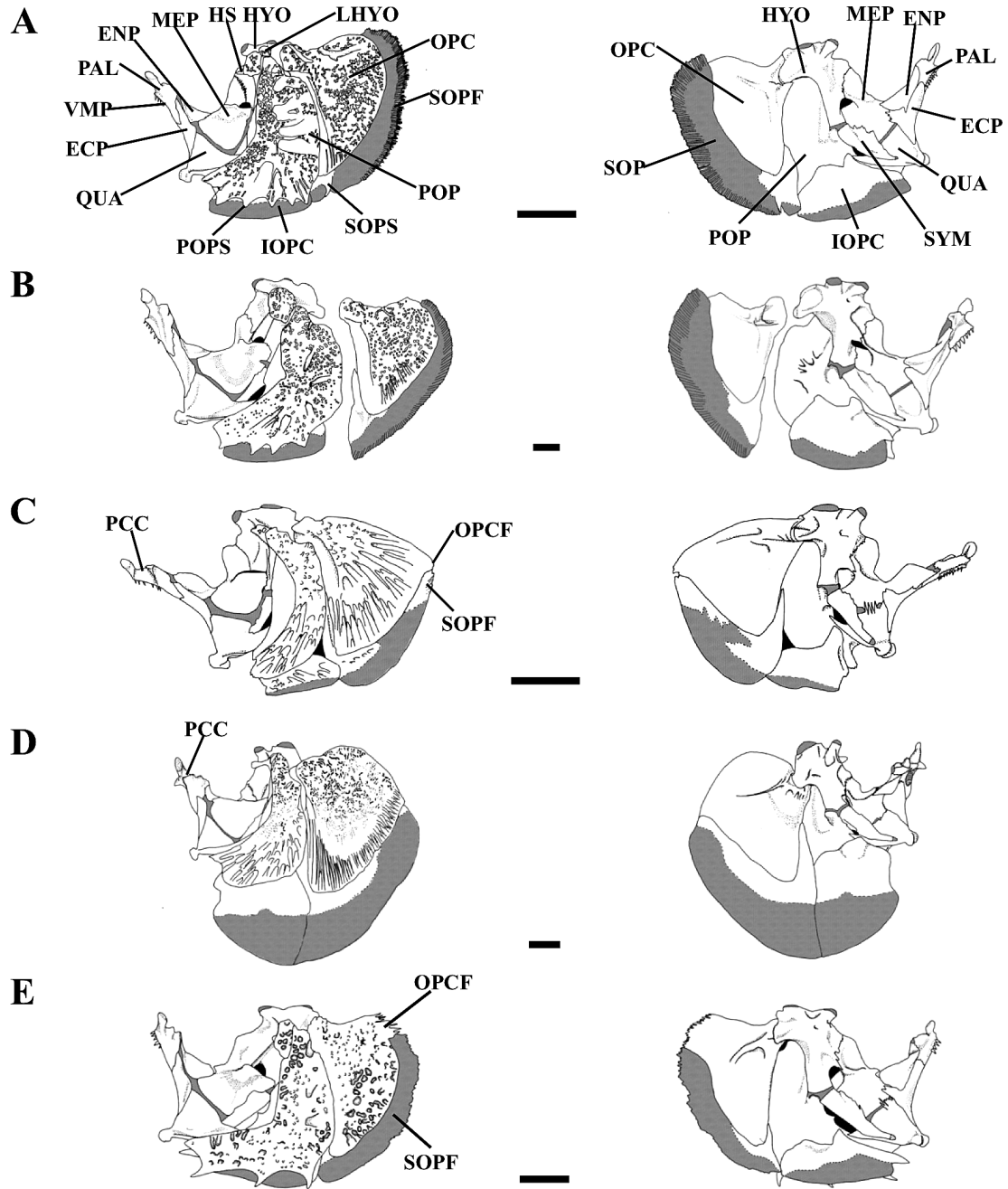


Fig. 24. Lateral (left) and mesial (right) views of suspensorium and opercular bones of left side. A, *Uranoscopus tosaе*; B, *Selenoscopus turbisquamatus*; C, *Genyagnus monopterygius*; D, *Ichthyscopus lebeck*; E, *Kathetostoma cubana*. ECP, ectopterygioid; ENP, endopterygioid; HS, hyomandibular spur; HYO, hyomandibula; IOPC, interopercle; LHYO, lateral process of hyomandibula; MEP, metapterygioid; OPC, opercle; OPCF, opercular fringe; PAL, palatine; PCC, palatine concavity; POP, preopercle; POPS, preopercular spines; QUA, quadrate; SOP, subopercle; SOPF, subopercular fringe; SOPS, subopercular spine; SYM, symplectic; VMP, ventral margin of palatine. Bars indicate 5 mm.

suspensorium. It possesses three condyles, two articulating with the lateral portion of the cranium dorsally and one with the opercle posteriorly. The hyomandibula is sutured with the metapterygioid anteriorly and connects with the preopercle posteriorly. A lateral process, located anterior to the anterodorsal edge of the preopercle, is the attachment site for the adductor mandibulae section 1. It is well developed and

extends anteriorly. The dorsal portion of the lateral process is exposed and sculptured in all uranoscopids (Figs. 24A-C, E, 25A, C-E), except for *Ichthyscopus lebeck* and *Pleuroscopus pseudodorsalis*, which have this portion embedded under skin and smooth (Figs. 24D, 25B). The hyomandibular spur, projecting from the dorsal side of the lateral process, is present in all uranoscopids.

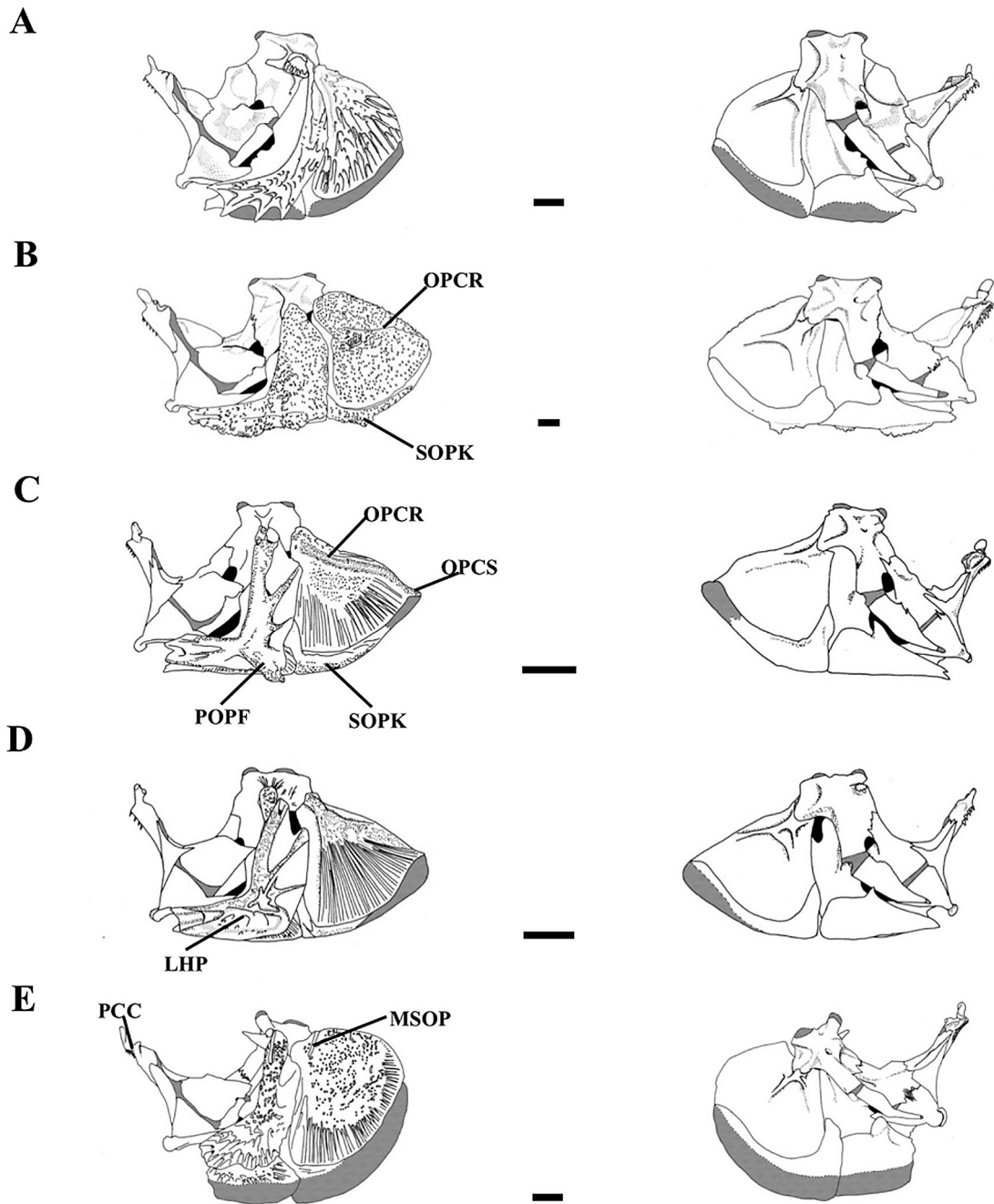


Fig. 25. Lateral (left) and mesial (right) views of suspensorium and opercular bones of left side. A, *Kathetostoma levae*; B, *Pleuroscopus pseudodorsalis*; C, *Xenocephalus egregius*; D, *X. elongatus*; E, *Astroscopus y-graecum*. LHP, lateral surface of horizontal limb of preopercle; sensory canal on lateral surface of opercle: MSOP, mid-dorsal canal; OPCR, opercular ridge; OPCS, opercular spine; PCC, palatine concavity; POPF, preopercular flange; SOPK, subopercular knob. Bars indicate 5 mm.

The metapterygoid is a large rectangular bone, situated in the middle of the suspensorium. It is sutured with the hyomandibula posterodorsally, and is connected to the quadrate ventrally, the endopterygoid and ectopterygoid anteriorly, and the symplectic posteroventrally. The metapterygoid lamina provides the attachment site for the levator arcus palatine dorsomesially, and is well developed.

The quadrate is a triangular bone with a condyle for articu-

lation with the anguloarticular anteriorly. It is connected to the ectopterygoid anteriorly, the endopterygoid anterodorsally, the preopercle posteroventrally, the metapterygoid dorsally, and the symplectic dorsomesially.

The symplectic is a long rod-like bone attached to the quadrate anterolaterally, the preopercle posterolaterally, and the metapterygoid anteriorly. The junction between the symplectic and hyomandibula is occupied by a large cartilage

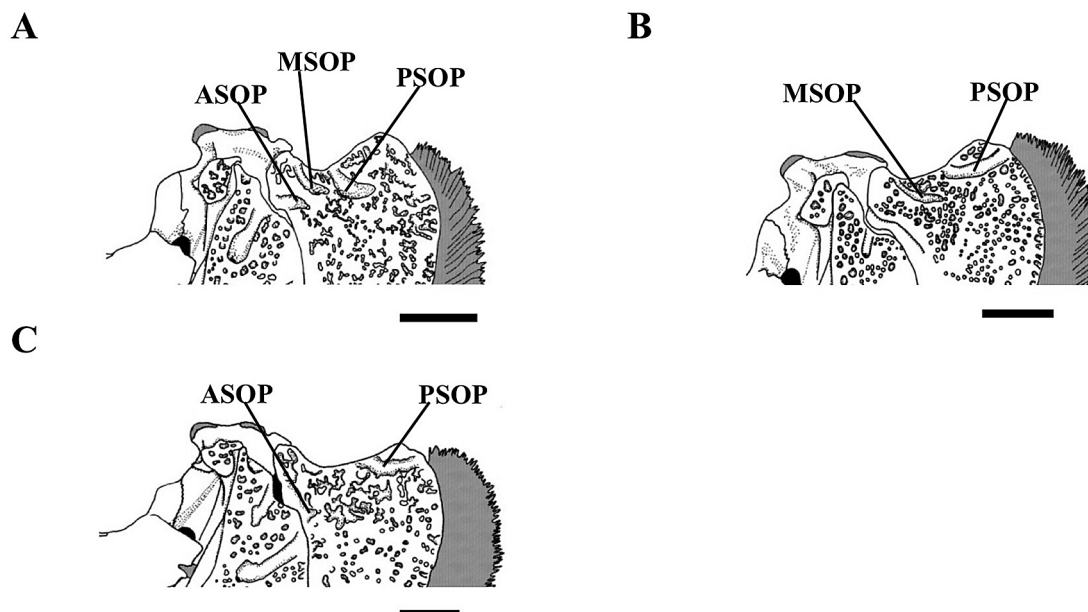


Fig.26. Lateral view of posterodorsal portion of suspensorium and opercular bones of left side. A, *Uranoscopus albesca*; B, *U. bicinctus*; C, *U. scaber*. Sensory canals on lateral surface of opercle: ASOP, anterodorsal canal; MSOP, mid-dorsal canal; PSOP, posterodorsal canal. Bars indicate 5 mm.

with a socket posteromesially for articulation with the interhyal. The ventral tip of this bone is covered with a small cartilaginous cap.

The endopterygoid is a thin, laminar bone. It is connected to the palatine anteriorly, the ectopterygoid ventrally, the metapterygoid posteriorly, and the quadrate posteroventrally. The endopterygoid is large in all uranoscopids (Figs. 24, 25A-B, E), except for *Xenocephalus* spp., that have a small endopterygoid (Fig. 25C-D).

The ectopterygoid is a boomerang-shaped bone connected with the palatine anterodorsally, the endopterygoid dorsomesially, and the quadrate posteriorly. It has a posterolateral process extending and connecting to the anterolateral surface of the metapterygoid in *Xenocephalus* spp. (Fig. 25C-D), that is missing in other uranoscopids (Figs. 24, 25A-B, E).

The palatine is a stout, stick-like bone connected to the endopterygoid posteriorly and the ectopterygoid posteroventrally. It has a band of conical teeth ventrally in all uranoscopids (Figs. 24A-C, E, 25), except for *Ichthyoscopus* spp., which have a broad band of villiform teeth (Fig. 24D). The anterior process of the palatine is directed dorsolaterally and attaches to the first infraorbital. It also has two facets dorsally for articulation with the lateral ethmoid. The dorsolateral surface of the palatine attaches to the first infraorbital. The ventral margin of palatine is almost straight in *Xenocephalus* spp., *Kathetostoma* spp. and *Pleuroscopus pseudodorsalis* (Figs. 24E, 25A-D), but is concave in the remaining uranoscopids (Figs. 24A-D, 25E). The base of the anterior process is grooved laterally, forming a concavity that is contiguous with nasal and oral cavities in *Astroscopus* spp., *Ichthyoscopus* spp. and *Genyganus monopterygius*

(Figs. 24C-D, 25E); other uranoscopids lack this concavity (Figs. 24A-B, E, 25A-D).

The preopercle is a large, crescent-shaped bone connected to the hyomandibula anterodorsally, the quadrate anterovertrally, the symplectic anteromesially, and the opercle posteriorly. It also suspends the interopercle and subopercle ventromesially. The lateral surface of the preopercle is covered with pits and tubercles and roofs the operculo-mandibular canal, which has several posterior branches. The posterior edge of the vertical limb of this bone lacks spines, but the ventral edge of the horizontal limb has large spines in species of *Kathetostoma* spp., *Uranoscopus* spp. and *Sele noscopus turbisquamatus* (Figs. 24A-B, E, 25A) that are absent in other genera (Figs. 24C-D, 25B-E). The lateral surface of horizontal limb is almost flattened in most uranoscopids (Figs. 24, 25A-C, E), but is deeply hollowed in *Xenocephalus australiensis* and *X. elongatus* (Fig. 25D). A preopercular flange extends from the lateral surface of preopercle in *X. egregius* (Fig. 25C), but is absent in other uranoscopids (Figs. 24, 25A-B, D-E).

The enlarged and posteriorly expanded opercle articulates with the hyomandibula and the preopercle anteriorly, and overlies the subopercle ventromesially. Its lateral surface is sculptured with numerous pits and tubercles and has sensory canals dorsally on the surface in *Uranoscopus* spp., *Sele noscopus turbisquamatus*, *Astroscopus guttatus*, *A. sexspinosus* and *A. y-graecum*, which do not reach the surface in other uranoscopids. A sensory canal is present on the middle part of the dorsal surface in *A. guttatus*, *A. sexspinosus* and *A. y-graecum* (Fig. 25E). Two sensory canals are apparent on the middle and posterior parts of the dorsal surface in *U.*



*bicinctus* and *U. oligolepis* (Fig. 26B), while two canals are located on the anterior and posterior parts in *U. scaber* (Fig. 26C). Three sensory canals are present on the anterior, middle and posterior parts of this area in *S. turbisquamatus* and the remaining species of *Uranoscopus* (Fig. 26A). The posterior margin of the opercle has a spine in *Xenocephalus* spp. (Fig. 25C-D), but lacks a spine in other genera (Figs. 24, 25A-B, E). A horizontal opercular ridge on the lateral surface of the opercle in *Pleuroscopus pseudodorsalis*, *X. egregius* and *X. armatus* (Fig. 25B-C) is absent in the remaining uranoscopids (Figs. 24, 25D-E). The posterodorsal margin of the opercle is fringed in *Genyagnus monopterygius*, *Kathetostoma averruncus*, *K. albigutta* and *K. cubana* (Fig. 24C, E), but smooth in the other uranoscopids (Figs. 24A-B, D, 25).

The interopercle is an elliptical bone attached to the ventromesial surface of the preopercle dorsally, overlapping the anterior margin of the subopercle posteriorly, and connected to the retroarticular anteriorly via a strong ligament. The dorsal margin of the interopercle has a prominent process that is bound to the posterolateral surface of the epihyal mesially. The ventral margin of the interopercle is thin and partly unossified in all uranoscopids (Figs. 24, 25A, E) except *Pleuroscopus pseudodorsalis* and *Xenocephalus* spp., which have a thick and completely ossified margin (Fig. 25B-D).

The subopercle is an L-shaped bone with the anterior vertical arm attached to the mesial surface of the anteroventral margin of the opercle, and the posterior arm partly covered by the opercle's lower edge. The lateral surface of the subopercle is smooth in all uranoscopid (Figs. 24, 25A, E), except for *Pleuroscopus pseudodorsalis* and *Xenocephalus* spp., which have the surface covered with numerous tubercles (Fig. 25B-D). The ventral margin of the posterior arm is fringed in *Kathetostoma albigutta*, *K. averruncus*, *K. cubana*, *Genyagnus monopterygius*, *Selenoscopus turbisquamatus*, and *Uranoscopus* spp. (Fig. 24A-C, E), but smooth in other uranoscopids (Figs. 24D, 25). A knob is present on the lateral surface of the subopercle in *P. pseudodorsalis*, *X. armatus* and *X. egregius* (Fig. 25B-C), but absent in other uranoscopids (Figs. 24, 25A, D-E). A subopercular spine is formed on the anteroventral corner of this bone in *Uranoscopus* spp. (Fig. 24A), but absent in other uranoscopids (Figs. 24B-E, 25).

#### Characters variable among Uranoscopidae

**TS 31.** *Dorsal portion of lateral process of hyomandibula.* 0: embedded under skin and smooth; 1: exposed and sculptured.

*Ingroup.* The dorsal portion of the hyomandibula's lateral process is embedded under the skin and smooth in *Ichthyoscopus lebeck* and *Pleuroscopus pseudodorsalis* (character 31-0), but exposed and sculptured in other uranoscopids (character 31-1).

*Outgroup.* The dorsal portion of the lateral process is

embedded under skin and smooth in most percoids (character 31-0) (Tominaga, 1968; Fraser, 1972; Sasaki, 1989; this study).

**TS 32.** *Endopterygoid.* 0: large; 1 small.

*Ingroup.* The endopterygoid is large in all uranoscopids (character 32-0), except *Xenocephalus* spp., in which it is small (character 32-1).

*Outgroup.* The endopterygoid is large in most percoids (character 32-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 33.** *Posterolateral process of ectopterygoid.* 0: absent; 1: present.

*Ingroup.* The posterolateral process is absent from the ectopterygoid in all uranoscopids (character 33-0), except *Xenocephalus* spp., which have a process on the bone (character 33-1).

*Outgroup.* The posterolateral process is absent from the ectopterygoid in most percoids (character 33-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 34.** *Ventral margin of palatine.* 0: almost straight; 1: concave.

*Ingroup.* The ventral margin of the palatine is almost straight in *Xenocephalus* spp., *Kathetostoma* spp. and *Pleuroscopus pseudodorsalis* (character 34-0), while the margin is concave in other uranoscopids (character 34-1).

*Outgroup.* The ventral margin of the palatine is almost straight in most percoids (character 34-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 35.** *Palatine concavity contiguous with narsal and oral cavities.* 0: absent; 1: present.

*Ingroup.* A concavity on the palatine contiguous with narsal and oral cavities is present in *Ichthyoscopus* spp., *Astroscopus* spp. and *Genyagnus monopterygius* (character 35-1), but absent in other uranoscopids (character 35-0).

*Outgroup.* The concavity is typically absent in percoids (character 35-0) (this study).

**TS 36.** *Preopercular spines.* 0: absent; 1: present.

*Ingroup.* Preopercular spines are absent in all uranoscopids (character 36-0), except *Kathetostoma* spp., *Uranoscopus* spp. and *Selenoscopus turbisquamatus*, which have strong preopercular spines (character 36-1).

*Outgroup.* Preopercular spines are typically absent in percoids (character 36-0) (Otero, 2004; this study).

**TS 37.** *lateral surface of horizontal limb of preopercle.* 0: almost flat; 1: deeply hollow.

*Ingroup.* The lateral surface of the horizontal limb of the preopercle is almost flat in most uranoscopids (character 37-0), but deeply hollow in *Xenocephalus australiensis* and *X. elongatus* (character 37-1).

*Outgroup.* The lateral surface of the horizontal limb of the preopercle is typically almost flat in percoids (character 37-0) (this study).

**TS 38.** *Sensory canal anterodorsally on lateral surface of*

*opercle*. 0: absent; 1: present.

*Ingroup*. A sensory canal is present anterodorsally on the lateral surface of the opercle in *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. archionema*, *U. cognatus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. polli*, *U. scaber* and *U. tosae* (character 38-1), but absent in other uranoscopids (character 38-0).

*Outgroup*. This sensory canal is absent from the anterodorsal part of the lateral surface of the opercle in examined percoids (character 38-0) (this study).

**TS 39.** *Sensory canal mid-dorsally on lateral surface of opercle*. 0: absent; 1: present.

*Ingroup*. A sensory canal is present mid-dorsally on the lateral surface of the opercle in *Selenoscopus turbisquamatus*, *Astroscopeus guttatus*, *A. sexspinus*, *A. y-graecum*, *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. oligolepis*, *U. polli* and *U. tosae* (character 39-1), but absent in other uranoscopids (character 39-0).

*Outgroup*. A sensory canal mid-dorsally on the lateral surface of the opercle is absent in examined percoids (character 39-0) (this study).

**TS 40.** *Sensory canal posterodorsally on lateral surface of opercle*. 0: absent; 1: present.

*Ingroup*. A sensory canal is present posterodorsally on the lateral surface of the opercle in *Uranoscopus* spp. and *Selenoscopus turbisquamatus* (character 40-1), but absent in other uranoscopids (character 40-0).

*Outgroup*. A sensory canal is absent posterodorsally on the lateral surface of the opercle in examined percoids (character 40-0) (this study).

**TS 41.** *Opercular spine*. 0: absent; 1: present.

*Ingroup*. A spine is present on the posterior margin of the opercle in *Xenocephalus* spp. (character 41-1), but absent in the other uranoscopids (character 41-0).

*Outgroup*. A spine is typically absent from the posterior margin of the opercle in percoids (character 41-0) (Fraser, 1968; this study).

**TS 42.** *Opercular ridge*. 0: absent; 1: present.

*Ingroup*. A ridge is present on the lateral surface of the opercle in *Pleuroscopus pseudodorsalis*, *Xenocephalus egregius* and *X. armatus* (character 42-1), but absent in other uranoscopids (character 42-0).

*Outgroup*. A ridge is typically absent from the lateral surface of the opercle in percoids (character 42-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 43.** *Posterodorsal margin of opercle*. 0: smooth; 1: fringed.

*Ingroup*. The posterodorsal margin of the opercle is fringed in *Genyagnus monopterygius*, *Kathetostoma averrun-cus*, *K. albigutta* and *K. cubana* (character 43-1), but smooth in other uranoscopids (character 43-0).

*Outgroup*. The posterodorsal margin of the opercle is

typically smooth in percoids (character 43-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 44.** *Ventral margin of interopercle*. 0: thin and partly unossified; 1: thick and completely ossified.

*Ingroup*. The ventral margin of the interopercle is thin and partly unossified in all uranoscopids (character 44-0), except *Pleuroscopus pseudodorsalis* and *Xenocephalus* spp., which have a thick and completely ossified margin (character 44-1).

*Outgroup*. The ventral margin of the interopercle is typically thin and partly unossified in percoids (character 44-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 45.** *Lateral surface of subopercle*. 0: smooth; 1: covered with tubercles.

*Ingroup*. The lateral surface of the subopercle is smooth in all uranoscopids (character 45-0), except *Pleuroscopus pseudodorsalis* and *Xenocephalus* spp., which have the lateral surface covered with numerous tubercles (character 45-1).

*Outgroup*. The lateral surface of the subopercle is typically smooth in percoids (character 45-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 46.** *Ventral margin of posterior arm of subopercle*. 0: smooth; 1: fringed.

*Ingroup*. The ventral margin of the posterior arm of the subopercle is fringed in *Kathetostoma albigutta*, *K. averrun-cus*, *K. cubana*, *Genyagnus monopterygius*, *Selenoscopus turbisquamatus* and *Uranoscopus* spp. (character 46-1), but smooth in other uranoscopids (character 46-0).

*Outgroup*. The ventral margin of the posterior arm of the subopercle is typically smooth in percoids (character 46-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 47.** *Subopercular knob*. 0: absent; 1: present.

*Ingroup*. A knob is present on the lateral surface of the subopercle in *Pleuroscopus pseudodorsalis*, *Xenocephalus armatus* and *X. egregius* (character 47-1), but absent in other uranoscopids (character 47-0).

*Outgroup*. The lateral surface of the subopercle typically lacks a knob in percoids (character 47-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 48.** *Subopercular spine*. 0: absent; 1: present.

*Ingroup*. A spine is present on the anteroventral corner of the subopercle in *Uranoscopus* spp. (character 48-1), but absent in other uranoscopids (character 48-0).

*Outgroup*. The anteroventral corner of the subopercle typically lacks a spine in percoids (character 48-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

#### Characters synapomorphic for Uranoscopidae

*Presence of hyomandibular spur*: A hyomandibular spur is present in uranoscopids (Pietsch, 1989; this study), but typically absent in percoids (Yabe, 1985; Imamura and Matsuura, 2003; this study).

*Opercle enlarged and expanded posteriorly*: The opercle

is enlarged and expanded posteriorly in uranoscopids (Pietsch, 1989; this study), but typically small and not expanded in percoids (this study).

#### Autapomorphies for terminal taxa

*Presence of preopercular flange.* A preopercular flange is present in *Xenocephalus egregius*, but absent in other uranoscopids and typically in percoids (this study). Consequently, this character is considered an autapomorphy of *X. egregius*, and not included in the phylogenetic analysis.

#### Other observed variations

*Villiform tooth band of palatine.* The palatine has a ventral band of villiform teeth in *Ichthyoscopus* spp., but a band of conical teeth in other uranoscopids. As villiform and conical teeth are present ventrally on the palatine in percoids examined for this study, these characters cannot be polarized and have been excluded from the phylogenetic analysis.

### 1–6. Branchial complex (Figs. 27–28)

**Description.** The branchial complex, a series of bilaterally paired bony arches on either side of the pharynx supporting the gill filaments and rakers, is each composed of five elements, the epibranchial and pharyngobranchial in the upper limb, and the basibranchial, hypobranchial and ceratobranchial in the lower limb. An interarcual cartilage is absent.

The basibranchials are unpaired bones situated on the midline of the lower branchial arch comprising of three elements. The anteriormost first basibranchial, is a nodule-like bone, sutured with the urohyal ventrally, loosely attached to the basihyal anteriorly and sandwiched by the anterior end of the hyoid arches of the two sides laterally. The second basibranchial is a plate-like bone that is ossified in most uranoscopids (Fig. 27A–D, H–I), but cartilaginous in *Uranoscopus* spp., *Selenoscopus turbisquamatus* and *Ichthyoscopus barbatus* (Fig. 27E–G, J). The second basibranchial is sandwiched by the hypobranchials of the first arch on the two sides anterolaterally, and is connected to the hypobranchials of the second arch posteriorly. It articulates with the first basibranchial anteriorly and the third basibranchial posteriorly. It also articulates with the urohyal anteroventrally in *Genyagnus monopterygius*, *Ichthyoscopus* spp. and *Xenocephalus* spp. The third basibranchial is situated between the hypobranchials of second and third arches. This bone is composed of a single cartilaginous element in *Kathetostoma canaster*, *K. laeve*, *K. nigrofasciatum*, *S. turbisquamatus*, *U. oligolepis* and *U. polli* (Fig. 27D, G), one ossified anterior element and one cartilaginous posterior element in *Astroscopus sexspinosus* and *X. australiensis* (Fig. 27B), one cartilaginous anterior element and one ossified posterior element in *I. barbatus* (Fig. 27J), two cartilaginous elements in *U. albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. japonicus*, *U. scaber* and *U. tosae* (Fig. 27E–F), and a single

rod-like ossified element in the remaining uranoscopids examined (Fig. 27A, C, H–I).

The hypobranchials, situated between the basibranchials and ceratobranchials, are three bilaterally paired bones which gradually become smaller from the first to third arches. The first hypobranchial (the hypobranchial of the first arch), a slightly flattened, rod-like bone, articulates with the first and second basibranchials proximally, and the first ceratobranchial (the ceratobranchial of the first arch) distally. The second hypobranchial is rod-like, and connected to the second and third basibranchials proximally, and the second ceratobranchial distally. The third hypobranchial is a fork-like bone. The bones of the two sides meet proximally and articulate with the third ceratobranchial distally. The distal and proximal cartilaginous caps of the third hypobranchial are present in all uranoscopids (Fig. 27B–I), except for *Ichthyoscopus* spp. and *Pleuroscopus pseudodorsalis*, in which the posterior margin of this bone is cartilaginous including the proximal and distal tips (CPHB3) (Fig. 27A, J).

The ceratobranchials consists of five bilaterally bones. The first to third ceratobranchials are rod-like and articulate with the hypobranchials proximally and the epibranchials distally. The fourth ceratobranchial is a long and rod-like bone that articulates with the fourth epibranchial posteriorly. The fourth ceratobranchials of the two sides are attached proximally to a small cartilage situated posterior to the third basibranchial in all uranoscopids, except for *Astroscopus guttatus*, *Uranoscopus cognatus*, *Kathetostoma laeve*, *K. canaster* and *K. nigrofasciatum*. The fourth ceratobranchial of the left side is fused with the cartilage in *Astroscopus guttatus* and *U. cognatus* specimens examined (Fig. 27C), while the bones on both sides are fused with the cartilage in specimens of *K. laeve*, *K. canaster* and *K. nigrofasciatum* (Fig. 27D). The fifth ceratobranchial is a triangular, tooth bearing bone. That is bonded directly to the bone of the opposite side proximally by connective tissue in all uranoscopids, except for *U. bicinctus*, which has a small cartilage between them (Fig. 27F).

The epibranchials are four short, rod-like bones. The first epibranchial articulates with the first pharyngobranchial proximally, when it is present, and the first ceratobranchial distally. It has a broad, flat process on the posterodorsal surface and a rod-like process directed mesially. The second epibranchial articulates with the anterolateral region of the second and third pharyngobranchials proximally and the second ceratobranchial distally. The second epibranchial lacks a tooth plate in all uranoscopids (Fig. 28A, C–I), except *Astroscopus sexspinosus*, which has a tooth plate fused with the middle portion of the bone ventrally (Fig. 28B). The third epibranchial has a sail-like crest, which is bound to the fourth epibranchial by a ligament, and articulates with the lateral region of the third pharyngobranchial proximally and the third ceratobranchial distally. A tooth plate is absent on the third epibranchial. The fourth epibranchial articulates with the

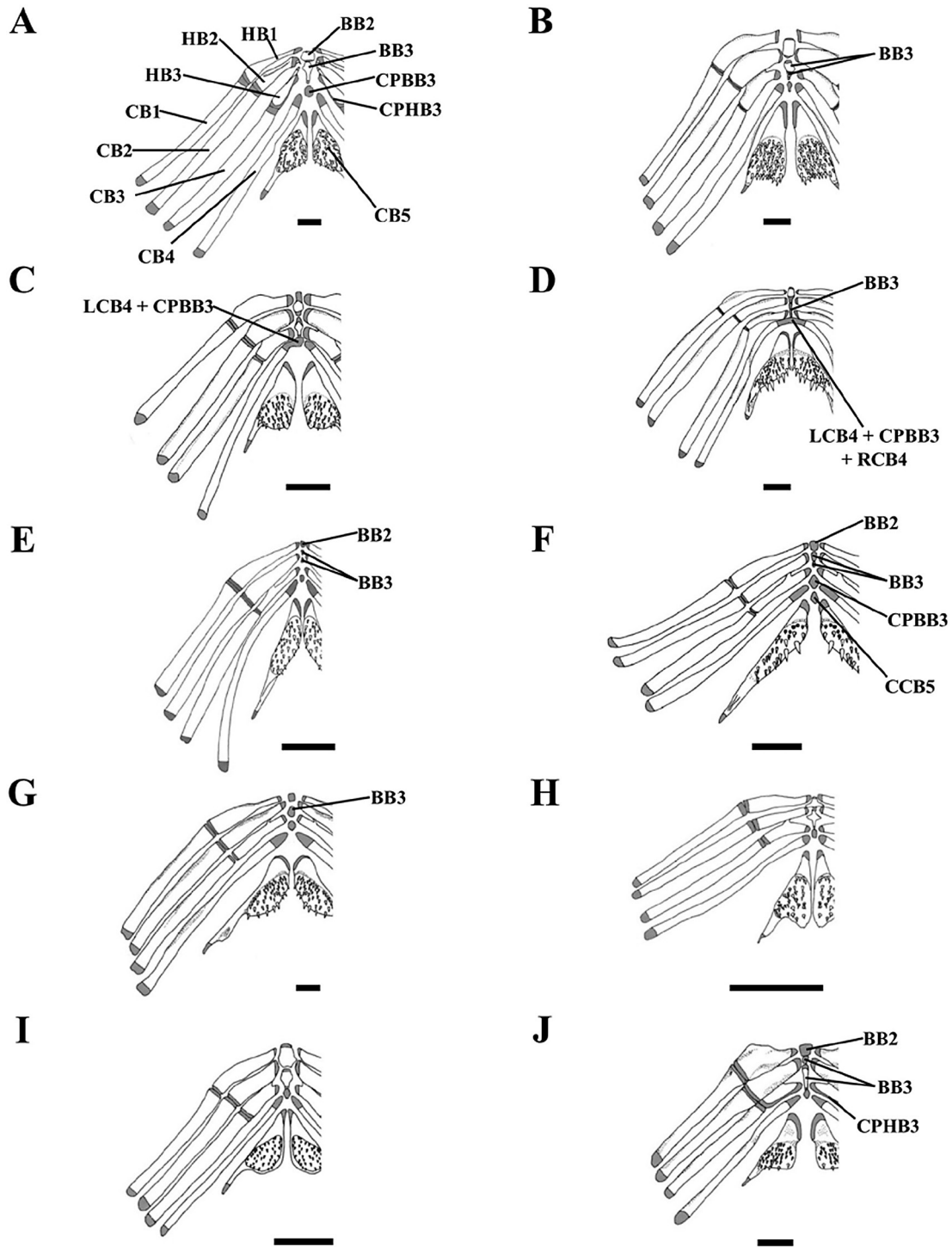


Fig. 27. Dorsal view of lower branchial arches after removal of first basibranchial and urohyal. A, *Pleuroscopus pseudodorsalis*; B, *Astroscopus sexspinosus*; C, *A. guttatus*; D, *Kathetostoma nigrofasciatum*; E, *Uranoscopus tosa*; F, *U. bicinctus*; G, *Selenoscopus turbisquamatus*; H, *Genyagnus monopterygius*; I, *Xenocephalus egregius*; J, *Ichthyoscopus barbatus*. BB2-3, second and third basibranchials; CB1-5, first to fifth ceratobranchials; CCB5, cartilage situated between proximal tips of fifth ceratobranchials; CPBB3, cartilage situated posterior to third basibranchial; CPHB3, cartilaginous portion on posterior margin of third hypobranchial; HB1-3, first to third hypobranchials; LCB4 + CPBB3, fusion of fourth ceratobranchial on left side and cartilage situated posterior to third basibranchial; LCB4 + CPBB3 + RCB4, fusion of fourth ceratobranchials on both sides and cartilage situated posterior to third basibranchial. Bars indicate 5 mm.



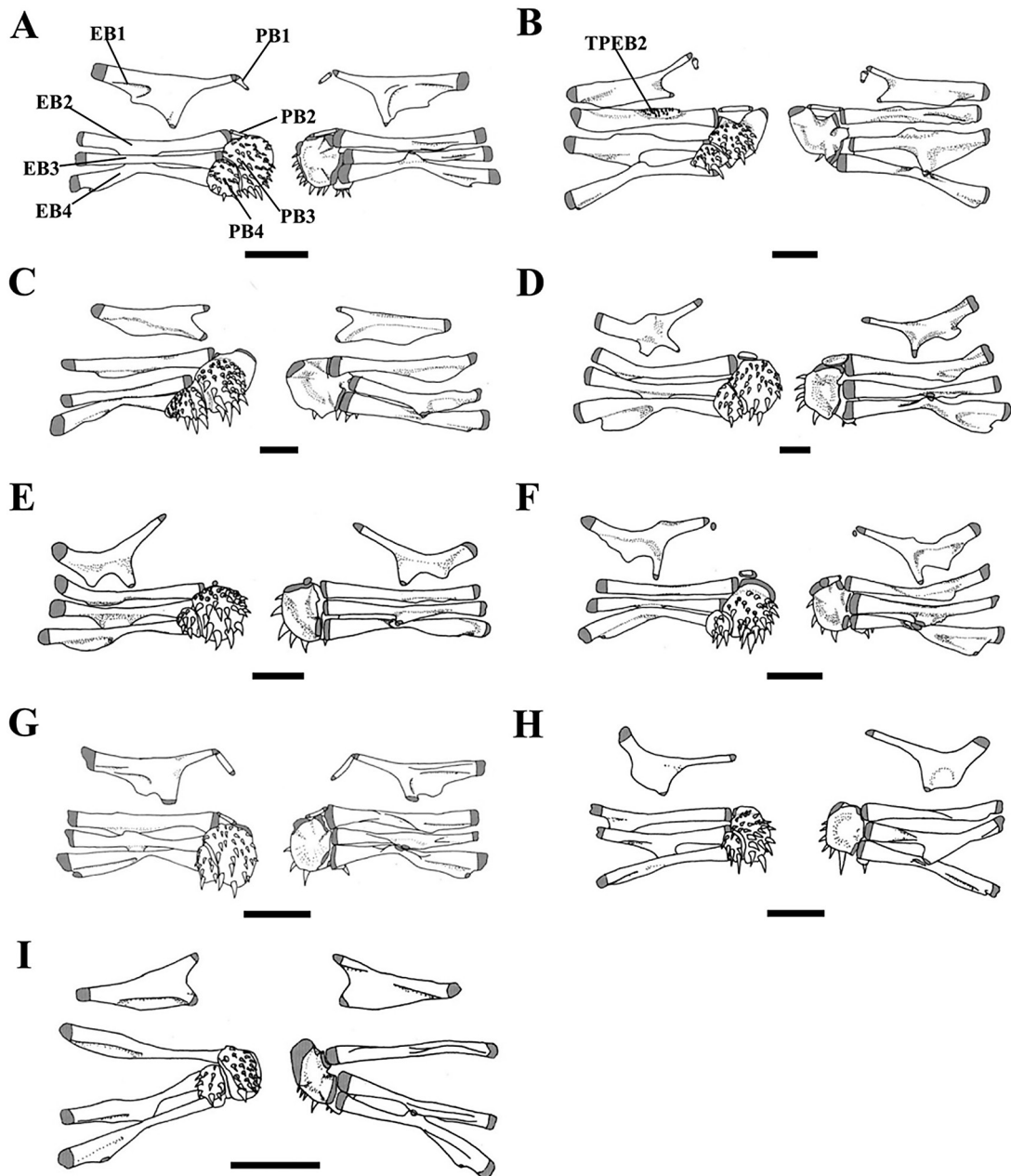


Fig. 28. Ventral (left) and dorsal (right) views of upper branchial arch of right side. A, *Pleuroscopus pseudodorsalis*; B, *Astroscopus sexspinosus*; C, *Ichthyoscopus sannio*; D, *Selenoscopus turbisquamatus*; E, *Uranoscopus japonicus*; F, *U. crassiceps*; G, *Xenocephalus egregius*; H, *Kathetostoma albigutta*; I, *Genyagnus monopterygius*. EB1-4, first to fourth epibranchials; PB1-4, first to fourth pharyngobranchials; TPEB2, tooth plate on second epibranchial. Bars indicate 5 mm.

posterior cartilage of the third pharyngobranchial and the anteromedial portion of the fourth pharyngobranchial proximally, and the fourth ceratobranchial distally.

The pharyngobranchials consist of two bones with teeth and two without. The first pharyngobranchial is tiny and toothless, and is connected with the rod-like process of the first epibranchial posteroventrally. It is ossified in *Xenocephalus* spp., *Pleuroscopus pseudodorsalis*, *Astroscopus sexspinosus*, *Uranoscopus cognatus*, *U. polli* and *U. tosae* (Fig. 28A-B, G), cartilaginous in *U. albesca* and *U. crassi-*

*ceps* (Fig. 28F), and absent in the remaining uranoscopids examined. The second pharyngobranchial, when present, is situated anterior to the third pharyngobranchial. It is present but lacks tooth plate in *P. pseudodorsalis*, *Xenocephalus* spp., *A. sexspinosus*, *A. zephyreus*, *Selenoscopus turbisquamatus*, *U. albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. oligolepis*, *U. polli*, *U. tosae* and *U. japonicus*. The second pharyngobranchial is ossified, small and rod-like, and connected to the second epibranchial distally and the third pharyngobranchial proximally in *P. pseudodorsalis*, *Xeno-*

*cephalus* spp., *A. sexspinosus* and *A. zephyreus* (Fig. 28A–B, G), ossified, small and plate-like, and connected to the second epibranchial distally and the third pharyngobranchial proximally in *S. turbisquamatus*, *U. albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. oligolepis*, *U. polli* and *U. tosae* (Fig. 28D, F), small, cartilaginous, and situated anterior to the anterior border of the third pharyngobranchial in *U. japonicus* (Fig. 28E), and absent in the remaining uranoscopids (Fig. 28C, H–I). The third pharyngobranchial is the largest tooth bearing bone, and articulates with the second and third epibranchials laterally. The fourth pharyngobranchial is the posteriormost toothed bone, and is attached to the fourth epibranchial laterally and the third pharyngobranchial anteriorly.

### Characters variable among Uranoscopidae

**TS 49.** *Second basibranchial.* 0: ossified; 1: cartilaginous.

*Ingroup.* The second basibranchial is ossified in most uranoscopids (character 49-0), while it is cartilaginous in *Uranoscopus* spp., *Selenoscopus turbisquamatus* and *Ichthyoscopus barbatus* (character 49-1).

*Outgroup.* The second basibranchial is typically ossified in percoids (character 49-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 50.** *Composition of third basibranchial.* 0: single rod-like and ossified element; 1: single cartilaginous element; 2: one ossified anterior element and one cartilaginous posterior element; 3: one cartilaginous anterior element and one ossified posterior element; 4: two cartilaginous elements (unordered).

*Ingroup.* The third basibranchial is composed of a single cartilaginous element in *Kathetostoma canaster*, *K. laeve*, *K. nigrofasciatum*, *Selenoscopus turbisquamatus*, *Uranoscopus oligolepis* and *U. polli* (character 50-1), one ossified anterior element and one cartilaginous posterior element in *Astroscopus sexspinosus* and *Xenocephalus australiensis* (character 50-2), one cartilaginous anterior element and one ossified posterior element in *Ichthyoscopus barbatus* (character 50-3), two cartilaginous elements in *U. albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. japonicus*, *U. scaber* and *U. tosae* (character 50-4), and a single rod-like and ossified element in the remaining uranoscopids (character 50-0).

*Outgroup.* The third basibranchial is typically comprised of a single rod-like and ossified element in percoids (character 50-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 51.** *Cartilaginous portions of third hypobranchial.* 0: posterior margin; 1: distal and proximal caps.

*Ingroup.* The third hypobranchial has a cartilaginous posterior margin including the proximal and distal tips in *Ichthyoscopus* spp. and *Pleuroscopus pseudodorsalis* (character 51-0), whereas it has cartilaginous proximal and distal caps in

other uranoscopids (character 51-1).

*Outgroup.* This bone typically has a cartilaginous posterior margin in percoids (character 51-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 52.** *Fourth ceratobranchials and proximal small cartilage situated posterior to third basibranchial.* 0: fourth ceratobranchials on both sides attached to cartilage proximally; 1: element on left side fused with cartilage; 2: elements on both sides fused with cartilage (ordered as 0-1-2).

*Ingroup.* The fourth ceratobranchials on both sides are attached proximally to a small cartilage situated posterior to the third basibranchial in most uranoscopids (character 52-0). The element on the left side is fused with the cartilage in *Astroscopus guttatus* and *Uranoscopus cognatus* (character 52-1), and the bones on both sides are fused with the cartilage in *Kathetostoma laeve*, *K. canaster* and *K. nigrofasciatum* (character 52-2).

*Outgroup.* The fourth ceratobranchials on both sides are typically attached to a small cartilage proximally in percoids (character 52-0).

**TS 53.** *First pharyngobranchial.* 0: ossified; 1: cartilaginous; 2: absent (unordered).

*Ingroup.* The first pharyngobranchial is ossified in *Xenocephalus* spp., *Pleuroscopus pseudodorsalis*, *Astroscopus sexspinosus*, *Uranoscopus cognatus*, *U. polli* and *U. tosae* (character 53-0). This bone is cartilaginous in *U. albesca* and *U. crassiceps* (character 53-1), and is absent in the remaining uranoscopids (character 53-2).

*Outgroup.* The first pharyngobranchial is typically ossified in percoids (character 53-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study).

**TS 54.** *Tooth plate on second pharyngobranchial.* 0: present; 1: absent.

*Ingroup.* The tooth plate is absent on the second pharyngobranchial in *Pleuroscopus pseudodorsalis*, *Xenocephalus* spp., *Astroscopus sexspinosus*, *A. zephyreus*, *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. oligolepis*, *U. polli*, *U. tosae*, and *U. japonicus* (character 54-1). In the remaining uranoscopids lacking the second pharyngobranchial, their character for this transformation series is coded as “?”, because presence or absence of the tooth plate in them cannot be evaluated.

*Outgroup.* The tooth plate is typically present on the second pharyngobranchial in percoids (character 54-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989).

**TS 55.** *Second pharyngobranchial.* 0: ossified, large and plate-like; 1: ossified, small and rod-like; 2: ossified, small and plate-like; 3: small and cartilaginous; 4: absent (unordered).

*Ingroup.* The second pharyngobranchial is ossified, small and rod-like in *Pleuroscopus pseudodorsalis*, *Xenocephalus* spp., *Astroscopus sexspinosus* and *A. zephyreus* (character

55-1), ossified, small and plate-like in *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. oligolepis*, *U. polli* and *U. tosae* (character 55-2), small and cartilaginous in *U. japonicus* (character 55-3), and absent in the remaining uranoscopids (character 55-4).

*Outgroup.* The second pharyngobranchial is typically ossified and large in percoids (character 55-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989).

#### Characters synapomorphic for Uranoscopidae

*Absence of tooth plate on third epibranchial.* The third epibranchial lacks a tooth plate in uranoscopids. This plate is typically present on that bone in percoids (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; Imamura, 1996; this study).

*Absence of interarcual cartilage.* An interarcual cartilage is absent in uranoscopids. This cartilage is usually present in percoids (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; Imamura, 1996; this study).

#### Autapomorphies for terminal taxa

*Presence of tooth plate on second epibranchial.* A tooth plate is present and fused with the second epibranchial ventrally in *Astroscopus sexspinosus*. This plate is absent in other uranoscopids and percoids, although most percoids have an autogenous tooth plate at the articulation between the second pharyngobranchial and second epibranchial (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; Imamura, 1996, 2004; this study). Therefore, this character is considered an autapomorphy of *A. sexspinosus*.

*Presence of cartilage between proximal tips of fifth ceratobranchials.* A cartilage is present between the proximal tips of the fifth ceratobranchials on both sides in *Uranoscopus bicinctus*. This cartilage is absent in other uranoscopids and typically absent in percoids (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; this study). Consequently, this character is regarded as an autapomorphy of *U. bicinctus*.

#### Other observed variations

None.

#### 1-7. Pectoral and pelvic girdles (Figs. 29-32)

**Description.** The pectoral and pelvic girdles form a united structure with the pectoral girdle attached to the lateral surface of the pelvic girdle ventromesially. The anterior portion of pelvic girdle projects well in front of the ventral arm of the pectoral girdle.

The pectoral girdle is a strong, broad bony structure consisting of the extrascapulae (described previously in section treating the cranium), posttemporal, supracleithrum, cleithrum, scapula, coracoid, postcleithra and actinosts.

The posttemporal is a thick and sculptured bone with dor-

sal and ventral limbs that articulate with the cranium anteriorly. The dorsal limb, articulating with the epiotic anteriorly, is short and flattened in all uranoscopids, except *Astroscopus* spp., which has a very elongate, spine-like element. The ventral limb is rod-like and attached to the intercalar by a short ligament. The posttemporal is connected to the supracleithrum posteromesially and has a sensory canal that is continuous with those of the lateral extrascapula anteriorly and the supracleithrum posteriorly.

The supracleithrum is a plate-like, sculptured bone, that is connected with the posttemporal anterolaterally, the dorsal limb of the cleithrum ventromesially and the anteriormost lateral line scale posteromesially. A spine is present on the posterior portion of the supracleithrum in *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. oligolepis*, *U. polli*, *U. scaber* and *U. tosae* (Fig. 30E, G-H), and a second spine (SSCLD) is present on the dorsomesial portion of the bone in *Uranoscopus* spp., *Kathetostoma albigutta* and *S. turbisquamatus* (Fig. 30D-G). The dorsal surface of the second spine dorsomesially is covered by tubercles and lacks ridges in *S. turbisquamatus*, *U. albesca*, *U. archionema*, *U. filibarbis*, *U. japonicus*, *U. polli* and *U. scaber* (Fig. 30G), but lacks tubercles and has a longitudinal ridge in *K. albigutta* and the remaining species of *Uranoscopus* (Fig. 30D-F). The mesial surface of this bone is connected to the cranium by Baudelot's ligament.

The cleithrum is a long, slightly curved bone with the dorsal and ventral limbs each ending in a spine. The cleithral spine arising from the posterior portion of the dorsal limb, is long and exposed distally in all uranoscopids, except *Astroscopus* spp. and *Ichthyoscopus* spp., which have a short spine that is embedded under skin. The ventral limb is prolonged. The cleithrum is connected to the supracleithrum dorsolaterally, the scapula posterodorsally and the coracoid posteroventrally, and suspends the postcleithrum posteromesially, when present. A flange lateral to the attachment site for the protractor pectoralis extends from the cleithrum in *Uranoscopus* spp., *Kathetostoma averruncus*, *K. cubana* and *Selenoscopus turbisquamatus* (Fig. 29G-I), but is absent in other uranoscopids (Fig. 29A-F).

The postcleithra comprises two bones, a leaf-like upper element and rod-like lower element, in *Astroscopus* spp., *Ichthyoscopus* spp., *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis* (Fig. 29A-D), but only a single elongate element that attaches with the mesial surface of the cleithrum in *Kathetostoma* spp. and *Genyagnus monopterygius* (Fig. 29E-F), or a single short element that is free from the pectoral girdle in *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. crassiceps*, *U. oligolepis* and *U. polli* (Fig. 29G). The postcleithrum is absent in the remaining species of *Uranoscopus* (Fig. 29H-I).

The scapula is a rectangular bone, containing a large fora-

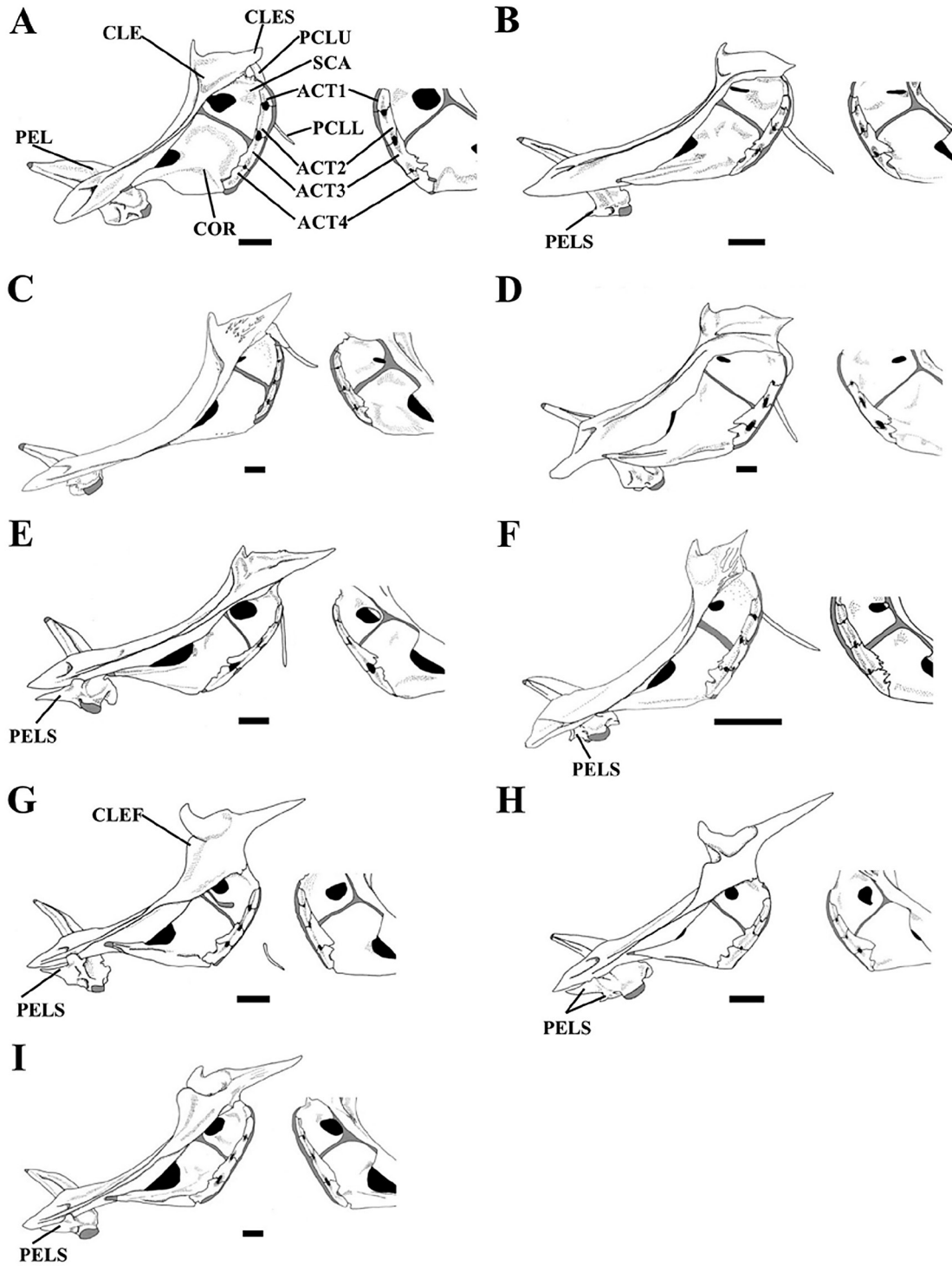


Fig. 29. Lateral view of pectoral and pelvic girdles (left) and mesial view of posteroventral portion of pectoral girdle (right) of left side. A, *Xenocephalus australiensis*; B, *Astroscopus zephyreus*; C, *Pleuroscopus pseudodorsalis*; D, *Ichthyoscopus sannio*; E, *Kathetostoma nigrofasciatum*; F, *Genyagnus monopterygius*; G, *Uranoscopus albesca*; H, *U. cognatus*; I, *Selenoscopus turbisquamatus* (postcleithra are not examined). ACT1-4, actinost one to four; CLE, cleithrum; CLEF, cleithral flange; CLES, cleithral spine; COR, coracoid; PCLL, lower element of postcleithra; PCLU, upper element of postcleithra; PEL, pelvis; PELS, pelvic spur; SCA, scapula. Bars indicate 5 mm.

men anteriorly that is sutured with the cleithrum anterodorsally and separated from the coracoid by a narrow cartilaginous band ventrally. The scapula is connected with

two and a half actinosts posteriorly and supports some upper pectoral fin rays posterodorsally.

The coracoid is a rather broad bone with a ventral arm that



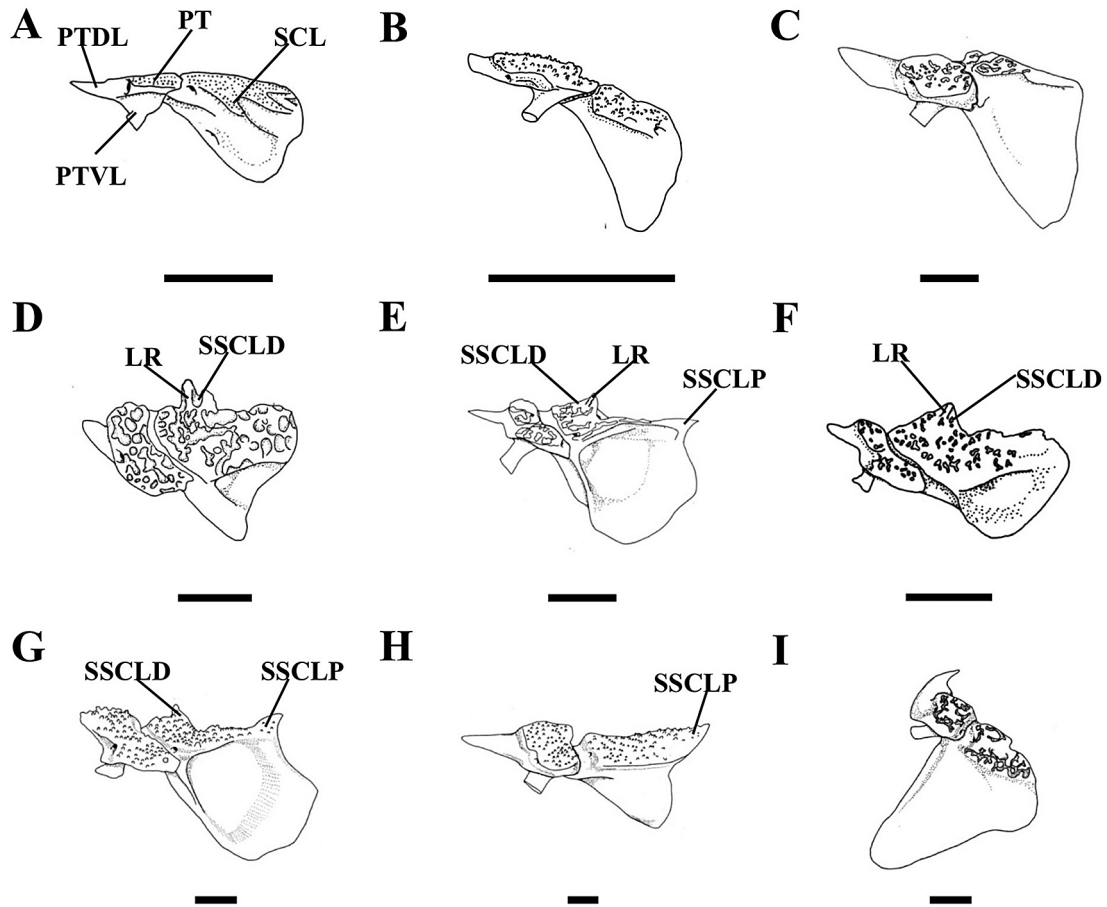


Fig. 30. Lateral view of posttemporal and supracleithrum of left side. A, *Xenocephalus egregius*; B, *Genyagnus monopterygius*; C, *Ichthyoscopus lebeck*; D, *Kathetostoma albigutta*; E, *Uranoscopus tosae*; F, *U. cognatus*; G, *Selenoscopus turbisquamatus*; H, *Pleuroscopus pseudodorsalis*; I, *Astroscopus sexspinosus*. LR, longitudinal ridge; PT, posttemporal; PTDL, dorsal limb of posttemporal; PTVL, ventral limb of posttemporal; SCL, supracleithrum; SSCLD, spine on dorsomesial portion of supracleithrum; SSCLP, spine on posterior portion of supracleithrum. Bars indicate 5 mm.

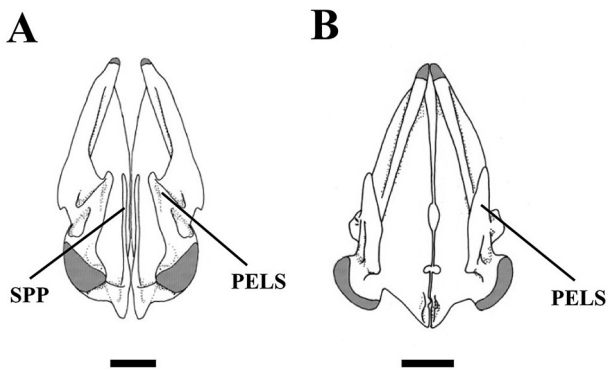


Fig. 31. Ventral view of pelvis. A, *Astroscopus y-graecum*; B, *Kathetostoma giganteum*. PELS, pelvic spur; SPP, subpelvic process. Bars indicate 5 mm.

attaches to the cleithrum anteroventrally. It is directly connected to the mesial expansion of the lower two actinosts in *Pleuroscopus pseudodorsalis*, *Xenocephalus australiensis* and *X. elongatus* (Fig. 29A, C), but is sandwiched by the lateral and mesial expansions of the lower two actinosts in other ura-

noscopids (Fig. 29B, D-I).

The actinosts are serially arranged, short and broad elements that are firmly attached to each other and to the posterior portions of the scapula and coracoid, forming a single strong and rigid unified pectoral plate. Four actinosts are present in all uranoscopids (Fig. 29A-C, E-I), except *Ichthyoscopus* spp., which lacks the uppermost actinost (Fig. 29D).

The pelvic girdle consists of a paired pelvis, each of which supports a pelvic fin with a single spine and five soft rays. The base of the pelvic spine has a dorsal process in *Kathetostoma* spp., *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis* (Fig. 32A, E, G), which is absent in other uranoscopids (Fig. 32B-D, F, H).

The pelvis is a large, thick, triangular bone with a small cartilaginous cap at the anterior tip and a large cartilaginous condyle, supporting the pelvic fin rays posteriorly. An accessory subpelvic keel is absent. A subpelvic process, situated on the posteromedial portion of the pelvis, is long in *Astroscopus* spp., *Ichthyoscopus* spp., *Xenocephalus* spp., *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. crassiceps*

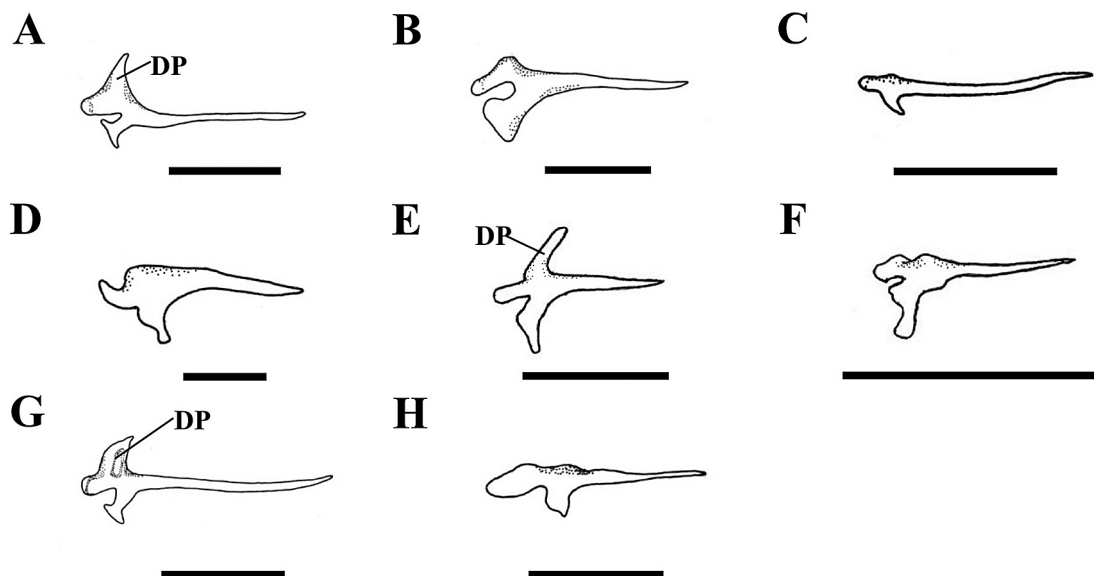


Fig. 32. Lateral view of pelvic spine of left side. A, *Pleuroscopus pseudodorsalis*; B, *Ichthyscopus barbatus*; C, *Astroscopus zephyreus*; D, *Selenoscopus turbisquamatus*; E, *Kathetostoma giganteum*; F, *Genyagnus monopterygius*; G, *Xenocephalus egregius*; H, *Uranoscopus cognatus*. DP, dorsal process of pelvic spine. Bars indicate 5 mm.

and *U. oligolepis* (Fig. 31A), but is very short in other uranoscopids (Fig. 31B). A postpelvic process is absent. Posteroventrally, the pelvis has a single poorly developed pelvic spur (sensu Pietsch, 1989) in *Astroscopus* spp. and *Genyagnus monopterygius* (Fig. 29B, F), two prominent and sharp spurs in *U. cognatus* (Fig. 29H), and single prominent and sharp spur in *Kathetostoma* spp., *Selenoscopus turbisquamatus* and other species of *Uranoscopus* (Fig. 29E, G, I). Spurs are absent in the remaining uranoscopids.

#### Characters variable among Uranoscopidae

**TS 56.** *Dorsal limb of posttemporal.* 0: short and flattened; 1: very elongate and spine-like.

*Ingroup.* The dorsal limb of the posttemporal is short and flattened in all uranoscopids (character 56-0), except *Astroscopus* spp., which has a mesially very elongate and spine-like limb (character 56-1).

*Outgroup.* The dorsal limb of the posttemporal is usually short and flattened in percoids (character 56-0) (Tominaga, 1968; Sasaki, 1989; this study).

**TS 57.** *Spine on posterior portion of supracleithrum.* 0: absent; 1: present.

*Ingroup.* A spine is present on the posterior portion of the supracleithrum in *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. oligolepis*, *U. polli*, *U. scaber* and *U. tosae* (character 57-1), but is absent in the remaining uranoscopids (character 57-0).

*Outgroup.* The posterior portion of the supracleithrum typically lacks a spine in percoids (character 57-0) (Tominaga, 1968; Sasaki, 1989; this study).

**TS 58.** *Spine on dorsomesial portion of supracleithrum.* 0:

absent; 1: present.

*Ingroup.* A spine is present on the dorsomesial portion of the supracleithrum in *Kathetostoma albigutta*, *Selenoscopus turbisquamatus* and *Uranoscopus* spp. (character 58-1), but is absent in the remaining uranoscopids (character 58-0).

*Outgroup.* The dorsomesial portion of the supracleithrum usually lacks a spine in percoids (character 58-0) (Tominaga, 1968; Sasaki, 1989; this study).

**TS 59.** *Dorsal surface of spine dorsomesially on supracleithrum.* 0: covered by tubercles and lacking ridges; 1: lacking tubercles but with a longitudinal ridge.

*Ingroup.* The dorsal surface of the spine on the dorsomesial portion of the supracleithrum is covered by tubercles and lacks ridges in *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. archionema*, *U. filibarbis*, *U. japonicus*, *U. polli* and *U. scaber* (character 59-0), but lacks tubercles and has a longitudinal ridge in *Kathetostoma albigutta* and the remaining species of *Uranoscopus* (character 59-1). The spine on the dorsomesial portion of the supracleithrum is absent in other uranoscopids (coded as "?").

*Outgroup.* A supracleithral spine is typically absent in percoids (Tominaga, 1968; Sasaki, 1989; this study). Therefore, the outgroup is coded as "?".

**TS 60.** *Flange of cleithrum situated lateral to attachment site of protractor pectoralis.* 0: absent; 1: present.

*Ingroup.* A flange situated lateral to the attachment site of the protractor pectoralis is present on the cleithrum in *Uranoscopus* spp., *Kathetostoma averruncus*, *K. cubana* and *Selenoscopus turbisquamatus* (character 60-1), but absent in other uranoscopids (character 60-0).

*Outgroup.* The flange is typically absent in percoids (character 60-0) (Tominaga, 1968; Sasaki, 1989).

**TS 61.** *Postcleithra*. 0: two; 1: single, elongate, attaching to cleithrum; 2: single, short, free from pectoral girdle; 3: absent (unordered).

*Ingroup.* The postcleithra comprises two elements in *Astroscopus* spp., *Ichthyoscopus* spp., *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis* (character 61-0), but only a single elongate element that attaches to the mesial surface of the cleithrum in *Kathetostoma* spp. and *Genyagnus monopterygius* (character 61-1) or a single short element free from the pectoral girdle in *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. crassiceps*, *U. oligolepis* and *U. polli* (character 61-2). The postcleithrum is absent in the remaining species of *Uranoscopus* (character 61-3).

*Outgroup.* In percoids, the postcleithra comprises two elements (character 61-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989).

**TS 62.** *Coracoid*. 0: articulating with lower two actinosts that lack expansions; 1: connecting directly to mesial expansion of lower two actinosts; 2: sandwiched by lateral and mesial expansions of lower two actinosts (ordered as 0-1-2).

*Ingroup.* The coracoid is directly connected to mesial expansions of the lower two actinosts in *Pleuroscopus pseudodorsalis*, *Xenocephalus australiensis* and *X. elongatus* (character 62-1), but is sandwiched by lateral and mesial expansions of the lower two actinosts in other uranoscopids (character 62-2).

*Outgroup.* The coracoid typically articulates with the lower two actinosts, which lack expansions, in percoids (character 62-0) (Imamura and Matsuura, 2003; this study).

**TS 63.** *Uppermost actinost*. 0: present; 1: absent.

*Ingroup.* The uppermost actinost is absent in *Ichthyoscopus* spp. (character 63-1), but is present in other uranoscopids (character 63-0).

*Outgroup.* The uppermost actinost is typically present in percoids (character 63-0) (Fraser, 1968; Tominaga, 1968; Sasaki, 1989; Imamura, 1996).

**TS 64.** *Dorsal process on base of pelvic spine*. 0: present; 1: absent.

*Ingroup.* A dorsal process is present on the base of the pelvic spine in *Kathetostoma* spp., *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis* (character 64-0), but absent in other uranoscopids (character 64-1).

*Outgroup.* The dorsal process is typically present in percoids (character 64-0) (this study).

**TS 65.** *Subpelvic process*. 0: long; 1: short.

*Ingroup.* The subpelvic process is long in *Astroscopus* spp., *Ichthyoscopus* spp., *Xenocephalus* spp., *Uranoscopus albesca*, *U. archionema*, *U. bicinctus*, *U. crassiceps* and *U. oligolepis* (character 65-0), but short in the other uranoscopids (character 65-1).

*Outgroup.* In percoids, the subpelvic process is typically long (character 65-0) (this study).

**TS 66.** *Pelvic spur*. 0: absent; 1: single poorly devel-

oped spur present; 2: single prominent and sharp spur present; 3: two prominent and sharp spurs present (ordered as 0-1-2-3).

*Ingroup.* The posteroventral portion of the pelvis has a single poorly developed pelvic spur in *Astroscopus* spp. and *Genyagnus monopterygius* (character 66-1), two prominent sharp spurs in *Uranoscopus cognatus* (character 66-3), a single prominent sharp spurs in *Kathetostoma* spp., *Selenoscopus turbisquamatus* and the other species of *Uranoscopus* (character 66-2), but no spur in the remaining uranoscopids (character 66-0).

*Outgroup.* In percoids, the posteroventral portion of the pelvis lacks spur (character 66-0) (this study).

*Remarks.* Pietsch (1989) considered the presence of the pelvic spur to be a synapomorphy supporting the monophyly of 11 trachinoid families, including the Uranoscopidae, Cheimarrichthyidae, Pinguipedidae, Percophidae, Trichonotidae, Creediidae, Champsodontidae, Chiasmodontidae, Leptoscopidae and Trachinidae. However, observations for this study revealed the absence of a pelvic spur in several uranoscopids. Placing doubt on the validity of the character as a synapomorphy for the suborder.

#### Characters synapomorphic for Uranoscopidae

*Anterior portion of pelvic girdle projecting beyond the ventral arm of pectoral girdle.* The anterior portion of the pelvic girdle projects in advance of the ventral arm of the cleithrum in uranoscopids. In contrast, the anterior end of the pelvic girdle typically does not reach the ventral arm of the cleithrum in percoids (Imamura and Matsuura, 2003; this study).

*Presence of cleithral spine.* A cleithral spine is present on the posterior portion of the dorsal limb of the cleithrum in uranoscopids, a feature that is typically absent in percoids (Imamura and Matsuura, 2003; this study).

*Actinosts short, broad and firmly attached to each other and to the posterior portions of scapula and coracoid.* The actinosts are short, broad and firmly attached to each other and to the posterior portions of the scapula and coracoid, forming a single strong, unified pectoral plate in uranoscopids. In contrast, percoids typically have the uppermost actinost smallest and lower elements becoming progressively longer ventrally (Imamura, 1996; this study).

*Absence of postpelvic process.* The postpelvic process situated posterior to the subpelvic process is absent in the uranoscopids. Contrarily, this process is present in typical percoids (Tominaga, 1968; Sasaki, 1989).

*Absence of accessory subpelvic keel.* Uranoscopids lack an accessory subpelvic keel that is typically well developed in percoids (Tominaga, 1968; Sasaki, 1989).

#### Autapomorphies for terminal taxa

None.

**Other observed variations**

*Configuration of cleithral spine.* Pietsch (1989) considered a large cleithral spine as being a derived character for his analysis of uranoscopid relationships. However, the configuration of the spine is serially changed among uranoscopids examined in this study; therefore it is impossible to divide them into any morphotypes, and characters associated with the configuration of the spine are not used for the analysis.

**1-8. Axial skeleton and median fin supports (Figs. 33-41)**

**Description.** The axial skeleton forms the central axis of the body and consists of the vertebrae, epineurals and pleural ribs. The median fins include the dorsal and anal fins with their spines and soft rays, and supporting proximal and distal pterygiophores, and stays. Supraneurals and medial pterygiophores are absent.

*Axial skeleton.* The vertebrae are situated on the midline of the body. The total number of vertebrae vary between genera and species: 24 in *Astroscopus* spp. and *Selenoscopus turbisquamatus*, 24-25 in *Uranoscopus* spp., 25-26 in *Ichthyoscopus* spp., *Kathetostoma albigutta* and *K. cubana*, 26-27 in *Xenocephalus* spp., 27 in *K. nigrofasciatum* and *K. averruncus*, 28 in *Pleuroscopus pseudodorsalis*, 29 in *Genyagnus monopterygius*, 31 in *K. laeve* and *K. canaster*, and 32-33 in *K. giganteum*. The vertebral column is separated into two continuous sections, abdominal and caudal vertebrae.

Abdominal vertebrae have a large neural spine with a basal neural arch dorsally. Except for several anterior elements, they also possess a bilateral pair of parapophysis ventrolaterally. The abdominal vertebrae consist of 9-10 elements in *Astroscopus* spp., 9 in *Ichthyoscopus* spp., 10-11 in *Uranoscopus* spp., 11 in *Xenocephalus* spp., *Selenoscopus turbisquamatus*, *Genyagnus monopterygius*, *Kathetostoma albigutta* and *K. cubana*, 12-13 in *K. giganteum*, *K. averruncus*, *K.*

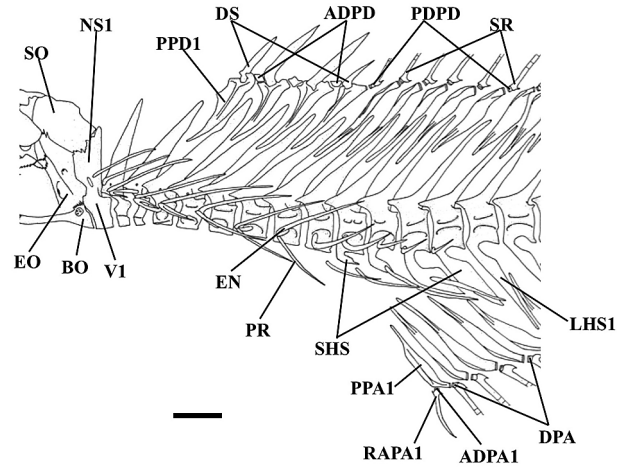


Fig. 33. Lateral view of abdominal vertebrae and associated bones on the left side in *Astroscopus y-graecum*. ADPA1, anterior distal pterygiophore on anterodistal base of first anal proximal pterygiophore; ADPD, anterior distal pterygiophore of dorsal fin; BO, basioccipital; DPA, distal pterygiophore of anal fin; DS, dorsal spine; EN, epineural; EO, exoccipital; LHS1, first long hemal spine; NS1, first neural spine; PDPD, posterior distal pterygiophore of dorsal fin; PPA1, first proximal pterygiophore of anal fin; PPD1, first proximal pterygiophore of dorsal fin; PR, pleural rib; RAPA1, first ray on anterodistal base of first proximal pterygiophore of anal fin; SHS, short hemal spine; SO, supraoccipital; SR, soft ray; V1, first vertebra. Bar indicates 5 mm.

*nigrofasciatum*, *K. canaster* and *K. laeve*, and 14 in *Pleuroscopus pseudodorsalis*. The centrum and neural spine of the first vertebra are firmly attached to the posterior portion of the cranium. A short ligament binds the prezygapophysis of the second vertebra to the posterior portion of the first vertebra in all uranoscopids (Fig. 34A), except *K. nigrofasciatum*, which has a long ligament binding the prezygapophysis of the sec-

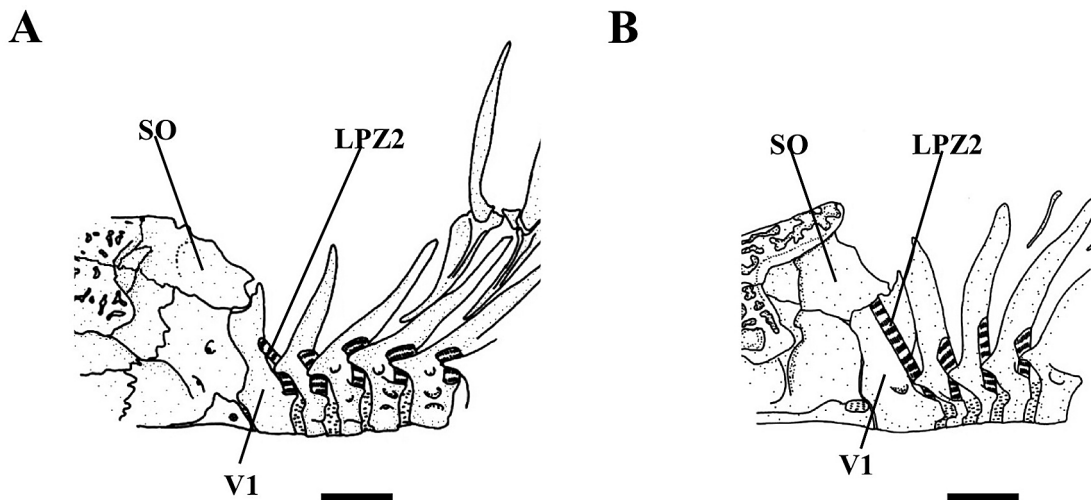


Fig. 34. Lateral view of anterior abdominal vertebrae and associated bones after removal of epineurals and pleural ribs. A, *Astroscopus zephyreus*; B, *Kathetostoma nigrofasciatum*. LPZ2, ligament from prezygapophysis of second vertebra; and other abbreviations are as in Fig. 33. Scales indicate 5 mm.



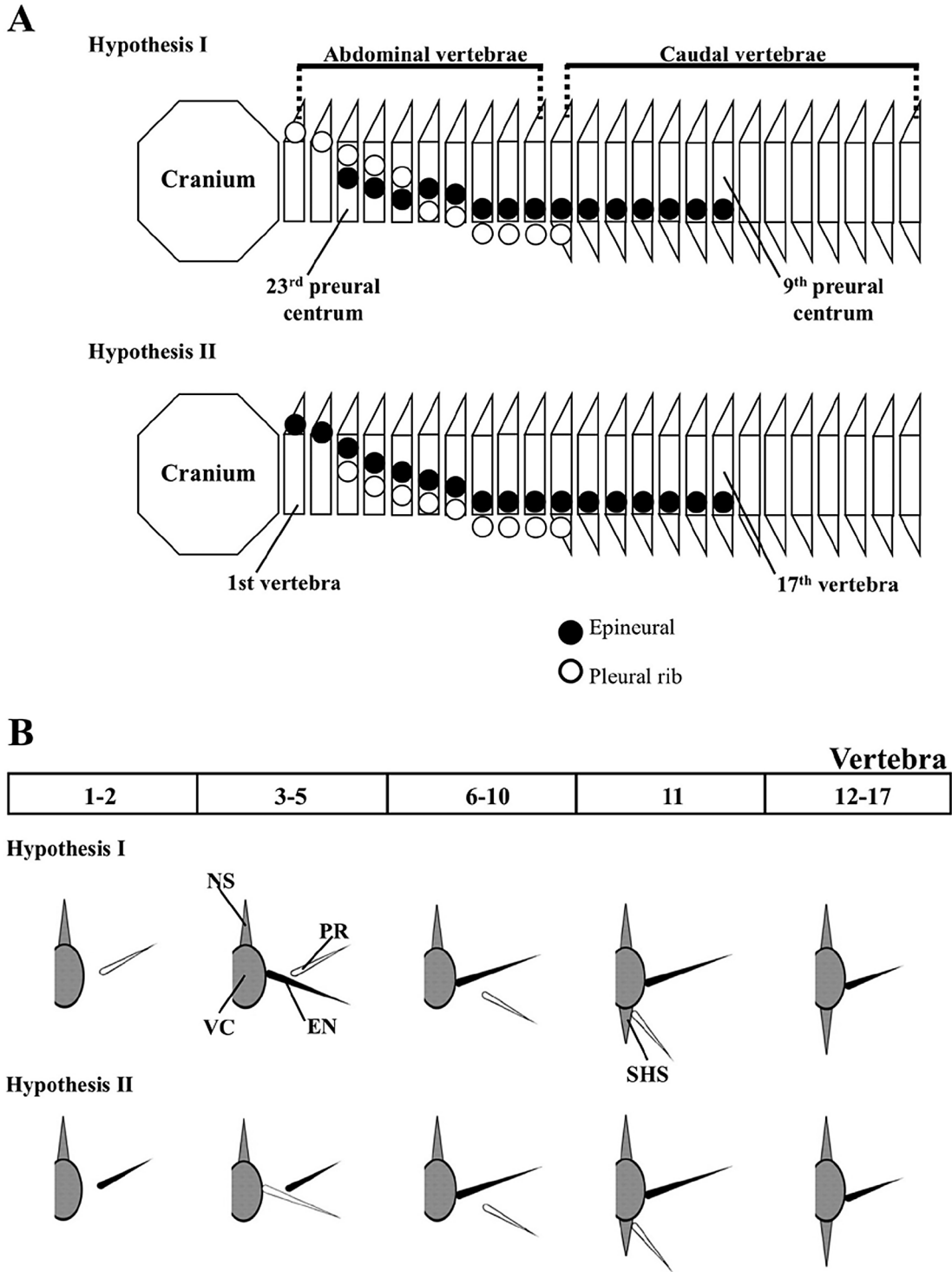


Fig. 35. Diagrams showing two hypotheses (Hypothesis I of Pietsch, 1989; Hypothesis II of Patterson and Johnson, 1995) of relationships between epineurals and pleural ribs in *Uranoscopus scaber*. A, lateral view of axial skeletons; B, cross sectional views of vertebrae and associated elements. VC, vertebral centrum; and other abbreviations are as in Fig. 33.

ond vertebra to the supraoccipital (Fig. 34B). The bases of the parapophyses of the abdominal vertebrae are narrow and short in *Kathetostoma* spp., *Uranoscopus* spp., *Xenocephalus* spp., *S. turbisquamatus* and *P. pseudodorsalis* (Fig. 38A), but are rudimentary in *Astroscopus* spp. and *Ichthyoscopus* spp.

(Fig. 38B), and are both wide and very expanded ventrolaterally in *G. monopterygius* (Fig. 38C).

The caudal vertebrae are situated between the abdominal vertebrae and caudal skeleton. Each element possesses a neural spine and neural arch dorsally, and a hemal spine and

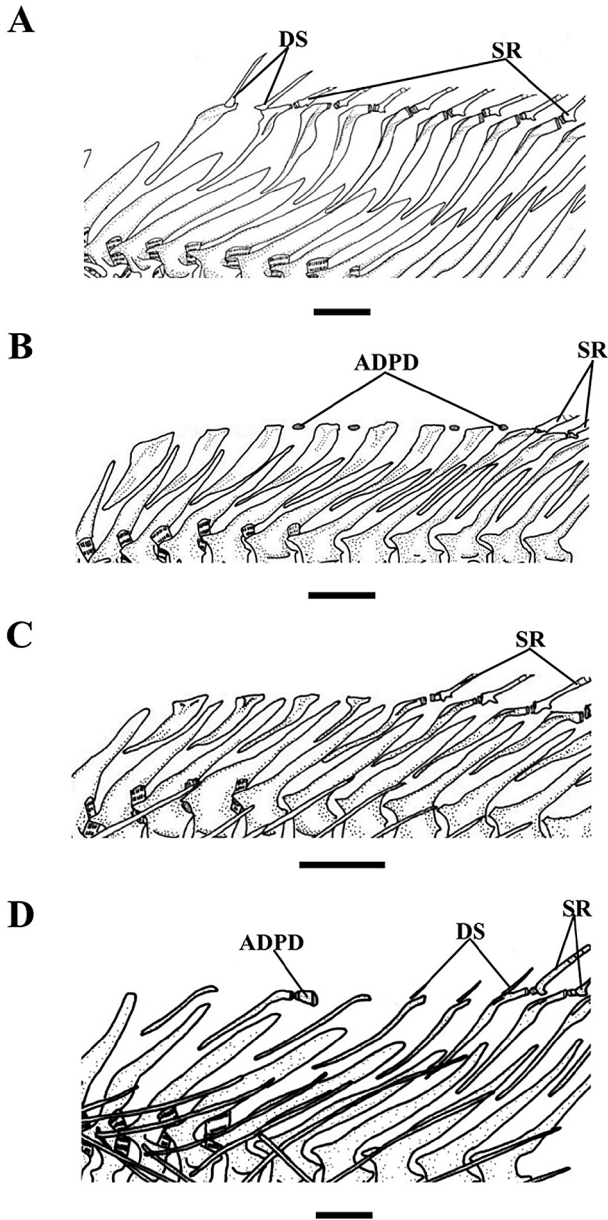


Fig. 36. Lateral view of anterior elements of dorsal fin and associated vertebrae from left side. A, *Ichthyoscopus lebecki*; B, *Xenocephalus egregius*; C, *Genyagnus monopterygius*; D, *Kathetostoma canaster*. Abbreviations are as in Fig. 33. Bars indicate 5 mm.

hemal arch ventrally, except for the last caudal vertebrae, in which the neural spine is reduced. The number of the caudal vertebrae varies: 13 in *Selenoscopus turbisquamatus*, 13–14 in *Uranoscopus* spp., 14 in *Pleuroscopus pseudodorsalis*, 14–15 in *Kathetostoma albigutta*, *K. averruncus*, *K. cubana* and *Astroscopus* spp., 15–16 in *Xenocephalus* spp., 16–17 in *Ichthyoscopus* spp., 18 in *Genyagnus monopterygius*, 18–19 in *K. laeve* and *K. canaster*, and 20 in *K. giganteum*. Anterior caudal vertebrae bear a short hemal spine respectively, while other caudal vertebrae have a long hemal spine. The number of the short hemal spines varies between

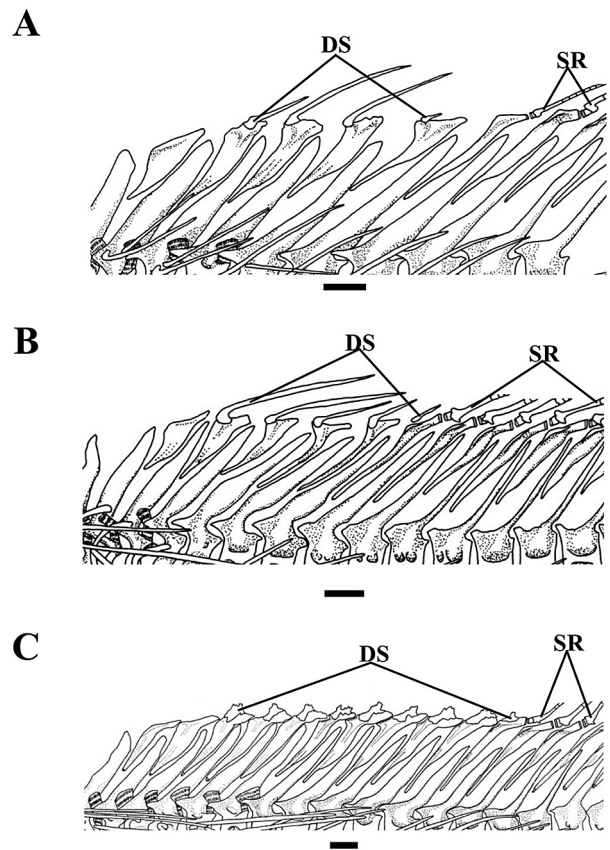


Fig. 37. Lateral view of anterior elements of dorsal fin and associated vertebrae from left side. A, *Selenoscopus turbisquamatus*; B, *Uranoscopus oligolepis*; C, *Pleuroscopus pseudodorsalis*. Abbreviations are as in Fig. 33. Bars indicate 5 mm.

species: one in *Xenocephalus* spp., *U. polli*, *U. japonicus* and *U. albesca*, two in *Ichthyoscopus* spp., *A. zephyreus*, *K. albigutta*, *K. cubana*, *K. giganteum*, *P. pseudodorsalis*, *S. turbisquamatus*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. oligolepis*, *U. scaber* and *U. tosae*, three in *Astroscopus guttatus*, *A. sexspinosus*, *G. monopterygius*, *K. averruncus*, *K. laeve*, *K. nigrofasciatum*, *U. archionema*, and four in *A. y-graecum* and *K. canaster*.

The epineurals are bilaterally paired bones that are slender and lie on the horizontal septum, which divides myomeres into dorsal (epaxialis) and ventral (hypaxialis) masses. The first two epineurals are connected with the neural arch of the first and second vertebrae via a ligament, the subsequent two or three epineural are attached to the dorsal surface of the pleural ribs, and the remaining epineurals posteriorly are attached to the adjacent vertebral centra in most uranoscopids. The number of epineurals is variable: 9–14 in *Ichthyoscopus* spp., 10–15 in *Astroscopus* spp., 15–18 in *Uranoscopus* spp., 16–18 in *Kathetostoma* spp., 18–19 in *Xenocephalus* spp., 20 in *Pleuroscopus pseudodorsalis* and 21 in *Genyagnus monopterygius*.

Pleural ribs are bilaterally paired, slender bones situated

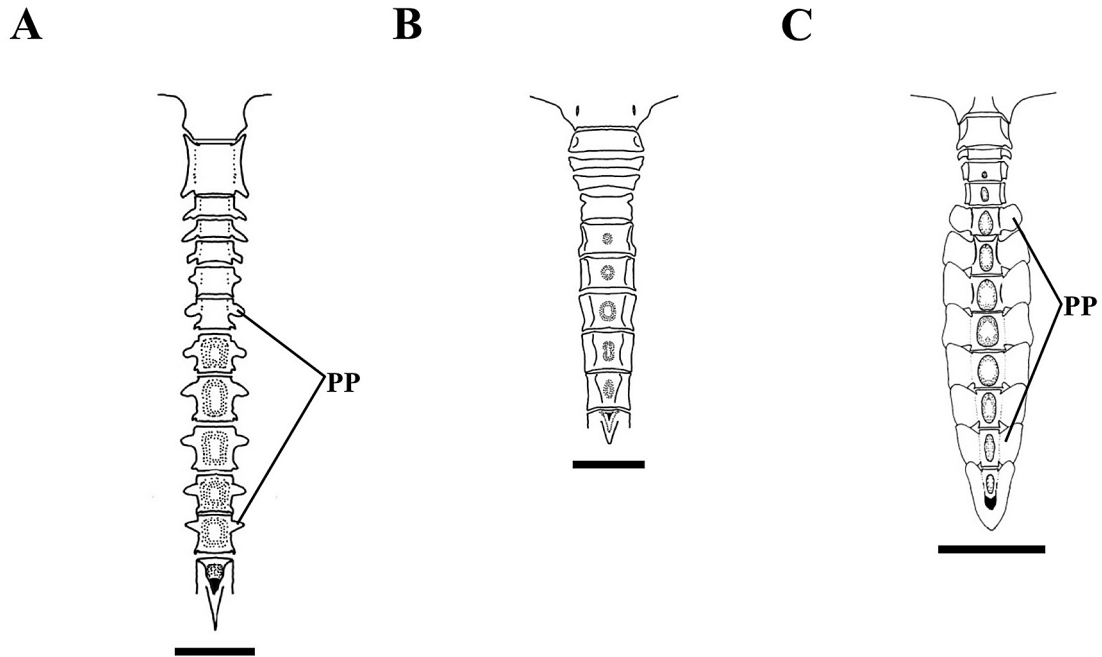


Fig. 38. Ventral view of abdominal vertebrae (cranium at top). A, *Kathetostoma albigutta*; B, *Ichthyoscopus lebeck*; C, *Genyagnus monopterygius*. PP, parapophyses. Bars indicate 5 mm.

under the epineurals and extending into the hypaxialis. The anterior two or three elements attach directly to vertebral centra, and several subsequent elements are free from vertebrae and the epineurals under which they are positioned, and posterior ribs on caudal vertebrae are attached to the anterior short hemal spine proximally. Pleural ribs are absent on several abdominal vertebrae in *Ichthyoscopus* spp. The number of pleural ribs vary between genera: 3 in *Ichthyoscopus* spp., 6–13 in *Kathetostoma* spp., 8–10 in *Uranoscopus* spp., 9–10 in *Astroscopus* spp., 10 in *Pleuroscopus pseudodorsalis*, 10–11 in *Xenocephalus* spp. and 11 in *Genyagnus monopterygius*.

**Median fin supports.** Proximal pterygiophores of the dorsal and anal fins are situated between the neural spines and between the hemal spines, respectively. Each proximal pterygiophore inserts into an interspace between either neural or hemal spines in all uranoscopids. The number of proximal pterygiophores of the dorsal fin varies from 17 to 24, and of the anal fin from 10 to 17 in the Uranoscopidae.

The first proximal pterygiophore of the dorsal fin inserts between the third and fourth neural spines. This element supports a spine in *Astroscopus* spp., *Ichthyoscopus* spp. and *Uranoscopus archionema* (Figs. 33, 34A, 36A), but lacks a spine in other uranoscopids (Figs. 34B, 36B–D, 37). The first proximal pterygiophore of the dorsal fin is a large, leaf-like bone in all uranoscopids (Figs. 33, 34A, 36A–C, 37), except *Kathetostoma* spp., in which has a reduced rod-like pterygiophore (Figs. 34B, 36D).

A number of anterior proximal pterygiophores of the anal fin are situated anterior to the first long hemal spine in all ura-

noscopids (Figs 33, 39). The proximal tips of the first and second proximal pterygiophores of the anal fin are separated from each other in all uranoscopids (Figs 33, 39A–F, H), except *Pleuroscopus pseudodorsalis*, which has the tips fused (Fig. 39G). The number of anterior proximal pterygiophores of the anal fin before the first long hemal spine varies between species: four in *Xenocephalus* spp., *P. pseudodorsalis*, *Astroscopus guttatus*, *A. sexspinosus*, *A. zephyreus*, *Uranoscopus albesca*, *U. cognatus*, *U. japonicus*, *U. polli* and *U. scaber*; five in *Ichthyoscopus* spp., *A. y-graecum*, *Genyagnus monopterygius*, *Kathetostoma cubana*, *K. giganteum*, *K. nigrofasciatum*, *Selenoscopus turbisquamatus*, *U. bicinctus*, *U. crassiceps*, *U. filibarbis*, *U. oligolepis* and *U. tosaie*; and six in the remaining uranoscopids.

Distal pterygiophores include ossified or cartilaginous elements. These of the dorsal fin are divided into three sections: the anterior elements situated behind the distal base of anterior proximal pterygiophores of the dorsal fin each bearing or lacking a spine; the posterior elements, except for the terminal element, each bearing a soft ray; and the terminal element bearing one or two soft rays and attached to the terminal proximal pterygiophore of the dorsal fin. Anterior elements of the distal pterygiophores of the dorsal fin are present in *Astroscopus* spp., *Xenocephalus* spp., *Kathetostoma giganteum*, *K. canaster*, *K. nigrofasciatum* and *K. laevis* (Figs. 33, 36B, D), but are absent in other uranoscopids (Figs. 36A, C, 37). Anterior distal pterygiophores consist of one ossified element in *K. canaster*, 3–5 ossified elements in *Astroscopus* spp., 4–7 ossified elements in *X. australiensis* and *X. elongatus*, one anterior ossified and one posterior carti-



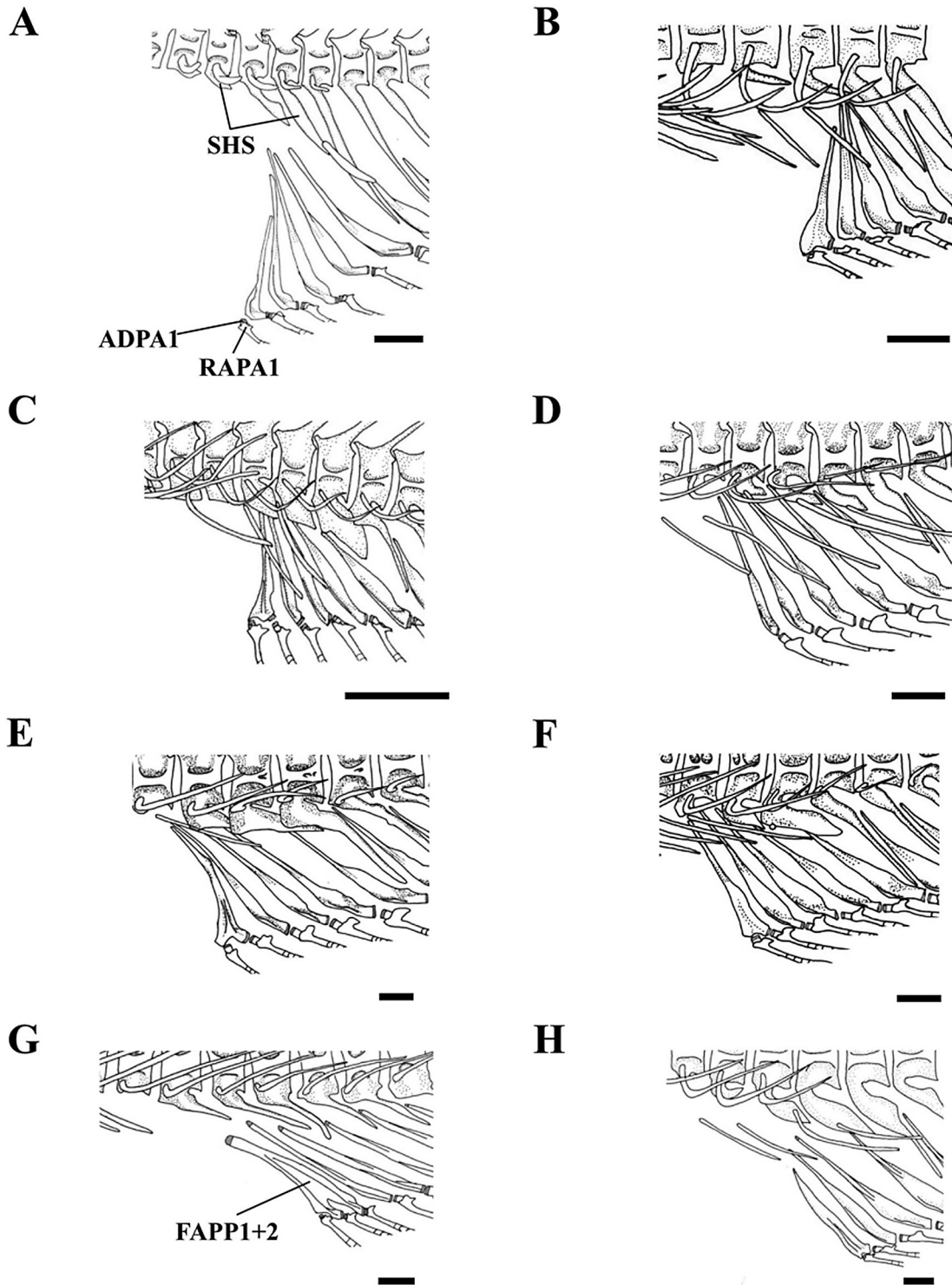


Fig. 39. Lateral view of anterior elements of anal fin and associated vertebrae from left side. A, *Ichthyoscopus lebeck*; B, *Xenocephalus egregius*; C, *Genyagnus monopterygius*; D, *Kathetostoma nigrofasciatum*; E, *Selenoscopus turbisquamatus*; F, *Uranoscopus oligolepis*; G, *Pleuroscopus pseudodorsalis*; H, *Astroscopus sexspinus*. FAPP1 + 2, fused proximal tips of first and second proximal pterygiophores of anal fin; other abbreviations are as in Fig. 33. Bars indicate 5 mm.

laminous elements in *K. nigrofasciatum*, one cartilaginous element in *X. armatus*, *Kathetostoma laeve* and *K. giganteum*, and 4 cartilaginous elements in *X. egregius*. Each ossified anterior element is attached to proximal pterygiophore anteriorly

and articulate with a dorsal spine and subsequent proximal pterygiophore posteriorly in *Astroscopus* spp. and *K. canaster*, but free from those latter bones in *K. nigrofasciatum*, *X. elongatus* and *X. australiensis*. Cartilaginous ante-



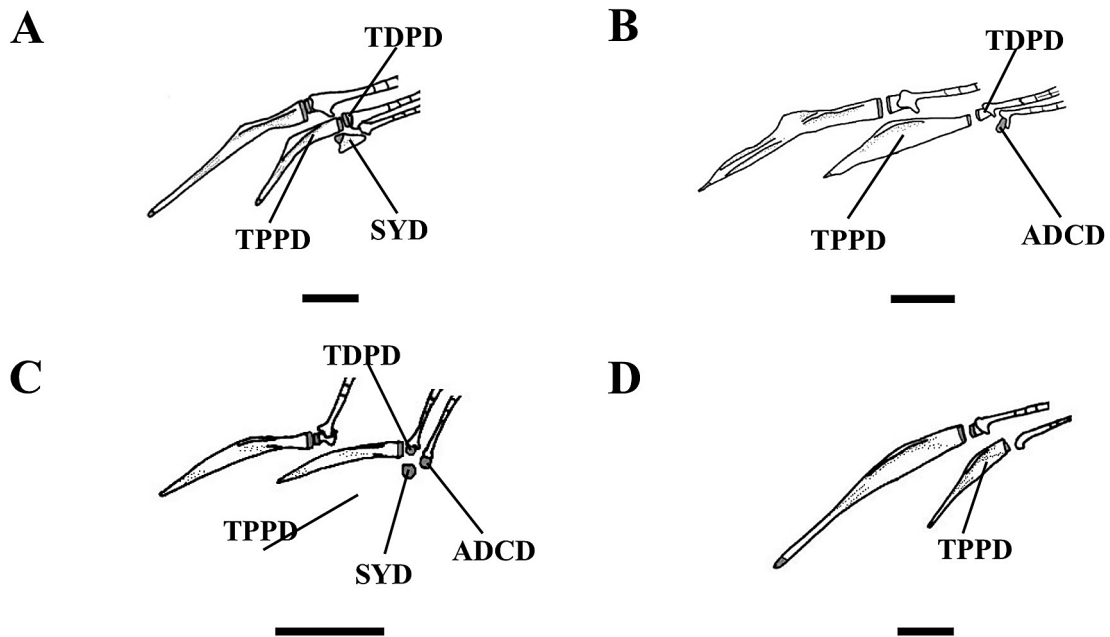


Fig. 40. Last two dorsal proximal pterygiophores and associated elements (left lateral view). A, *Pleuroscopus pseudodorsalis*; B, *Astroscopus sexspinosus*; C, *Kathetostoma giganteum*; D, *Ichthyoscopus barbatus*. ADCD, small additional distal pterygiophore cartilage of terminal proximal pterygiophore of dorsal fin; SYD, stay of dorsal fin; TDPD, terminal distal pterygiophore of dorsal fin; TPPD, terminal proximal pterygiophore of dorsal fin. Bars indicate 5 mm.

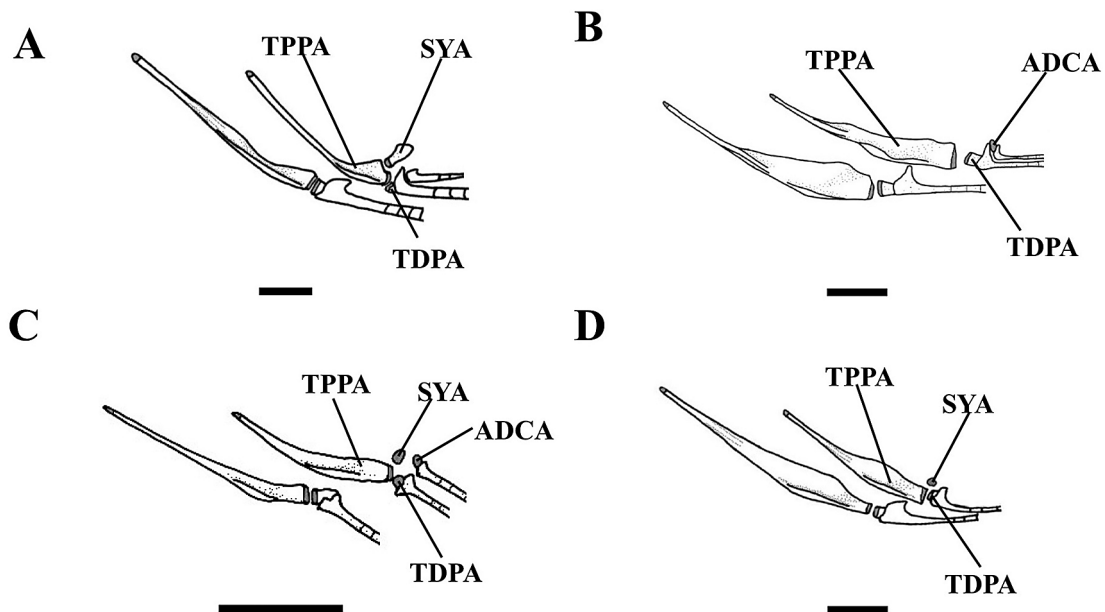


Fig. 41. Last two anal proximal pterygiophores and associated elements (left lateral view). A, *Pleuroscopus pseudodorsalis*; B, *Astroscopus sexspinosus*; C, *Kathetostoma giganteum*; D, *Ichthyoscopus barbatus*. ADCA, small additional distal pterygiophore cartilage of terminal proximal pterygiophore of anal fin; SYA, stay of anal fin; TDPA, terminal distal pterygiophore of anal fin; TPPA, terminal proximal pterygiophore of anal fin. Bars indicate 5 mm.

rior elements are attached to proximal pterygiophores in *K. nigrofasciatum* and *K. laeve*, but are free from them in *K. giganteum*, *X. egregius* and *X. armatus*. The distal pterygiophore on the terminal proximal pterygiophore of the dorsal fin is ossified in most uranoscopids (Fig. 40A-B), but is cartilaginous in *K. canaster*, *K. averruncus*, *K. giganteum*, *K. laeve*,

*Uranoscopus oligolepis*, *U. crassiceps*, *Ichthyoscopus sannio* and *X. australiensis* (Fig. 40C), and absent in *K. cubana*, *Ichthyoscopus barbatus* and *Genyagnus monopterygius* (Fig. 40D).

A single distal pterygiophore, each bearing a soft ray, is present on the posterodistal base of all proximal pterygio-

phores of the anal fin, except for the first and terminal proximal pterygiophores. Two distal pterygiophores are present anteriorly and posteriorly distal base of the first proximal pterygiophore of the anal fin. The more posterior element is ossified, while the nature of the anterior element on the anterodistal base of the first proximal pterygiophore of the anal fin varies among uranoscopids; the anterior element is cartilaginous in *Astroscopus sexspinosus* (Fig. 39H), absent in *Kathetostoma* spp. (Fig. 39D), and is ossified in the remaining uranoscopids (Figs. 33, 39A–C, E–G). The distal pterygiophore on the terminal proximal pterygiophore of anal fin is ossified in all uranoscopids (Fig. 41A–B, D), except *Uranoscopus scaber* and *K. giganteum*, in which it is cartilaginous (Fig. 41C).

Dorsal fin spines are situated in the anterior portion of the dorsal fin in species that have them. They are present in *Astroscopus* spp., *Ichthyoscopus* spp., *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus*, *Uranoscopus* spp., *Kathetostoma laeve*, *K. canaster*, *K. nigrofasciatum*, *K. giganteum* and *Xenocephalus australiensis* (Figs. 33, 36A, D, 37), but are absent in other uranoscopids (Fig. 36B–C). Spines are composed of one strong, rigid element in *K. laeve*, four to six strong, rigid elements in *Astroscopus* spp., three soft, flexible elements anteriorly and one strong, rigid element posteriorly in *S. turbisquamatus*, four soft, flexible elements anteriorly and one strong, rigid element posteriorly in *U. oligolepis*, one soft, flexible element in *X. australiensis* and *K. giganteum*, two soft, flexible elements in *Ichthyoscopus* spp., four to five soft, flexible elements in *U. scaber*, *U. polli*, *U. albesca*, *U. japonicus*, *U. tosae*, *U. bicinctus*, *U. cognatus*, *U. crassiceps* and *U. archionema*, three tiny soft elements and one soft, flexible element in *K. canaster*, one tiny soft element in *K. nigrofasciatum*, and nine rudimentary, knob-like elements in *P. pseudodorsalis*. Dorsal spines articulate with the proximal pterygiophores of the dorsal fin and are depressible in *Astroscopus* spp., *Ichthyoscopus* spp., *Uranoscopus* spp., *S. turbisquamatus*, *K. laeve*, *K. giganteum*, *K. nigrofasciatum*, *K. canaster* and *X. australiensis*. In contrast, the anterior eight and last dorsal spines are firmly attached to a proximal pterygiophore posteriorly and are not depressible in *P. pseudodorsalis*. A single dorsal spine is present on the first proximal pterygiophore of the dorsal fin in *Astroscopus* spp., *Ichthyoscopus* spp. and *U. archionema*, but is absent from the pterygiophore in other uranoscopids.

The terminal proximal pterygiophore of dorsal fin has two soft rays in most uranoscopids (Fig. 40A–C), but one is present in *Ichthyoscopus* spp., *Astroscopus zephyreus*, *Genyagnus monopterygius*, *Kathetostoma albigutta*, *K. averruncus*, *K. cubana*, *K. nigrofasciatum*, *Uranoscopus archionema*, *U. crassiceps*, *U. filibarbis*, *U. polli*, *Xenocephalus armatus*, *X. egregius* and *X. australiensis* (Fig. 40D).

The first ray on the anterodistal base of the first proximal pterygiophore of the anal fin is a soft ray in most uranosc-

pids (Fig. 39A–C, E–H), while it is a spine in *Astroscopus y-graecum* (Fig. 33), and absent in *Kathetostoma* spp. (Fig. 39D). The second ray on the posterodistal base of the first proximal pterygiophore of the anal fin is a soft ray. The number of soft rays on the terminal proximal pterygiophore is two in all uranoscopids (Fig. 41A–C), except for *K. albigutta* and *Ichthyoscopus barbatus*, that have one (Fig. 41D).

The stay is a small bony element, situated on the posterodistal base of the terminal proximal pterygiophores of dorsal and anal fins. The stay of the dorsal fin is ossified in *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis* (Fig. 40A), but cartilaginous in *Astroscopus y-graecum*, *A. guttatus*, *A. zephyreus*, *Ichthyoscopus lebeck*, *I. sannio*, *Kathetostoma albigutta*, *K. canaster*, *K. giganteum*, *K. laeve*, *K. nigrofasciatum*, *Selenoscopus turbisquamatus*, *Uranoscopus albesca*, *U. bicinctus* and *U. crassiceps* (Fig. 40C), and absent in the remaining uranoscopids (Fig. 40B, D). The stay of the anal fin (SYA) is ossified in *Xenocephalus* spp., *P. pseudodorsalis*, *A. zephyreus* and *A. y-graecum* (Fig. 41A), but cartilaginous in *Ichthyoscopus* spp., *A. guttatus*, *Genyagnus monopterygius*, *K. canaster*, *K. giganteum*, *K. laeve*, *K. nigrofasciatum*, *U. archionema*, *U. crassiceps*, *U. oligolepis* and *U. tosae* (Fig. 41C–D), and absent in the remaining uranoscopids (Fig. 41B).

A small additional distal pterygiophore cartilage is present in the space between the terminal distal pterygiophore and the stay of the dorsal fin in *Kathetostoma giganteum*, *K. laeve*, *Astroscopus sexspinosus* and *Uranoscopus cognatus* (Fig. 40B–C), and of the anal fin in *K. giganteum*, *U. cognatus* and *A. sexspinosus* (Fig. 41B–C), but absent in both the dorsal and anal fin in other.

**Identification of epineurals and pleural ribs (Fig. 35).** Pietsch (1989) first proposed the relationship of epineurals (as epipleurals) and pleural ribs in the Uranoscopidae. In his hypothesis (termed “Hypothesis I” here), all pairs of epineurals are attached to the third to the 17th vertebrae (= ninth to the 23rd preural centra in Pietsch, 1989: Fig. 31), while all pairs of pleural ribs are free from other bones, of which the four anteriormost pairs lying dorsal to the epineurals and the remaining six passing ventral to the epineurals. Patterson and Johnson (1995) reinterpreted the structure of epineurals and pleural ribs in uranoscopids. They proposed an alternative hypothesis (termed “Hypothesis II” here), treating the upper series as the epineurals and the lower series as the pleural ribs. Hypothesis I implies a shift of the pleural ribs from above the epipleurals to below them, whereas Hypothesis II switch of the attachments of pleural ribs and epineurals to the vertebral centra.

In percoids (e.g., Sasaki, 1989; Patterson and Johnson, 1995; this study), the epineurals (as epipleurals in Sasaki, 1989) are confined to the first four to eight vertebrae and lie on the horizontal septum, with the first two epineurals originating from the neural arches of the first and second vertebrae,

and the remaining elements attached to the pleural ribs. The pleural ribs are situated in hypaxialis and attached with the vertebrae proximally, with the first element always attached to the third vertebra.

In all uranocopids examined, all upper ribs lie in the horizontal septum, with the first two connected to the neural arch of the first and second vertebrae via a ligament, the subsequent two or three attached to the dorsal surface of the first to third lower ribs, respectively, and the remaining posterior ribs attached to the vertebral centra. In contrast, the lower ribs of abdominal vertebrae extend into the hypaxialis, with the anteriormost two or three directly attached to the vertebral centra and the ribs subsequent ribs lying under upper free from vertebrae and upper ribs. Ribs of caudal vertebrae also extend in the hypaxialis and are attached to the anterior short hemal spine proximally. Consequently, the upper and lower ribs can be identified as the epineurals and the pleural ribs, respectively.

Based on this, the attachment of the epineurals and the pleural ribs to the centra have switched in the Uranoscopidae, supporting "Hypothesis II" proposed by Patterson and Johnson (1995).

#### Characters variable among Uranoscopidae

**TS 67.** *Parapophyses.* 0: rudimentary; 1: narrow and short; 2: wide and very expanded (ordered as 0-1-2).

*Ingroup.* The parapophyses of abdominal vertebrae are rudimentary in *Astroscopus* spp. and *Ichthyoscopus* spp. (character 67-0), whereas they are narrow and short in *Kathetostoma* spp., *Uranoscopus* spp., *Xenocephalus* spp., *Pleuroscopus pseudodorsalis* and *Selenoscopus turbisquamatus* (character 67-1), and wide and very expanded in *Genyagnus monopterygius* (character 67-2).

*Outgroup.* The parapophyses of abdominal vertebrae are typically narrow and short in percoids (character 67-1) (Tomimaga, 1968; this study).

**TS 68.** *Configuration of first proximal pterygiophore of dorsal fin.* 0: leaf-like; 1: rod-like.

*Ingroup.* The first proximal pterygiophore of the dorsal fin is leaf-like in all uranocopids (character 68-0), except for *Kathetostoma* spp., which has a rod-like first proximal pterygiophore (character 68-1).

*Outgroup.* The first proximal pterygiophore of the dorsal fin is typically leaf-like in percoids (character 68-0) (this study).

**TS 69.** *Form of distal pterygiophore on anterodistal base of first proximal pterygiophore of anal fin.* 0: absent; 1: ossified; 2: cartilaginous (unordered).

*Ingroup.* The distal pterygiophore on the anterodistal base of the first proximal pterygiophore of the anal fin is cartilaginous in *Astroscopus sexspinosus* (character 69-2), absent in *Kathetostoma* spp. (character 69-0), and ossified in the remaining uranocopids (character 69-1).

*Outgroup.* Percoids typically lack a distal pterygiophore on the anterodistal base of the first proximal pterygiophore of the anal fin (character 69-0) (Fraser, 1968; Tomimaga, 1968; Sasaki, 1989).

**TS 70.** *Dorsal spine on first proximal pterygiophore.* 0: strong and rigid; 1: soft and flexible, 2: absent (unordered).

*Ingroup.* The dorsal spine on the first proximal pterygiophore is strong and rigid in *Astroscopus* spp. (character 70-0), soft and flexible in *Ichthyoscopus* spp. and *Uranoscopus archionema* (character 70-1), and absent in other uranocopids (character 70-2).

*Outgroup.* The dorsal spine on the anterior proximal pterygiophores are typically strong and rigid in percoids (character 70-0) (Tomimaga, 1968; Sasaki, 1989; Imamura, 1996).

**TS 71.** *Number of soft rays on terminal proximal pterygiophore of dorsal fin.* 0: two; 1: one.

*Ingroup.* The number of soft rays on the terminal proximal pterygiophore of the dorsal fin is two in most uranocopids (character 71-0), but one in *Ichthyoscopus* spp., *Astroscopus zephyreus*, *Genyagnus monopterygius*, *Kathetostoma albigutta*, *K. averruncus*, *K. cubana*, *K. nigrofasciatum*, *Uranoscopus archionema*, *U. crassiceps*, *U. filibarbis*, *U. polli*, *Xenocephalus armatus*, *X. egregius* and *X. australiensis* (character 71-1).

*Outgroup.* Percoids typically have two soft rays on the terminal proximal pterygiophore of the dorsal fin (character 71-0) (this study).

**TS 72.** *First ray on anterodistal base of first proximal pterygiophore of anal fin.* 0: spine; 1: soft ray; 2: absent (unordered).

*Ingroup.* The first ray on the anterodistal base of the first proximal pterygiophore of the anal fin is a soft ray in most uranocopids (character 72-1), while it is a spine in *Astroscopus y-graecum* (character 72-0), and it is absent in *Kathetostoma* spp. (character 72-2).

*Outgroup.* Spines are typically present on the anterodistal base of the first proximal pterygiophore of the anal fin in percoids (character 72-0) (Tomimaga, 1968; Sasaki, 1989).

**TS 73.** *Number of soft rays on terminal proximal pterygiophore of anal fin.* 0: two; 1: one.

*Ingroup.* The number of soft rays on the terminal proximal pterygiophore of the anal fin is two in all uranocopids (character 73-0), except *Kathetostoma albigutta* and *Ichthyoscopus barbatus*, which have one (character 73-1).

*Outgroup.* The typical number of soft rays on the terminal proximal pterygiophore of the anal fin is two in percoids (character 73-0) (this study).

#### Characters synapomorphic for the Uranoscopidae

*First vertebra firmly attached to posterior portion of cranium.* The centrum and neural spine of the first vertebra are firmly attached to the posterior portion of the cranium in

Uranoscopidae. Typically, the centrum of the first vertebra articulates with the cranium and the neural spine is free from it in percoids (Fraser, 1968; Sasaki, 1989).

*Posterior elements of epineurals attached to vertebrae and pleural ribs separated from vertebrae.* In percoids, epineurals are attached to pleural ribs, and pleural ribs are attached to vertebrae (Sasaki, 1989). In contrast, the attachments of the epineurals and pleural ribs have switched in Uranoscopidae with epineurals attached to vertebrae and pleural ribs free from them.

*First proximal pterygiophore of dorsal fin inserted between third and fourth neural spines.* The first proximal pterygiophore of the dorsal fin is inserted between the third and fourth neural spines in all uranoscopids. The pterygiophore is typically inserted between the second and third neural spines in percoids (Fraser, 1968; Sasaki, 1989). It is unclear if the first pterygiophore in uranoscopids is homologous with that typically in percoid, because two possible evolutionary interpretations exist: the pterygiophore inserting in the space between the second and third neural spines (= first pterygiophore of typical percoids) has been lost; or the fin and its supporting pterygiophore have shifted posteriorly. Both characters, however, can be considered to be derived.

*Absence of supraneurals.* Supraneurals are absent in the Uranoscopidae, while three rod-like supraneurals are typically inserted in the space between the posterior border of the supraoccipital crest and the third neural spine in percoids (Fraser, 1968; Sasaki, 1989).

*Each proximal pterygiophores individually inserts in an interspace between adjacent neural and hemal spines.* Each proximal pterygiophore individually inserts in an interspace between adjacent neural and hemal spines in all uranoscopids. Two or more pterygiophores typically insert in an interspace between adjacent neural and hemal spines in percoids (Sasaki, 1989; Imamura and Matsuura, 2003).

*Second ray on posterior portion of first proximal pterygiophore of anal fin being soft ray.* The second ray on the posterior portion of the first proximal pterygiophore of the anal fin is a soft ray in all uranoscopids. This ray is homologous with a third anal spine, which is situated on the posterior portion of the first proximal pterygiophore of anal fin in most percoids (Sasaki, 1989; Imamura, 1996).

#### Autapomorphies for terminal taxa

*Long ligament bonding prezygapophysis of second vertebra with supraoccipital.* A long ligament binds the prezygapophysis of the second vertebra to the supraoccipital in *Kathetostoma nigrofasciatum*. A short ligament binds the prezygapophysis of the second vertebra with the posterior portion of the first vertebra in other uranoscopids and percoids (this study). Consequently, the former character is regarded as an autapomorphy of this species.

*Proximal tips of first and second proximal pterygiophores*

*of anal fin fused.* The proximal tips of the first and second proximal pterygiophores of the anal fin are fused in *Pleuroscopus pseudodorsalis*. In contrast, they are separated from each other in other uranoscopids and percoids (this study). The condition present in *P. pseudodorsalis* is regarded as an autapomorphy for the species.

#### Other observed variations

*Characters associated with proximal and distal pterygiophores, dorsal spines and number of vertebrae.* Homologies of individual proximal pterygiophores supporting a spine and distal pterygiophore are unclear, as numbers of dorsal and anal proximal pterygiophores and vertebrae vary in Uranoscopidae (17–24 dorsal proximal pterygiophores, 10–17 anal proximal pterygiophores, and 24–33 vertebrae), it is unclear which proximal pterygiophores have been added or lost. Therefore, except for the first and last proximal pterygiophores of the dorsal and anal fins, characters associated with proximal pterygiophores, distal pterygiophores, dorsal spines, the number of vertebrae, are not used in the analysis. The “first and last” dorsal proximal pterygiophores among uranoscopids are considered homologous and are used in the analysis, because the former is consistently inserted between the third and fourth neural spines in all members of the family, and the last proximal pterygiophore is associated with the stay in both the Uranoscopidae and typical percoids (Johnson, 1984; this study).

*Additional distal pterygiophore cartilage on the terminal proximal pterygiophores of dorsal and anal fins.* A small additional distal pterygiophore cartilage is present in the space between the last distal pterygiophore and the stay of the terminal proximal pterygiophore of the dorsal fin in *Kathetostoma giganteum*, *K. laeve*, *Astroscopus sexspinosus* and *Uranoscopus cognatus*, and on the terminal proximal pterygiophore of the anal fin in *K. giganteum*, *U. cognatus* and *A. sexspinosus*. These cartilages are absent from the dorsal and anal fins in the remaining uranoscopids and typically in percoids (this study). These cartilages are situated in the space between the last distal pterygiophore and stay and could be derived from the last distal pterygiophore or stay. Therefore, although the presence of additional cartilages is considered to be derived, the homology in those species having them is unclear. This character is not used for the analysis.

#### 1–9. Caudal skeleton (Fig. 42)

**Description.** The caudal skeleton comprises a series of fan-like elements spreading out from the posteriormost centrum that includes the hypurals, parhypural, uroneural, epurals and urosyle, plus the second and third preural centra. The posterior margin of the caudal skeleton supports the caudal rays and radial cartilages.

The hypurals are situated on the posterior part of the urostyle and consist of three plate-like bones: an autogenous





style in *Astroscopus* spp., *X. armatus*, *X. australiensis* and *X. elongatus* (Fig. 42A–B), but fused with the urostyle in the others (Fig. 42C–H). The lower hypural plate is formed by a fusion of the first and second hypurals and is attached to the parhypural in all uranoscopids (Fig. 42A, C–F, H), except *Ichthyoscopus barbatus* and *X. australiensis* which have the two elements fused (Fig. 42B, G). A process is present on the anterolateral surface of the lower hypural plate in *Xenocephalus* spp., *Genyagnus monopterygius*, *K. albigutta* and *K. nigrofasciatum* (Fig. 42B, H), but absent in the remaining uranoscopids (Fig. 42A, C–G).

The parhypural is plate-like and situated below the lower hypural plate. The bone has the parhypurapophysis on its lateral surface. The parhypural is attached to the lower hypural plate in all uranoscopids, except *Ichthyoscopus barbatus* and *Xenocephalus australiensis*, which have the two bones fused.

The uroneural is a single rod-like bone (= first uroneural), lying above the urostyle and the fifth hypural. It is attached to the urostyle in *Astroscopus y-graecum*, *A. guttatus*, *A. zephyreus*, *Selenoscopus turbisquamatus*, *Uranoscopus archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. japonicus*, *U. scaber* and *U. tosae* (Fig. 42A, F), but fused to it in other uranoscopids (Fig. 42B–E, G–H). The second uroneural is absent in all uranoscopids.

The rod-like epurals are situated above the uroneural. All uranoscopids have three epurals (Fig. 42A–B, D–F, H), except *Pleuroscopus pseudodorsalis*, *Ichthyoscopus barbatus*, *Uranoscopus bicinctus* and *U. oligolepis*, which have two (Fig. 42C, G).

The urostyle is a triangular bone, formed from the fusion of the ural and first preural. It is connected to the second preural centrum anteriorly, the uroneural dorsally, the hypurals posteriorly, and the parhypural ventrally. The urostyle is fused with the upper hypural plate in *Ichthyoscopus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Genyagnus monopterygius*, *Pleuroscopus pseudodorsalis*, *Selenoscopus turbisquamatus* and *Xenocephalus egregius*.

The second and third preural centra are situated anterior to the urostyle and the parhypural. Each is attached ventrally to an autogenous plate-like long hemal spines. These second and third preural centra are attached to each other in all uranoscopids (Fig. 42A–C, E–H), except *Kathetostoma cubana* which have the two fused (Fig. 42D).

The caudal fin rays comprise principal rays and procurvent rays. Principal rays are the branched rays plus one unbranched and segmented ray at the upper and lower margins of the fin. The number of principal rays is 6 (upper) + 6 (lower) in *Kathetostoma* spp., *Selenoscopus turbisquamatus* and *Genyagnus monopterygius*, 6 + 7 in *Pleuroscopus pseudodorsalis*, 6–7 + 6 in *Astroscopus* spp., *Uranoscopus* spp. and *Ichthyoscopus* spp., and 6–7 + 6–7 in *Xenocephalus* spp. Procurvent rays consist of short anterior unsegmented and

posterior segmented elements. The number of the procurvent rays is 6–8 (upper) + 4–5 (lower) in *Astroscopus* spp., 4–8 + 4–5 in *Uranoscopus* spp., 4–5 + 2–4 in *Ichthyoscopus* spp., 5–8 + 4–7 in *Kathetostoma* spp., 9–11 + 6–9 in *Xenocephalus* spp., 6 + 5 in *G. monopterygius*, 8 + 7 in *P. pseudodorsalis*, and 6 + 4 in *S. turbisquamatus*.

Radial cartilages are present on the distal tips of the neural spine of the third preural centrum, the epurals, the fifth hypural and the hemal spines of the second and third preural centra.

### Characters variable among Uranoscopidae

**TS 74. Fifth hypural.** 0: attached to urostyle and upper hypural plate; 1: attached to urostyle and fused with upper hypural plate; 2: fused with urostyle and upper hypural plate (unordered).

*Ingroup.* The fifth hypural is attached to the urostyle and the upper hypural plate in *Uranoscopus* spp., *Xenocephalus* spp., *Astroscopus y-graecum*, *A. sexspinosus*, *A. zephyreus* and *Selenoscopus turbisquamatus* (character 74–0), attached to the urostyle and fused with the upper hypural plate in *A. guttatus* (character 74–1), and fused with the urostyle and the upper hypural plate in remaining uranoscopids (character 74–2).

*Outgroup.* The fifth hypural is typically attached to the urostyle and the upper hypural plate or fourth hypural, which forms the upper part of the upper hypural plate, in percoids (character 74–0) (Tominaga, 1968; Sasaki, 1989; Fujita, 1990).

**TS 75. Upper hypural plate and urostyle.** 0: attached; 1: fused.

*Ingroup.* The upper hypural plate is attached to the urostyle in *Astroscopus* spp., *Xenocephalus armatus*, *X. australiensis* and *X. elongatus* (character 75–0), but fused with the urostyle in remaining uranoscopids (character 75–1).

*Outgroup.* The third and fourth hypurals, forming the upper hypural plate in Uranoscopidae, are typically attached to the urostyle in percoids (character 75–0) (Tominaga, 1968; Sasaki 1989; Fujita, 1990; Imamura, 1996).

**TS 76. Lower hypural plate and parhypural.** 0: attached; 1: fused.

*Ingroup.* The lower hypural plate and parhypural are attached in all uranoscopids (character 76–0), except *Ichthyoscopus barbatus* and *Xenocephalus australiensis*, which have the two elements fused (character 76–1).

*Outgroup.* The lower hypural plate or the first hypural, which forms the lower part of the lower hypural plate, typically articulates with the parhypural in percoids (character 76–0) (Tominaga, 1968; Sasaki 1989; Fujita, 1990; Imamura, 1996).

**TS 77. Process on anterolateral surface of lower hypural plate.** 0: absent; 1: present.

*Ingroup.* A process is present on the anterolateral surface

of the lower hypural plate in *Xenocephalus* spp., *Genyagnus monopterygius*, *K. albigutta* and *K. nigrofasciatum* (character 77-1), but absent in other uranoscopids (character 77-0).

**Outgroup.** This process is typically absent on the anterolateral surface of the lower hypural plate, or the first and second hypurals forming the lower hypural plate, in percoids (character 77-0) (Tominaga, 1968; Sasaki, 1989; Fujita, 1990).

**TS 78.** *Uroneural and urostyle.* 0: attached; 1: fused.

**Ingroup.** The uroneural is attached to the urostyle in *Astroscopus y-graecum*, *A. guttatus*, *A. zephyreus*, *Selenoscopus turbisquamatus*, *Uranoscopus archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. japonicus*, *U. scaber* and *U. tosa* (character 78-0), but fused with it in other uranoscopids (character 78-1).

**Outgroup.** The uroneural is typically attached to the urostyle in percoids (character 78-0) (Tominaga, 1968; Sasaki, 1989; Fujita, 1990).

**TS 79.** *Number of epurals.* 0: three; 1: two.

**Ingroup.** The number of the epurals is three in all uranoscopids (character 79-0), except for *Pleuroscopus pseudodorsalis*, *Ichthyoscopus barbatus*, *Uranoscopus bicinctus* and *U. oligolepis*, which have two (character 79-1).

**Outgroup.** Percoids typically have three epurals (character 79-0) (Tominaga, 1968; Sasaki, 1989; Fujita, 1990).

### Characters synapomorphic for Uranoscopidae

**First and second hypurals fused.** The first and second hypurals are fused in all uranoscopids, while they are typically autogenous in percoids (Tominaga, 1968; Sasaki, 1989; Fujita, 1990).

**Third and fourth hypurals fused.** The third hypural is fused with the fourth hypural in all uranoscopids, but are typically autogenous in percoids (Tominaga, 1968; Sasaki, 1989; Fujita, 1990).

**Second uroneural absent.** The second uroneural is absent in Uranoscopidae, but is typically well developed in percoids (Tominaga, 1968; Sasaki, 1989; Fujita, 1990).

### Autapomorphies for terminal taxa

**Second and third preural centra fused.** The second and third preural centra are fused in *Kathetostoma cubana*. These two bones are attached to each other in other uranoscopids and percoids (Tominaga, 1968; Sasaki, 1989; Fujita, 1990; this study). The former condition in *K. cubana* is considered to be an autapomorphy.

### Other observed variations

**Number of principal caudal fin rays.** The number of principal caudal fin rays in uranoscopids is 6-7 (upper) + 6-7 (lower), but typically 9 (upper) + 8 (lower) in percoids (Johnson 1984; this study). Although the former character may be a derived character, the homology of fin rays in uranoco-

pids relative to percoids is unclear, so it is not possible to tell if the same rays have been lost in all uranoscopids. Therefore, this character is not used for the phylogenetic analysis.

## 2. Myology

### 2-1. Cheek muscle (Figs. 43-44)

**Description.** The cheek muscular structure comprises the adductor mandibulae (A) that is divided into three sections, A1, A2 and A $\omega$ . A1 and A2 occupy the region between the jaws and preopercle, while A $\omega$  is situated on the mesial surface of lower jaw. A distinct section A3 is absent.

Section A2 is smaller than A1, and its posterodorsal portion (PDPA2) lies under A1 in *Pleuroscopus pseudodorsalis* and *Xenocephalus* spp. (Fig. 43A). In contrast, A2 is larger than A1 and its posterodorsal portion covers A1 in other uranoscopids (Fig. 43B-C). Section A1 originates from the metapterygoid, the hyomandibula and the preopercle in *P. pseudodorsalis*, *Xenocephalus* spp. and *Kathetostoma averuncus*, and from the metapterygoid and the hyomandibula in other uranoscopids. Section A1 inserts onto the dorsal half of the ligamentum primordium via tendinous tissue and has a short tendon for attachment with the proximal portion of maxilla anteriorly. Section A2 originates from the preopercle, metapterygoid, quadrate, symplectic and hyomandibula and inserts onto the ligamentum primordium anterodorsally and the anguloarticular anteroventrally.

Section A $\omega$  lies on the mesial surface of the lower jaw and is connected to the anteroventral side of the quadrate by a strong ligament. This section is restricted to the anterior region of the anguloarticular in all uranoscopids (Fig. 44A), except *Kathetostoma* spp., in which it expands posteriorly and mostly reaches to the quadrate (Fig. 44B).

The ligamentum primordium connects the posterior portion of the proximal arm of the maxilla with the lateral surface of the anguloarticular. The attachment site of this ligament on the maxilla is posterior to the dorsal attachment of A1 on the bone in all uranoscopids (Fig. 43A-B), except for *Astroscopus* spp., which has the ligament attaching anterior to the dorsal attachment of A1 (Fig. 43C).

### Characters variable among Uranoscopidae

**TS 80.** *Adductor mandibulae section A2.* 0: small and its posterodorsal portion lying under A1. 1: large and its posterodorsal portion covering A1.

**Ingroup.** Section A2 of the adductor mandibulae is small and its posterodorsal portion lies under the section A1 in *Pleuroscopus pseudodorsalis* and *Xenocephalus* spp. (character 80-0), but is large and its posterodorsal portion covers section A1 in other uranoscopids (character 80-1).

**Outgroup.** Section A2 of the adductor mandibulae is typically small and its posterodorsal portion lies under the section A1 in percoids (character 80-0) (Sasaki, 1989; Johnson, 1980; this study).



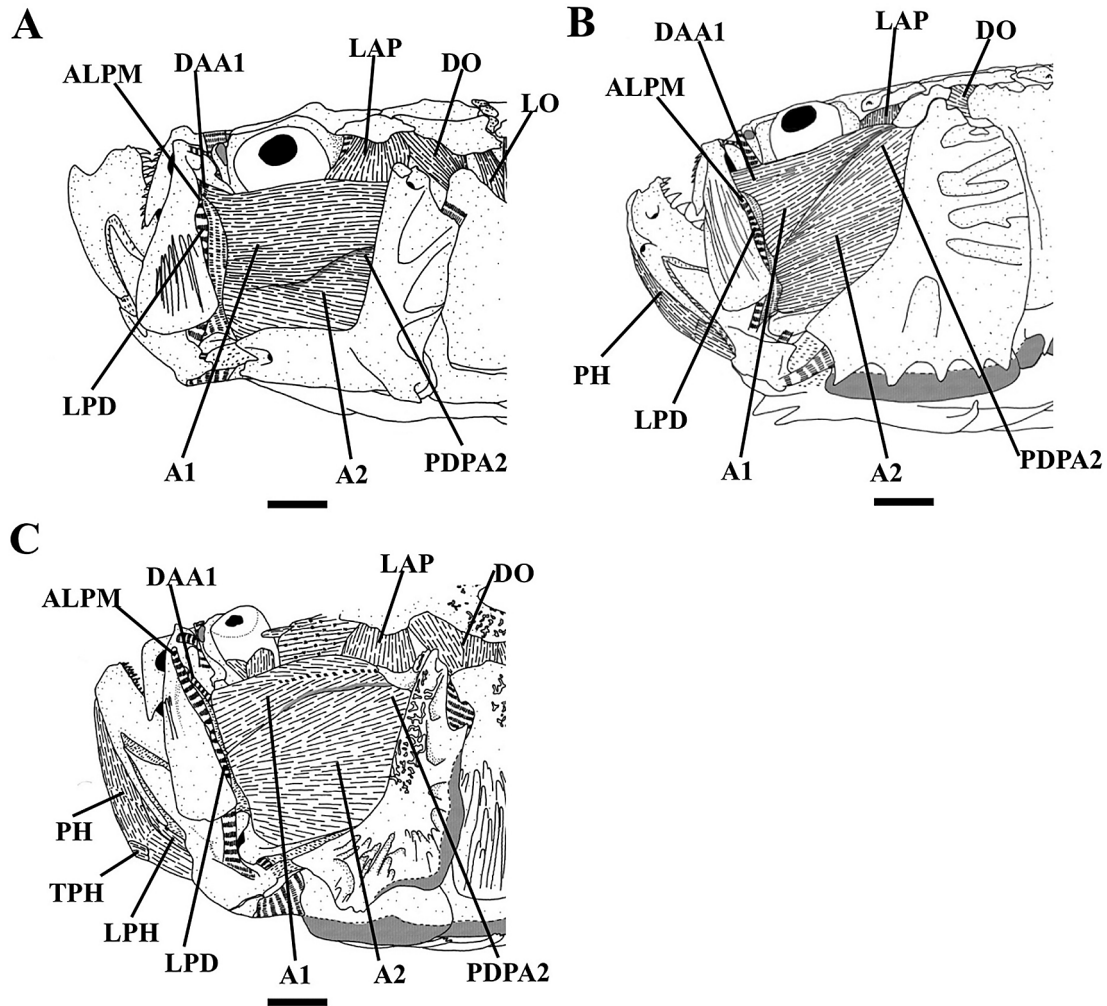


Fig. 43. Lateral aspect of cheek and cephalic muscles of left side. A, *Xenocephalus egregius*; B, *Uranoscopus tosae*; C, *Astroscopus zephyreus*. A1 and A2, adductor mandibulae sections 1 and 2, respectively; ALPM, attachment site of ligamentum primordium on maxilla; DAA1, dorsal attachment of A1 on maxilla; DO, dilatator operculi; LAP, levator arcus palatini; LO, levator operculi; LPD, ligamentum primordium; LPH, lateral fold of protractor hyoidei; PDPA2, posterodorsal portion of A2; PH, protractor hyoidei; TPH, transversus protractor hyoidei. Bars indicate 5 mm.

**TS 81.** *Adductor mandibulae section A $\omega$* . 0: restricted to anterior region of anguloarticular; 1: expanding posteriorly and mostly reaching to quadrate.

*Ingroup.* Section A $\omega$  of the adductor mandibulae is restricted to the anterior region of the anguloarticular in all uranoscopids (character 81-0), except *Kathetostoma* spp., which has A $\omega$  expanded posteriorly and mostly reaches to the quadrate (character 81-1).

*Outgroup.* Section A $\omega$  is typically restricted to the anterior region of the anguloarticular in typical percoids (character 81-0) (Imamura and Matsuura, 2003; this study).

**TS 82.** *Attachment site of ligamentum primordium on maxilla.* 0: posterior to dorsal attachment of A1; 1: anterior to dorsal attachment of A1.

*Ingroup.* The attachment site of the ligamentum primordium on the maxilla is posterior to the dorsal attachment of A1 in all uranoscopids (character 82-0), except *Astroscopus*

spp., which has the ligament attaching anterior to the dorsal attachment of A1 (character 82-1).

*Outgroup.* The attachment site of the ligament is typically posterior to the dorsal attachment of A1 in percoids (character 82-0) (Sasaki, 1989; Johnson, 1980; this study).

**Characters synapomorphic for the Uranoscopidae**

None.

**Autapomorphies for terminal taxa**

None.

**Other observed variations**

None.



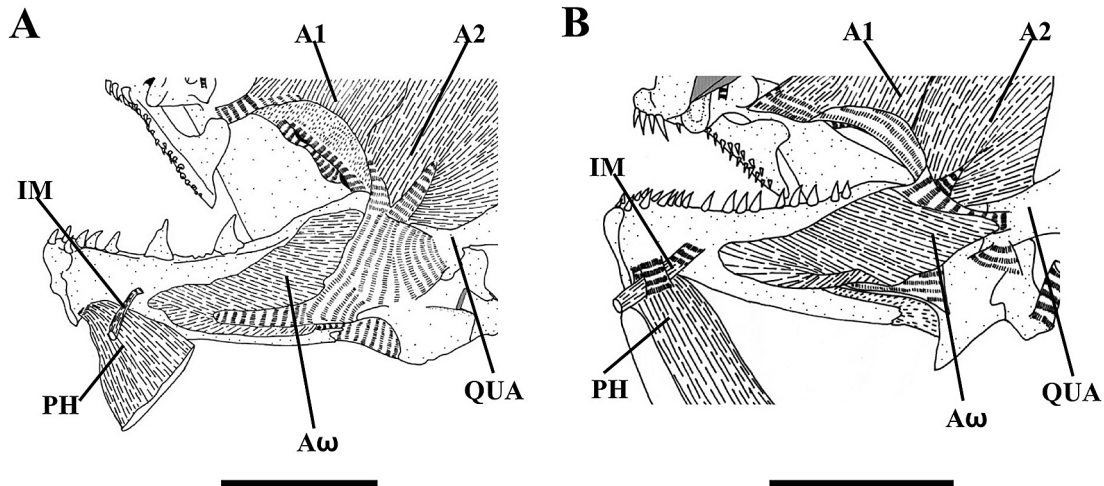


Fig. 44. Mesial aspect of cheek muscle, and upper and lower jaws of right side. A, *Uranoscopus cognatus*; B, *Kathetostoma giganteum*. A $\omega$ , adductor mandibulae sections  $\omega$ ; IM, intermandibularis; QUA, quadrate; other abbreviations are as in Fig. 43. Bars indicate 5 mm.

## 2-2. Cephalic muscles between cranium and suspensorium-operculum (Figs. 43, 45)

**Description.** The cephalic muscles between the cranium and suspensorium-operculum comprise of the levator arcus palatini, adductor arcus palatini, dilatator operculi, adductor operculi, adductor hyomandibulae and levator operculi.

The levator arcus palatini is located on the posterodorsal part of the suspensorium. It originates on the sphenotic and inserts onto the preopercle, hyomandibula, metapterygoid and symplectic.

The adductor arcus palatini is situated on the floor of the orbit. It originates on the lateral ethmoid, parasphenoid and prootic in *Xenocephalus* spp., *Pleuroscopus pseudodorsalis*, *K. canaster* and *K. nigrofasciatum*, and on the prevomer, lateral ethmoid, parasphenoid and prootic in *Uranoscopus* spp., *Ichthyoscopus* spp., *Astroscopus* spp., *Genyagnus monopterygius*, *K. cubana*, *K. averruncus*, *K. giganteum*, *K. laeve* and *K. albigutta*. This muscle inserts onto the lateral surface of the palatine and endopterygoid, and the mesial surface of the metapterygoid and hyomandibula.

The dilatator operculi originates on the sphenotic, pterotic and hyomandibula, and inserts onto the anterodorsal portion of the opercle.

The adductor hyomandibulae and adductor operculi are fused to each other at their origin. The fused muscular complex originates on the pterotic, prootic, exoccipital and intercalar. The adductor hyomandibulae insert on the posteromesial portion of the hyomandibula anteriorly and the adductor operculi inserts on the anteromesial portion of the opercle posteriorly.

The levator operculi is a large muscle that originates on the hyomandibula, pterotic, posttemporal and supracleithrum, and inserts onto the dorsomesial aspect of the opercle.

## Characters variable among Uranoscopidae

None.

## Characters synapomorphic for Uranoscopidae

*Levator operculi originating from supracleithrum.* The levator operculi originates on the hyomandibula, pterotic, posttemporal and supracleithrum in Uranoscopidae. In contrast, the muscle primitively originates only on the pterotic in percoids (Sasaki, 1989).

## Autapomorphies for terminal taxa

None.

## Other observed variations

None.

## 2-3. Ventral muscles of head (Figs. 43-50)

**Description.** The ventral muscles of the head include the intermandibularis, protractor hyoidei, hyohyoidei inferioris, hyohyoidei abductores, hyohyoidei adductores and newly recognized transversus protractor hyoidei.

The intermandibularis is a small bundle, binding the mesial sides of two dentaries.

The protractor hyoidei is a huge muscle situated mesial to the lower jaw. It originates on the anteromesial region of the dentary via a short tendon and inserts onto the posterolateral surface of the ceratohyal. The dorsal margin of this muscle is folded laterally and extends posteriorly for insertion on the mesial surface of the interopercle in *Astroscopus* spp. and *Ichthyoscopus* spp. (Figs. 43C, 46C, 47B), but is unfolded and does not extend posteriorly in other uranoscopids (Figs. 43B, 46A-B, 47A).

The transversus protractor hyoidei, first described here; developed on the mid-ventral part of the protractor

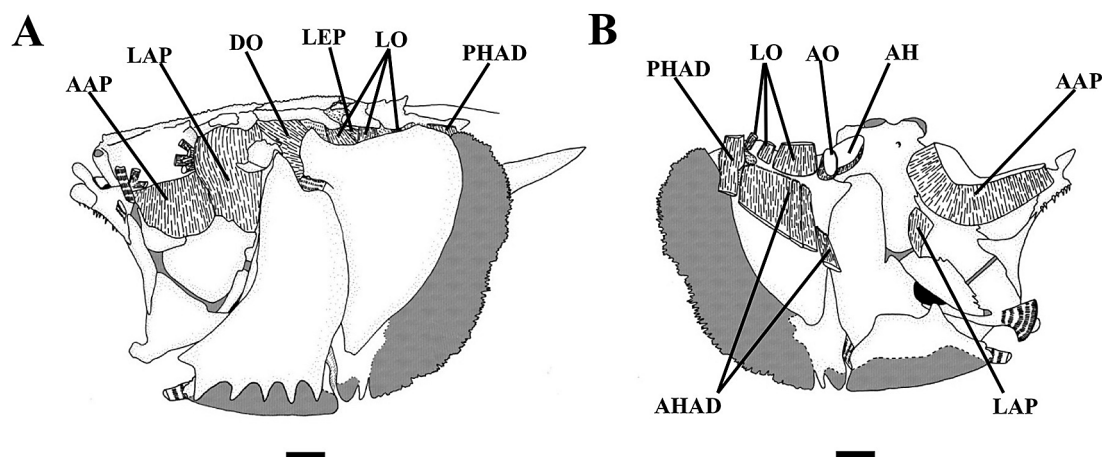


Fig. 45. Lateral (A) and mesial (B) views of cephalic and ventral muscles after removal of jaws and cheek muscles of left side in *Uranoscopus archionema*. AAP, adductor arcus palatini; AH, adductor hyomandibulae; AHAD, anterodorsal section of hyohyoidei adductores; AO, adductor operculi; DO, dilatator operculi; LAP, levator arcus palatini; LEP, levator pectoralis; LO, levator operculi; PHAD, posterodorsal section of hyohyoidei adductores. Bar indicates 5 mm.

hyoidei just anterior to its second myoseptum. The muscle is present in *Astroscopus* spp. and *Uranoscopus crassiceps* (Figs. 43C, 46B-C), but is absent in other uranoscopids.

The hyohyoidei inferioris is a slender muscle situated ventral to the anterior portion of the hyoid arch and anterior to the hyohyoidei abductor section 2. It originates from a raphe on the ventral midline formed by a fusion of the tendon from the anteroventral surface of the hypohyal and the hyohyoidei abductor section 2 from the second or third branchiostegal ray. It inserts onto the mesial face of the ceratohyal just anterior to the base of the fourth branchiostegal ray.

The hyohyoidei abductores comprises two sections, 1 and 2. Section 1 originates from the anteroventral region of the ceratohyal and inserts proximally on all branchiostegal rays, except the last. Section 2 originates on the raphe on which the hyohyoidei inferioris is inserted, and inserts on the second branchiostegal ray in all uranoscopids (Fig. 48A), except *Xenocephalus* spp., in which it inserts onto the third ray (Fig. 48B).

The hyohyoidei adductores is sheet-like and composed of two sections, the anterodorsal and posterodorsal sections. The anterodorsal section connects the mesial aspects of the branchiostegal rays and originates from the mesial surface of the opercle. The posterodorsal section connects the distal tips of the branchiostegal rays and is fused with the hyohyoidei abductor section 2 anteriorly. This section originates from the lateral surfaces of the supracleithrum and cleithrum in *Xenocephalus* spp., *Ichthyoscopus* spp., *Astroscopus* spp., *Genyanus monopterygius*, *Pleuroscopus pseudodorsalis*, *Uranoscopus cognatus*, *Kathetostoma canaster*, *K. giganteum*, *K. nigrofasciatum* and *K. laeve* (Fig. 50), while it originates on the lateral surface of the supracleithrum in other uranoscopids (Figs. 45A, 49).

### Characters variable among Uranoscopidae

**TS 83.** *Dorsal margin of protractor hyoidei.* 0: unfolded; 1: folded laterally and extending for insertion on mesial surface of interopercle.

*Ingroup.* The dorsal margin of the protractor hyoidei is unfolded in all uranoscopids (character 83-0), except *Astroscopus* spp. and *Ichthyoscopus* spp., which have the margin folded laterally and extending for insertion on the mesial surface of the interopercle (character 83-1).

*Outgroup.* The dorsal margin of the protractor hyoidei is unfolded in all percoids examined (character 83-0) (this study).

**TS 84.** *Transversus protractor hyoidei.* 0: absent; 1: present.

*Ingroup.* The transversus protractor hyoidei is present in *Astroscopus* spp. and *Uranoscopus crassiceps* (character 84-1), but is absent in other uranoscopids (character 84-0).

*Outgroup.* This muscle is absent in all percoids examined (character 84-0) (This study).

**TS 85.** *Insertion site of hyohyoidei abductor section 2.* 0: first branchiostegal ray; 1: second branchiostegal ray; 2: third branchiostegal ray (ordered as 0-1-2).

*Ingroup.* The hyohyoidei abductor section 2 is inserted on the second branchiostegal ray in all uranoscopids (character 85-1), except *Xenocephalus* spp., which has it inserted on the third (character 85-2).

*Outgroup.* The hyohyoidei abductores section 2 inserts on the first branchiostegal ray in all percoids examined (character 85-0) (this study).

*Remarks.* Seven branchiostegal rays are present in *Uranoscopus tosae* and *Kathetostoma cubana*, but all other uranoscopids have six. The first branchiostegal ray appears to be lost in those with six, making their anteriormost branchiostegal ray homologous with the second branchiostegal ray of

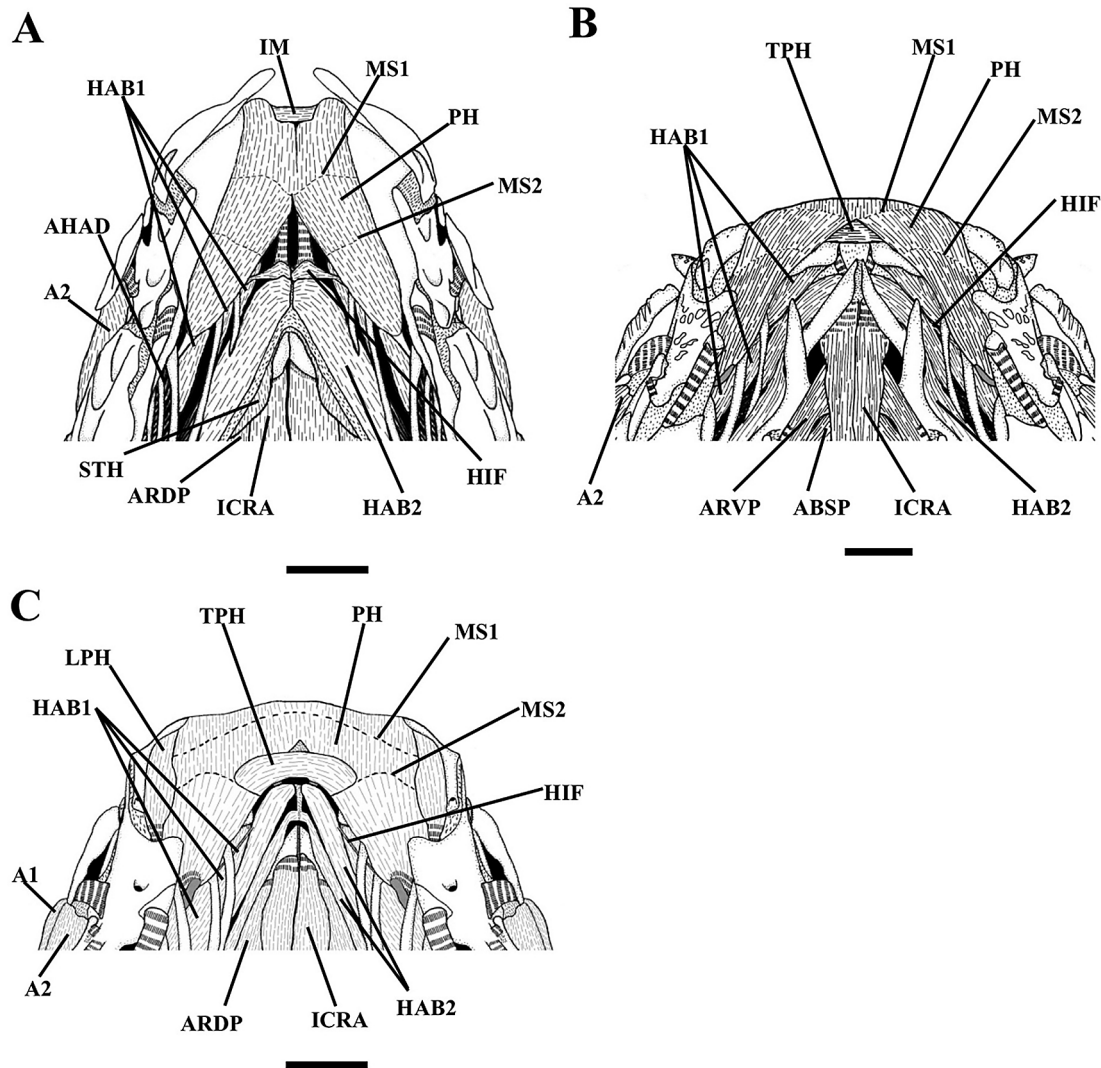


Fig. 46. Ventral aspect of ventral muscles of head (anterior at the top). A, *Xenocephalus elongatus*; B, *Uranoscopus crassiceps*; C, *Astroscopus zephyreus*. A1 and A2, adductor mandibulae sections 1 and 2, respectively; AHAD, anterodorsal section of hyohyoidei adductores; ARDP, arrector dorsalis pelvici; ARVP, arrector ventralis pelvici; HAB1, 2, first and second hyohyoidei abductores respectively; HIF, hyohyoidei inferioris; ICRA, infracarinalis anterior; IM, intermandibularis; LPH, lateral fold of protractor hyoidei; MS1,2, first and second myosepta respectively; PH, protractor hyoidei; STH, sternohyoideus; TPH, transversus protractor hyoidei. Scales indicate 5 mm.

*U. tosa* and *K. cubana*.

**TS 86.** Origin of posterodorsal section of hyohyoidei adductor: 0: mesial surface of opercle; 1: lateral surface of supra-cleithrum and cleithrum; 2: lateral surface of supra-cleithrum (unordered).

**Ingroup.** The posterodorsal section of the hyohyoidei adductor originates on the lateral surfaces of the supra-cleithrum and cleithrum in *Xenocephalus* spp., *Ichthyoscopus* spp., *Astroscopus* spp., *Genyagnus monopterygius*, *Pleuroscopus pseudodorsalis*, *Uranoscopus cognatus*, *Kathetostoma canaster*, *K. giganteum*, *K. nigrofasciatum*, and *K. laeve* (character 86-1), while it originates on the lateral surface of just the supra-cleithrum in other uranoscopids (character 86-2).

**Outgroup.** The section originates from the mesial surface of the opercle in all percoids examined (character 86-0) (this

study).

**Remarks.** Pietsch (1989) regarded the posterodorsal section of the hyohyoidei adductor originating on the posttemporal as a synapomorphy supporting the sister relation of *Uranoscopus* spp. and *Kathetostoma* spp. However, his examination of species was incomplete and his conclusion was therefore erroneous.

**Characters synapomorphic for the Uranoscopidae**

None.

**Autapomorphies for terminal taxa**

None.



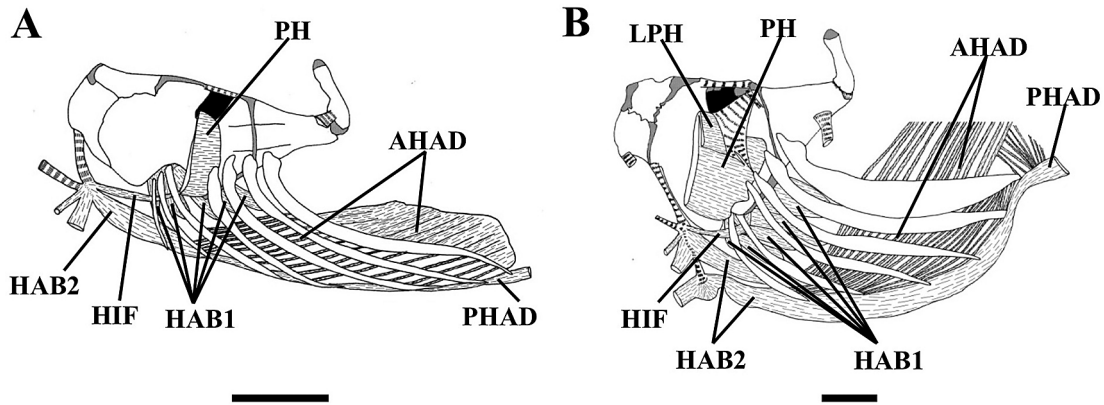


Fig. 47. Lateral aspects of ventral muscles on left side of head. A, *Uranoscopus tosaе*; B, *Ichthyoscopus lebecki*. PHAD, posterodorsal sections of hyohyoidei adductores; other abbreviations are as in Fig. 46. Bars indicate 5 mm.

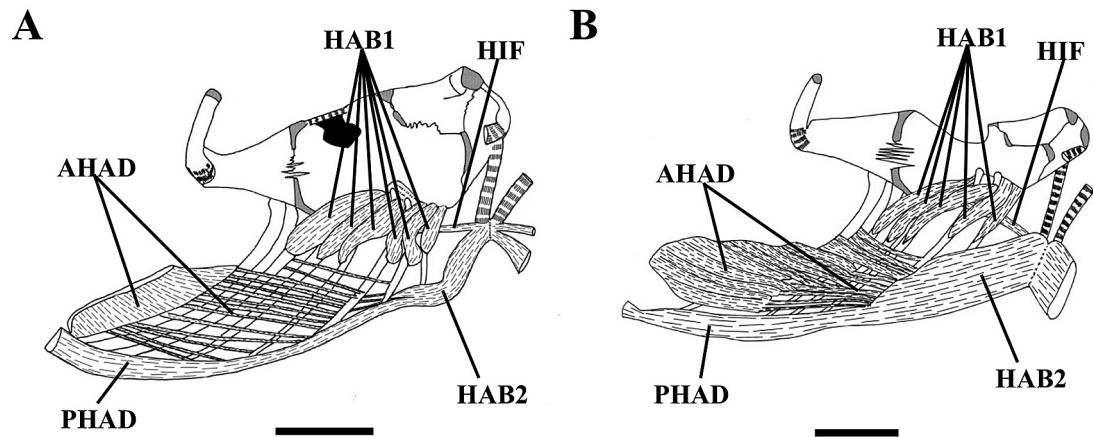


Fig. 48. Mesial aspects of ventral muscles on left side of head. A, *Uranoscopus tosaе*; B, *Xenocephalus elongatus*. Abbreviations are as in Figs. 46-47. Bars indicate 5 mm.

**Other observed variations**

None.

**2-4. Branchial muscles (Figs. 49-52)**

**Description.** The branchial muscles include the levator externus, levator internus, levator posterior, adductores, transversus dorsalis, obliquus dorsalis, retractor dorsalis, rectus communis, pharyngoclavicularis, rectus ventralis, obliquus ventralis, transversus ventralis, sphincter oesophagi and obliquus posterior.

The levator externus comprises three elements, the first, second and fourth levator externus. This muscle originates from the dorsolateral region of the prootic and pterotic, and inserts on the dorsal surface of the first, second and fourth epibranchials. The third element, that inserts on the third epibranchial, is absent. The lateral surface of the levator externus is covered by a thin muscular sheath.

The levator internus, situated mesial to the origin of the levator externus, consists of two elements, the anterior (= first levator internus) and posterior (= second levator internus) elements originating on the pterotic and prootic respectively.

The anterior element inserts on the anterior region of the third pharyngobranchial, and the posterior element on both the lateral region of the third pharyngobranchial and the proximal tip of the third epibranchial.

The levator posterior is a slender muscle that connects the exoccipital and intercalar to the posterodorsal edge of the fourth epibranchial.

The adductores has five sections. The first to third sections are small muscles that interconnect the anteromesial faces of the first to third epibranchials and ceratobranchials, respectively. The fourth and fifth sections are robust muscles, the fourth interconnecting the posteromesial portions of the fourth epibranchial and ceratobranchial, and the fifth interconnecting the posteromesial portion of the fourth ceratobranchial with the posterodorsal portion of the fifth ceratobranchial.

The transversus dorsalis comprises two elements, the transversus dorsalis anterior and posterior. The transversus dorsalis anterior, formed from the transversus epibranchial 2 and connecting the proximal tips of the right and left second epibranchials, is situated in the anterodorsal part of the upper gill



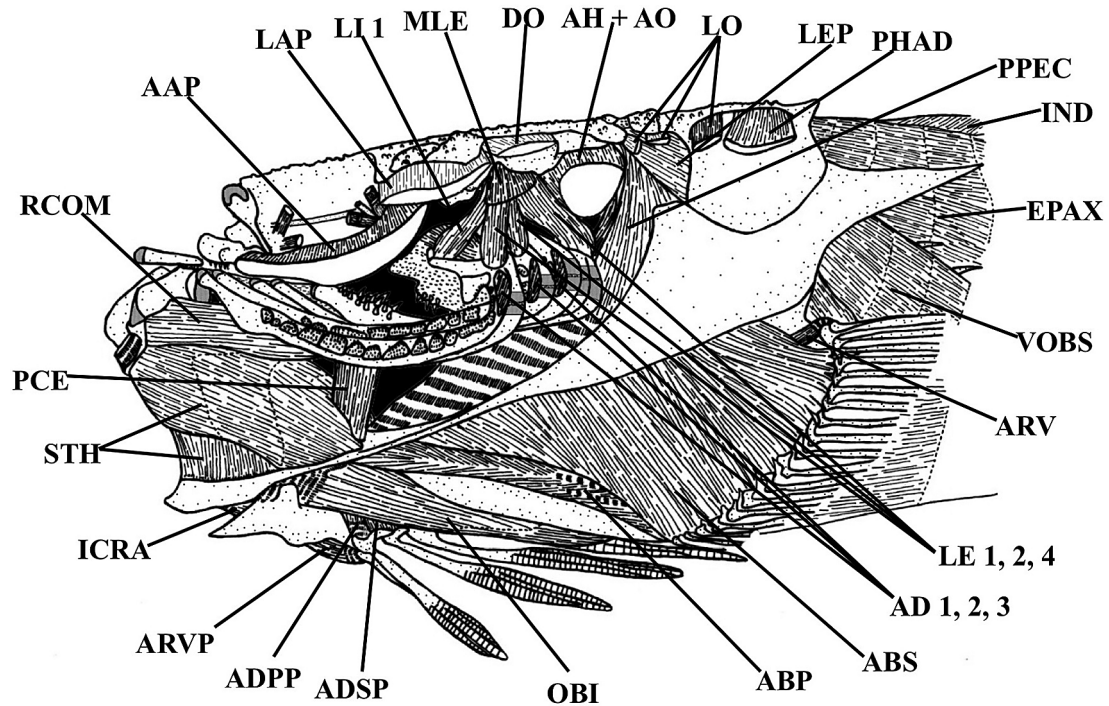


Fig. 49. Lateral aspect of head in *Uranoscopus crassiceps* after removal of infraorbitals, jaws, suspensorium, hyoid arch and their associated muscles. AAP, adductor arcus palatini; ABP, abductor profundus; ABS, abductor superficialis; AD1, 2, 3, adductor 1, 2 and 3 respectively; ADPP, adductor profundus pelvici; ADSP, adductor superficialis pelvici; AH + AO, fusion of adductor hyomandibulae and adductor operculi; ARV, arrector ventralis; ARVP, arrector ventralis pelvici; DO, dilatator operculi; EPAX, epaxialis; ICRA, infracarinalis anterior; IND, inclinatores dorsales; LAP, levator arcus palatini; LE1, 2, 4, levator externus 1, 2 and 4 respectively; LEP, levator pectoralis; LI1, levator internus 1; LO, levator operculi; MLE, muscular sheath covering lateral aspect of levatores externi; OBI, obliquus inferioris; PCE, pharyngoclavicularis externus; PHAD, posterodorsal section of hyohyoidei adductores; PPEC, protractor pectoralis; RCOM, rectus communis; STH, sternohyoideus; VOBS, ventral section of obliquus superioris. Bar indicates 5 mm.

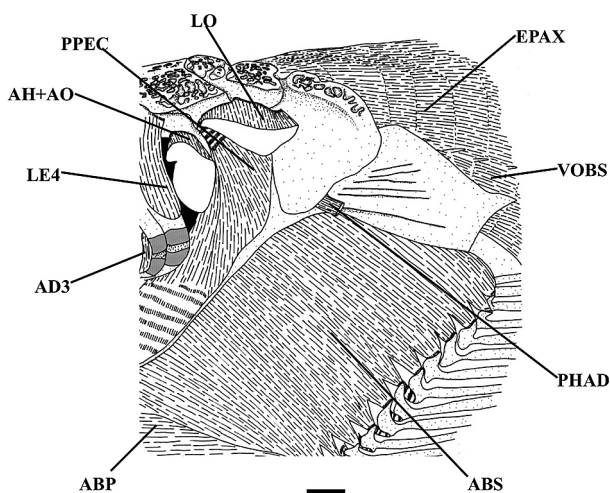


Fig. 50. Lateral aspect of pectoral fin girdle on left side in *Ichthyoscopus barbatus* after removal of infraorbitals, jaws, suspensorium, hyoid arch and their associated muscles. Abbreviations are as in Fig. 49. Bar indicates 5 mm.

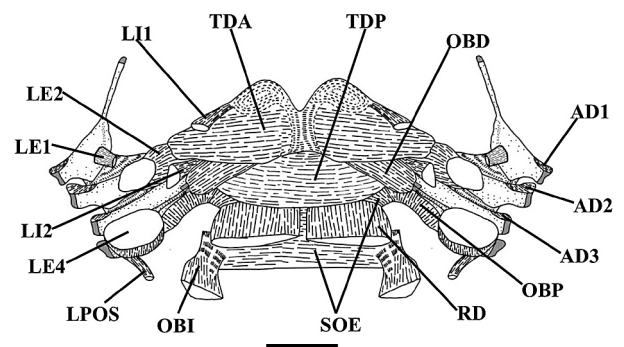


Fig. 51. Dorsal aspect of muscles serving upper branchial arches in *Kathetostoma nigrofasciatum* (anterior at top). AD1, 2, 3, adductor 1, 2 and 3 respectively; LE1, 2, 4, levator externus 1, 2 and 4 respectively; LI1, 2, levator internus 1 and 2; LPOS, levator posterior; OBD, obliquus dorsalis; OBI, obliquus inferioris; OBP, obliquus posterior; RD, retractor dorsalis; SOE, sphincter oesophagi; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior. Bar indicates 5 mm.

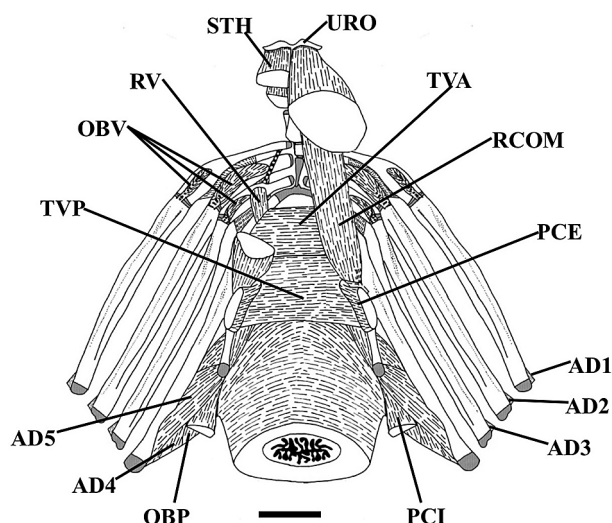


Fig. 52. Ventral aspect of muscles serving lower branchial arches in *Kathetostoma nigrofasciatum* (anterior at top). AD1, 2, 3, 4, 5, adductor 1, 2, 3, 4 and 5 respectively; OBP, obliquus posterior; OBV, obliquus ventralis; PCE, pharyngoclavicularis externus; PCI, pharyngoclavicularis internus; RCOM, rectus communis; RV, rectus ventralis; STH, sternohyoideus; TVA, transversus ventralis anterior; TVP, transversus ventralis posterior; URO, urohyal. Bar indicates 5 mm.

arch. A transversus pharyngobranchial 2 is absent. The transversus dorsalis posterior binds the third and fourth epibranchials of the two sides in *Astroscopus* spp., *Xenocephalus* spp., *Genyagnus monopterygius*, *Pleuroscopus pseudodorsalis*, *Uranoscopus bicinctus*, *U. archionema* and *U. polli*, but binds the fourth epibranchials of the two sides in the remaining uranoscopids.

The obliquus dorsalis originates on the third pharyngobranchial and inserts on the third and fourth epibranchials.

The retractor dorsalis is a thick longitudinal muscle that connects the third and fourth pharyngobranchials with the ventrolateral corners of the anterior vertebrae. The rectus communis originates on the posterolateral surfaces of the urohyal and the first basibranchial, and inserts on the ventrolateral face of the fifth ceratobranchial.

The pharyngoclavicularis, connecting the fifth ceratobranchial with the cleithrum, has two elements, the externus and internus. The pharyngoclavicularis externus inserts on the ventral portion of the fifth ceratobranchial, while the pharyngoclavicularis internus insert on the dorsal aspect of the posterior portion of the fifth ceratobranchial. The origin of the pharyngoclavicularis externus on the cleithrum is sandwiched by the posterior portion of the sternohyoideus.

The rectus ventralis connects the third hypobranchial with the fourth ceratobranchial.

The obliquus ventralis, consists of three elements that interconnect the first to third hypobranchials with the first to third ceratobranchials, respectively. The third element connecting the third hypobranchial with the third ceratobranchial is pres-

ent in all uranoscopids, except *Kathetostoma albigutta*, which lacks it.

The transversus ventralis comprises two muscles, the transversus ventralis anterior and posterior, interconnecting the fourth and fifth ceratobranchials of the two sides, respectively. The posterodorsal margin of the transversus ventralis anterior is overlapped by the anteroventral margin of the transversus ventralis posterior in all uranoscopids, except *Kathetostoma albigutta*, in which the muscles are separated.

The sphincter oesophagi surrounds the esophagus in the posterior portion of the branchial arch and partially attaches to the posterior margin of the third and fourth pharyngobranchials. The muscle is also connected with a body muscle, the obliquus inferioris, on the lateral surface of the esophagus.

The obliquus posterior connects the fourth epibranchial with the fifth ceratobranchial.

#### Characters variable among Uranoscopidae

None.

#### Characters synapomorphic for Uranoscopidae

*Absence of third levator externus.* The third levator externus is absent in the Uranoscopidae. In contrast, this muscle is present in percoids (Sasaki, 1989).

*Presence of first, second and third adductores.* The first, second, and third adductores, interconnecting the anteromedial faces of the first to third epibranchials and ceratobranchials respectively, are present in Uranoscopidae. The muscles are typically absent in percoids (Imamura and Matsuura, 2003; this study).

*Pharyngoclavicularis internus inserted onto dorsal aspect of fifth ceratobranchial.* The pharyngoclavicularis internus inserts on the dorsal aspect of the posterior portion the fifth ceratobranchial in all uranoscopids, but typically inserts on the ventral portion of the fifth ceratobranchial in percoids (Sasaki, 1989).

*Absence of transversus pharyngobranchial 2.* A transversus pharyngobranchial 2 is absent in all uranoscopids, whereas the element is primitively present in percoids (Springer and Johnson, 2004; this study).

#### Autapomorphies for terminal taxa

*Absence of third obliquus ventralis.* The third obliquus ventralis is absent in *Kathetostoma albigutta*, but is present in other uranoscopids and typically present in percoids (Sasaki, 1989). The absence of the muscle is regarded as an autapomorphy of *K. albigutta*.

*Transversus ventralis anterior and posterior separated.* The transversus ventralis anterior and posterior are separated in *Kathetostoma albigutta*, but overlap in other uranoscopids and typically in percoids (Sasaki, 1989; Imamura, 1996). The former character state is regarded as an autapomorphy of *K. albigutta*.

**Other observed variations**

None.

**2-5. Pectoral and pelvic muscles (Figs. 49-50, 53-58)**

**Description.** The pectoral and pelvic muscles are composed of a pair of muscles on each side of the pectoral and pelvic girdles. The sternohyoideus, levator pectoralis and protractor pectoralis, are associated with these girdles, and described in this section.

Pectoral muscles include the levator pectoralis, protractor pectoralis, abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor profundus and arrector dorsalis. A coracoradialis is absent.

The abductor superficialis is an outer muscle on the lateral surface of the pectoral girdle that originates on the posterior surface of the cleithrum and inserts on the bases of the pectoral fin rays. The origin of the abductor superficialis on the lower limb of the cleithrum is posterior to that of the abductor profundus in all uranoscopids (Fig. 54A), except *Astroscopus* spp., in which the origin is anterior to it (Fig. 55A). The abductor superficialis is narrow and restricted to the ventral part of lateromedial aspect of the cleithrum in all uranoscopids (Figs. 49, 53A, 54A), except *Astroscopus* spp. and *Ichthyoscopus* spp., in which have a broad muscle that expands to occupy midlateral most portion of the cleithrum (Figs. 50, 55A).

The abductor profundus is an inner muscle of the lateral surface of the pectoral muscles that originates on the mesial surface of the cleithrum and the lateral surfaces of the coracoid, scapula and actinosts. It inserts on the bases of all pectoral fin rays.

The arrector ventralis is situated mesial to the abductor superficialis and dorsal to the abductor profundus. The

muscle is large and originates on the mesial surface of the middle portion of the cleithrum in all uranoscopids (Fig. 54B), except *Astroscopus* spp. and *Ichthyoscopus* spp., which have a small muscle that originates on the lateral surface of upper limb of the cleithrum (Fig. 55B). The arrector ventralis inserts on the base of the mesial segment of the uppermost ray.

The adductor superficialis is a dorsomesial muscle on the mesial surface of the pectoral girdle that originates on the dorsomesial aspect of the cleithrum and inserts on all rays, except the uppermost.

The adductor profundus is situated lateral to the adductor superficialis. It originates on the mesial surfaces of the cleithrum, scapula, coracoid and actinosts, and inserts on the bases of all rays, except the uppermost.

The arrector dorsalis is located lateral to the adductor superficialis and dorsal to the adductor profundus. It originates on the mesial surface of the cleithrum and scapula, and inserts on the base of the uppermost ray.

Pelvic muscles comprise dorsal and ventral elements. The dorsal elements include the adductor superficialis pelvius, adductor profundus pelvius, arrector dorsalis pelvius and extensor proprius, while the ventral elements include the abductor superficialis pelvius, abductor profundus pelvius and the arrector ventralis pelvius.

The adductor superficialis pelvius covers the posterior portion of the adductor profundus pelvius anteriorly, and is attached to the extensor proprius laterally and the pelvis posteromesially. It inserts on the bases of the soft rays and spine in *Pleuroscopus pseudodorsalis*, *Xenocephalus* spp. and *Kathetostoma* spp. (Figs 56A, D), but inserts only on the bases of the soft rays in *Uranoscopus* spp., *Ichthyoscopus* spp., *Astroscopus* spp. and *Genyagnus monoptyerygius* (Figs. 49,

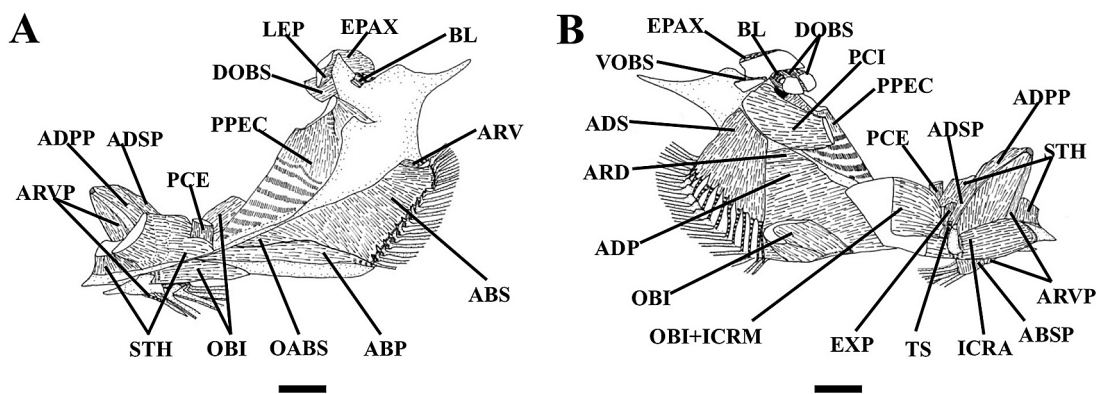


Fig. 53. Lateral (A) and mesial (B) aspects of pectoral and pelvic girdles on left side of *Uranoscopus polli*. ABP, abductor profundus; ABS, abductor superficialis; ABSP, abductor superficialis pelvius; ADP, adductor profundus; ADPP, adductor profundus pelvius; ADS, adductor superficialis; ADSP, adductor superficialis pelvius; ARD, arrector dorsalis; ARV, arrector ventralis; ARVP, arrector ventralis pelvius; BL, Baudelot's ligament; DOBS, dorsal section of obliquus superioris; EPAX, epaxialis; EXP, extensor proprius; ICRA, infracarinalis anterior; LEP, levator pectoralis; OABS, origin of abductor superficialis on lower limb of cleithrum; OBI, obliquus inferioris; OBI + ICRM, fusion of obliquus inferioris and infracarinalis medius; PCE, pharyngoclavicularis externus; PCI, pharyngoclavicularis internus; PPEC, protractor pectoralis; STH, sternohyoideus; TS, transverse septum; VOBS, ventral section of obliquus superioris. Bars indicate 5 mm.



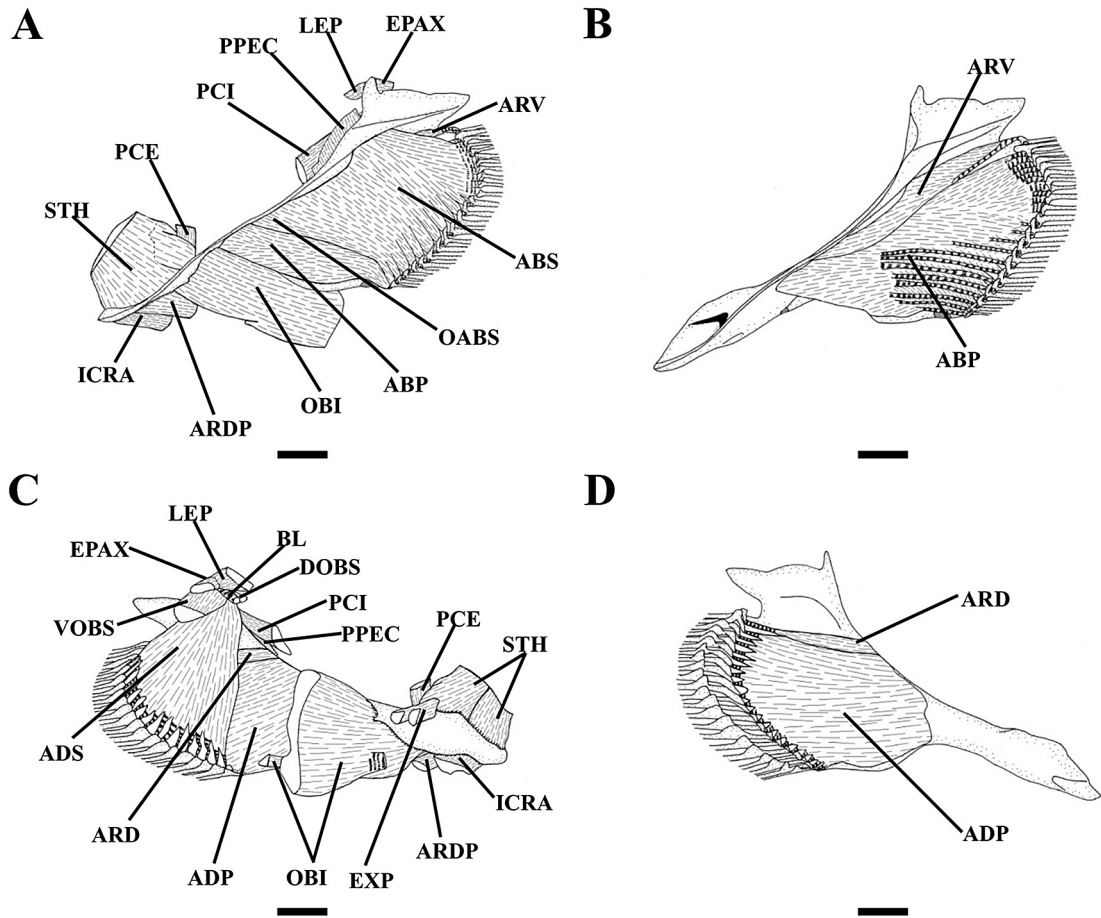


Fig. 54. Lateral (A and B) and mesial (C and D) aspects of pectoral girdle on left side of *Xenocephalus elongatus*. B and D, after removal of ABS, ADS, ARDP, BL, DOBS, EPAX, EXP, ICRA, LEP, OBI, PCE, PCI, PPEC, STH and VOBS. ARDP, arrector dorsalis pelvici; other abbreviations are as in Fig. 53. Bars indicate 5 mm.

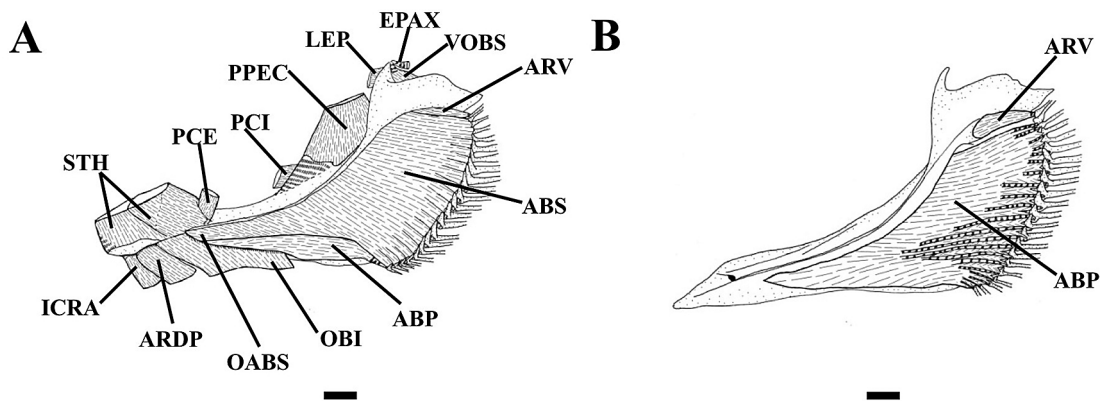


Fig. 55. Lateral aspects of pectoral girdle on left side of *Astroscopus y-graecum*. A, after removal of skin; B, after removal of ABS, ADS, ARDP, BL, DOBS, EPAX, EXP, ICRA, LEP, OBI, PCE, PCI, PPEC, STH and VOBS. Abbreviations are as in Figs. 53-54. Bars indicate 5 mm.

53A, 58B).

The adductor profundus pelvici originates on the dorsal surface of the pelvis and inserts on the bases of the soft rays via tendons.

The arrector dorsalis pelvici originates on the anteroventral aspect of the cleithrum and lateral surface of the pelvis in

*Astroscopus* spp., *Kathetostoma* spp., *Xenocephalus* spp., *Pleuroscopus pseudodorsalis* and *Genyagnus monopterygius* (Figs. 54A, C, 55A, 56A, C-D), while it originates on the lateral surface of the pelvis in *Ichthyoscopus* spp. (Fig. 58). It inserts on the base of the pelvic fin spine. The muscle is absent in *Uranoscopus* spp.



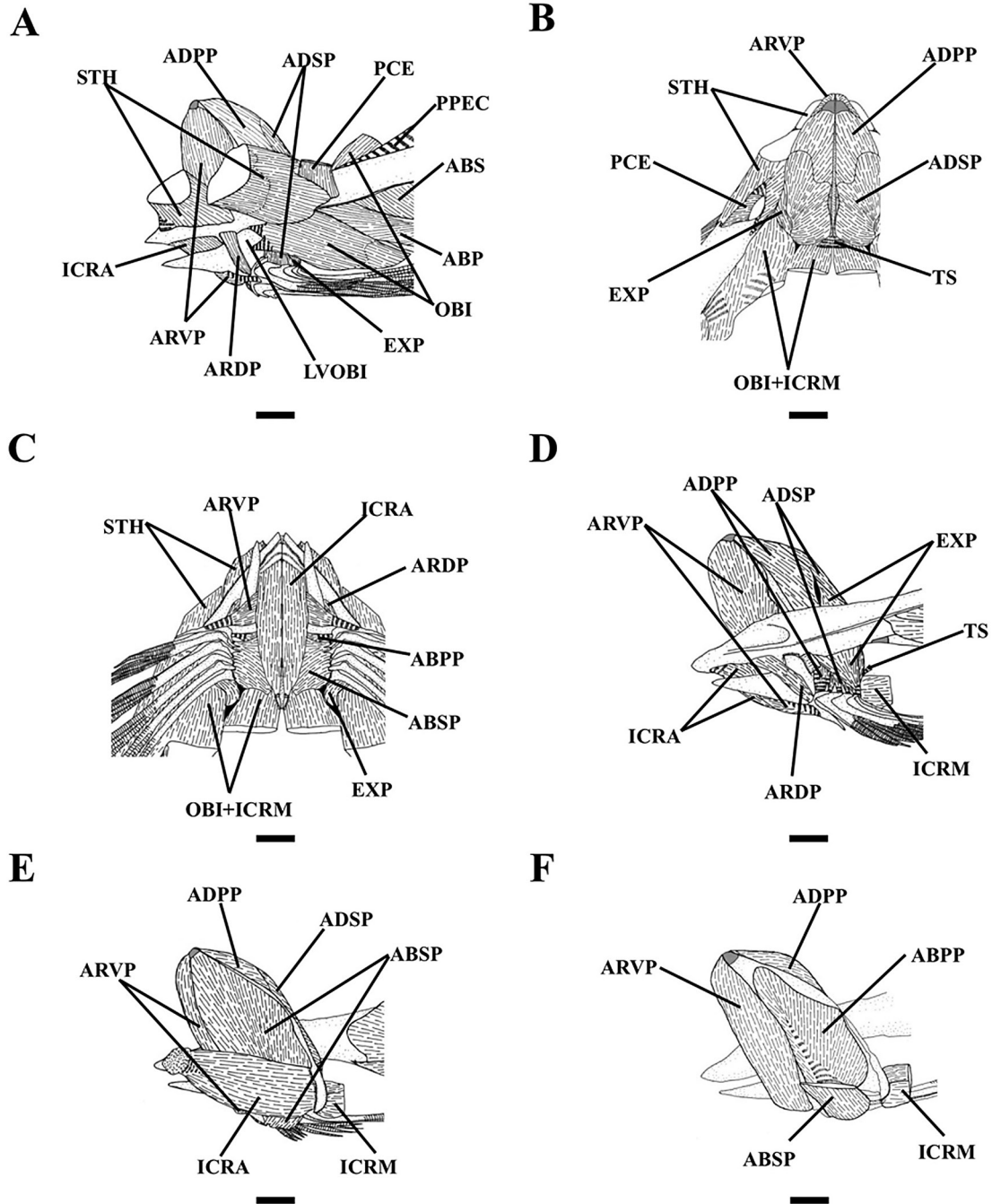


Fig. 56. Pelvic and associated muscles in *Kathetostoma laeve*. Lateral (A), dorsal (B) and ventral (C) aspects of pelvic girdle; lateral (D) and mesial (E) aspects of pelvic girdle after removal of STH, PCE, PPEC and OBI; mesial (F) aspect of pelvic girdle after removal ABSP, ADSP and ICRA. ABPP, abductor profundus pelvis; LVOBI, lateral surface of pelvis for attachment with obliquus inferioris; other abbreviations are as in Figs. 53-54. Bars indicate 5 mm.

The extensor proprius lies above the adductor superficialis pelvis and adductor profundus pelvis, and originates on the dorsolateral border of the pelvis and mesial aspect of the cleithrum. It inserts on the innermost ray.

The abductor superficialis pelvis lies under the abductor profundus pelvis, and originates on the ventral surface of the pelvis. It inserts on the bases of the soft rays and spine.

The abductor profundus pelvis, situated above the abduc-

tor superficialis pelvis and arrector ventralis pelvis, originates on the ventral surface of the pelvis, and inserts on the bases of the soft rays.

The arrector ventralis pelvis originates on the lateral margin of the ventral surface of the pelvis and inserts on the spine.

The other muscles associated the pectoral and pelvic girdles comprise the sternohyoideus, levator pectoralis, protractor pectoralis, epaxialis, obliquus superioris, obliquus

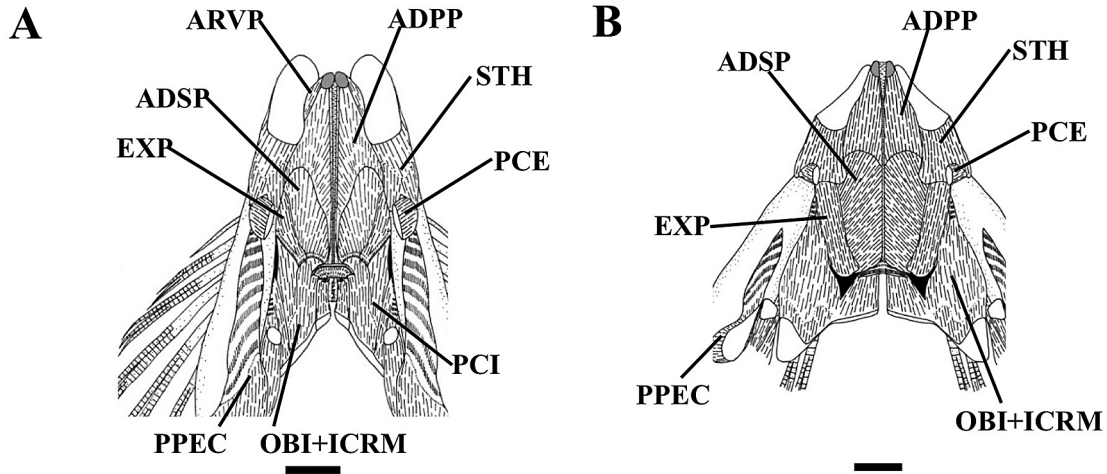


Fig. 57. Dorsal aspects of pelvic muscles (anterior at top). A, *Astroscopus zephyreus*; B, *Xenocephalus australiensis*. Abbreviations are as in Figs. 53-54. Bars indicate 5 mm.

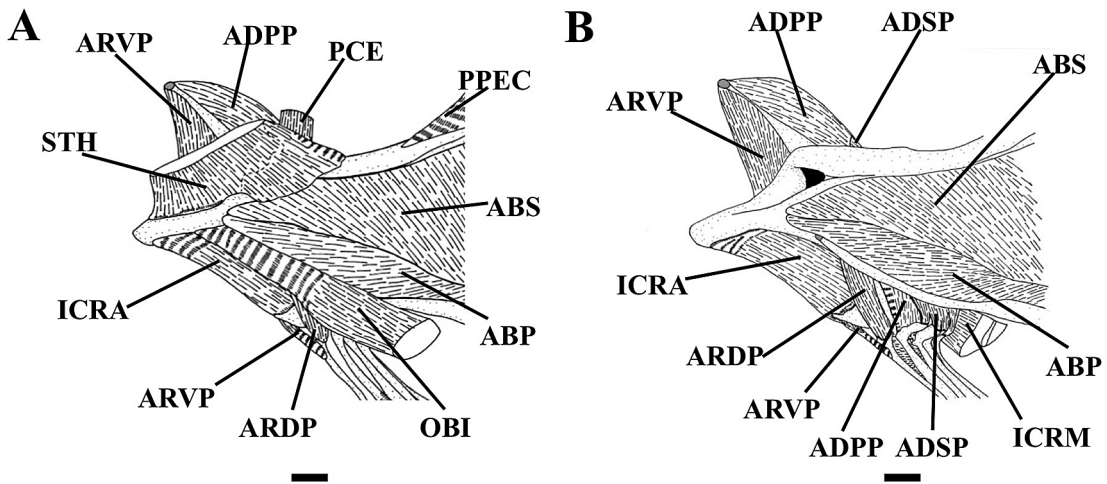


Fig. 58. Lateral aspects of pelvic muscles on left side of *Ichthyoscopus sammio*. A, after removal of skin; B, after removal of STH, PCE, PPEC and OBI. Abbreviations are as in Figs. 53-54. Bars indicate 5 mm.

inferioris, infracarinalis anterior and infracarinalis medius (the last five muscles are described in other sections).

The sternohyoideus is a massive muscle that originates on the anterior portion of the cleithrum, and inserts on the ventrolateral aspects of the urohyal. It extends mesially where it attaches to the adductor superficialis pelvicus in *Xenocephalus elongatus* and *X. australiensis* (Fig. 57B), but is separated from that muscle in other uranoscopids (Fig. 57A).

The levator pectoralis originates on the posterior aspect of the cranium, including the pterotic, intercalar and exoccipital, and inserts on the dorsal portion of the pectoral girdle, including the posttemporal, supracleithrum and cleithrum.

The protractor pectoralis connects the cranium and cleithrum. It originates on the pterotic and inserts on the cleithrum. It is thick and massive posterodorsally and becomes thin and sheet-like, changing to connective tissue anteroventrally.

#### Characters variable among Uranoscopidae

**TS 87.** *Origin of abductor superficialis on lower limb of cleithrum.* 0: posterior to that of abductor profundus; 1: anterior to that of abductor profundus.

*Ingroup.* The origin of the abductor superficialis on the lower limb of the cleithrum is anterior to that of the abductor profundus in *Astroscopus* spp. (character 87-1), but posterior to that of the abductor profundus in other uranoscopids (character 87-0).

*Outgroup.* The origin of the abductor superficialis on the lower limb of the cleithrum is posterior to that of the abductor profundus in primitively percoids (character 87-0) (Sasaki, 1989; this study).

**TS 88.** *Abductor superficialis.* 0: narrow and restricted to ventral part of lateromedial aspect of cleithrum; 1: broad and expanding to occupy midlateral most portion of cleithrum.

*Ingroup.* The abductor superficialis is narrow and restricted to the ventral part of the lateromedial aspect of the

cleithrum in all uranoscopids (character 88-0), except *Astroscopus* spp. and *Ichthyoscopus* spp., which have a broad muscle that expands to occupy midlateral most portion of the cleithrum (character 88-1).

**Outgroup.** The muscle is typically narrow and originates from the ventral part of the lateromedial aspect of the cleithrum in percoids (character 88-0) (Sasaki, 1989; Shinohara, 1994; this study).

**TS 89.** *Arrector dorsalis pelvicius*. 0: present, originating on pelvis; 1: present, originating on cleithrum and pelvis; 2: absent (unordered).

**Ingroup.** The arrector dorsalis pelvicius is present and originates on the cleithrum and pelvis in *Kathetostoma* spp., *Astroscopus* spp., *Xenocephalus* spp., *Genyagnus monopterygius* and *Pleuroscopus pseudodorsalis* (character 89-1), and from the pelvis in *Ichthyoscopus* spp. (character 89-0). This muscle is absent in *Uranoscopus* spp. (character 89-2).

**Outgroup.** The muscle is typically present and originates on the pelvis in percoids (character 89-0) (Sasaki, 1989; this study).

**TS 90.** *Sternohyoideus* and *adductor superficialis pelvicius*. 0: separated; 1: attached.

**Ingroup.** The sternohyoideus is attached to the adductor superficialis pelvicius in *Xenocephalus elongatus* and *X. australiensis* (character 90-1), but is separated from the latter muscle in other uranoscopids (character 90-0).

**Outgroup.** The sternohyoideus and the adductor superficialis pelvicius are separated in all percoids examined (character 90-0) (this study).

**Characters synapomorphic for the Uranoscopidae**

**Absence of coracoradialis.** The coracoradialis is absent in all uranoscopids, while it is primitively present in percoids (Yabe, 1985; this study).

**Extensor proprius originating from pelvis and cleithrum.** The extensor proprius originates on the pelvis and cleithrum in the Uranoscopidae. In contrast, this muscle primitively originates only on the pelvis in percoids (Sasaki, 1989).

**Autapomorphies for terminal taxa**

None.

**Other observed variations**

None.

**2-6. Muscles associated with median fins (Figs. 53-61, 62B)**

**Description.** Three categories of muscles (erector, depressor and inclinator) are present in both dorsal and anal fins, connecting the proximal and distal pterygiophores to the fin ray bases by aponeuroses. As carinal muscles, epaxialis and hypaxialis are associated with the dorsal and anal fins, as well as other skeletal parts they are also described in this

chapter.

**Dorsal fin muscles.** The dorsal fin muscles comprise the inclinatores dorsales, erectores dorsales, depressores dorsales, and fibres of epaxialis associated with the dorsal fin. The erectores dorsales and depressores dorsales, are present only for soft rays in *Genyagnus monopterygius*, *Pleuroscopus pseudodorsalis*, *Xenocephalus elongatus*, *X. egregius*, *X. armatus*, *Kathetostoma albigutta*, *K. averruncus*, *K. cubana* and *K. nigrofasciatum* (Fig. 60B), whereas those for both spines and soft rays are present in other uranoscopids (Figs. 59, 60A).

The inclinatores dorsales are superficial muscles that are continuous, thin, sheet-like, and well developed anteriorly and become gradually reduced posteriorly. These muscles overlie the epaxialis and originate from the fascia between the skin and epaxialis. They insert onto the bases of dorsal fin rays, the distal aspects of proximal pterygiophores and the distal pterygiophores.

The erectores dorsales include elements for spines and soft rays. The elements for the spines, if present, originate on the anterolateral aspect of the proximal pterygiophore with which the ray articulates, and the posterolateral aspect of the preceding pterygiophore, while the elements for the soft rays originate on the lateral aspect of the proximal pterygiophore with which the ray articulates. The erectores dorsales insert on the anteromesial portion of the ray bases.

The depressores dorsales comprise elements for spines and soft rays. The elements for spines, if present, originate on the posterolateral aspect of the proximal pterygiophores, with which the ray articulates, while the elements for soft rays originate on the anterolateral aspect of the subsequent proximal pterygiophore. The depressores dorsales insert on

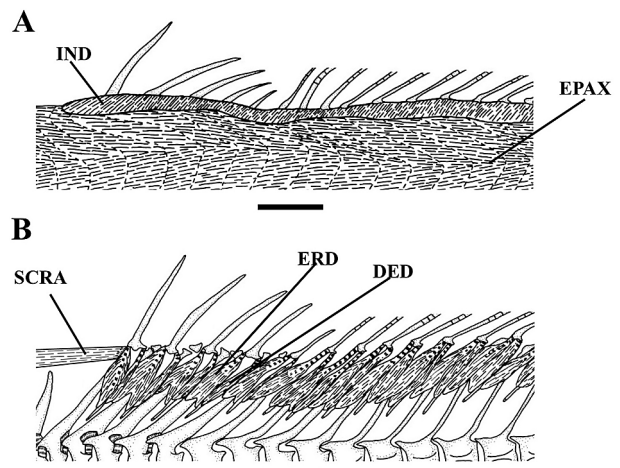


Fig. 59. Lateral aspect of median fin muscles on left side in *Astroscopus zephyreus*. A, anterior part of dorsal fin after removal of skin; B, after removal of epaxialis and inclinatores dorsales. DED, depressores dorsales; ERD, erectores dorsales; EPAX, epaxialis; IND, inclinatores dorsales; SCRA, supracarinalis anterior. Bars indicate 5 mm.



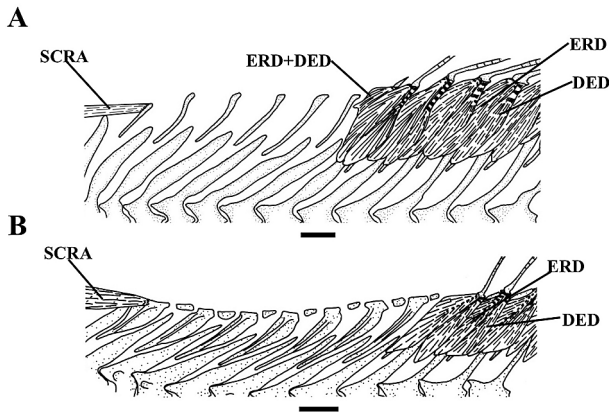


Fig. 60. Lateral aspects of median fin muscles of anterior part of dorsal fin on left side after removal of epaxialis and inclinatores dorsales. A, *Kathetostoma laeve*; B, *Xenocephalus elongatus*. ERD + DED, fusion of erectores dorsales and depressores dorsales; other abbreviations are as in Fig. 59. Bars indicate 5 mm.

the posterolateral portion of the ray bases.

The epaxialis covers the erectores dorsales and depressores dorsales and inserts on the distal aspect of the proximal pterygiophores of dorsal fin rays.

*Anal fin muscles.* Anal fin muscles consist of the inclinatores anales, erectores anales and depressores anales. Some fibres of the hypaxialis are also associated with the anal fin.

The inclinatores anales are superficial muscles that are well developed anteriorly and gradually reduce in mass posteriorly. They originate from the fascia between the skin and the hypaxialis, and insert on the base of the anal fin rays.

The erectores anales each originate on the lateral aspect of

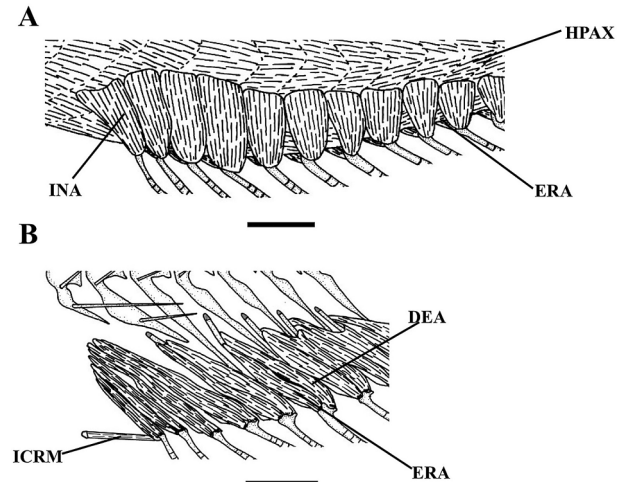


Fig. 61. Lateral aspects of median fin muscles on left side of *Astroscopus zephyreus*. A, anterior part of anal fin after removal of skin; B, after removal of hypaxialis and inclinatores anales. DEA, depressores anales; ERA, erectores anales; HPAX, hypaxialis; ICRM, infracarinalis medius; INA, inclinatores anales. Bars indicate 5 mm.

the proximal pterygiophore with which a ray articulates and inserts on the anteromesial aspect of the anal ray base.

The depressores anales originate from the posterolateral aspects of the proximal pterygiophores, with which the rays articulate, and the anterolateral aspect of the subsequent proximal pterygiophore for all anal fin rays, except the ray on the anteroventral portion of the first proximal pterygiophore. The muscle for this ray originates on the lateral aspect of the first proximal pterygiophore. The muscles insert on the posterolateral aspects of the bases of the anal fin rays.

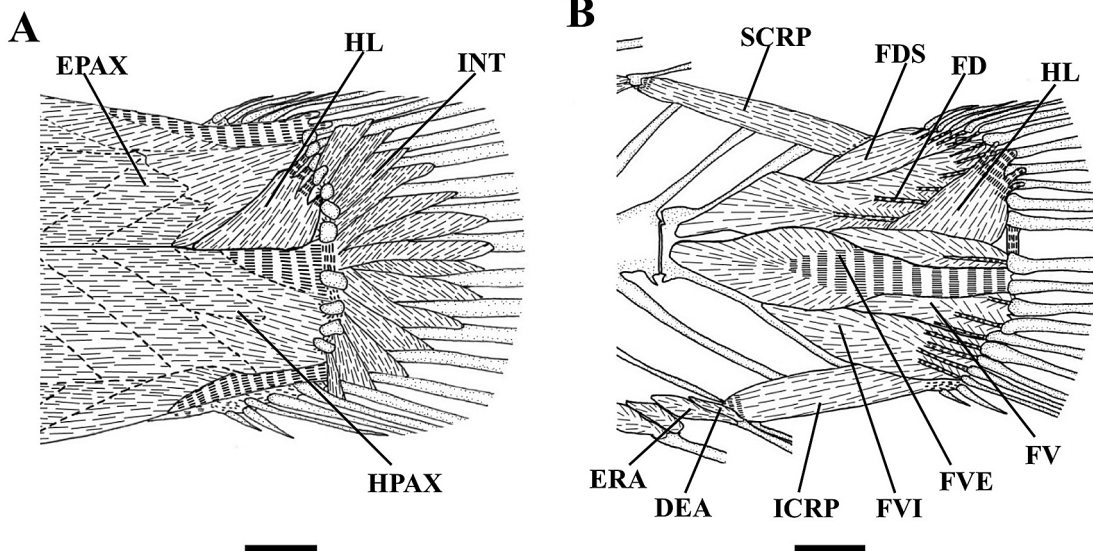


Fig. 62. Lateral views of caudal muscles on left side of *Kathetostoma albigutta*. A, superficial view after removal of skin; B, after removal of epaxialis (EPAX) and hypaxialis (HPAX). DEA, depressores anales; ERA, erectores anales; FD, flexor dorsalis; FDS, flexor dorsalis superior; FV, flexor ventralis; FVE, flexor ventralis externus; FVI, flexor ventralis inferior; HL, hypochochordal longitudinalis; ICRP, infracarinalis posterior; INT, interradians; SCRP, supracarinalis posterior. Bars indicate 5 mm.



The hypaxialis covers the erectores anales and depressores anales and inserts on the distal faces of the proximal pterygiophores of the anal fin rays.

**Carinal muscles.** The carinal muscles are paired muscles, lying on the dorsal and ventral midlines of the body. They comprise five independent elements: the supracarinalis anterior, supracarinalis posterior, infracarinalis anterior, infracarinalis medius and infracarinalis posterior. A supracarinalis medius is absent. The supracarinalis anterior and infracarinalis medius are mostly fused with body muscles.

The supracarinalis anterior is a thick muscle, connecting the posterodorsal aspect of the supraoccipital and the anterolateral aspect of the first proximal pterygiophore of the dorsal fin.

The supracarinalis posterior is a rod-like muscle linking the terminal pterygiophore of dorsal fin and the neural spine of the third preural centrum.

The infracarinalis anterior is a thick muscle connecting the anteroventral aspect of the cleithrum to the posteroventral portion of pelvis (or pelvic spur) and the subpelvic process.

The infracarinalis medius is a paired thick muscle connecting the posterior portion of the pelvis and the anteroventral aspect of the first proximal pterygiophore of the anal fin.

The infracarinalis posterior is a rod-like muscle interconnecting the terminal proximal pterygiophore of the anal fin and the hemal spine of the third preural centrum.

#### Characters variable among Uranoscopidae

None.

#### Characters synapomorphic for the Uranoscopidae

None.

#### Autapomorphies for terminal taxa

None.

#### Other observed variations

*Presence of erectores dorsales and depressores dorsales for only soft rays.* The erectores dorsales and depressores dorsales are present only for soft rays in *Genyagnus monopterygius*, *Pleuroscopus pseudodorsalis*, *Xenocephalus elongatus*, *X. egregius*, *X. armatus*, *Kathetostoma albigutta*, *K. averruncus*, *K. cubana* and *K. nigrofasciatum*, but for both spines and soft rays in other uranoscopids and those percoids examined for this study. Although the former character is likely to be a derived character, the homology of the spines, soft rays and distal and proximal pterygiophores of the dorsal fin with which erectores dorsales and depressores dorsales are associated is unclear among uranoscopids (see discussion under section 1-8. Axial skeleton and medial fin supports). Therefore, they are omitted from the phylogenetic analysis.

#### 2-7. Caudal fin muscles (Fig. 62)

**Description.** Muscles supporting the caudal fin include the interradians, hypochordal longitudinalis, flexor dorsalis superior, flexor dorsalis, flexor ventralis, flexor ventralis externus and flexor ventralis inferior. An adductor dorsalis is absent.

The interradians are situated between the caudal fin rays and consist of dorsal and ventral sections that lie on the dorsal and ventral lobes of the caudal fin, respectively.

The hypochordal longitudinalis is a small, triangular muscle that originates on the urostyle, parhypural, and upper and lower hypural plates. It inserts on several fin rays on the dorsal lobe of the caudal fin via tendons.

The flexor dorsalis superior originates on the neural spines of the second to fourth preural centra, epurals, urostyle, uroneural and upper hypurals, and insert on the caudal fin rays at the posterodorsal corner of the fin.

The flexor dorsalis adjoins the flexor dorsalis superior dorsally, and the flexor ventralis externus, flexor ventralis and hypochordal longitudinalis ventrally. It originates on the epurals, uroneural, urostyle, neural arches and centra of the second to fourth preural centra and upper hypurals, and inserts on the bases of the caudal fin rays forming the upper lobe.

The flexor ventralis, located mesial to the flexor ventralis externus, originates on the urostyle, lower hypural plate, parhypural, and hemal arches and centra of the second to fifth preural centra. It inserts on the bases of the caudal fin rays forming the lower lobe of the fin.

The flexor ventralis externus is a thin muscle that originates from the third and fourth preural centra, and inserts on the bases of several caudal fin rays in the lower lobe by a long tendon. The muscle is present in *Xenocephalus* spp., *Uranoscopus* spp., *Pleuroscopus pseudodorsalis*, *Kathetostoma albigutta*, *K. averruncus* and *K. cubana*, but is absent in the remaining uranoscopids.

The flexor ventralis inferior originates on the parhypural, and the hemal arches, hemal spines and centra of the third and fourth preural centra. It inserts on the bases of caudal fin rays at the anteroventral corner of the lower lobe of the fin.

#### Characters variable among Uranoscopidae

**TS 91.** *Flexor ventralis externus*. 0: present; 1: absent.

Ingroup. The flexor ventralis externus is present in *Xenocephalus* spp., *Uranoscopus* spp., *Pleuroscopus pseudodorsalis*, *Kathetostoma albigutta*, *K. averruncus* and *K. cubana* (character 91-0), but absent in other uranoscopids (character 91-1).

Outgroup. The flexor ventralis externus is primitively present in percoids (character 91-0) (Sasaki, 1989; this study).

**Characters synapomorphic for the Uranoscopidae**

None.

**Autapomorphies for terminal taxa**

None.

**Other observed variations**

None.

**2-8. Body muscles (Figs. 49-51, 53-59, 61-63, 74)**

**Description.** Body muscles comprise serially arranged myomeres, each separated from its adjacent myomeres via myocomma. The muscle mass is separated into two major parts, the epaxialis and hypaxialis, by a horizontal septum.

The epaxialis is a large muscle that forms the dorsal component of the body muscles. It is attached to the pterotic, parietal, supraoccipital, epiotic and exoccipital anteriorly, and the urostyle, parhypural, hypural plates and bases of the caudal fin rays in the dorsal lobe posteriorly. This muscle is also connected to the posttemporal, supracleithrum, mesial aspect of the anterodorsal portion of the upper limb of the cleithrum, neural arches, neural spines and centra of vertebrae, and the proximal pterygiophores of the dorsal fin.

The hypaxialis is the ventral component of body muscles, separated from the epaxialis by the horizontal septum. It consists of two subdivisions, the obliquus superioris and obliquus inferioris. The obliquus superioris is divided into dorsal and ventral sections. The dorsal section of obliquus superioris originates on the exoccipital and intercalar anteriorly, and inserts on Baudelot's ligament and the anteromesial aspect of the upper limb of the cleithrum posteriorly. The ventral section of the obliquus superioris is attached to the

posteromesial surface of the upper limb of the cleithrum and postcleithra anteriorly, and lies just below the horizontal septum posteriorly. It is connected to the proximal pterygiophores of the anal fin, hemal arches, hemal spines and centra of vertebrae, and bases of several rays in the ventral lobe of the caudal fin.

The obliquus inferioris originates on the posterior aspects of the pelvis, lateral and medial surfaces of the cleithrum, ventral aspect of the coracoid and lateral aspect of the esophagus. The anteroventral portion of the obliquus inferioris fused to the infracarinalis medius ventrally. This portion also originates on the posterior portion of pelvis in all uranoscopids, except *Astroscopeus* spp., in which it originates on the dorsal surfaces of the extensor proprius and adductor superficialis pelvici, and the posterior portion of the pelvis. The obliquus inferioris and lateral surface of the pelvis are attached together in all uranoscopids, except *Ichthyoscopeus* spp., in which they are separated. The muscle is fused with the sternohyoideus anteriorly in *Astroscopeus y-graecum*, *A. guttatus*, *A. sexspinosus*, *Kathetostoma canaster*, *K. giganteum*, *K. laeve*, *K. nigrofasciatum* and *Pleuroscopeus pseudodorsalis*, but is separated from it by a lateral expansion of the cleithrum in the remaining uranoscopids. The obliquus inferioris is fused with the obliquus superior posteriorly.

**Characters variable among Uranoscopidae**

**TS 92.** Anteroventral portion of obliquus inferioris and infracarinalis medius. 0: originating from dorsal portion of extensor proprius and adductor superficialis pelvici, and posterior portion of pelvis; 1: originating from posterior portion of pelvis.

*Ingroup.* The anteroventral portion of the obliquus inferi-

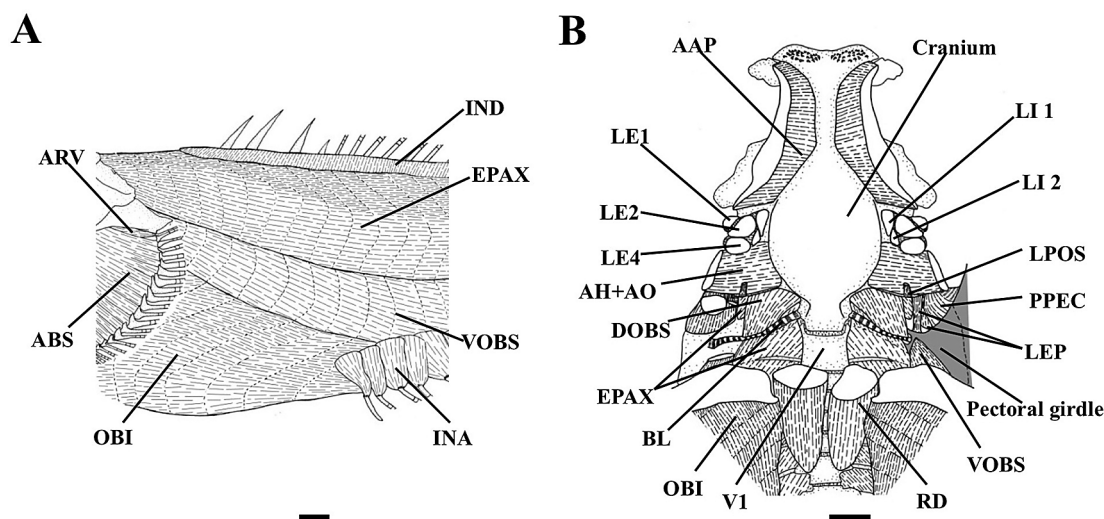


Fig. 63. Anterior body musculature. A, lateral view of body muscles after removal of skin on left side of *Astroscopeus y-graecum*; B, ventral view of body muscles after removal of infraorbitals, jaws, suspensorium, hyoid arches, branchial arches, pelvic girdle and visceral organs in *Uranoscopeus tosaе*. BL, Baudelot's ligament; DOBS, dorsal section of obliquus superioris; EPAX, epaxialis; OBI, obliquus inferioris; VOBS, ventral section of obliquus superioris; other abbreviations are as in Figs. 33, 49, 51, 59 and 61. Scales indicate 5 mm.

oris and the infracarinalis medius originate from the posterior portion of the pelvis in all uranoscopids (character 92-1), except *Astroscopus* spp., in which they originate from dorsal portions of the extensor proprius and adductor superficialis pelvici, and the posterior portion of the pelvis (character 92-0).

*Outgroup.* This portion of the obliquus inferioris and the infracarinalis medius originate from the dorsal portion of the extensor proprius and adductor superficialis pelvici, and the posterior portion of the pelvis in all percoids examined (character 92-0) (this study).

**TS 93.** *Obliquus inferioris and lateral surface of pelvis.* 0: attached; 1: separate.

*Ingroup.* The obliquus inferioris and the lateral surface of pelvis are attached together in all uranoscopids (character 93-0), except *Ichthyoscopus* spp., in which they are separated (character 93-1).

*Outgroup.* This muscle is attached to the lateral surface of the pelvis in all percoids examined (character 93-0) (this study).

**TS 94.** *Obliquus inferioris and sternohyoideus.* 0: fused; 1: separated by cleithrum.

*Ingroup.* The obliquus inferioris is fused with the sternohyoideus in *Astroscopus guttatus*, *A. y-graecum*, *A. sexspinosus*, *Kathetostoma canaster*, *K. giganteum*, *K. laeve*, *K. nigrofasciatum* and *Pleuroscopus pseudodorsalis* (character 94-0), but is separated from it by the lateral expansion of the cleithrum in other uranoscopids (character 94-1).

*Outgroup.* The obliquus inferioris is connected to and fused with the sternohyoideus in all percoids examined (character 94-0) (this study).

### Characters synapomorphic for the Uranoscopidae

*Obliquus superioris divided into two sections.* The obliquus superioris is divided into dorsal and ventral sections. The dorsal section of the obliquus superioris inserts on Baudelot's ligament and the anteromesial aspect of the upper limb of the cleithrum posteriorly in all uranoscopids. This muscle is continuous and penetrated by Baudelot's ligament in all percoids examined for this study.

*Remark.* This derived condition was described as "musculaire latéro-craniale sur l'opisthotique" by Danois (1962) in *Uranoscopus scaber*.

*Obliquus inferioris originating from esophagus.* The obliquus superioris originates on the esophagus in the Uranoscopidae. This muscle is separated from the esophagus in all percoids examined for this study.

### Autapomorphies for terminal taxa

None.

### Other observed variations

None.

### 3. Other morphology (Figs. 64-75)

Morphological variation was observed in the body scales, lateral line, gill opening, nostrils, orbit, cutaneous cirri on the lips, cutaneous cirri on the nostrils, cutaneous cirri on the lower surface of the head, cutaneous cirri on the ventral membrane of the cleithral spine, labial flap on the upper lip, median belly fold, mental barbels, cutaneous axillary appendage associated with the pectoral fin, and tubercles and pits on bony elements. Characters recognized in these morphological features are described and discussed in this section. The transverse septum separating the pericardial cavity and the pleuroperitoneal cavity, the swimbladder and other accessory organs, the lingual lure and electric organs, are also described here.

**Description.** *Body scales* (Fig. 64). Body scales are present in all uranoscopids, except *Kathetostoma* spp. Scales are exposed posteriorly in *Xenocephalus australiensis*, *X. elongatus* and *Selenoscopus turbisquamatus*, modified into small blunt spinules in *Pleuroscopus pseudodorsalis*, covered with skin and forms oblique rows in *Ichthyoscopus* spp., *Uranoscopus* spp., *Astroscopus y-graecum*, *A. sexspinosus* and *A. zephyreus*, and completely embedded under the skin in *Genyagnus monopterygius*, *A. guttatus*, *X. armatus* and *X. egregius*.

*Lateral line* (Figs. 65-67). The posterior portion of the lateral line is situated close to the lateral midline of side of body in *Pleuroscopus pseudodorsalis*, close to but separate from the dorsal fin base in *Kathetostoma* spp. and *Xenocephalus* spp., and mostly attached to the dorsal fin base in other uranoscopids. Lateral lines dorsally on the either side of the caudal peduncle are separate in all uranoscopids, except *Ichthyoscopus* spp., in which they are fused dorsally. The posterior end of the lateral line reaches to near the middle portion

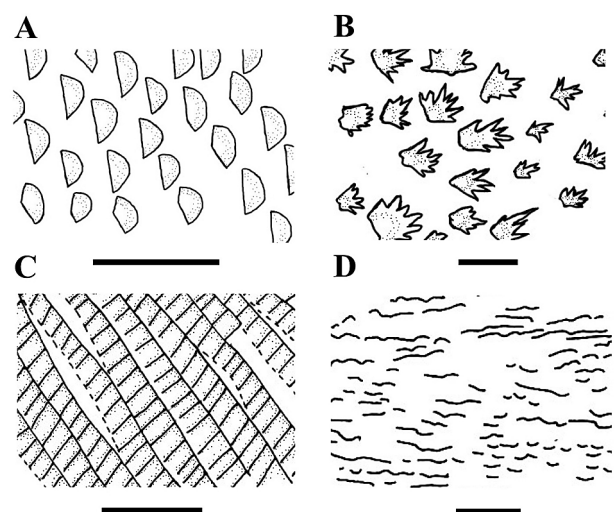


Fig. 64. Body scales. A, *Xenocephalus elongatus*; B, *Pleuroscopus pseudodorsalis*; C, *Ichthyoscopus lebecki*; D, *Genyagnus monopterygius*. Bars indicate 5 mm.

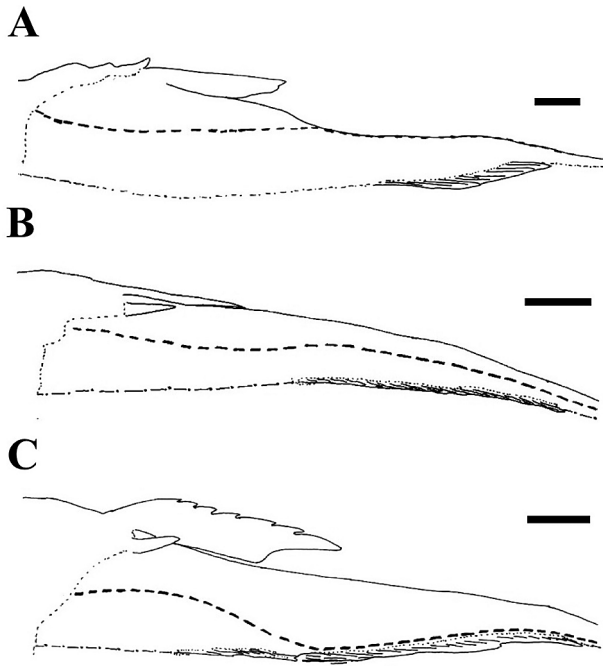


Fig. 65. Patterns of lateral line on right side in dorsal view. A, *Pleuroscopus pseudodorsalis*; B, *Kathetostoma giganteum*; C, *Uranoscopus tosaе*. Bars indicate 10 mm.

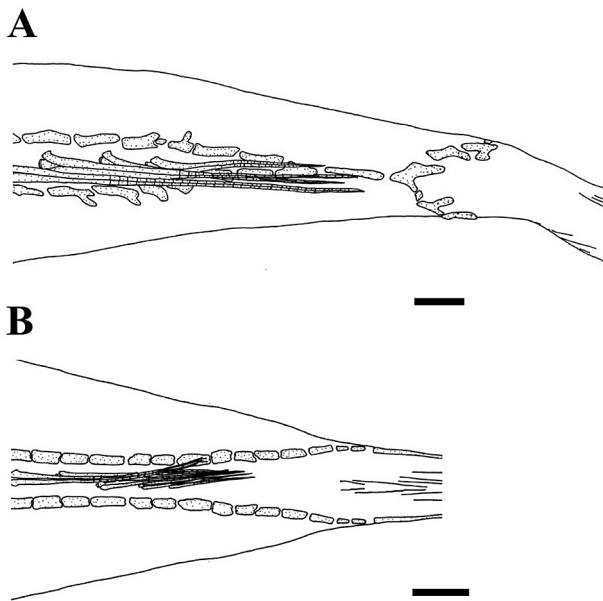


Fig. 66. Patterns of lateral line posteriorly on body in dorsal view of caudal peduncle. A, *Ichthyoscopus sannio*; B, *Uranoscopus bicinctus*. Bars indicate 5 mm.

of the caudal fin in all uranoscopids, except *Astroscopus* spp. in which the end curves down and joints to the lateral line of the opposite side mid-ventrally.

**Gill opening** (Fig. 68). The gill opening is narrow with the dorsal edge reaching the cleithrum in *Astroscopus* spp., *Xenocephalus* spp., *Ichthyoscopus* spp., *Genyagnus monopterygius*, *Pleuroscopus pseudodorsalis*, *Uranoscopus cognatus*,

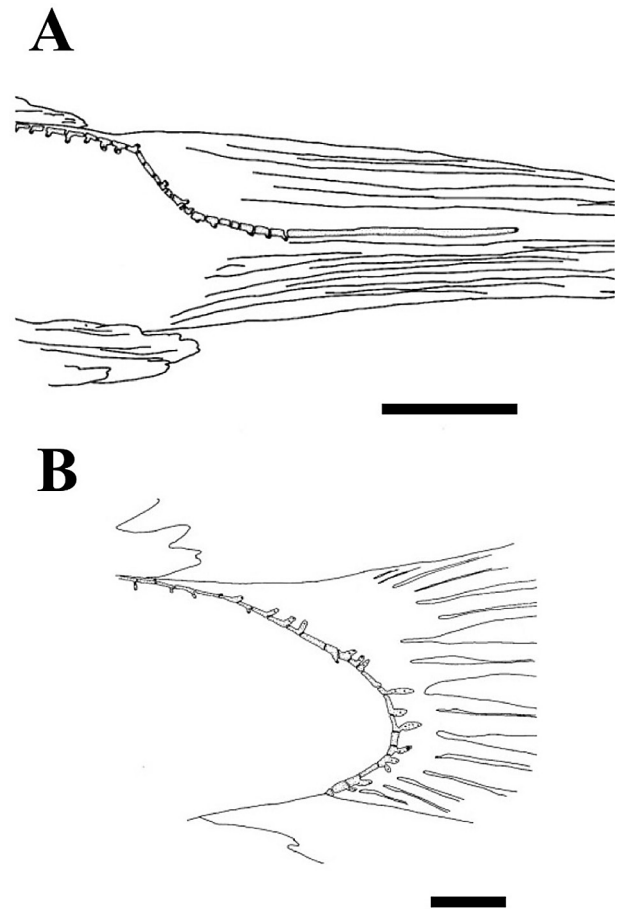


Fig. 67. Lateral view of left side of caudal peduncle and fin showing termination of lateral line. A, *Genyagnus monopterygius*; B, *Astroscopus y-graecum*. Bars indicate 5 mm.

*Kathetostoma canaster*, *K. giganteum*, *K. laeve* and *K. nigrofasciatum*, but large with the dorsal edge extending to the supracleithrum in other uranoscopids.

**Nostrils** (Fig. 69). The nostrils comprise two pairs of openings, the anterior and posterior nostrils. The openings are large in *Astroscopus* spp. and *Ichthyoscopus* spp., but are small in other uranoscopids. The nostrils are confined to the nasal region in all uranoscopids, except *Astroscopus* spp., which has the posterior nostril extending into the orbital region.

**Orbit** (Fig. 69). The orbit is formed by the frontal, lateral ethmoid, sphenotic and infraorbitals. It is large in *Astroscopus* spp., but small in other uranoscopids.

**Cutaneous cirri of lips** (Fig. 69). Cirri are present on the edges of the upper and lower lips in all uranoscopids. They are short and poorly developed in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Pleuroscopus pseudodorsalis*, *Genyagnus monopterygius* and *Selenoscopus turbisquamatus*, but are long and well developed in *Astroscopus* spp. and *Ichthyoscopus* spp. The cirri on lips are conical in *Xenocephalus* spp., *Kathetostoma* spp., *Selenoscopus turbisquamatus* and *Pleuroscopus pseudodorsalis*, and com-



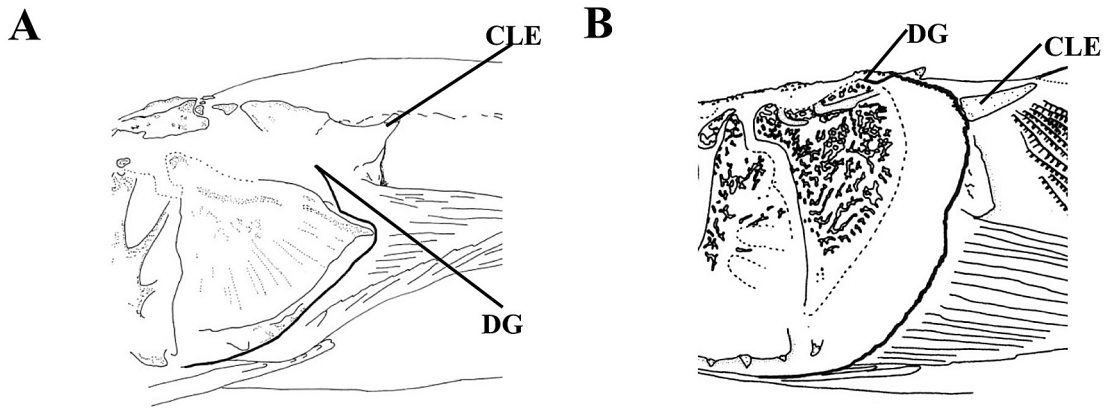


Fig. 68. Lateral view of posterior portion of left side of head. A, *Xenocephalus egregius*; B, *Uranoscopus bicinctus*. CLE, cleithrum; DG, dorsal margin of gill opening. Bars indicate 5 mm.

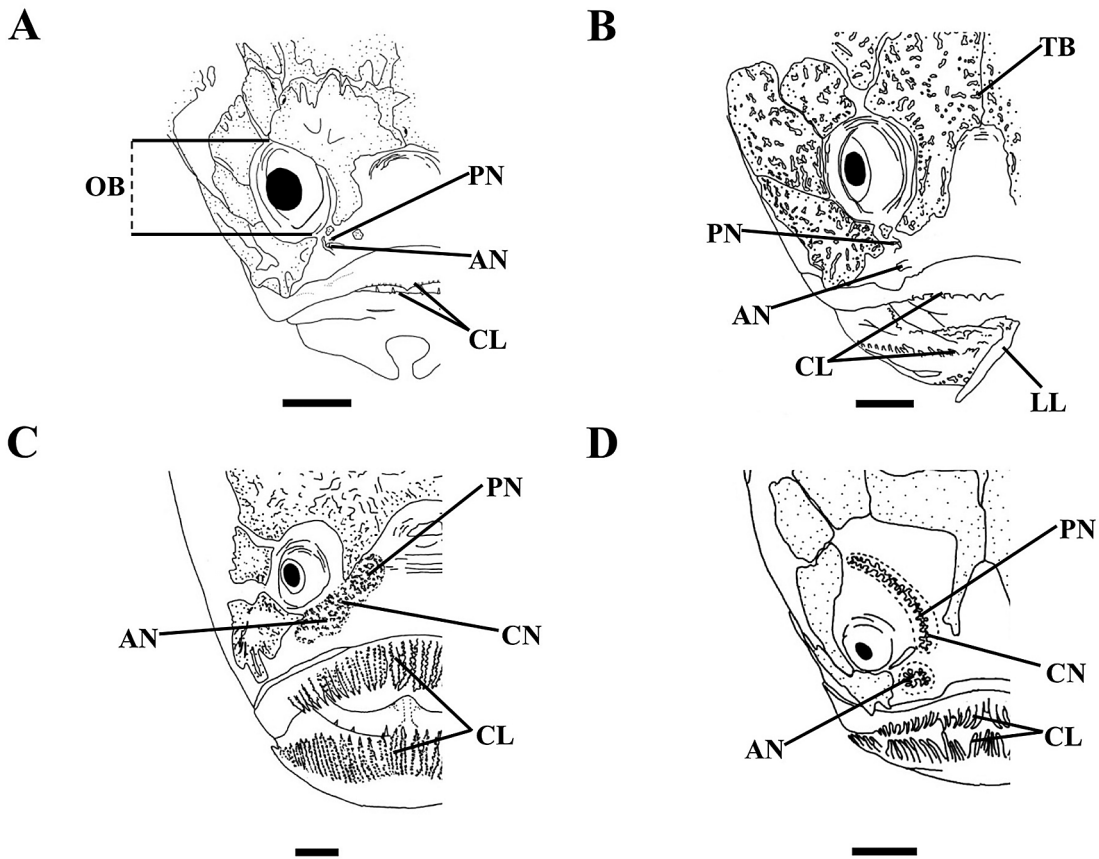


Fig. 69. Dorsal view of right side of head. A, *Xenocephalus egregius*; B, *Uranoscopus tosaе*; C, *Ichthyoscopus lebeck*; D, *Astroscopus guttatus*. AN, anterior nostril; CN, cutaneous cirri of nostrils; CL, cutaneous cirri of lips; LL, lingual lure organ; OB, orbit; PN, posterior nostril; TB, tubercle. Bars indicate 5 mm.

pressed in other uranoscopids. The cirri of lips are comprised of unbranched and branched elements in *Uranoscopus* spp., *Kathetostoma* spp., *Selenoscopus turbisquamatus*, only branched elements in *Ichthyoscopus sannio* and *I. lebeck*, and only unbranched elements in the remaining uranoscopids.

*Cutaneous cirri of nostrils* (Fig. 69). Cirri on the rims of the nostrils are large and well developed in *Astroscopus* spp. and *Ichthyoscopus* spp., but absent or poorly developed in other uranoscopids.

*Cutaneous cirri on underside of lower jaw* (Fig. 70). Several series of cirri, originating from horizontal fleshy ridges on

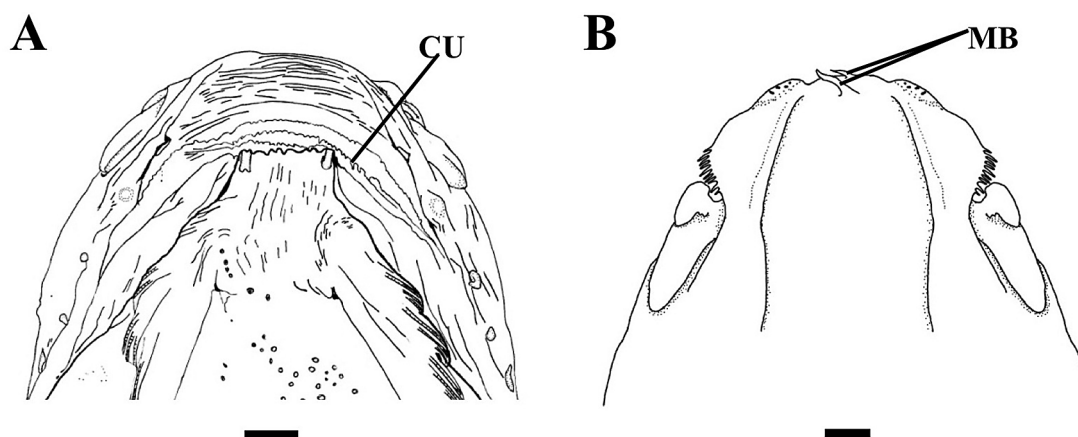


Fig. 70. Ventral view of head. A, *Kathetostoma giganteum*; B, *Ichthyscopus barbatus*. CU, cutaneous cirri on underside of lower jaw; MB, mental barbels. Scales indicate 5 mm.

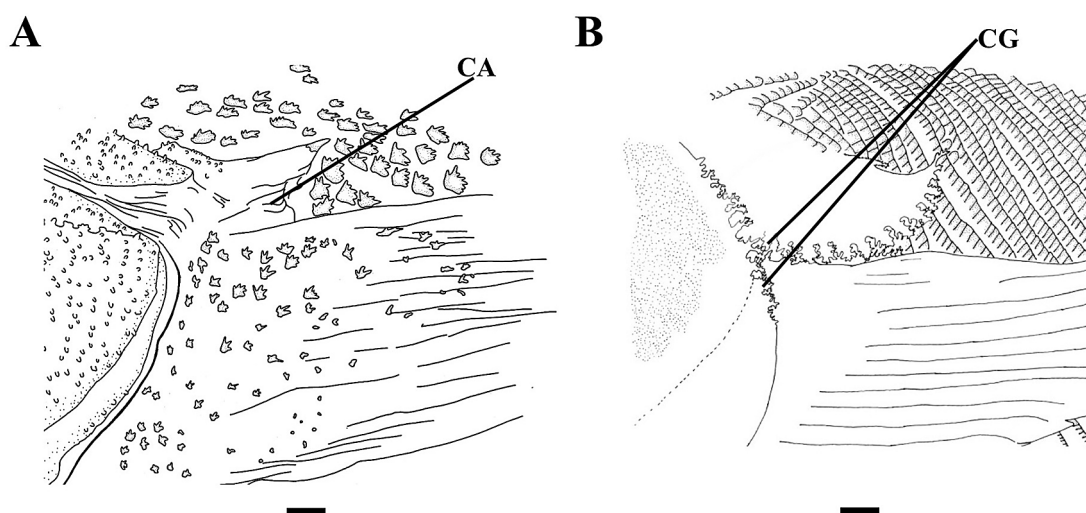


Fig. 71. Lateral view of left side of head posteriorly. A, *Pleuroscopus pseudodorsalis*; B, *Ichthyscopus lebeck*. CA, cutaneous axillary appendage; CG, cutaneous cirri of gill opening. Scales indicate 5 mm.

the underside of the lower jaw, are present in *Kathetostoma* spp., but are absent in other uranoscopids.

**Cutaneous cirri of gill opening** (Fig. 71). Cirri associated with the gill opening, are present on the membrane of the cleithral spine, and posterior margins of the subopercle and opercle in *Ichthyscopus* spp. but are absent in other uranoscopids.

**Labial flap on upper lip** (Fig. 72). A labial flap forms on the outer rim of the upper lip in *Kathetostoma albigutta*, *K. canaster*, *K. cubana*, *K. giganteum*, *K. laeve* and *K. nigrofasciatum*, but not in other uranoscopids.

**Mental barbels** (Figs 70B, 73A). Mental barbels are cutaneous rod-like elements, arising from the anteromedial surface of the lower jaw. A single barbel is present in *Genyagnus monopterygius* and *Uranoscopus filibarbis*, and *Ichthyscopus barbatus* has two. The structure is absent in other uranoscopids.

**Median belly fold** (Fig. 73). A longitudinal fleshy fold is

present on the midline of the ventral surface of the abdomen in *Astroscopus* spp. and *Ichthyscopus* spp., but absent in other uranoscopids.

**Cutaneous axillary appendage associated with pectoral fin** (Fig. 71). A cutaneous axillary appendage is associated with the posterodorsal region of the pectoral girdle in all uranoscopids.

**Tubercles and pits on bony elements** (Fig. 69). Numerous tubercles and pits are present on the outer surface of the infra-orbitals, cranium, opercular bones, and dorsal elements of the pectoral girdle in all species of the family Uranoscopidae.

**Transverse septum** (Fig. 74). A transverse septum, separating the pericardial cavity and the pleuroperitoneal cavity, is attached to the posterior portion of the pelvis ventrally in all uranoscopids.

**Lingual lure organ** (Fig. 69). The lingual lure is an elongate soft tissue organ on the lower oral valve. It is present in *Genyagnus monopterygius*, *Kathetostoma albigutta*, *Sele-*

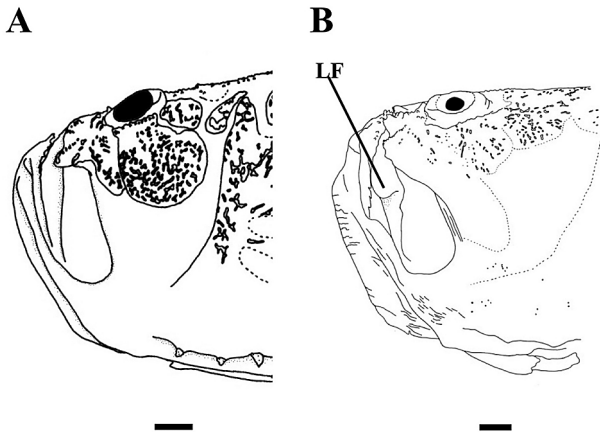


Fig. 72. Lateral view of anterior portion of left side of head. A, *Uranoscopus bicinctus*; B, *Kathetostoma laeve*. LF, labial flap. Scales indicate 5 mm.

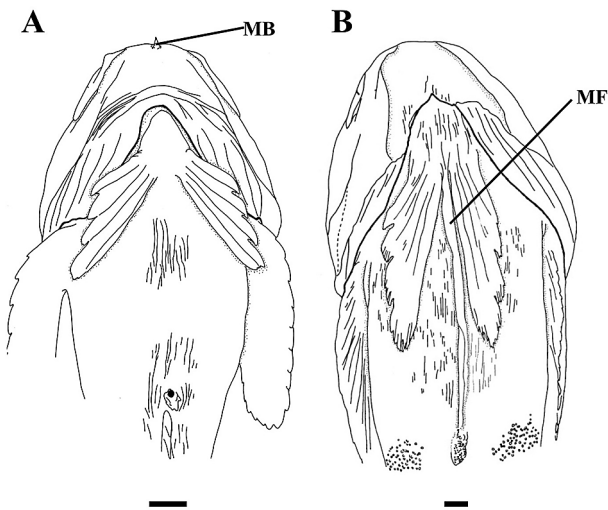


Fig. 73. Ventral view of head and abdomen. A, *Genyagnus monopterygius*; B, *Astroscopus y-graecum*. MB, mental barbel; MF, median belly fold. Scales indicate 5 mm.

*noscopus turbisquamatus*, *Uranoscopus archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. oligolepis*, *U. polli*, *U. scaber* and *U. tosae*, but absent in other uranoscopids. The configuration of the lure organ is depressed in *K. albigutta*, *S. turbisquamatus*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. oligolepis*, *U. polli*, *U. scaber* and *U. tosae*, and compressed in *G. monopterygius*.

**Orbital electric organ** (Fig. 75). The orbital electric organ, is an oval-shaped, specialised organ, just posterior to the eye ball. It is formed from numerous layers of soft tissue, optic nerves, and optic muscles that are innervated by the oculomotor nerve (III). The organ is unique to *Astroscopus* spp.

**Swimbladder.** The swimbladder is absent in all uranoscopids.

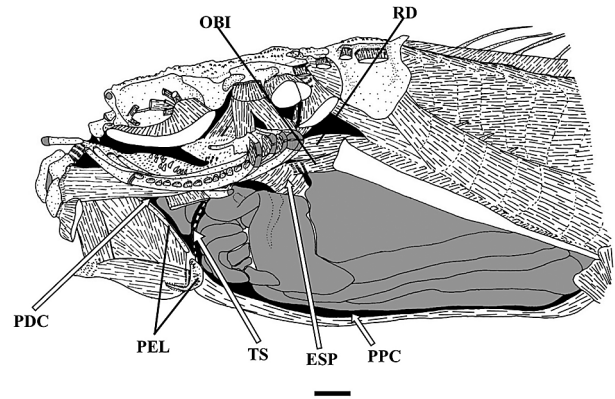


Fig. 74. Lateral aspects of left side of head and body of *Uranoscopus bicinctus* after removal of infraorbitals, jaws, suspensorium, hyoid arches, pectoral and pelvic girdles and associated muscles. ESP, esophagus; OBI, obliquus inferioris; PDC, pericardial cavity; PPC, pleuroperitoneal cavity; PEL, pelvis; RD, retractor dorsalis; TS, transverse septum. Scale indicates 5 mm.

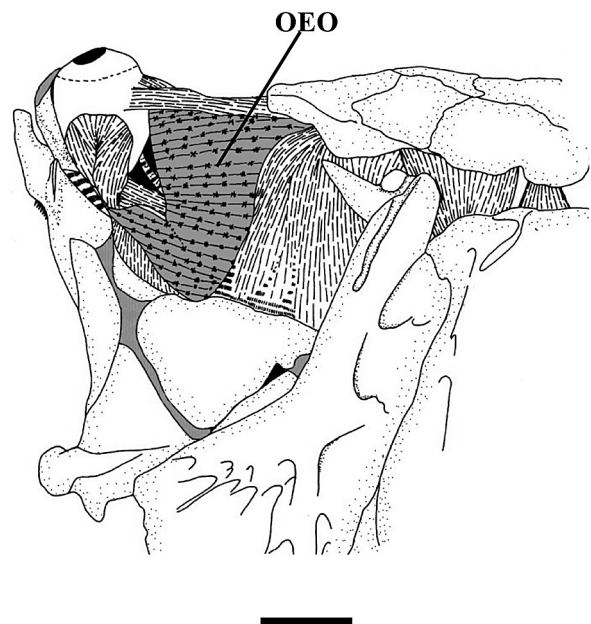


Fig. 75. Lateral view of left side of *Astroscopus y-graecum* head after removal of circumorbital bones, jaw, and cheek muscles. OEO, orbital electric organ. Scale indicates 5 mm.

#### Characters variable among Uranoscopidae

**TS 95. Body scales.** 0: present, exposed posteriorly; 1: present, modified into small blunt spinules; 2: present, covered with skin and forming oblique rows; 3: present, completely embedded under skin; 4: absent (unordered).

**Ingroup.** Scales are present on the body in all uranoscopids, except *Kathetostoma* spp., which lack them (character 95-4). The posterior edges of scales are exposed in *Xenocephalus australiensis*, *X. elongatus* and *Selenoscopus turbisquamatus* (character 95-0), modified into small blunt



spinules in *Pleuroscopus pseudodorsalis* (character 95-1), covered with skin and forming oblique rows in *Ichthyoscopus* spp., *Uranoscopus* spp., *Astroscopus y-graecum*, *A. sexspinosus* and *A. zephyreus* (character 95-2) and completely embedded under skin in *Genyagnus monoptyerygius*, *A. guttatus*, *X. armatus* and *X. egregius* (character 95-3).

*Outgroup.* Scales are typically present with posterior edge exposed in percoids (character 95-0) (this study).

**TS 96.** *Posterior portion of lateral line.* 0: close to lateral midline of side; 1: close to but separated from dorsal fin base; 2: mostly attached to dorsal fin base (ordered as 0-1-2).

*Ingroup.* The posterior portion of the lateral line is close to the lateral midline of the side in *Pleuroscopus pseudodorsalis* (character 96-0), close to but separated from the dorsal fin base in *Kathetostoma* spp. and *Xenocephalus* spp. (character 96-1), and mostly attached to the dorsal fin base in other uranoscopids (character 96-2).

*Outgroup.* The posterior portion of the lateral line is situated close to the lateral midline of the side in percoids examined (character 96-0) (this study).

**TS 97.** *Lateral lines on either side of caudal peduncle.* 0: separated; 1: fused dorsally.

*Ingroup.* The lateral line on either side of the caudal peduncle are separated from each other in all uranoscopids (character 97-0), except *Ichthyoscopus* spp., in which they are fused dorsally (character 97-1).

*Outgroup.* The lateral line on either side of the caudal peduncle are separated in percoids examined (character 97-0) (this study).

**TS 98.** *Posterior end of lateral line.* 0: reaching to near middle portion of caudal fin; 1: curved downward and joining lateral line of opposite side.

*Ingroup.* The posterior end of the lateral line reaches to near the middle of the caudal fin in all uranoscopids (character 98-0), except *Astroscopus* spp., in which the end curves downward and joins the lateral line of the opposite side (character 98-1).

*Outgroup.* The posterior end of the lateral line is typically near the middle of the caudal fin in percoids (character 98-0) (Waldman, 1986).

**TS 99.** *Gill opening.* 0: large, its dorsal edge extending to supracleithrum; 1: narrow, its dorsal edge reaching to cleithrum.

*Ingroup.* The gill opening is narrow with its dorsal edge reaching to the cleithrum in *Astroscopus* spp., *Xenocephalus* spp., *Ichthyoscopus* spp., *Genyagnus monoptyerygius*, *Pleuroscopus pseudodorsalis*, *Uranoscopus cognatus*, *Kathetostoma canaster*, *K. giganteum*, *K. laeve* and *K. nigrofasciatum* (character 99-1), while the opening is broad with its dorsal edge extending to the supracleithrum in other uranoscopids (character 99-0).

*Outgroup.* The gill opening is typically broad with its dorsal edge extending to the supracleithrum in percoids (char-

acter 99-0).

*Remarks.* Pietsch (1989) considered a large gill opening to be a synapomorphy that supports a sister relationship between *Uranoscopus* spp. and *Kathetostoma* spp. However, observations in this study indicate his hypothesis is erroneous.

**TS 100.** *Nostril openings.* 0: small; 1: large.

*Ingroup.* Nostril openings are large in *Astroscopus* spp. and *Ichthyoscopus* spp. (character 100-1), but small in other uranoscopids (character 100-0).

*Outgroup.* Nostril openings are small in all percoids examined for this study (character 100-0).

**TS 101.** *Posterior nostrils.* 0: confined to nasal region; 1: extending into orbital region.

*Ingroup.* Posterior nostrils are confined to the nasal region in all uranoscopids (character 101-0), except *Astroscopus* spp., in which the posterior nostril extend into the orbital region (character 101-1).

*Outgroup.* Posterior nostrils are confined to the nasal region in all percoids examined for this study (character 101-0).

**TS 102.** *Orbit.* 0: large; 1: small.

*Ingroup.* The orbit is large in *Astroscopus* spp. (character 102-0), but is small in other uranoscopids (character 102-1).

*Outgroup.* The orbit is large in all percoids examined for this study (character 102-0).

**TS 103.** *Cutaneous cirri on lips.* 0: short and poorly developed; 1: long and well developed.

*Ingroup.* Cutaneous cirri on the edges of the upper and lower lips, are short and poorly developed in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Pleuroscopus pseudodorsalis*, *Genyagnus monoptyerygius*, and *Selenoscopus turbisquamatus* (character 103-0), but large and well developed in *Astroscopus* spp. and *Ichthyoscopus* spp. (character 103-1).

*Outgroup.* All percoids examined for this study lack cirri on the lips. Therefore, the outgroup is coded as “?”.

**TS 104.** *Shape of cutaneous cirri on lips.* 0: conical; 1: compressed.

*Ingroup.* Cutaneous cirri are conical on the lips in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Selenoscopus turbisquamatus* and *Pleuroscopus pseudodorsalis* (character 104-0), and compressed in other uranoscopids (character 104-1).

*Outgroup.* All percoids examined for this study lack cirri on the lips. The outgroup is coded as “?”.

**TS 105.** *Branched cutaneous cirri on lips.* 0: only unbranched cirri present; 1: both branched and unbranched cirri present; 2: only branched cirri present (unordered).

*Ingroup.* Both unbranched and branched cirri are present on the lips of *Uranoscopus* spp., *Kathetostoma* spp. and *Selenoscopus turbisquamatus* (character 105-1), while *Ichthyoscopus sannio* and *I. lebeck* have only branched cirri on the lips



(character 105-2). Remaining uranoscopids have only unbranched cirri on the lips (character 105-0).

*Outgroup.* All percoids examined for this study lack cirri on the lips. The outgroup is coded as “?”.

**TS 106.** *Cutaneous cirri on nostrils.* 0: absent or poorly developed; 1: large and well developed.

*Ingroup.* Cutaneous cirri are large and well developed on the nostrils in *Astroscopus* spp. and *Ichthyoscopus* spp. (character 106-1), but poorly developed or absent in other uranoscopids (character 106-0).

*Outgroup.* All percoids examined for this study lack cirri on the nostrils (character 106-0).

**TS 107.** *Cutaneous cirri on underside of lower jaw.* 0: absent; 1: present.

*Ingroup.* The cutaneous cirri on the underside of the lower jaw present in *Kathetostoma* spp. (character 107-1) that are absent in other uranoscopids (character 107-0).

*Outgroup.* All percoids examined for this study lack cirri on the underside of the lower jaw (character 107-0).

**TS 108.** *Cutaneous cirri on membrane on gill opening.* 0: absent; 1: present.

*Ingroup.* *Ichthyoscopus* spp. have cutaneous cirri on the membrane of the cleithral spine, and posterior margins of the subopercle and opercle (character 108-1), which are absent in other uranoscopids (character 108-0).

*Outgroup.* All percoid examined for this study lack cirri associated with gill opening (character 108-0).

**TS 109.** *Labial flap on upper lips.* 0: absent; 1: present.

*Ingroup.* A labial flap on the outer rim of the upper lip is present in *Kathetostoma albigutta*, *K. canaster*, *K. cubana*, *K. giganteum*, *K. laeve* and *K. nigrofasciatum* (character 109-1), but absent in other uranoscopids (character 109-0).

*Outgroup.* No percoids examined for this study have a labial flap on the outer rim of the upper lip (character 109-0).

**TS 110.** *Mental barbels.* 0: absent; 1: one; 2: two (ordered as 0-1-2).

*Ingroup.* A single medial barbel, originating from the anterior medial surface of the lower jaw, is present in *Genyagnus monopterygius* and *Uranoscopus filibarbis* (character 110-1), whereas two barbels are present in *Ichthyoscopus barbatus* (character 110-2). Mental barbels are absent in other uranoscopids (character 110-0).

*Outgroup.* No percoids examined for this study have one or more mental barbels on the anterior medial surface of the lower jaw (character 110-0) (this study).

*Remarks.* Cuvier in Cuvier and Valenciennes (1829) described *Uranoscopus filibarbis* on the basis of a unique medial barbel generating on the symphysis of lower jaw. However, the character can not be examined from the holotype of *U. filibarbis*, MNHN 3098, as the chin of the specimen was destroyed (Brüss and Klausewitz, 1984). As no other specimens are known, the character for this species is coded as 110-1 base on the original description.

**TS III.** *Median belly fold.* 0: absent; 1: present.

*Ingroup.* A median belly fold is absent in all uranoscopids (character 111-0), except *Astroscopus* spp. and *Ichthyoscopus* spp., which have a belly fold (character 111-1).

*Outgroup.* A belly fold is absent all in percoids examined for this study (character 111-0).

**TS 112.** *Configuration of elongate lingual lure organ.* 0: elongate lingual lure organ absent; 1: depressed; 2: compressed (unordered).

*Ingroup.* The configuration of the elongate lingual lure organ is depressed in *Kathetostoma albigutta*, *Selenoscopus turbisquamatus*, *Uranoscopus archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. oligolepis*, *U. polli*, *U. scaber* and *U. tosae* (character 112-1), whereas it is compressed in *Genyagnus monopterygius* (character 112-2). A lingual lure organ is absent in the other uranoscopids (character 112-0).

*Outgroup.* Percoids typically lack this lure (character 112-0).

**TS 113.** *Orbital electric organ.* 0: absent; 1: present.

*Ingroup.* A specialised orbital electric organ, situated posterior to the eye, is present in *Astroscopus* spp. (character 113-1), but absent in other uranoscopids (character 113-0).

*Outgroup.* An orbital electric organ is absent in all percoids examined for this study (character 113-0).

#### Characters synapomorphic for the Uranoscopidae

*Cutaneous axillary appendage associated with pectoral fin.* A cutaneous axillary appendage associated with the posterodorsal region of the pectoral girdle is present in all uranoscopids. The appendage is absent in percoids (Imamura and Matsuura, 2003).

*Tubercles and pits on bony elements.* Tubercles and pits are present on the outer surface of the infraorbitals, cranium, opercular bones, and dorsal elements of the pectoral girdle in all uranoscopids, while they are typically absent in percoids (Imamura and Matsuura, 2003).

*Transverse septum attached to posterior portion of pelvis.* Transverse septum separating the pericardial cavity and the pleuroperitoneal cavity is attached to the posterior portion of the pelvis ventrally in all uranoscopids. The septum is attached to the cleithrum or the anterior tip of the pelvis ventrally in all percoids examined for this study.

*Absence of swimbladder.* The swimbladder is absent in all uranoscopids, but typically present in percoids (Sasaki, 1989; Imamura, 1996).

#### Autapomorphies for terminal taxa

None.

#### Other observed variations

None.

## V. Monophyly of Family Uranoscopidae

Monophyly of the Uranoscopidae was shown by Pietsch (1989) based on cladistical methodology. He considered that 12 synapomorphies to support the relationship: (1) lateral surface of head and shoulder region rugose and highly sculptured; (2) orbital foramen greatly reduced; (3) parietal exceptionally large, nearly contiguous or meeting on the midline; (4) intercalar greatly reduced; (5) four infraorbitals; (6) fourth infraorbital fused to dorsal surface of the cranium; (7) opercle entire, enlarged, and expanded posteriorly; (8) urohyal greatly reduced, wing-like extension absent, closely attached to the first basibranchial; (9) third hypobranchial forked; (10) second pharyngobranchial severely reduced or lost; (11) caudal vertebrae and anal-fin rays reduced in number; and (12) cleithral spine large. Most of these characters are recognized as synapomorphies of the Uranoscopidae in the current study, although several presented by Pietsch (1989) are expressed differently here. Four of his characters (3, 6, 9 and 11), however, are not considered synapomorphies here. In this study, the exceptionally large parietal and the forked third hypobranchial are not regarded as derived characters, as similar conditions were found in percoids examined. A detailed examination of the fourth infraorbital (= dermosphenotic) in uranoscopids, revealed that this element is firmly attached to the cranium, but not fused with it. With regard to the number of caudal vertebrae in uranoscopids, since Pietsch (1989) used trachinoids as his outgroup, and this study uses percoids, inferences of the two studies for this character cannot be compared.

This study reconfirms the monophyly of the family Uranoscopidae, as supported by 42 synapomorphies: (1) two facets of first infraorbital separated by dorsomedial ridge; (2) presence of subocular shelf on first infraorbital; (3) absence of infraorbital homologous with percoid second infraorbital; (4) dorsal surface of cranium broad and flat; (5) presence of interorbital fossa; (6) absence of posttemporal fossa; (7) presence of maxillo-lateral ethmoid ligament; (8) presence of anterior socket for articulation with anterior condyle of hyomandibula on posterolateral corner of sphenotic; (9) supraoccipital crest formed on posterior portion of supraoccipital; (10) urohyal sutured with first basibranchial; (11) absence of posterior projection of urohyal; (12) presence of hyomandibular spur; (13) opercle enlarge and expanded posteriorly; (14) absence of tooth plate on third epibranchial; (15) absence of interarcual cartilage; (16) anterior portion of pelvic girdle projecting beyond the ventral arm of pectoral girdle; (17) presence of cleithral spine; (18) short and broad actinosts firmly attached to each other and to posterior portions of scapula and coracoid; (19) absence of post-pelvic process; (20) absence of accessory subpelvic keel; (21) first vertebra firmly attached to posterior portion of cranium; (22) posterior elements of epineurals attached to

vertebrae and pleural ribs separated from vertebrae; (23) first proximal pterygiophore of dorsal fin inserted between third and fourth neural spines; (24) absence of supraneurals; (25) each proximal pterygiophore individually inserting into interspace between adjacent neural and hemal spines; (26) second ray on posterior portion of first proximal pterygiophore of anal fin being soft ray; (27) first and second hypurals fused; (28) third and fourth hypurals fused; (29) absence of second uroneural; (30) levator operculi originating from supracleithrum; (31) absence of third levator externus; (32) presence of first, second and third adductores; (33) pharyngoclavicularis internus inserted onto dorsal aspect of fifth ceratobranchial; (34) absence of transversus pharyngobranchial 2; (35) absence of coracoradialis; (36) extensor proprius originating from pelvis and cleithrum; (37) obliquus superioris divided into two sections; (38) obliquus inferioris originating from esophagus; (39) presence of cutaneous axillary appendage associated with pectoral fin; (40) tubercles and pits on bony elements; (41) transverse septum attached to posterior portion of pelvis; and (42) absence of swimbladder.

## VI. Phylogenetic Relationships of Uranoscopidae (Fig. 76; Table 2)

Phylogenetic relationships of the Uranoscopidae are inferred from characters in 113 transformation series. A matrix of characters is shown in Table 2. A single most parsimonious tree of relationships for the Uranoscopidae was obtained from a phylogenetic analysis (Fig. 76). A consistency index for the tree was 0.52, a rescaled consistency index was 0.43 and the tree length was 288. Reversed characters are labeled "r". An asterisk identifies autapomorphic characters.

The monophyly of the Uranoscopidae (clade 1A) is also unambiguously supported by 17 synapomorphies in the phylogenetic analysis: 9-1, 15-2\*, 19-1\*, 27-1, 28-1, 54-1\*, 62-1, 70-2, 72-1, 78-1, 85-1\*, 86-1, 89-1, 92-1, 102-1, 103-0\* and 104-0\*. In addition, 11 synapomorphies (11-1, 26-2, 31-1, 51-1, 65-1, 69-1, 74-2, 75-1, 94-1, 96-1 and 99-1) also support the family based on ACCTRAN.

### Relationships of uranoscopid genera and species

*Clade 1A.* Divides into clades 2A and 2B.

*Clade 2A.* Includes species of *Pleuroscopus* and *Xenocephalus*. Clade 2A is unambiguously supported by eight synapomorphies: 3-1, 10-1, 14-1\*, 24-1\*, 44-1\*, 45-1\*, 55-1 and 105-0; and further supported by two synapomorphies (42-1 and 47-1) based on ACCTRAN, and by four synapomorphies (11-1, 26-2, 69-1 and 99-1) based on DELTRAN. Clade 2A is divided into clades 3A and 3B.

*Clade 3A.* Comprises *Pleuroscopus pseudodorsalis*. This clade is characterized by eight apomorphies: 17-1, 31-0r, 51-0r, 57-1, 79-1, 94-0r, 95-1\* and 96-0r, and is also

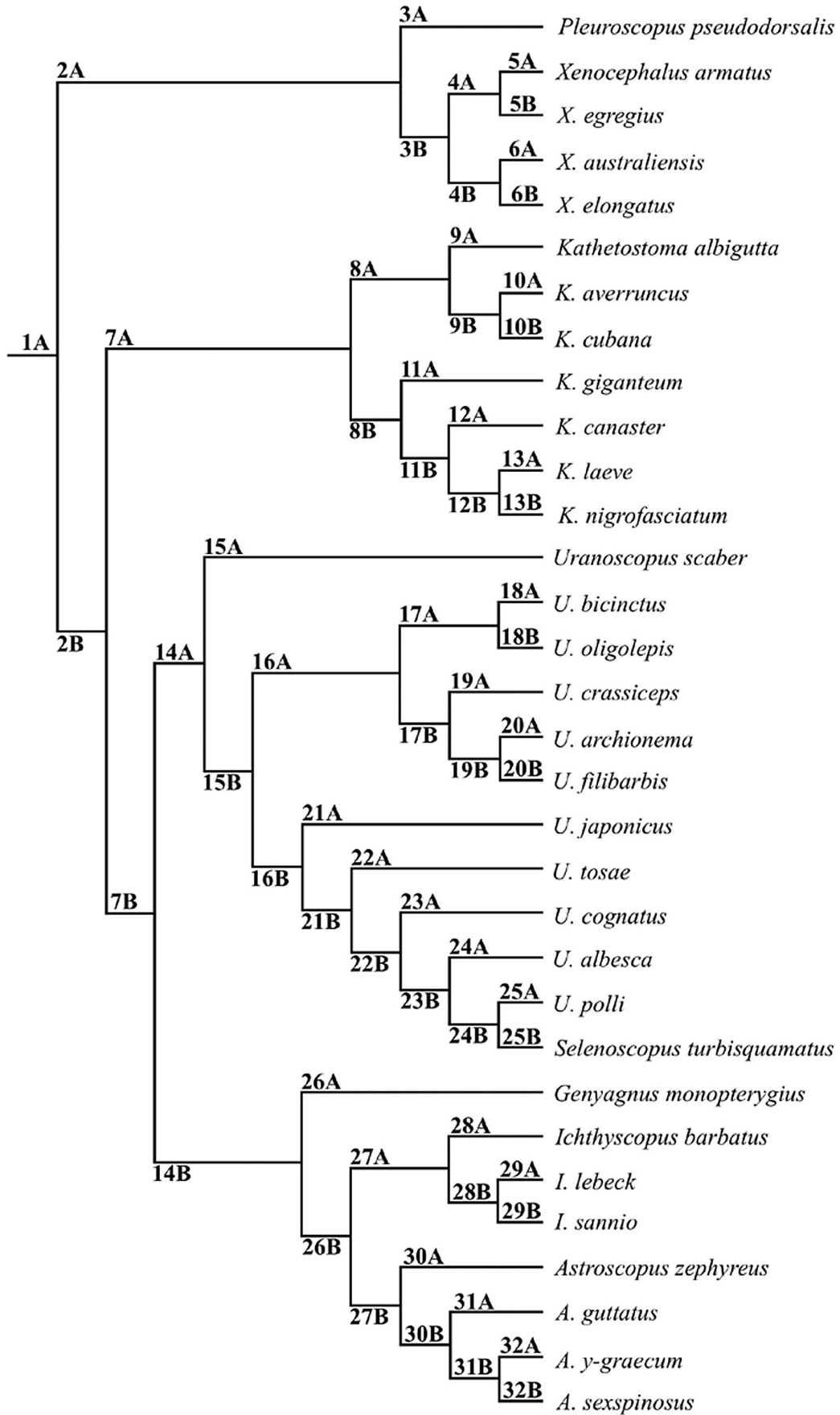


Fig. 76. Cladogram of phylogenetic relationships of Uranoscopidae.

Table 2. Matrix of characters in transformation series used in phylogenetic analysis

Taxon	Transformation series and characters													
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60		
Outgroup	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000		
1. <i>Astroscopus y-graecum</i>	11001	01A11	01001	00121	11001	20100	10011	00010	00000	00000	102?4	100?0		
2. <i>A. guttatus</i>	11001	01010	01201	00111	11001	20100	10011	00010	00000	00000	112?4	100?0		
3. <i>A. sexspinosus</i>	10000	01011	01001	00121	11001	20100	10011	00010	00000	00002	10011	100?0		
4. <i>A. zephyreus</i>	11001	01A11	01202	00111	21001	20100	10011	00000	00000	00000	10211	100?0		
5. <i>Genyagnus monopterygius</i>	20100	11010	01102	10011	11000	21111	10011	00000	00100	10000	102?4	000?0		
6. <i>Ichthyoscopus barbatus</i>	00100	11000	11102	10011	01000	20111	10011	00000	00000	00013	002?4	000?0		
7. <i>I. lebeck</i>	00100	11000	11102	10011	01000	10110	00011	00000	00000	00000	002?4	000?0		
8. <i>I. sannio</i>	00100	11000	11102	10011	01000	20110	10011	00000	00000	00000	002?4	000?0		
9. <i>Kathetostoma albigutta</i>	00010	00010	10002	10010	00000	01100	10000	10000	00100	10000	102?4	00110		
10. <i>K. averruncus</i>	00110	00010	10002	10010	00000	01100	10000	10000	00100	10000	102?4	000?1		
11. <i>K. canaster</i>	00000	00010	10002	10010	00100	00100	10000	10000	00000	00001	122?4	000?0		
12. <i>K. cubana</i>	00110	00010	10002	10010	00000	01000	10000	10000	00100	10000	102?4	000?1		
13. <i>K. giganteum</i>	00000	00010	10002	10010	00000	00100	10000	10000	00000	00000	102?4	000?0		
14. <i>K. laeve</i>	01000	00010	10002	10010	00100	00100	10000	10000	00000	00001	122?4	000?0		
15. <i>K. nigrofasciatum</i>	01010	00010	10002	10010	00100	10100	10000	10000	00000	00001	122?4	000?0		
16. <i>Pleuroscopus pseudodorsalis</i>	00100	00011	10012	01010	00010	21100	00000	00000	01011	01000	00011	010?0		
17. <i>Selenoscopus turbisquamatus</i>	00100	00010	01002	10010	10000	211??	10010	10111	00000	10011	10?12	01101		
18. <i>Uranoscopus albesca</i>	00100	00010	01002	20010	20000	21100	10010	10111	00000	10114	10112	01101		
19. <i>U. archionema</i>	00000	01010	01002	20010	21000	21100	10010	10111	00000	10114	10212	01101		
20. <i>U. bictinctus</i>	01000	00010	01002	20010	20001	21100	10010	10011	00000	10114	10212	01111		
21. <i>U. cognatus</i>	00100	00010	01002	20010	20000	21100	10010	10111	00000	10114	11012	00111		
22. <i>U. crassiceps</i>	00100	01010	01002	20010	20000	21100	10010	10111	00000	10114	10112	01111		
23. <i>U. filibarbis</i>	0?000	?10?0	?0?0?	?0?0?	20?0?	?1?0?	1?0?0?	10111	000?0	101?0	?????	0110?		
24. <i>U. japonicus</i>	00100	01010	01002	20010	20000	21100	10010	10111	00000	10114	10213	01101		
25. <i>U. oligolepis</i>	01000	01010	01002	20010	22000	21100	10010	10011	00000	10111	10212	01111		
26. <i>U. polli</i>	00100	00010	01002	10010	20000	21100	10010	10111	00000	10111	10012	01101		
27. <i>U. scaber</i>	02000	11010	01002	10010	21000	21100	10010	10101	00000	10114	102?4	01101		
28. <i>U. tosaie</i>	00100	11010	01002	20010	20000	21000	10010	10111	00000	10114	10012	01111		
29. <i>Xenocephalus armatus</i>	00100	01011	10012	00010	00010	21110	11100	00000	11011	01000	10011	000?0		
30. <i>X. australiensis</i>	00100	01001	10012	00010	00010	21110	11100	01000	10011	00002	10011	000?0		
31. <i>X. egregius</i>	00100	01011	10012	11010	00010	21110	11100	00000	11011	01000	10011	000?0		
32. <i>X. elongatus</i>	00100	01011	10012	10010	00010	21110	11100	01000	10011	00000	10011	000?0		



Table 2. continued.

Taxon	Transformation series and characters											
	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101-105	106-110	111-113	
Outgroup	00000	01000	00000	00000	00000	00000	00000	00000	00???	00000	000	
1. <i>Astroscoptes y-graecum</i>	02010	10010	00000	00001	01111	11110	10002	20111	10110	10000	101	
2. <i>A. guttatus</i>	02010	10010	01010	00001	01111	11110	10003	20111	10110	10000	101	
3. <i>A. sexspinosus</i>	02010	10020	01000	00101	01111	11110	10002	20111	10110	10000	101	
4. <i>A. zephyreus</i>	02010	10010	11000	00001	01111	11110	10012	20111	10110	10000	101	
5. <i>Genyagnus monopterygius</i>	12011	12012	11021	01101	00001	10010	11013	20010	01010	00001	020	
6. <i>Ichthyoscopus barbatus</i>	02110	00011	11121	10111	00101	10100	11112	21011	01110	10102	100	
7. <i>I. lebeck</i>	02110	00011	11021	00101	00101	10100	11112	21011	01112	10100	100	
8. <i>I. sannio</i>	02110	00011	11021	00101	00101	10100	11112	21011	01112	10100	100	
9. <i>Kathetostoma albigutta</i>	12001	21102	12121	01101	10001	20010	01014	10000	01001	01010	010	
10. <i>K. averruncus</i>	12001	21102	12021	00101	10001	20010	01014	10000	01001	01000	000	
11. <i>K. canaster</i>	12001	21102	02021	00101	10001	10010	11004	10010	01001	01010	000	
12. <i>K. cubana</i>	12001	21102	12021	00101	10001	20010	01014	10000	01001	01010	000	
13. <i>K. giganteum</i>	12001	21102	02021	00101	10001	10010	11004	10010	01001	01010	000	
14. <i>K. laeve</i>	12001	21102	02021	00101	10001	10010	11004	10010	01001	01010	000	
15. <i>K. nigrofasciatum</i>	12001	21102	12021	01101	10001	10010	11004	10010	01001	01010	000	
16. <i>Pleuroscopus pseudodorsalis</i>	01001	01012	01021	00110	00001	10010	01001	00010	01000	00000	000	
17. <i>Selenoscopus turbisquamatus</i>	?2011	21012	01001	0000?	?????	2????	?????	20000	01001	00000	01?	
18. <i>Uranoscopus albesca</i>	22010	21012	01001	00101	00001	20020	01012	20000	01001	00000	000	
19. <i>U. archionema</i>	22010	21011	11001	00001	00001	20020	01012	20000	01001	00000	010	
20. <i>U. bicinctus</i>	22010	21012	01001	00011	00001	20020	01012	20000	01001	00000	010	
21. <i>U. cognatus</i>	32011	31012	01001	00001	00001	10020	01012	20010	01001	00000	010	
22. <i>U. crassiceps</i>	22010	21012	11001	00001	00011	20020	01012	20000	01001	00000	010	
23. <i>U. filibarbis</i>	?????	21072	1?0??	?????	?????	?????	?????	20000	01????	0?001	?1?	
24. <i>U. japonicus</i>	32011	21012	01001	00001	00001	20020	01012	20000	01001	00000	010	
25. <i>U. oligolepis</i>	22010	21012	01001	00111	00001	20020	01012	20000	01001	00000	010	
26. <i>U. palli</i>	22011	21012	11001	00101	00001	20020	01012	20000	01001	00000	010	
27. <i>U. scaber</i>	32011	21012	01001	00001	00001	20020	01012	20000	01001	00000	010	
28. <i>U. tosaе</i>	32011	21012	01001	00001	00001	20020	01012	20000	01001	00000	010	
29. <i>Xenocephalus armatus</i>	02000	01012	11000	01100	00002	10010	01013	10010	01000	00000	000	
30. <i>X. australiensis</i>	01000	01012	11000	11100	00002	10011	01010	10010	01000	00000	000	
31. <i>X. egregius</i>	02000	01012	11001	01100	00002	10010	01013	10010	01000	00000	000	
32. <i>X. elongatus</i>	01000	01012	01000	01100	00002	10011	01010	10010	01000	00000	000	

A, both 0 and 1 are coded.

supported by five apomorphies (42-1, 47-1, 65-1, 74-2 and 75-1) based on DELTRAN. This species has three autapomorphies not included in the analysis: presence of parietal spine; presence of frontal spine; presence of frontal spine; and proximal tips of first and second anal fin proximal pterygiophores fused.

*Clade 3B.* Includes species of the genus *Xenocephalus*. Monophyly of clade 3B is unambiguously supported by nine synapomorphies: 7-1, 29-1, 32-1\*, 33-1\*, 41-1\*, 65-0r, 74-0r, 77-1 and 85-2\*; and further supported by two synapomorphies (71-1 and 75-0r) based on ACCTAN, and four synapomorphies (31-1, 51-1, 94-1 and 96-1) based on DELTRAN. Clade 3B is divided into clades 4A and 4B.

*Clade 4A.* Includes *Xenocephalus armatus* and *X. egregius*. This clade is unambiguously supported by two synapomorphies 62-2 and 95-3 and also supported by three synapomorphies (42-1, 47-1 and 71-1) based on DELTRAN. Clade 4A is separated into clades 5A and 5B.

*Clade 5A.* Comprises *Xenocephalus armatus* and is characterized by a single apomorphy (75-0r) based on DELTRAN.

*Clade 5B.* Comprises *Xenocephalus egregius*, characterized by three autapomorphies: 16-1, 17-1 and 75-1, as well as an autapomorphy, presence of preopercular flange, not included into the analysis.

*Clade 4B.* Comprises the two species: *Xenocephalus australiensis* and *X. elongatus*. It is unambiguously supported by two synapomorphies 37-1\* and 90-1\*, and further supported by two synapomorphies (42-0r and 47-0r) based on ACCTAN and a synapomorphy (75-0rD) based on DELTRAN. Clade 4A is divided into clades 6A and 6B.

*Clade 6A.* Comprises *Xenocephalus australiensis*, characterized by three apomorphies: 9-0r, 50-2 and 76-1, and further supported by an apomorphy (71-1) based on DELTRAN.

*Clade 6B.* Comprises *Xenocephalus elongatus*, characterized by an apomorphy 16-1, and supported by an apomorphy (71-0r) based on ACCTAN.

*Clade 2B.* Comprises species of *Kathetostoma*, *Uranoscopus*, *Ichthyoscopus* and *Astroscopus*, *Selenoscopus turbisquamatus* and *Genyagnus monopterygius*. Monophyly of clade 2B is unambiguously supported by five synapomorphies: 16-1, 53-2, 55-4, 62-2 and 80-1\*, and further supported by five synapomorphies (36-1, 46-1, 61-1, 66-2 and 105-1) based on ACCTAN, and six synapomorphies (31-1, 51-1, 65-1, 66-1, 75-1 and 96-1) based on DELTRAN. This clade is divided into clades 7A and 7B.

*Clade 7A.* Includes species of the genus *Kathetostoma*. It is unambiguously supported by eight synapomorphies: 26-0r, 68-1\*, 69-0r, 72-2\*, 81-1\*, 95-4\*, 107-1\* and 109-1, and further supported by six synapomorphies (11-1, 36-1, 61-1, 66-2, 74-2 and 105-1) based on DELTRAN. Clade 7A is divided into clades 8A and 8B.

*Clade 8A.* Comprises three species: *Kathetostoma albigutta*, *K. averruncus* and *K. cubana*. This clade is unambiguously supported by five synapomorphies: 4-1, 43-1, 71-1, 86-2 and 99-0r, and further supported by two synapomorphies (46-1 and 94-1) based on DELTRAN. Clade 8A is split into clades 9A and 9B.

*Clade 9A.* Comprises *Kathetostoma albigutta*. It is characterized by five apomorphies: 58-1, 59-1, 73-1, 77-1 and 112-1, and further supported by two autapomorphies not included into the analysis: absence of third obliquus ventralis; and transversus ventralis anterior and posterior separated.

*Clade 9B.* Comprises two species: *Kathetostoma averruncus* and *K. cubana*. The clade is unambiguously supported by two synapomorphies 3-1 and 60-1. Clade 9B is divided into clades 10A and 10B.

*Clade 10A.* Includes *Kathetostoma averruncus*. It is characterized by an apomorphy 109-0r.

*Clade 10B.* Includes *Kathetostoma cubana*. This clade is characterized by an apomorphy 28-0r, and further supported by an autapomorphy, second and third preural centra fused, which was not included into the analysis.

*Clade 8B.* Comprises four species: *Kathetostoma giganteum*, *K. canaster*, *K. laeve* and *K. nigrofasciatum*. It is unambiguously supported by three synapomorphies: 27-0r, 91-1 and 94-0r, and further supported by a synapomorphy (46-0r) based on ACCTAN, and a synapomorphy (99-1) based on DELTRAN. Clade 8B is separated into clades 11A and 11B.

*Clade 11A.* Includes *Kathetostoma giganteum*. This clade lacks any apomorphies.

*Clade 11B.* Comprises three species: *Kathetostoma canaster*, *K. laeve* and *K. nigrofasciatum*. It is unambiguously supported by three synapomorphies: 23-1\*, 50-1 and 52-2\*. This clade is separated into clades 12A and 12B.

*Clade 12A.* Includes *Kathetostoma canaster*. It lacks any apomorphies.

*Clade 12B.* Comprises two species: *Kathetostoma laeve* and *K. nigrofasciatum*. It is unambiguously supported by a synapomorphic 2-1. This clade is divided into clades 13A and 13B.

*Clade 13A.* Includes *Kathetostoma laeve*. It lacks any apomorphies.

*Clade 13B.* Includes *Kathetostoma nigrofasciatum*. This clade is characterized by four apomorphies: 4-1, 26-1, 71-1 and 77-1, and supported by an autapomorphy, long ligament bonding prezygapophysis of second vertebra with supraoccipital, which was not included into the analysis.

*Clade 7B.* Comprises species of *Uranoscopus*, *Ichthyoscopus*, and *Astroscopus*, *Selenoscopus turbisquamatus* and *Genyagnus monopterygius*. It is unambiguously supported by seven synapomorphies: 7-1, 11-0r, 12-1\*, 34-1\*, 64-1\*, 95-2 and 96-2\*, and further supported by two synapomor-

phies (6-1 and 22-1) based on ACCTAN, and three synapomorphies (26-2, 69-1 and 94-1) based on DELTRAN. This clade is divided into clades 14A and 14B.

*Clade 14A.* Comprises species of the genus *Uranoscopus* and *Selenoscopus turbisquamatus*. It is unambiguously supported by 17 synapomorphies: 21-2, 38-1, 40-1\*, 48-1, 49-1, 50-4, 57-1, 58-1, 59-1, 60-1, 61-3, 74-0r, 78-0r, 86-2, 89-2\*, 99-0r and 112-1, and further supported by four synapomorphies (36-1, 46-1, 66-2 and 105-1) based on DELTRAN. Clade 14A is separated into clades 15A and 15B.

*Clade 15A.* Includes *Uranoscopus scaber*. It is characterized by two apomorphies: 2-2\* and 59-0, and further supported by two apomorphies (6-1D and 22-1D) based on DELTRAN.

*Clade 15B.* Comprises 11 species: *Uranoscopus bicinctus*, *U. oligolepis*, *U. crassiceps*, *U. archionema*, *U. filibarbis*, *U. japonicus*, *U. tosae*, *U. cognatus*, *U. albesca*, *U. polli* and *Selenoscopus turbisquamatus*. It is unambiguously supported by three synapomorphies: 16-2, 39-1 and 55-2\*, and further supported by two synapomorphies (6-0r and 22-0r) based on ACCTAN. Clade 15B is separated into clades 16A and 16B.

*Clade 16A.* Comprises five species: *Uranoscopus bicinctus*, *U. oligolepis*, *U. crassiceps*, *U. archionema* and *U. filibarbis*. This clade is unambiguously supported by two synapomorphies 61-2 and 65-0r. Clade 16A is divided into clades 17A and 17B.

*Clade 17A.* Comprises two species: *Uranoscopus bicinctus* and *U. oligolepis*. It is unambiguously supported by three synapomorphies: 2-1, 38-0r and 79-1. Clade 17A is split into clades 18A and 18B.

*Clade 18A.* Includes *Uranoscopus bicinctus*. This clade is characterized by two autapomorphies: 7-0r and 25-1, and supported by an autapomorphy, presence of cartilage between proximal tips of fifth ceratobranchials, which was not included into the analysis.

*Clade 18B.* Includes *Uranoscopus oligolepis*. It is characterized by three apomorphies: 22-2\*, 50-1 and 78-1.

*Clade 17B.* Comprises three species: *Uranoscopus crassiceps*, *U. archionema* and *U. filibarbis*. This clade is unambiguously supported by a synapomorphy 71-1. Clade 17B is divided into clades 19A and 19B.

*Clade 19A.* Includes *Uranoscopus crassiceps*. It is characterized by three apomorphies: 3-1, 53-1 and 84-1.

*Clade 19B.* Comprises two species: *Uranoscopus archionema* and *U. filibarbis*. It is unambiguously supported by a synapomorphic 59-0. Clade 19B is divided into clades 20A and 20B.

*Clade 20A.* Includes *Uranoscopus archionema*. This clade is characterized by two apomorphies: 22-1 and 70-1.

*Clade 20B.* Includes *Uranoscopus filibarbis*. It is characterized by an apomorphic 110-1.

*Clade 16B.* Comprises six species: *Uranoscopus japonicus*, *U. tosae*, *U. cognatus*, *U. albesca*, *U. polli* and *Selenoscopus turbisquamatus*. It is unambiguously supported by a synapomorphy 3-1. Clade 16B is divided into clades 21A and 21B.

*Clade 21A.* Includes *Uranoscopus japonicus*. It is characterized two apomorphies: 55-3\* and 59-0.

*Clade 21B.* Comprises five species: *Uranoscopus tosae*, *U. cognatus*, *U. albesca*, *U. polli* and *Selenoscopus turbisquamatus*. This clade is unambiguously supported by a synapomorphic 53-0r. Clade 21B is separated into clades 22A and 22B.

*Clade 22A.* Includes *Uranoscopus tosae*. It is characterized by two apomorphies: 6-1 and 28-0r.

*Clade 22B.* Comprises four species: *Uranoscopus cognatus*, *U. albesca*, *U. polli* and *Selenoscopus turbisquamatus*. It is unambiguously supported by a synapomorphy: 7-0r. Clade 22B is separated into clades 23A and 23B.

*Clade 23A.* Includes *Uranoscopus cognatus*. It is characterized five apomorphies: 52-1, 57-0r, 66-3\*, 86-1 and 99-1.

*Clade 23B.* Comprises three species *Uranoscopus albesca*, *U. polli* and *Selenoscopus turbisquamatus*. It is unambiguously supported by two synapomorphies 59-0 and 61-2, and further supported by a synapomorphy (78-1) based on ACCTAN. Clade 23B is divided into clades 24A and 24B.

*Clade 24A.* Includes *Uranoscopus albesca*. It is characterized by three apomorphies 53-1, 65-0r, and 112-0r, and further supported by an apomorphy (78-1) based on DELTRAN.

*Clade 24B.* Comprises *Uranoscopus polli* and *Selenoscopus turbisquamatus*. This clade is unambiguously supported by two synapomorphies 16-1r and 50-1. Clade 24B is divided into clades 25A and 25B.

*Clade 25A.* Includes *Uranoscopus polli*. It is characterized by an apomorphy 71-1, and further supported by an apomorphy (78-1) based on DELTRAN.

*Clade 25B.* Includes *Selenoscopus turbisquamatus*. It is characterized by three apomorphies: 21-1, 48-0r and 95-0r, and further supported by an apomorphy (78-0r) based on ACCTAN.

*Clade 14B.* Comprises species of *Ichthyscopus* and *Astroscopus*, and *Genyagnus monopterygius*. It is unambiguously supported by seven synapomorphies: 13-1, 20-1\*, 35-1\*, 71-1, 91-1, 104-1\* and 105-0, and further supported by five synapomorphies (3-1, 21-1, 29-1, 36-0r and 66-1r) based on ACCTAN, and two synapomorphies (22-1 and 99-1) based on DELTRAN. Clade 14B is separated into clades 26A and 26B.

*Clade 26A.* Includes *Genyagnus monopterygius*. It is characterized by eight apomorphies: 1-2\*, 30-1, 43-1, 67-2\*, 77-1, 95-3, 110-1 and 112-2\*, and also supported by

seven apomorphies (3-1, 6-1, 21-1, 29-1, 46-1, 61-1 and 74-2) based on DELTRAN. This species has an autapomorphy, anteroventral region of frontal connected with parasphenoid, which was not included into the analysis.

**Clade 26B.** Comprises species of *Ichthyoscopus* and *Astroscopus*. This clade is unambiguously supported by nine synapomorphies: 27-0r, 65-0r, 67-0\*, 83-1\*, 88-1\*, 100-1\*, 103-1\*, 106-1\* and 111-1\*, and also supported by two synapomorphies (46-0r and 61-0r) based on ACCTRAN. Clade 26B is divided into clades 27A and 27B.

**Clade 27A.** Includes species of the genus *Ichthyoscopus*. The clade is unambiguously supported by 10 synapomorphies: 9-0r, 11-1, 51-0r, 63-1\*, 66-0r, 70-1, 89-0r, 93-1\*, 97-1\* and 108-1\*, and also supported by a synapomorphy (21-0r) based on ACCTRAN, and four synapomorphies (3-1, 6-1, 29-1 and 74-2) based on DELTRAN. Clade 27A is divided into clades 28A and 28B.

**Clade 28A.** Includes *Ichthyoscopus barbatus*. It is characterized by seven apomorphies: 30-1, 49-1, 50-3\*, 73-1, 76-1, 79-1 and 110-2\*.

**Clade 28B.** Comprises two species: *Ichthyoscopus lebeck* and *I. sannio*. This clade is unambiguously supported by a synapomorphy 105-2\*. Clade 28B is separated into clades 29A and 29B.

**Clade 29A.** Includes *Ichthyoscopus lebeck*. It is characterized by two apomorphies 26-1 and 31-0r.

**Clade 29B.** Includes *Ichthyoscopus sannio*. It lacks any apomorphies supported.

**Clade 27B.** Comprises species of the genus *Astroscopus*. This clade is unambiguously supported by 20 synapomorphies: 1-1\*, 2-1, 5-1, 13-2, 16-0r, 18-1\*, 25-1, 56-1\*, 70-0r, 74-0r, 75-0r, 78-0r, 82-1\*, 84-1, 87-1\*, 92-0r, 98-1\*, 101-1\*, 102-0r and 113-1\*, and further supported by four synapomorphies (3-0r, 6-0r, 10-1 and 29-0r) based on ACCTRAN. Clade 27B is divided into clades 30A and 30B.

**Clade 30A.** Includes *Astroscopus zephyreus*. It is characterized by two apomorphies: 21-2 and 55-1, and also supported by an apomorphy (10-1) based on DELTRAN.

**Clade 30B.** Comprises three species: *Astroscopus guttatus*, *A. y-graecum* and *A. sexspinosus*. The clade is unambiguously supported by four synapomorphies: 15-1\*, 39-1, 71-0r and 94-0r, and further supported by a synapomorphy (21-1) based on DELTRAN. Clade 30B is separated into clades 31A and 31B.

**Clade 31A.** Includes *Astroscopus guttatus*. It is characterized by three apomorphies: 52-1, 74-1\* and 95-3, and also supported by an apomorphy (10-0r) based on ACCTRAN. This species has an autapomorphy, presence of free three cartilages anterior to basihyal, which was not included into the analysis.

**Clade 31B.** Comprises two species: *Astroscopus y-graecum* and *A. sexspinosus*. The clade is unambiguously sup-

ported by two synapomorphies 13-0r and 19-2\*, and further supported by a synapomorphy (10-1) based on DELTRAN. Clade 31B is separated into clades 32A and 32B.

**Clade 32A.** Includes *Astroscopus y-graecum*. It is characterized by an apomorphy 72-0r.

**Clade 32B.** Includes *Astroscopus sexspinosus*. It is characterized by seven apomorphies: 2-0r, 5-0r, 50-2, 53-0r, 55-1, 69-2\* and 78-1, as well as an autapomorphy, presence of tooth plate on second epibranchial, not included into the analysis.

## VII. Comparison with Previous Study

Relationships of Uranoscopidae have been inferred phylogenetically only by Pietsch (1989), who analyzed them at the generic level based on cladistic methodology and anatomical data. He hypothesized: (1) *Pleuroscopus* and *Xenocephalus* (as *Gnathagnus*, considered a junior synonym of *Xenocephalus* by Springer and Bauchot, 1994) are a monophyletic group that diverged initially from other taxa; (2) a monophyletic group comprising *Kathetostoma* and *Uranoscopus* have a sister relationship with a monophyletic group comprising *Genyagnus*, *Ichthyoscopus* and *Astroscopus*; and (3) *Genyagnus* has a sister relationship with a monophyletic *Ichthyoscopus* and *Astroscopus*. The phylogenetic position of the monotypic genus *Selenoscopus* described by Okamura and Kishimoto (1993) was not treated remains unknown.

Firmly relationships reconstructed here mostly resemble those of the previous study, but differ for *Kathetostoma* and *Uranoscopus*. In the present study, these two genera are regarded as paraphyletic, i.e., *Kathetostoma* has a sister relationship with a monophyletic group comprising *Uranoscopus*, *Genyagnus*, *Ichthyoscopus* and *Astroscopus*. *Selenoscopus* is inferred as nesting deeply within *Uranoscopus*, making *Uranoscopus* as currently recognized paraphyletic. *Selenoscopus* is therefore regarded as a junior synonym of *Uranoscopus*.

## VIII. Sister Group of Uranoscopidae (Fig. 77; Table 3)

The Uranoscopidae has been considered to have a sister relationship with the Trachinidae by several authors (e.g., Pietsch, 1989; Pietsch and Zabetian, 1990; Imamura and Matsuura, 2003), as the two families share a number of derived characters. Pietsch (1989) regarded nine characters as synapomorphies of the two families: (1) the epiotic with a large, rounded, posterolaterally directed expansion that serves to support the medial process of the posttemporal; (2) infra-orbital bones forming a subocular shelf; (3) large, well-ossified lateral and medial extrascapulae; (4) medial extrascapulae fused to the posteromedial margin of the supra-occipital; (5) rugose, highly sculptured, and superficially placed supracleithral bones; (6) anterodorsal section of hyo-



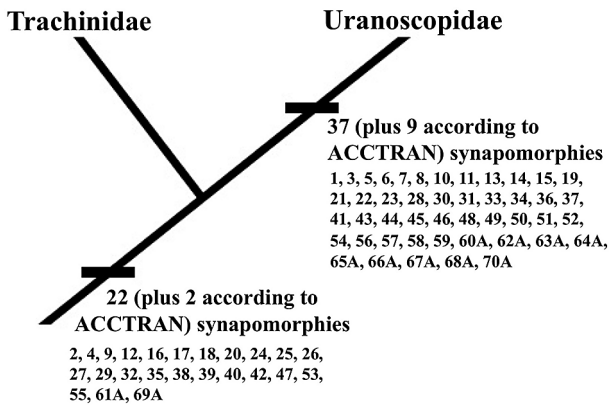


Fig. 77. Sister relationship of Uranoscopidae and Trachinidae. Numbers of characters correspond to those in Table 3. “A” indicates synapomorphy recognized according to ACC-TRAN.

hyoidei adductors muscle narrow, its origin restricted to the anterodorsal-medial surface of the opercle; (7) an elevated lateral line that turns ventrally on the caudal peduncle and extends out onto the middle rays of the caudal fin; (8) epidermal covering of scales fully united between adjacent scales, forming discrete, oblique scale rows that extend across the body in an anterodorsal-posteroventral direction; and (9) scales oriented at right angles to oblique scale rows. Characters 2, 5 and 7 are considered in this study to be valid synapomorphies of the two families, although they are expressed differently. Characters 1 and 6 were not adjudged derived characters, when compared with percoids, while character 3, the size of medial extrascapulae, are continuously variable among the family and cannot be separated into morphotypes. Character 4, fusion between the medial extrascapula(e) and posteromedial margin of the supraoccipital, cannot be evaluated as the homology between the medial extrascapula(e) and the sensory canal on the supraoccipital is unclear among uranoscopids (see section 1-2. Cranium). As characters 8 and 9 were present in only several uranoscopids examined for this study, they were inferred as not being synapomorphic for the family. Imamura and Matsuura (2003) listed 16 derived characters that are present in both the Uranoscopidae and Trachinidae: (1) the supratemporal sensory canal of the two sides continuous with each other; (2) six branchiostegal rays; (3) three or more anal-fin pterygiophores anterior to the first hemal spine; (4) presence of soft ray on posterior portion of the first anal pterygiophore; (5) relationship of the neural spines and dorsal fin pterygiophores 1: 1; (6) absence of the first supraneural; (7) branched caudal fin rays fewer than 15; (8) the parasphenoid and pterospheonoid attached; (9) the cranium with many tubercles and/or lumps; (10) presence of a developed hyomandibular process; (11) the cleithrum with a strong spine posteriorly; (12) the lateral and mesial sides of the lower two actinosts expanded anteriorly and sandwiching the coracoid; (13) the pelvic girdle strongly extended in front

of the pectoral girdle anteriorly; (14), lower two hypurals fused; (15) scale forming discrete, oblique rows; and (16) a cutaneous axillary appendage associated with the pectoral fin. These characters, with the exception of characters 1, 3, 7, 8, 12 and 15, are also accepted as synapomorphies of two families in this study. Characters 1, 3 and 7 cannot be evaluated as the homologies of the medial extrascapulae, anal fin proximal pterygiophores and branched caudal fin rays are unclear (sections 1-2. Cranium; 1-8. Axial skeleton and median fin supports; and 1-10. Caudal skeleton). Characters 8, 12 and 15 were found in some uranoscopids, but were not inferred to be synapomorphies of the family by the analysis.

On the basis of this study, the following 22 (plus two based on ACCTTRAN) synapomorphies of Uranoscopidae are also present in Trachinidae: 2, 4, 9, 12, 16, 17, 18, 20, 24, 25, 26, 27, 29, 32, 35, 38, 39, 40, 42, 47, 53 and 55 (plus 61 and 69 based on ACCTTRAN) (Fig. 77, Table 3). No other families having more derived characters than Trachinidae have not been examined or reported. Therefore, the sister relationship of the Uranoscopidae and Trachinidae is also strongly supported here. Of the above-listed characters, 4, 9, 18, 20, 29, 32, 38, 42, 53 and 55 (plus 61 based on ACCTTRAN) are new synapomorphies of the two families. As a result, the number of synapomorphies directly supporting the monophyly of the Uranoscopidae is reduced from 59 (plus 11 based on ACCTTRAN) to 37 (plus nine based on ACCTTRAN).

## IX. Classification (Figs. 78-85)

### 1. Family Uranoscopidae

**Diagnosis.** Two facets on first infraorbital for articulation with tip of anterior process of palatine and lateral ethmoid mesially separated by dorsomesial ridge; infraorbital homologous with percoid second infraorbital absent; interorbital fossa present; posttemporal fossa absent; maxillo-lateral ethmoid ligament present; anterior socket for articulation with anterior condyle of hyomandibula present on posterolateral corner of sphenotic; urohyal sutured with first basibranchial; posterior projection of urohyal absent; opercle enlarged and expanded posteriorly; third epibranchial without tooth plate; interacual cartilage absent; postpelvic process absent; first vertebra firmly attached to posterior portion of cranium; posterior elements of epineurals attached to vertebrae and pleural ribs separated from vertebrae; first proximal pterygiophore of dorsal fin inserted between third and fourth neural spines; third and fourth hypurals fused; levator operculi originating from supracleithrum; third levator externus absent; pharyngoclavicularis internus inserted onto dorsal aspect of fifth ceratobranchial; transversus pharyngobranchial 2 absent; extensor proprius originating from pelvis and cleithrum; obliquus superioris divided into two sections, dorsal obliquus superioris inserted onto Baudelet's ligament and anteromesial aspect of upper limb of

Table 3. List of synapomorphies supporting monophyly of Uranoscopidae and sister relation of Uranoscopidae and Trachinidae

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*I. Characters common to Uranoscopidae*

1. Two facets of first infraorbital separated by dorsomesial ridge.
- 2\*. Presence of subocular shelf on first infraorbital.
3. Absence of infraorbital homologous with percoid second infraorbital.
- 4\*. Dorsal surface of cranium broad and flat.
5. Presence of interorbital fossa.
6. Absence of posttemporal fossa.
7. Presence of maxillo-lateral ethmoid ligament.
8. Anterior socket for articulation with anterior condyle of hyomandibula present on posterolateral corner of sphenotic.
- 9\*. Supraoccipital crest formed on posterior portion of supraoccipital.
10. Urohyal sutured with first basibranchial.
11. Absence of posterior projection of urohyal.
- 12\*. Presence of hyomandibular spur.
13. Opercle enlarge and expanded posteriorly.
14. Absence of tooth plate on third epibranchial.
15. Absence of interacual cartilage.
- 16\*. Anterior portion of pelvic girdle projecting beyond ventral arm of pectoral girdle.
- 17\*. Presence of cleithral spine.
- 18\*. Actinosts short, broad firmly attached to each other and to posterior portions of scapula and coracoid.
19. Absence of postpelvic process.
- 20\*. Absence of accessory subpelvic keel.
21. First vertebra firmly attached to posterior portion of cranium.
22. Posterior elements of epineurals attached to vertebrae and pleural ribs separated from vertebrae.
23. First proximal pterygiophore of dorsal fin inserted between third and fourth neural spines.
- 24\*. Absence of supraneurals.
- 25\*. Each proximal pterygiophore individually inserting in interspace between adjacent neural and hemal spines.
- 26\*. Second ray on posterior portion of first proximal pterygiophore of anal fin being soft ray.
- 27\*. First and second hypurals fused.
28. Third and fourth hypurals fused.
- 29\*. Absence of second uroneural.
30. Levator operculi originating from supracleithrum.
31. Absence of third levator externus.
- 32\*. Presence of first, second and third adductores.
33. Pharyngoclavicularis internus inserted onto dorsal aspect of fifth ceratobranchial.
34. Absence of transversus pharyngobranchial 2.
- 35\*. Absence of coracoradialis.
36. Extensor proprius originating from pelvis and cleithrum.
37. Obliquus superioris divided into two sections.
- 38\*. Obliquus inferioris originating from esophagus.
- 39\*. Cutaneous axillary appendage associated with pectoral fin.
- 40\*. Presence of tubercles and pits on bony elements.
41. Transverse septum attached to posterior portion of pelvis.
- 42\*. Absence of swimbladder.

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cleithrum posteriorly, and ventral obliquus superioris attached to posteromesial surface of upper limb of cleithrum and post-cleithra anteriorly; transverse septum separating pericardial cavity and pleuroperitoneal cavity, attached to posterior portion of pelvis ventrally.

## 2. Genera of the family Uranoscopidae

Seven genera are recognized in the family.

Genus *Pleuroscopus* Barnard, 1927

Genus *Xenocephalus* Kaup, 1858

Genus *Kathetostoma* Günther, 1860

Table 3. Continued.

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*II. Characters recognized as synapomorphies of Uranoscopidae based on phylogenetic analysis*

43. Two vomerine tooth plates (= character 9-1).  
 44. Absence of basisphenoid (= character 15-2).  
 45. Intercalar small, separated from prootic (= character 19-1).  
 46. Rod-like posteriormost branchiostegal ray (= character 27-1).  
 47\*. Six branchiostegal rays (= character 28-1).  
 48. Absence of tooth plate on second pharyngobranchial (= character 54-1).  
 49. Coracoid connecting directly to mesial expansion of lower two actinosts (= character 62-1).  
 50. Absence of dorsal spine on first proximal pterygiophore (= character 70-2).  
 51. Presence of soft ray on anterodistal base of first proximal pterygiophore of anal fin (= character 72-1).  
 52. Uroneural and urostyle fused (= character 78-1).  
 53\*. Insertion of hyohyoidei abductor section 2 onto second branchiostegal ray (= character 85-1).  
 54. Origin of posterodorsal section of hyohyoidei adductor onto lateral surface of supracleithrum and cleithrum (= character 86-1).  
 55\*. Presence of arrector dorsalis pelvis originating from cleithrum and pelvis (= character 89-1).  
 56. Anteroventral portion of obliquus inferioris and infracarinalis medius originating from posterior portion of pelvis (= character 92-1).  
 57. Orbit small (= character 102-1).  
 58. Cutaneous cirri on lips short and poorly developed (= character 103-0).  
 59. Conical shape of cutaneous cirri on lips (= character 104-0).  
 60A. Absence of ethmoid (= character 11-1).  
 61A\*. Absence of beryciform foramen of ceratohyal (= character 26-2).  
 62A. Dorsal portion of lateral process of hyomandibula exposed and sculptured (= character 31-1).  
 63A. Presence of distal and proximal cartilaginous caps of third hypobranchial (= character 51-1).  
 64A. Subpelvic process short (= character 65-1).  
 65A. Presence of ossified distal pterygiophore on anterodistal base of first proximal pterygiophore of anal fin (= character 69-1).  
 66A. Fifth hypural fused with urostyle and upper hypural plate (= character 74-2).  
 67A. Upper hypural plate fused with urostyle (= character 75-1).  
 68A. Obliquus inferioris and sternohyoideus separated by cleithrum (= character 94-1).  
 69A\*. Posterior portion of lateral line close to but separated from dorsal fin base (= character 96-1).  
 70A. Gill opening narrow and its dorsal edge reaching to cleithrum (= character 99-1).

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“A” indicates characters recognized as uranoscopid synapomorphy according to ACCTRAN. Asterisk indicates synapomorphy shared between Uranoscopidae and Trachinidae.

- Genus *Uranoscopus* Linnaeus, 1758
- Genus *Genyagnus* Gill, 1861
- Genus *Ichthyoscopus* Swainson, 1839
- Genus *Astroscopus* Brevoort, 1860

*Remark.* The classification of Uranoscopidae at the generic level, for clades 3A (*Pleuroscopus*), 3B (*Xenocephalus*), 7A (*Kathetostoma*), 14A (*Uranoscopus*), 26A (*Genyagnus*), 27A (*Ichthyoscopus*) and 27B (*Astroscopus*), is proposed in this study on the basis of their phylogenetic relationships and minimization of taxonomic changes in the family (Fig. 78). Seven genera herein recognized are mostly similar with the recent classification proposed by Nelson (2006), except for *Selenoscopus*, which is synonymized with *Uranoscopus*, because the relationship reconstructed here inferred the former is deeply nested in *Uranoscopus*, and the genus *Uranoscopus* is paraphyletic if *Selenoscopus* is regarded as valid. New discussions and definitions of genera are expressed under “Remarks” for each taxon. Only anatomical characters considered to be important in this study are

included in generic diagnoses.

**2-1. Key to the genera of Uranoscopidae**

- 1a. Ventral flange of dentary present; adductor mandibulae section A2 small and its posterodorsal portion lying under section A1 .....2
- 1b. Ventral flange of dentary absent; adductor mandibulae section A2 large and its posterodorsal portion covering section A1 .....3
- 2a. Opercle without spine; posterolateral process of ectopterygoid absent .....*Pleuroscopus*
- 2b. Opercle with spine; posterolateral process of ectopterygoid present .....*Xenocephalus*
- 3a. Posterior portion of lateral line close to dorsal fin base; cutaneous cirri present on lower surface of lower jaw .....*Kathetostoma*
- 3b. Posterior portion of lateral line mostly attached to dorsal fin base; no cutaneous cirri on lower surface of lower jaw .....4

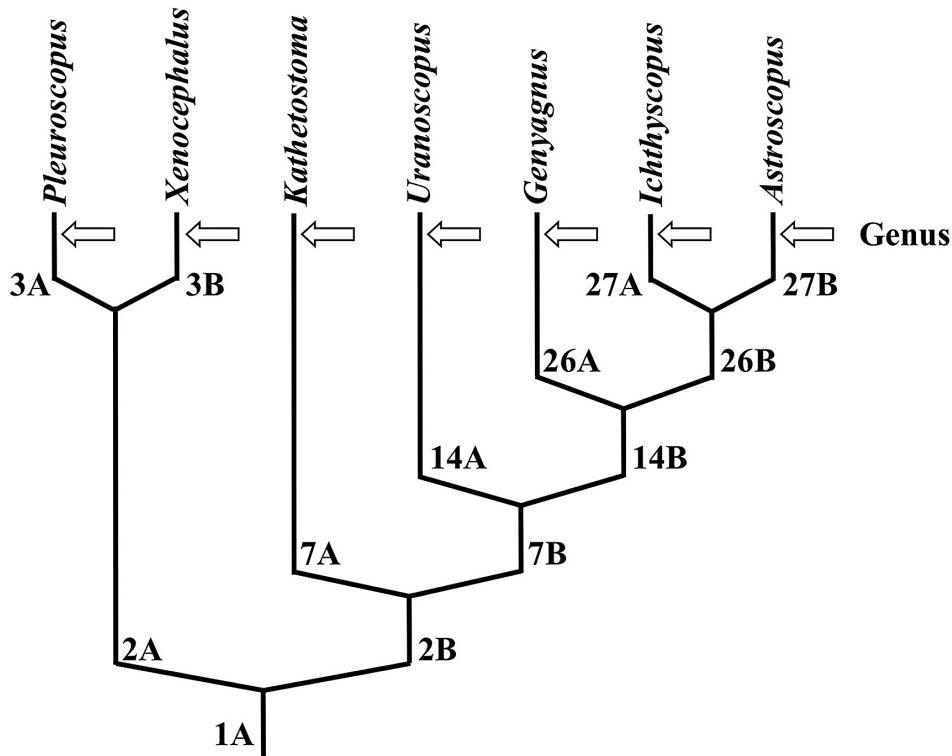


Fig. 78. Cladogram of phylogenetic relationships of Uranoscopidae inferred in this study, demonstrating taxonomic ranking for the “genus”. Arrows indicate clades provided the generic rank.

- 4a. Preopercle with spines; posterior portion of supra-cleithrum with spine; cutaneous cirri on lips conical .....*Uranoscopus*
- 4b. Preopercle without spines; posterior portion of supra-cleithrum without spine; cutaneous cirri on lips compressed .....5
- 5a. Median belly fold absent; parapophyses wide and very expanded; dorsal margin of protractor hyoidei not folded .....*Genyagnus*
- 5b. Median belly fold present; parapophyses rudimentary; dorsal margin of protractor hyoidei folded laterally and extending for insertion on mesial surface of interopercle .....6
- 6a. Cutaneous cirri present on membrane of gill opening; posterior nostrils confined to nasal region; orbital electric organ absent .....*Ichthyscopus*
- 6b. Cutaneous cirri absent on membrane of gill opening; posterior nostrils extending into orbital region; orbital electric organ present .....*Astroscopus*

**2-2. Genus *Astroscopus* Brevoort, 1860**

*Astroscopus* Brevoort in Gill, 1860: 20 (type species: *Uranoscopus anoplos* Valenciennes in Cuvier and Valenciennes, 1832 = *Uranoscopus y-graecum* Cuvier in Cuvier and Valenciennes, 1829).

*Agnus* Günther, 1860: 229 (type species: *Uranoscopus anoplos* Valenciennes in Cuvier and Valenciennes, 1832 =

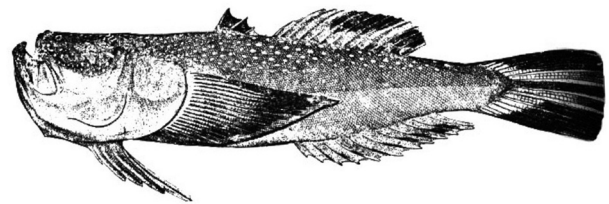


Fig. 79. Lateral view of *Astroscopus y-graecum*, type species of the genus (from Jordan and Everman, 1896).

*Uranoscopus y-graecum* Cuvier in Cuvier and Valenciennes, 1829).

*Upselonphorus* Gill, 1861: 113 (type species: *Uranoscopus y-graecum* Cuvier in Cuvier and Valenciennes, 1829).

**Diagnosis.** Two spines present on anterior portion of first infraorbital; third infraorbital not forming part of orbit; nasal exposed and sculptured; ethmoid present; parietal with unroofed sensory canal or sensory canal absent; posterodorsal portion of parasphenoid separated from pterosphenoid and frontal; epiotic process absent; supraoccipital with roofed sensory canal; lateral extrascapula composed of two elements, each with canal and two pores; coronomackelian expanded ventrally, almost attached to ventral edge of Meckelian cartilage; ventral margin of palatine concave; palatine with concavity contiguous with nasal and oral cavities; dorsal limb of posttemporal very elongate and spine-like; posterior and dorsomesial portions of supra-cleithrum lacking



spines; postcleithra composed of two elements; no dorsal process on base of pelvic spine; subpelvic process long; pelvic spur with single poorly developed spur; parapophyses of abdominal vertebrae rudimentary; dorsal fin with spine on first proximal pterygiopore strong and rigid; ligamentum primordium attaching to maxilla anterior to dorsal attachment of section A1; dorsal margin of protractor hyoidei folded laterally and extending to insert on mesial surface of interopercle; transversus protractor hyoidei present; origin of abductor superficialis on lower limb of cleithrum located anterior to origin of abductor profundus; abductor superficialis broad and expanding to occupy most of cleithrum midlaterally; anteroventral portion of obliquus inferioris and infracarinalis medius originating on dorsal portion of extensor proprius and adductor superficialis pelvici, and on posterior portion of pelvis; body scales covered with skin and forming oblique rows or embedded under skin; posterior portion of lateral line mostly attached to dorsal fin base; posterior end of lateral line curved downwardly and joining lateral line of opposite side; opening of nostrils large; posterior nostril extending into orbital region; orbit large; cutaneous cirri on nostrils large and well developed; lips with long, compressed, unbranched cutaneous cirri; orbital electric organ present.

*Remark.* The genus includes four living species: *Astroscopus guttatus* Abbott, 1860, *A. sexspinosus* (Steindachner, 1876), *A. γ-graecum* (Cuvier in Cuvier and Valenciennes, 1829) (= type species) (Fig. 79) and *A. zephyreus* Gilbert and Starks in Gilbert, 1897. In addition, a fossil species, *Astroscopus countermani* Carnevale, Godfrey and Pietsch, 2011, was recently described (Carnevale et al., 2011).

### 2-3. Genus *Genyagnus* Gill, 1861

*Genyagnus* Gill, 1861: 115 (type species: *Uranoscopus monopterygius* Schneider in Bloch and Schneider, 1801).

*Synnema* Haast, 1873: 274 (type species: *Uranoscopus monopterygius* Schneider in Bloch and Schneider, 1801).

**Diagnosis.** Three spines present on anterior portion of first infraorbital; third infraorbital with subocular shelf and contacting frontal; ethmoid present; parietal with roofed sensory canal; supraoccipital with roofed sensory canal; lateral extrascapula composed of two elements, each with canal and two pores; urohyal attached to second basibranchial posterodorsally; anterior edge of basihyal with two cartilaginous caps; ventral margin of palatine concave, with concavity for contiguous with nasal and oral cavities; ventral margin of posterior arm of subopercle fringed; first and second pharyngobranchials absent; postcleithra composed of elongate single element attached to cleithrum; no dorsal process on base of pelvic spine; subpelvic process short; pelvic spur with single poorly developed spur; parapophyses of abdominal vertebrae wide and distinctly expanded; process on anterolateral surface of lower hypural plate present; body scales completely embedded under skin; posterior portion of

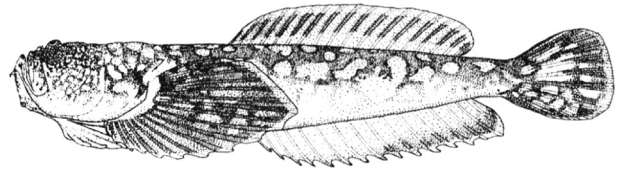


Fig. 80. Lateral aspect of *Genyagnus monopterygius*, type species of the genus (from Kishimoto, 2001).

lateral line mostly attached to dorsal fin base; opening of nostrils small; cutaneous cirri on nostrils poorly developed; single mental barbel present; lips with short, compressed, unbranched cutaneous cirri; compressed, elongate lingual lure present.

*Remark.* Pietsch (1989) included median extrascapula tightly fused to the posterodorsal surface of the supraoccipital among the characters in his diagnosis of this genus. This character is considered not to be available as the homology between the sensory canals of the supraoccipital and medial extrascapulae is unclear among uranoscopids (see section 2-1. Cranium).

The genus is monotypic, including only *Genyagnus monopterygius* (Schneider in Bloch and Schneider, 1801) (Fig. 80).

### 2-4. Genus *Ichthyscopus* Swainson, 1839

*Ichthyscopus* Swainson, 1839: 181, 269 (type species:

*Uranoscopus inermis* Cuvier in Cuvier and Valenciennes, 1829 = *Uranoscopus lebeck* Bloch and Schneider, 1801).

*Anema* Günther, 1860: 226, 230 (type species: *Uranoscopus lebeck* Bloch and Schneider, 1801).

**Diagnosis.** Third infraorbital contacted to frontal; prevomer with single tooth plate; ethmoid absent; parietal with roofed sensory canal; supraoccipital without sensory canal; lateral extrascapula composed of two elements, each with canal and two pores; urohyal attached to second basibranchial posterodorsally; ventral margin of palatine concave, with concavity contiguous with nasal and oral cavities; third hypobranchial with cartilaginous posterior margin, including proximal and distal tips; first and second pharyngobranchials absent; posterior and dorsomesial portions of supracleithrum without spines; postcleithra composed of two elements; uppermost actinost absent; no dorsal process on base of pelvic spine; subpelvic process long; pelvic spur absent; parapophyses of abdominal vertebrae rudimentary; dorsal fin with dorsal spine on first proximal pterygiopore soft and flexible; dorsal margin of protractor hyoidei folded laterally and extending to insert on mesial surface of interopercle; abductor superficialis broad and expanding to occupy most of cleithrum midlaterally; arrector dorsalis pelvici present, originating on pelvis; obliquus inferioris separated from lateral surface of pelvis; body scales covered with skin and forming oblique rows; posterior portion of lateral line mostly attached to dorsal fin base; lateral lines on either side of cau-

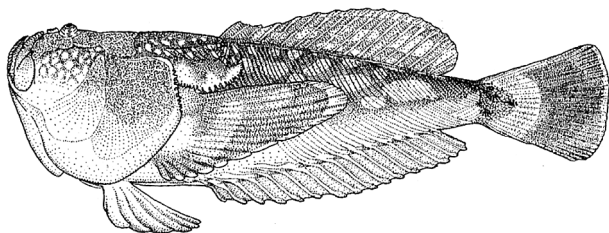


Fig. 81. Lateral view of *Ichthyscopus lebeck*, type species of the genus (from Kishimoto, 2001).

dal peduncle fused dorsally; opening of nostrils large; cutaneous cirri on nostrils large and well developed; cutaneous cirri present on membranes of gill opening; lips with long, compressed, unbranched or branched cutaneous cirri.

*Remark.* Pietsch (1989) included median and medial extrascapulae tightly fused to the posterior margin of the parietal and posterodorsal surface of the supraoccipital among the characters diagnosing *Ichthyscopus*. This character is considered not valid as the homology between the sensory canal of the parietal and supraoccipital and medial extrascapulae is unclear among uranoscopids (see section 2-1. Cranium).

The genus comprises eight species: *Ichthyscopus barbatus* Mees, 1960, *I. fasciatus* Haysom, 1957, *I. insperatus* Mees, 1960, *I. lebeck* (Bloch and Schneider, 1801) (= type species) (Fig. 81), *I. malacopterus* [Anonymous (Bennett), 1830], *I. nigripinnis* Gomon and Johnson, 1999, *I. sannio*, Whitley, 1936 and *I. spinosus* Mees, 1960.

## 2-5. Genus *Kathetostoma* Günther, 1860

*Kathetostoma* Günther, 1860: 231 (type species: *Uranoscopus laevis* Bloch and Schneider, 1801).

**Diagnosis.** Beryciform foramen of ceratohyal present, bridge above it ossified or cartilaginous; preopercle with spines ventrally; ventral margin of posterior arm of subopercle smooth or fringed; postcleithra composed of single elongate element, attached to cleithrum; dorsal process present on base of pelvic spine; subpelvic process short; pelvic spur with single prominent, sharp spine; first proximal pterygiophore of dorsal fin rod-like; anal fin without distal pterygiophore on anterodistal base of first proximal pterygiophore; no dorsal spine on first proximal pterygiophore of dorsal fin; anal fin without first ray on anterodistal base of first proximal pterygiophore; adductor mandibulae section A $\omega$  expanding posteriorly and mostly reaching to quadrate; body scales absent; posterior portion of lateral line close to, but separated from, dorsal fin base; openings of nostril small; cutaneous cirri on nostrils poorly developed or absent; cutaneous cirri on underside of lower jaw present; labial flap on upper lips present or absent; lips with short, conical, unbranched and branched cutaneous cirri; depressed, elongate lingual lure absent or present.

*Remark.* *Kathetostoma* (Clade 7A) is separated into two

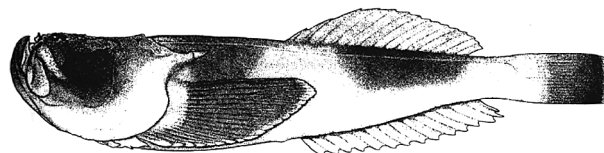


Fig. 82. Lateral view of *Kathetostoma laeve*, type species of the genus (from Last et al. 1983).

clades (8A and 8B), supported by several synapomorphies and having widely separated geographical distributions. Clade 8A, including *K. albigutta*, *K. cubana* and *K. averruncus*, is distributed in the western Central Atlantic and eastern Central Pacific, while Clade 8B, comprising *K. giganteum*, *K. canaster*, *K. nigrofasciatum* and *K. laeve*, are confined to Australasian waters. It is cladistically reasonable to recognize the two clades as separate genera or retain generic status for Clade 7A. To minimized taxonomic change, *Kathetostoma* retained as the genus name for clade 7A.

Pietsch (1989) included the following four characters in his diagnosis of *Kathetostoma*: spinous-dorsal fin absent; lateral line located just beneath insertion of dorsal fin; lingual lure organ usually present; and gill opening extremely wide, terminating dorsally far forward, well beyond posterior margin of supracleithrum. Based on material examined in this study, dorsal spines are present in *K. laeve*, *K. canaster*, *K. nigrofasciatum* and *K. giganteum*, and the character should therefore not be included for the phylogenetic analysis as the homology of dorsal fin spines among uranoscopids is unclear (see the section 1-8. Axial skeleton and median fin supports). In addition, the lateral line in *Kathetostoma* is located close to the dorsal fin base, not just beneath the base, and the lingual lure and configuration of gill opening vary among species (see section 3. Other morphology).

The genus includes eight species: *Kathetostoma albigutta* Bean, 1892, *K. averruncus* Jordan and Bollman, 1890, *K. binigrasella* Gomon and Roberts, 2011, *K. canaster* Gomon and Last, 1987, *K. cubana* Barbour, 1941, *K. giganteum* Haast, 1873, *K. laeve* (Bloch and Schneider, 1801) (= type species) (Fig. 82) and *K. nigrofasciatum* Waite and McCulloch, 1915.

## 2-6. Genus *Pleuroscopus* Barnard, 1927

*Pleuroscopus* Barnard, 1927: 67 (type species: *Pleuroscopus pseudodorsalis* Barnard, 1927).

**Diagnosis.** Third infraorbital with subocular shelf; nasal exposed and sculptured; frontal, parietal and pterotic each with spine; sphenotic lacking posterolateral process; posterodorsal portion of parasphenoid separated from pterosphenoid and frontal; supraoccipital without sensory canal; dentary with ventral flange; dorsal portion of lateral process of hyomandibula embedded under skin and smooth; dorsolateral surface of opercle with longitudinal ridge; ventral margin of interopercle thick and completely

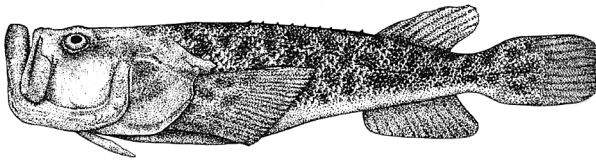


Fig. 83. Lateral view of *Pleuroscopus pseudodorsalis*, type species of the genus (from Last et al. 1983, based on Barnard, 1927).

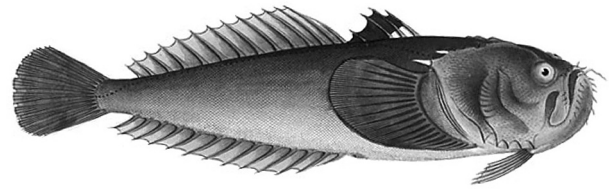


Fig. 84. Lateral view of *Uranoscopus scaber*, type species of the genus (from Bloch, 1786).

ossified; lateral surface of subopercle covered with tubercles and knob, but without spine; third hypobranchial with cartilaginous posterior margin that includes proximal and distal tips; first pharyngobranchial ossified; second pharyngobranchial ossified small, and rod-like; spine on posterior portion of supracleithrum but not at middle; postcleithra composed of two elements; subpelvic process short; pelvic spur absent; dorsal spine on first proximal pterygiopore of dorsal fin absent; upper hypural plate fused with urostyle; epurals composed of two elements; body scales modified into small blunt spinules; posterior portion of lateral line close to lateral midline of body; gill opening narrow, its dorsal edge reaching to cleithrum; opening of nostrils small; cutaneous cirri of nostrils absent or poorly developed; lips with short, conical, unbranched cutaneous cirri.

*Remark.* Pietsch (1989) included the pelvic spur short and lips lacking cutaneous cirri in his diagnosed *Pleuroscopus*. However, based on specimens examined for this study, the genus lacks a pelvic spur, and has short, conical, unbranched cutaneous cirri on the lips.

The genus is monotypic, including only *Pleuroscopus pseudodorsalis* Barnard, 1927 (Fig. 83).

## 2-7. Genus *Uranoscopus* Linnaeus, 1758

*Uranoscopus* Linnaeus, 1758: 250 (type species: *Uranoscopus scaber* Linnaeus, 1758).

*Nematagnus* Gill, 1861: 113 (type species: *Uranoscopus filibarbis* Cuvier in Cuvier and Valenciennes, 1829).

*Zalescopsis* Jordan and Hubbs, 1925: 312 (type species: *Zalescopsis tosae* Jordan and Hubbs, 1925).

*Selenoscopus* Okamura and Kishimoto, 1993: 311 (type species: *Selenoscopus turbisquamatus* Okamura and Kishimoto, 1993)

**Diagnosis.** Posterodorsal portion of parasphenoid connected to pterosphenoid or to pterosphenoid and frontal; supraoccipital with unroofed or roofed sensory canal; ventral margin of palatine concave, without concavity contiguous nasal and oral cavities; preopercle with spines ventrally; anterior and posterior part of lateral surface of opercle with sensory canal dorsally; midlateral surface of opercle with or without sensory canal dorsally; ventral margin of posterior arm of subopercle fringed; second basibranchial cartilaginous; third basibranchial composed of one or two cartilaginous elements; posterior portion of supracleithrum with or

without spine; dorsomesial portion of supracleithrum with spine; flange present on cleithrum lateral to attachment site of protractor pectoralis; postcleithra composed of short single element free from pectoral girdle or absent; no dorsal process on base of pelvic spine; pelvic spur with one or two prominent, sharp spurs; fifth hypural attached to urostyle and upper hypural plate; uroneural attached to or fused with urostyle; arrector dorsalis pelvici absent; body scales present, covered with skin and forming oblique rows or exposed posteriorly; posterior portion of lateral line mostly attached to dorsal fin base; opening of nostrils small; cutaneous cirri of nostrils poorly developed or absent; mental barbel present or absent; lips with short, conical, unbranched and branched cutaneous cirri; depressed, elongate lingual lure usually present.

*Remark.* The monotypic genus *Selenoscopus* is deeply nested with other species of *Uranoscopus* in Clade 14A. If *Selenoscopus* is regarded as valid, *Uranoscopus* is paraphyletic. Therefore, *Selenoscopus* is treated as a junior synonym of *Uranoscopus* here.

At present, *Uranoscopus* comprises 25 described living species: *U. affinis* Cuvier in Cuvier and Valenciennes, 1829, *U. albesca* Regan, 1915, *U. archionema* Regan, 1921, *U. bauchotae* Brüß, 1987a, *U. bicinctus* Temminck and Schlegel, 1843, *U. cadenati* Poll, 1959, *U. chinensis* Guichenot in Sauvage, 1882, *U. cognatus* Cantor, 1849, *U. crassiceps* Alcock, 1890, *U. dahlakensis* Brüß, 1987c, *U. dollfusi* Brüß, 1987a, *U. filibarbis* Cuvier in Cuvier and Valenciennes, 1829, *U. fuscomaculatus* Kner, 1868, *U. guttatus* Cuvier in Cuvier and Valenciennes, 1829, *U. japonicus* Houuttuyn, 1782, *U. kaianus* Günther, 1880, *U. marisrubri* Brüß, 1987b, *U. marmoratus* Cuvier in Cuvier and Valenciennes, 1829, *U. oligolepis* Bleeker, 1878, *U. polli* Cadenat, 1951, *U. rosette* Randall and Arnold, 2012, *U. scaber* Linnaeus, 1758 (= type species) (Fig. 84), *U. sulphureus* Valenciennes in Cuvier and Valenciennes, 1832, *U. tosae* (Jordan and Hubbs, 1925) and *U. turbisquamatus* (Okamura and Kishimoto, 1993). In addition, a fossil species, *Uranoscopus ciabatta* Girono, Nolf and Cavallo, 2010, was recently described from an otolith.

## 2-8. Genus *Xenocephalus* Kaup, 1858

*Xenocephalus* Kaup, 1858: 85 (type species: *Xenocephalus armatus* Kaup, 1858).

*Gnathagnus* Gill, 1861: 115 (type species: *Uranoscopus*



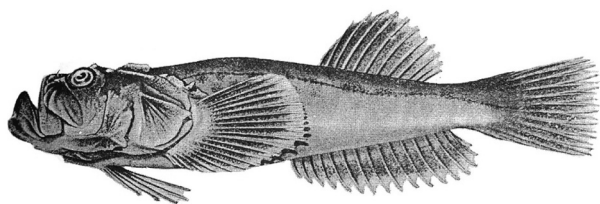


Fig. 85. Lateral view of *Xenocephalus armatus*, type species of the genus (from Last et al. 1983, based on Waite, 1904).

*elongatus* Temminck and Schlegel, 1843).

*Ariscopus* Jordan and Snyder, 1902: 479 (type species:

*Ariscopus iburius* Jordan and Snyder, 1902 = *Uranoscopus elongatus* Temminck and Schlegel, 1843).

*Excectides* Jordan and Thompson, 1905: 253 (type species:

*Excectides egregius* Jordan and Thompson, 1905).

*Gnathagnoides* Whitley and Phillipps, 1939: 235 (type

species: *Gnathagnus innotabilis* Waite, 1904 = *Xenocephalus armatus* Kaup, 1858).

*Benthoscopus* Longley and Hilderbrand, 1940: 264 (type

species: *Benthoscopus laticeps* Longley and Hilderbrand, 1940 = junior synonym of *Excectides egregius*, Jordan and Thompson, 1905).

**Diagnosis.** Third infraorbital with subocular shelf; fourth infraorbital not forming part of orbit; nasal exposed and sculptured; ethmoid absent; sphenotic without posterolateral process; dentary with ventral flange; urohyal attached to second basibranchial; endopterygoid small; posterolateral process on ectopterygoid present; opercle with spine posteriorly; ventral margin of interopercle thick and completely ossified; lateral surface of subopercle covered with tubercles; subopercle with or without knob; first pharyngobranchial ossified; second pharyngobranchial ossified, small and rod-like; supracleithrum without spines; postcleithra composed of two elements; subpelvic process long; pelvic spur absent; process on anterolateral surface of lower hypural plate present; hyohyoidei abductor section 2 inserted on third brachioistegal ray; body scales present, exposed posteriorly / or completely embedded under skin; posterior portion of lateral line close to, but separated from, dorsal fin base; opening of nostrils small; cutaneous cirri of nostrils poorly developed or absent; lips with short, conical, unbranched cutaneous cirri.

*Remark.* Pietsch (1989) listed pelvic spur short, dorsal spines absent and cutaneous cirri on lips absent, as characters diagnosing *Xenocephalus* (as *Gnathagnus*). Based on specimens of *Xenocephalus* examined for this study, the pelvic spur is absent and short, conical, unbranched cutaneous cirri are present on lips in all species of this genus, while one soft, flexible dorsal spine is present in *X. australiensis*, a species not included in Pietsch's (1989) study.

*Xenocephalus* contains the following five species: *X. armatus* Kaup, 1858 (= type species) (Fig. 85), *X. australien-*

*sis* (Kishimoto, 1989), *X. cribratus* (Kishimoto, 1989), *X. egregius* (Jordan and Thompson, 1905) and *X. elongatus* (Temminck and Schlegel, 1843).

## X. General Discussion (Figs. 76, 86–91, Table 4)

Uranoscopids are benthic fishes adapted to live in sand or mud on the seafloor. They are carnivorous, ambush predators that are typically solitary and nocturnal. Individuals bury into sand or mud during the day time with only their eyes and mouth exposed (Kishimoto, 2001; Carpenter, 2002). Uranoscopids generally occur from the littoral zone to depths of 550 m, although *Pleuroscopus pseudodorsalis* inhabits depths of 600 to 900 m (Nakabo, 2002; Capenter, 2002; Gomon 2008).

In this chapter, uranoscopid adaptations for a benthic life style are discussed, focusing on apomorphic characters common to the Uranoscopidae. Other adaptations based on the nature of character modifications varying among the family are also discussed.

### 1. Characters modified for a benthic existence present in all uranoscopids

This study found 70 synapomorphies that support the monophyly of Uranoscopidae. Among them, six synapomorphies are considered to be adaptive for a benthic life style.

*Dorsal surface of cranium.* The dorsal surface of the cranium is flat and broad in all members of the Uranoscopidae. A flat and broad cranium is often present in highly specialized bottom-dwelling fishes, such as the Lophiidae, Ogocephalidae and Platycephalidae (e.g., Gregory, 1933; Marshall, 1965; Imamura, 1996).

*Pectoral girdle.* Uranoscopids have the coracoid directly connected with a mesial expansion of the lower two actinosts, and short and broad actinosts that are firmly attached to each other and to the posterior portions of the scapula and coracoids, forming a single strong and rigid pectoral plate. In several bottom-dwelling fishes (e.g., Gobiidae, Cottidae and Blenniidae), the actinosts are broad, plate-like, and firmly connected to the scapula and coracoid. This structure is likely to provide a solid and strong site for the attachment of pectoral fin muscles supporting the large pectoral fin and a broad margin for the articulation of pectoral fin rays.

*Swimbladder.* The swimbladder is absent in all uranoscopids, as it is in many bottom-dwelling fishes (e.g., Cottidae and Pleuronectidae) (Helfman et al. 1997). Lack of this organ in benthic species is considered to be helpful in maintaining an individual's position on the bottom (Bond, 1996).

*Cutaneous cirri on lips.* Cutaneous cirri are present on lips of uranoscopids. These types of cirri are unique to some benthic-dwelling fishes (e.g., Leptoscopidae, Dactyloscopidae and Trichodontidae) (Last, 2001; Nakabo, 2002; Nelson 2006) and may help in preventing the intake of sand or mud



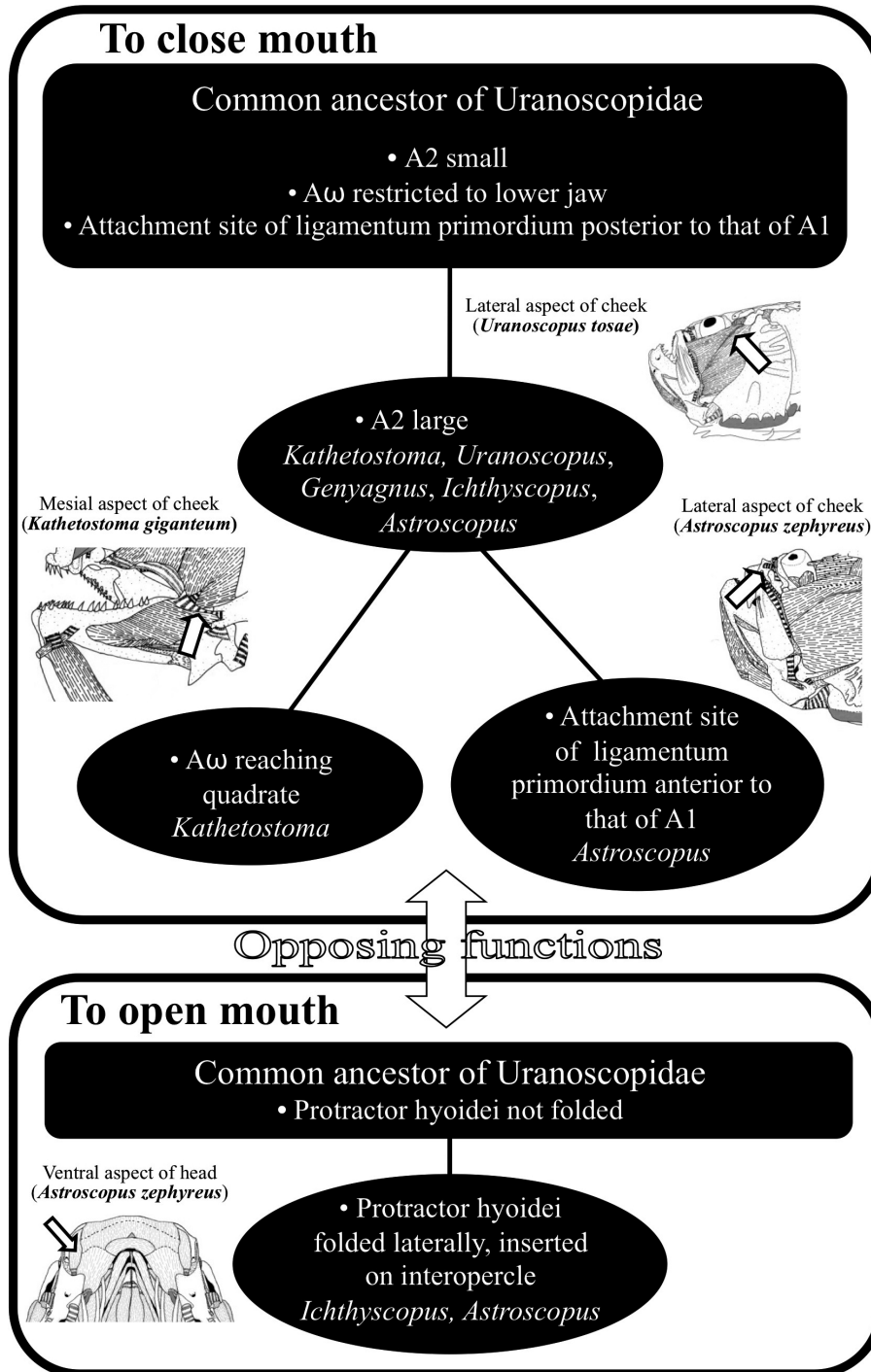


Fig. 86. Diagram showing hypothesised evolution of feeding mechanism in Uranoscopidae.

when uranoscopids burrow into seabottom and take in water for respiration.

*Lateral line.* The lateral line is situated close to the dorsal fin base in members of Uranoscopidae. This condition is rare in bony fishes, and is only known in some benthic-dwelling families (e.g., Trachinidae, Trichodontidae and Ammodytidae) (Roux, 1981; Nakabo, 2002). The closal position of the lateral line would make it possible to function as a sen-

sory organ when uranoscopids bury in the seabottom.

Among the six characters discussed above, four of them (i.e., cranium, actinosts of pectoral girdle, swimbladder and lateral line) are also present in the Trachinidae, the sister group of Uranoscopidae, although uranoscopids have a much broader cranium. The remaining two characters, the coracoid of the pectoral girdle and cirri on the lips, as well as the broader cranium do not occur in the Trachinidae, and are

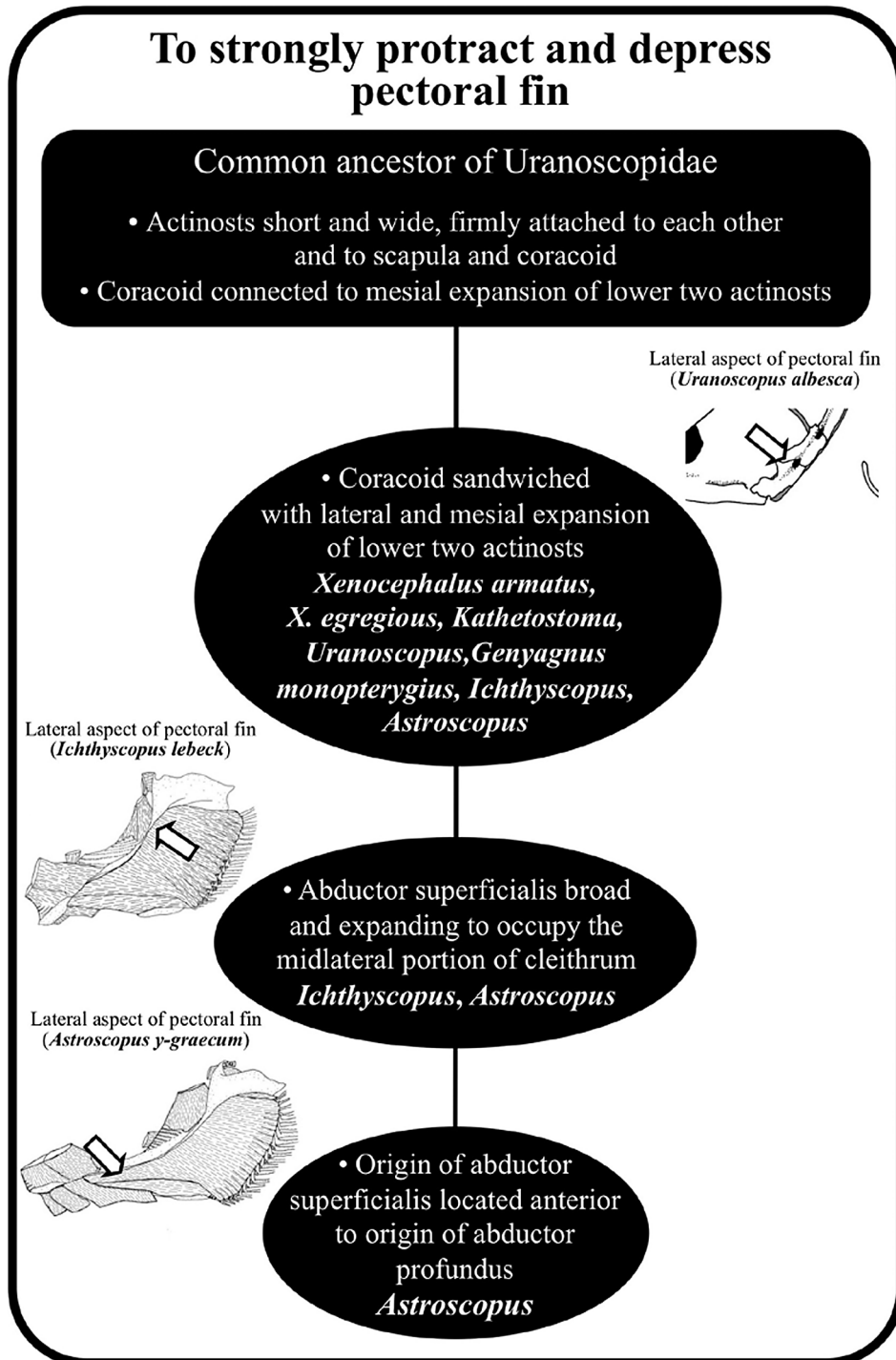


Fig. 87. Diagram showing hypothesised evolution of pectoral-fin mechanism in Uranoscopidae.

likely to have been acquired by the common ancestor of the Uranoscopidae.

In addition, all uranoscopids have a strongly oblique mouth, a character not used for the phylogenetic analysis. This character may be considered a derived character, because this form of mouth is not found in the vast majority of percoids (this study). An oblique mouth may be regarded as an adaptation for benthic life, as it makes the capture of prey eas-

ier, owing to the upward direction of the opening and closing of the mouth, when uranoscopids approach their prey from the seabottom. Although members of the Trachinidae have a slightly oblique mouth, it is much more highly modified in uranoscopids. Therefore, Uranoscopidae is considered to be a more adaptive group for benthic life style than Trachinidae.

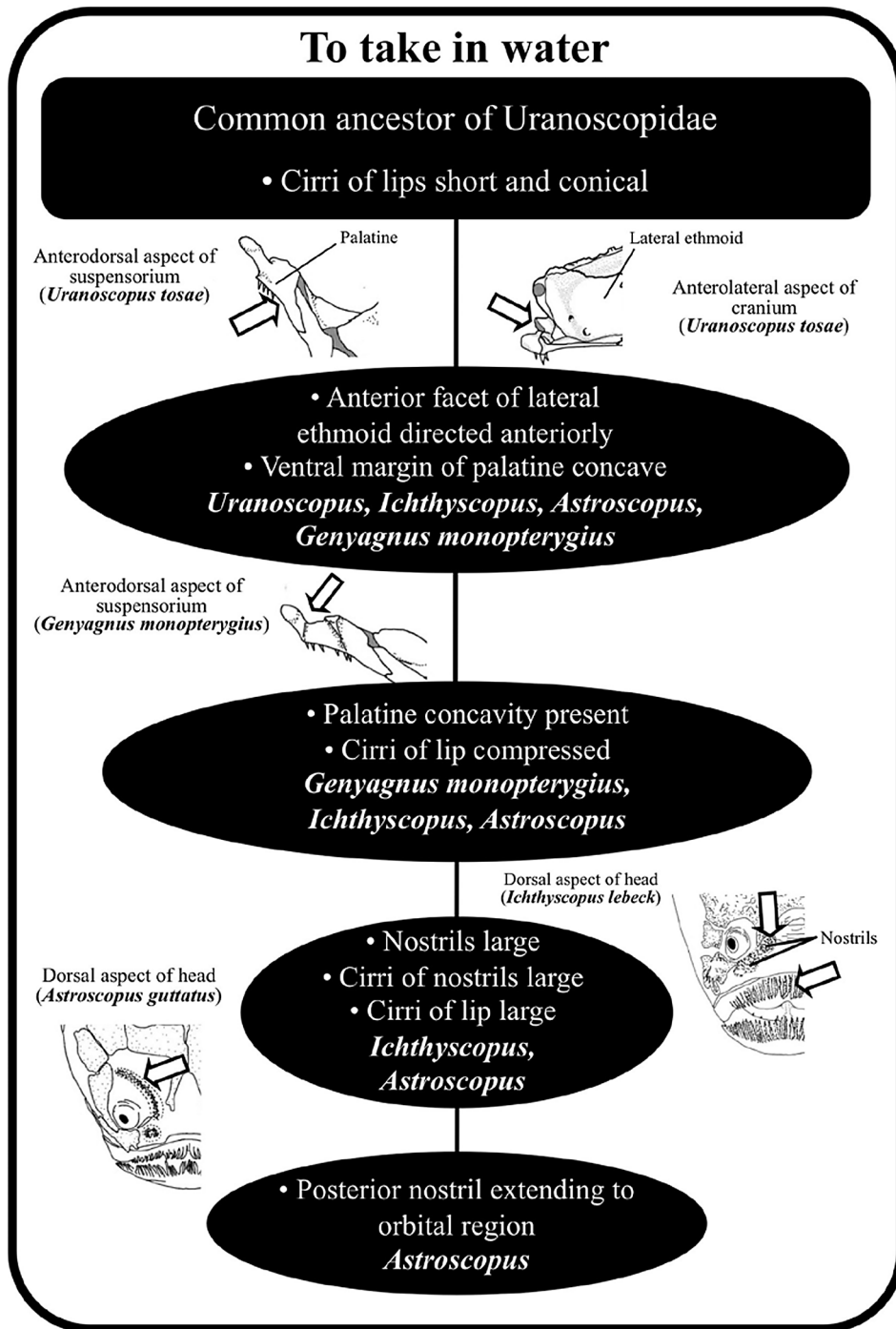


Fig. 88. Diagram presenting hypothesized evolution of respiratory mechanism associated with taking in water in Uranoscopidae. Characters associated with branched cirri on lips are not included because of their ambiguity in supporting phylogenetic relationships of Uranoscopidae.

## 2. Benthic adaptations varying among the Uranoscopidae

Besides the six adaptive characters mentioned above, additional specialized morphologies considered to be adaptations for a benthic life style occur variously among uranoscopids. These adaptations are mainly correlated with six physical mechanisms: feeding, pectoral fin locomotion, breathing,

sensory systems, lingual lure attraction and electrical production. They are described and discussed in this section.

### 2-1. Feeding mechanism

The feeding mechanism of uranoscopids is considered to be more highly advanced than most other perciforms. In the cheek region, morphological variations occur in the adductor

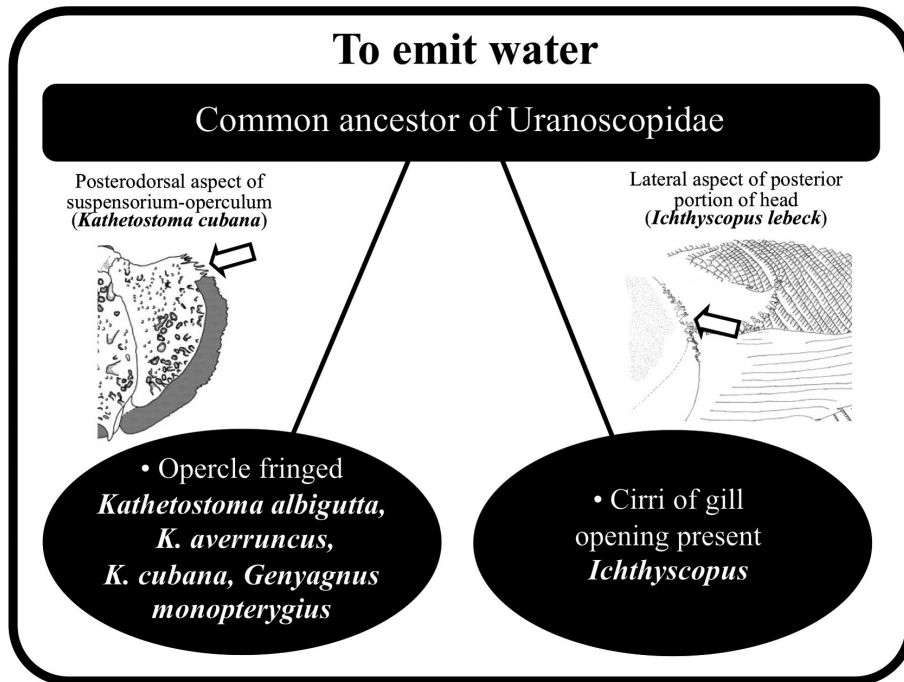


Fig. 89. Diagram showing evolution on respiratory mechanism associated with emitting water in Uranoscopidae. Characters associated with size of gill opening are not included because of their instability in the phylogenetic relationships of Uranoscopidae.

mandibulae and ligamentum primordium. The adductor mandibulae section A2 is small and the posterodorsal portion of it lies under section A1 in *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis*, as well as in percoids (character 80-0 in this study). *Uranoscopus* spp., *Kathetostoma* spp., *Ichthyscopus* spp., *Astroscopus* spp. and *Genyagnus monopterygius* have a large section A2 with its posterodorsal portion covering section A1 (character 80-1). In acanthopterygians, the closure of the mouth is produced by the adductor mandibulae (Lauder, 1985), and section A2, associated with the lower jaw, is the largest element of the adductor mandibulae in percoids (this study). Therefore, a well developed A2 in terms of muscle mass is considerably a specialized character which provides powerful and speedy closure of the mouth.

The adductor mandibulae section A $\omega$  is apparently different among uranoscopids. The section A $\omega$ , which is also considered to be associated with closing the mouth, is restricted to the anterior region of the anguloarticular in all uranoscopids, as in percoids (character 81-0), except *Kathetostoma* spp., in which section A $\omega$  expands posteriorly and mostly reaches to the quadrate (character 81-1). Posterior expansion of the section A $\omega$  is regarded as a specialization providing a stronger and more rapid closure of the mouth.

The attachment site of the ligamentum primordium also varies among uranoscopids. The site of attachment of the ligamentum primordium on the maxilla is posterior to the dorsal attachment of section A1 in all uranoscopids, as in percoids (character 82-0), except for *Astroscopus* spp., it attaches

anterior to dorsal attachment of the section A1 (character 82-1). The ligamentum primordium connects the adductor mandibulae and maxilla; therefore on anterior shift of the connection site is considered to make mouth closure more effective.

In the ventral region of the head, variations are apparent in the protractor hyoidei. The dorsal margin of protractor hyoidei is folded laterally and extends posteriorly to insert on the mesial surface of the interopercle in *Ichthyscopus* spp. and *Astroscopus* spp. (character 83-1), while it is not folded in other uranoscopids and percoids (character 83-0). In acanthopterygians, a ventral depression of the lower jaw involves the hyoid apparatus (Lauder, 1985). Consequently, the dorsal margin of the protractor hyoidei folded laterally and extending to insert on the mesial surface of the interopercle is regarded as a specialized structure providing a rapid opening of the mouth.

The four specialized structures mentioned above can be classified as strategies for opposite functions, closing and opening the mouth. The common ancestor of uranoscopids is inferred to have had a small muscular mass for section A2, section A $\omega$  restricted to the lower jaw, the attachment site of the ligamentum primordium posterior to that of section A1, and the protractor hyoidei not folded and not inserted on the interopercle. The evolution of the strategy for a powerful and rapid closure of the mouth initially occurred in the common ancestor of *Kathetostoma*, *Uranoscopus*, *Genyagnus*, *Ichthyscopus* and *Astroscopus* (branch 2B), having a large



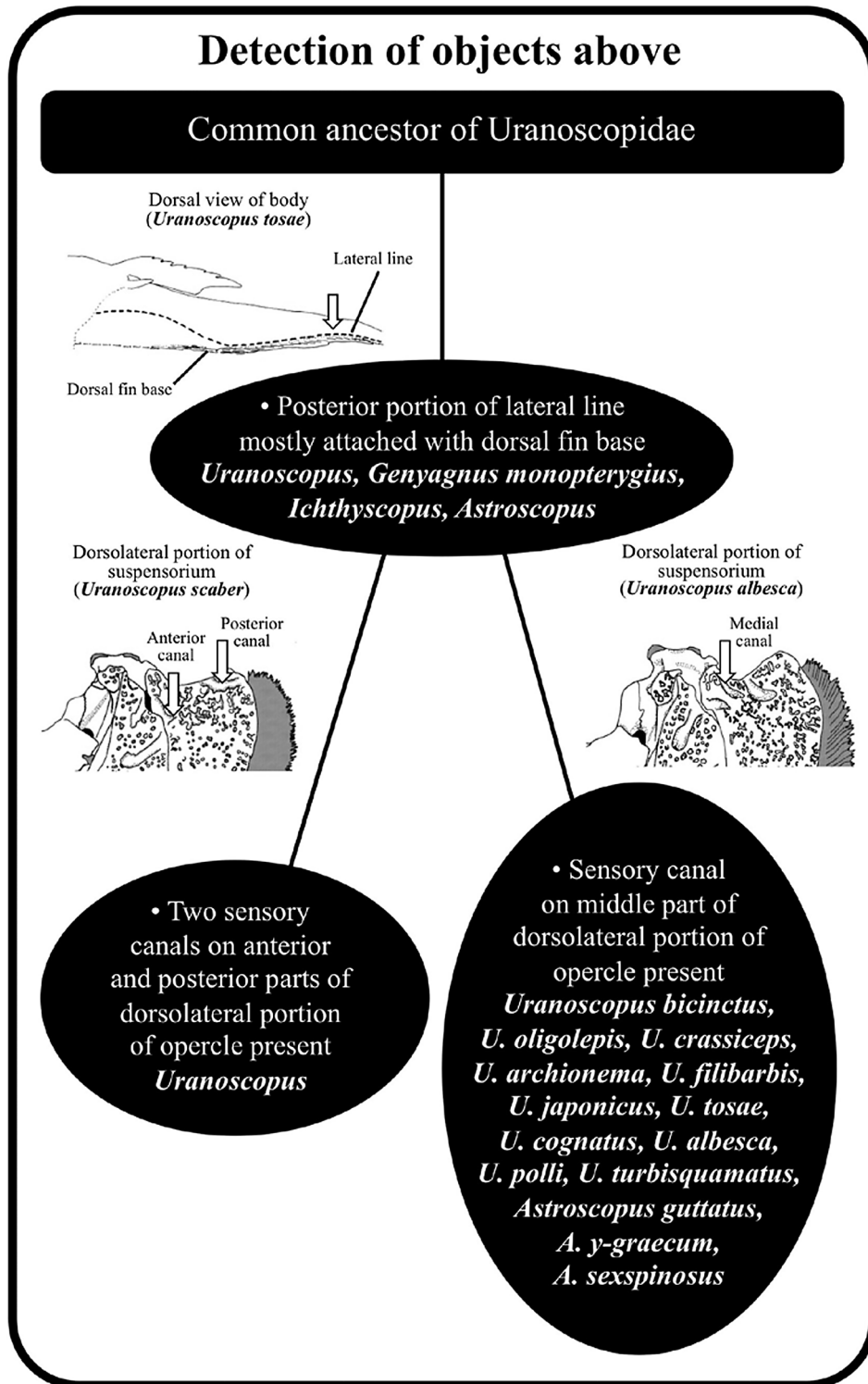


Fig. 90. Diagram presenting hypothesized evolution of sensory adaptations in Uranoscopidae.

muscle mass of section A2. Two independent adaptations are considered to have occurred subsequently in the common ancestors of *Kathetostoma* and *Astroscopus*. The adductor mandibulae section A $\omega$  became well developed and expanded posteriorly reaching the quadrate in the common ancestor of *Kathetostoma* (clade 7A), while the ligamentum primordium

became prolonged with its attachment site situated anterior to that of the section A1 in the common ancestor of *Astroscopus* (clade 27B). In contrast, the converse strategy of opening the mouth speedily, was evolved only in the common ancestor of *Ichthyscopus* and *Astroscopus* (clade 26B), in which the protractor hyoidei became folded laterally and extended pos-

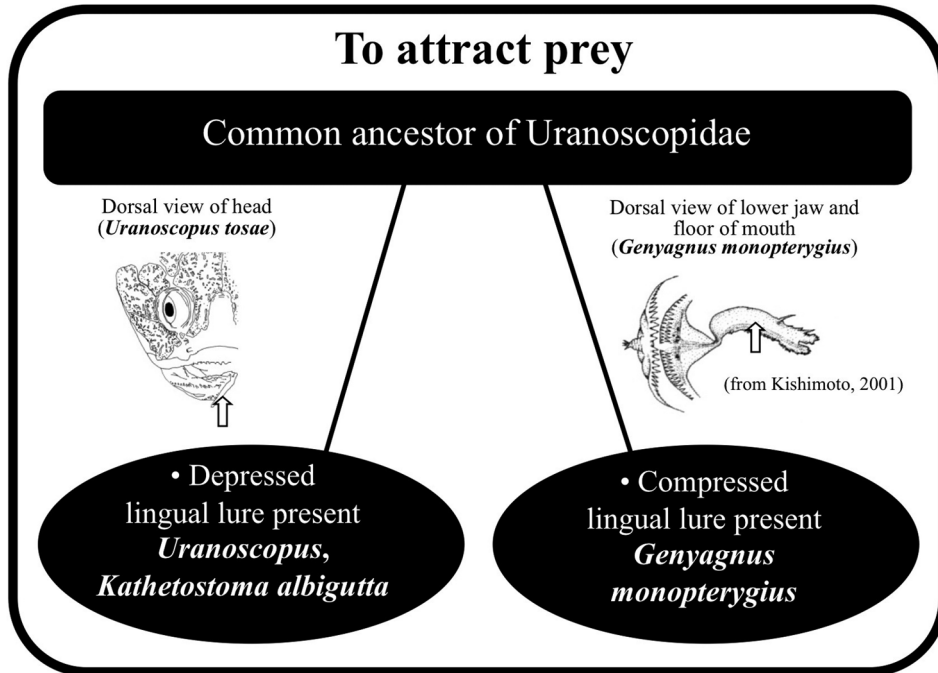


Fig. 91. Diagram presenting hypothesized evolution lingual lure organ mechanism in Uranoscopidae.

teriorly to insert on the mesial surface of the interopercle. Powerful and speedy closing and opening mechanisms of the mouth are considered to be effective in capturing prey swimming near the sea bottom where uranoscopids bury. The inferred evolution of the feeding mechanism is shown in Fig. 86.

## 2-2. Pectoral-fin mechanism

The pectoral-fin mechanism in the Uranoscopidae is considered to be more highly modified than other perciforms. Uranoscopids commonly have short and wide actinosts that are firmly attached with each other and with the scapula and coracoid. The structure provides a solid and strong attachment site for pectoral fin muscles supporting the large pectoral fin and a broad margin for attachment of the pectoral fin rays. In addition, a synapomorphy of the family recognized after the analysis, the coracoid directly connected with the mesial expansion of the lower two actinosts (character 62-1), also provides an attachment site for the pectoral muscles. In addition to these characters, two other, which are considered to be adaptive for a benthic life style, are found in the pectoral fin of uranoscopids. The coracoid is sandwiched by the lateral and mesial expansions of lower the two actinosts in *Kathetostoma* spp., *Uranoscopus* spp., *Ichthyoscopus* spp., *Astroscopus* spp., *Genyagnus monoptyerygius*, *Xenocephalus egregius* and *X. armatus* (character 62-2). As the coracoid articulates with the lower actinosts, which lack expansions in most acanthopterygians (Sasaki, 1989; Helfman et al., 1997; Imamura and Matsuura, 2003), the character found in uranoscopids is considered to be a specialized solid and strong

attachment site for pectoral muscles.

The abductor superficialis is broad and expands to occupy the midlateral most portion of the cleithrum in *Astroscopus* spp. and *Ichthyoscopus* spp. (character 88-1). In contrast, this muscle is narrow and confined to the ventral part of lateromedial aspect of the cleithrum in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Pleuroscopus pseudodorsalis* and *Genyagnus monoptyerygius* (character 88-0). In addition, the abductor superficialis has another variation in its origin on the lower limb of the cleithrum. The origin of this muscle is anterior to the origin of the abductor profundus in *Astroscopus* spp. (character 87-1), but is located posterior to the origin of the abductor profundus in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Ichthyoscopus* spp., *P. pseudodorsalis* and *G. monoptyerygius* (character 87-0). The abductor superficialis generally originates posterior to the origin of the abductor profundus in acanthopterygians (Sasaki, 1989; Drucker and Jensen, 1997; Westneat et al. 2004; this study). Consequently, the origin of the abductor superficialis anterior to the origin of the abductor profundus is assumed to be a specialized character, and may extend the abductor superficialis increasing its volume. In acanthopterygians, the abductor superficialis functions to protract and depress the fin (Drucker and Jensen, 1997). Therefore, the expansion of the abductor superficialis to occupy the midlateral portion of the cleithrum more anteriorly can be considered to strengthen the protraction and depression of the pectoral fin.

All adaptive characters discussed above may be regarded as the specialized functions of the pectoral-fin mechanism, energetic protraction and depression of the fin. The com-

Table 4. Adaptive characters for a benthic life style in the Uranoscopidae (-, primitive condition; D, derived condition)

Function	Character	Genus						
		<i>Pleuroscopus</i>	<i>Xenocephalus</i>	<i>Kathetostoma</i>	<i>Uranoscopus</i>	<i>Genyagnus</i>	<i>Ichthyoscopus</i>	<i>Astroscopus</i>
Feeding mechanism	1) A2 large and its posterodorsal portion covering A1	-	-	D	D	D	D	D
	2) A $\omega$ expanding posteriorly and reaching to quadrate	-	-	D	-	-	-	-
	3) Attachment site of ligamentum primordium on maxilla situated anterior to dorsal attachment of A1	-	-	-	-	-	-	D
	4) Dorsal margin of protractor hyoidei folded laterally and extending for insertion on mesial surface of interopercle	-	-	-	-	-	D	D
Pectoral fin mechanism	5) Coracoid connected directly to mesial expansion of lower two actinosts	D	-/D	-	-	-	-	-
	6) Coracoid sandwiched by lateral and mesial expansions of lower two actinosts	-	-/D	D	D	D	D	D
	7) Abductor superficialis broad and expanding to occupy most of midlateral portion of cleithrum	-	-	-	-	-	D	D
	8) Origin of abductor superficialis on lower limb of cleithrum located anterior to origin of abductor profundus	-	-	-	-	-	-	D
Respiratory mechanism	9) Anterior facet of lateral ethmoid directing anteriorly	-	-	-	D	D	D	D
	10) Ventral margin of palatine concave	-	-	-	D	D	D	D
	11) Palatine concavity contiguous with nasal and oral cavities present	-	-	-	-	D	D	D
	12) Nostril openings large	-	-	-	-	-	D	D
Respiratory mechanism	13) Posterior nostrils extending into orbital region	-	-	-	-	-	-	D
	14) Cutaneous cirri on nostrils large and well developed	-	-	-	-	-	D	D
	15) Cutaneous cirri on lips short and poorly developed	D	D	D	D	D	-	-
	16) Cutaneous cirri on lips long and well developed	-	-	-	-	-	D	D
	17) Cutaneous cirri on lips conical	D	D	D	D	-	-	-
	18) Cutaneous cirri on lips compressed	-	-	-	-	D	D	D
	19) Cutaneous cirri on lips with only unbranches	D	D	-	-	D	-/D	D
	20) Cutaneous cirri on lips with both branches and unbranches	-	-	D	D	-	-	-
	21) Cutaneous cirri on lips with only branches	-	-	-	-	-	-/D	-
	22) Posterodorsal margin of opercle fringed	-	-	-/D	-	D	-	-
	23) Ventral margin of posterior arm of subopercle fringed	-	-	-/D	D	D	-	-
	24) Cutaneous cirri on membrane of gill opening	-	-	-	-	-	D	-
Sensory system mechanism	25) Sensory canal present anterodorsally on lateral surface of opercle	-	-	-	-/D	-	-	-
	26) Sensory canal present mid-dorsally on lateral surface of opercle	-	-	-	-/D	-	-	-/D
	27) Sensory canal present posterodorsally on lateral surface of opercle	-	-	-	D	-	-	-
	28) Posterior portion of lateral line close to but separated from dorsal fin base	-	D	D	-	-	-	-
	29) Posterior portion of lateral line mostly attached with the dorsal fin base	-	-	-	D	D	D	D
Lingual lure organ mechanism	30) Elongate lingual lure organ depressed	-	-	-/D	-/D	-	-	-
	31) Elongate lingual lure organ compressed	-	-	-	-	D	-	-
Electric organ mechanism	32) Orbital electric organ present	-	-	-	-	-	-	D
Number of derived conditions in total		4	6	10	13	12	15	18

mon ancestor of uranoscopids is thought to have had a strong attachment site for the pectoral muscles with the coracoid directly connected to a mesial expansion of the lower two actinosts, and the short and broad actinosts firmly attached to each other and to the posterior portions of the scapula and

coracoids. The evolution of a more solid and strong connection between the coracoids and lower two actinosts appear to have occurred independently in the common ancestors of *Xenocephalus armatus* and *X. egregius*, and *Kathetostoma*, *Uranoscopus*, *Ichthyoscopus*, *Astroscopus* and *Genyagnus*

*monopterygius* (clades 4A and 2B) with the coracoid sandwiched by the lateral and mesial expansions of lower two actinosts. The evolution of a specialised more effective protraction and depression of the fin is assumed to have occurred in the common ancestor of *Ichthyoscopus* and *Astroscopus* (clade 26B,, with a broad abductor superficialis. Within this clade, an independent adaptation occurred in the common ancestor of *Astroscopus* (clade 27B), in which the abductor superficialis expanded to the lower limb of the cleithrum anterior to the origin of the abductor profundus. A strong protraction and depression of the fin would be highly efficient in burying the body in sand or mud, as well as moving up from the seabottom for capturing prey and escaping predators. The inferred evolution of the pectoral-fin mechanism is summarized in Fig. 87.

### 2-3. Respiratory mechanism

Characters associated with respiratory mechanism vary considerably in uranoscopids. When uranoscopids bury in the seabottom, they need to draw in water for respiration. For such a peculiar habitat, characters to enable them to do so are considered to be acquired.

In the nasal region, morphological variations are recognized on the lateral ethmoid, palatine and nostrils. The anterior facet of lateral ethmoid is directed ventrally (character 12-0) and the ventral margin of palatine is almost straight (character 34-0) in *Kathetostoma* spp., *Xenocephalus* spp. and *Pleuroscopus pseudodorsalis*, whereas the anterior facet of lateral ethmoid is directed anteriorly (character 12-1) and the ventral margin of the palatine is concave (character 34-1) in *Uranoscopus* spp., *Ichthyoscopus* spp., *Astroscopus* spp. and *Genyagnus monopterygius*. A palatine concavity contiguous nasal and oral cavities is present in *Ichthyoscopus* spp., *Astroscopus* spp. and *Genyagnus monopterygius* (character 35-1), while the concavity is absent in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp. and *Pleuroscopus pseudodorsalis* (character 35-0). In most acanthopterygians, the palatine does not form such a concavity (Kapoor and Khanna, 2004). A palatine concavity is thought to be a specialized character for passing water from the nostrils to the oral cavity. It is likely that the palatine concavity arose because of the closer proximity of the oral and nasal cavities with the anteriorly directed anterior facet of the lateral ethmoid (character 12-1) and the concave ventral margin of the palatine (character 34-1).

The openings of the anterior and posterior nostrils are small in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Pleuroscopus pseudodorsalis* and *Genyagnus monopterygius* (character 100-0), but large in *Astroscopus* spp. and *Ichthyoscopus* spp. (character 100-1). The posterior nostril is confined to the nasal region in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Ichthyoscopus* spp., *P. pseudodorsalis* and *G. monopterygius* (character 101-0), but extends into the

orbital region in *Astroscopus* spp. (character 101-1). As the anterior and posterior nostrils are small in acanthopterygians (this study), the large anterior and posterior nostrils and the posterior nostril extending into the orbital region are considered to be specialized characters for increasing the volume of water passing through the palatine concavity.

Cutaneous cirri associated with the nostrils are absent or poorly developed in *Pleuroscopus pseudodorsalis*, *Genyagnus monopterygius*, *Xenocephalus* spp., *Kathetostoma* spp. and *Uranoscopus* spp. as well as in most percoids (character 106-0), while the cirri are large and well developed in *Ichthyoscopus* spp. and *Astroscopus* spp. (character 106-1). As cutaneous cirri are absent or poorly developed on the nostrils in acanthopterygians, larged cirri around the nostrils are considered to be a specialized character for filtering grains of sand or mud from water passing through the palatine concavity.

In the mouth region, a number of variations occur in the cutaneous cirri of the lips. Cutaneous cirri are short and poorly developed in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp., *Pleuroscopus pseudodorsalis* and *Genyagnus monopterygius* (character 103-0), while cirri are long and well developed in *Ichthyoscopus* spp. and *Astroscopus* spp. (character 103-1). Cutaneous cirri in *Xenocephalus* spp., *Kathetostoma* spp., *Uranoscopus* spp. and *P. pseudodorsalis* are conical (character 104-0), but compressed in *Ichthyoscopus* spp., *Astroscopus* spp. and *G. monopterygius* (character 104-1). The cutaneous cirri of lips comprise only unbranched elements in *Xenocephalus* spp., *Astroscopus* spp., *P. pseudodorsalis*, *G. monopterygius* and *I. barbatus* (105-0), both unbranched and branched elements in *Kathetostoma* spp. and *Uranoscopus* spp. (105-1), and only branched in *I. lebeck* and *I. sannio* (105-2). As cutaneous cirri are usually absent on the lips of acanthopterygians (the outgroup is coded as “?” in transformation series 103, 104 and 105). Their presence and the various morphological variations of them are considered to be specialized characters for filtering grains of sand or mud from water passing through the closed mouth under the bottom substrate, although the evolution of branched cirri on lips is not stable in the relationships of the family when both ACCTRAN and DELTRAN are used. As the result of the phylogenetic analysis in this study, long cirri appeared to have evolved from short cirri; therefore, the former condition is considered to be more effective in filtering sand and mud grains. In addition, the results supported the evolution of compressed cirri from conical cirri (clade 14). The Coefficient of Drag value for liquid flowing through the compressed shape is less than that of the conical shape. Therefore, compressed cirri can be regarded as a speciality for allowing water to flow easier. The lateral branches on cirri can be also regarded as a speciality for filtering grains of sand or mud more efficiently.

In the opercular region, morphological variations are pres-



ent on the opercle, subopercle and membrane at the edge of gill opening. The posterodorsal margin of the opercle is fringed in *Genyagnus monopterygius*, *Kathetostoma albigutta*, *K. averruncus* and *K. cubana* (character 43-1), while it is smooth in *Uranoscopus* spp., *Ichthyoscopus* spp., *Astroscopus* spp., *Xenocephalus* spp., *Pleuroscopus pseudodorsalis*, *K. giganteum*, *K. laeve*, *K. canaster* and *K. nigrofasciatum* (character 43-0). The ventral margin of the posterior arm of the subopercle is fringed in *Uranoscopus* spp., *G. monopterygius*, *K. albigutta*, *K. averruncus* and *K. cubana* (character 46-1), whereas it is smooth in *Xenocephalus* spp., *Ichthyoscopus* spp., *Astroscopus* spp., *P. pseudodorsalis*, *K. giganteum*, *K. laeve*, *K. canaster* and *K. nigrofasciatum* (character 46-0). The gill opening is large and its dorsal edge extends to the supracleithrum in *K. albigutta*, *K. averruncus*, *K. cubana*, *U. tubisquamatus*, *U. albesca*, *U. archionema*, *U. bicinctus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. oligolepis*, *U. polli*, *U. scaber* and *U. tosae* (character 99-1), while the opening is narrow and its dorsal edge reaches to the cleithrum in *Xenocephalus* spp., *Ichthyoscopus* spp., *Astroscopus* spp., *K. giganteum*, *K. laeve*, *K. canaster*, *K. nigrofasciatum*, *P. pseudodorsalis*, *U. cognatus* and *G. monopterygius* (character 99-0). Cutaneous cirri are continuously developed on the membrane of the cleithral spine, and posterior margin of the subopercle and opercle, in *Ichthyoscopus* spp. (character 108-1), but not in other uranoscopids (character 108-0). In acanthopterygians, the margin of the opercle and subopercle are smooth, the gill opening is large with the dorsal edge extending to the supracleithrum, and the gill opening lacks cutaneous cirri. Therefore, the fringes on the opercle and subopercle, and presence of cutaneous cirri on the membrane of the gill opening can be considered to be adaptive characters for preventing sand or mud grains from entering the gill chamber while the gill opening emits water. The phylogenetic analysis inferred that a narrow gill opening supported the monophyly of the Uranoscopidae and a wide gill opening is a reversed character (thus a derived character) when ACC-TRAN is used, while it is unclear which character associated with the size of the gill opening supports the monophyly of the family and whether a wide gill opening is primitive or derived when DELTRAN is used. Therefore, the polarities of characters associated with the size of the gill opening are unsolved.

The respiratory mechanism can be separated into two strategies, to take in and to emit water, operating while the mouth and operculum are immovable when buried the substrate. With regard to the withdrawal of water through the mouth and nostrils, the common ancestor of the Uranoscopidae would have been provided with short, conical cirri on the lips (clade 1A). The evolution of the strategy for taking in water through the mouth initially occurred in the common ancestor of *Uranoscopus*, *Ichthyoscopus*, *Astroscopus* and *Genyagnus monopterygius* (clade 7B), having the anterior facet of the lat-

eral ethmoid directed anteriorly and the ventral margin of the palatine concave, resulting in a closer juxta position of the oral and nasal cavities. Within the clade, one adaptation is considered to have occurred in the common ancestor of *Ichthyoscopus*, *Astroscopus* and *G. monopterygius* (clade 14B), possessing the palatine concavity contiguous the nasal and oral cavities and the cutaneous cirri of the lips compressed. In the lineage comprising *Ichthyoscopus*, *Astroscopus* and *G. monopterygius*, one adaptation is apparent in the common ancestor of *Ichthyoscopus* and *Astroscopus* (clade 26B), with the nostril openings large, cutaneous cirri of the nostrils large and cutaneous cirri of the lips long. Among *Ichthyoscopus* and *Astroscopus*, one adaptation occurred in the common ancestor of *Astroscopus* spp. (clade 27B) with the posterior nostril extending to the orbital region. Although branched cirri on the lips are regarded as an adaptive character as mentioned above, the evolution of this character is unstable within uranoscopids according to both ACC-TRAN and DELTRAN. Therefore, this adaptive character is not useful.

With regard to the emission water from the gill opening, the evolution of adaptations is unclear in the Uranoscopidae, as two of four variations correlated with the function, the ventral margin of the posterior arm of the subopercle and gill opening, were inferred to be unstable according to ACC-TRAN and DELTRAN. However, as it is most likely that a fringed subopercle is derived, three of four characters can be regarded as adaptive characters: (1) opercle fringed in *Kathetostoma albigutta*, *K. averruncus*, *K. cubana* and *Genyagnus monopterygius*; (2) subopercle fringed in *Uranoscopus*, *K. albigutta*, *K. averruncus*, *K. cubana* and *G. monopterygius*; and (3) cirri present on gill opening in *Ichthyoscopus*. However, as mentioned above, it is unclear whether a wide gill opening is primitive or derived when DELTRAN is used.

The withdrawing and emitting of water enhanced by the adaptive characters as part of respiratory mechanism can be considered to be highly effective in burying the body in a seabottom for long period of time while waiting to ambush and capture prey or remain concealed from predators. The inferred evolution of the respiratory mechanism is presented in Figs. 88 and 89.

#### 2-4. Sensory system mechanism

Adaptive characters associated with the sensory system occur in the opercle and lateral line. A sensory canal is present anterodorsally on the lateral surface of the opercle in *Uranoscopus scaber*, *U. tubisquamatus*, *U. albesca*, *U. archionema*, *U. cognatus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. polli* and *U. tosae* (character 38-1), while it is absent from this area in other uranoscopids (character 38-0). A sensory canal is present mid-dorsally on the lateral surface of the opercle in, *Astroscopus guttatus*, *A. sexspinosus*, *A. y-graecum*, *U. albesca*, *U. archionema*, *U. bicinctus*, *U. cognatus*, *U. crassiceps*, *U. filibarbis*, *U. japonicus*, *U. oligolepis*,

*U. polli*, *U. turbisquamatus* and *U. tosae* (character 39-1), whereas it is absent from this area in other uranoscopids (character 39-0). A sensory canal is present posterodorsally on the lateral surface of the opercle in *Uranoscopus* spp. (character 40-1), but absent from this area in other uranoscopids (character 40-0). In most acanthopterygians, sensory canals on the head are comprised of supra- and infraorbital canals, without additional sensory canals on the opercle (Mogdans and Bleckmann, 2001; Kapoor and Khanna, 2004). Therefore, the addition of sensory canals on the lateral surface of the opercle is considered to a specialization for supporting the cephalic lateral line system in perceiving water movement from above more effectively.

The posterior portion of the lateral line, is close to the lateral midline of side in *Pleuroscopus pseudodorsalis* (character 96-0), close to but separated from the dorsal fin base in *Xenocephalus* spp. and *Kathetostoma* spp. (character 96-1), and mostly attached to the dorsal fin base in *Uranoscopus* spp., *Ichthyoscopus* spp., *Astroscopus* spp. and *Genyagnus monopterygius* (character 96-2). In most acanthopterygians, the posterior portion of the lateral line is close to the lateral midline of side (Webb, 1990). As the lateral line of piscivorous fish is thought to assist with the detection of prey (Enger et al., 1989), the posterior portion of the lateral line located close to the dorsal fin base and mostly attached to the dorsal fin base are considered to be adaptive characters for detecting prey approaching from above more sufficiently.

All adaptive characters associated with the sensory system mechanism of uranoscopids are involved with the function of sensing movement in the above water mass. Although the positioning of the posterior portion of the lateral line close to the dorsal fin base can be regarded as adaptive, it is unclear whether this condition was present in the common ancestor of the Uranoscopidae or those of uranoscopids expecting *Pleuroscopus*, *Xenocephalus* and *Kathetostoma* when DELTRAN is accepted. Consequently, the posterior portion of lateral line close to the dorsal fin base is regarded as unresolved. However, it is apparent that the lateral line close to the dorsal fin base was acquired prior to the acquisition of other adaptive characters discussed above. The evolution of adaptive characters associated with the sensory system, except for character omitted, initially occurred in the common ancestor of *Uranoscopus*, *Genyagnus monopterygius*, *Ichthyoscopus* and *Astroscopus* (clade 7B) with the posterior portion of the lateral line mostly attached to the dorsal fin base. Within the clade, two independent adaptations were apparent in the lineage of *Uranoscopus* and that of *A. guttatus*, *A. sexspinosus* and *A. y-graecum*. An adaptation was acquired by the common ancestor of *Uranoscopus* (clade 14A) with two sensory canals developed anterodorsally and posterodorsally on the lateral surface of the opercle. Another adaptation appeared in the common ancestor of *U. bicinctus*, *U. oligolepis*, *U. crassiceps*, *U. archionema*, *U. filibarbis*, *U. japonicus*, *U. tosae*, *U.*

*cognatus*, *U. albesca*, *U. polli* and *U. turbisquamatus* (clade 15B) and that of *A. guttatus*, *A. sexspinosus* and *A. y-graecum* (clade 30B) with a sensory canal developed mid-dorsally on the lateral surface of the opercle. These specializations are thought to be strongly efficient for detecting prey or predators approaching from above. The inferred evolution of the sensory adaptations is shown in Fig. 90.

## 2-5. Lingual lure organ mechanism

The lingual lure is an elongate and worm-like extension of the median portion of the respiratory valve of the lower jaw. It is present in *Kathetostoma albigutta*, *Uranoscopus scaber*, *U. bicinctus*, *U. oligolepis*, *U. crassiceps*, *U. archionema*, *U. filibarbis*, *U. japonicus*, *U. tosae*, *U. cognatus*, *U. polli*, *U. turbisquamatus* and *Genyagnus monopterygius*, but absent in other uranoscopids, as well as typical percoids (character 112-0). The lingual lure is depressed in *Kathetostoma albigutta*, *U. scaber*, *U. bicinctus*, *U. oligolepis*, *U. crassiceps*, *U. archionema*, *U. filibarbis*, *U. japonicus*, *U. tosae*, *U. cognatus*, *U. polli* and *U. turbisquamatus* (character 112-1), whereas it is compressed in *G. monopterygius* (character 112-2). In general, acanthopterygians lack a lure on the median portion of the respiratory valve of the lower jaw. The presence of lingual lure is regarded as an adaptive character for enticing a prey closer for ease of capture.

The median portion of the respiratory valve of the lower jaw evolved into two independent adaptations, depressed and compressed elongate lure organs, which involved the function to attract preys closer. An adaptation of a depressed lure occurred in the common ancestor of *Uranoscopus* (clade 14A) and *Kathetostoma albigutta* (clade 9A); whereas, another adaptation of the compress lure appeared in *Genyagnus monopterygius* (clade 26A). These adaptive characters can be assumed to be highly efficient for impersonating a worm in attracting prey. The inferred evolution of the lingual lure mechanism is shown in Fig. 91.

## 2-6. Orbital electric organ mechanism

The orbital electric organ is formed in the posterior portion of the eye ball and innervated by the oculomotor nerve (III). The organ is present only in *Astroscopus* spp. (character 115-1). As most acanthopterygians lack an orbital electric organ, the presence of this organ can be regarded as an adaptive character for the production of electricity to catch prey or protection from predators.

The evolution of the orbital electric organ is considered to have occurred only in the common ancestor of *Astroscopus* (clade 27B).

## 3. Conclusion

Based on the adaptive mechanisms and evolutionary processes described and discussed above, the most likely conclusion is that the evolutionary changes in uranoscopid

morphology are directly influenced by the harm of predation. Many adaptive characters for a benthic life style are found in the common ancestor of the Uranoscopidae and all the uranoscopid evolutionary processes. This implies that the common ancestor had already established a life style adapted to the benthic zone.

As discussed above, recent uranoscopids have 32 adaptive characters for benthic life style summarized in Table 4, which are variable among the family. Within the Uranoscopidae, the genus *Astroscopus* (or common ancestor of *Astroscopus*) has 18 adaptive characters, the greatest numbers for the family, while *Ichthyoscopus* has 15 adaptive characters, *Uranoscopus* has 13, *Genyagnus* has 12, and *Kathetostoma* has 10. These genera belong to clade 2B (Fig. 78). Consequently, further adaptations for a benthic life style from the ancestral morphology of the Uranoscopidae were acquired in clade 2B. On the other hand, the genus *Pleuroscopus* with only four adaptive characters, and *Xenocephalus* with six, the two genera belonging clade 2A have retained the basic adaptive plan of the Uranoscopidae. In reflecting on the phylogenetic relationships of the family Uranoscopidae, there is a tendency for the number of adaptive characters in genera to increase following the sequence of branching clades. This supports the notion that the evolutionary trend among uranoscopids is for an adaptation to a benthic life style, although the degree of adaptations vary within the family.

In conclusion, after obtaining many adaptive characters for a benthic life style, including burying in the seabottom, detecting prey and predators, waiting for and catching prey, and avoiding predation, uranoscopids can be considered to have acquired a unique diversity.

## XI. Summary

This study describes the osteological and myological anatomy and other morphological characters of the family Uranoscopidae (sensu Nelson, 2006) in detail, reconfirms the monophyly of the Uranoscopidae, reconstructs the phylogenetic relationships of the family based on characters recognized, evaluates synapomorphies supporting the sister relationship of the Uranoscopidae and Trachinidae, redefines the classification of the Uranoscopidae, and discusses adaptations and evolutionary processes for a benthic life style in the Uranoscopidae.

The conclusions of this study are summarized as:

1. The monophyly of Uranoscopidae is reconfirmed to be strongly supported by 59 synapomorphies (plus 11 according to ACCTAN).

2. The phylogenetic relationships were analyzed based on the morphological characters in 113 transformation series for the eight genera and 32 species in the family. As a result, a single most parsimonious hypothesis of relationships was obtained. The relationships of the family reconstructed in

this study mostly resemble those of Pietsch (1989), but differ with regard to the relationship of *Kathetostoma* and *Uranoscopus*. In the present study, the two genera are regarded as paraphyletic with *Kathetostoma* in a sister relationship with a monophyletic group that includes *Uranoscopus*, *Genyagnus*, *Ichthyoscopus* and *Astroscopus*. In addition, *Selenoscopus* was inferred to be deeply nested within *Uranoscopus*, making *Uranoscopus* paraphyletic if *Selenoscopus* is retained.

3. A sister relationship of the Uranoscopidae and Trachinidae is strongly supported by 22 synapomorphies (plus two according to ACCTAN). Of these, 10 (plus one according to ACCTAN) are newly recognized in this study.

4. The classification of the family Uranoscopidae is redefined to comprise seven genera: *Pleuroscopus*, *Xenocephalus*, *Kathetostoma*, *Uranoscopus*, *Genyagnus*, *Ichthyoscopus* and *Astroscopus*. The monotypic genus *Selenoscopus* described by Okamura and Kishimoto (1993) is synonymized with *Uranoscopus*, because the phylogenetic relationships reconstructed here infer it to be deeply nested within *Uranoscopus*.

5. The benthic life style of Uranoscopidae is described and discussed. In this study, 38 adaptive characters associating the benthic life style are recognized. Among them, six characters are synapomorphies of the Uranoscopidae and 32 are variable among genera and species. These characters are mainly correlated with six physical mechanisms: feeding, pectoral fins, respiration, sensory system, lingual lure organ and electric organ. The number of variable characters is four in *Pleuroscopus*, six in *Xenocephalus*, 10 in *Kathetostoma*, 13 in *Uranoscopus*, 12 in *Genyagnus*, 15 in *Ichthyoscopus* and 18 in *Astroscopus*. Based on these numbers, *Pleuroscopus* and *Xenocephalus* are considered to have retained the basic adaptive plan for a benthic life style in the Uranoscopidae, while *Uranoscopus*, *Genyagnus*, *Ichthyoscopus* and *Astroscopus* have further adaptations evolved from the basic plan. With regard to the phylogenetic relationships of the family, there is a tendency for the number of adaptive characters in genera to increase following the sequence of branching clades. Consequently, because of many adaptive characters obtained, including burying into the seabottom, detecting prey and predators, waiting for and catching prey, and avoiding predation, uranoscopids could be considered to have acquired a unique diversity.

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