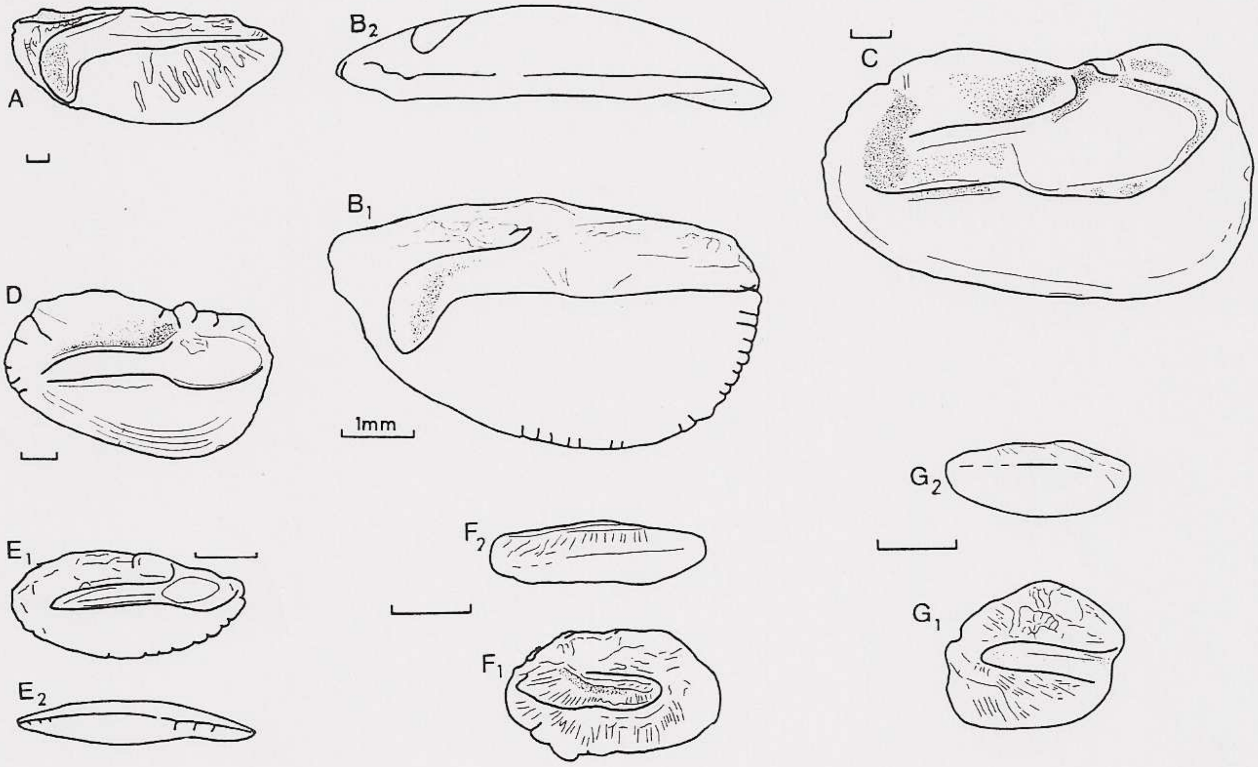


Fig. 35. Saccular otoliths of the suborder Albuloidei. A, *Albula vulpes* (Linnaeus 1758); Recent; Gulf of Mexico (Coll. Nolf); left otolith; B, *Albula dorsalis* (Priem 1914); Lower Miocene; Aquitaine, France; B_1, inner face; B_2, ventral view of left otolith; C, *Pterothrissus belloci* Cadenat 1937; Recent; South Atlantic (Coll. Nolf); left otolith; D, *Pterothrissus umbonatus* (Koken 1884); Middle Miocene; Aquitaine, France; left otolith; E. *Pterothrissus protensus* Stinton 1977; Middle Eocene; Paris Basin; E_1, inner face; E_2, ventral view of left otolith; F, *Aldrovandia phalacra* (Vaillant 1888); Recent; Atlantic, Florida (Coll. Fitch); F_1, inner face; F_2, ventral view of right otolith; G, *Notacanthus sexpinis* Richardson 1846; Recent; New Zealand (Coll. Fitch); G_1, inner face; G_2, ventral view of left otolith.

**Albula dorsalis* Priem 1914) (incertae sedis). Lower Miocene; Aquitaine, France. (Fig. 35 B).

Albula eppsi White & Frost 1931 (skeleton). Paleocene; Southern England.

Albula incurvata Stinton 1975. Upper Eocene; Southern England.

Albula rhaphiodon Stinton 1975. Lower Eocene; Southern England.

«*genus Albulidarum*» *alabamae* (Frizzell 1965) *(Archaealbula)*. Paleocene; Alabama, U. S. A.

«*genus Albulidarum*» *meridiana* (Frizzell 1965) *(Eoalbula)*. Eocene; Mississippi, U. S. A.

«*genus Albulidarum*» *sohli* (Frizzell 1965) *(Protalbula)*. Upper Cretaceous; Georgia, U. S. A.

«*genus Albulidarum*» *weileri* Frizzell 1965 *(Prealbula)*. Upper Cretaceous; Alabama, U. S. A.

Family Pterothrissidae Gill 1893

Figured Recent example: *Pterothrissus belloci* Cadenat 1937 (Fig. 35 C).

Pterothrissid otoliths have been found in many neritic Tertiary deposits, but they are never common in the associations. The two known living species of *Pterothrissus* are confined to rather deep water, and probably many of the fossil pterothrissid otoliths were carried into the neritic environment in the excreta of predators, foraging in deeper water. However, the fossil *P. protensus* (Eocene) seems to be confined to shallow deposits and also presents a more aberrant morphology.

Seven valid fossils species are known, but several of them need extensive revision:

Pterothrissus angulatus Stinton 1966. Lower Eocene; Southern England.

Pterothrissus antiquus Stinton 1965. Paleocene; Southern England.

Pterothrissus prevetustus Stinton 1958. Oligocene; Victoria, Austrailia.

**Pterothrissus protensus* Stinton 1975. Lower Eocene; Southern England (Fig. 35 E).

Pterothrissus tardinensis (Leriche 1908) *(Dentex)*. Paleocene; France.

**Pterothrissus umbonatus* (Koken 1884) (incertae sedis). Oligocene; Germany (Fig. 35 D).

«*genus* aff. *Pterothrissus*» *elongatus* Weiler 1942. Upper Oligocene; Germany.

Albuloidea incertae sedis

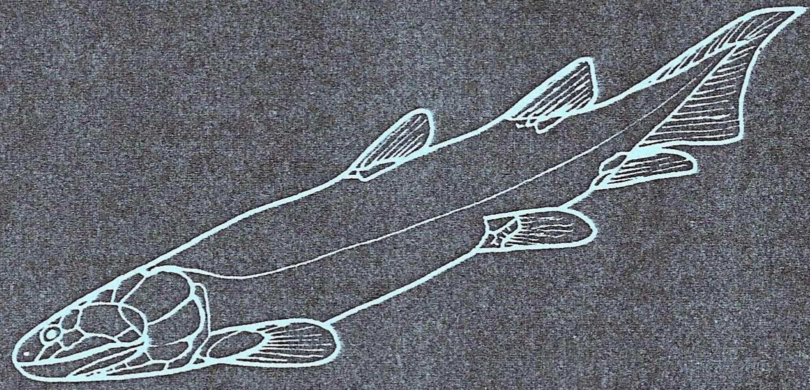
«*genus Albuloideorum*» *ahlumensis* (Stolley 1912) *(Otolithus)*. Lower Cretaceous; Germany.

«*genus Albuloideorum*» *cantianus* (Shepherd 1916) *(Atherina)*. Middle Cretaceous; England.

HANDBOOK OF PALEOICHTHYOLOGY

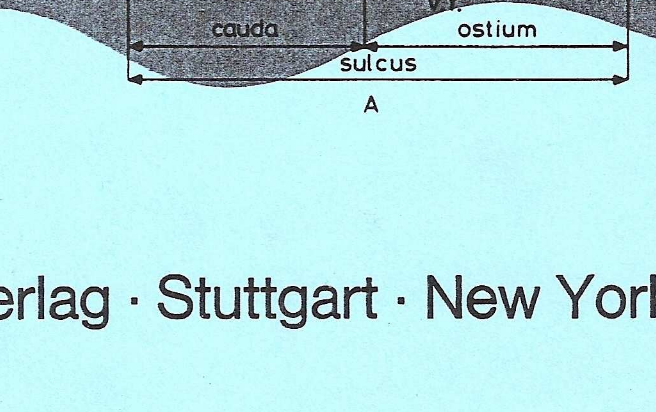
Edited by Prof. Dr. H.-P. SCHULTZE, Lawrence
Initiated by Prof. Dr. O. KUHN, München

VOLUME 10



D. NOLF

OTOLITHI PISCIUM



SEMPER BONIS ARTIBUS
Gustav Fischer Verlag · Stuttgart · New York

Handbook of Paleoichthyology

Edited by Professor Dr. Hans-Peter Schultze,
Lawrence, Kansas, USA

Initiated by Professor Dr. Oskar Kuhn, München

Contributions by

S. E. Bendix-Almgreen, Kopenhagen · H. Cappetta, Montpellier · M. Chang, Bejing ·
R. Denison, Lincoln/Mass. · P. Forey, London · B. Gardiner, London ·
L. B. Halstead, Reading/England · H. Jessen, Köln · D. Nolf, Brussels · C. Patterson, London ·
H.-P. Schultze, Lawrence/Kansas · S. Turner, Brisbane · E. Vorobyeva, Moskau ·
R. Zangerl, Rockville/Indiana

Volume 10: D. Nolf, Otolithi piscium

SEMPER BONIS ARTIBUS

Gustav Fischer Verlag · Stuttgart · New York · 1985

Otolithi piscium

By Dirk Nolf, Brussels (Belgium)

With a contribution by V. Talimaa,
Vilnius (Lituania, USSR)

With 81 figures

SEMPER BONIS ARTIBUS

Gustav Fischer Verlag · Stuttgart · New York · 1985

Volume 1	Halstead, Schultze, Turner: Interrelationships of agnaths and fishes, Agnatha
Volume 2	Denison: Placodermi
Volume 3A	Zangerl: Chondrichthyes I (Paleozoic Elasmobranchii)
Volume 3B	Cappetta: Chondrichthyes II (Mesozoic and Cenozoic Elasmobranchii)
Volume 4	Bendix-Almgreen: Chondrichthyes III (Holocephali, «Bradyodonti»)
Volume 5	Denison: Acanthodii
Volume 6	Schultze: Dipnoi
Volume 7	Chang, Forey, Jessen, Schultze, Vorobyeva: Crossopterygii
Volume 8	Forey, Gardiner: Actinopterygii I
Volume 9	Patterson: Actinopterygii II
Volume 10	Nolf: Otolithi piscium

Editor:
Professor Dr. Hans-Peter Schultze, University of Kansas, Museum of Natural History, Lawrence, Kansas 66045, USA

The Handbook of Paleoichthyology presents a complete survey of Agnatha and Pisces in the style and arrangement of the Encyclopedia of Paleoherpetology. The morphology, histology, interrelationships, taxonomy, occurrence, time range, and habitat of all groups will be described.
Emphasis is placed on comparative presentations of complete specimens and many details. The reader will thus be able to obtain characteristic features of all groups, down to the genus and sometimes to the species making the Handbook useful for identification.

CIP-Kurztitelaufnahme der Deutschen Bibliothek

Handbook of paleoichthyology : [in 10 vol.] / ed. by Hans-Peter Schultze. Initiated by Oskar Kuhn. Contributions by S. E. Bendix-Almgreen ... – Stuttgart ; New York : Fischer

NE: Schultze, Hans-Peter [Hrsg.]; Bendix-Almgreen, Sevend E. [Mitverf.]

Vol. 10. Nolf, Dirk: Otolithi piscium. – 1985

Nolf, Dirk :
Otolithi piscium / by Dirk Nolf. With contribution by V. Talimaa. – Stuttgart ; New York : Fischer, 1985. –
(Handbook of paleoichthyology ; Vol. 10)
ISBN 3-437-30399-6 (Stuttgart ...)
ISBN 0-89574-211-X (New York ...)

Wollgrasweg 49, D-7000 Stuttgart 70

Production: Fotosatz Jovanović, Neuhaus/Vornbach and Pustet, Regensburg
Printed in Germany

ISBN 3-437-30399-6
ISBN 0-89574-211-X NY

Editor's Preface

Agassiz's beautifully illustrated opus in five volumes «Recherches sur les poissons fossiles» (1833–1844) was the real beginning of paleoichthyology. In this, Agassiz has given the first comprehensive presentation of fossil agnathans and fishes. In the following years numerous descriptions of forms, mostly from Europe and North America have been published. This has been compiled by A. S. Woodward (1889–1901) in his famous «Catalogue of Fossil Fishes in the British Museum (Natural History)». The Catalogue was so well compiled that it is still used by specialists in paleoichthyology.

A. S. Woodward was one of many excellent paleoichthyologists in Great Britain from the past to today. In Scandinavia E. A. Stensiö founded an important school in paleoichthyology after World War I. He and his followers have done extremely detailed investigations, which put great emphasis on anatomical interpretations. There arose a strong controversy between the Scandinavian and the English-American schools about the interpretation of morphological data and the interrelationships of different groups of agnathans and fishes. The controversy still exists; and the Russian, German and French paleoichthyologists find themselves on one side or the other or in between. Between 1960 and 1970 one synopsis in Russian (1964: Osnovy paleontologii, vol. 11; 1967: Engl. translation) and one synopsis in French (1964 to 1969: Traité de Paléontologie, vol. 4) have been published in journals representing the whole field of paleontology. Osnovy shows the systematic view point, Traité the morphological-anatomical view point.

At this time, new and young paleoichthyologists have begun to replace the older, so well reputed generation. New findings especially in until now less searched regions (Asia, Southern continents, and northern and southern polar regions) revealed a great amount of new information about Paleozoic agnathans and fishes. In addition another event has influenced and will continue to influence paleoichthyology: Hennig's book «Grundzüge einer Theorie der phylogenetischen Systematik» (1950) translated 1966 into English («Phylogenetic systematics») by R. Zangerl, a contributor to the Handbook. Thus the revision, verification and falsification of the old ideas on the interrelationships of agnathans and fishes started with new view points within the seventies.

The Handbook of Paleoichthyology will summarize as far as possible all known data as a base for comparison with new findings and for interpretation of interrelationships. Nevertheless the reader will find the newest analysis of interrelationships, sometimes even contrary ones in different volumes.

Each volume deals with the anatomy and fossil record of agnathans or of a group (class, subclass, etc.) of fishes, except for volume 10 which deals with one organ of osteichthyan fishes, otoliths or ear stones. There are two important reasons to devote a separate volume to otoliths as planned by O. Kuhn. First, otoliths in situ (within the labyrinth) are rare, they often occur isolated from other fish fossils, and of necessity are usually described independently of other remains. Therefore a whole separate taxonomy has been built up. Second, as small forms with many features, otoliths are important stratigraphic indicators for Tertiary sediments, thus of great interest to geologists.

Within the osteichthyans, otoliths are well formed within teleost actinopterygians. Fossil forms have been described in many cases without sufficient knowledge of Recent otoliths. Today the tendency is to integrate otolith taxa with fish taxa. Dr. D. Nolf puts special emphasis on the comparison of fossil otoliths with Recent ones in this volume.

Lawrence, March 1983 H.-P. Schultze

Acknowledgements of the Author

It is a pleasure for me to express my sincere gratitude to Dr. C. Patterson of the British Museum (Natural History), London, and to the Drs. A. Gautier and E. Steurbaut of the State University of Gent, Belgium, for the many hours which they spent in discussing and correcting the manuscript of this book, and especially for the many improvements in English they suggested.

Contents

General Morphology 1
Membranous labyrinth and otolith organs 2
Function 3
Composition 3
Preservation 5
Nomenclature 6
Taxonomic value 8
Ontogenetic changes 8
Variability 11
Dissymmetry 14
Dimorphism 15
Convergence, symplesiomorphy and parallel variations 16
Relation otolith length/fish length 17
Biogeography 18
Taphonomy 19
Recent versus fossil habitat 19
Origin of fossil otolith associations 19
Otolith associations and the paleoenvironment 19
Evolution 23
Evolution below the species level 23
Evolution on the species level 24
Evolution of whole faunas 25
Evolution of biotas 25
Stratigraphic Use 27
Taxonomy of Fossil Otoliths 30
Generic determination 30
Otoliths in situ 33
Systematics 34
Superclass Gnathostomata 35
Class Osteichthyes 35
Subclass Acanthodii 35
Subclass Actinoptergii 35
Infraclass Cladistia 35
Infraclass Actinopteri 36
Superseries Chondrostei 36
Order Palaeonisciformes 36
Order Acipenseriformes 37
Superseries Neopterygii 37
Division Ginglymodi 37
Order Lepisosteiformes 37
Division Halecostomi 37
Subdivision Halecomorphi 37
Order Amiiformes 37
Subdivision Teleostei 37
Supercohort Osteoglossomorpha 38
Order Osteoglossiformes 38
Order Mormyriformes 39
Supercohort Elopocephala 39
Cohort Elopomorpha 39
Order Elopiformes 39
Order Megalopiformes 39
Order Anguilliformes 39
Cohort Clupeocephala 45
Subcohort Clupeomorpha 45
Order Clupeiformes 45
Subcohort Euteleostei 48
Infracohort Ostariophysi 48
Series Anotophysi 48
Order Gonorhynchiformes 48
Series Otophysi 48
Subseries Cypriniphysi 48
Order Cypriniformes 48
Subseries Characiphysi 48
Order Characiformes 48
Order Siluriformes 48
Infracohort Neognathi 48
Supersection Protacanthopterygii 48
Order Salmoniformes 48
Supersection Neoteleostei 52
Section Stenopterygii 52
Order Stomiiformes 52
Section Eurypterygii 53
Subsection Cyclosquamata 53
Order Aulopiformes 53
Subsection Ctenosquamata 55
Sept Scopelomorpha 55
Order Myctophiformes 55
Sept Acanthomorpha 57
Order Ctenothrissiformes 57
Superorder Paracanthopterygii 57
Order Percopsiformes 57
Order Batrachoidiformes 57
Order Gobiesociformes 57
Order Lophiiformes 57
Order Gadiformes 59
Order Ophidiiformes 63
Superorder Acanthopterygii 67
Series Atherinomorpha 67
Order Atheriniformes 67
Series Percomorpha 69
Order Beryciformes 69
Order Zeiformes 72
Order Lampriformes 73
Order Gasterosteiformes 74
Order Channiformes 75
Order Synbranchiformes 75
Order Scorpaeniformes 75
Order Dactylopteriformes 79
Order Pegasiformes 79
Order Perciformes 79
Order Pleuronectiformes 102
Order Tetraodontiformes 105
Subclass Sarcopterygii 107
Infraclass Actinistia 107
Infraclass Dipnoi 107
References and Bibliography 108
Abbrevations used in Figures 110
Annotated list of the nominal otolith-based fossil fish species 110
Index generum 134
Index of higher categories 141

General Morphology

Otoliths, or ear stones, are unique among vertebrate fossils in the sense that they are not parts of the skeleton, but integral and specialised hard parts of the acoustico-lateralis system.

Since recognition of their taxonomic utility by Cuvier in 1836, and their application in paleontology nearly 100 years ago (Koken 1884A), about 2000 nominal otolith-based species have been described. They range from Jurassic to Recent strata. From older strata, a few skeletons of palaeonisciform (Carboniferous, Permian) and pholidopleuriform (Triassic) chondrosteans with otoliths in situ are known, but isolated otoliths from the Devonian only.

If, following Patterson & Rosen (1977), leptolepids and lycopterids are considered teleosts, nearly all identifiable otolith-based fossil fishes are teleosts. In reconstructions of teleost faunas, the saccular otoliths play much the same role as teeth in the reconstruction of shark or mammal faunas. While complete skeletons are normally very scarce, otoliths often occur in great quantities in many marine deposits and allow reconstruction of rather extensive faunas just as shark teeth, or as mammal teeth in terrestrial deposits.

Notwithstanding a long paleontological tradition and practice, many contemporary ichthyologists and paleontologists view systematic otolith studies with suspicion. This negative judgment reflects a reasonable evaluation of the bulk of otolith literature and should not disturb those who are conscious of the value and utility of otoliths in paleontology and taxonomy. Indeed, except for a few competent workers, otolith paleontology has mainly been carried out in a rather amateur way, often by geologists untrained in fish taxonomy, ecology and biogeography or in the intraspecific variability of zoological objects. Therefore, the main aim of the present paper consists in a thorough revision of the whole otolith-based (nominal) fossil record, after careful evaluation of all aspects of otolith ontogeny, variability, post-mortem changes (e.g. abrasion, etching) etc.

Besides the above cited imperfections of previous work, it should also be emphasized that in spite of increasing interest in recent otoliths during the last decade, our knowledge of the subject still remains rather poor, and that for many fish families, otoliths are only known by four or five scientists in the world with access to extensive collections. I try to remedy this situation by figuring an otolith of at least one species of almost every extant family of osteichthyan fishes, disregarding whether the family concerned has a fossil record or not. To appreciate the narrow basis on which most previous otolith research has been conducted, one only has to realize that for about 40 % of the Recent families, otoliths have never been figured previously.

Before going into the various aspects of otoliths and otolith paleontology, this introduction can be completed with a brief historical survey of previous work. In this review, I do not aim at completeness, but rather emphasize the most pertinent and constructive previous contributions on otolith paleontology. An almost complete survey of otolith bibliography can be found in Weiler (1968A) for the period to 1968 and in Huyghebaert & Nolf (1979) for the period after 1968; a good survey of pre-Linnean and old data is given by Chaine & Duvergier (1934).

One can conveniently accept that the basis of otolith paleontology was laid down by Koken. In his 1884 paper, he insisted on the fact that nearly every osteichthyan species is characterized by features of its saccular otoliths, and extensively discussed the principle of comparative morphological studies on Recent and fossil otoliths to elucidate the taxonomic affinities of fossils. The publication is provided with careful illustrations of the most pertinent Recent otoliths known to him, and 21 fossils species are introduced with very accurate descriptions and illustrations. Apart from this he developed a nomenclatural system for *incertae sedis* otoliths, the principle of which is still in use, slightly modified (see chapter on taxonomy of fossil otoliths, p. 30).

This publication was followed by three other important papers on the same basis : Koken (1885: Paleocene otoliths, Denmark; 1888: Paleogene otoliths, southern USA; 1891A: mainly Oligocene and Miocene otoliths from Germany). In the light of present day knowledge, many of Koken's generic attributions need revision, but his work may still be called extremely precise considering the very poor knowledge of Recent otoliths at that time.

The next major contribution to otolith paleontology is the series of papers by Schubert between 1902A and 1916A, mainly on the Miocene of the Vienna basin. Although these studies are less precise than those of Koken, especially as a result of the choice of eroded types and the unnecessary splitting of species, many of his names are still valid, covering the bulk of common teleosts in the Miocene deposits of the Paratethys-area. The complete work of Schubert has been revised by Nolf (1981).

About the same time, Bassoli (1906A) published his paper on the Tortonian otoliths of Italy. Notwithstanding the fact that many of his generic attributions are incorrect, all his type material consists of almost perfectly preserved, carefully selected otoliths, a quality unfortunately lacking in the work of many later otolith-paleontologists. In 1924, Frost started his work on otoliths, regularly issued in short papers until 1935. He made a major contribution to the knowledge of Recent otoliths, and also published many fossil species from New Zealand, Sumatra and Nigeria, but the main part of his work concerns material from the Eocene and occasionally the Jurassic of England.

Frost's work is important because of the tremendous quantitiy of published material, but unfortunately his figures are often inaccurate, and almost none of his species can be judged on basis of his very schematic drawings. As most of Frost's type material is deposited in the British Museum, evaluation of most of his species is fortunately possible.

In 1932 appeared Sulc's paper on the Paleogene otoliths of Biarritz, southwestern France. By competent selection of type material and excellent illustrations, this paper is one of the best on otoliths of the period, although according to present day standards many of the generic identifications are subject to revision.

About the same time, Chaine & Duvergier (1934) started their «Recherches sur les otolithes des poissons», continued by Chaine until 1958 (9 volumes). These contain an excellent atlas of the otoliths of many Recent species and their variability. They are documents of major importance for paleontological otolith studies.

In the same period, Weiler (1942) concentrated most of his activities on otolith paleontology and worked intensively in this field until 1972. Most of his publications are of a quality exceeding that of previous work. In North America, Frizzell and collaborators published some papers among which Frizzell & Dante (1965) may be considered the most important. Indeed it constitutes the first faunistic study on North American Tertiary otoliths since Koken (1888), but unfortunately suffers from various imperfections which are dealt with in the chapter on the taxonomy of fossil otoliths.

Since about 1964, J. Fitch, a fishery biologist and Scientific Director of the California Department of Fish and Game, became interested in otolith paleontology, studying mainly California Pliocene and Pleistocene deposits. This resulted in several excellent reports in which he was able to trace back to the Pliocene and Pleistocene many of the fishes of the Californian coast. These analyses differ from previous ones in that they were conducted with the aid of a quantity of Recent comparative material that had never been available to any of the previous otolith paleontologists. Moreover the influence of Fitch on present day otolith paleontology has been marked because he has distributed Recent otoliths to workers throughout the world. Hence, there are today very few otolith workers who have not acquired otoliths of some hundred species from J. Fitch.

With this emphasis on a more extensive knowledge of Recent otoliths we can now turn to the otolith-research of the last decade. Whereas Weiler's collection of Recent otoliths hardly exceeded 1000 species at the end of his career, contemporary otolith workers like Fitch, Schwarzhans, Stinton, Steurbaut and the present author currently work with comparative collections containing 2000 to 6000 species. As to the work on fossil forms, here progress has been made mainly in the study of faunal successions in the Tertiary of the Belgian Basin (Nolf), Holland (Gaemers), the Paratethys (Brzobohaty), the Paris Basin (Nolf & Lapierre), southern England (Stinton) Aquitaine, southwestern France (Steurbaut 1984) and New Zealand (Schwarzhans).

Besides these extensive faunal reconstructions, many more restricted regional studies have been undertaken, some of which are excellent, but others still very poor.

Outside Europe and North America, we note an increasing interest in otoliths during the last decade in Japan. The various reports on Recent Japanese otoliths by Ohe (1976–1980) are of especial interest to otolith paleontologists.

Finally, the basis for the monographic study of systematic groups, both recent and fossil, has been laid by the treatment of the ophidiiform otoliths (Nolf 1980).

Membranous labyrinth and otolith organs

Calcareous crystals in the inner ear or labyrinth occur in all vertebrates. In agnathans, selachians and tetrapods, only numerous minute crystals, called statoconia, are known. Their dimensions vary between 1 and 50 microns. In nearly all actinopterygians and non-tetrapod sarcopterygians, these crystals are agglutinated and form solid masses with a well-defined morphology: the otoliths.

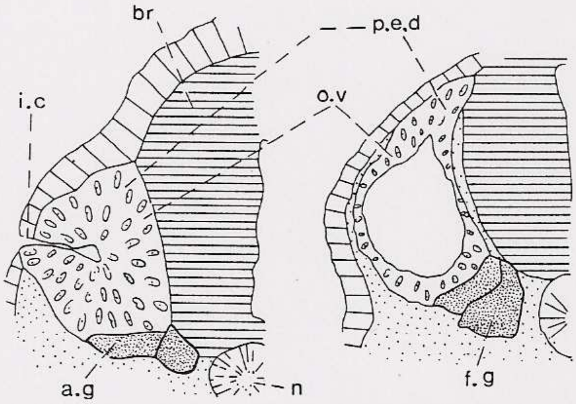


Fig. 1. Origin of the otic vesicle in early embryos of *Lampetra fluviatilis* (Linnaeus 1758), after Hagelin in Jarvik 1980.

The origin of otoliths is associated with that of the labyrinth. The labyrinth itself originates from the otic placodes which are paired ectodermal thickenings on each side of the head. These placodes, that originally formed part of the lateral line system, migrate inward, and form the otic vesicle or otocyst (Fig. 1).

Early in ontogenetic development, the otic vesicle is pinched off from the epidermis; cells from the lower part of the otic vesicle migrate and form the otic ganglion with the associated eighth cranial nerve. The sac-like structure of the otic vesicle is gradually divided into a complicated dorsal chamber or *utriculus* and a ventral chamber or *sacculus*. A further diverticle of the sacculus is called the *lagena* in lower vertebrates and corresponds to the complicated cochlea in mammals. From the upper part of the utriculus originate the three semicircular canals with their ampullae (swellings at the end of each canal) and the endolymphatic duct. All these membranous structures are located in the part of the skull called the auditory capsule. Various portions of the labyrinth are surrounded by cartilage, which is later replaced by bone in most vertebrates (Yapp 1965).

In the utriculus, sacculus and lagena, a patch of sensory and supportive cells exist, called macula. These maculae resemble neuromasts (clumps of sensory hair cells and supportive cells) of the lateral line system, but are somewhat larger.

Each sensory cell has a clump of short cilia (stereocilia) and one larger cilium (kinocilium). The cilia are embedded in a modified cupula (fragile, transparent sac, capping the cilia of a neuromast). In the maculae of the labyrinth, the cupulae are made heavy by deposits of calcium carbonate (Hildebrand 1974). In some groups (agnathans, selachians, tetrapods) these deposits consist of very small

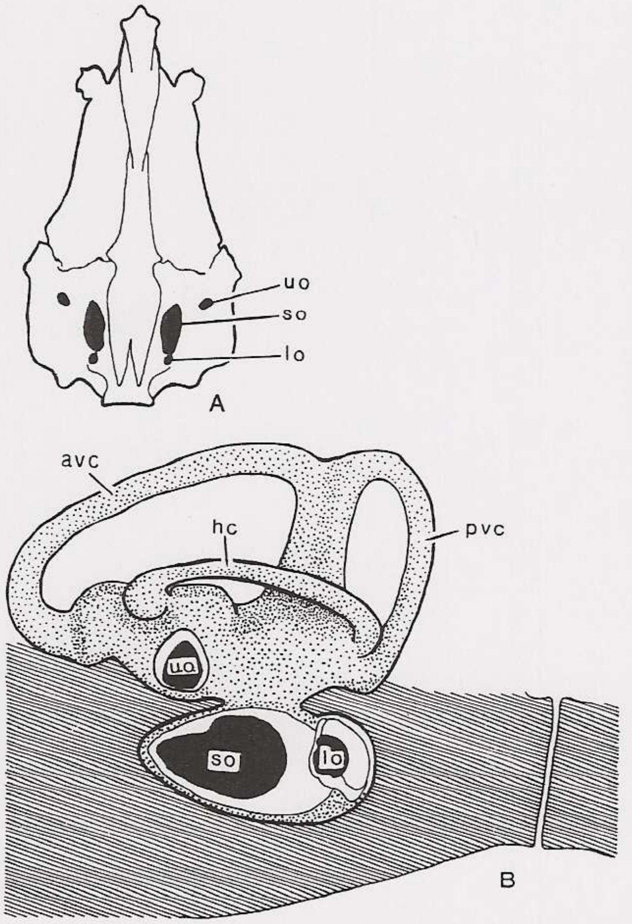


Fig. 2. A, Position of otoliths in the braincase (ventral view) of *Salmo mykiss* Walbaum 1792; B, Position of the otoliths in the labyrinth of *Salvelinus fontinalis* (Mitchill 1815), after Rosen & Greenwood 1970.

crystals; in osteichthyans (except Tetrapoda), they form solid otoliths, statoliths, or ear stones. According to Norman & Greenwood (1975) otoliths are secreted by the walls of the labyrinth. They increase in size by deposition of concentric layers of calcium carbonate and organic material, giving the well known concentric ring pattern in sections. Most actinopterygians have three otoliths (Fig. 2) saccular, utricular and lagenar. The saccular otolith is usually the biggest and the most important for taxonomic use.

In sarcopterygians, only a saccular otolith is known in *Latimeria*, while in lungfishes only saccular and utricular otoliths are reported. In the literature several special names have been applied to the three types of otoliths: saccular otolith = sagitta = sacculith; utricular otolith = lapillus = utriculith; lagenar otolith = asteriscus = lagenalith. In my opinion, the descriptive terms saccular, utricular and lagenar otolith are most easily understood and are used in this work.

Function

Most of the relevant data on the function of fish labyrinths and their associated otoliths have been summarized by Cordier & Dalq (1954) and Lowenstein (1957). From these and various other reports, one striking conclusion can be drawn: there is a relatively suitable understanding of the function of fish-labyrinths, but knowledge on the precise role of otoliths and especially on the physiology how they operate is very poor.

According to the above cited reports, the labyrinth has four main functions: (1) maintenance and regulation of muscle tone; (2) reception of angular accelerations; (3) gravity reception (equilibrium); (4) sound reception.

Total extirpation of both labyrinths results in temporary or lasting loss in muscle tone, but there are no positive indications that the otoliths properly are involved in this function, while the perception of angular and acceleration movements is mainly assured by the sensory cells in the ampullae of the semicircular canals.

Separate functional elimination of parts of the labyrinth showed that the whole range of postural responses to positional changes is controlled by the utriculus. Although, equilibrium in fishes is not controlled by the labyrinth alone; visual orientation also takes a considerable importance in the control of posture and movement. So, if the utricular otolith is removed and light is illuminated from the side or from below, the fish will swim on its side, or upside down.

While the equilibrium function of the labyrinth resides in the superior part (utriculus and semicircular canals), the inferior part (sacculus and lagena) is chiefly responsible for sound perception.

Ostariophysi show the best performances concerning detection of frequency range, pitch discrimination and threshold of sounds, and it is also striking that those fishes have highly modified saccular and lagenar otoliths. Very big and modified saccular otoliths are also recorded in sound-producing fishes like sciaenids and morids. In the two last groups, otolith specialization essentially affects the morphology of the sulcus, which constitute the contact-patch with the sensory cells.

As stated in the beginning of this section, there are no unequivocal data on the precise way how an otolith functions, but their strong piezoelectric properties (Morris & Kittelman 1967) might be of some use in frequency analysis, depth perception or both.

Composition (Fig. 3)

Otoliths consist of calcium carbonate and organic matter, called otoline. Otoline has been investigated by Degens, Deuser & Haedrich (1969). The total quantity of otoline may constitue from 0.2 to 10% of an otolith. This organic matter is a fibrous protein with a molecular weight greater than 150,000 and characterized by abundance of acidic amino acids. The protein is chemically rather uniform through various taxonomic groups of fishes, in contrast to shelled invertebrates which have species-specific organic constituents in the shell.

In most otolith-forming vertebrates the calcium carbonate occurs in the crystal form aragonite, the aragonite crystals oriented with their long axes radiating from the center to the surface of the otolith. In lower actinopterygians, otoliths may be partly or entirely constituted by another crystal form of calcium carbonate, vaterite, while statoconia of warm blooded tetrapods (Aves and Mammalia) are calcite. In

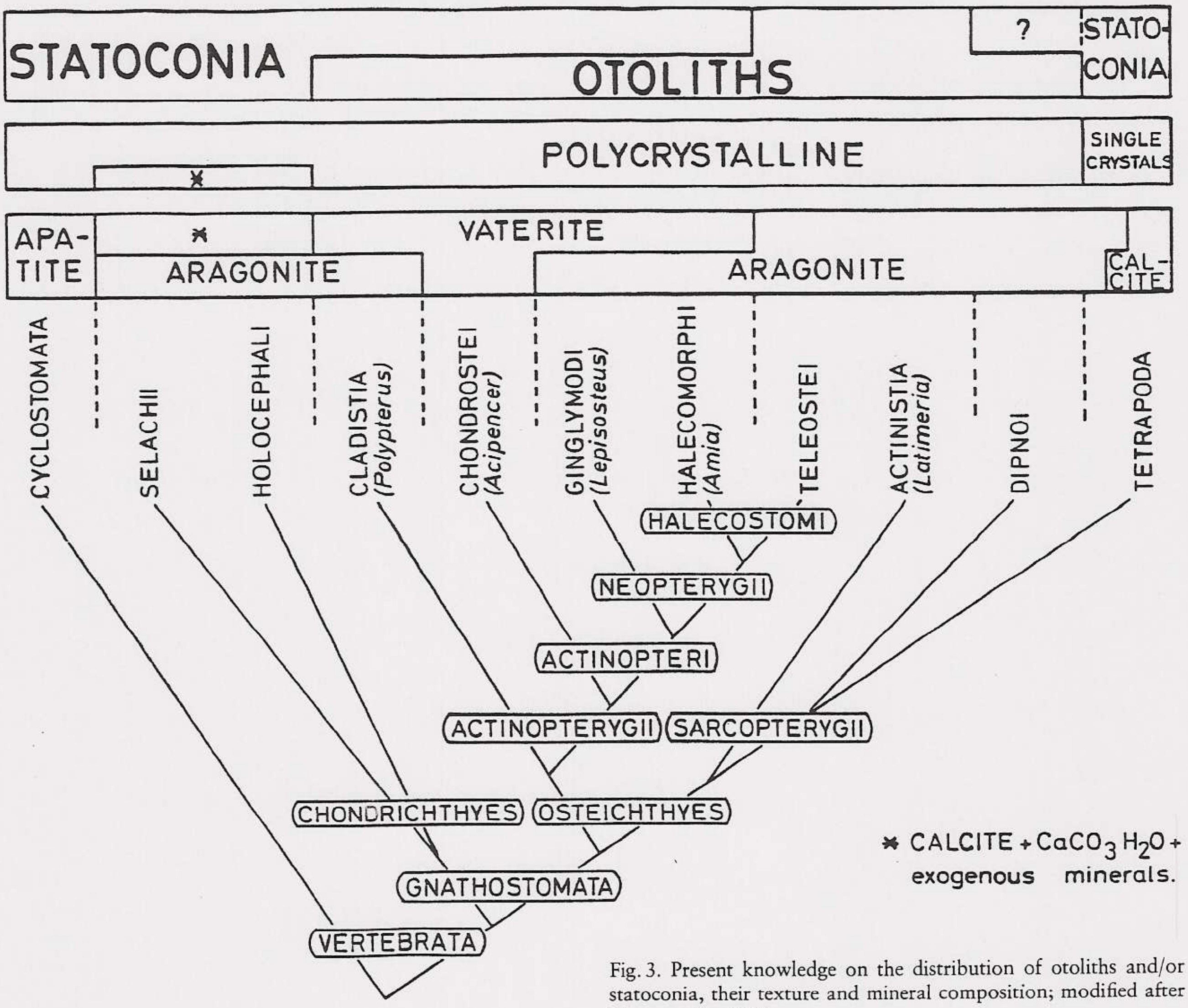


Fig. 3. Present knowledge on the distribution of otoliths and/or statoconia, their texture and mineral composition; modified after Carlström 1963.

most investigated species of reptiles statoconia consist of a mixture of aragonite and calcite. The highest percentage of calcite was found in turtles (Carlström 1963). In selachians, crystals mostly consist of aragonite, but exogenous minerals, supposed to enter in the labyrinth through the endolympahtic duct, are also present. Statoconia of Cyclostomata are formed by a different compound, apatite, a calcium phosphate forming the mineral component of vertebrate bones. In otoliths the presence of vaterite probably reflects the evolutionary primitive condition since this mineral normally occurs in the plesiomorph groups of actinopterygians. In nearly all teleosts, otoliths are constituted of aragonite, but in the collicula of the most primitive living forms like albulids and anguilliforms, vaterite may also occur.

Pathological teleost otoliths also may show irregularly shaped parts, made of vaterite (Fig. 4). This phenomenon has been called otocony by Frizzel & Exline (1958). Usually, the labyrinth of fishes with otoconic otoliths also contains isolated bodies of polycrystalline vaterite without definite morphology. These bodies are called ossiculiths by Frizzell & Exline (1958). Their dimensions range between 0.05 and 0.5 mm. In lower actinopterygians, such as *Lepisosteus*, usually both otoliths and ossiculiths occur. In these fishes, the presence of ossiculiths is not a pathological feature. Ossiculiths have been recorded as fossils by Frizzell & Exline (1958), but they cannot yet be used for taxonomic work.

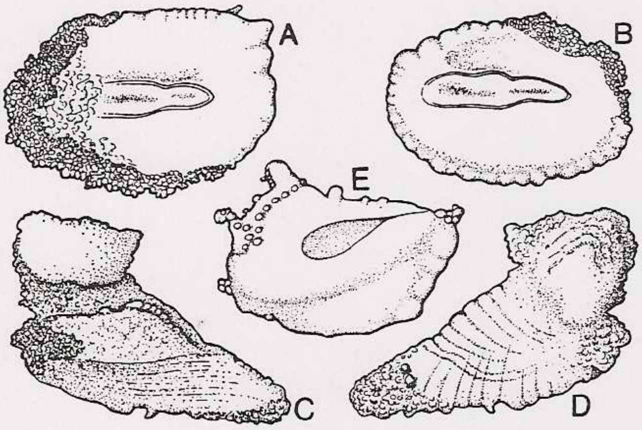


Fig. 4. Otoconic otoliths. A, *Pleuronectes platessa* (Linnaeus 1758); B, *Lophius piscatorius* (Linnaeus 1758); C, normal vaterite otoliths of *Acipenser sturio* (Linnaeus 1758); after Weiler 1959.

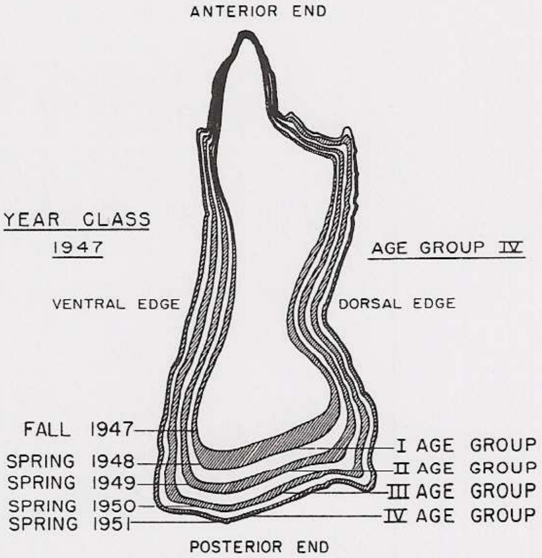


Fig. 5. Annual ring patterns and age groups in a right saccular otolith of southern California *Pneumatophorus japonicus* Houttuyn 1872 (from Fitch 1951).

Data on the presence of otoliths, ossiculiths and statoconia in the labyrinth of dipnoans are contradictory. Carlström (1963) reports only statoconia, while Retzius (1881) figures well formed otoliths, ossiculiths and statoconia. Shepherd (1914) reports statoconia from *Lepidosiren* and both saccular and utricular otoliths from *Neoceratodus*. Personally, I have observed well formed saccular and utricular otoliths in *Protopterus aethiopicus* and *Lepidosiren paradoxus* (Fig. 81). In the specimen of *Protopterus aethiopicus*, that I investigated, the saccular and utricular otoliths were fused in their upper part, but I do not think that this is the rule in this species.

Oxygen and carbon isotope data of otoliths have been investigated by Devreux (1967) and Degens, Deuser & Haedrich (1969) for various teleostean fishes and indicate that the isotopic composition of otolith aragonite is close to that of the sea. It is hence similar to that commonly observed in marine and fresh water invertebrate shell material. Therefore, otoliths can be used for investigations on paleotemperatures and paleoecology (Devreux 1967).

Other aspects of otolith crystallographic properties have been investigated by Morris & Kittleman (1967). They have shown that the saccular otoliths in the two species examined by them, a notothaeniid and a flatfish, have strong piezoelectric properties. They conclude that „Hence, in theory, they constitute a mechanism for depth perception or frequency analysis or both".

Another aspect of the composition of otoliths consists in the concentric ring structure of their organic and inorganic material. The rings are growth rings due to the continuous formation of new organic and calcareous material on the surface of the otolith. These patterns have a very fine structure, but rapid observation of a broken otolith with a pocket lens, reveal small, dark or opaque zones, alternating with larger, light or translucent zones. Sections tangential to the medial longitudinal plane of maximum growth show the growth bands best. One set of rings usually corresponds to the annual growth of an otolith.

The large light-colored or «translucent» zone corresponds to a period of fast deposition (usually summer and fall). In this period, production of organic fibers is high, but calcification is even higher. The ratio of organic/inorganic material is overwhelmingly in favor of the inorganic portion. The dark or «opaque» zone corresponds to a period of slow deposition. In this period, fewer organic fibers are produced, but the ratio of organic/inorganic material is in favor of the organic portion, since calcification is almost nil. The thickness ration between slow growth and fast growth zones ranges from 1:20 in early stages to 1:3 in later stages.

This primary pattern of light and dark rings is most obvious in fishes inhabiting cold and temperate waters, where the influence of seasons is strong. For such fishes, annual ring patterns have been used for age identification in fishery biology (Fig. 5). Techniques used in such investigations have been described by Blacker (1974) und Williams & Bedford (1974). In tropical zones, where seasonal variability has less importance in the annual life cycle of fishes, these patterns are less clear or even nonexistent.

In paleontology virtually no investigations on annual rings of otoliths have been carried out, except for the casual mention of these structures in two Belgium Miocene gadid species by Gaemers (1972).

More detailed investigations on ring structure of Recent otoliths has been carried out by Panella (1971). Using acetate replicas of etched otolith sections, he observed a pattern of growth rings finer than the annual one. Within the global two zones of fast and slow growth, he recorded a pattern of monthly, fortnightly and even daily rings. His observations on saccular otoliths of *Merluccius bilinearis* indicated a winter pattern with around 100 to 110 days and a summer pattern with approximately 230 to 260 days. Concerning these daily rings, he stated (Panella 1971, p. 1125) «The specific cause or causes of this daily cycle of calcium deposition can only be a matter of speculation, but it is probably related to the known circadian rhythms in the behavior, metabolism and physiology of fishes».

Preservation

The correct evaluation of the state of preservation of fossils is a general problem in paleontology, and not a specific one of otoliths. However, because so many species of fossil otoliths have been based on strongly eroded specimens with the result that they have to be rejected, a section on preservation seems appropriate.

There are three factors that cause otolith erosion: postmortem transport of otoliths in turbulent water; action of the digestive acids in the stomachs of predators, and decalcification of the sediment in which the otoliths are imbedded. In some cases, otoliths may be affected by all three types of erosion.

Erosion occurs in all evironments where the water is turbulent enough to transport otoliths, such as intertidal and infralittoral environments, estuaries, etc. Usually the action of turbulence and transport is also visible on other fossils (e.g. molluscs) in the association. The Eocene sands of Le-Bois-Gouet in Brittany, France form a good example of an otolith locality in which transport played a major role.

Great quantities of transport-eroded otoliths also occur in basement gravels and associated transgressive beds. Usually such otoliths have the surface covered with little pits and all their salient structures are more or less smoothed off.

Erosion by digestive acids mainly depends on the predator that ate the otolith-bearing prey. Among predators rejecting or excreting otoliths, predatory fishes have to be named first, but also marine mammals, otters, various sea birds, crabs and probably several other invertebrates. Very little is known about the digestive action on otoliths in fish stomachs. However, as most otoliths will pass through the digestive system of a fish before they enter the sediment, and as otoliths from non-turbulent and non-decalcified deposits are usually in perfect condition, digestion by fishes probably has very little influence on otoliths. Well preserved otoliths are also reported from regurgitation pellets of birds and otters, but otoliths from stomachs of marine mammals may be eroded to various degrees. In the strongly altered gadid otoliths that I have seen from the stomachs of Pinnipedia, relief-inversion of prominent rims and lobes was characteristic.

Erosion by decalcification of otoliths may be synsedimentary or postsedimentary. Recent otoliths affected by nearly synsedimentary decalcification have been described from the seas around southern Norway by Gaemers (1978). Postsedimentary erosion of otoliths can be observed in many places where originally calciferous sands or clays are subject to infiltrating acid surface waters. Otoliths from such beds, if not entirely decalcified, show rugous surfaces and their central body is hollowed out. This central body may communicate with the surface through holes of various diameters and sizes, due also to decalcification. The formation of such holes starts in the sulcus area and otoliths affected by the process are quickly reduced to fragments of no use to paleontology.

It is difficult to establish standards to measure the degree to which otoliths are affected by erosion. My advice is again that students of otoliths should look very carefully at many freshly extracted Recent otoliths (otoliths from formalin-preserved specimens may suffer from chemical erosion). A good impression of the various degrees of erosion can be obtained from the figures in Anfossi & Mosna (1975), where various stages of degradation of fossil *Maurolicus muelleri* (Gmelin 1789) are interpreted as ten different species.

Finally, it should also be mentioned that fossil otoliths containing pyrite, even if they look perfect when collected, may disintegrate completely after some years as a result of oxidation of the pyrite.

Nomenclature

As stated above, the great majority of actinopterygians, and nearly all teleosteans, have three pairs of otoliths: an utricular, a saccular and a lagenar. Except for a few siluriforms and the sciaenid genus *Bairdiella*, only saccular otoliths have been used in otolith-based reconstructions of fossil fish faunas and taxonomic investigations. Consequently a consistent morphological nomenclature has been developed for saccular otoliths only. The various morphological elements of saccular otoliths seem to be so consistent that they can be applied almost throughout actinopterygian fishes, except ostariophysans. Ostariophysans have such highly modified saccular otoliths that nobody has been able to explain the homologies of their complicated morphology in a satisfactory way. Their morphology is so unusual that a competent otolith worker like Schwarzhans (1978), who made a tentative morphological interpretation of a so called right otolith, was in reality describing its partner from the left side.

Some taxonomic investigations have also been carried out on utricular and lagenar otoliths of ostariophysans, but their morphology remains nearly unknown for all other groups. A consistent morphological nomenclature for their structure, usuable in all groups, has not yet been worked out, but one should do so only after detailed investigations in the various groups. A preliminary nomenclature for ostariophysan lagenar otoliths is given by Frizzell & Koenig (1973) and for the practical purpose of description, I worked out a provisional nomenclature for utricular ariid otoliths (Nolf 1976). This nomenclature will not be repeated here, less it should be considered as standard, which certainly was not my intention.

For the saccular otolith, an extensive series of more or less useful morphological terms has been proposed by various authors. In Fig. 6 the most frequently used terms of otolith morphology are indicated on schematic drawings of an otolith of the acanthopterygian type and of the paracanthopterygian type. All of them apply to the rims or to the inner (= medial) face of otoliths; no terminology has been developed for the external (= lateral) face.

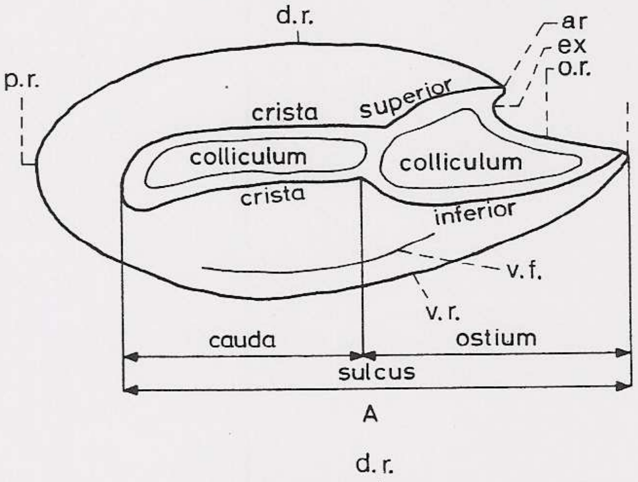


Fig. 6. Morphological nomenclature of the inner face of a saccular otolith. A, Acanthopterygian type; B, Paracanthopterygian type.

Besides these widely used morphological terms, which are usually sufficient to describe the various features of an otolith, many others have been introduced, but seem not to be of primary necessity. Furthermore several of these terms only apply to otoliths of particular taxa.

All morphological terms which have been applied in the past to otoliths are listed alphabetically and explained below. Each name is followed by the author who introduced it.

Alar prolongation (FRIZZELL & LAMBER 1961): an anterodorsal expansion of the rostrum.

Anterodorsal angle (CHAINE & DUVERGIER 1934): angular outline of the anterior part of the dorsal rim in some species.

Anteroventral angle (CHAINE & DUVERGIER 1934): angular outline of the anterior part of the ventral rim in some species.

Area (KOKEN 1884 A) as used by KOKEN, the term refers to a depression in the internal face, just above the crista superior. In general Latin, French and English usage «area» means a part of a surface, and has been used as such by various authors (e.g. the area situated below the posterior part of the cauda). For this reason, the use of the term area in the sense of KOKEN is inadvisable.

Caudal keel (FRIZZELL & LAMBER 1961): slightly concave or flat dorsal expansion of the area situated between the crista superior and the dorsal rim of Myripristinae.

Collum (CHAINE & DUVERGIER 1934): junction of ostial and caudal portions of the sulcus.

Excissura minor (MESSIEH 1972): notch in the posterior rim of certain clupeiform fishes.

Excisural formation (CHAINE & DUVERGIER 1934): small, often irregular, expansion of the part of the ostium between the rostrum and the excissura.

Ostial channel (FRIZZELL & LAMBER 1962): in many anguilliform, pterothrissid, ophidiiform, etc. otoliths, the ostium does not reach the anterior rim, but is linked to the anterior or the dorsal rim by a small gutterlike depression called ostial channel.

Pararostrum (MESSIEH 1971): small expansion of the posterior rim, just above the excissura minor in certain clupeiform fishes.

Postcaudal notch (FRIZZELL 1965): small notch in the posteroventral rim of some albulids, reaching the posterior part of the cauda.

Postcaudal keel (FRIZZELL 1965): expansion of the posterior part of the dorsal area in certain albulids.

Postcaudal trough (CHAINE & DUVERGIER 1934): depression linking the posterior end of the cauda with the posterior or the ventral rim.

Posterodorsal angle (CHAINE & DUVERGIER 1934): angular outline of the posterior part of the dorsal rim.

Postrostrum (MESSIEH 1972): small expansion of the posterior rim, just below the excissura minor in certain clupeiform fishes.

Pseudocolliculum (SCHWARZHANS 1978): small collicular crest just above the crista inferior in certain gadiforms, myctophids, apogonids, beryciforms, etc.

Umbo (KOKEN 1884 A): center of growth, visible on the external face of certain otoliths.

It is evident that all these named structures, even those mentioned in Fig. 6 are not necessarily found in the otoliths of each species: gobiids have no rostrum, bythitids have no division of the sulcus, gadids have no excissura, etc.

Besides this nomenclature of isolated morphological elements, SCHWARZHANS (1972, 1978) developed a rather complicated terminology for a number of structural conditions in the patterns of the colliculi, the sulcus opening and the sulcus outline. This terminology is explained here for the sake of completeness and because it is used in a few recent otolith papers. However, it is my opinion that such technical jargon is complicating rather than simplifying otolith descriptions. Most of the terms can be avoided by a few words of normal language and are directly evident in illustrations.

Condition of colliculi

Homomorph: flat colliculi or one undivided flat colliculum (e.g. Elopidae, Gadidae, Ophidiidae, Percoidei).

Heteromorph: a flat ostial and a crest-like caudal colliculum (e.g. Moridae).

Scombroid: no clear colliculi; sulcus deep (e.g. Scombridae, Clupeidae) with a v-shaped cross section.

Condition of sulcus opening and position

Biostial: sulcus opens widely to both anterior and posterior rims (e.g. Paralepididae, Oreosomatidae).

Caudal: cauda opens widely on the posterior rim (e.g. Moridae).

Medial: sulcus is isolated on the central part of the inner face (e.g. Gobiidae).

Ostial: sulcus with an ostium opening widely to the anterior rim (e.g. Serranidae).

Pseudo ostial: ostium is only connected to anterior or upper rim by an ostial channel (e.g. Congridae).

Pseudo biostial: both anterior and posterior ends of the sulcus do not open clearly on the anterior and posterior rims (e.g. Gadidae).

Condition of sulcus pattern

Archesulcoid: no clear division into ostium and cauda (e.g. *Elops*, Osteoglossidae).

Heterosulcoid: clearly distinct ostium and cauda; two types are defined: Ostial-heterosulcoid with large ostium and small straight cauda (e.g. *Beryx*, *Apogon*, Atherinidae) and caudal-heterosulcoid with not enlarged ostium combined with a bent cauda (e.g. Cyprinodontidae).

Homosulcoid: ostium and cauda are clearly distinguishable, a constriction present at the junction of ostial and caudal portions (at least in the crista inferior). Ostium and cauda look more or less symmetrical (e.g. Gadidae, Macrouridae).

Incisive: one of the colliculi has developed into an elongate crest. SCHWARZHANS (1978) distinguishes two types. In the caudal incisive, the caudal collicum is incisive (Moridae); in the ostial incisive the ostal colliculum is incisive. The example cited by SCHWARZHANS for the last condition is the ostariophysan saccular otolith, but as he considered a left otolith to be a right one, the crest-like structure that he interpreted is not ostial but caudal.

Taxonomic Value

Except for a very few ostariophysan species, where utricular and lagenar otoliths have been used, the saccular otolith is the usual tool for taxonomic investigations and the reconstruction of fossil faunas. By «otolith» in the following discussion, we always mean the saccular one.

The main diagnostic features of an otolith are its outline, the pattern and the degree of incision of the sulcus with any associated colliculi, the convexity of the inner face, the convexity or concavity of the external face and the thickness. The convexity and thickness of an otolith are best illustrated by a view from the ventral side, because this side is much less subject to morphological variation than the dorsal one.

One can fill hundreds of pages with the description of the various aspects which these diagnostic features may present throughout the actinopterygians (sarcopterygians have no sulcus comparable to the actinopterygian one), but a simple glance at Figs. 26–79 gives more information than any description can provide.

Sometimes the shape of the dorsal rim provides useful features, but it should be noted that this rim is usually the most variable part of an otolith. Therefore, statements on the morphology of the dorsal rim in poorly sampled species cannot be trusted as good diagnostic features.

Sometimes, the ornamentation of the external face also provides useful characteristics, but in most cases it is impossible to recognize species, genera or even families by the ornamentation of the external face alone. As a general rule, the external faces of plesiomorph teleostean otoliths show little ornamentation. In acanthopterygians, ornamentation may vary between an elaborate pattern of small, usually radial lobes (Fig. 7A) and a nearly flat surface. Many gadiform otoliths show a strong ornamentation with large lobes of swollen aspect (Fig. 7B), while flatfish otoliths usually have very smooth external faces (Fig. 7C). But none of the foregoing statements should be considered as absolute: we have seen smooth external faces on otoliths of gadiform species which usually are strongly lobated. Ornamentation of the external face is subject also to strong ontogenetic changes which will be discussed in the next section.

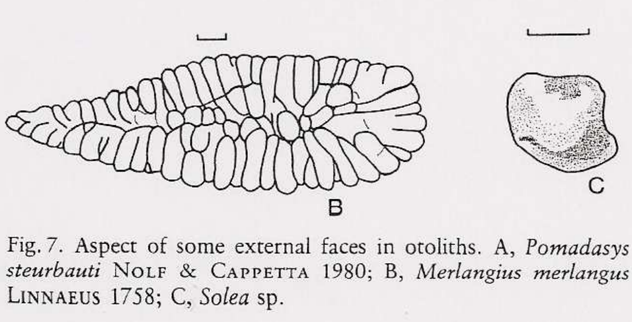


Fig. 7. Aspect of some external faces in otoliths. A, *Pomadasys steurbauti* Nolf & Cappetta 1980; B, *Merlangius merlangus* Linnaeus 1758; C, *Solea* sp.

Concluding this section on features, I turn to the ever returning question of non-otolith taxonomists: «Do otoliths really permit one to distinguish species, genera, families, etc.?» To this, I can answer in exactly the same way as if the question was posed for whole animals: in some cases, distinction of species, etc. is very easy, in others it is hardly possible.

In Recent Gadidae, distinction of the various species on the basis of whole fishes is relatively easy, but in a family like the Cynoglossidae, it becomes very difficult. Transposed to otoliths, one can say that sciaenid species can readily be identified by their otoliths, but in the Scaridae, the task becomes nearly impossible.

The same is true for the definition of genera and families. Above the family level, definition of higher groups by otolith features often becomes more hazardous, because few families or higher groups are yet definable by otolith synapomorphies. A glance, for example, at the otoliths of the various families of the suborder Photichthyoidei (Fig. 45) hardly suggests strong relationships. On the other hand, otoliths of Gadiformes (Figs. 49–50) have synapomorphies and even relationships between the orders Gadiformes and Ophidiiformes (Fig. 51) are supported by synapomorphies of their otoliths. In using otoliths for species identification, problems of variability, ontogenetic changes, etc. arise just as when using whole animals. For example, the adult stage of the beryciform *Anoplogaster cornutus* Valenciennes 1833 looks so different from the juvenile that it was named as a distinct genus, *Caulolepis longidens* Gill 1883. In otoliths, an analogous confusion could arise with regard to the adult and juvenile otoliths of *Hoplostethus atlanticus* Collett 1889 (Fig. 8B_1, B_3) if the intermediate specimen (Fig. 8B_2) was lacking.

In the following paragraphs, problems concerned with ontogenetic changes, variability, various types of otolith dimorphism, etc. will be discussed.

Ontogenetic changes

Nearly all otoliths are subject to more or less manifest ontogenetic changes. Little is known about the very early stages of otoliths in larval and very young fishes, except that the otoliths do not yet show such typical features as in later stages. As a rule, I can state that otoliths of very juvenile fishes have a rather smooth external face and comparable rims. Often the pattern of the sulcus is also not so obvious as in later stages. In the late juvenile and early adult stages, all morphological features become most clearly expressed. In the late adult and senile stages, the growth rate of the otoliths usually declines: the otolith length/fish length ratio

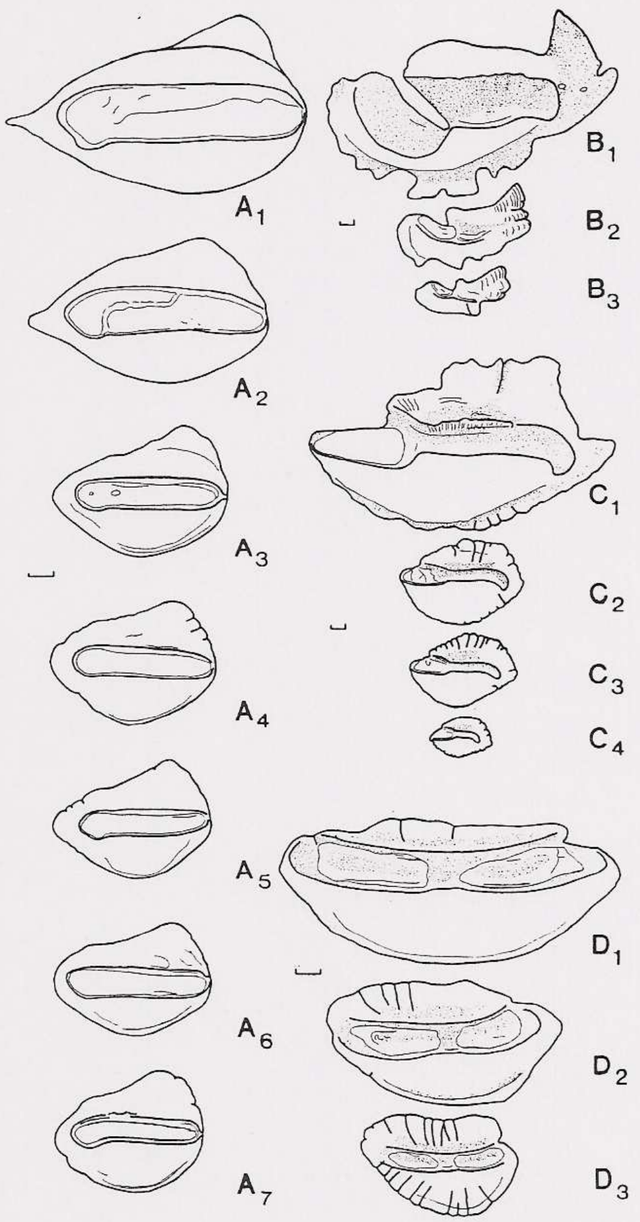


Fig. 8. Four examples of allometric growth in teleostean otoliths. A, *Lepophidium cervinum* (GOODE & BEAN 1885) (Ophidiidae); B, *Hoplostethus atlanticus* COLLETT 1889 (Trachichthyidae); C, *Pagellus erytherinus* (LINNAEUS 1758) (Sparidae); D, *Ventrifossa ctenomelas* (GILBERT & CRAMER 1896) (Macrouridae).

decreases in most species. Moreover, all ornamentation becomes smoother, even the sulcus pattern. Studies on allometric growth in gadid otoliths have been carried out by GAEMERS (1976) and growth series of *Merlangius merlangus* (LINNAEUS 1758) and *Trisopterus luscus* (LINNEAUS 1758) have been figured by NOLF (1977). Important changes during the early growth stages of herring otoliths are illustrated by HEMPEL & TREKEL (1959). Strong ontogenetic changes are known in the otoliths of sciaenids and have been illustrated by OHE (1980) for *Pennahia argentata* (HOUTTUYN 1782) and *Nibea mitsukurii* (JORDAN & SNYDER 1900).

The most important ontogenetic change in sciaenid otoliths concerns the progressive widening of the ostium. Very juvenile sciaenid otoliths (coll. HUDDLESTONE), not figured by OHE (1980), look like generalized perciform otoliths and have not yet acquired the typical sciaenid sulcus pattern. For the present discussion, I have chosen some very obvious examples of ontogenetic changes in Recent fishes (Fig. 8). The clearest one is *Hoplostethus atlanticus* COLLETT 1889 where the whole rim shape and sulcus pattern

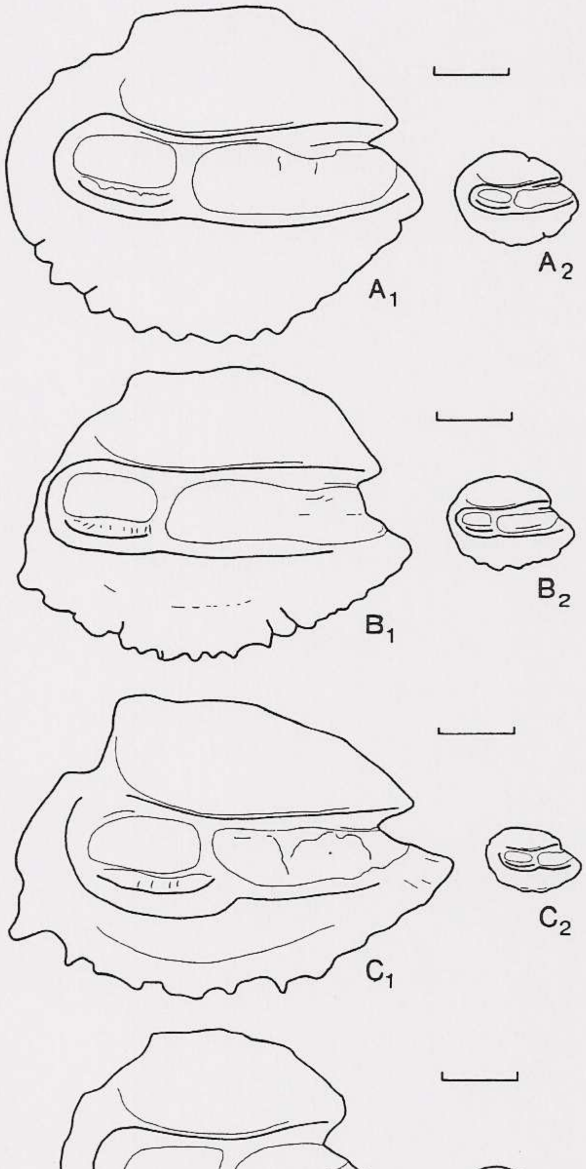


Fig. 9. Adult (A_1, B_1 . . .) and juvenile (A_2, B_2 . . .) otoliths of five Atlantic *Diaphus* species. A, *D. effulgens* (GOODE & BEAN 1896); B, *D. lucidus* (GOODE & BEAN 1896); C, *D. splendidus* (BRAUER 1904); D, *D. metopoclampus* (COCCO 1829); E, *D. dumerili* (BLEEKER 1856).

alters in the process. In *Lepophidium cervinum* (Goode & Bean 1885), it is obvious that the spinous process of the posterior rim is only acquired in the adult stage; moreover the height/length ratio of the otolith decreases during growth. Somewhat less spectacular, but still obvious changes are demonstrated for *Pagellus erythrinus* (Linneaus 1758). The series indicates a change from otoliths rather generalized in form to a more characteristic morphology in later stages. This is the kind of ontogenetic change that occurs in the otoliths of most fishes of the large suborder Percoidei. Finally, a quite obvious change is illustrated by the macrourid *Ventrifossa ctenomelas* (Gilbert & Cramer 1896). In this series, I see an evolution from rather high, round otoliths with a large area between the crista superior and the upper rim to very elongate otoliths with a crista superior close to the upper rim. The adult otoliths of this

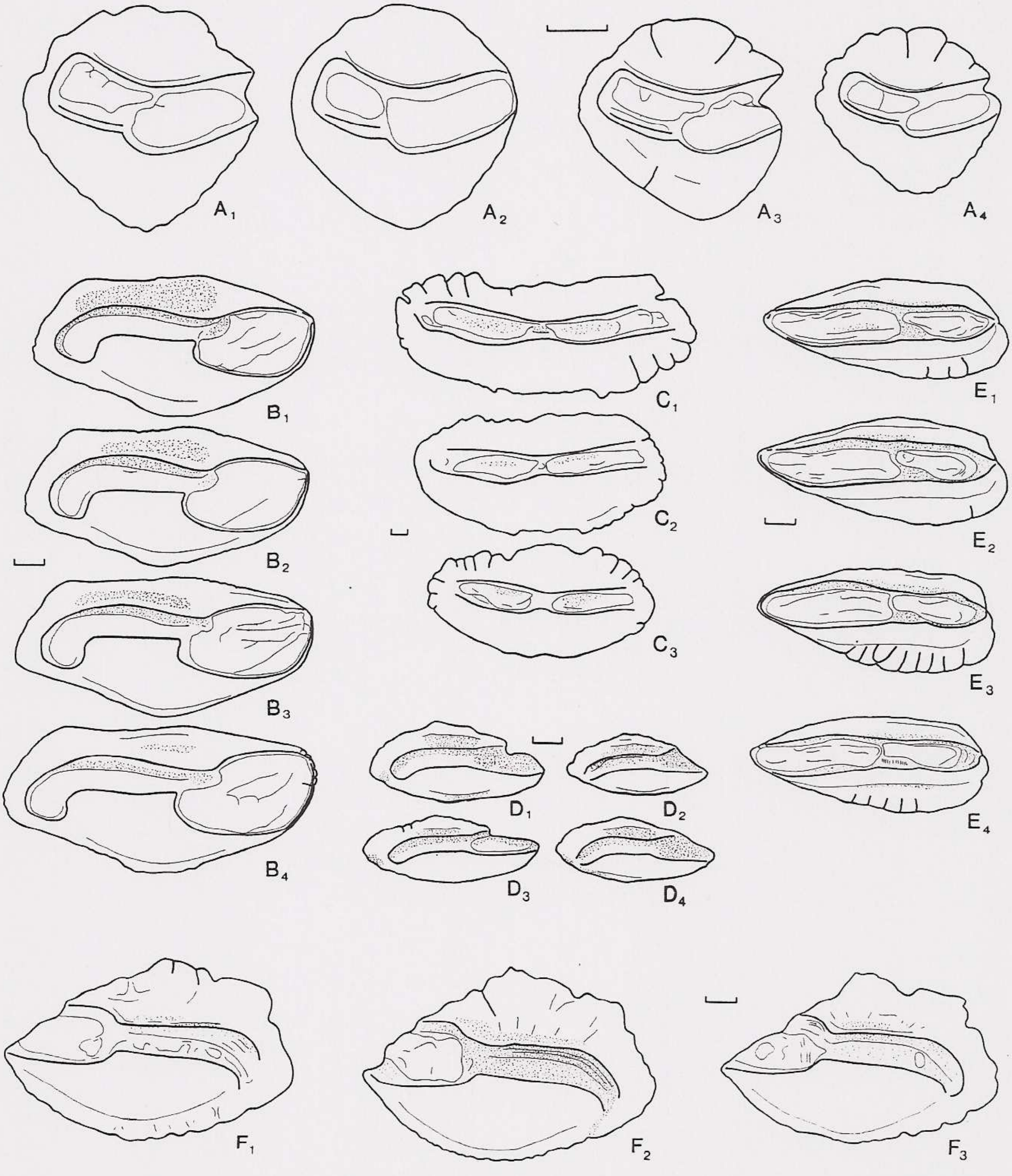


Fig. 10. Species with slightly or moderately variable otoliths. A, *Myctophum selenops* Taaning 1928 (Myctophidae); B, *Cynoscion analis* (Jenyns 1842) (Sciaenidae); C, *Macrourus berglax* Lacepede 1802 (Macrouridae); D, *Serranus tabacarius* (Cuvier 1829) (Serranidae); E, *Trisopterus esmarkii* (Nilsson 1855) (Gadidae); F, *Pagellus natalensis* Steindachner 1902 (Sparidae).

species may be considered as quite typical, but the juvenile one (Fig. 8 D_3) reflect the plesiomorph condition of otoliths in macrourine fishes. Considered without knowledge of their later stage, they could be easily confused with those of the genus *Nezumia*, that has a more plesiomorph type of macrourine otoliths. In fact, such ontogenetic series as *Pagellus erythrinus* and *Ventrifossa ctenomelas* are perfect illustrations of the biogenetic law of Haeckel. The statement that juvenile otoliths usually reflect a more plesiomorph condition, while typical apomorph features only turn up in later stages, brings us to another problem concerned with otolith identification. It will be illustrated with Atlantic *Diaphus* otoliths. Adult and juvenile otoliths of five Recent Atlantic *Diaphus* species are shown (Fig. 9). Comparison of the adult otoliths shows that they are excellent tools for specific identification, but if one should only have juvenile material, distinction is hardly possible. Various analogous examples could be given, e.g. in gobiids, serranids, scorpaenids, pomadasyids, etc. This means that in dealing with fossil otoliths of these groups, reliable identifications are only possible on adult otoliths, and paleontologists waste their time if they attempt to identify juvenile material at the species level. This also means that the choice of holotypes for new fossil species among such juvenile otoliths, even if they are perfectly preserved, only results in doubtful species of no further use.

Variability

Two kinds of variability will be considered: intraspecific variability, and the variation throughout the species that constitute a genus. All examples are chosen among Recent species because in fossil examples variability within a group can only be inferred. One should study variability on Recent otoliths and interpret fossil variability in the light of knowledge from the Recent material. The inverse way is never free of speculation.

Concerning intraspecific variability of otoliths, statements again can be made in exact analogy with data on whole fishes. There are species where variability is almost nil and others where it is very great. In the example of *Cynoscion analis* (Fig. 10B), all otoliths look almost like replicas; in all other examples variability is obvious, but may be called moderate. Fortunately for paleontology such moderate variability is the rule in otoliths of many species.

In Fig. 11, some species with rather strongly variable otoliths are figured. In *Arnoglossus laterna (*WALBAUM 1792) and *Phanerodon furcatus* GIRARD 1854 variability is high, but if one has a good series of otoliths, the characters of the species can still be recognized. This is true of the otoliths of many flatfishes and certain perciform and scorpaenid fishes. In the eels *Ophichthus triserialis* (KAUP 1856) and *Gymnothorax mordax* (AYRES 1859) and in the cottid *Myoxocephalus quadricornis* (LINNAEUS 1758), otoliths are highly variable in several features such as rims, sulcus delimitation and thickness. Such species may present problems in paleontological investigations. If such cases turn up in a paleontological analysis, open nomenclature will be preferable to the arbitrary lumping or splitting of form groups.

Finally, the most excessive otolith variation has been observed in the gulpher *Eurypharynx pelicanoides* VAILLANT 1828 (Fig. 11C). In such species, otoliths are of no use for identification.

Intraspecific variability of otoliths has been illustrated accurately for many species by CHAINE & DUVERGIER 1934 and CHAINE (1935 to 1958).

An evident problem in studying intraspecific variability is the question that always turns up: which difference can be attributed to variability, and which truly delimit species?

Therefore I now study another aspect of variability: differences between species within one genus, or what one could call «generic variability». Evidently, genera should not be considered in the same way as species. If species are (or should be) real entities in nature, genera are in part the result of our cirteria of grouping species together, and there are no clearly defined rules for doing so nor are the criteria of various authors uniform.

On the generic level, just as on the specific, I can say that there are genera with rather uniform morphology, genera with clear variability, and genera with strong variations. All three cases are illustrated in Fig. 12.

Genera like *Apogon* (Fig. 12 A–F) are quite easy for paleontologists if they have to decide on the generic identification of their fossils, but problems turn up when they have to decide on the distinction of fossil species. Because, in a genus like *Apogon*, specific features consists of minute differences in shape and rim pattern, extensive series of perfectly preserved fossils are required to define species.

In genera like *Chloropthalmus* (Fig. 12 G–J), criteria for generic identification of fossils are less evident, but once one has established that the fossils should be included in the genus, distinction between the various species presents no problem.

Finally, I have to deal with the case of genera like *Myoxocephalus* (Fig. 12 K–N). Here, the morphology of the species is so divergent that one could almost say that the only character they have in common is the absence of consistent structural patterns. The problem is still more complicated because each of the various species is also subject to strong intraspecific variability.

When dealing with fossils of such a genus, generic identification is usually based on a synapomorphy with only one of the Recent species, but specific identification is complicated because it is very difficult to distinguish between intraspecific variability and variation above the species level. For such species, the use of open nomenclature (*Myoxocephalus* sp.) will often be the best solution. Obviously, the three examples chosen in Fig. 12 are three extremes, chosen to illustrate explicitly the various conditions which may occur. Fortunately, in most cases, specific differences are well expressed in the various members of a genus, and specific features are clear enough that they are not obliterated by intraspecific variability. The generic variability of two different genera is illustrated in Fig. 13. In both examples, specific differences are clear and need not further comment. This is the situation found in the otoliths of very many teleostean fishes; in these cases, they are excellent tools for specific identification.

The same kind of discussion could be continued for the taxonomic value of otoliths above the generic level, family

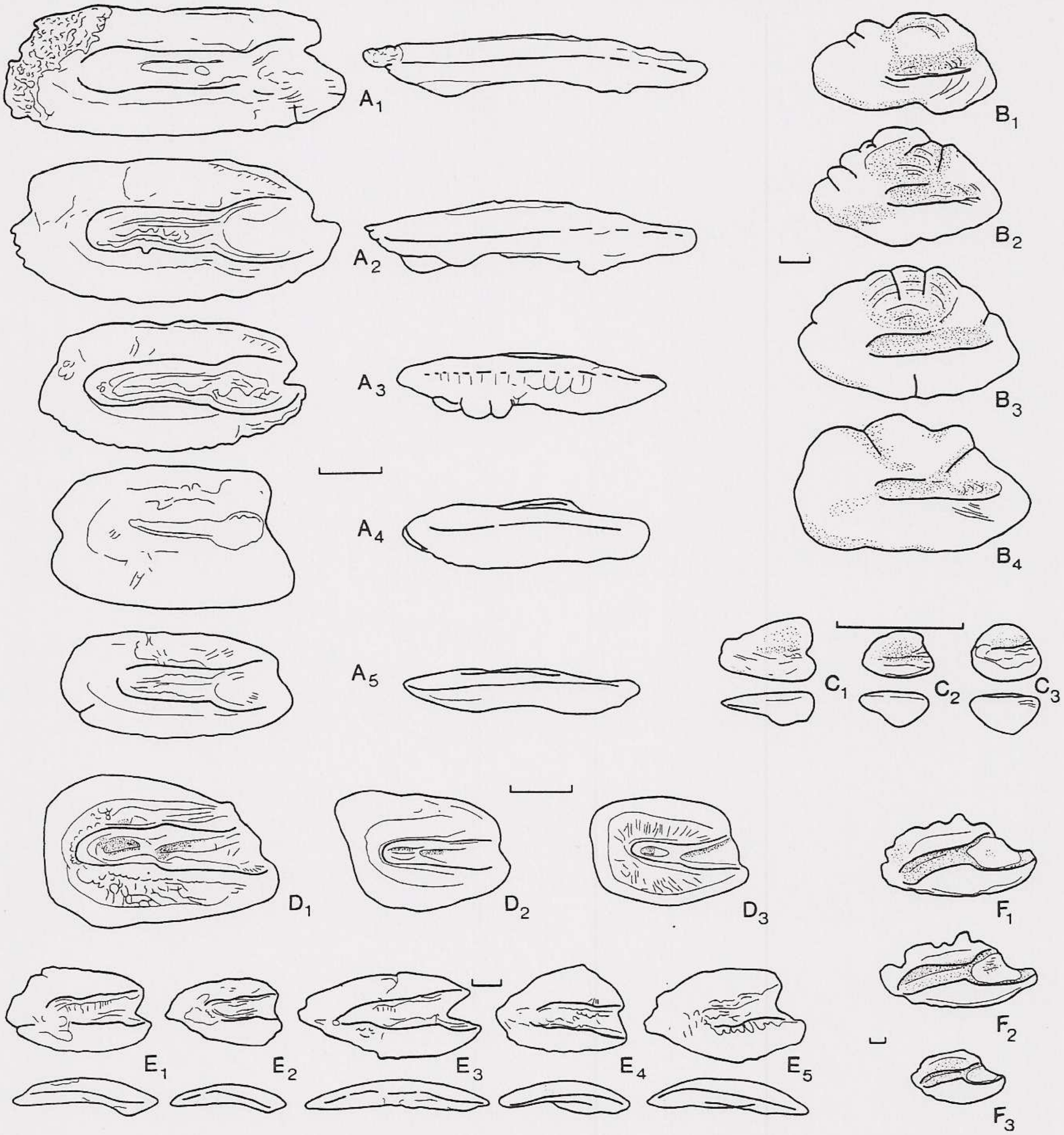


Fig. 11. Species with strong or obvious otolith-variability, A, *Ophichthus triserialis* (KAUP 1856) (Ophichthidae); B, *Myoxocephalus quadricornis* (LINNAEUS 1758) (Cottidae); C, *Eurypharynx pelicanoides* VAILLANT 1882 (Eurypharingidae); D, *Arnoglossus laterna* (WALBAUM 1792) (Bothidae); E, *Gymnothorax mordax* (AYRES 1859) (Muraenidae); F, *Phanerodon furcatus* GIRARD 1854 (Embiotocidae).

level, etc.; at each level the conclusion will be that there are groups in which otolith morphology is very helpful and others where it is less so, with all possible intermediate situations.

My comments on variability can be concluded with an example where both variation of species constituting a genus and intraspecific variability are involved. In Fig. 14, variability is shown in otoliths of four pomadasyid species living together in the same neritic areas of the Caribbean. This means that their otoliths are expected to be found together in the otolith association of a bottom sample from the area; analogous situations will turn up in otolith paleontology. At a first glance (Fig. 14), all the otoliths look the same, but careful examination shows that *Haemulon flavolineatum* is characterized by a very regularly curved cauda, while the posterior part of the cauda is slightly angular in all the other species. One also learns that *H. plumieri* has a marked angle in the central portion of the dorsal rim and a marked posterodorsal angle. Otoliths of *H. aurolineatum* are slightly more elongate than those of the

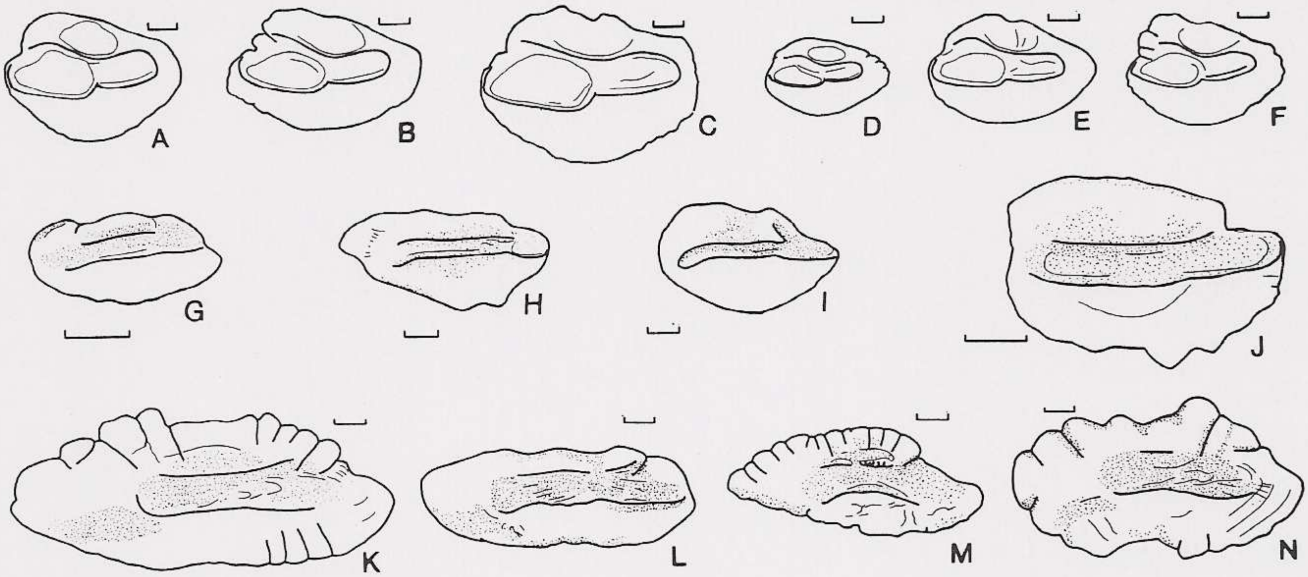


Fig. 12. Otolith variations in species of one genus. A–F, *Apogon*, a genus with restricted variation: A, *A. aureus* (Lacepede 1803); B, *A. ellioti* Day 1875; C, *A. fleurieu* (Lacepede 1802); D, *A. fraenatus* Valenciennes 1832; E, *A. quadrifasciatus* Cuvier 1828; F, *A. striatus* Smith & Radcliffe 1942; G–J, *Chlorophthalmus*, a genus with clear variation: G, *C. agassizi* Bonaparte 1840; H, *C. atlanticus* Poll 1953; T, *C. nigripinnis* Guenther 1878; J, *C. fraserbrunneri* Poll 1953; K–N, *Myoxocephalus*, a genus with strong variation; *M. jaok* (Cuvier 1829); L, *M. octodecemspinosus* (Mitchill 1815); M, *M. stelleriraninus* Jordan & Starks 1904; N, *M. verrucossus* (Bean).

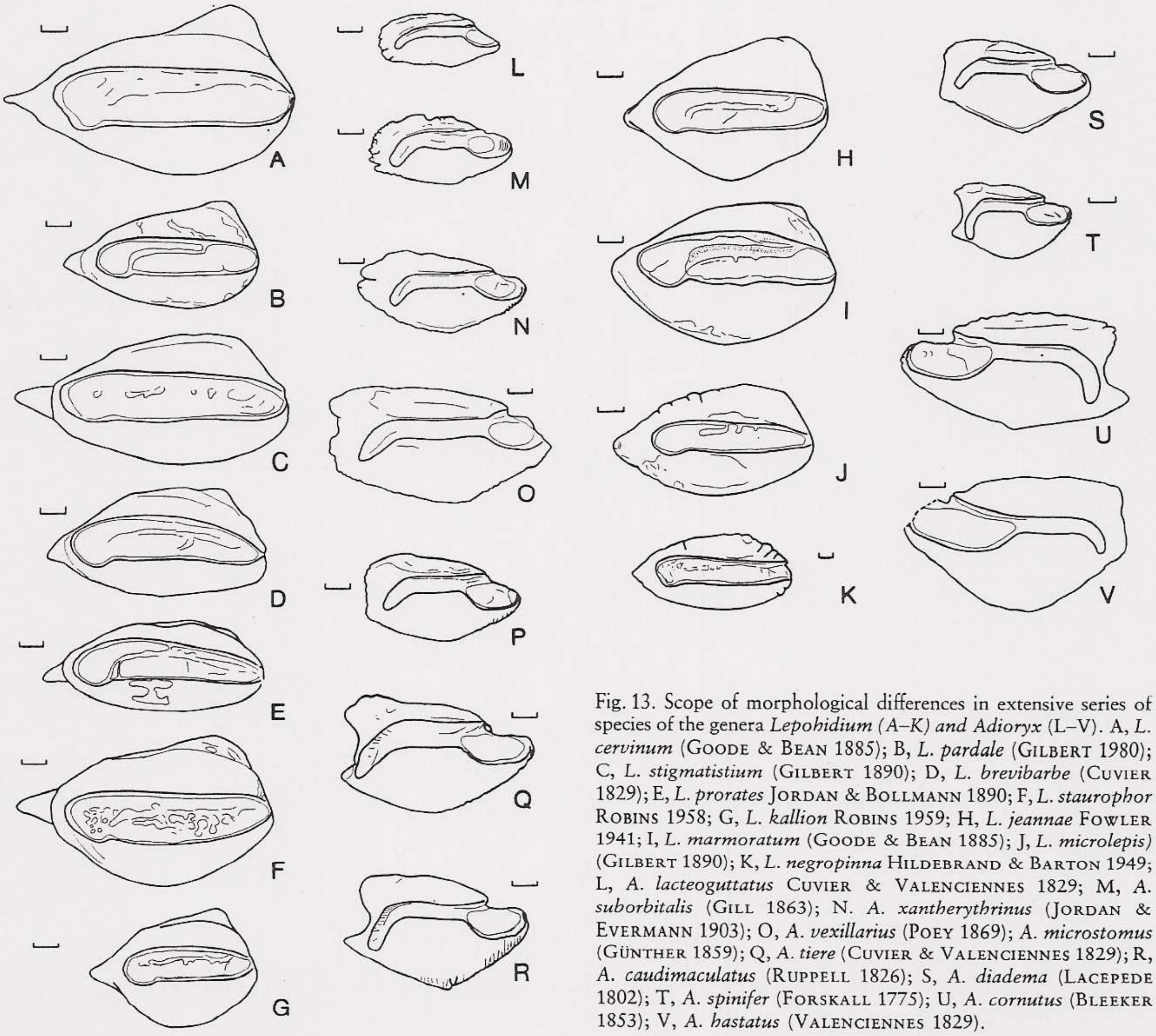


Fig. 13. Scope of morphological differences in extensive series of species of the genera *Lepohidium (A–K) and Adioryx* (L–V). A, *L. cervinum* (Goode & Bean 1885); B, *L. pardale* (Gilbert 1980); C, *L. stigmatistium* (Gilbert 1890); D, *L. brevibarbe* (Cuvier 1829); E, *L. prorates* Jordan & Bollmann 1890; F, *L. staurophor* Robins 1958; G, *L. kallion* Robins 1959; H, *L. jeannae* Fowler 1941; I, *L. marmoratum* (Goode & Bean 1885); J, *L. microlepis)* (Gilbert 1890); K, *L. negropinna* Hildebrand & Barton 1949; L, *A. lacteoguttatus* Cuvier & Valenciennes 1829; M, *A. suborbitalis* (Gill 1863); N. *A. xantherythrinus* (Jordan & Evermann 1903); O, *A. vexillarius* (Poey 1869); *A. microstomus* (Günther 1859); Q, *A. tiere* (Cuvier & Valenciennes 1829); R, *A. caudimaculatus* (Ruppell 1826); S, *A. diadema* (Lacepede 1802); T, *A. spinifer* (Forskall 1775); U, *A. cornutus* (Bleeker 1853); V, *A. hastatus* (Valenciennes 1829).

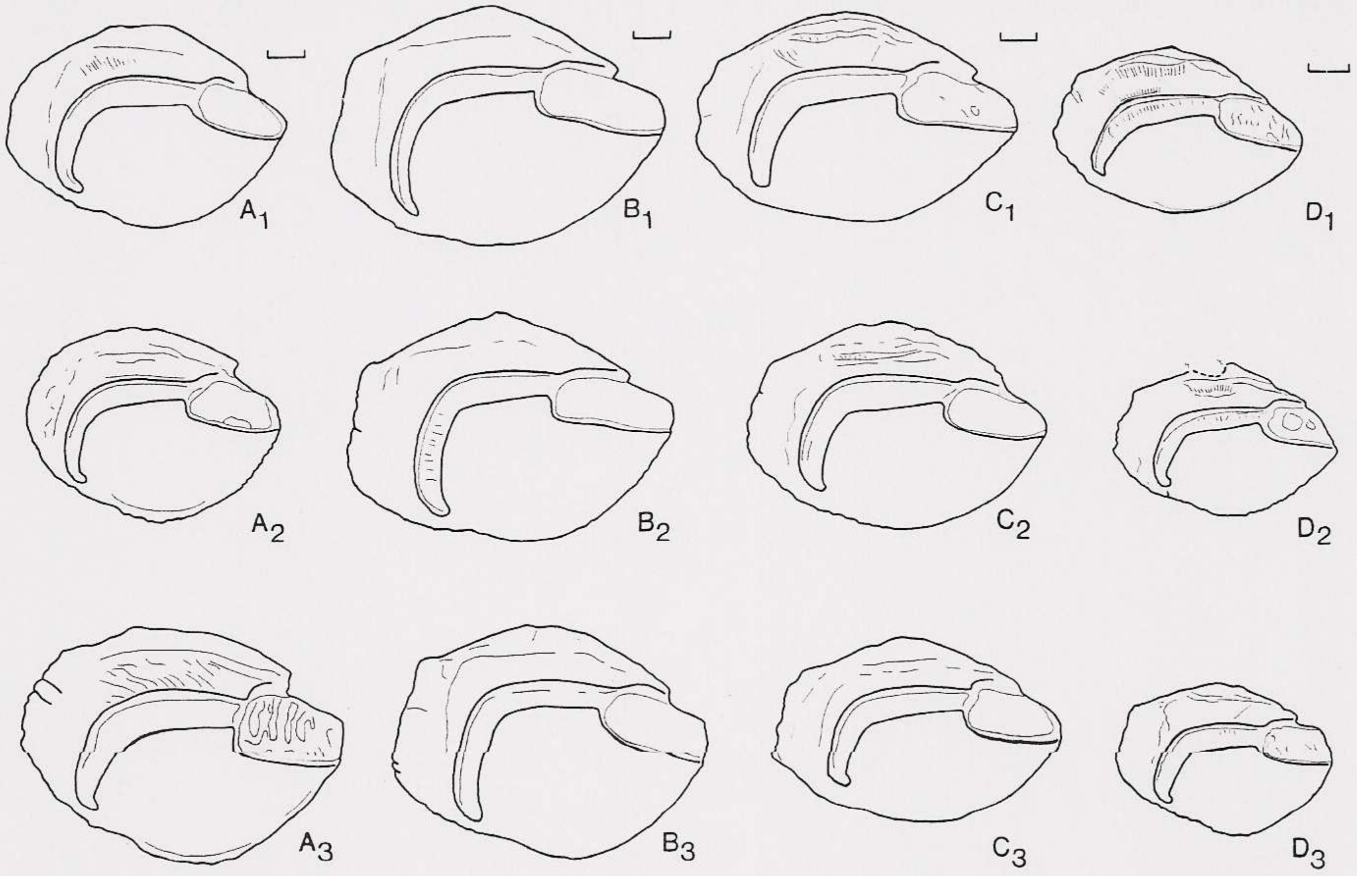


Fig. 14. Intraspecific variation of four Recent Caribbean species of the genus *Haemulon* (Pomadasyidae). A. *H. flavolineatum* (Desmarest 1823); B, *H. plumieri* (Lacepede 1802); C, *H. aurolineatum* Cuvier 1830; D, *H. bonariensis* Cuvier 1830.

other species. Finally *H. bonariensis* has a slightly concave stretch in the posterior ventral rim and the ventrally directed part of the cauda is relatively short.

This example stresses that notwithstanding apparent similarity, diagnostic features may be discovered even in cases where distinction is difficult. It also illustrates the limitations of identification work: all the otoliths figured were extracted from fishes with a total length varying between 15 and 25 cm, but it is almost certain that otoliths of fishes of the same species with a length of 5 to 10 cm will not yet have acquired the diagnostic features discussed. In such a case, distinction will be possible for the adult portion of the otolith association, but the juvenile portion will not be identifiable at the specific level. A fossil example is the pomadasyid otolith association from the Middle Eocene of the Paris Basin (Nolf & Lapierre 1979).

Finally, I may conclude that all paleontological investigations on otoliths should be accompanied by extensive studies on Recent material; other approaches are more speculation.

Dissymmetry

In all actinopterygians except flatfishes, left and right otoliths are symmetrical in every specimen. This does not mean that the left otolith is the exact mirror image of the right in all its details: they are symmetrical in the sense of left and right hand symmetry.

In fishes with bilateral symmetry (all non-flatfishes) marked aberrations from this symmetry are rare but have been recorded from time to time. In Fig. 15 C and D, the normal situation is shown for the ophidiid *Dicrolene intronigra* Goode & Bean 1883, but in Fig. 15 A and B, presenting the left and right otolith of one specimen, an apparent dissymmetry is visible. Such cases are considered to be anomalous.

In flatfishes, on the other hand, dissymmetry of the entire head is usually reflected to a certain extent in the otoliths. This is illustrated for *Lepidorhombus whiffiagonus* (Walbaum 1792), *Hippoglossoides platessoides* (Fabricius 1780) and *Bothus lunatus* (Linnaeus 1758) (Fig. 15). However, the dissymmetry of flatfish otoliths should not be considered absolute: while in a specimen of *Bothus lunatus* (Fig. 15 C). I found strongly dissymmetric otoliths, those of a *Bothus podas* (Delaroche 1809) (Fig. 15 D) are nearly symmetrical. In collections of flatfish otoliths dissymmetry is often hidden by intraspecific variability, which is unusually wide in this group.

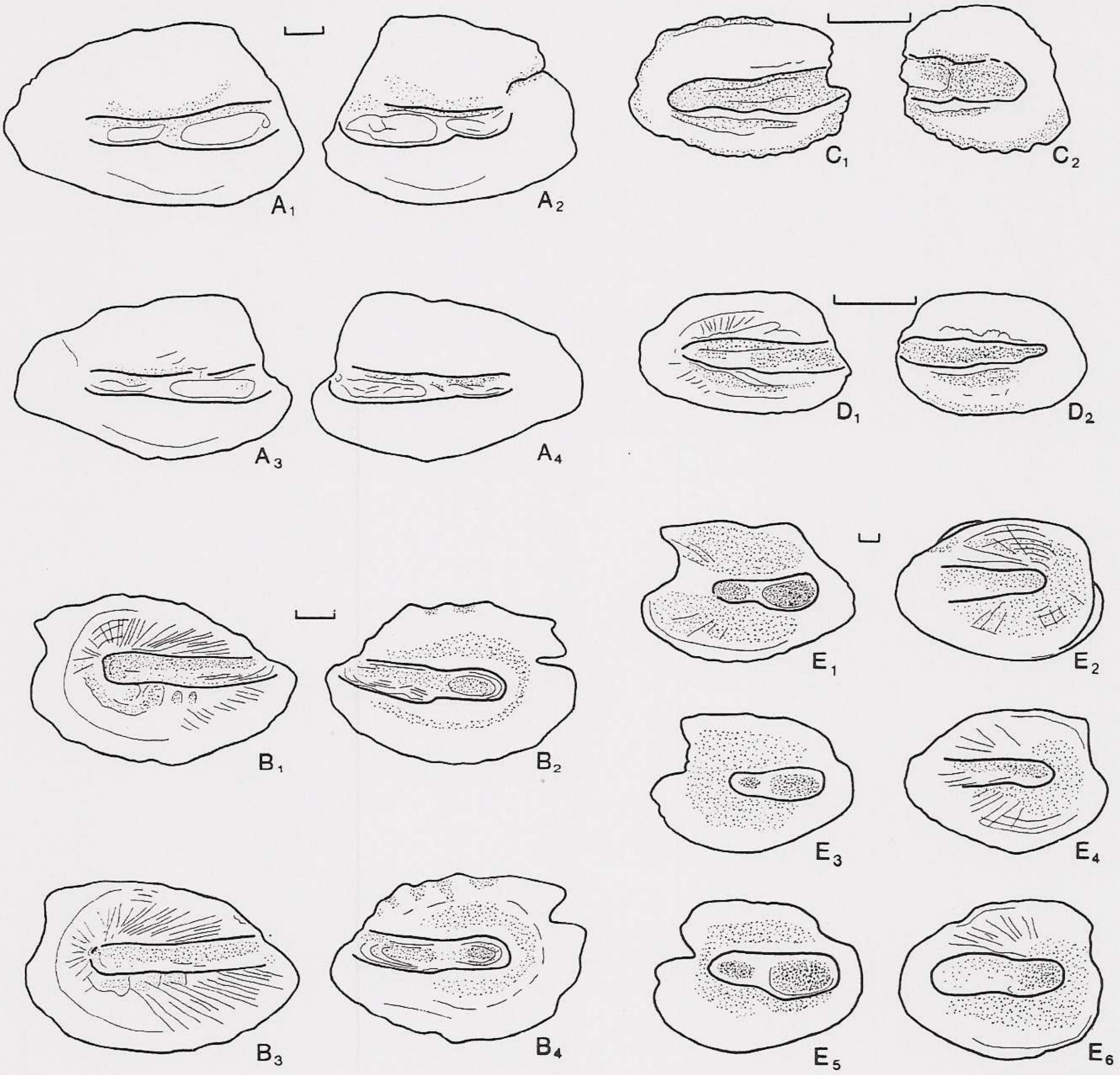


Fig. 15. Dissymmetry of teleost otoliths. A, *Dicrolene intronigra* Goode & Bean 1883 (Ophidiidae); B, *Lepidorhombus whiffiagonus* (Walbaum 1792) (Bothidae); C, *Bothus lunatus* (Linnaeus 1758); D, *Bothus podas* (Delaroche 1809) (Bothidae); E, *Hippoglossoides platessoides* (Fabricius 1780) (Pleuronectidae).

Dimorphism

Although few studies have been carried out on otoliths of different populations within one species, such differences are known. Messieh (1972) was able to find slight but significant differences between otoliths of the spring spawning population and the autumn spawing population of *Clupea harengus* Linnaeus 1758 in the Gulf of St. Lawrence, Canada. Such differences probably occur in other species, but have never been investigated. In my opinion, there are probably slight differences between otoliths of North American and European populations of species like *Gadus morrhua* Linnaeus 1758 and *Melanogrammus aeglefinus* (Linnaeus 1758) but the evidence is still incomplete. Anyhow, the fact that significant differences have been observed between herring populations and probably also occur in other species, is important for paleontologists. It implies that they should not split up species on the basis of very minute differences in otoliths from different localities or stratigraphical horizons, because in many cases they may just represent population differences.

Sexual dimorphism of otoliths has never been demonstrated in fish otoliths, but no extensive investigations have been carried out. If it occurs, it should be most likely in fishes which show marked sexual dimorphism, such as cyprinodonts. If gender should have any influence on otolith morphology, the differences are probably so slight that they are hidden by normal intraspecific variability.

Convergence, symplesiomorphy and parallel variations

In many works on comparative morphology, similarities that cannot be ascribed to phylogenetic affinity are lumped as convergences. Generally, they are attributed to functional adaptation.

The term «convergence», in the sense in which it is generally used, is a compilation of different phenomena. In my opinion the application of the term «convergence» should be restricted to cases where similar features occur in two or more groups which evidently have no direct phylogenetic affinity. Such a case is illustrated by the otoliths of ophidiiforms, superorder Paracanthopterygii, and Congridae, order Anguilliformes (Fig. 16). Similarities are evident in the outline and thickness of the otoliths and in the loss of the division between ostial and caudal portion of the sulcus. In both groups this finally leads to a reduced, centrally placed sulcus with poorly defined limits.

Notwithstanding the striking resemblance, the process of sulcus transformation is entirely different in the two groups. In ophidiiforms, the undivided sulcus results from the disappearance of a well individualized cauda, while in congrids the cauda remains very clear but the ostium becomes indistinct and finally disappears. Because of the analogous way of life in congrids and ophidiiforms (benthic fishes on soft, muddy bottom) one is tempted to consider the convergence of their otoliths as functional adaptation to the environment. This explanation seems acceptable, but even without it we can speak here about convergence.

Another example of convergence is provided by the otoliths of three unrelated teleost families: clupeids, carangids and scombrids (Fig. 17). All three are characterized by small elongate otoliths with a deeply incised sulcus and a very prominent rostrum. But in the details of their morphology they have little in common, and the similarities cited are probably convergences related to a similar epipelagic habitat in the three families.

Entirely different are those similarities that can often be observed among related taxonomic groups, where sometimes species seem to be more closely related to species outside their own group than to those in it. These false «convergences» can be divided into two different categories. I have chosen an example in the order ophidiiforms and the first type is illustrated by the otoliths of *Genypterus* (Ophidiinae), *Hoplobrotula* (Neobythitinae) and *Dipulus* (Bythitidae) (Fig. 18). Resemblance between otoliths of these three genera, which belong to rather different groups,

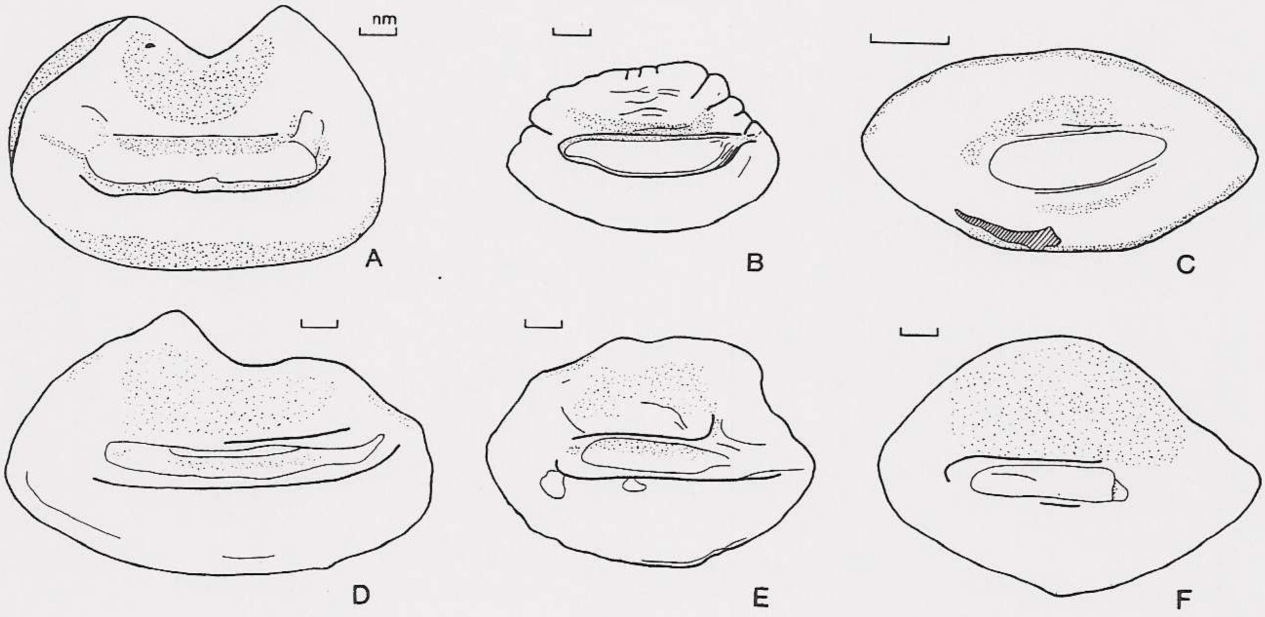


Fig. 16. Otoliths of three species of ophidiiforms (A–C), compared to three species of congrids (D–F). A, *Alcockia rostrata* (Guenther 1878); B, *Selachophidium guentheri* Gilchrist 1903; C; *Oligopus robustus* (Smith & Radcliffe 1913); D, *Coloconger meadi* Kanazawa 1957; E, *Paraxenomystax* sp.; F, *Rhechias bullisi* Smith & Kanazawa 1977.

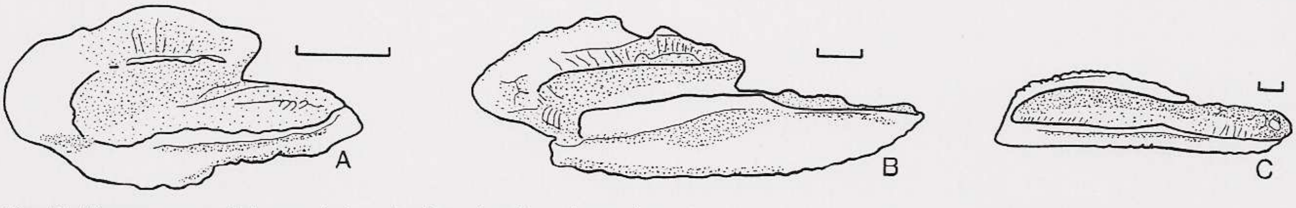


Fig. 17. Convergent otolith morphology in three families of epipelagic fishes. A, *Sardina pilchardus* (Walbaum 1792) (Clupeidae); B, *Caranx lutescens* (Richardson 1843) (Carangidae); C, *Thunnus thynnus* (Linnaeus 1758) (Scombridae).

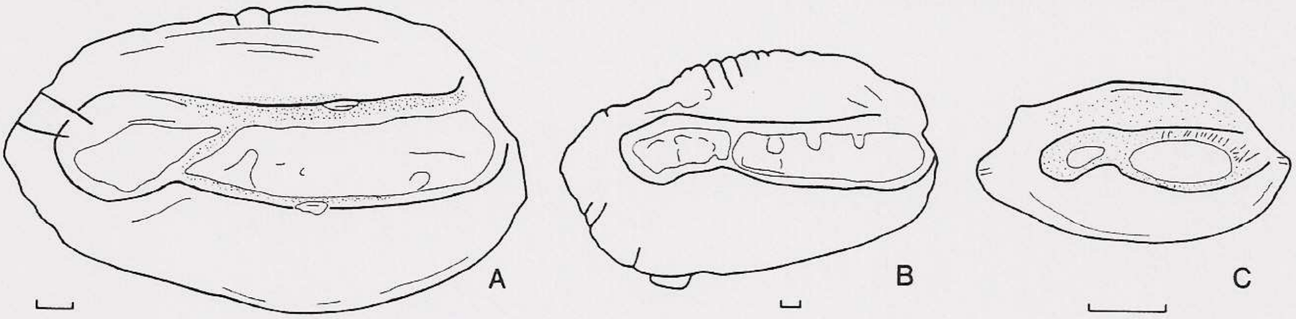


Fig. 18. Resemblance based on symplesiomorphies between three distantly related ophidiiform fishes. A, *Hoplobrotula gnathophus* REGAN 1921 (Ophidiidae, Neobythitinae); B, *Genyptenus blacodes* (BLOCH & SCHNEIDER 1801) (Ophidiidae, Ophidiinae); C, *Dipulus caecus* WHITE 1905 (Bythitidae).

is due only to conservation of primitive features. Therefore we deal here with symplesiomorphy, that has nothing to do with convergence.

The second type of false convergence can be documented with numerous examples in ophidiiform otoliths (see NOLF 1980 for illustrations): resemblance of the undivided, central sulcus in *Onuxodon*, *Taureophidium*, *Barathrites*, the Bythitini, *Lucifuga* and *Dermatopsis;* resemblance of the ventral profile in *Echiodon*, *Acanthonus*, *Leucicorus* and *Cataetyx;* convexity of the inner face in *Parophidium*, *Sirembo* and certain *Neobythites;* the strong notch in the dorsal rim of certain *Glyptophidium* and *Luciobrotula;* the very strong anterodorsal angle in *Ophidion* and *Typhlonus*, etc.).

All these similarities are examples illustrating VAVILOV's law (see KIRIAKOFF 1957 for comments). This law states that in related taxa, comparable variations will occur frequently; they are called parallel variations. This is the logical result of the fact that the genetic make up of related taxa is necessarily similar, often resulting in comparable phenetic traits.

Such similarities are often considered convergence, but this is not correct if one accepts the definition of the term given here. Moreover it is absolutely false to attribute this type of similarity to functional adaptation. It is essentially the expression of the similar genetic content of the groups concerned.

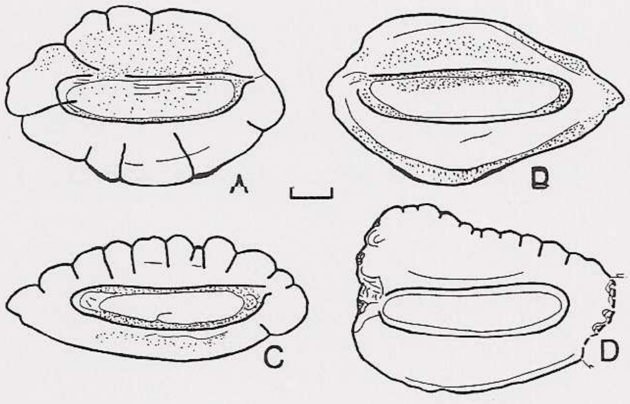


Fig. 19. Parallel variations in the sulcus morphology of ophidiiforms. A, *Pycnocraspedium squamipinne* ALOCK 1889, Recent; B, «genus *Neobythitinorum boulangeri* NOLF 1980, Oligocene; C, *Hypopleuron caninum* SMITH & RADCLIFFE 1913, Recent ; D, «genus *Neobythitinorum*» *ornatissimus* (NOLF 1974), Oligocene.

In paleontology also, results of VALVILOV's law have to be considered and may cause problems. The sulcus of the living genera *Pycnocraspedium* and *Hypopleuron* (Fig. 19) suggests close relationship, but analysis of other somatic features in these fishes is not at all indicative of such a situation. The same type of sulcus exists in various fossil species, e.g. «*genus Neobythitinorum*» *hilgendorfi* (KOKEN 1891A) and «*genus Neobythitinorum*» *ornatissimus* (NOLF 1974) (Fig. 19). If it is true that no close affinity exists between the Recent *Hypopleuron* and *Pycnocraspedium*, one has to consider the similarity of their sulci as a parallel variation. For this reason, one cannot consider this feature as an indicative of relationship and suggest relationships between the fossil species as exemplified in Fig. 18.

Relation otolith length/fish length

A simple glance at the otoliths of various fish families shows that their relative size varies greatly. A few examples of the ratio of otolith length to fish length are given to illustrate this fact:

Chirocentrus dorab (CHIROCENTRIDAE): 0.8 %
Diaphus metopoclampus (MYCTOPHIDAE): 5.4 %
Gadus morrhua (GADIDAE): 1.5 %
Brotula barbata (BROTULIDAE): 5.7 %
Epinephelus striatus (EPINEPHELIDAE): 1.5 %
Cynoscion striatus (SCIAENIDAE): 1.8 %
Scomberomorus guttatus (SCOMBRIDAE): 0.9 %

In a very general sense, the relative size of an otolith constitutes one of its features, but it seems not to be a very important one in estimating relationships. Our otoliths of various ophidiiform species show relative sizes varying between 1.5 to 7.1 % of fish length. It seems to us that the relative length of an otolith is partly related to function. Fishes that make noise have big otoliths, most of the bottom-dwelling species have relatively big otoliths, while nearly all epipelagic fishes (except flying fishes) have very little otoliths. In mesopelagic fishes, however, no general rules can be stated. Myctophids have big otoliths, stomiatids very little ones; intermediate situations occur in other groups of mesopelagic fishes. As long as we have no good account of the precise function of otoliths, the reasons of the given size distributions can only be a matter of speculation.

My investigations on ophidiiform otoliths produced some evidence that the ratio otolith length/fish length could be subject to allometric changes, but investigations by DUPONT (1972) have shown a nearly linear relation between fish growth and otolith growth for Mediterranean *Merluccius merluccius* (LINNAEUS 1758). Anyhow, observations on the relation between otolith length and fish length in growth series of Recent species can be used to estimate the size of a given related fossil species. This aspect remains an almost totally unexplored field of otolith paleontology.

Biogeography

As in some of the previous chapters, what will be said here applies to the general paleontological context of comparative studies of fossil and Recent organisms. However, since it seems that many previous otolith workers ignored the distribution of Recent fishes, some discussion appears justified.

If one observes that nearly a hundred of the European Eocene otolith species are closely related to Recent shallow water Indo-West Pacific genera, attribution of such species to Indo-West Pacific genera seems justified. An uninformed neontologist might suggest that affinity with Atlantic genera is more likely, but our conclusions are supported by investigations of other animal groups, and the paleogeographic data for the period considered.

If, on the other hand, one states that otoliths of *Diaphus theta* EIGENMANN & EIGENMANN 1890 and *Stenobrachius leucopsarus* (EIGENMANN & EIGENMANN 1890), both Northern Pacific mesopelagic myctophids, are present in the Mediterranean Pliocene, as was recently done by some European paleontologists, one is talking biogeographic nonsense. The example given is spectacular, but unfortunately, otolith literature is full of generic identifications that are incompatible with biogeography past and present: *Atherinopsis*, a genus endemic to the American Pacific coast, is cited in the Mediterranean Pliocene; *Gadus*, a northern hemisphere coldwater genus, is cited from the Oligocene of South Australia; *Raniceps*, a Recent eastern Atlantic endemic, from the Miocene of New Zealand; *Trachinus*, a Recent eastern Atlantic endemic, also from the Miocene of New Zealand; several embiotocids, Recent endemic littoral fishes of the Northern Pacific, from the Eocene of Europe (the present author made this error in an early paper); *Prionotus*, *Leurestes*, *Paralabrax*, *Centropomus* and several other typical Recent New World genera from the Eocene of Europe.

These are all examples of the many generic otolith identifications that are improbable in terms of biogeography, and demand careful checking in terms of morphology. In all of the cited cases, a detailed morphological analysis of the specimens shows that the generic identifications are incorrect. This shows that generic identification of fossil otoliths should be performed in a much more careful way, but this is marginal to the present discussion. My main conclusion is that even if morphologic evidence persistently suggests realtionships of fossils incompatible with biogeographic data, one should treat the identification with extreme scepticism. I therefore hope that the publication of figures of otoliths of all Recent fish families in the present work will not result, for example, in the appearance in the European Tertiary of otoliths of notothaeniids, normanichthyids, galaxiids and the like.

Taphonomy

Recent versus fossil habitat

Usually, publications on otolith-based faunal reconstructions for a given stratum conclude with a section on paleoenvironmental conditions. In this section, conclusions about depth, temperature, salinity, substrate etc. are formulated on the basis of comparisons of the habitat and behaviour of related living species, on the assumption that their fossil relatives had the same way of life. On the other hand, we know that evolution happened and that, for example, the Eocene fauna is different from that of today. Therefore, can we take it for granted that the fossil forms had exactly the same way of life as their Recent relatives?

This aspect of otoliths has been dealt with in my monograph on ophidiiforms (NOLF 1980). In the suborder Ophioidei most of the living species are confined to bathybenthic habitats, or at least to deep neritic ones. In the Eocene, however, I observe that the very abundant subfamily Neobythitinae is represented by tremendous quantitites of otoliths in shallow water deposits. Eocene deep-sea Neobythitinae are not known, but this does not mean that they did not existed at that time, because no real deep-sea Eocene deposits have ever been investigated for otoliths. Anyhow, it may be stated without doubt that the shallow-water Eocene Neobythitinae were much more numerous than the whole Recent fauna of this subfamily. This means, that in this case, the principle of actualism cannot be applied back to Eocene times. However, a careful taxonomic analysis indicates that nearly all the Eocene shallow-water Neobythitinae belong to extinct genera, while in the Miocene, shallow-water Neobythitinae disappeared, and living genera such as *Hoplobrotula*, *Neobythites* and *Glyptophidium* are recorded from deep-water deposits.

Together with congrids, which had also during Eocene times a much more neritic habitat than most of their living relatives, ophidiiforms seem to be rare exceptions where there is a marked discrepancy between past and present habitat.

A more shallow habitat, even during Neogene time, has also been suggested for the bathybenthic family Macrouridae and for the mesopelagic family Myctophidae (GAEMERS & SCHWARZHANS 1979; HEINRICH 1969; TAKAHASHI 1976), but this seems due to incorrect interpretation of the taphonomy of the otolith associations studied by these authors. Data on Eocene faunas show that macrourid and myctophid otoliths are completely absent in all neritic deposits of the whole Anglo-Paris-Belgium Basin, but that they are present in more oceanic deposits of the Aquitaine Basin (southwest France). Hence, their pelagic habitat was already established in the Eocene.

From the foregoing, I may conclude that for nearly all fossil otoliths that belong to living genera, data on the present habitat may be applied. In many, but not all cases, identifications at the family level still allow some comparison with present habitats, but should be evaluated much more prudently, as data on Eocene ophidiiforms and congrids showed discrepancies from their present bathymetric distribution.

Origin of fossil otolith associations

When we use otoliths to estimate the total length of the animals from which they came, it is obvious that in nearly every known fossil association, all the fishes were about hardly 10 to 15 cm long (there are only a few exceptions, mainly among albulids, pterothrissids and macrourids).

In most cases, it is also striking that the bones of all the fishes, represented by thousands of otoliths, are totally absent in the sediment. Therefore, it is very probably that most otoliths are derived from small fishes constituting the prey of larger predators (sharks, actinopterygians, marine mammals, sea birds, etc). This hypothesis is supported by an analysis of the osteological material from strata where both otoliths and fish bones, teeth or skeletons are known (e.g. London Clay; Belgium Eocene; Middle Oligocene Septaria Clay of the Mainz Basin). In the osteological material from such deposits, nearly all the species represented by otoliths in the sediment are lacking, and most of the bones and teeth belong to bigger fishes, among which predatory species are well represented (e.g. sphyraenids, trichiurids, large scombrids, blochiids and xiphiids in the deposits cited above as examples). In the otolith assemblages these predators are much less numerous than their prey, and their otoliths occur only very occasionally.

According to SCHÄFER (1966), otoliths are regularly found in the excreta of large fishes, while bone is nearly entirely digested. This observation makes our hypothesis even more likely: most of the otoliths enter the sediment through predators. This model also explains why otoliths of mesopelagic fishes or deep water bottom fishes, for example, are recorded from associations that mainly consist of shallow water fishes. They are brought into these associations by predators foraging in more oceanic environments. With this statement we do not exclude all other factors that may contribute to the origin of otolith taphocoenoses, such as mass mortality caused by red tides, deep water fishes brought to the surface by upwelling water, etc., but we think that predation is the commonest way in which otoliths enter sediments.

Otolith associations and paleoenvironment

Very little is known about the occurrence of otoliths on Recent sea bottoms. Among the most relevant papers on the subject, we may cite those of WRIGLEY & STINTON (1973), on marine sediments off Massachusetts, and GAEMERS (1978), on the seas around southern Norway. Although both papers contain precise observations on the quantitative composition of otolith associations at various depths and in various types of sediment, the information they provide can only be applied on a very restricted regional scale.

It is my opinion that such reports provide the key to the most objective interpretation of fossil otolith associations. But working on such a basis will only be possible for paleontologists, when hundreds of such reports from various stations all over the world are available. WRIGLEY & STINTON (1973) clearly demonstrate that sediments deposited at depths less than 100 m in the investigated area are very poor in otoliths, while those deposited between 150 and 567 m are quite rich. Unfortunately, this is of no help in explaining the very rich fossil otolith associations in the Middle Eocene of the Paris Basin and various others, which were certainly deposited in environments shallower than 50 m.

From GAEMERS' 1978 report, it is obvious that in the North Sea shallow deposits exist containing otolith associations in which Gadidae and Pleuronectiformes are about equally important, but none of the shallow water deposits investigated in the Pliocene of the North Sea Basin contains an association of this type.

The two examples given show that in the present state of knowledge, interpretation of fossil otolith assemblages with the help of precise data on Recent assemblages is impossible in most cases.

For this reason, most paleoenvironmental conclusions on fossil otolith associations are arrived at by the indirect method of comparison with the mode of life of Recent fishes. Because in practice nearly each case is different, and because too rigorous tentatives of interpretation usually turn out in highly speculative statements, I will give here only some very generalized considerations.

It should be taken as a rule that the otolith association of a given site gives only a rough idea of the fauna inhabiting the area and never exactly reflects the quantitative composition of the fish fauna that lived there. In the preceding section, I explained that most otoliths probably enter the sediment through the excreta of predators. As some of these predators feed in both neritic and more oceanic environments, they may bring into neritic associations otoliths of deep-water fishes such as myctophids, gonostomatids and sometimes macrourids. It is even known that several cetaceans routinely forage in depths of 200–300 m, where they eat mainly myctophids, but also macrourids, morids, etc. FITCH & BROWNELL (1968) reported 18.164 otoliths from only 17 cetacean stomachs. Furthermore, many small mesopelagic fishes such as myctophids and gonostomatids live during the day at depths varying between 200 and 1000 m. At night, they migrate to the surface, where they may be eaten by epipelagic predators which may transport their otoliths into neritic environments.

As a second rule, we can state that nearly all collected fossil otolith associations consist either of fishes inhabiting sandy and muddy environments, or of mesopelagic fishes, or both accompanied by a few epipelagic forms, but almost never by inhabitants of rocky shores or reefs. This is simply the consequence of the fact that rocky shore environments do not provide good chances for fossilization and that reef environments usually fossilize in consolidated rocks in which it is impossible to collect otoliths.

Taking the two rules formulated above as general statements on the nature of otolith associations, I may consider other aspects of their taphogenesis, e.g. the various biotic and abiotic influences.

As biotic influences I can cite burrowing organisms, such as worms and crabs, which are responsible for a mixing sediment, and consequently of the otoliths they contain. There are also more sedentary burrowing predators (some ophichthyid eels burrow deep in the sediment). Otoliths of fishes eaten by such predators are brought directly deep in the sediment and as many of the burrowing eels are very sedentary, otolith associations resulting from their activities will strongly reflect the diet of the predator rather than the fauna inhabiting the area. A very rich and very localized otolith association that had to be interpreted in this sense was discovered by me in the sands of Lede (Belgian Eocene, NOLF, not published). It is also a well known fact that in the London Clay (Lower Eocene, England), one often finds important otolith concentrations around big pieces of fossil wood. When big trunks of floating wood are saturated by water and sink to a flat uniform bottom like that of the London Clay, they form very suitable microenvironments for sedentary predators which concentrate otoliths in their vicinity.

As abiotic factors influencing taphogenesis, I may cite mechanical transport by water currents and turbidite slumping along the continental slope. Water currents are known to be responsible for much transport of sediment and the embedded otoliths. This action may transport otoliths over various distances, but also is responsible for hydraulic selection of otoliths. At a distance of only 70 m in the same layer of the Sands of Wemmel (Belgian Eocene), I observed two different otolith associations, the first one contained mainly species with flat otoliths with a rounded shape, the second mainly species with thick, elongate otoliths. These two types of bodies react differently during mechanical transport, and I suggest that in this case, mechanical sorting was involved in the origin of these two different associations (NOLF, not published). Very little is known about otoliths in turbidite deposits, but it is likely that otoliths may also be transported by slumping of sediments along the continental slope.

Almost nothing is known about otolith taphonomy of fresh-water fishes, except that nearly all known associations come from lacustrine and not from fluviatile habitats; indeed, in fluviatile conditions, transport prevails over sedimentation.

In marine environments, euryhaline deposits are usually characterized by groups such as atherinids, mugilids, sphyraenids, small clupeids, moronids, cyprinodontids, sciaenids, eleotrids and others, according to the geographic position of the locality considered. In stenohaline deposits, the composition of the association depends upon the geographic provenience and varies greatly according to paleotemperature, substrate, turbulence, etc.; therefore no general characterization can be given.

Concerning depth and the interaction between neritic and oceanic environments, some general statements can often be deduced from the ratio of neritic fishes/myctophids/macrourids for most Cenozoic deposits:

Otolith associations that are almost free of myctophids and macrourids are indicative of neritic environments with little communication with the oceanic area. Such associations are encountered in all the Eocene deposits of southern England, the Paris Basin and the Belgian Basin.

Associations with both neritic species and myctophids, but few or no macrourids, are indicative of neritic environments exposed to oceanic influence. In such areas the proportion of myctophid otoliths becomes higher in the deeper parts of the continental shelf. Many such associations were deposited in areas that hardly exceeded 200 m in depth. The Pliocene marls of Figueras, northeast Spain (see Nolf & Martinell 1981) may be cited as an example of such association in a very shallow neritic environment. The marls of Brihande (Eocene), the Clay of Saint-Etienne d'Orthe (Oligocene) and the marls of Saubrigues (Miocene), all found in Aquitaine, southwest France, are examples of deposits where such associations occur in rather deep neritic environments.

Associations with many macrourid (bathybenthic fishes) otoliths are indicative of continental slope sediments, deposited at depths of at least 250 m. Usually, they are accompanied by great quantities of myctophid otoliths. The Tortonian and the Tabianian stratotype are good examples of strata containing such otolith associations.

Finally, otolith associations are also much influenced by the paleobiogeographic province in which they occur: the whole Neogene of the North Sea Basin is characterized by otolith associations dominated by gadids, while this family is very rare or absent in most of the Neogene strata of Aquitaine, southwestern France. In case of paleobiogeographic evaluation, each association has to be considered as separate, according to its geographic and chronostratigraphic position. Considerations on such evaluations largely exceed the purpose of the present book. It may however be good to note that mixture of elements from different provinces by biotic or mechanical transport is very improbable.

Mesozoic fishes are too different from Recent fishes, and their otolith associations too little known to make evaluations.

Evolution

Like all organisms or parts of organisms, otoliths are subject to evolution. Since otoliths are common fossils which can be collected in large quantities in successive strata and in different geographical areas, evolutionary trends can sometimes be demonstrated or at least hypothesized. However, one should be very careful with such reconstructions; many phylogentic trees with species nicely derived one from another in successive stratigraphic levels are highly speculative. Often the degree of complexity of such trees is a good measure of the fantasy of their authors. I entirely agree with PATTERSON'S (1977) statement that paleontologists do not have unique access to evidence of phylogeny. The theory of evolution gives them a method of interpreting fossils, but the interpretation of the structure and relationships of fossils is necessarily secondary to these aspects of Recent organisms.

Evolution below the species level

Often, one otolith-based species is present throughout a series of deposits. In such cases, it is not uncommon to observe little morphological difference between populations of the species in successive strata. Frequently these differences may be attributed to environmental changes. Differences in temperature, depth, paleogeography, water currents, etc., may cause changes in the distribution pattern of populations within one species, or age groups of the same species, reflected in small morphological differences between the otoliths. But there are cases in which the morphological changes show a well defined trend with the result that the youngest population shows marked differences from the oldest while we see a gradual change in the intermediate populations. This may be interpreted as the evolutionary change of a species and can be illustrated with the species *Gadiculus labiatus* (SCHUBERT 1905) (Fig. 20).

In the successive layers of both the North Sea Basin and the Aquitaine Basin, the Lower Miocene populations of this species have rather elongate otoliths, which gradually changed into more round ones higher in the succession. In Fig. 20 this is demonstrated by a Lower Miocene and a Middle Miocene population from the Belgium Basin. Such gradual changes are very useful for stratigraphical correlations. They provide a method by which strata of unknown age but containing *Gadiculus labiatus*, can be correlated to the standard evolutionary series established in an area with well known stratigraphy.

Noteworthy evolutionary changes have also been observed in otoliths of the ophidioid *«genus Neobythitinorum» regularis* (PRIEM 1911) in which slender, elongate otoliths in the Middle Eocene of the Anglo-Paris-Belgium Basin change to more robust and higher otoliths in the Upper Eocene of the same area.

Because species like the two cited above are very useful in biozonation, people working mainly on biostratigraphy tend to split them into so called chronospecies on the basis of minute morphological differences which, in many cases, do not exceed differences due to intraspecific variability in Recent species, e.g. the splitting of *Trisopterus sculptus* (KOKEN 1891 A), in the work of GAEMERS (1976). With the

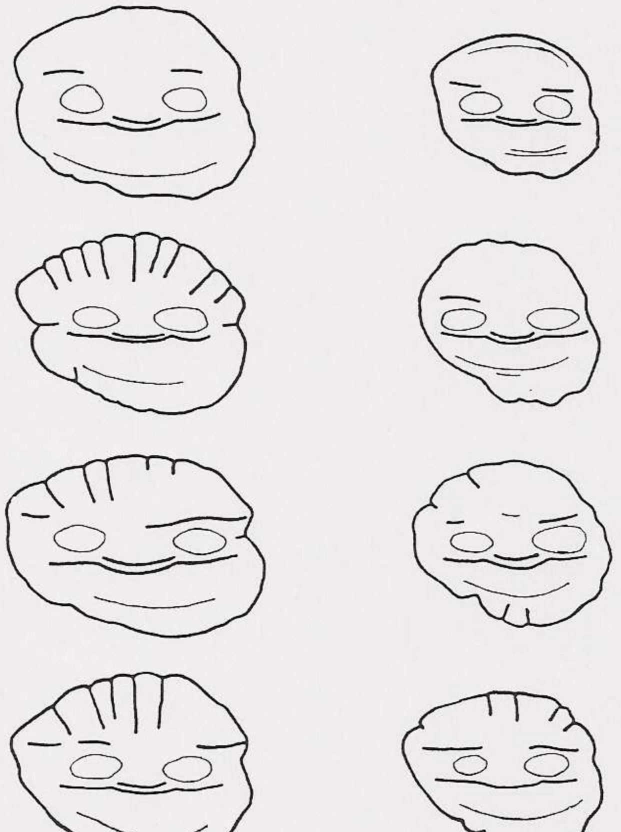


Fig. 20. Morphology and variability of *Gadiculus labiatus* (SCHUBERT 1905) A, Population from the Sands of Edegem, Lower Miocene; Belgium; B, Population from the Sands of Zonderschot, Middle Miocene; Belgium.

foregoing I do not deny that in cases where the gradual changes in a lineage are striking, it is legitimate to establish different species, but it is a wrong principle that species status should be accorded to very minute differences with the justification that such species are useful for stratigraphy. Between contemporary species, fossil or Recent, such minute differences are never accredited specific status and there should not be two different standards to evaluate species. It is my opinion that minute differences in evolutionary lineages should be demonstrated with biometric analysis rather than hypothesized with the aid of doubtful species, the diagnostic features of which consist in their stratigraphic position mainly.

Evolution on the species level

With this section I enter one of the most speculative fields of paleontology. Therefore the already cited statement by Patterson (1977) that paleontologists do not have unique access to evidence of phylogeny should be emphasized again. Indeed, it is a simplistic approach to problems of phylogenesis, to think that thorough investigation of the stratigraphic succession of a taxon allows conclusions as to how all of the species concerned evolved one from the other. For this reason, I feel that beyond the specific level, it is much more appropriate to make statements in terms of interrelationships between species than in terms of ancestor-descendent relations. For the evaluation of interrelationships, the cladistic method seems the most appropriate.

One of the rare examples where ancestor-descendent relationship seems documented with both morphological and paleontological evidence is the series *Gadiculus antwerpiensis* (Gaemers 1971), *G. miocenicus* (Heinrich 1969), *G. benedeni* (Leriche 1926B), *G. verticalis* (Gaemers & Schwarzhans 1973) succeeding each other from the Lower Miocene to the Pliocene in the North Sea Basin. But the relationship between these species can as well be expressed in a cladogram, in which they are arranged in terms of common origin and sister groups (Fig. 21). This way of presenting relationships does not require the always speculative assumption that this or that species certainly descends from another one. If all the species involved form a series of ancestors and descendants, the cladogram can be reconverted into a lineage by placing all species except *G. verticalis* at their respective branch point, but this is not required to demonstrate their relationships.

I also stress that many genealogical trees figuring species derived from each other in a definite time sequence only illustrate some overall similarity of features, combined with the argument of a logical succession in the stratigraphical context. Many stratigraphic oriented paleontologists are tempted by the fallacious idea that the correctness of their phylogeny is proved by the stratigraphical succession of taxa. The fallacy of this reasoning is obvious (see Patterson 1980).

At a first glance, my statement may sound destructive to evolutionary paleontology, which certainly is not my intention. Therefore, this section on evolution will be concluded with an example of a different approach, where the study of both Recent and fossil otoliths demonstrates

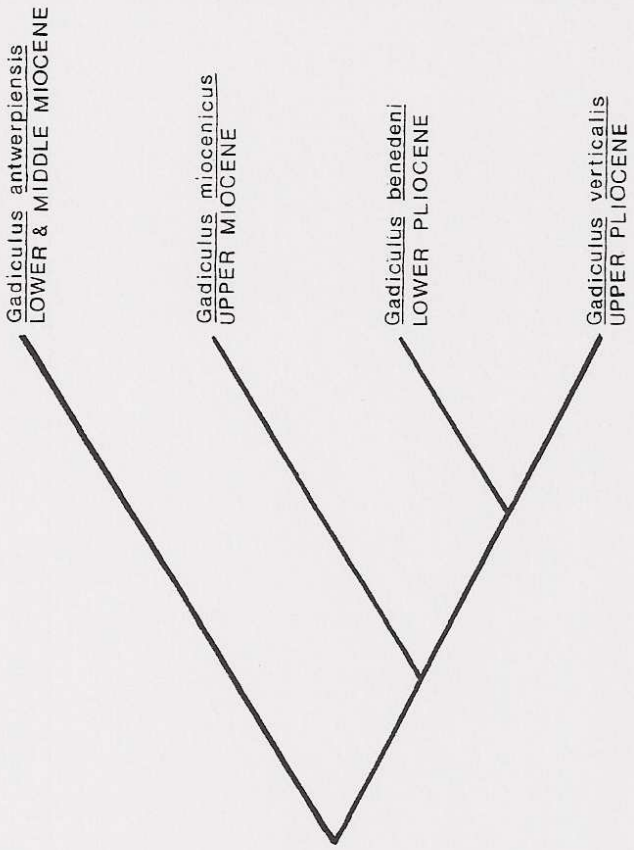


Fig. 21. Cladogram of interrelationship of some *Gadiculus* species.

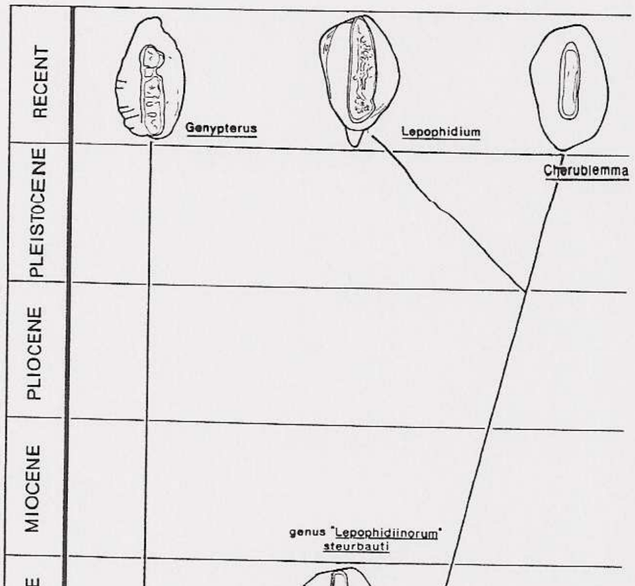


Fig. 22. Interrelationships of some fossil and Recent *Lepophidiini*.

what they teach about interrelationships and evolutionary changes in the tribe Lepophidiini (Fig. 22).

In this example, interrelationships between the three living genera of the tribe Lepophidiini and two of their fossil relatives are examined, disregarding stratigraphy. Comparison with other ophidiids outside the group shows that in *Genypterus* otoliths reflect the most plesiomorph condition among Leopophidiini, because of their well divided sulcus which opens on the anterior rim, while the central, undivided sulcus of *Cherublemma* shows the most derived (apomorph) condition. In *Lepophidium*, division of the sulcus is also nearly lost. The undivided sulcus is a synapomorphy that allows one to conclude that *Lepophidium* and *Cherublemma* are more closely related to each other than to the other genera.

The fossils «*Lepophidiinorum*» *lamberi* and «*Lepophidiinorum*» *steurbauti* have three synapomorphies: a sulcus opening on the anterior rim, having a very short, rounded, but well individualized cauda; the spinous posterior end; and the very marked anteriodorsal angle. The last two features are conserved in *Lepophidium* where they should be considered as symplesiomorphies. Finally *Genypterus* otoliths show only plesiomorph characters, but other somatic features of the fish are indicative of relationships to Leopohidiini. All this indicates: 1) that otoliths of Lepophidiini show an evolutionary tendency to lose the division of the sulcus, and to form an anterodorsal angle and a spinous posterior end. 2) Although fossils are unknown, *Genypterus* existed in the Eocene, since a more evolved fossil *(Lepophidiinorum» lamberi)* was already present in the Eocene. 3) That the Lepophidiini, now restricted to tropical and subtropical American seas, formerly also existed in European coastal waters, because «*Lepophidiinorum steurbauti* from the Lower Oligocene of Aquitaine, southwestern France, is closely related to the American «*Lepophidiinorum*» *lamberi*. 4) That nothing in the suggested scheme of relationships is contradicted by the stratigraphical evidence; ist just shows that *Genypterus* otoliths have not yet been recorded as fossils, but may be expected in the Eocene or even earlier.

Evolution of whole faunas

By this topic, I mean the degree of relationship of the fauna of a definite stratigraphic level, on the world scale, to the Recent fauna or to faunas from different stratigraphic levels.

In the Jurassic, otoliths only show generalized teleostean features. Virtually, none of them shows relationships with Recent fishes at the family level, or even at a higher level. In the Cretaceous, especially the Upper Creataceous, there are already species whose otoliths show relationships at the family level, but at the generic level all of them differ from Recent genera.

In the Paleocene one first observes otoliths of living genera, but the bulk of the fauna belongs to extinct ones. After the beginning of the Eocene there is a marked change, many Recent genera existed during that epoch, besides a few extinct genera which gradually become rarer in the Oligocene and Neogene. In the Lower and Middle Miocene, the first Recent species appear, especially among deep-water fishes. In the deep sea, fish evolution is probably slower because the uniform environmental conditions through time, and many species apparently persist during considerable time. In littoral species, the situation is less clear: only since the Lower Miocene, a slow increase of Recent species progress in successive faunas.

Finally, the geographic position of the fauna considered should also be taken in account in such evaluations. In the Belgian Pliocene, which formed part of the rather isolated North Sea Basin, 23 of the 47 otolith-based species (= about 50 %) belong to Recent forms (Nolf 1978b), while in the Californian Pliocene, a largely oceanic exposed area, only one of more than 150 recorded species of marine teleosts from Pliocene and Pleistocene deposits is now extinct (Fitch & Lavenberg 1971). For the Mediterranean Pliocene, the proportion of Recent species in the total fauna (unpublished data) is higher than in the North Sea Pliocene, but not so overwhelming as in the California Pliocene deposits.

Evolution of biotas

As otoliths are very common fossils that may be collected by the thousand in the successive strata of various countries, they allow well documented reconstructions of the successive fish biotas in various geographic areas. Changes in composition and biogeographic affinities have been studied in various otolith-based teleost faunas of the European Tertiary.

From these observations, some conclusions about the evolution of the biogeographic affinities of these faunas can be drawn.

It is accepted, as a general trend in historical biogeography of marine organisms, that during the Late Cretaceous, the Tethys formed a circumtropical ocean with a rather uniform marine fauna in which two subregions can be distinguished: European-Malayan and Middle American (Banarescu & Boscaiu 1978). This view is supported by the observation that among the Eocene teleosts of both the Anglo-Paris-Belgium Basin and Aquitaine, southwestern France, there are many species belonging to genera that now live only in the Indo-west Pacific area, while typical Atlantic genera are almost entirely lacking in these Eocene faunas. The Indo-west Pacific affinity of the marine Eocene teleost fauna of Europe is supported not only by otolith evidence, but also by the extensive skeleton-based fauna from Monte Bolca, northern Italy.

During the Oligocene, the junction of the Mediterranean with the Indian ocean was progressively closed, and has been ruped since the early Miocene. During the Oligocene, in both the North Sea and Aquitaine Basins species with Indo-west Pacific affinities were gradually replaced by new ones with Atlantic affinities. In the North Sea Basin, the former Indo-Pacific fauna is nearly entirely replaced by one of Atlantic-Mediterranean type at the beginning of the Miocene. In the Aquitaine Basin and the Mediterranean area, the bulk of Miocene teleosts have Atlantic-Mediterranean affinities, but probably because of higher water temperatures than in the North Sea Basin, several species with Indo-Pacific affinities were able to persist. They are recorded relatively regularly in the Lower Miocene, but become extremely rare at the end of the Middle Miocene. The Pliocene marine fauna of Europe is a typical Atlantic one. In the Mediterranean area, it still shows considerable affinities with the Recent fauna, but in the North Sea Basin and Paratethys area, it is marked by endemism.

Evidently, analysis like the present one can only be treated in a very general way within the scope of a book like this, but otolith-reconstructed faunas offer good possibilities for a much more detailed analysis. My aim here is to stress the great importance of otoliths to paleobiogeography. Finally I can conclude this section with the statement that observed changes in faunal composition through time in a given area are the result of interaction between organic evolution and the ever-changing biogeographic pattern. Consideration of both these aspects may provide good results in biostratigraphy.

Stratigraphic Use

The principal conditions required for marine fossils, to be useful for stratigraphic correlation are:

1. They should be common enough to be regularly found.
2. They should not be too strictly confined to particular facies.
3. They should have a relatively wide geographic distribution.
4. The species should have a limited time range.

In order to judge the value of otoliths for biostratigraphy I will in this chapter, discuss to which measure fishes, and more precisely otoliths, fulfill the conditions cited above.

Speaking about the first condition, we can say that in the Tertiary, otoliths are the most common of all osteichthyan fossil remains. They are found in nearly all non-decalcified marine deposits of various facies. In many cases they furthermore occur in tremendous quantitites, allowing extensive faunal reconstructions. The same cannot be said about Mesozoic strata. Although some Jurassic deposits contain considerable quantitites of otoliths (e.g. the «Aldorfer Otolithen-Pflaster», Upper Jurassic of Northern Germany), many Mesozoic rocks are almost devoid of these fossils. For the whole of the Cretacous, less than 20 valid otolith-based species are actually known. This can partly be due to inadequate prospection and to the fact that chalk facies are inappropriate for otolith collecting. Such reasons may partially explain the poor otolith record in Mesozoic strata, but I do not expect that otoliths will ever allow a detailed biostratigraphy of these deposits.

The situation is still worse for Paleozoic strata, since otoliths are known only from the Devonian of northernmost Europe. The below described Devonian palaeoniscoid otoliths, where known, occur in the same stratigraphic levels, thus they could be used for biozonation (Fig. 23). Otoliths of type «B» make up only 2–3 % of all otoliths in residues from Spitsbergen, while they are even more rare or completely missing in residues of other regions. The two varieties of otoliths of type «B» are found at different levels in Spitsbergen. The first variety (Fig. 28 A–D) is typical for most of the higher parts of the Grey Hoek Formation, Eifelian (Mount Tavlefjellett, Wijdefjord, Spitsbergen) while the other variety (Fig. 28 E–I) is found in the Wood Bay Formation, Upper Emsian or Lower Eifelian (Mount Watson, Austfjord, Spitsbergen). It is not possible to see a similar difference in type «A» between the two levels. Therefore, type «A» could be considered characteristic for the lower Eifelian. The occurrence of these incertae sedis palaeoniscoid otoliths yields in no ways information of the quality provided by the otolith-associations of Tertiary strata. I can thus conclude that only Tertiary deposits seem to be appropriate for extensive biostratigraphic zonation and correlation with otoliths.

As to our second and third conditions, the measure in

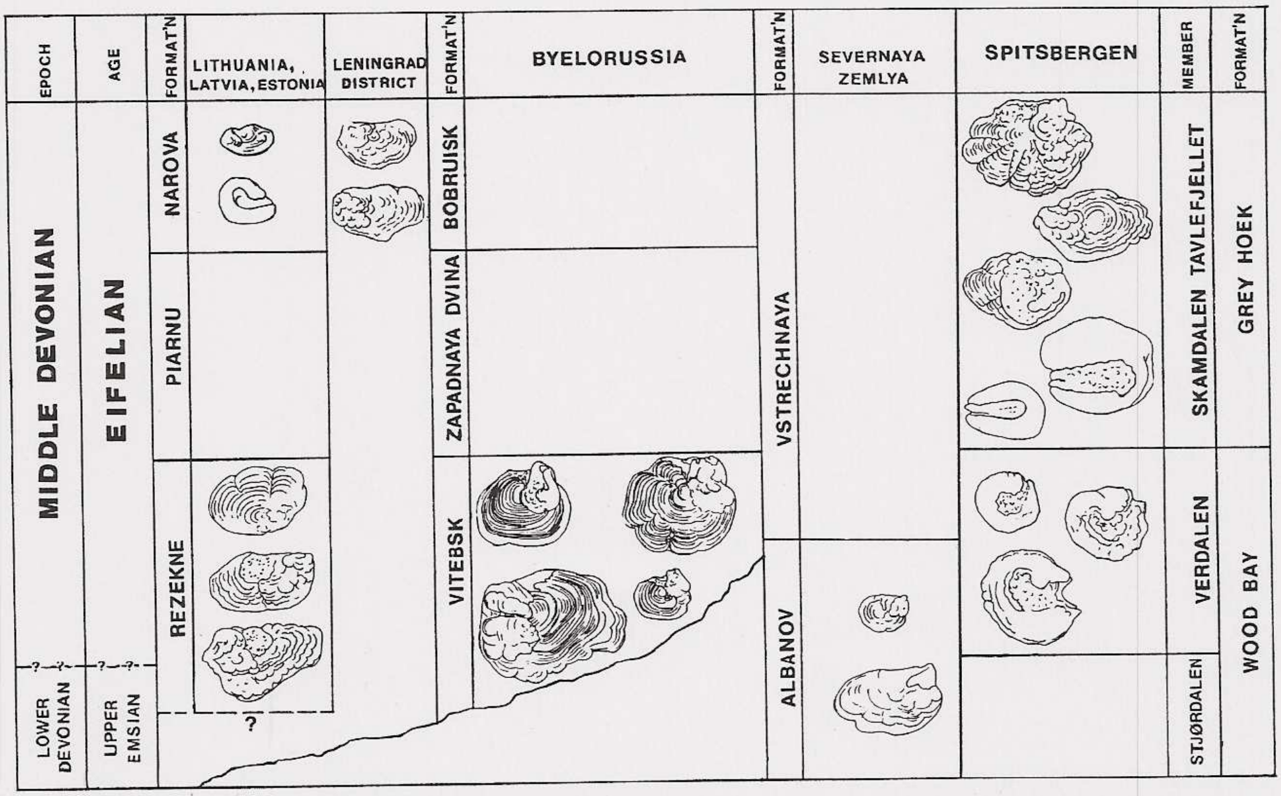


Fig. 23. Stratigraphic distribution of incertae sedis palaeoniscoid otoliths in the Lower and Middle Devonian in Spitsbergen and in different parts of U.S.S.R. (contribution V. Talimaa).

which otoliths are facies-bound and their geographic repartition, we need to consider the ecology of the various fish groups. Some fish families such as the gobiesocids, the trypterygiids, the smaller blenniids, etc., are restricted to very limited neritic environments, but they seem not to play a very important role in fossil otolith associations. Hence they can be neglected.

As said in the chapter on otolith associations and the paleoenvironment, nearly all otolith associations consist either of fishes inhabiting flat relief sandy or muddy environments, or mesopelagic forms, or both. In shallow facies, the neritic portion of the association will dominate. The more the facies becomes oceanic, the more the mesopelagic and bathybenthic portion will characterize the association.

Many neritic fish species of flat relief environments have a geographic range of one thousand to a few thousands km. Therefore, the stratigraphic use of their otoliths will be restricted to geographic areas of the same dimensions. A good example is provided by the gadids, which are very abundant and useful as stratigraphic fossils in the Oligocene and Neogene of the North Sea Basin, while in the Aquitaine Basin, southwestern France, they are so scarce that they can hardly be taken in consideration for the local biostratigraphy.

For mesopelagic fishes, the situation is quite different. Among them, myctophids and gonostomatids are particuarly abundant in many otolith associations. Their geographic distributions coincide with that of oceanic water masses with typical chemical and physical properties. As such water masses form huge compartments of the oceanic basins, the distribution range of mesopelagic fishes is often of the order of 10,000 km and more. Therefore, we may expect that they will be appropriate for biostratigraphic zonations on this scale.

Actually most of the mesopelagic otolith-biostratigraphy has still to be worked out, and much taxonomic work is needed to provide a solid basis for it. Nerverthless, it is my opinion that mesopelagic otoliths, especially those of myctophids, will provide very good biozonations, covering areas of the dimensions of important parts of oceanic basins.

Although there are several species with a worldwide distribution, the actual composition of mesopelagic fish biocoenoses show considerable differences according to the oceanic basins they are found in. Therefore, I do not expect that mesopelagic otolith zonations of worldwide application (such as those based on planctonic foraminifers and on calcareous nannoplancton) are possible. Nevertheless, this does not exclude the possibility of correlation between the zonations of different oceanic basins.

Another aspect of the otoliths of mesopelagic fishes has been touched on in the taphonomic analysis of otolith associations, where I have said that otoliths of mesopelagic fishes are often encountered in neritic environments well exposed to the ocean. For this reason, such otoliths can be very useful in the correlation of neritic and oceanic facies.

To evaluate the average time interval that can be covered by otolith-based zones, we need to discuss our fourth condition: the time-range of fish species.

According to my experience, nearly all otolith-represented fossil fish species have a vertical range varying between 2 and 20 million years. Neritic species, especially the smaller ones, have ranges of lower values, while oceanic fishes usually have a more considerable time-range.

STRATIGRAPHY			ASSEMBLAGE-ZONES					
			Marine				Continental	
MIOCENE	Middle Miocene = Sallomacian		8	b	*Diplodus karrerae- Boops neogenicus zone*	*Gadiculus labiatus* round form		
				a		*Gadiculus labiatus* elongate form		
	Lower Miocene	Marls of Saubrigues	7		*"genus aff. Valenciennellus" kotthausi - Acropoma nolfi zone*			
		Burdigalian	6		*Spicara sp. - Pomadasys steurbauti zone*			
		Aquitanian	5		*"genus Chandidarum" rhenanus - Serranus sp. zone*		II	*"genus Cyprinodontidarum" angulosus zone*
							I	*Prolebias praecursor zone*
OLIGO-MIOCENE TRANSITION			4		*Polymetme supraoligocenica - Polyipnus sp. zone*			
OLIGOCENE	Upper Oligocene		3		*"genus Lepophidiinorum" steurbauti - Sillago sp. zone*			
	Middle Oligocene		2		*Apogon sp. 2 zone*			
	Lower Oligocene		1		*"genus Neobythitinorum" boulangeri - Cepola sp. zone.*			

Fig. 24. Otolith-based biozonation of the Oligo-Miocene in the Aquitaine Basin, France (from STEURBAUT 1984).

Using all possible combinations applied in biostratigraphy such as lineage-zones, association-zones, acme-zones, concurrent range zones, etc., the minimal time for otolith-zones probably lies in the dimension of one or two million years. This means a precision of one to maximally three zones in our stages of the classic type such as the Ypresian, the Lutetian or the Tortonian.

In the foregoing paragraphs, emphasis has been placed on theoretical aspects of the stratigraphic use of otoliths. Few examples were cited, because very few areas where both correctly identified otolith-faunas and suitable stratigraphical successions of otolith-bearing strata are known. In fact, the only areas that can be cited in this respect are the Belgian Basin where we find a relative complete succession of otolith faunas from the Middle Paleocene to the Pleistocene (data in NOLF 1976, 1977, 1978 and unpublished thesis, 1974) and the Aquitaine Basin which offers a good succession from the Lower Eocene to the uppermost Middle Miocene (STEURBAUT 1984, and NOLF, unpublished data for the Eocene).

In the Belgian Basin, a succession of about 18 different otolith associations has been recognized but these reflect essentially differences of facies, rather than strong faunal breaks between the successive layers. Indeed many of the otolith associations are essentially concordant with lithological units, and this bears out their facies-related nature. Major changes not influenced by facies are mostly due to the changing paleobiogeographic affinities of the fauna inhabiting the area (see chapter on the evolution of biota) and probably can be used throughout the whole North Sea Basin.

In the Aquitaine Basin, about 11 successive otolith associations have been recognized (Fig. 24). Here also and even more than in the Belgian Basin, some of the faunal breaks reflect different facies. In contrast to the Belgian Basin which contains nearly exclusively neritic faunas, several of the Aquitaine-Basin associations are rich in mesopelagic material, which may provide in the future some of the reference-horizons for the whole southern European Tertiary.

Other areas with relative extensive otolith-associations are the Paratethys area in Central Europe (Lower Oligocene – Pliocene), and New Zealand (Lower Eocene – Recent). But in those areas, prospection has been less intense and faunal knowledge is restricted to some rich associations that are essentially concordant with certain lithostratigraphic units, separated by important faunal hiatuses or deposits with very poor faunas.

Except for southern England, where a Middle Paleocene-Upper Eocene succession is known very similar to the Belgian one, all published otolith associations from other points of the world should rather be considered as reference points or horizons, up to now isolated from their stratigraphical context.

As a conclusion of this chapter on the stratigraphic use of otoliths, some major faunistic events and changes in the marine Tertiary of Europe are summarized in Fig. 25.

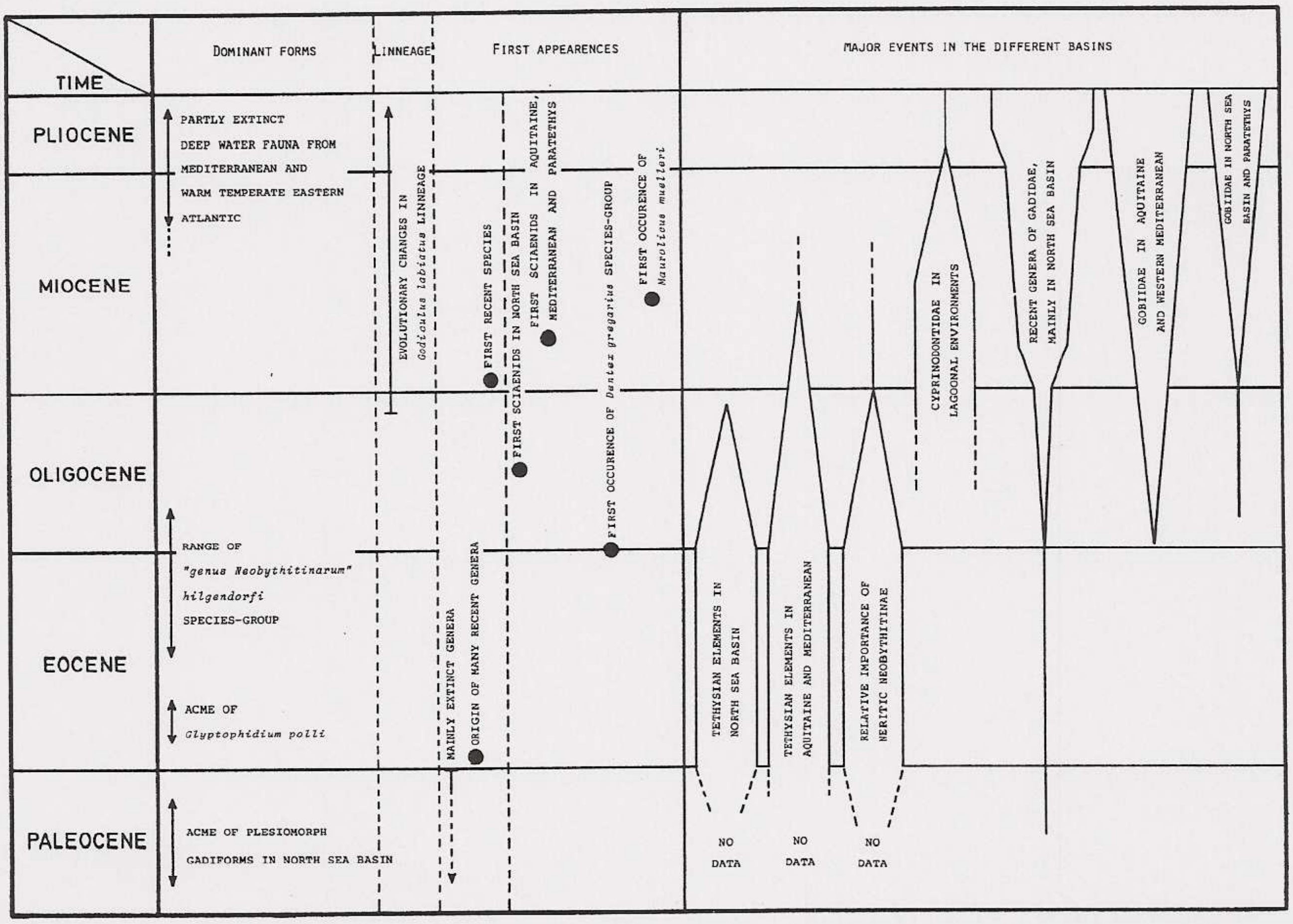


Fig. 25. Some major faunistic characters of the marine Tertiary of Europe, as indicated by otoliths.

Taxonomy of Fossil Otoliths

Generic determination

Since the early days of otolith paleontology, generic identification of otolith-based species has certainly been the most troublesome aspect of taxonomic work. In principle, the primary separation of the different species in a given sample on a purely typological basis is a job which any well-trained paleontologist or student of systematic zoology should be able to do. The real problem only begins when going on to generic identification.

Appreciation of the systematic position of a fossil otolith is only possible by comparison with properly identified Recent ones, or by comparison with otoliths in situ, observed in identifiable fossil fish skeletons.

As discoveries of fossil skeletons with otoliths in situ are extremely rare, in nearly all cases the relations of a fossil otolith are evaluated by comparison with Recent forms. It is evident that the precision of the identification largely depends upon the extent of the Recent reference collection. For this reason Koken (1884A), in the early history of otolith paleontology, having disposed only of a restricted collection of Recent otoliths, proposed a kind of open generic nomenclature. In his system, all species were called «*Otolithus*», followed by a Recent genus name in brackets, or, if such identification was not possible, by the name of the family or higher taxonomic category in the plural genitive, e.g. *Otolithus (Gadidarum) planus*. The only inconveniences of this system were that a normal fish genus *Otolithus* Cuvier 1817 was already introduced, which could cause confusion, and that the denomination *Otolithus* is superfluous for those species that can be attributed to Recent genera.

In more recent literature this is remedied by citing species that can be attributed to Recent genera by their genus name, omitting «*Otolithus*», while those species which do not fit in known Recent genera are cited by plural genitive names, preceded by «*genus*» instead of «*otolithus*», as suggested by Richter (1948, p. 147: «Art ohne Gattung»). Thus a hypothetical species *circularis* might be cited under the following names, according to the precision of the identification:

Albula circularis
«*genus* aff. *Albula*» *circularis*
«*genus Albulidarum*» *circularis*
«*genus Albuloideorum*» *circularis*
«*genus Elopiformorum*» *circularis*

Such incertae sedis otoliths could also be designated by the names of fossil genera, but the situation is more complex. It is evident, in the context of general paleontology, that fossil teleost faunas from various strata, from Jurassic to Quaternary, may contain both extinct and living genera. But the proportion of the two categories is not directly evident, especially in Tertiary strata, which contains the most abundant otolith faunas.

Thus, an otolith of uncertain systematic position may belong either to an extinct genus, or to a Recent genus of which the otoliths are unknown. Use of a fossil genus name therefore implies deciding arbitrarily in favor of the first hypothesis (and refuting the second). Even in those rare cases where knowledge of the Recent otoliths of a group is very extensive (except ophidiiforms, gadids, macrourids, perhaps myctophids, and a few monotypic groups, there are no such families). I think it is a wise rule not to use exclusively otolith-based fossil genera. Although collective generic nomenclature does not conform to usual taxonomic practice, it exactly and objectively reflects the state of knowledge about the position of the given species, while using fossil genera, suggests a precision that does not exist, and merely hints that the species are incertae sedis.

Apart from this theoretical objection against the use of otolith-based genera, there is another more practical one. Considering the restricted Recent collections of many otolith paleontologists, we may expect chaotic results from the «fossil genus routine»: no need for careful examination of the taxonomic position of your fossil or for this tiresome comparison with Recent species; put it in a fossil genus, and if it does not obviously fit in a Recent family, make a fossil one, and so on till you arrive at a splendid pseudotaxonomy! In my opinion, otolith literature is already full enough with speculations for us to avoid doing things in this way.

Although most otolith workers made use of collective generic names for their incertae sedis species, several otolith-based genera have been introduced, mostly by Stinton, Frizzell & his collaborators, and Gaemers. Before an evaluation of these genera it is important to emphasize the rather divergent concepts of fossil genera held by these authors.

Going through all Stinton's work, one has the impression that for him, the introduction of fossil genera is based on the axiom that since the beginning of the Eocene, all otoliths can be referred to Recent genera. If a given post-Paleocene species does not fit very well within any Recent genus, he refers it to the «least different» Recent genus he knows, while in all pre-Eocene faunas, he erects fossil genera for analogous cases. Although the axiom that all post-Paleocene species can be attributed to Recent genera is unacceptable, it should be said that in my opinion nearly all of Stinton's genera represent true extinct genera.

Frizzell's genera (mostly published in 1965) are more hazardous. He stated that collective generic names are taxonomically artifical and not compatible with zoological nomenclature (which is not true, according to Article 42 C of the International Code of Zoological Nomenclature and R. Richter 1948, p. 147). He introduced fossil genera for nearly every species that was not clearly integrated in one of the Recent genera known to him. Many of the genera introduced by Frizzell & Dante (1965) have type-species of which the authors certainly never examined the type material (*Genartina*, *Allomorone*, *Ekokenia*, *Bauzaia*, *Eosolea*). Some of these genera may be regarded as good fossil genera, if restricted to their type-species, as may a few others. But as defined by these authors, they are catch-all groups for very heterogeneous assemblages of genera (see analysis of the taxonomic postion of all the species referred to *Bauzaia* by FRIZZELL & DANTE 1965; NOLF 1980).

GAEMERS' concept of otolith-based genera again represents a different view as he states himself: «The concept of genus as used here is different from the convential idea. Therefore, I call this sort of genus *Neogenus*...» (GAEMERS 1976a, p. 11). In the opinion of GAEMERS, there is a very clear resemblance between the ontogenetic change of otoliths during the life of a given individual and the change of otoliths through geological time in the lineage of species to which that individual belongs. At the beginning of a lineage, otoliths should present a morphology with juvenile features, evolving to senile-looking otoliths near the end of the lineage. In this light, each genus introduced by GAEMERS should correspond to a lineage of species. Unfortunately, some of GAEMERS' (1976a, 1976b, 1978) lineages are highly tentative, and so are the corresponding genera. Apart from this, his morphological criteria are very small differences, and result in unnecessary splitting of many well established genera (e.g. the Recent subspecies *Gadiculus argenteus argenteus* (GUICHENOT 1850) and *Gadiculus argenteus thori* SCHMIDT 1905 are put in two different genera by GAEMERS (1976), and *Trisopterus esmarkii* (NILSSON 1855) is split off from *Trisopterus* on no other morphological argument than the otoliths).

All these examples stress the rather doubtful and fragile nature of otolith-based genera erected in the past, and I think paleontologists should not continue in this way. Although it is my opinion that otolith-based genera should not be used, there is no rule of zoological nomenclature that invalidates such names and every author who wishes to use them rather than collective generic names is free to do so. For this reason an alphabetical list of all otolith-based general is given below, with my opinion of each. The deadline for inclusion in the list has been put on 31st of December 1980.

Actuariolum KARRER 1971. Type species: *Actuariolum bicaudatum* (FROST 1924). A true fossil genus.

Allomorone DANTE & FRIZZELL in FRIZZELL & DANTE (1965). Type species: *Otolithus (Carangidarum) americanus* KOKEN 1888, a nominal valid fossil genus of the family Pomadasyidae. The otoliths of the type species differ from all living pomadasyids known by otoliths, but otoliths are not yet known for several Recent genera of the family. If used, the genus has to be restricted to the type species, as probably none of the species included by DANTE & FRIZZELL is congeneric with it.

Archaealbula FRIZZELL 1965. Type species: *Archaealbula alabamae* FRIZZELL 1965, a true fossil genus.

Archaegadiculus SCHWARZHANS 1979 (subgenus). Type species: *Otolithus (Hymenocephalus) labiatus* SCHUBERT 1905, a junior synonym of *Gadiculus* GUICHENOT 1850. The name introduced by SCHWARZHANS can be retained as a fossil subgenus of *Gadiculus*.

Archaeotolithus STOLLEY 1910A. Type species: *Archaeotolithus trigonalis* STOLLEY 1910, a true fossil genus, but incertae sedis, difficult to evaluate on the basis of the iconography.

Archegadus STINTON 1965. Type species: *Archegadus comptus* STINTON 1965, probably a synonym of *Archemacrouroides* STINTON 1965 (see NOLF 1978a, p. 225).

Archemacrouroides STINTON 1965. Type species: *Archemacrouroides ornatus* STINTON 1965, a true fossil genus.

Archengraulis STINTON in STINTON & TORRENS (1968). Type species: *Archengraulis productus* STINTON in STINTON & TORRENS 1968, cannot be evaluated on the basis of the iconography.

Austrocentris SCHWARZHANS 1980. Type species: *Cleidopus cavernosus* STINTON 1958, a synonym of *Monocentris* SCHNEIDER 1801.

Bauzaia DANTE & FRIZZELL in FRIZZELL & DANTE (1965). Type species: *Otolithus (Gadidarum) mucronatus* KOKEN, 1888, a true fossil genus if restricted to the type species and *Bauzaia lamberi* DANTE & FRIZZELL 1965.

Brazosiella DANTE & FRIZZELL in FRIZZELL & DANTE (1965). Type species: *Brazosiella kokeni* DANTE & FRIZZELL in FRIZZELL & DANTE (1965), a junior synonym of *Lactarius* CUVIER & VALENCIENNES 1833.

Citharopsettodus SCHWARZHANS 1979. Type species: *Citharopsettodes angustus* SCHWARZHANS 1979, a nominal valid fossil genus, but this means little, as the otoliths of many Recent flatfishes are still unknown.

Claybornichthys FRIZZELL & DANTE 1965. Type species: *Claybornichthys troelli* DANTE & FRIZZELL in FRIZZELL & DANTE (1965). The knowledge of Recent siluroid utricular otoliths is so poor that it is hardly possible to evaluate such otolith-based genera and species.

Cleidogonia STINTON in STINTON & TORRENS (1968). Type species: *Cleidogonia antiqua* STINTON in STINTON & TORRENS (1968), cannot be evaluated on the basis of the iconography.

Colliolus GAMERS & SCHWARZHANS 1973. Type species: *Gadus friedbergi* CHAINE & DUVERGIER 1928 = *Trisopterus sculptus* (KOKEN 1891), a junior synonym of *Trisopterus* RAFINESQUE 1814.

Egregioberyx SCHWARZHANS 1980. Type species: *Monocentris sphaeroides* STINTON 1958, a synonym of *Monocentris* SCHNEIDER 1801.

Ekokenia DANTE & FRIZZELL in FRIZZELL & DANTE (1965). Type: *Otolithus (Sciaenidarum) eporectus* KOKEN 1888, probably a true fossil genus.

Ensigadus GAEMERS 1978. Type species: *Ensigadus ensiformis* (STEURBAUT & HERMAN 1978), a true fossil genus.

Eoalbula FRIZZELL 1965. Type species: *Eoalbula meridiana* FRIZZELL 1965, a true fossil genus.

Eosolea FRIZZELL & DANTE 1965. Type species: *Otolithus (Solea) bartonensis* FROST, 1934 = *«genus Heterenchelyidarum» circularis* SHEPHERS 1916, probably a true fossil genus.

Gadichthys GAEMERS & SCHWARZHANS 1973. Type species: *Gadus benedeni;* LERICHE 1926, a junior synonym of *Gadiculus* GUICHENOT 1850.

Gadophycis STINTON 1965. Type species: *Otolithus (Merluccius) ovalis* FROST 1931, a true fossil genus.

Generatina FRIZZELL & DANTE 1965. Type species: *Otolithus* (incertae sedis) *hampshirensis* SCHUBERT 1916, closely related to *Osmerus* LACÉPÈDE 1803, but perhaps a true fossil genus.

Jefitchia DANTE & FRIZZELL in FRIZZEL & DANTE (1965). Type species: *Jefitchia copelandi* DANTE & FRIZZELL in

Frizzell & Dante (1965), cannot be evaluated on the basis of the iconography (holotype of *J. copelandi* not figured; two figured paratypes are different species, if not different genera).

Karrerichthys Schwarzhans 1980. Type species: *Karrerichthys admirabilis* Schwarzhans 1980, a true fossil genus, but very closely related to *Melanonus* Günther 1878.

Krebsiella Schwarzhans 1980. Type species: *Krebsiella diversa* Schwarzhans 1980, cannot be evaluated as a true fossil genus due to our incomplete knowledge of Recent hemerocoetine otoliths.

Latirhynchus Stinton 1965. Type species: *Latrihynchus grumosus* Stinton 1965, a synonym of *Archemacrouroides* Stinton 1965 (see Nolf 1978a, p. 225).

Lycoclupea Gowda 1967. Type species: *Lycoclupea menakiae* Gowda 1967, cannot be evaluated on the basis of the iconography.

Macrurulus Schwarzhans 1980. Type species: *Macrurulus immanis* Schwarzhans 1980, a true fossil genus.

Maorigadus Schwarzhans 1980. Type species: *Maorigadus anarchicus* Schwarzhans 1980, a true fossil genus.

Maxwelliella Schwarzhans 1980. Type species: *Maxwelliella urbana* Schwarzhans 1980. Nominally valid, but more intensive study of various Recent congrid otoliths is needed to make sure that this genus represents a true fossil one.

Merlangiogadus Gaemers 1973. Type species: *Otolithus (Merlangus) cognatus* Koken 1891, a junior synonym of *Micromesistius* Gill 1864 (see Nolf 1977, p. 25–26).

Metalbula Frizzell 1965. Type species: *Metalbula bashiana* Frizzell 1965, a junior synonym of *Albula* Scopoli 1777.

Microgadiculus Schwarzhans 1979, (subgenus). Type species: *Macrurus rumanus* Weiler 1943. This subgenus is based on a type species of doubtful status (uninterpretable juvenile specimens of a gadiform, sensu latu).

Neocolliolus Gaemers 1976. Type species: *Gadus esmarkii* Nilsson 1855, a junior synonym of *Trisopterus* Rafinesque 1814.

Nolfophidion Schwarzhans 1980. Type species: *Gadus refertus* Stinton 1958, a true fossil genus.

Ophidypterus Stinton 1965. Type species: *Ophidypterus retusus* Stinton 1965, a true fossil genus.

Palaeomorrhua Gaemers & Schwarzhans 1973. Type species: *Otolithus (Morrhua) sollingenensis* Koken 1891 A, a true fossil genus.

Palaeoraniceps Gaemers 1976. Type species: *Otolithus (Gadi) tuberculosus* Koken 1884 A, a junior synonym of *Raniceps* (Cuvier) Oken 1817.

Palaeumbra Weiler 1973. Type species: *Palaeumbra moguntina* Weiler 1973, a true fossil genus.

Palealbula Frizzell 1965. Type species: *Otolithus (Clupeidarum) neocomiensis* Priem 1908 C, a true fossil genus according to Priem's figure, but neither Frizzell or the present author have seen the specimen.

Paleosciaena Ohe 1976. Type species: *Paleosciaena mizunamiensis* Ohe 1976, a doubtful genus, based on eroded type material.

Parabatmya Frizzell, Lamber & Dante in Frizzell & Dante (1965). Type species: «*Conger*» *fornicatus* Frizzell & Lamber 1962, a nominal valid fossil genus, but our knowledge of Recent congrid otoliths is too restricted to decide if it is really extinct.

Paralactarius Schwarzhans 1980. Type species: *Paralactarius ornatus* Schwarzhans 1980, a potential catch-all genus for plesiomorph otoliths of various families of the suborder Percoidei.

Platysepta Stinton 1965. Type species: *Platysepta prima* Stinton 1965, an invalid genus, as the type species is to be rejected.

Polyperca Stinton 1965. Type species: *Polyperca serranoides* Stinton 1965, a nominal valid fossil genus, but our knowledge of Recent serranid otoliths is too restricted to decide if it is really extinct.

Prealbula Frizzell 1965. Type species: *Prealbula weileri* Frizzell 1965, a true fossil genus.

Praehoplichthys Schwarzhans 1980. Type species: *Praehoplichthys pulcher* Schwarzhans 1980, probably a true fossil genus.

Preophidium Frizzell & Dante 1965. Type species: *Preophidium petropolis* Dante & Frizzell in Frizzell & Dante (1965), possibly a true fossil genus, but very closely related to *Sirembo* Bleeker 1858. As otoliths of only two of the four living *Sirembo* species are known, further investigation may reveal complete synonymy with this Recent genus. As defined by Frizzell & Dante (1965), *Preophidium* is a catch-all genus and has to be restricted to the type species, *Otolithus (Gadidarum) elevatus* Koken 1888 and *Sirembo convexus* Stinton 1977.

Primaevomesus Stinton 1965. Type species: *Primaevomesus tricrenulatus* Stinton 1965, probably a true fossil genus.

Proraniceps Stinton 1965. Type species: *Proraniceps leiopleurus* Stinton 1965, a synonym of *Archemacrouroides* Stinton 1976 (see Nolf 1978a, p. 225).

Protalbula Frizzell 1965. Type species: *Protalbula sohli* Frizzell 1965, a true fossil genus.

Protocolliolus Gaemers 1976. Type species: *Otolithus (Gadus) eocenicus* Frost 1931, a true fossil genus.

Pseudocolliolus Gaemers 1978. Type species: *Pseudocolliolus cuykensis* Gaemers 1978, probably a junior synonym of *Gadiculus* Guichenot 1850.

Pteralbula Stinton 1973. Type species: *Ot. (Atherina) cantiana* Shepherd 1916, a true fossil genus.

Signata Dante & Frizzell in Frizzel & Dante (1965). Type species: *Signata stenzeli* Dante & Frizzell in Frizzell & Dante (1965), a true fossil genus.

Sphaeronchus Stinton in Stinton & Torrens (1968). Type species: *Sphaeronchus dorsetensis* Stinton in Stinton & Torrens (1968), a true fossil genus.

Stintonia Frizzell & Lamber 1961. Type species: *Otolithus (Sciaenidarum) priemi* Schubert 1916 A, a true fossil genus.

Vorhisia Frizzell 1965. Type species: *Vorhisia vulpes* Frizzell 1965, probably a true fossil genus, but this cannot be stated confidently as otoliths of most Recent cypriniform genera are unknown.

Waitakia Schwarzhans 1980. Type species: *Waitakia robusta* Schwarzhans 1980, cannot be evaluated as a true fossil genus due to our incomplete knowledge of Recent hemerocoetine otoliths.

Weileria Frizzell & Lamber 1961. Type species: *Weileria louisiana* Frizzell & Lamber 1961, a doubtful genus, based on a doubtful type species.

Otoliths in situ

Although osteological material with otoliths in situ or with associated otoliths is very rarely found, it has been possible for a few species to establish the relation between both kinds of fossils. Several such occurrences are known in localities of the Messinian (Upper Miocene) in Italy, but unfortunately the faunas of these sites are in need of extensive revision, both for the osteological and otolith fossils. In several other cases, otoliths have been observed in identifiable skeletons, but they are too poorly preserved to be of any utility for taxonomical investigations. Skeletons with otoliths in situ are very important in the study of Mesozoic fishes, where direct comparison with Recent otoliths usually only provides a very general idea of their affinities.

In the following list, we enumerate, as far as known to us, the species for which osteological material with associated otoliths has been recorded. All species for which the otoliths are well enough preserved or suitable oriented to show taxonomically useful features, are marked with*. For the others, the otoliths are not in such condition, or the osteological material needs revision e.g. the various myctophids cited by D'Erasmo (1929).

Amblypterus vratislavensis Fritsch 1895 – Fritsch (1895A).
*_Ampheristus toliapicus_ König 1825 – Casier (1966).
*_Anthracoperca siebergi_ Voigt 1934 – Voigt (1934).
Amia kehreri Andreae 1893B – Jermanzka (1977).
*_Apogon macrolepis_ Storms 1898 – Taverne & Nolf (1979).
Australosomus kochi Stensiö 1932B – Stensiö (1932B).
*_Bregmaceros albyi_ (Sauvage 1880)– Bachmayer & Weinfurter (1965).
Clupea humilis von Meyer 1851 – Weiler (1955).
*_Coryphaenoides karaginensis_ Gretshina 1973.
*_Dapalis formosus_ (von Meyer 1851) – Weiler (1955).
Dapalis ? rotundus (Weiler 1963) – Best (1975).
*_Dapalis sieblosensis_ (Winkler 1880B) – Martini (1965).
*_Dentex laekeniensis_ van Beneden – Taverne & Nolf (1979).
Elonichthys robisoni (Hibbert 1835) – Traquair (1901 [1914C]).
Felichthys stauroforus Lynn & Melland (1939).
Gobius francofurtanus Koken 1891 – Best (1975).
*_Gobius multipinnatus_ (von Meyer 1851) – Weiler (1955).
Gobius papyraceus (Agassiz 1839) – Gaudant (1978).
*_Lepisosteus fimbriatus_ Wood 1846 – Stinton (1975).
*_Leptolepis coryphaenoides_ (Bronn 1830A) – Patterson (personal communication).
*_Lycoptera middendorfi_ (Müller 1861) – Reis (1909A).
Mimia toombsi Gardiner & Bartram 1977 – Gardiner (1984).
*_Morone aequalis_ (Koken 1891) – Best (1975).
*_Notogoneus longiceps_ (von Meyer 1851) – Weiler (1963).
Novumbra oregonensis Cavender 1969A – Cavender (1969A).
Nyctophus columnae (Sauvage 1873D) – D'Erasmo (1929).
Nyctophus dorsalis (Sauvage 1837D) – D'Erasmo (1929).
Nyctophus (Diaphus) larteti (Sauvage 1873D) – D'Erasmo (1929).
Nyctophus (Lampanyctus) edwardsi (Sauvage 1873D) – D'Erasmo (1929).
Nyctophus (Lampanyctus) licatae (Sauvage 1873D) – D'Erasmo (1929).
Nyctophus (Lampanyctus) microsoma (Sauvage 1873D) – D'Erasmo (1929).
*_Palaeoesox fritzschei_ Voigt 1934 – Voigt (1934).
*_Palaeogadus atropatanus_ Bogatshov 1933 – Fedotov (1976).
*_Palaeogadus germanus_ Fedotov 1970 – Fedotov (1976).
*_Palaeogadus intergerinus_ Danilchenko 1947 – Fedotov (1976).
*_Palaeogadus latebrosus_ Danilchenko 1960 – Fedotov (1976).
Palaeoniscum freieslebeni Blainville 1818A – Hennig (1915C), Hunger (1939).
*_Paratrisopterus avus_ Fedotov 1971 – Fedotov (1976).
*_Prolebias praecursor_ Weiler 1929 – Weiler (1963).
Rhabdoderma huxleyi Traquair 1881 – Nolf (unpublished).
Rhadinichthys carinatus (Agassiz 1835) – Traquair (1911 [1914C]).
*_Solea kirchbergana_ von Meyer 1851 – Weiler (1955).
*_Thaumaturus spannuthi_ Voigt 1934 – Voigt (1934).
Trigla arambourgi Weiler 1928 – Schwarzhans & Weiler (1971).
Trisopterus macropterygius (Kramberger 1883A) – Jerzmańska (1962).

Systematics

Here otoliths of Recent species and all otolith-based fossil species, except those which are doubtful, rejected or could not be evaluated on the basis of the iconography (see p. 112–133) are listed and examples are figured. All fossil species are cited with the generic name that now appears correct. If this is not the original one, the generic name of the original follows the author's name, without the prefix *Otolithus* or genus. Fossil species based on skeletons with otoliths in situ, but which do not have exclusively otolith-based primary types, are also included. They are followed by the notation «skeleton». For ervery species, the stratigraphic and geographic source of the type material is given in a rather generalised terminology, e.g. Middle Miocene, Aquitaine, France instead of perhaps more precise but not widely understood terms like Sallomacian, Sallespisse.

In principle, one species has been illustrated for each Recent family, but in a few families which are very well represented in the paleontological record, more species are figured. The survey may be considered as fairly complete, and except in the ostariophysans, the few missing families are all rare, often monotypic groups. In the Ostariophysans, there is no pretence of completion. Except for some ariids, ostariophysan otoliths have hardly been recorded in paleontological investigations. In consequence, otolith paleontologist never have spent much time collecting Recent otoliths of these fishes.

In each family, an iconographical example of a Recent species is given first, followed by a list of the valid fossil species, and a list of the fossil record of otoliths of Recent species. All Recent species are cited by the modern name now considered as correct and are not followed by a possible different generic name derived from the original description, since we are here not concerned with synonymies of extant species. For each of these species only the earliest stratigraphical record is given, followed by the bibliographic reference to this record.

The classification followed is principally that of GREENWOOD, ROSEN, WEITZMAN & MEYERS (1966), taking in account amendments by ROSEN & PATTERSON (1969: superorder Scopelomorpha; position of the Atherinomorpha and Ateleopodoidei), GREENWOOD & ROSEN (1970: ostariophysian and gonorhynchiform fishes), NELSON (1970: Clupeiformes), GREENWOOD & ROSEN (1971: Alepocephaloidei), ROSEN (1973: higher classification of Euteleostei), WEITZMAN (1974: Stomiatiformes), GREENWOOD (1977: Elopomorpha), PATTERSON & ROSEN (1977: higher classification of Teleostei), COHEN & NIELSEN (1978: Ophidiiformes), FINK & FINK (1981: Ostariophysi).

It is editorial policy in the Handbook of Paleoichthyology that authors be cited for all higher taxa. In the teleosts, where virtually all the very numerous suprageneric taxa are extant and neontological classification has a long and intricate history, citing authors is a particularly difficult task for the paleontologist. The names and authors used in this work have been compiled in collaboration with C. PATTERSON (British Museum (Natural History), London), who is preparing volume 9 of the Handbook. Our aim has been only to find acceptable authors for names currently in use among ichthyologists. With family-group names, this is theoretically practicable, since the Code provides guidance. Above superfamily level, no rules exist and we had to make our own. Several systems are possible, each with its own problems. Aiming for uniformity, objectivity and simplicity, we have decided to adapt those articles of the Code covering family-group names to order-group names. By order-group, we mean categories from order downwards to the category immediately above superfamily. Above the category order, usage is varied and unstable, but the names and categories are few, and authorship is readily established. Deciding the lower limit of this order-group is sometimes arbitrary, especially with older work. For example, BOULENGER (1904) and GOODRICH (1909) introduced many new names between the ranks of order and family in categories such as Division (BOULENGER), Subdivision, Tribe, Sub-Tribe (GOODRICH). BOULENGER's Division names end in -formes, and we have decided that these are family-group names, not order-group, on the basis of a statement by REGAN (1909), who collaborated with BOULENGER, that the -formes termination means Superfamily. We have decided that GOODRICH's (1909) Divisions, Tribes etc. are order-group names because in his hierarchy a Sub-Tribe may include superfamilies (p. XIII).

Article 29 of the Code covers formation of family-group names. Adapting this to order-group names, they must be based on the stem of a family (and ultimately genus) name, with the addition of an appropriate suffix. The suffixes in common use in ichthyology, and adopted here, are -iformes (order) and -oidei (suborder): e.g. Elopiformes, Elopoidei. The category infraorder is as yet so rarely used that no standard termination exists.

Article 36 of the Code covers co-ordination of categories in the family-group. Adapting this to order-group names means that names given, or first given, to a suborder, will apply, with the original authority, to order after change of suffix: e.g. REGAN (1909), who proposed a suborder Stomiatoidei, becomes author of the order Stomiiformes, despite the fact that this order (as Stomiatiformes) was first proposed by ROSEN in 1973.

Article 11(e) of the Code covers availability of family-group names, and states that correct orthography is not essential. Adapting this to order-group names means that names based on a valid family within the group take the original data and authorship, with emended termination: e.g. BLEEKER's (1895) Ordo Clupeae makes him the author of the order Clupeiformes and suborder Clupeoidei.

In family-group names, the law of priority applies (Article 23(d)), but in cases where this would upset general usage application is to be made to the Commission. Since the Commission does not rule on order-group names this article cannot be adapted. We have followed usage rather than priority: e.g. the suborder Opisthoproctoidei BERG (1937) does not take priority over the suborder Argentinoidei BERTELSEN (1958) (see COHEN 1964: 1).

We repeat that our aim is simplicity and uniformity. Very probably we have missed earlier or original citations of names, both in the family-group and order-group. If so, we shall be glad to hear from anyone interested in such drudgery. But we feel that nothing is to be gained from logic-chopping or metaphysical disputes on order-group names and their authorship. Usage and stability are all that matters.

Superclass Gnathostomata Gegenbaur 1874
Class Osteichthyes Huxley 1880
? Subclass Acanthodii Owen 1846E

It still remains a matter of discussion if acanthodians have otoliths or not. Calcified bodies with the appearance and position of otoliths are known in a few acanthodians (see Miles 1973 and Ørvig 1972, for a review of the literature and figures). In a skull af *Acanthodes ovensi* White 1927 from the Lower Carboniferous of Scotland, I have seen pairs of one big and one somewhat smaller body on both sides of the head, in the right topographical position for otoliths. However, these bodies do not look like otoliths in osteichthyans; moreover the material of which they are made of looks different. If these bodies were presented to me isolated, I would never imagine that they might be otoliths.

X-ray cristallography analyses mentioned by Miles (1973, p. 80) proved that the otolith-like bodies collected from acanthodian heads consist of calcite, with a few traces of dolomite, They hence differ from the vaterite or aragonite otoliths in osteichthyans. However that does not proof definitely that the objects are not otoliths. It is furthermore not known whether the calcite or the dolomite in acanthodian «otoliths» do not result from diagenetic processes.

Subclass Actinopterygii Klein 1885
Infraclass Cladistia Cope 1871

Order Polypteriformes Bleeker 1859

Family Polypteridae Bonaparte 1832

Figured recent example: *Calamoichthys calabaricus* (Smith 1866) (Fig. 26). No otolith-based fossil record.

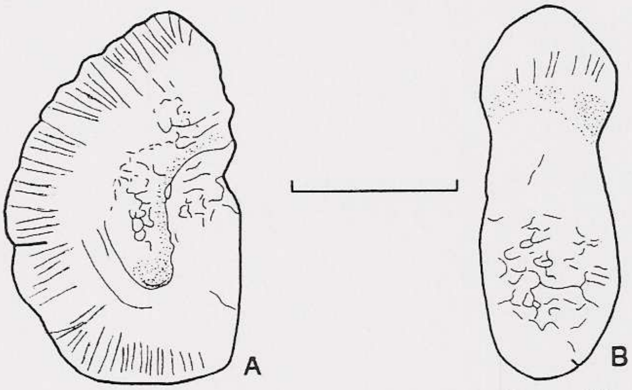


Fig. 26. *Calamoichthys calabaricus* (Smith 1866); Recent; West Africa (Coll. Nolf). A, left? lagenar otolith; B, left? utricular otolith.

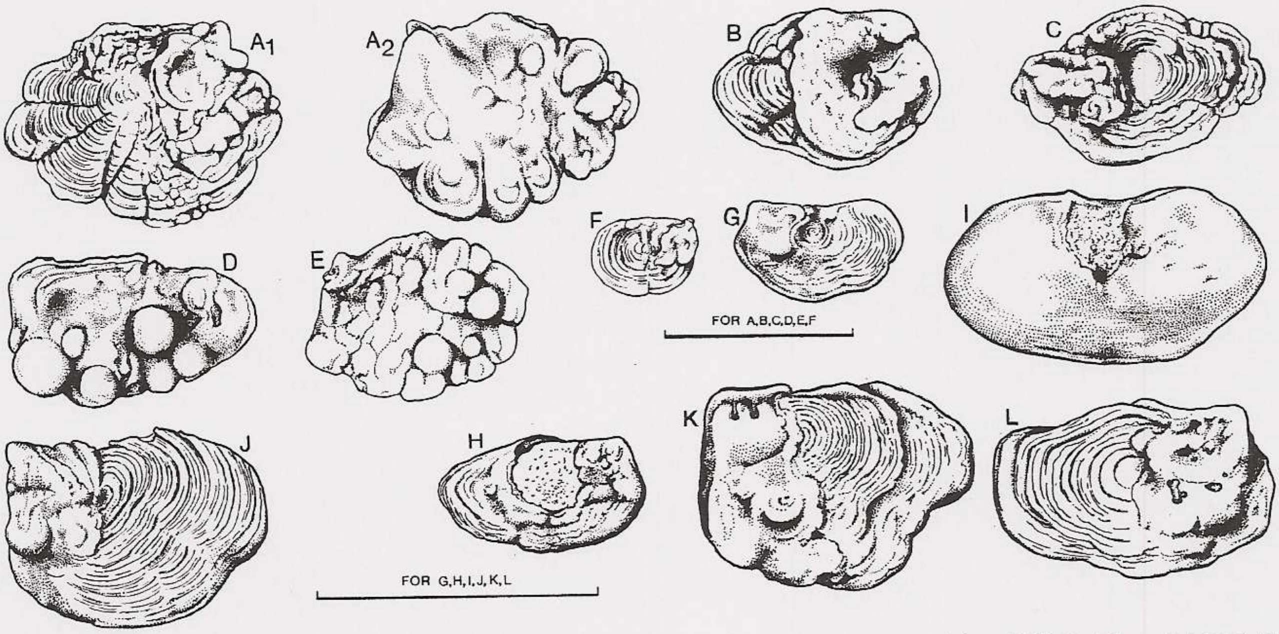


Fig. 27. Palaeoniscoid otolith type «A». A, Holotype LGJ 45–632, right otolith; A_1, inner, A_2, external face, X25; B, right otolith LGJ 45–532, inner face, X25; C, left otolith LGJ 45–628, inner face, X25; D, right otolith LGJ 45–630, external face, X25; E, right otolith LGJ 45–634, external face, X25; A–E, D2, Tavlefjellet Member, Grey Hoek Formation, Eifelian, Middle Devonian; Tavlefjellet, Wijdefjord, Spitsbergen; F, right otolith LGJ 35–168, inner face, X25; D1, Albanov Formation, Upper Emsian or lowermost Eifelian, Lower/Middle Devonian; Prionier island, Severnaja Zemlya, U.S.S.R; G, left otolith LGJ 60–010, inner face, X38; D2, Narova formation, Eifelian, Middle Devonian; Leningrad district, U.S.S.R.; H, right otolith LGJ 25–0543, inner face, X38; ? D1–D2, Rezekne horizon, Upper Emsian or lowermost Eifelian, Lower/Middle Devonian; 431,3 m depth of Ludza drilling, Latvia, U.S.S.R.; I, ? left otolith LGJ 60–008, inner face, X38; D2, Narova horizon, Eifelian, Middle Devonian; Leningrad district, U.S.S.R.; M, right otolith LGJ 55–003, inner face, X38; K, right otolith LGJ 55–005, inner face, X38; L, left otolith LGJ 55–004, inner face, X38; K–L, ? D1–D2, Vitebsk horizon, Upper Emsian or lowermost Eifelian, Lower/Middle Devonian; 287,3–290,4 m depth of drilling Chaschniki, Byelorussia, U.S.S.R. (contribution V. Talimaa).

Infraclass Actinopteri Cope 1871

Superseries Chondrostei Müller 1846
Order Palaeonisciformes Goodrich 1909
(contribution by V. Talimaa)

The oldest known otoliths occur in the uppermost Lower Devonian or in the Lowermost Middle Devonian of Spitsbergen (Verdalen Member, Wood Bay Formation; Tavlefjellet Member, Grey Hoek Formation), of Severnaja Zemlja (Albanov Formation), of the Baltic region (Rezekne horizon, and Upper Narova horizon), and of Byelorussia (Vitebsk horizon). These phosphatic otoliths were obtained by dissolving the rocks with weak acetic acid. Two morphological types can be distinguished. Otoliths of type «A», are usually shiny, and nearly transparent with yellowish brown to nearly black color, they vary widely in external shape. Specimens of type «A» may represent the saccular otolith. Otoliths of type «B» make up only 2–3 % of all otoliths in residues from Spitsbergen, while they are even more rare or completely missing in residues of other regions. Type «B» otoliths may represent the lagenar otolith. A third type different from type «A» and «B» occurs extremely rarely in the residues, it may represent the utricular otolith.

Type «A» (Fig. 27)

Otoliths of type «A» are 0.4–3.0 mm in diameter, they are elongated oval or irregular in shape, very flat and low. The margin of small specimens is rounded, while large specimens have processes along the margin separated from each other by shallow grooves. A growth center surrounded by concentric growth lines can be observed on the inner face (Fig. 27 A, B, C, F–L); the growth lines prescribe the outline.

Left and right otoliths can be distinguished because the anterior part of the inner face is characterized by an elevation (b) with an uneven, irregular tuberculated surface. Depth, size and shape of the elevation and its surface vary, and the elevation occupies up to half of the inner face in some otoliths (Fig. 27 B). The center of the inner face is formed by a depression which can be filled with a light mat and porous substance in old otoliths with a very smooth inner face (Fig. 27 H, I).

The external face of specimens of type «A» (Fig. 27 A_2, D, E) is smooth or occupied by small irregular or round elevations. These round elevations are sometimes arranged in radial rows in continuation with the processes on the margin.

Type «B» (Fig. 28)

Otoliths of type «B» are oval or sometimes spherical with a diameter of 0.3–1.5 mm. They are domed or compressed. A longitudinal furrow occupies the middle part of the inner face, it may be compared with the colliculum of the saccular otolith of acanthopterygians. The furrow runs straight (Fig. 28 C), or turns upwards and widens at the center of the inner face (Fig. 28 E, F, G, I). The furrow passes over to the external face and continues to the growth center. Beside the furrow, the inner face is somewhat elevated, smooth or with faint concentric furrows. Deep otoliths of type «B» can have a deep and narrow (Fig. 28 D_1, F) or a broad marginal furrow. Some have a ridge in the middle (Fig. 28 B). The marginal furrow occupy more than half of the circumference.

The external face is smooth and elevated like a cone in many otoliths, others have a distinct protuberance (Fig. 28 A_2, C_2, D_2, G_2: a) which occupies about a third of

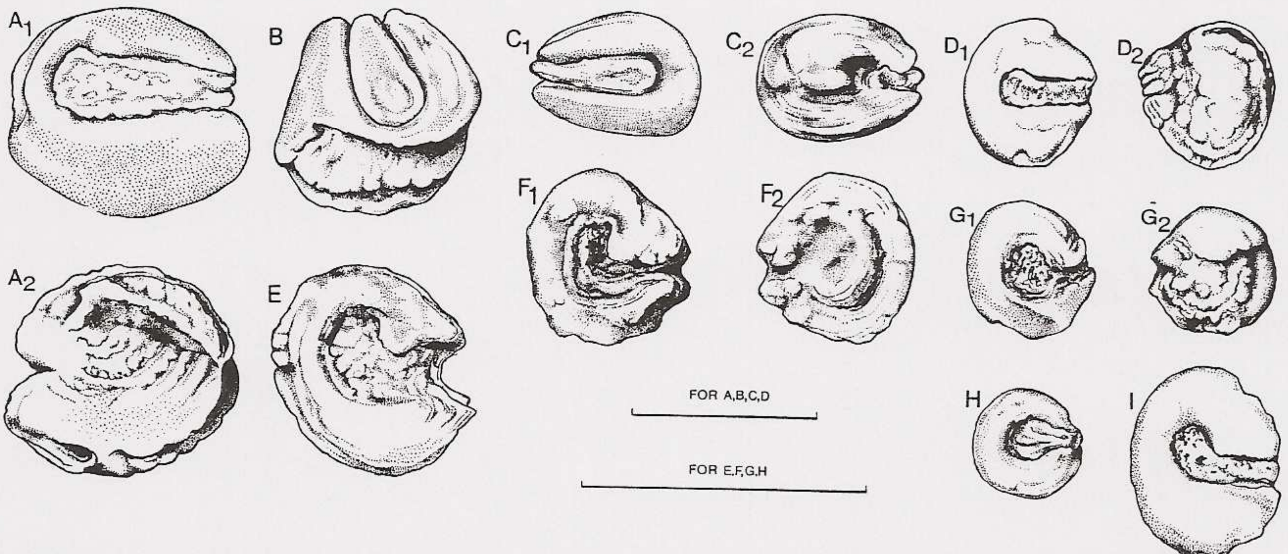


Fig. 28. Palaeoniscoid otolith type «B». A, Holotype LGJ 45–625, left otolith; A_1, inner face; A_2, external face, X38; B, right otolith LGJ 45–625, inner face, X38; C, right otolith LGJ 45–599, C_1, inner face, C_2, external face, X25; D, left otolith LGJ 45–624, D_1, inner face, D_2, external face, X25; A–D, D2, Tavlefjellet Member, Grey Hoek Formation, Eifelian, Middle Devonian; Mount Tavelefjellet, Wijdefjord, Spitsbergen; E, left otolith LGJ 45–598, inner face, X38; F, left otolith LGJ 45–594, F_1, inner face, F_2, external face, X38; G, left otolith LGJ 45–596, G_1, inner face, G_2, external face, X38; H, left otolith LGJ 45–597, inner face, X38; I, left otolith LGJ 45–595, inner face, X38; E–I, D2, Verdalen Member, Wood Bay Formation, Eifelian, Middle Devonian; Mount Watson, Austfjord, Spitsbergen (contribution V. Talimaa).

the surface. Small elevations are developed on the remaining depressed external face. A low depression occupies the central part of the external face in cases where no protuberance is formed (Fig. 28F_2).

Two varieties can be distinguished within type «B»: elevated specimens with or without marginal furrow and nearly straight longitudinal furrow on the inner face (Fig. 28 A–D), and flat specimens without marginal furrow and with dorsally curved longitudinal furrow (Fig. 28 E–F).

Both types of otoliths probably belong with high probability to paleoniscoid and actinopterygians of the *Orvikuina* type. They are always found together with scales of *Orvikuina* or related formes. They (type «A») resemble otoliths described in *Palaeoniscum* from the Upper Permian of Thuringia, Germany (HUNGER 1939).

Order Acipenseriformes GOODRICH 1909

Family Acipenseridae BONAPARTE 1832

Figured Recent example: *Acipenser transmontanus* RICHARDSON 1836 (Fig. 29 A). No otolith-based fossil record.

Family Polyodontidae BONAPARTE 1832

Figured Recent example: *Polyodon spathula* (WALBAUM 1892) (Fig. 29 B). No otolith-based fossil record.

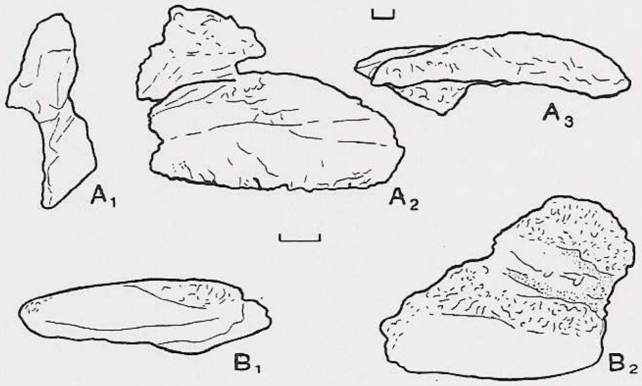


Fig. 29. A, *Acipenser transmontanus* RICHARDSON 1836; Recent; California, U.S.A. (Coll. FITCH); left saccular otolith; A_1, posterior view; A_2, inner face; A_3, ventral view. B, *Polyodon spatula* (WALBAUM 1792); Recent; U.S.A. (Coll. FITCH); B_1, right saccular otolith, ventral view; B_2, inner face.

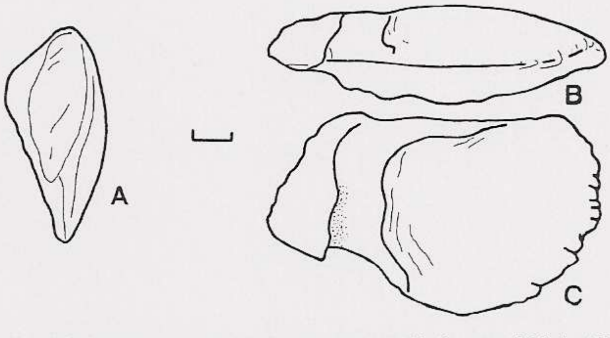


Fig. 30. *Lepisosteus osseus* (LINNAEUS 1758); Recent; U.S.A. (Coll. FITCH); left saccular otolith A, posterior view; B, ventral view; C, inner face.

Chondrostei incertae sedis

«genus Chondrosteiformorum» subdeltoideus STINTON 1968 *(Gyrosteus)* Bathonian; Southern England.

Superseries Neopterygii REGAN 1923
Division Ginglymodi COPE 1871
Order Lepisosteiformes HUXLEY 1861

Family Lepisosteidae CUVIER 1825

Figured Recent example: *Lepisosteus osseus* (LINNAEUS 1758) (Fig. 30).

Otolith-based fossil species:

Lepisosteus fimbriatus (WOOD 1846) (skeleton). Upper Eocene; Southern England.

Division Halecostomi REGAN 1923
Subdivision Halecomorphi COPE 1871
Order Amiiformes HUXLEY 1861

Family Amiidae BONAPARTE 1832

Figured Recent example: *Amia calva* LINNAEUS 1766 (Fig. 31). No otolith-based fossil record.

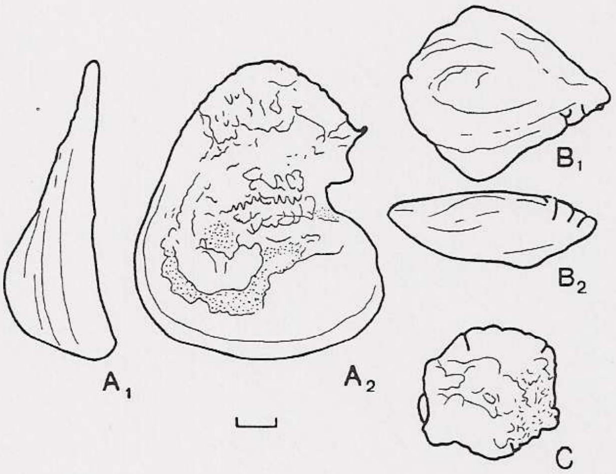


Fig. 31. *Amia calva* LINNAEUS 1766; Recent; U.S.A. (Coll. FITCH); A, left lagenar otolith in posterior A_1 and inner face A_2 view; B, left saccular otolith in inner face B_1 and ventral B_2 view; C, left utricular otolith.

Subdivision Teleostei MÜLLER 1846

Family Leptolepididae NICHOLSON & LYDEKKER 1889

Many Mesozoic otoliths have been attributed to the fossil family Leptolepididae. These attributions are based only on the observation that many strata containing little plesiomorph teleost-otoliths, often also contain leptolepid skeletons. In our opinion, this is a very poor argument for a taxonomic identification. The only known true leptolepid

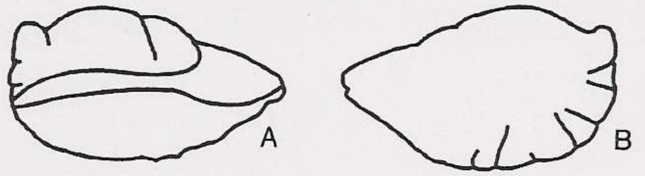


Fig. 32. Otolith found in situ in a skull of *Leptolepis coryphaenoides* (BRONN 1830); Callovian (Middle Jurassic); Calvados, France; A, inner face; B, external face. Drawn by STINTON.

otoliths are those found in situ in a skull of *Leptolepis coryphaenoides* (BRONN 1830), collected from in the stomach content of a *Pholidophorus* from the Callovian (Middle Jurassic) of Calvados, Western France (PATTERSON 1975, p. 284). The otoliths were preserved as phosphatic shells amongst the acid residues, after cleaning treatment of the skull. They have been drawn by STINTON (see Fig.32), but we were not in the opportunity to examine them.

Supercohort Osteoglossomorpha GREENWOOD et al. 1966
Order Osteoglossiformes REGAN 1909
Suborder Osteoglossoidei REGAN 1909

Family Osteoglossidae BONAPARTE 1832

Figured Recent examples: *Osteoglossum bicirrhosum* (AGASSIZ 1829) (Fig. 33 A); *Arapaima gigas (*CUVIER 1817) (Fig. 33 C).

All living osteglossids are exclusively freshwater fishes, but the fossil record in various marine deposits clearly indicates that several extinct species had marine representatives.

Osteoglossids from marine deposits are known by otoliths from the Bathonian of Southern England and by osteological remains from several Paleogene sites (Angola, England, Monte Bolca, Turkmenia). Paleogene osteoglossid otoliths are known from the continental lower Paleocene of Belgium (Montian, unpublished); marine Paleocene of Belgium (NOLF 1978a) and the Eocene of the Anglo-Franco-Belgian Basin (two species). Osteoglossid otoliths show very marked ontogenetic changes.

There are three nominal otolith-based species:

«genus Osteoglossidarum» acutangulus (STINTON 1977) *(Heterotis)*. Middle Eocene; Southern England. (Fig. 33 B).
«genus Osteoglossidarum» rhomboidalis (STINTON 1977) *(Polymixia)*. Lower Eocene; Southern England.
«genus Osteoglossidarum» pentangulus (FROST 1924) *(Leptolepidarum)*. Kimmeridgian; Southern England.

Family Pantodontidae PETERS 1876

Figured Recent example: *Pantodon buchholzi* PETERS 1876 (Fig. 33 D). No otolith-based fossil record.

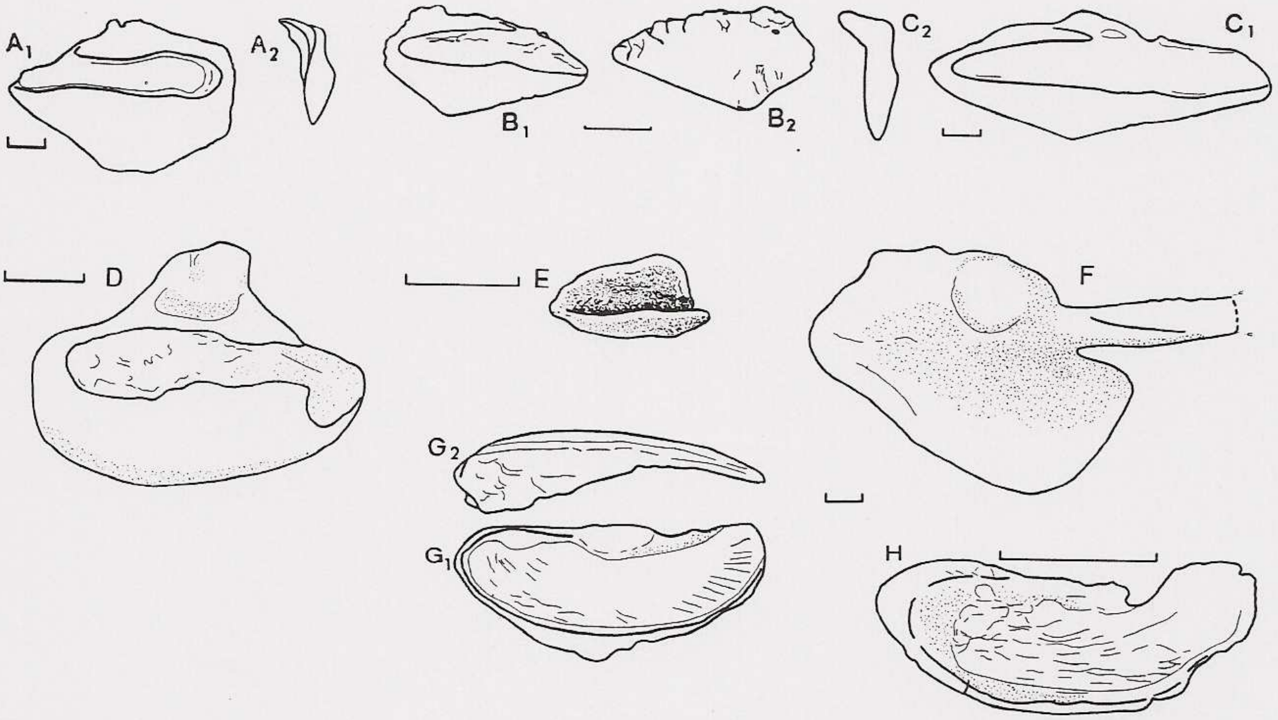


Fig. 33. Osteoglossomorph otoliths. A, *Osteoglossum bicirrhosum* (AGASSIZ 1829); Recent; Brazil (Coll. FROST, BMNH); right saccular otolith. B, *«genus Osteoglossidarum» acutangulus* (STINTON 1977); Middle Eocene0 Belgium; B_1, inner face; B_2, posterior view; B_3, external face of left saccular otolith; C, *Arapaima gigas* (CUVIER 1817); Recent; Amazone (Coll. FITCH); C_1, cross section; C_2 inner face of left saccular otolith; D, *Pantodon buchholzi* PETERS 1876; Recent; Zaire, Africa (Coll. NOLF); left saccular otolith; E, *Hiodon alosoides* (RAFINESQUE 1819); Recent; Western U.S.A (after TAVERNE 1977); left saccular otolith; F, *Notopterus* sp.; Recent; South Asia (Coll NOLF); left saccular otolith; G, *Gnathonemus petersii* (GÜNTHER 1862); Recent; Central Africa (Coll. NOLF); G_1, inner face; G_2, ventral view of left saccular otolith; H, *Campylomormyrus tamandua* (GÜNTHER 1864); Recent; Central Africa (Coll. NOLF); left saccular otolith.

Suborder Notopteroidei Jordan 1923
Superfamily Hiodontoidea Valenciennes 1846

Family Lycopteridae Cockerell 1925

The only otoliths that undoubtless can be attributed to lycopterids are those found in situ in the skulls of several specimens of *Lycoptera middendorfi* (Müller 1861) from the Lower Cretaceous of Transbaikalia, Russia (Reis 1909).

Many other isolated otoliths from various Jurassic localities have also been attributed to lycopterids, especially by Weiler (1957). For none of them, there exists convincing morphological evidence that they really belong to this family (see comments on p. 111).

Family Hiodontidae Valenciennes 1846

Figured Recent example: *Hiodon alosoides (*Rafinesque 1819) (Fig. 33 E). No otolith-based fossil record.

Superfamily Notopteroidea Bleeker 1859

Family Notopteridae Bleeker 1859

Figured Recent example: *Notopterus* sp. (Fig. 33 F). No otolith-based fossil record.

Order Mormyriformes Berg 1937

Family Mormyridae Bonaparte 1832

Figured Recent examples: *Gnathonemus petersi (*Günther 1862) (Fig. 33 G); *Campylomormyrus tamandua* (Günther 1864) (Fig. 33 H). No otolith-based fossil record.

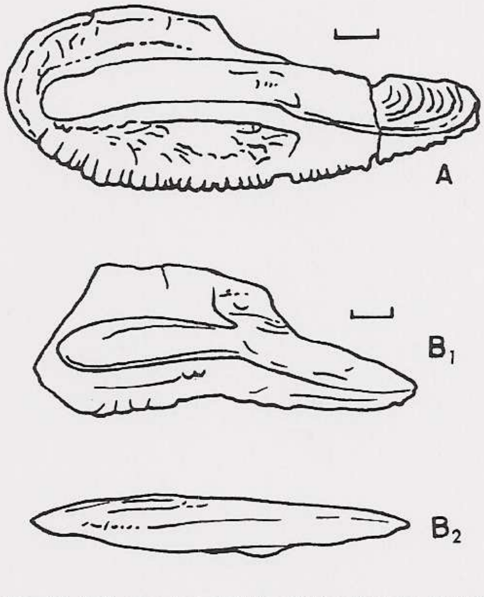


Fig. 34. Left saccular otoliths of Elopiformes and Megalopiformes. A, *Elops affinis* Regan 1909; Recent; Pacific, Mexico (Coll. Fitch); B, *Megalops cyprinoides* (Broussonet 1782); Recent; Samoa (Coll Fitch); B_1, inner face; B_2, ventral view.

Family Gymnarchidae Günther 1868

No useful data on Recent otoliths (only very formaline-eroded otoliths figured by Taverne 1972). No otolith-based fossil record.

Supercohort Elopocephala Patterson & Rosen 1970
Cohort Elopomorpha Greenwood et al. 1966
Order Elopiformes Greenwood et al. 1966

Family Elopidae Bonaparte 1832

Figured Recent example: *Elops affinis* Regan 1909 (Fig. 34 A).

Otolith-based fossil species:

Elops undulatus Stinton 1966. Lower Eocene; Southern England.
«*genus? Elopidarum*» *rhenanus* (Weiler) in Martin & Weiler 1954 *(Lycopteridarum)*. Dogger; Germany.

Elopiformes incertae sedis

«*genus Elopiformorum*» *recurvus* Frost 1931. Paleocene; Southern England.

Order Megalopiformes Patterson & Rosen 1977

Family Megalopidae Jordan & Gilbert 1882

Figured Recent example: *Megalops cyprinoides* (Broussonet 1782) (Fig. 34 B).

Otolith-based fossil species:

«*genus Megalopidarum*» *bicrenulatus* (Stinton 1973) *(Megalops)*. Albian, Lower Cretaceous; Southern England.

Order Anguilliformes Regan 1909
Suborder Albuloidei Jordan 1923
Superfamily Albuloidea Bleeker 1859

Family Albulidae Bleeker 1859

Figured Recent example: *Albula vulpes* (Linnaeus 1758) (Fig. 35 A).

Although albulid otoliths are never common in fossil associations, a rather high number of species has been discovered, probably due to the large size of their otoliths. Several of these fossil species belong to extinct genera.

Otolith-based fossil species:

Albula bashiana (Frizzel 1965) *(Metalbula)*. Eocene; Mississippi, U.S.A.
Albula bellevoyei (Priem 1908) *(Trachinus)*. Middle Oligocene; Paris Basin, France.