

**OTOLITH-MORPHOLOGY AND ITS USAGE FOR HIGHER SYSTEMICAL UNITS,
WITH SPECIAL REFERENCE TO THE MYCTOPHIFORMES s.l.**

by

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Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. — Meded. Werkgr. Tert. Kwart. Geol., 15 (4): 167 - 185, 9 Figs., 3 Pl. Rotterdam, December 1978.

Some necessary technical terms are introduced with regard to the main morphological structures of the sulcus that can be found in the teleostean otoliths. Most of these named structures do not implicate monophyletic origin by any means, as they can obviously have originated within different lineages. Nevertheless, phylogenetical discussion of higher taxa within the Teleostei can be based on these structures. The important role of the Myctophiformes, with regard to the evolution and origin of the Acanthopterygii and Paracanthopterygii, is a special purpose of this paper. Other problems, such as the Atherinomorpha and the relationship of Gadiformes and Ophidioidei, are discussed. The limits of phylogenetic studies based on otoliths are pointed out (possibilities of numerous analogies because of a not very complex morphology, loss of advanced features because of different types of reductions).

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THE IMPORTANCE OF OTOLITHS

Fossil

The advantages of otoliths are, that they are the only identifiable isolated remains of Teleosteans so far and that they are millions of times more common in the fossil record than complete fish-skeletons. Except for the European Tertiaries our knowledge of fossil otoliths is still in a beginning stage of discovery and description. Nevertheless they turn out to be of interest for the following further investigations:

Regional biostratigraphy

First steps in this field have been done by Brzobohatý (Neogene, Paratethys), Gaemers and Schwarzahns (Oligocene and Neogene, North Sea Basin) and Nolf (Paleogene, Belgian Basin and Paris Basin). Certain groups (Gadidae in the Neogene and Ophidioidei in the Paleogene) contain a number of short living species and quite well known lineages on which these studies are based.

Paleogeography

These investigations are becoming exceedingly important as our knowledge of oversea fossil faunas is increasing. A first regional work has been done by Brzobohatý (Neogene, Paratethys).

Recent

A good estimation on the number of living teleostean species would be placed somewhere between 30.000 and 50.000. In the ten largest private and institutional collections about a tenth to a fifth of these are represented by otoliths. It is an unpleasant misproportion that of only about 1.000 recent species otoliths have been figured and quite often in an incorrect or even misleading way. However, that is the most necessary work to be done, as all studies on recent or fossil material should be based on a proper zoological background. An example of how this can be done is shown by Karrer's marvellous work on Moridae otoliths. A better co-operation between otolith specialists and a better exchange of recent material will be necessary.

In the past several small attempts have been published on phylogenetic relationships based on otoliths by Hecht, Karrer, Nolf, Schwarzahns, Stinton and Weiler. All of them realized that otoliths are conservative enough in their characters to allow phylogenetic interpretations on the level of species, genera and families. In the higher hierarchy, however, this becomes somewhat problematical. The most conservative and consequently the most important structure for these purposes is the sulcus (fig. 1); this has also been the opinion of most previous workers.

THE MORPHOLOGICAL STRUCTURES

Purely empirically I would like to make the following statements on the value of certain otolith structures.

On the species level such characters as small differences in the outline, sculpture (on the margins or outside), L:H and L:T ratios are the most important, whereas other characteristics usually are constant.

On the somewhat higher genus or family level other characters, such as small differences in the sulcus margins, the outline in general, curvatures, cristae and larger structures on the outside (tubercles and ridges) are of increasing importance.

For higher taxa there is more or less only one useful character left, concerning the principal

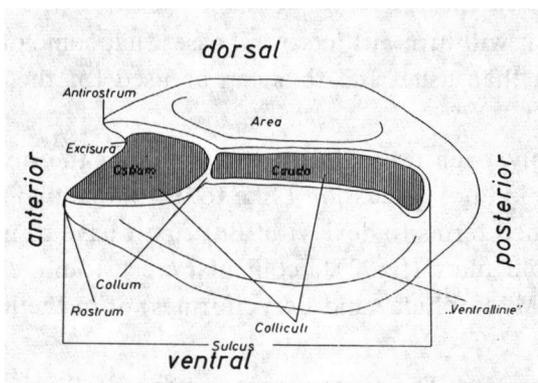


Fig. 1. Orientation and explanation of the morphological structures of a teleostean otolith (right sagitta).

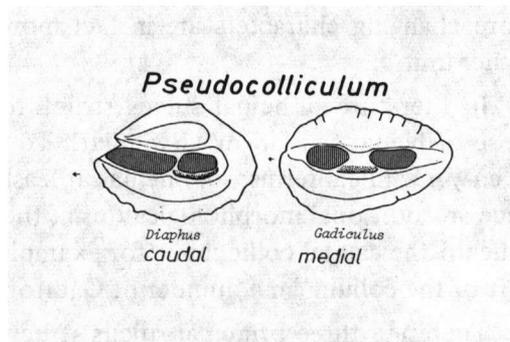


Fig. 2. Explanation of the new morphological term pseudocolliculum with two examples (colliculi are hatched, pseudocolliculum is dotted).

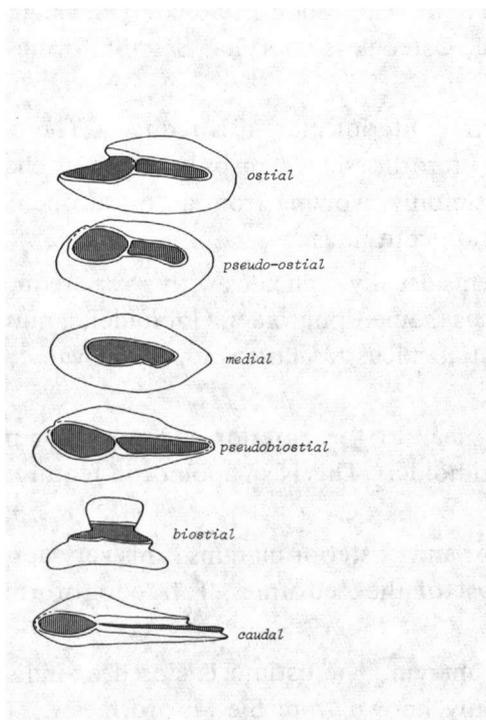


Fig. 3. Explanation of the six principal types of sulcus openings (colliculi are hatched). Right sagittas.

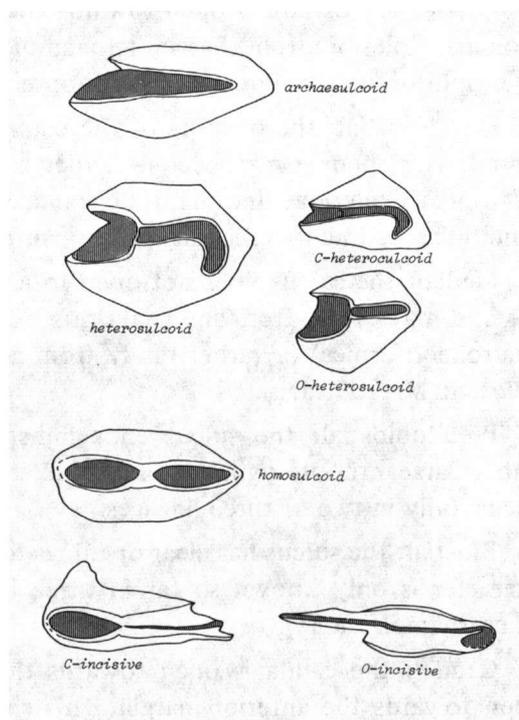


Fig. 4. Explanation of the four principal types of sulcus margins, including four important variations (colliculi are hatched). Right sagittas.

structure of the sulcus, unless one likes to use parallelisms as evidence (Personally I think that parallelisms are too dangerous and dubious to be of any use for phylogenetical purposes).

This statement had a very general character and it will turn out in several cases that some of the more changing characters are in fact more constant than usual and thus can be used for the next higher unit.

In literature principal sulcus structures have only been used circumscriptive or in the normal sense of being 'similar' or 'dissimilar'. To avoid this kind of discussion I like to introduce two sorts of easy technical terms; so, one has at least well-defined terms to deal with. But first I have to introduce an additional morphological term, the pseudocolliculum (fig. 2), a collicular crest, found either beneath the caudal colliculum (for example in some Myctophidae and Beryciformes) or in the lower part of the collum (in a number of Gadiformes).

There are three principal sulcus structures to consider. The first is the number of colliculi. The sulcus can be filled with one undivided colliculum, either as a primitive character or a secondary, when formerly divided colliculi are fused together again. The division into an ostial and a caudal colliculum is an apomorph character, that originated gradually and was obviously realized in at least three different lineages.

Secondly the opening of the sulcus is an important feature. We are able to recognize six principal possibilities (fig. 3):

Ostial: the ostium is open towards the anterior margin. The cauda is closed. This is, generally spoken, a plesiomorph character (examples: Elopidae, Osteoglossomorpha, Salmoniformes, most Myctophiformes, a number of Acanthopterygii).

Pseudo-ostial: the opening of the ostium towards the anterior margin is reduced. The cauda is closed. The opening may become either indistinctive (Pterothrissidae), or only an ostial channel is left (most Congridae and many Sciaenidae), quite commonly evolving from an ostial opening and sometimes leading to a medial sulcus position, if reduction continues.

Medial: the sulcus does not open to any margin. This usually coincides with a very reduced sulcus and may evolve from an ostial or pseudo-ostial sulcus (some Congroidei, Gobioidi, a number of Pleuronectiformes) or rather rarely from a pseudobiostial sulcus (*Macruroides*, *Squalogadus*, *Typhlonus*, all Macrouridae).

Pseudobiostial: the sulcus ends indistinctly very near to the anterior and posterior margins (most Paracanthopterygii, Alepisauroidi and few Ophidioidei). This is an apomorph feature, which occurs only in two or three lineages.

Biostial: the sulcus has clear openings to the anterior and posterior margins. This very apomorph character is only known so far in three lineages (most of the Zeiformes, Tetraodontiformes and Macrorhamphosidae).

Caudal: the cauda is open towards the posterior margin. The ostium is closed or indistinctly open towards the anterior margin. This character is only known from the Moriformes s.s. (within Paracanthopterygii).

Last but not least the general outline of the sulcus is important. We distinguish four categories (fig. 4):

Fig. 5. Possible phylogenetic meaning and evolution of the sulcus structures, modified after Greenwood et al., 1966.

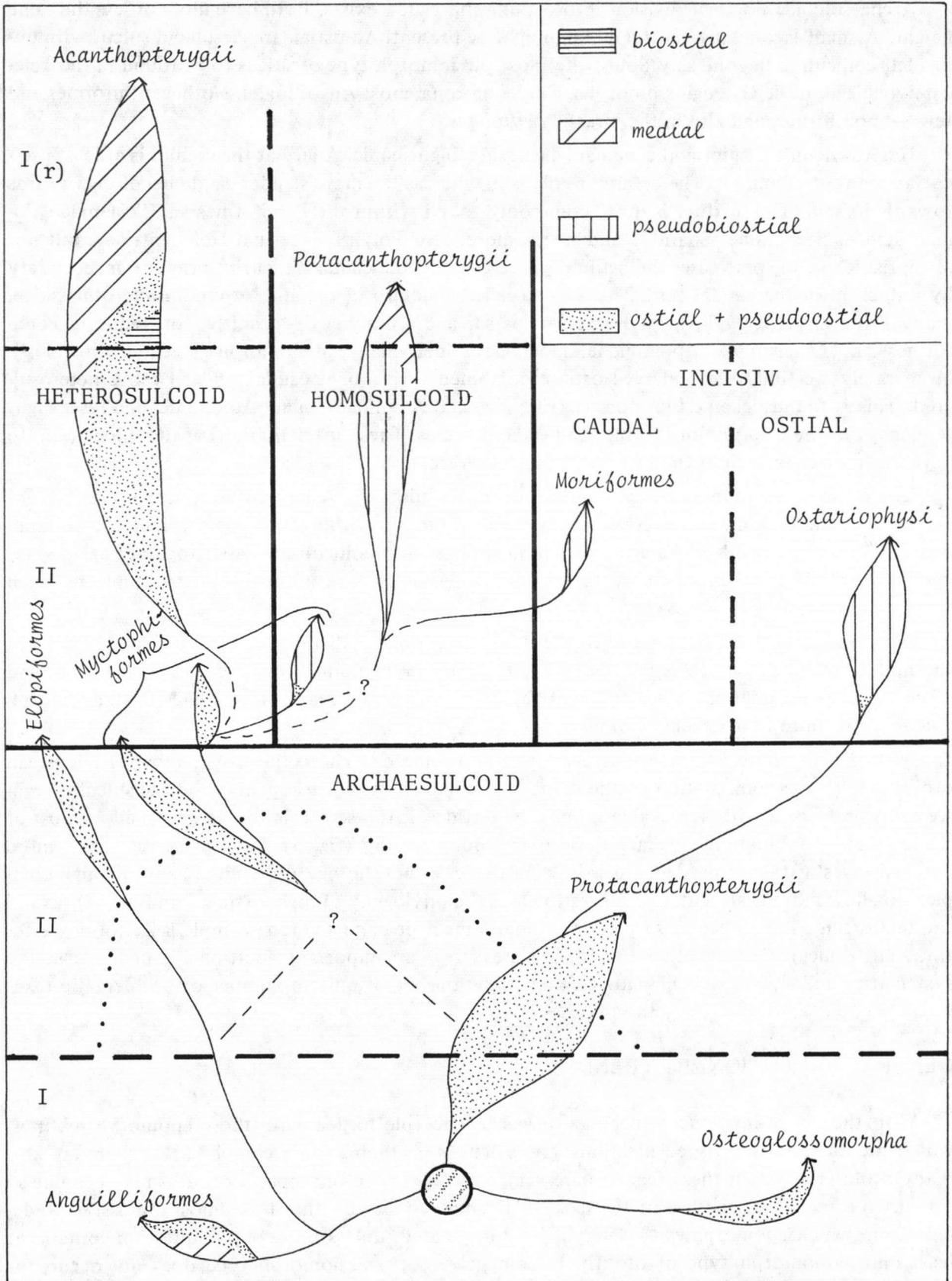


Fig. 5

Archaesulcoid: no clear division into ostium and cauda exists. Both have more or less the same height. A small lace at the ventral margin might be present. An ostial, archaesulcoid sulcus with undivided colliculi is beyond any doubt the most plesiomorph type of sulcus to be found in the Teleostei, realized in the Osteoglossomorpha, Clupeomorpha, most Anguilloidei, Nothacanthiformes and few Salmoniformes and also in the jurassic *Leptolepis*.

Heterosulcoid: ostium and cauda are clearly distinguishable. A lace at the collum is at least present at the ventral margin. The ostium is enlarged, whereas the more slender cauda bends downwards towards its end. This feature is quite commonly found within the Perciformes s.l. (Sciaenidae, Pomadasyidae, Serranidae, Sparidae and many more, also Polymixiidae and Holocentridae, but not Myripristidae). In some cases the ostium is enlarged, but the cauda is straight, primary or secondary by reduction of the caudal bent. That can be called O-heterosulcoid and is found in Pterothrissidae, many Protacanthopterygii, most Beryciformes s.l. and a number of 'primitive' or 'reduced' Perciformes s.l. (Atherinidae, Apogonidae, most Gobioidi, many plesiomorph 'Pleuronectiformes'). More rarely we find a not enlarged ostium combined with a bent cauda, which I call C-heterosulcoid. This is found in some Elopiformes (Elopidae and Albulidae), many Aulopoidei and (as a slight tendency) in the Cyprinodontiformes and Galaxiiformes. These specialisations of the sulcus seem to have taken place in each of the three possibilities several times.

Homosulcoid: ostium and cauda are clearly distinguishable. A lace at the collum is present. Ostium and cauda look more or less symmetrical. This is found within the Alepisauroidi, the Zenionidae (ex Zeiformes) and all Paracanthopterygii unless their colliculi are fused together again. This apomorph character seems to have taken place only twice, one group only containing the small family Zenionidae.

Incisive: this character is due to the development of one colliculum towards a ridge-like crest in the middle of the sulcus. This may be either the ostial colliculum (O-incisive - all Ostariophysi and *Chanos*), or the caudal colliculum (C-incisive - Moriformes ex Paracanthopterygii). Both apomorph characters seem to have developed only once.

With these technical terms we are able to bring some order into the vast number of teleostean otoliths. With the combination of the number of colliculi, the sulcus opening and the sulcus margin we are able to deal with surveyable groups. Nevertheless, the screen is too coarse to allow most of the possible combinations to have derived monophyletically (fig. 5). In special cases much more detailed investigation is needed, thus showing that the morphology of otoliths is not enough complex to allow more than tentative suggestions for the phylogeny of higher (than family-level) taxa in the teleosts. A number of surprising analogies must be expected (an example is Zeiformes - Tetraodontiformes). On the other hand, they are surely an important additional expedient for the systematics and might well help to clear the relationship of quite a number of problematic taxa.

GENERAL EVOLUTIONARY TRENDS

With the above introduced technical terms we are able to deal with those apomorph features, which are due to certain specializations: the sulcus is becoming more complex. But there are also many otoliths in which these features are very reduced. In the final stages, otoliths may become so similar to each other, because of the lack of distinctive features, that it is almost impossible to decide from which apomorphies they might have originated, unless the group in question contains at least one plesiomorph type of otolith. In some cases this plesiomorph type does not occur, for

example the Lophiiformes and Beloniformes. In other cases, viz. the Zeiformes, Tetraodontiformes and Pleuronectiformes it is present, and there are also cases, where its occurrence is doubtful as in the Ophidioidei.

In general we can state that the mode of life is somehow affecting the morphology of the otoliths. Thus benthic living fishes tend to develop thick, more or less unsculptured otoliths. The sulcus tends to reduce the opening towards a medial position and the colliculi are quite commonly fusing together. The sulcus is often flattening out. The margins of the sulcus may be reduced to a totally indistinctive oval shape. More pelagic living fishes tend to develop thin, strongly sculptured otoliths (these two features are obviously affected most easily). The sulcus tends to become very deep, so that the margins of the colliculi are almost disappearing (naturally they are still present as they mark the very points where the nerves touch the surface of the otolith). The margins of the sulcus will equalize and in some cases the sulcus breaks through to the posterior end of the otolith, thus forming a biostial opening.

There are a number of exceptions, of course, but this possibility and not yet known other possible influences should be kept in mind.

PHYLOGENETIC STUDIES

The study of otoliths has already yielded a number of certain lineages based on good synapomorphies. Some of the best examples are: the evolution of the Zeiformes via Grammicolepidae, Oreosomatidae, *Capros*, *Antigonia* out of a typical O-heterosulcoid Berycoidei-type of otolith, probably near the Trachithyidae (evolution of a strong biostial sulcus; Parazenidae and Zenionidae are certainly to be excluded of the Zeiformes); the Tetraodontiformes via Ballistoidei very likely out of the Acanthuroidei (another case of evolution of a strong biostial sulcus); the line *Gonorhynchus*, *Chanos*, *Ostariophysa* (evolution of an O-incisive sulcus, already realized in *Chanos*); the much reduced features commonly found in the Pleuronectiformes have in the most plesiomorph genus *Psettodes* a typical heterosulcoid otolith, which might originate from some not very advanced Percoidei, possibly near *Micropterus* ex Centrarchidae (*Micropterus* and *Psettodes* are hardly to distinguish on the generic level).

Myctophiformes (sensu Greenwood et al., 1966).

The Myctophiformes are thought to be an important group for the origin of the Acanthopterygii as well as of the Paracanthopterygii. When studying the otoliths we can easily recognize three principal types of otoliths (fig. 6). The most plesiomorph type of sulcus we find within the Aulopoidei (aulopid otolith) containing the families Aulopidae, Chlorophthalmidae, Synodidae, Bathypteroidae, Scopelosauridae, Ipnopidae and Harpodontidae. With the exception of one case (*Trachinocephalus* ex Synodidae) the colliculi are not yet clearly divided. The opening is ostial or pseudo-ostial. The sulcus is more or less archaesulcoid with a trend towards the C-heterosulcoid development (some Chlorophthalmidae, Aulopidae and, most distinctive, some advanced Synodidae as *Synodus* and *Trachinocephalus*). The Chlorophthalmidae and Aulopidae show some surprising similarities with several Elopiformes, such as Elopidae and Megalopidae. Anyhow, all these characters must be regarded as being very plesiomorph and therefore they don't give any good evidence with respect to the origin of the Myctophiformes. The Harpodontidae might be most related with the second group, the Myctophoidei.

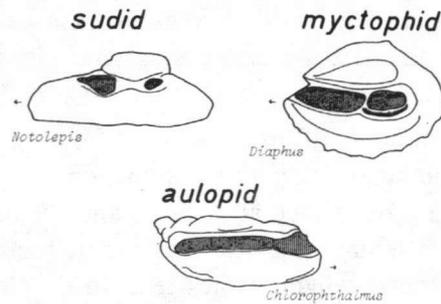


Fig. 6. The three principal types of otoliths found within the Myctophiformes s.l. (colliculi are hatched).

The Myctophoidei (myctophid otolith) only contain the families Myctophidae and Neoscolecidae. They still have an archaesulcoid sulcus with a tendency towards an O-heterosulcoid sulcus. The colliculi are clearly divided. In some Myctophidae a caudal pseudocolliculum is present. All these characters are commonly found in most Berycoformes (a plesiomorph character-combination in this group, with a much stronger developed O-heterosulcoid sulcus), thus giving a good argument for the origin of the Acanthopterygii somewhere out of or near to the Myctophoidei. Otoliths of the Ctenothrissiformes are not yet known.

A sistergroup to the Myctophoidei could be the Alepisauroidei (sudid otolith), containing the families Paralepididae, Sudidae, Omosudidae, Evermannellidae and Scopelarchidae (otoliths of the Anopteridae and Alepisauridae are not yet known). These otoliths have clearly divided colliculi. The sulcus is homosulcoid in such a way that the ostium is still larger than the cauda, thus suggesting an ostial, more or less O-heterosulcoid origin near to the Myctophoidei. The presence of a homosulcoid sulcus suggests furthermore that the Paracanthopterygii have originated from somewhere near to the Alepisauroidei. This would logically mean that the homosulcoid sulcus is a primary character within the Paracanthopterygii, which matches good with what we find in the Gadiformes, Percopsiformes and Batrachoidiformes (fig. 7).

Atherinomorpha (sensu Greenwood et al., 1966).

The systematic position and extensiveness of the Atherinomorpha has always been a serious problem in ichthyological work. Greenwood et al. placed the Sphyraenidae, Mugilidae and Polynemidae within the Perciformes, which is strongly supported by the otolith point of view, as they all show advanced heterosulcoid otoliths, which is common in that group. The Gasterosteiformes are problematical, as it is hard to say, whether their O-heterosulcoid sulcus is a primary or reduced (from true heterosulcoid) character. Anyhow, they quite certainly belong to the Acanthopterygii. The Atherinidae (including Pseudomugilidae and Melanotaeniidae of some authors) to which the Atherinomorpha should be reduced (then Atheriniformes) have an ostial, O-heterosulcoid sulcus in the same way as most Berycoidei and few 'primitive' Perciformes; also their colliculi are divided (fig. 8).

Fig. 7. Possible relationship within the Myctophiformes s.l., also showing possible origin of Acanthopterygii and Paracanthopterygii based on otoliths (colliculi are hatched).

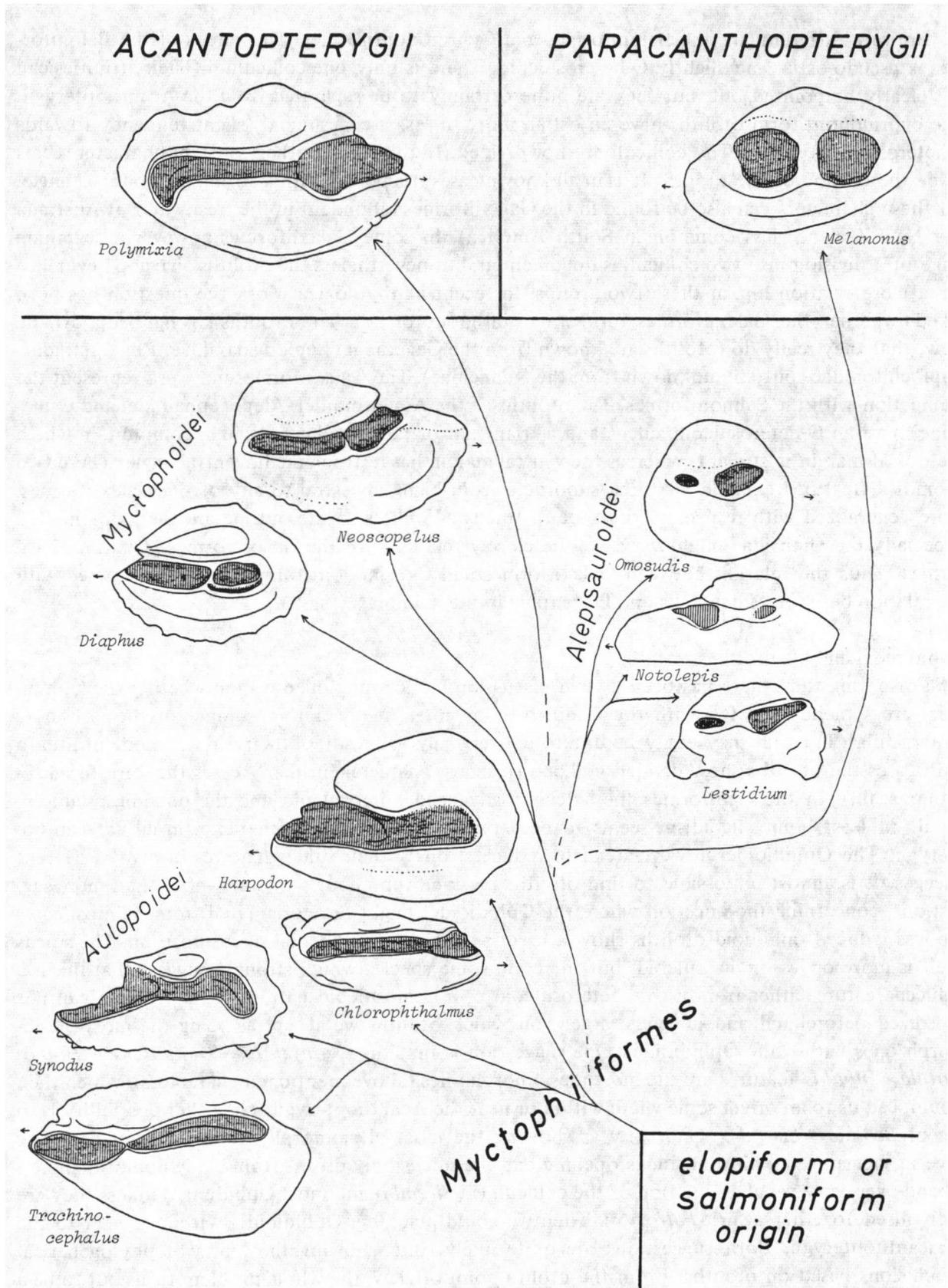


Fig. 7

Entirely different are the Beloniformes and Cyprinodontiformes. The sulcus of the Beloniformes is pseudo-ostial and slightly O-heterosulcoid. There is only one colliculum. Their affinities can not clearly be pointed out, but they are quite certainly to be separated from the Acanthopterygii. The cyprinodontiform otoliths have an ostial, more or less archaesulcoid (slight tendency towards C-heterosulcoid) sulcus. The colliculi are not divided. In this case another constant character seems to be the outline of the otolith. It is in all known cases triangular, with a strong mediodorsal angle. All these characters can also be found in the Galaxiiformes (abundant in the freshwater of Australia and New Zealand, less common in South America). In some Galaxiiformes however a beginning stage of a division into two colliculi is documented, but nevertheless the otoliths give good evidence for a close relationship of these two groups. In recent ichthyological work the question has been asked, whether the Galaxiiformes form a natural group or not. The otoliths strongly support the view, that they really do (otoliths are known from the Galaxiidae, Lepidogalaxiidae, Retropinnidae, Haplochitonidae, but still unknown from the Salangidae). The Galaxiiformes may also represent the connection with the Salmoniformes. The otoliths of the Argentinioidei, Alepocephaloidei and Osmeroidae have an O-heterosulcoid sulcus and a triangular or pentangular outline in common, in which the dorsal margin is straight, whereas the ventral margin has a strong medioventral angle. These two apomorph features exclude all three suborders from being ancestral to any of the Galaxiiformes. More generalized with respect to the type of sulcus as well as to the outline are the Salmonoidei. Especially the Umbridae might very well be closely related with the Galaxiiformes - Cyprinodontiformes. Thus the relation between Galaxiiformes and Cyprinodontiformes can be compared with the relation between Marsupialia and Placentalia in the mammals (fig. 9).

Ophidioidei and Gadiformes

For a long time there has been a vivid discussion, concerning the question whether the Ophidioidei are somehow related with the Gadiformes or not. The general appearance of these fishes is quite similar, but that may easily be due to convergency as a result of their similar mode of life. In both cases the otoliths show divided colliculi (primary character, in many cases they are fused together again). In the Gadiformes the sulcus is advanced homosulcoid and the opening pseudobiostial. At least homosulcoidism seems to be a primary, plesiomorph character in all Paracanthopterygii. The Ophidioidei however tend to reduce strongly their sulcus features in many different lineages. It is almost impossible to find otoliths plesiomorph enough to state more than mere suggestions, concerning the question where the Ophidioidei might have originated from. In most cases the less reduced ophidioid otoliths show a pseudo-ostial or even medial sulcus position. The sulcus itself is more or less archaesulcoid, but there are some species which strongly suggest that this is a reduced feature either from a true heterosulcoid or a homosulcoid pattern. This problem can not be solved beforehand and depends largely on which otoliths we accept as being the most plesiomorph ones within the Ophidioidei. One suggestion is that the *Neobythites* - *Genypterus* - *Hoplobrotula* - *Dipulus* features are the most plesiomorph ones (above mentioned characters), which then would lead us to an origin somewhere within or near the Acanthopterygii. The other possibility is to accept *Brotula* - *Sirembo* - *Petrotyx* as showing the most plesiomorph otolith features. Here we have in fact a pseudobiostial sulcus opening and the sulcus only differs from being homosulcoid by a bend-over, very peculiar junction of the colliculi (in *Sirembo* and most Ophidiinae) unless they are both fused together again (*Petrotyx*). Then we could place the Ophidioidei within or near to the Paracanthopterygii. Both suggestions are quite likely, thus showing the limits of phylogenetical conclusions based on otoliths. From the otolith point of view, the whole problem turns out to be a mere believing of what are the connecting synapomorphies. There are of course some parallelisms

on other otolith features between Ophidioidei and Gadiformes. There is a particular tuberculation on the outside and a praedorsal lobe of the dorsal margin (common within the Gadiformes, rare within the Ophidioidei). The last character has also been found in some Congridae, most Apogoniidae and a number of Stephanoberycoidei. I have strong objections against regarding them as synapomorphies for the relationship between Ophidioidei and Gadiformes. These characters are usually not constant enough for phylogenetical conclusions on this high systematic level and therefore they should better be considered to be mere parallelisms.

Another group, the Zoarcidae, is quite often placed near the Gadiformes. They have an ostial, somewhat reduced heterosulcoid sulcus, which offers no good argument to place them somewhere near the Paracanthopterygii. They fit well within the Blennioidei, as has been suggested by previous workers.

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Plate I

Plain numbers show the inside of the otoliths; a) view from dorsal; b) view from anterior.

ELOPIFORMES

Elopidae

Fig. 1. *Elops hawaiiensis* Regan. Recent, off Hawaii. 7.5 x.

Megalopidae

Fig. 2. *Megalops cyprinoides* (Broussonet). Recent, east Australia. 16 x.

MYCTOPHIFORMES

Aulopoidei

Chlorophthalmidae

Fig. 3. *Chlorophthalmus nigripinnis* Günther. Recent, east Australia, 16 x.

Fig. 4. *Chlorophthalmus agassizi* Bonaparte. Recent, Gulf of Mexico. 16 x.

Aulopidae

Fig. 5. *Aulopus curtirostris* Thomson. Recent, Queensland, Australia. 16 x.

Synodontidae

Fig. 6. *Saurida tumbil* (Bloch). Recent, West Australia. 6 x.

Fig. 7. *Saurida undosquamis* (Richardson). Recent, West Australia. 6 x.

Fig. 8. *Synodus variegatus* (Lacepède). Recent, West Australia. 16 x.

Fig. 9. *Synodus lucioiceps* (Ayres). Recent, California. 16 x.

Fig. 10. *Trachinocephalus myops* (Bloch & Schneider). Recent, Madagascar. 6 x.

Bathypteroidae

Fig. 11. *Bathypterois longifilis* Günther. Recent, east Australia. 10 x.

Scopelosauridae

Fig. 12. *Scopelosaurus harryi* (Mead). Recent, California. 30 x.

Plate I

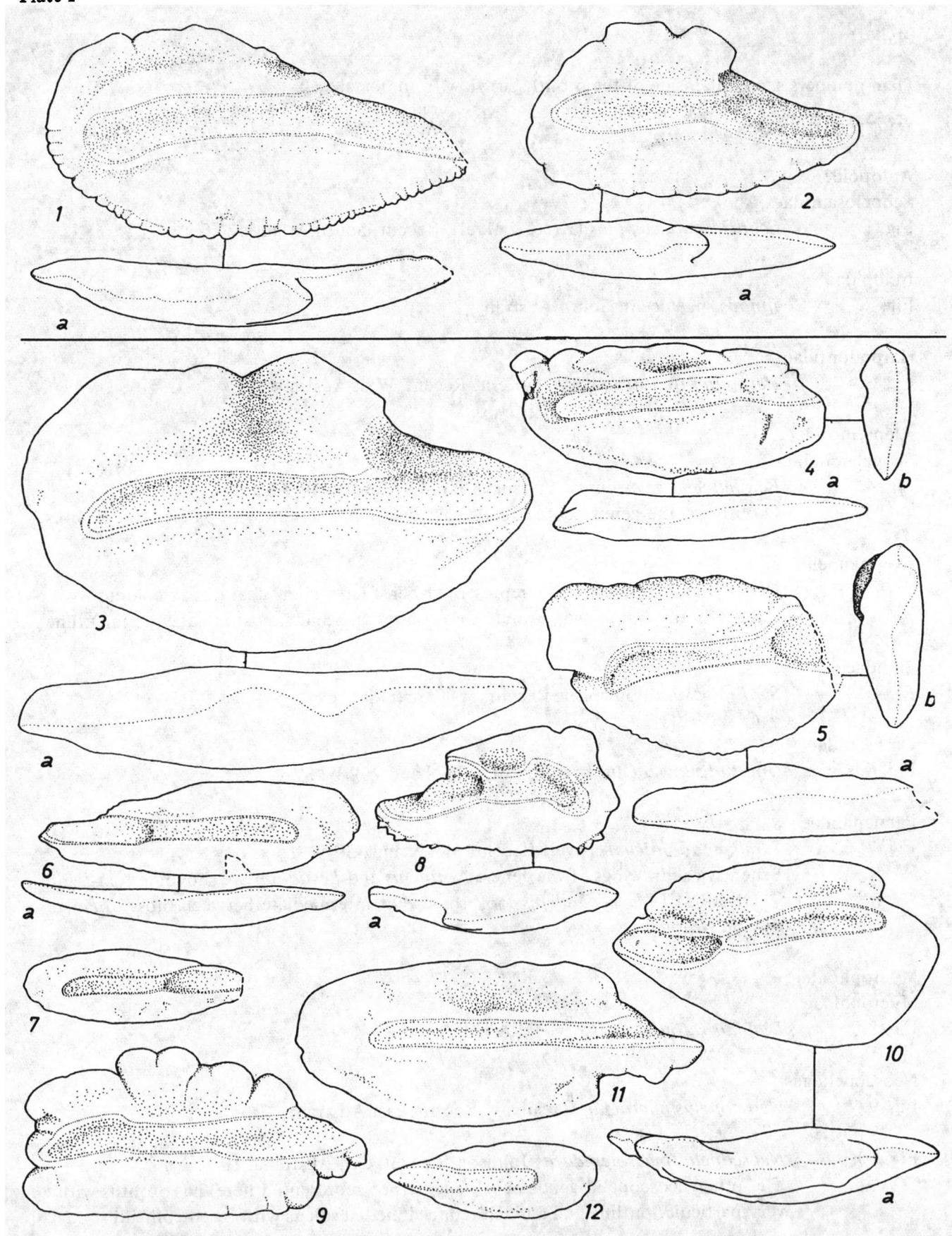


Plate II

Plain numbers show the inside of the otoliths; a) view from dorsal.

MYCTOPHIFORMES

Aulopoidei

Scopelosauridae

Fig. 1. *Scopelosaurus lepidus* (Kreft & Maul). Recent, South-Atlantic. 7.5 x.

Ipnopidae

Fig. 2. *Ipnopis* sp. Recent, South Australia. 30 x.

Harpodontidae

Fig. 3. *Harpodon translucens* Saville-Kent. Recent, West Australia. 16 x.

Alepisauroidae

Scopelarchidae

Fig. 4. *Benthalbella macropinna* Bussing & Bussing. Recent, 39° S and 21° W. 16 x.
Otoliths of the genus *Scopelarchus* have much in common with paralepidid otoliths.

Evermannellidae

Otoliths of this family (not represented here) have many features in common with sudid otoliths, but are somewhat more compressed and almost rectangular in outline.

Sudidae

Fig. 5. *Sudis jayakara* Boulenger. Recent, east Australia. 16 x.

Omosudidae

Fig. 6. *Omosudis lowei* Günther. Recent, 07° N and 20° W. 32 x.

Paralepididae

Fig. 7. *Paralepis atlanticus* Krøyer. Recent, 65° N and 33° W. 16 x.
Schematic drawings of the genera *Notolepis* and *Lestidium* are shown in text-figure 7. Otoliths of *Macroparalepis* look somewhat intermediate between those of *Paralepis* and *Notolepis*.

Myctophoidae

Myctophidae

Fig. 8. *Diaphus rafinesquei* (Cocco). Recent, Sicily. 14 x.

Neoscopelidae

Fig. 9. *Neoscopelus microchir* Matsubara. Recent, east Australia. 10 x.

Fig. 10. *Neoscopelus macrolepidotus* Johnson. Recent, east Australia. 10 x.

The other neoscopelid genus *Scopelengys* (not represented here) has otoliths with a very particular outline and a much reduced medial sulcus with fused colliculi.

Plate II

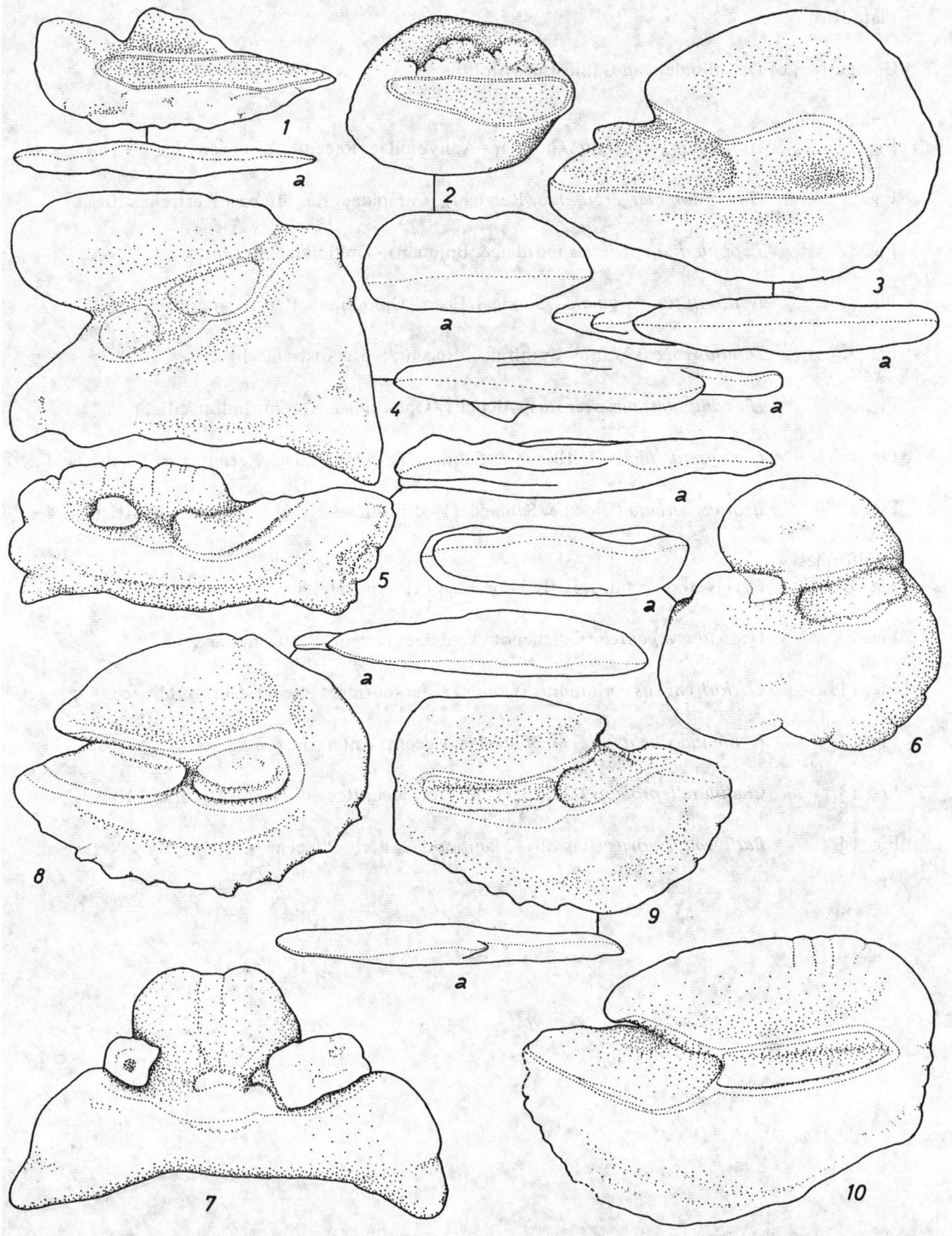


Plate III

Comparison of Ophidioidei and Gadiformes otoliths.

Ophidioidei

- Fig. 1. *Aphyonus gelatinosus* Günther - Aphyonidae. Recent, Caribbean. 9 x.
- Fig. 2. *Onuxodon margaretiferae* (Rendahl) - Carapidae. Recent, east Australia. 20 x.
- Fig. 3. *Lepophidium prorates* (Jordan & Bollman) - Ophidiidae. Recent, west. U.S.A. 4 x.
- Fig. 4. *Neobythites marginatus* Goode & Bean - Ophidiidae. Recent, Indopacific. 6 x.
- Fig. 5. *Dipulus caecus* Waite - Bythitidae. Recent, West Australia. 14 x.
- Fig. 6. *Holcomycteronus pterotus* (Alcock) - Ophidiidae. Recent, Indopacific. 6 x.
- Fig. 7. *Genypterus blacodes* (Bloch & Schneider) - Ophidiidae. Recent, east Australia. 4 x.
- Fig. 8. *Brotula barbata* (Bloch & Schneider) - Brotulidae. Recent, tropical east Atlantic. 4 x.

Gadiformes

- Fig. 9. *Phycis* sp. - Gadidae. Early Pliocene, northern Italy. 4 x.
- Fig. 10. *Gadiculus argenteus* Guichenot - Gadidae. Recent, Portugal. 6.5 x.
- Fig. 11. *Coelorhynchus carminatus* (Goode) - Macrouridae. Recent, Gulf of Mexico. 4 x.
- Fig. 12. *Hymenocephalus* sp. - Macrouridae. Recent, Antarctic. 6.5 x.
- Fig. 13. *Chalinura leptolepis* (Günther) - Macrouridae. Recent, North-Atlantic. 11 x.
- Fig. 14. *Bathygadus novus* (Bassoli) - Macrouridae. Early Pliocene, northern Italy. 4 x.

Plate III

