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The otoliths of the moridae (Teleostei, Gadiformes) and
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by
C. Karrer

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Introduction

The otoliths of the Moridae have been known since the detailed descriptions by Vaillant (1888) of Physiculus dalwigkii Kaup and Mora mora Risso; but no particular attention was paid to their structure which differs from all other otoliths. Frost (1926) apparently was not familiar with Vaillant's description since he does not refer to it in his presentation of the sagitta of Physiculus bacchus (Bl. Schn.). Schmidt (1968) describes, however only very briefly, the otoliths of 5 moridae species and points out their 'Moridic type'. Radiograms of the skulls of 4 species are reproduced in Svetovidov (1969) on which the otoliths are faintly recognizable. Kotthaus (1970) illustrates the sagitta of Physiculus peregrinus GTHR.

Several Moridae were caught during the voyages of the FFS 'E. Haeckel' (Fisheries research vessel of the Institute for Ocean Fisheries and Fish Processing, Rostock-Marienehe) in the Atlantic Ocean between 1966 and 1969. The great variety in form of the otoliths was discovered during their preparation (only the sagitta was considered) and this led to the suggestion to investigate their taxonomic significance. For this reason it was attempted to extend the investigation to as many genera as possible.

The Moridae were separated from the Gadidae by Svetovidov 1937 because of anatomical differences, and were elevated to a distinct family. They were the subject of investigations, by themselves or in conjunction with the Gadidae, in later

works by the same author (1940 to 1969). In his 1967 paper, Svetovidov emphasized that the taxonomy within Moridae is insufficiently known and is in urgent need of revision. Because of the small differences in external characteristics between the genera and the very large variability of e.g., the fin formulae, it is necessary to find phylogenetically useable differences for assessing relationships. The results shown below indicate that the structure of the otoliths is very suitable for this purpose.

I am truly grateful to many of my colleagues for their help: Prof. Bonnet, Sete; I.W. Brown, Melbourne; P. Buerton, Berlin; Dr. D.M. Cohen, Washington; L. Danke, Rostock; Dr. K. Diebel, Berlin; Dr. P. Kähsbauer, Vienna; B. Kossurok, Rostock; Dr. G. Kreft, Hamburg; Dr. R.M. McDowall, Wellington; G.E. Maul, Funchal; G. Palmer, London; Dr. J.R. Paxton, Sydney; Prof. M. Poll, Tervuren; Prof. T.S. Rass, Moscow; Dr. W. Schmidt, Abidjan; Mr. R.H. Scott, Hobart; Dr. F. Terofal, Munich; P.J.P. Whitehead, London; as well as the New Zealand Geological Survey, Lower Hutt. Special acknowledgement is due Prof. A.N. Svetovidov and his colleagues in Leningrad for the welcome accorded to me during my stay at the Zoological Institute of the Academy of Science. I am also very grateful to Prof. W. Weiler, Worms, not only for the loan of otoliths but also for his numerous valuable suggestions, his lively interest in the work, and particularly for proof-reading of the manuscript. I am indebted to Mrs. Jozsa, VEB Fotochemische Werke Berlin, for the preparation of radiograms.

Material

Unless indicated otherwise, all otoliths were prepared from freshly caught fish. The animals were to be damaged as little as possible, and the otoliths were removed through the bottom of the neurocranium by lifting the operculum as described by Kotthaus (1967). As to otoliths from preparations in collections, they were generally well preserved (even when the material was nearly 100 years old) in cases where the fishes had been kept continuously in alcohol. On the other hand, otoliths from

animals which had been exposed to formalin exhibited corrosion damage up to the point of complete decomposition of the otoliths. It is thus not true in every case that museum pieces are totally unsuitable for otolith investigations as was suggested by Luedemann (1941).

The preparation of otoliths from Moridae must be done with care since the tips break off easily. In all cases where only one Sagitta was prepared, the right-hand one was selected except for the illustrated sample / ^{from} Gadella maraldi (Risso). Otoliths which have not suffered damage by the conservation agent are sometimes recognizable quite well in radiograms.

We have investigated the otoliths (including those from the Tertiary and of Euclichtys polynemus McCulloch) of 16 genera with 23 species. They are described in the following. The whole fishes were also available for study except for Physiculus natalensis Gilchr., Laemonema barbatulum Goode and Bean, and L. yarelli (Lowe). In addition, the following species were available for comparison purposes, without preparation of the otoliths although their form was checked in some cases with the aid of radiograms.

Laemonema latifrons Holt and Byrne (I S H, 'A. Dohrn' St. 430/65, 63 N, 20 W; one specimen).

Laemonema sp. (ISH. WH-St. 83/68, 25 S, 44 W; two specimens).

Laemonema sp. (ZIAS 38936, SW-Atlantic; 7 specimens).

Laemonema longipes Schmidt (ZIAS 24477 and 25251 types, also 36021, 37841; ZMB 22439; North Pacific, one specimen each).

Lepidion inosimae (Günth.) (ZIAS 11726, Inosima; one specimen).

L. schmidti Svet. (ZIAS 22883, Misaki; holotype)

Lotella callarias Günth. (NMW 41643, Port Jackson; one specimen).

L. phycis (Schleg.) (ZIAS 22886, Nagasaki; 4 specimens; NMW 41632 Tokyo; one specimen).

Physiculus japonicus Hilg. (ZIAS 9689, type of Lotella maximowiczii Herzenstein, also 22885, 22887, 25195, Japan; one specimen each).

Ph. nematopus Gilb. (NMW 41954, Alaska; cotype)

Ph. rastrelliger Gilb. (NMW 41956, Alaska; cotype).

Ph. roseus Alcock (ZIAS 22884, Kagoshima; one specimen).
(Physiculus) marginatus (Gthr.) (ZIAS 38100, 38101,
SW-Atlantic; 3 and 6 specimens).

ISH = Institute für Seefischerei (Institute for Ocean
Fisheries), Hamburg

NMW = Naturhistorisches Museum, Wien (Museum of Natural
History, Vienna)

ZIAS = Zoological Institute of the Academy of Science,
Leningrad

ZMB = Zoological Museum, Berlin

And finally, the holotype of †? Palae^ogadus singularis (Koken)
(Otolith, Paleontological Museum, Berlin) as well as numerous
otoliths of Gadidae and Macrouridae of my own collection
were used for comparison.

Results

The sagittae of the Moridae differ conspicuously from all
otoliths described so far. Their form varies considerably
in spite of many common characteristics which are specific
to all sagittae of Moridae. Most of the genera that have
been studied can be divided into three groups which will
be described together. The investigations have led to
conclusions regarding the taxonomy which are discussed
further below.

We follow Chaine et Duvergier (1934) and Weiler (1942)
in the terminology of the structure of the otoliths. The
peculiarities of the otoliths of Moridae however made it
necessary to introduce a few new terms.

1. General Characteristics of the Otoliths of Moridae

Fig. 1 shows clearly the deviating form of the sagitta of
Moridae; the diagram of a right sagitta of Teleosteer is shown at
A, and that of another/^{right}sagitta, this time from a Morida, is given at B.

The sagittae of Moridae have an elongated shape and are often

extraordinarily thick (Fig. 1c). In such cases they are much reduced along the edges. Since there is neither an anterior nor a posterior edge, the definition of the dorsal edge (DR) and the ventral edge (VR) extends from the rostral tip of the otolith (or the opening of the ostium) to the tip of the posterior colliculum. Of the projections of the edges (pre- and postdorsal corner -PDE, and pre- and postventral corner -PVE) which are otherwise quite common in the sagittae of Teleosteer, only the predorsal corner is found in a few genera (of Moridae). Postcaudal region (PR) and postcaudal depression (PS) are absent since the end of the cauda is open. Inner and outer surfaces (see below) join dorsally in a rounded edge which is characterized by bulging projections. The ventral edge is almost always smooth. In the central and posterior parts, it consists of a sharp edge which forms the lower part of the ventral field. A more or less deep cut in the ventral edge separates the caudo-ventral tip (see below) from that of the posterior colliculum. Rostrum (R) and antirostrum (AR) are rarely present while an Excisura ostii in the typical form is always lacking.

The sulcus extends along the entire length of the otolith. At the collum (C) it is clearly divided into ostium and cauda, but there is never a separation. The sulcus is only lightly depressed in the ostium but very deeply in the cauda. The ostium is narrower than the cauda and, with a single exception (Auchenoceros), never exceeds it in length but is usually much shorter. The ostium ends closed near the edge, and is open in only few genera. It is filled by a flat or raised colliculum anterior (CA).

The cauda deepens continuously starting at the collum, and opens wide. It is confined by the sharp-edged cristae superior et inferior which end in substantial tips (caudo-dorsal-CDS) and caudo-ventral tip -CVS). This results in forms at the end of the cauda which are analogous to rostrum, antirostrum, and excisura ostii. The colliculum posterior (CP) is limited to a high very narrow crista which extends longitudinally throughout the cauda and exceeds it in height. This results

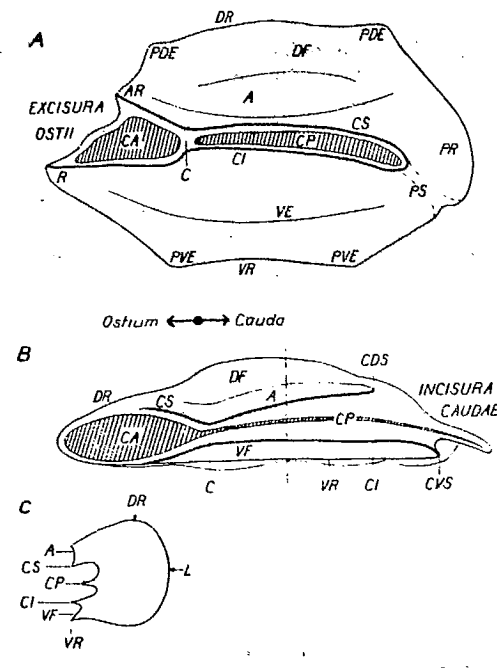


Fig. 1: Diagrams of a right sagitta: A from a Teleosteer (medial view); B of a Morida (medial view); C cross section of (B) along the broken line. A = area; AR = antirostrum; C = collum with upper and lower edge; CA = colliculum anterior; CDS = caudo-dorsal tip; CI = crista inferior; CP = colliculum posterior; CS = crista superior; CVS = caudo-ventral tip; DF = dorsal field; DR = dorsal edge; L = lateral line; PDE = pre- and post dorsal corner; R = rostrum; VE = ventral groove which separates internal zone and external margin; VF = ventral field; VR = ventral edge.

in the division of the cauda into a dorsal and a ventral groove. We have already mentioned the cut in the ventral edge which separates the CVS from the tip of the CP. The dorsal caudal groove is a much longer, partially very deep depression because the CDS ends a great distance from the tip of the CP. This depression is termed *incisura caudae*.

Crista superior (CS) and crista inferior (CI) are clearly developed from approximately the middle of the ostium all the way to the caudal tips. The first flattens out at the rostrum while the other merges with the ventral edge. An area (A) exists almost always and is usually differentiated from the dorsal field (DF) by a ridge. The area located ventrally to the sulcus is an undifferentiated surface, the ventral field (VF).

On the external surface (since the sagittae of Moridae are very thick this term has been chosen in favour of the more usual 'outside') we find that the structures (rounded or bumpy projections) stop ventrally before reaching the edge; the remaining space is more or less concave, smooth, or at least with a different structure than the rest of the external surface. This zone extends along the ventral edge. The lateral limit of the otolith, visible in dorsal and ventral views, is called the lateral line (L).

The descriptions that follow have been written as short as possible: the characteristics common to all genera precede the descriptions of the three groups, and are not repeated for each of the species.

Abbreviations for the dimensions are L = length, H = height, D = depth. The ratios of the dimensions are given in percent of the length. This appears to be preferable in broad otoliths rather than quoting length/height or length/width indices. The lengths of the collicula were measured as well, in order to characterize the different ratios of ostium and cauda.

Before each description, we have listed the number of specimens investigated, followed by the length of the illustrated otolith in brackets, and finally the average percentage values of the undamaged specimens. The dimensions of the

individual pieces are found in the tables.

2. Descriptions

Mora group

Form variable, highest near anterior end. The sequence 159
in which the genera are described corresponds to increasing
width which is coupled with a progressively reduced interior.
Rostrum and antirostrum are absent. CDS at moderate distance
from the end of the cauda. The incisura caudae is accordingly
relatively short (maximum 1/4 of the length of the otolith)
and very shallow. There is little difference in length
between CP and CVS. The crista inferior in most genera of
this group ends before the CVS which thus alone forms the
ventral edge.

Interior more or less flat but the crista superior always
retreats in an arch starting at the collum. As a result, the
straight CP and the CVS are visible in a dorsal view. The
ostium is shorter than the cauda, longitudinally elongated;
it ends, closed, some distance from the edge. An opening is
suggested only in Mora. The CA usually does not completely
fill the ostium. The two directly merging collicula are well
visible in all four genera: the colliculum anterior narrows at
the collum and continues in the crista of the C. posterior.
The cauda is flatter than in the other Moridae because of
the retreating crista superior, particularly its dorsal
groove. CP is straight and runs close to the crista superior.
The upper caudal groove is therefore narrower than the very
wide open lower one. CP and crista inferior are of approximate-
ly equal height.

The crista inferior projects into a pronounced upper corner
at the collum. The area is a conspicuous, elongated, shiny
surface of characteristic shape in all genera, including
Mora and Halargyreus for which they are not mentioned by
Schmidt (1968). The ventral limit of the area follows the
crista superior, its dorsal limit is a sinuate line, very
wide at the front, narrowing towards the rear as far as the
CDS. The crista inferior is less pronounced than the crista

superior. It drops behind the middle of the cauda and merges with the ventral edge. This creates at the end of the lower caudal groove a deep spate-like depression.

The external surface has little structure. The increase in width in Antimora and Lepidion results in the formation of a ventral surface which corresponds to a part of the external surface.

Mora mora (Risso) Fig. 2

Mora mediterranea, Vaillant 1888. Exped. Sc. 'Travailleur' et 'Talisman', Poissons (Scientific expeditions 'Travailleur' and 'Talisman', Fishes), p. 298, plate XXV, Figs. 6, 6a.

.... . Ventral field slightly concave; gradually it merges into the ventral edge towards the cauda. Two specimens have a shallow depression which extends to the edge.

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External surface smooth, anterior edge usually with two indentations. Larger bulge near the posterior end of the dorsal appendix caused by the deeper depression of the dorsal field. Flat groove above the cauda in place of the plain surface in Mora.

Variability: small, affecting the anterior dorsal edge.

The Sagitta illustrated by Fitch and Brownell undoubtedly belongs to H. johnsonii, the only species of this genus (H. affinis Collettis a synonym, according to Templeman 1968).

Antimora rostrata Gthr. Fig. 4

Antimora rostrata, Svetovidov 1969, Zool. Zh 48, p.1826 Fig. 1-6 (radiogram of skull with otoliths).

68 otoliths, (15.6mm), L:H:D - 100:37:25, CA:CP -1.6.

Preliminary remark: the large number of otoliths all come from animals which were caught at a depth of 550 to 1000m in the NW-Atlantic. The dimensions are summarized in Table 2.

Sagitta teardrop-shape, the pointed end caudal, thick. Dorsal edge rising at anterior with at least one indentation above the start of the ostium. The greatest height is attained above the middle of the ostium from where the dorsal edge falls more or less evenly towards the CP, sometimes undulating, sometimes smoothly. CDS ends at some distance before the CP and the incisura is consequently longer than in Mora or Halargyreus. The CVS exceeds the CP in the same measure as the CDS ends before it but it is not separated from it by an incision.

Inside even, only the dorsal field retreating slightly. Sulcus barely constricted at the collum. Ostium relatively wide, rounded at front, tapering evenly towards the rear. In most specimens the sulcus drops down to the edge in front of the crista inferior which ends below the middle of the ostium. A small indentation can thus occur in the ventral edge. CA tall, of granular consistency, not completely filling the ostium. Ventral caudal groove deeply excavated; the edge of the CP does not widen towards the rear; it is dentulated at the rear in the otoliths of very large fishes.

Cristae are weakly formed and start somewhat before the middle of the ostium resulting in shorter area and ventral field than in the other 3 genera. The area is depressed over its entire surface, not only in the central portion as in Mora. Crista inferior drops abruptly towards the ventral edge.

Exterior surface variable. The dorso-rostral part of the otolith dips strongly sideways so that no definite boundary between the dorsal field and the exterior surface can be determined. The indentation(s) of the dorsal edge above the ostium usually form short grooves. The posterior third, approximately, of the otolith is accompanied latero-ventrally by a comb which ends in a more or less high tip. This tip is also the extreme point of the roughly triangular ventral surface which has a small groove directly behind the ventral edge but which is otherwise even and glossy.

Variability: The shape of the anterior dorsal edge varies considerably. In small otoliths it always has 2 to 3 clearly differentiated bulges which flatten out with increasing size. The same thing happens in the dorsal field where otoliths of older animals have a more pronounced dorso-lateral drop with the result that the dorsal field ends in a tip pointing outwards. The shape of the CA does not always correspond to that shown in the illustration. The dorsal anterior bulge may be absent and the CA is narrow and elongated. But in numerous specimens - independantly of the size of the otolith the CA expands further dorsally; it may even cover the anterior end of the area and cover it in a caudal direction for a short distance.

As can be seen from the numbers in Table 2, no size-dependent differences in proportions can be found in the sagittae of the fishes which were investigated (total length ranging from 148 to 541mm). It might however, be desirable to measure a larger number of young specimens.

Lepidion eques (Gthr.) Fig. 5

Lepidion eques, Schmidt 1968, Arch. Fischereiwiss. (Archive of Fisheries Science), XIX, supplement 1, p. 13, Plate 2, fig. 22, Plate 15.

6 Otoliths, (11.4mm), L:H:D - 100:39:30, CP:CA-1.5.

Sagitta almost rectangular, rounded predorsal corner, very thick. Dorsal edge rising vertically at front, turning at a right angle and then running almost horizontally to CDS, with 2 larger bulges in front and a few very small bulges at the rear. Incisura short and very flat. Ventral edge smooth, convex at front, weakly concave at rear. CP and CDS of equal length with only a shallow indent between them.

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Discussion

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Since the discovery that the otoliths are specific to each species (Cuvier et Valenciennes 1828, Koken 1884, Ihering 1891) their importance in taxonomy has been

emphasized repeatedly. But in spite of this, until very recently authors have always limited themselves to merely descriptive representations of otolith morphology, even when larger taxonomic groups were treated (e.g. Berinke 1956, Hungarian Cyprinides; Bauza Kullan 1956, 1958 Pleureonectiformes). Conclusions regarding the taxonomy were not drawn. Only few works such as those of Frizzell (1965), Stinton (1967) and Weiler (1968a) point in this direction.

The sagittae of the Moridae are distinguished by a number of morphological particularities (wide sulcus which extends through the entire length of the otolith; cauda never shorter, and usually much longer than ostium). But the definitive characteristics are the deep, wide open cauda with the grate shaped collicum posterior and the incisura caudae. We cannot say how these unusual formations have developed because corresponding fossils are not available. Since such structures are not known in any other sagitta studied so far, the classification of otoliths with these characteristics as belonging to the Moridae must be undisputed. The structure of the sagitta thus adds to the anatomical peculiarities which Svetovidov (1937) pointed out in his works and which have led to the separation of the Moridae from the Gadidae - connection between the air bladder and the auditory organ, fontanelles in the rear wall of the skull, bony channel of the olfactory nerves, and the partially ossified interorbital septum. It thus confirms that the Moridae are a monophyletic group with a long separate development. Proof of this may be the presence of all typical characteristics of the Moridae-sagitta in the Tertiary otoliths. Okamura (1966) investigated the brain structure of gadiform fishes and found that the lobi optici in the Moridae are smaller than the telencephalon, in contrast with the Gadidae, and that the tractus olfactorii consist of a single bundle on each side. However, only two species from each family had been studied, and the subject requires further study.

Just as the uniform development of the cauda permits the classification of an otolith as belonging to Moridae, so does the variety of form permit the easy determination of the genera

and makes it possible to determine relationships within the family. But we must emphasize that the otoliths can only be one of many characteristics. A comprehensive study of as many species as possible was urged by Svetovidov (1967) and is being carried out by Cohen; it can uncover further commonly derived characteristics (synapomorphisms) between the individual taxa and thus facilitate the determination of sister groups (Hennig et al. 1953).

As a result of the present study, Fig. 20 is presented which illustrates the relationships between the genera of Moridae. The genera of each of the three groups described together are undoubtedly more closely related to each other than to those of the other two groups in each case, or to the remaining genera. It is certain that the Pseudophyscis group stands as a sister group apart from all other Moridae because of its completely aberrant form of the ostial section of the sagitta; but whether it can indeed be considered as an original group must be decided on the basis of other (perhaps osteological) characteristics. The same trends occur in the Mora and Physiculus groups which are considered to be sister groups: an increase in the width of the otoliths is connected with a reduction of the margin zones and the development of a ventral surface. The spindle shape of the sagitta of the Physiculus group with the deeply receding structures (sulcus, ventral field, area), the broad incisura caudae, and the stretched posterior colliculum, are interpreted as synapomorphisms. Not shown in the diagram are: Lotella whose position can not be determined on the basis of the otoliths; Actuariolum in order to avoid fixing a period; and genera whose otoliths are not known (Austrophycis Ogilby 1897, Eretmophorus Giglioli 1889, Gargilius Jensen in Schmidt 1906, Rhynchogadus Tortonese 1948 = Hypsirhynchus Facciola 1884).

A derivation of the otolith forms from one another is clearly discernible in the Mora group. Mora is the only genus which possesses a ventral field whose ventral boundary does not coincide with the ventral edge but leaves a narrow margin. The anterior colliculum of Halargyreus, Antimora, and Lepidion

has a raised granular structure, and never completely fills the ostium. On the other hand, the anterior colliculum of Mora has the form of a very flat carpet lying adjacent to the edge of the deeply depressed ostium. It is not possible to decide whether the 'open' ostium of Mora is an original condition or a secondary phenomenon. The genera Halargyreus, Antimora and Lepidion are a sister group opposite Mora.

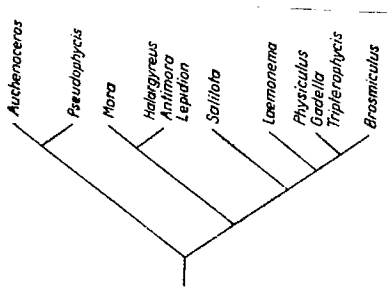


Fig. 20: Relationships between the genera of Moridae based on otolith studies.

Within the Physiculus group, the sagitta of Brosmiculus with its low height and extraordinary width constitutes a separate developmental branch towards a gracile, very fragile otolith, while the sagitta of Laemonema in its stout robust form represents another extreme of the spindle shape. There are more characteristics common among the otoliths of Physiculus, Gadella and Tripterophycis than they have in common with either of the genera mentioned above. The objection that considerable differences occur between the habits of these three genera can - considering our present insufficient knowledge of osteological characteristics - only be refuted with the statement that 'similar' does not necessarily mean related (see below). For Tripterophycis, the

only Moridae with three dorsalia, Whitley (1948) set up a separate family which was supposed to exhibit relationships with the Macrouridae. But the investigations of the otoliths do not in any way justify a separation from the Moridae.

Cohen (according to Svetovidov 1967) considers Lotella maximowiczi Herzenst. to be a synonym of Physiculus japonicus Hilg., based on the dentation of the jaw which differs from that of Lotella. Radiograms of the specimens at the Zoological Institute of Leningrad which Prof. Svetovidov was kind enough to make available to me, show the typical sagittae of Physiculus.

The otoliths of Salilota (limited to a single species in the area of Argentine/Chile) do not coincide in all characteristics with those of the remaining genera of the Physiculus group. They deviate in having a relatively short cauda and their area has a different shape. But since differences in the proportions of the sulcus are hardly decisive there can be no doubt that the genus belongs to this group.

The sagitta of Lotella has some characteristics which approach Salilota and the genus may perhaps have to be placed close to the Physiculus group. Relationships with the genera of the Mora group do not exist.

Günther established in 1862 the genus Pseudophyscis for the New Zealand species Lota breviscula Rich. and described the Australian species Ps. barbatus in 1863. In 1887 however he withdrew it, saw it as a synonym of Physiculus - as is to some extent still done today (Munro 1957; Scott 1962) - and also set Ph. bacchus = breviusculus. The equating of these two species is still found in recent literature. Only Graham (1938) first points out unambiguous differentiating characteristics. The investigation of the otoliths shows that there is no close relationship between Physiculus and Pseudophyscis (this genus also lacks the luminous organ (see below) which is seen as typical by Cohen according to Svetovidov 1967). Pseudophyscis can thus not be

considered as a subgenus of Physiculus (Whitley 1968). The otolith investigation further shows that in addition to breviusculus, this genus also includes barbatus and bacchus. The distribution of Pseudophyscis is limited to the area of Australia. The cosmopolitan genus Physiculus (it remains to be established to what extent the remaining 10 species not mentioned here do indeed belong to it) does thus not occur in the southwestern Pacific.

The genus Auchenoceros (Günther 1889), ^{which probably} because of the first dorsalis, which consists of a single ray, is placed near Bregmaceros and together with it into a separate family (Jordan 1923; Svetovidov 1948), belongs to the Moridae as was already conjectured by Svetovidov (1937): in addition to the typical otoliths this genus also has the connection between air bladder and auditory organ, the fontanelles in the posterior wall of the skull etc. Bregmaceros otoliths by the way, have a completely different form (Bachmayer and Weinfurter 1965; Kotthaus 1969).

There are areas of agreement in the formation of the cauda and its margins, between Actuariolum and the genera of the Pseudophyscis group; but because of the totally different structure of the ostium this fossil genus cannot be directly included in that group.

(Ph.) marginatus belongs to neither Physiculus nor any other genus of the Physiculus group. The species may perhaps be classified under Pseudophyscis or form a new genus, but this cannot be decided until undamaged otoliths have been studied or when other unambiguous characteristics differentiating the genera can be found.

Equally uncertain are the relationships within the genus Laemonema. I have already indicated in the section describing the otoliths that the species mentioned by Svetovidov (1967, 1969) but not described, exhibits remarkable differences in its otoliths relative to the species investigated here. This species also deviates in its habit from the majority of the Laemonema species but shows remarkable agreement with L. latifrons Holt and Byrne (1908) (the otoliths of the only investigated specimen of that species are destroyed in the

radiogram). A splitting up of the genus Laemonema will therefore probably be inevitable in a revision. Rass (1954) already indicated a grouping within the species. According to Rass, not only L. latifrons but also L. globiceps Gilchrist (1906) and L. multiradiatum Thompson (1916) possess an interorbital space which is considerably wider than the diameter of the eye, smaller rays in addition to the ventralis rays, and only a rudimentary barbel or none at all.

Rass (1954) raises L. longpipes Schmidt (1938) to a separate genus, Podonema (Whitley 1964/65 replaces the name with Podonematischys since Podonema is already preoccupied by Solier 1851). Lindberg and Legeza (1965) have restored the species to Laemonema until a final clarification of the matter. The investigation of the specimens at the Zoological Institute in Leningrad (including the types) and of a personally owned specimen (I am very grateful to Prof. Rass, Moscow for this gift) suggests that a separation, based on external characteristics, would be quite in order. A preparation of the otoliths was not possible because they were completely dissolved in our specimen. The radiogram of one of the Leningrad samples shows a very small otolith which cannot be recognized sufficiently to determine if it is identical with the typical Laemonema otoliths. However, no agreement appears to exist with the otoliths of L.sp. from the group around L. latifrons.

Norman (1957) classifies the genus Microlepidium Garman (1899) under Laemonema. Microlepidium includes the species M. verecundum (Gilbert 1897) and M. grandiceps Garman, each described only on the basis of a single small specimen. The protruding lower jaw at the symphysis is mentioned for both; for M. grandiceps, a V-shaped row of teeth on the vomer is mentioned also (Günther 1862 lists 'a small group of vomerine teeth' (sic) in the diagnosis for the genus Laemonema) as well as the small number of rays in the pectoral fin. These are the same characteristics that Rass (1954) lists for Podonematischys.

In the same year as Rass, Taki (1954) takes a critical view of the Laemonema species. Unfortunately he does not consider all the species, for instance L. latifrons and L. multiradiatum. His new subgenus Guttigadus (Type: L. rhodochir Gilbert) suggests a possible further subdivision of Laemonema s.str. in the sense of Rass.

Another problem is the position of Laemonemodes compressicauda Gilchrist (1903) which was also classified under Laemonema by Norman (1957). It is certain that the otoliths can contribute here as well in answering the many open questions. They should definitely also be considered in any revision of the genus Laemonema.

Svetovidov (1967) gives more examples of the uncertain position of species and genera. Let us also mention here Strinsia tinca described by Rafinesque in 1810 and considered a nomen dubium by Cohen and Torchio (1963). The specimens known under this name more recently were actually injured samples of Gadella maraldi (Risso). Whether the Strinsia alata Steindachner (1859) found in the Hungarian Tertiary belong to the same genus remains to be determined. The genus classification should also be rechecked for the remaining fossil species which have been described from impressions and were listed under Moridae (Danilchenko 1960 in the English translation of 1967).

The position of several juvenile forms for which separate genera have been established is also questionable. Mead, Bertelsen and Cohen (1964) consider Gargilius from the North Atlantic to be the pelagic stage of Lepidion eques (= lepidion). They assume they are also identical with the also North Atlantic Lotella maxillaris Bean (1885) and the Mediterranean Rhynchogadus hepaticus (Facciola). Eretmophorus kleinenbergi Giglioli, only known from the Mediterranean but in relatively large specimens (up to 105mm) is considered by D'Ancona (1931) to be the post-larval stage of Lepidion lepidion. Svetovidov (1967) concludes from the difference in larval forms that L. lepidion and L. eques must be two different species. This

has since been proved in a different way through the work of Templeman (1970). D'Ancona (1933) compiled the larval forms of the Mediterranean Moridae. There it is seen for instance that the normal number of rays is reached in Mora mora of 20mm and Gadella maraldi of 26mm length. We can therefore safely assume that this is also true for the very much larger specimens of Eretmophorus kleinenbergi. But a comparison of the fin formulae of this species (D 4-5/66-77, A 64-67 according to D'Ancona) with those of Lepidion lepidion (D5/54 - 58, A48-51 according to Templeman) shows a discrepancy which far exceeds the nevertheless large variability of the Moridae. Compared with the juvenile stage of the other Moridae Eretmophorus still exhibits very much larval traits at a length of 105 mm which makes it unlikely that this genus is the synonym of another. Gargilius vitellus Koefoed (1953) and Lotella maxillaris are unusual among the Moridae with 10 rays in the ventral fins. This indicates that they may perhaps be a separate species.

An investigations of the otoliths would in all these cases leave no doubt as to which genera the species belong to.

Svetovidov (1967) points out the insufficient knowledge of the relationships within the Moridae and explains the reasons for this. Furthermore there exist no comprehensive critical descriptions, particularly of the larger genera (Norman 1935, 1937 gave bibliographies for Physiculus and Lepidion, based on the material of the British Museum which are of course not complete; I have already mentioned the remarks of Rass 1954 and Taki 1954 regarding Laemonema). Svetovidov deploras also the insufficient weight of the characteristics used in the demarcation of the taxa. It is clear that the type of dentation, the presence or absence of vomer teeth (Salilota - Physiculus), or of an extended first (or second, according to Templeman, 1970) dorsalis ray (Lepidion - Salilota) can only be a determinative mark but never a sign of relationships. Kaup (1858) for instance notes the absence of vomer teeth in his short diagnosis of the genus Lotella. But Phillipps (1926) describes an unusually large specimen of L. rhacina which has them. This changes nothing in the status of the genus, it only shows how easy it is to classify species incorrectly when only

one such characteristic is the basis. This is particularly grave in rare species.

According to Stinton (1967), the otoliths evolve relatively slowly because they are not, due to their location, exposed to the selective pressure of the external conditions of life. It is therefore possible that Eocene otoliths can often only be distinguished with difficulty from those of recent genera. The conclusion is that genera, such as Auchenoceros and Pseudophycus, may be closely related although they differ in external appearance. Differences between the otoliths on the other hand indicate a long standing separation. The sagittae of Salilota and Lepidion for instance show that there is no relationship between the two genera (Norman 1937).

According to Cohen (footnote in Svetovidov 1967), the difference between Physiculus and Lotella (differentiated according to the dentation of the jaws so far) is mainly the presence or absence of a luminous organ. Franz (1910) already mentions a dark, scaleless spot in front of the anus in Ph. japonicus which has been considered since Kishitani (1930) to be a luminous organ. But this is not limited to the genus Physiculus (in addition to the species mentioned here it is also found in filifer Garman 1899 and, according to Jordan and Hubbs 1922, in fulvus Bean, nematopus Gilbert and rastrelliger Gilbert): it is also observed in Tripterophycis (Brauer 1905), Salilota (Thompson 1916), Gadella (Maul 1952) and according to our own studies, in Brosmiculus. It is noteworthy that among the Moridae, a luminous organ occurs only in the Physiculus group (only Laemonema lacks it; it remains to be determined whether this is true for all species).

Laemonema also differs in another characteristic from the other genera of the Physiculus group: the anal fin starts relatively far back, resulting in a large distance between ventralis and analis. This distance is also much greater in genera of the Mora group than in those of the Physiculus group.

This begs the question whether the otoliths can be a basis for determining the position of the Moridae within the

Gadiformes. The otoliths of all gadoids have been investigated with the exception of those of Arctogadus (not listed in Weiler 1968b; for the genera missing there see Skalkin 1961 and Schmidt 1968). Sanz Echeverria (1935) and Schmidt point out already that their form varies considerably. This is particularly true of the Lotinae which are certainly not a monophyletic group. The differences between the sagittae of Merluccius and the Gadinae are too small to justify a segregation of this genus from the Gadidae and the establishment of a separate family.

Svetovidov (1969) has shown that the position of the lobi olfactorii between the nasal capsule and the front of the brain is age dependent, and that this invalidates the main characteristic which originally led to segregation.

Koken (1885, 1891) describes 2 species of Gadidae from fossil otoliths and mentions a deeply depressed sulcus and collicular formations with a 'longitudinal keel'. But a re-investigation of the typus of ?Palaeogadus singularis showed that the longitudinal keel has not even a remote similarity with the ridge shaped colliculum posterior of the Moridae.

It has already been said that Euclichtys is not a Morida. The fragmentary otoliths which nevertheless show the central parts of the sulcus well, indicate fairly significant coincidences with Macruronus (from Frost 1926, and from a sagitta of M. magellanicus Lönnberg in my possession). It is also interesting in this context to find that the radiogram on which Svetovidov (1969) based his Figs. 1-10 of Melanonus gracilis, shows sagittae (Kotthaus 1970 has recently illustrated one of M. zugmayeri) which have a conspicuous similarity with those of Gaidropsarus gen. (Schmidt 1968, and otoliths of G. ensis in our own collection). The characteristic may help in resolving the question of the taxonomic position of Melanonus which was originally classified under the Moridae without having the family characteristics (Svetovidov 1967). Marshall (1966) considers a separate family to be necessary because of the position of the bulbi olfactorii.

As to the knowledge of the otoliths of the remaining Gadiform families (Muraenolepidae, Bregmacerotidae, Macrouridae, and Melanonidae, according to Svetovidov 1969), it is very poor except for the Macrouridae whose sagittae are quite uniformly shaped - even among the Ophidiidae (incl. Brotulidae), Carapidae and Zoarcidae which are now included in the order again, as well as Pyramodontidae (Greenwood et al. 1966).

Considering the otoliths and the numerous other anatomical differences (Svetovidov 1937) which led to the establishment of the family, we must strictly reject any relationship between one genus or a group of genera of the Moridae, and the Macrouridae as suggested for Tripterophycis by Whitley (1948), or the Gadidae as suggested for Laemonema (with respect to Urophycis) by Rass (1954). Numerous characteristics, adaptations to the mode of life, have evolved in parallel within the Gadiformes, e.g. the short and thickset shape and the complete, very fine covering with scales of groundling species such as Lotella - Raniceps; the splitting of dorsal and anal fins into several segments in Mora, Halargyreus - all Gadinae; the first dorsal fin consisting of a single ray in Auchenoceros - Bregmaceros; the elongated jaws in pelagic species such as Halargyreus, (Laemonema) longipes - Micromesistius, Merluccius. But in no instance are they an expression of a phylogenetic relationship.

In conclusion, let me point out again the taxonomic importance of the otoliths. The differences will not always be as conspicuous as in the Moridae but they make the otoliths of recent fishes suitable as additional determinant marks, an idea first proposed by Kotthaus 1967. It is certain that the otoliths can make a significant contribution to the resolution of taxonomic problems in other groups as well, for instance the Zeiformes (Stinton 1967) and should therefore be considered in relevant works.