MORIDAE: OVERVIEW

Chris D. Paulin

ABSTRACT. The family Moridae is defined by four features: a swim bladder-auditory capsule connection, a caudal skeleton with four or five hypurals and X-Y bones, a joined first neural spine, and distinctive otoliths.

About 95 species are currently known and these can be placed in 17 genera. In addition, five species representing three genera are known only from juvenile specimens.

On the basis of otolith structure the family can be divided into three groups. Although there is general agreement among workers on interrelationships, there is no consensus on the placement of some genera within the framework.

INTRODUCTION

The family Moridae is defined by the following characters: a swim bladder-auditory capsule connection, a caudal skeleton with four or five hypurals and X-Y bones, a joined first neural spine, and distinctive otoliths (Cohen, 1984). The group exhibits a high degree of morphological difference between some genera, but understanding of infrafamilial relationships is hindered by an equally high degree of morphological similarity among others. Convergence, reductive trends, and parallel specializations are evident throughout the group.

The family Moridae was proposed by Svetovidov (1937) based on the unique swim bladder connection with the auditory capsules, a character that was first described by Parker (1883) and subsequently by Beatie (1890) (Fig. 1). Svetovidov (1940, 1946, 1948) confirmed the validity of the specialized swim bladder as a diagnostic character for distinguishing morids from other gaidoids. Rosen and Patterson (1969) recorded additional unique characters in the morid caudal skeleton.

Although morid otoliths were illustrated and described by Vaillant (1888) and Beatie (1890) and have been reported in both paleontological and ichthyological literature during the twentieth century, Schmidt (1968) appears to have been the first to recognize their uniqueness at the family level. He illustrated sagittae from five Atlantic genera of morids and noted that, “although the form of the otolith within this family is by no means uniform, it is so characteristic that one can speak of a morid type.”

The character that makes the morid sagitta distinct is the deeply channeled bifurcate cauda (posterior portion of the sulcus or groove on the inner face of an otolith, Fig. 2), a feature first noted by Frost (1924) in his studies of fossil otoliths from New Zealand. The function of the bifurcate cauda is unknown, but may be related to the other morid auditory specialization, the swim bladder connection.

About 95 morid species are currently known and these can be placed in 17 genera. In addition, five species representing three genera are known only from juvenile specimens and may represent juvenile stages of other genera. Otoliths are unknown for at least four genera. Osteological information is not available for most genera. A summary of meristic characters is provided in Table 1.

CHARACTERISTICS OF INFRAFAMILIAL GROUPS AND COMPONENT GENERA

Two independent studies by Karrer (1971) and Fitch and Barker (1972) based on examination of otoliths from approximately two-thirds of the known morid genera reported that the diversity of characteristics found on the morid otolith are sufficiently consistent as to permit identification of the genera.
Morid genera were previously distinguished by characters of uncertain validity, and defining relationships between genera was difficult. From the results of their studies, both Karrrer, and Fitch and Barker were able to show that the morid otoliths fit into three natural groups (Fig. 2). In addition to these three groups, which possibly represent a basis for division at the subfamily level, there are three genera that Schwarzhans (1984) placed in a fourth group which he considered to be a specialized offshoot of the "Mora" group.

**"Mora" Group**

Characterized by a cup-shaped bend on the crista inferior. The ostium is shorter than the cauda, and the crista superior is more than three-fourths as long as the crista inferior.

Four genera can be placed within this group: *Mora*, *Halargyreus*, *Lepidion*, and *Antimora*. A shared character other than sagitta configuration is the complete or partial division of the anal fin (to a lesser extent in *Antimora*). Svetovidov (1948) assumed on functional grounds that a single fin is the primitive condition and arranged genera in a transition series based on increasing number of fins and their distance of separation. His hypothesis is supported by the presence in all gadiforms of a single continuous series of pterygiophores, present even over areas that lack fin rays. Complete division of the second dorsal fin has occurred in the morid genera *Tripterygius* and *Auchenoceros*. On the basis of otolith configuration it appears this is convergence and is not evidence for relationship.

All genera within the "Mora" group comprise deep-water fish, usually found in depths of 400-1200 m; *Antimora* is usually found in depths greater than 1000 m. All four genera are characterized by relatively few species: *Mora*—one, *Halargyreus*—one, *Antimora*—two, and *Lepidion*—six or seven. Most genera are widespread in temperate seas.

**Mora** Risso, 1826

The genus *Mora* is represented by a single Tethyan species *Mora moro* (Risso). Two separate species were previously recognized for southern hemisphere populations; however, examination of spec-
Table 1. Summary of meristic information for morid genera.

<table>
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<th>Genus</th>
<th>No. of species</th>
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<th>Caudal</th>
<th>Total</th>
<th>Fin rays</th>
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</table>

imens by Paulin (1983) showed no justification for separate taxa based on morphometric measurements or otolith shape. Although morid otoliths have been used for species determination, particularly in describing fossil taxa, the variability of configurations within living species makes the sagitta unreliable. Examples from juvenile specimens are particularly variable.

_Halargyreus_ Günther, 1862

The genus is represented by a single pelagic species, _Halargyreus johnsonii_ Günther, found in temperate waters (Tethyan) in 500-1000 m. _Halargyreus_ differs from the other genera within this group in the loss of the barbel and possessing a protruding lower jaw, which are adaptations related to ecology. The genus was revised by Templeman (1968) and Cohen (1973).

_Lepidion_ Swainson, 1838

Northern Atlantic _Lepidion_ were revised by Templeman (1970). The genus is represented by six or seven benthic species, and is found in all temperate waters in 500-1200 m. _Lepidion inosimae_ (Günther) reaches lengths in excess of 2 m and is the largest species within the family. Critical comparison of the nominal species in the North Atlantic with those in the Pacific is required.

_Antimora_ Günther, 1887

The genus is represented by two abyssal species found below 1000 m. _Antimora rostrata_ (Günther) is found worldwide except for the North Pacific, where it is replaced by a second species, _A. microlepis_ Bean (Small, 1981). _Antimora_ is distinguished from other genera in this group by the protruding snout, incomplete division of the anal fin and very high ratio of precaudal to caudal vertebrae.

"Pseudophycis" Group

Characterized by otoliths with the ostium approximately equal to the cauda and a crista superior more than three-fourths as long as the crista inferior.

Three genera can be placed in this group: _Pseudophycis_, _Lotella_, and _Eeyorius_. The species of all three are coastal dwellers, usually found in depths of less than 300 m. The group can be regarded as
manifesting the primitive condition within the Morididae, lacking any development of light organs or derived fin structure as found in the “Physicus” and “Mora” groups respectively.

**Pseudophycis** Günther, 1862

*Pseudophycis* is represented by three species (Paulin, 1983) confined to the Australasian region.

**Lotella** Kaup, 1858

*Lotella* is represented by at least six species and a revision of the genus is required. *Lotella* is distinguished from *Pseudophycis* by otolith shape and dentition (Paulin, 1983).

**Eeyorius** Paulin, 1986

*Eeyorius* closely resembles *Pseudophycis* in external morphology and dentition and differs from that genus in otolith shape. Otoliths of *Eeyorius* are similar to *Pseudophycis* in thickness and in having a crista superior almost as long as the crista inferior but differ in having a relatively smooth, unexpanded middorsal region and an ostium shorter than the cauda. *Eeyorius* is perhaps more closely related to *Lotella* but differs from that genus in having a brush-like band of teeth and lacking an outer row of relatively large, widely spaced pointed teeth. Otoliths of *Eeyorius* differ from those of *Lotella* in being thinner and in having a crista superior almost as long as the crista inferior.

**“Physicus” Group**

Characterized by spindle-type otoliths with a relatively short ostium and a crista inferior that is almost twice as long as the crista superior.

Seven genera can be placed within this group and are divided into two “subgroups” on the basis of presence or absence of a ventral light organ. The genera within the “Physicus” subgroup are the most specialized within the Morididae. These genera all possess light organs and one, *Tripterophycis*, has three dorsal fins.

**“Physicus” Subgroup**

Genera within this subgroup include *Physicus*, *Gadella*, *Salilota*, and *Tripterophycis*; all have very similar otoliths. Fortunately, these genera are widely divergent in external morphology and easily identifiable. All genera within this group possess a ventral light organ. No other morid genera have a light organ; although, there is a possibility of luminescent tissue occurring within genera of the *Laemonema* subgroup. Recently captured juveniles of *Lepidion schmidti* in New Zealand waters possess a midventral streak and ring around the anus of deeply pigmented tissue which is possibly luminescent. In specimens over 150 mm SL, the pigmented tissue is irregular and it is not visible in specimens over 200 mm SL. There appears to be no discrete light organ as in “Physicus” subgroup species (personal observation). Haneda (1951) and Marshall (1965) reported luminescence in juveniles of non-luminescent adult macrourids. The difference in structure of the light organ of “Physicus” group species and that of juvenile *L. schmidti* (“Mora” group) suggests independent phylogenetic origins.

**Physicus** Kaup, 1858

Morid fishes of the genus *Physicus* are distributed in all tropical, subtropical, and warm temperate regions of the world ocean in depths of 40–1500 m, usually 100–600 m. Most of the species are superficially very similar and easily confused. For this reason they are in general poorly known and not readily identifiable in most parts of the world. Despite the slow rate at which knowledge has accumulated on those features that are impor-
tant in diagnosing the species, very few names of species are synonyms; out of 33 available names, 31 are valid (Paulin, in preparation).

Norman (1937) presented a synopsis of the species of the genus based on material in the British Museum, giving brief synonyms and distributional data for 17 species. Three of the species recorded by Norman have subsequently been shown to belong to other genera (Karrer, 1971; Fitch and Barker, 1972; Paulin, 1983) on the basis of otolith shape. Otoliths of 13 Physicus species have been illustrated (Kotthaus, 1970; Karrer, 1971; Steurbaut, 1979; Paulin, 1983; Parin, 1985); they are not reliable for identification of species.

Cohen (1979) noted that Physicus had a ventral light organ and that there were more than 20 named species which had never been revised. Prior to Cohen (1979) few descriptions of Physicus species indicated the presence or absence of a ventral light organ. Alcock (1893) described P. argyropastus as having a pre-anal pigmented pit, and Garman (1899) described a small scaleless rounded space anterior to the vent in P. filifer.

Franz (1910) and Jordan and Hubbs (1925) reported a ventral fossa in P. japonicus Hilgendorf, P. fulvus Bean, P. nematopus Gilbert, and P. nastrellig Gilbert, which Hickling (1931) interpreted as a luminous organ.

Cohen (1980, personal communication) noted that the position of the light organ was important in diagnosing Physicus species. Okamura (1982) used the position of the light organ in relation to the anus, in addition to other characters, to diagnose three new species from the Kyushu-Palau ridge, and Parin (1985) noted the position of the light organ in his descriptions of three new species from the Nasca Ridge.

The results of my study (Paulin, in preparation) show that Physicus species can be identified by measurements of the size and position of the dermal fossa of the ventral light organ (expressed as a percentage of ventral fin base to anal fin origin distance). I recognize 31 previously described nominal species and describe another seven new species.

Most Physicus species have fairly restricted geographical distributions, and it is likely that other species will be found.

Gadella Lowe, 1843

A number of genera have been proposed for morid fishes that possess a ventral light organ and lack a mental barbel: Gadella Lowe, 1843, type species G. gracilis Lowe, 1843; Uraleptes Costa, 1858, type species Gadus maraldi Risso, 1810; Brosmiculus Vaillant, 1888, type species B. imberbis Vaillant, 1888; and Leptophyisc Garman, 1899, type species Leptophyisc filifer Garman, 1899.

Günther (1862) examined the holotype of Gadella gracilis and synonymized it with Uraleptes maraldi. Brauer (1908) considered Leptophyisc a junior synonym of Physicus. Examination of specimens of Brosmiculus and Leptophyisc (Paulin, in preparation) shows them to be congeneric with Gadella.

Gadella is represented by seven nominal and one undescribed species (Paulin, in preparation).

Salilota Günther, 1887

Salilota australa (Günther) is the sole representative of this genus, which is closely related to Physicus. It has a similar shaped otolith and light organs and differs in possessing vomerine teeth. It occupies a different habitat, viz., shallow water, and is found only in South American waters where it apparently replaces Pseudophysicus.

Tripteryhis Boulenger, 1902

Tripteryhis, represented by T. giglchristi Boulenger, is confined to the Southern Hemisphere. A second undescribed species of Tripteryhis has been reported from the southeastern Pacific (Park et al., 1981; Parin, 1985). The genus is distinguished in having three dorsal fins and the light organ restricted to an area around the anus and not separate as in Physicus, Gadella, and Salitola.

“Laemonema” Subgroup

The remaining genera in the “Physicus” group do not have distinct light organs but most show deeply pigmented tissue, particularly around the abdominal region, which may be luminous. Otoliths are very thick and robust, and as with the “Physicus” subgroup it is difficult to distinguish between genera using otoliths alone. At least four genera can be placed in this group: Laemonema, Microlepidium, Podonomatchay, and Momontaira.

It is unclear at present as to how many genera should be recognized. Most of these fishes are bathypelagic and are small in size. All are poorly known and more specimens are required.

Microlepidium Garman, 1899

Microlepidium is a monotypic genus confined to the Pacific coast of North America. Microlepidium verrucundum (Jordan and Cramer) is a pelagic species distinguished by having an otolith with a thin vertically directed blade (Fitch and Barker, 1972). Character states given for Podonomatchay are the same as those for Microlepidium and the two may be synonyms. I have not examined specimens of the former.

Laemonema Günther, 1862

Several studies have suggested that the 14 species within the genus Laemonema should be divided. There are two groups of species: broad-headed and narrow-headed forms (Rass, 1954; Taki, 1954; Karrer, 1971). The broad-headed species are characte
terized by jaws of either equal length or the lower jaw slightly protruding; the chin barbel is rudimentary or absent. Narrow-headed species have a shorter lower jaw and prominent chin barbel. Both groups differ from *Microlepidium* Garman, 1899, in numbers of branchial rays, the arrangement of the vomerine teeth, and lower numbers of pectoral fin rays.

**Momonatira** Paulin, 1985

This recently discovered but poorly represented monotypic genus in the *Laemonema* subgenus is from deep water (1100-1200 m) off South Canterbury, New Zealand. *Momonatira globosus* Paulin is characterized by having five developed rays in the ventral fin (*Laemonema* and *Microlepidium* have only two developed rays with rudimentary rays present in some species), a very high number of pectoral rays, an extremely well-developed head lateralis system, and broad fleshy bases to the dorsal and anal fins.

**Genera incertae sedis**

The following genera do not fit into any of the previous three groups, and do not form a natural group as considered by Schwarzhans (1984).

**Austrophycis** Ogilby, 1897

The genus is represented by one circumpolar species in cool temperate waters of the Southern Hemisphere, and one species apparently confined to Australia.

The relationships of this genus possibly lie close to the “*Pseudophycis*” group, but otoliths differ in having a short ostium (one-third or less of total otolith length cf. about half in *Pseudophycis*).

**Auchenoceros** Günther, 1889

*Auchenoceros* is a distinctive fish, differing from all other morids in having only one visible ray in the first of the three dorsal fins. It is a semipelagic species confined to the New Zealand region. Many of its character states appear convergent with *Laemonema*, but its relationships are unclear. It is probably closely related to the *Pseudophycis* group. The otolith differs from those of other morids in being very thin in fish of similar size.

**“Actuariolum”** Kar rer, 1971 (Fossil taxa)

This genus is based exclusively on otoliths, which seems to be diagnostic in the present instance. Although the Code does not forbid introduction of exclusively otolith-based genera or even higher taxonomic categories, such action is undesirable. Open nomenclature at the generic level is preferable (Nolf, 1985). Otoliths extremely thick, with maximum height at anterior end of otolith, quite variable in configuration. A number of new fossil species have recently been described by Schwarzhans (1984).

Fitch and Barker (1972) assigned an extant “Antarctic” species to this genus. Paulin (1983) demonstrated that Fitch and Barker’s specimens are *Austrophycis marginata*, and that *Actuariolum* is distinct from *Austrophycis* in otolitic structure.

Fossil morids were reviewed by Fitch and Barker (1972) and fossil otoliths of *Tripteroptychus*, *Physiculus*, and *Lotella* have recently been reported from early Miocene deposits in New Zealand (Grenfell, 1984; Schwarzhans, 1984), the North Sea Basin, and Aquitaine, SW France (Steurbaut, 1979: *Physiculus*), as well as the Late Miocene of northern Italy (Nolf and Steurbaut, 1983: *Laemonema*).

**JUVENILE FORMS**

Three nominal genera of morids, *Eretmophorus* Giglioli, 1889, *Stevoukodia* Cohen, 1973, and *Rhynchogadus* Tortonese, 1948, which may represent juveniles of other known or unknown morid genera, have been described. Otoliths for these genera are unknown, and their relationships are unclear.

**DISCUSSION**

Discovery of the diversity of form of the morid otolith by Schmidt (1968) has enabled relationships between genera to be more clearly defined and understood (Karrer, 1971; Fitch and Barker, 1972), and there is general agreement among various studies (Paulin, 1983; Schwarzhans, 1984) on a framework of interrelationships. There does not, however, seem to be a consensus on the placement of some genera.

All the studies have recognized three basic groups, which probably represent natural divisions within the family. Two of these groups, the “*Mura*” group and the “*Physiculus*” group are well defined. The third group, “*Pseudophycis*,” is less well defined. My placement of *Lotella* and *Eeyoria* within it is questioned by other workers (R. Lavenberg, personal communication). The short ostium of these two genera may indicate relationships elsewhere within the family and is an area for additional investigation. The genera incertae sedis, *Austrophycis* and *Auchenoceros*, also require further study. *Austrophycis*, although possibly close to the “*Pseudophycis*” group, may also represent a separate “group.” *Auchenoceros* is a highly specialized morid and has been described as a “morid anchovy” (D. M. Cohen, personal communication). The relationships of this genus within the family are unclear, and the understanding of its position may hold the key to the interrelationships of all the genera.

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