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THE MIOCENE FISH *MAROSICHTHYS*, A PUTATIVE TETRAODONTIFORM, ACTUALLY A PERCIFORM SURGEON FISH (ACANTHURIDAE) RELATED TO THE RECENT *NASO.*

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ABSTRACT

Marosichthys huismani (de Beaufort, 1926), a fish from the Miocene of the Celebes, was described in the tripod fish family Triacanthidae, Tetraodontiformes. It is shown here to be a valid genus of the surgeon fish family Acanthuridae, Perciformes, and closely related to the Recent genus *Naso. Marosichthys* is unique among all acanthurids in having the ventral shafts of the first two basal pterygiophores of the spiny dorsal fin in the preneural space (versus only one in front of the first neural spine) and no vacant interneural spaces (versus the third space vacant).

INTRODUCTION

De Beaufort (1926) described a fossil fish represented by the head and upper abdominal region as *Marosia huismani* in the family Triacanthidae, order Tetraodontiformes. The description was brief, but stated that there were at least six dorsal-fin spines, a well-developed pelvic-fin spine, and incisor-like teeth. De Beaufort related *Marosia* to the Recent genus *Triacanthus,* the Oligocene genus *Acanthopleurus* (now placed in the triacanthid subfamily Triacanthinae, along with *Triacanthus*), and the Eocene *Spinacanthus* (now placed among the balistoid tetraodontiforms).

The generic name was found by Whitley (1951) to be preoccupied in Lepidoptera and the replacement name *Marosichthys* was offered. Romer (1945, 1966) listed *Marosichthys* without explanation in the family Balistidae rather than Triacanthidae, but this probably was a lapsus because the described conditions of the dorsal- and pelvic-fin spines in *Marosichthys* clearly are those of triacanthids and not balistids.

Without having examined the specimen, Tyler (1968; 1980) accepted this fossil on the basis of its original description as a member of

Fig. 1. Photograph of the holotype of *Marosichthys huismani* (de Beaufort), Miocene of the Celebes, Geologisch Museum Amsterdam, Z 7478, length from snout to last preserved centrum 60 mm.

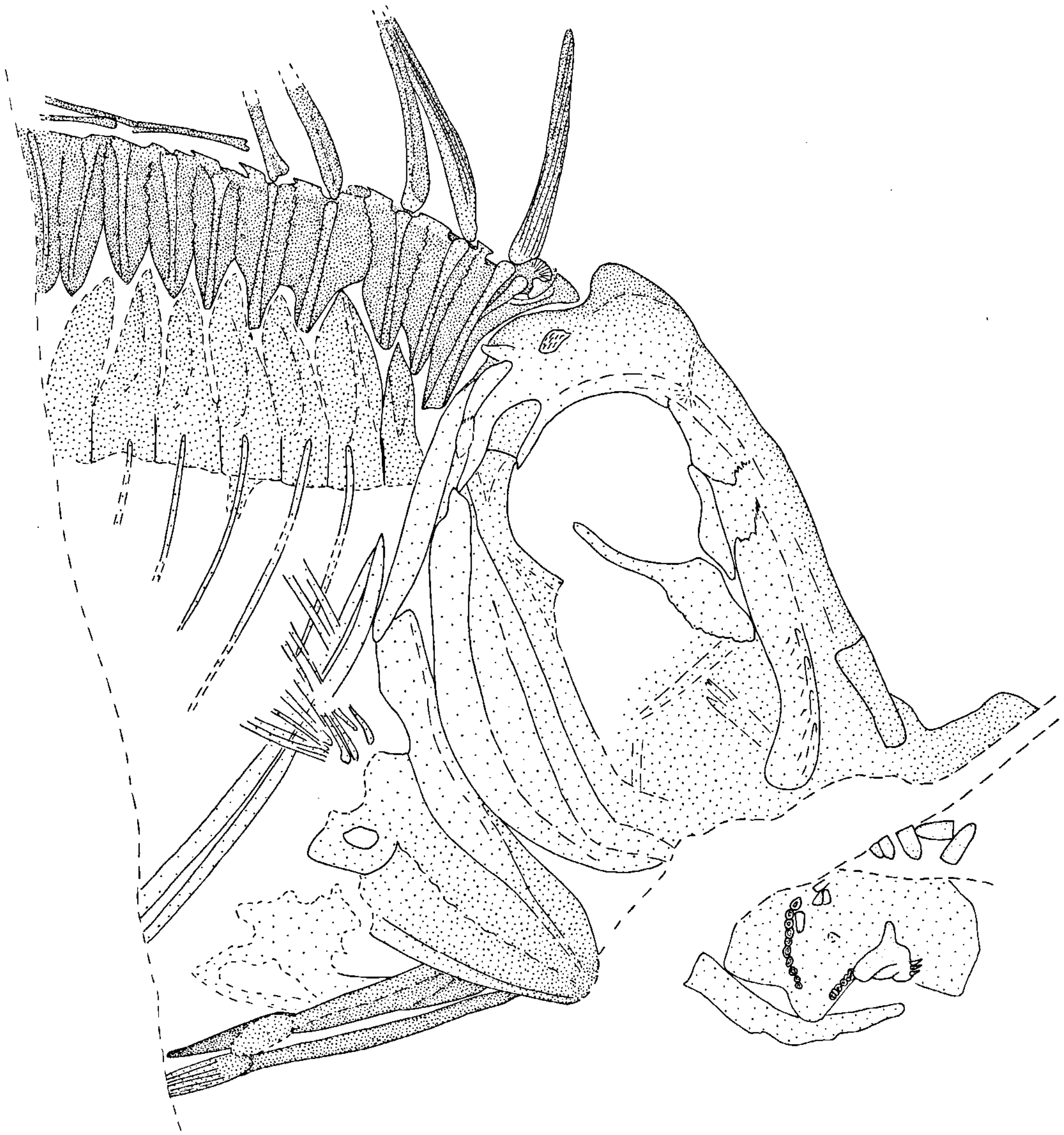

Fig. 2. Reconstruction of the holotype of *Marosichthys huismani* (camera lucida).

the subfamily Triacanthinae.

A recent examination of the holotype of *Marosichthys huismani* (Geologisch Museum Amsterdam, Z 7478) indicates that several important anatomical features were not mentioned in the original description and that the specimen is clearly a perciform surgeon fish, Acanthuridae. It is closely related to the Recent *Naso* but it has several such unique features that it merits generic level recognition within its newly assigned family.

REDESCRIPTION OF *MAROSICHTHYS HUISMANI*

Only the anterior half of the body is preserved, without the anal fin and caudal vertebrae, and there is a fracture through the jaws to the lower end of the cleithra (Figs. 1-2). The body ends posteriorly at a fracture that courses from the tenth dorsal-fin basal pterygiophore, through the centrum of the seventh vertebra, to the lower

Fig. 3. Photograph of the dorsal fin and its pterygiophores in the holotype of *Marosichthys huismani.*

end of the postcleithrum and basal region of the pelvic fin. The length of the body from the snout to the middle of the seventh centrum is 60 mm, and its depth between the spiny dorsal-fin base and the pelvic fin is 49 mm.

There are six dorsal-fin spines (Figs. 3-4). The first spine is very short and does not protrude to the exterior, being a cap of bone (not fully preserved posterodorsally) that is rotated downward into the deep indentation in front of the grooved median flange at the distal end of the first basal pterygiophore. This same pterygiophore bears the much longer second dorsal-fin spine at the posterior end of the distal edge of the median flange. Thus, there are two supernumerary dorsal-fin spines. The third spine is as well developed as the second spine and both of these spines have deep longitudinal grooves. The grooves are present over most of the anterior and lateral surfaces of the second spine but only on the anterior surface of the third spine. The third and fourth spines have their distal regions missing, and the fifth and sixth spines are even more incomplete distally. The third to sixth spines are borne individually on pterygiophores. The fourth spine is like the two preceding long spines except that it is strongly heteracanth and has a smooth, non-grooved surface. The fifth and sixth spines also are smooth, and the fifth is weakly heteracanth (the sixth is preserved in posterior view and its degree of heteracanthy cannot be determined). Behind the sixth spine are the remains of only three fin rays. The first ray is robust and well ossified, and there is evidence of distal branching.

The distal ends of the spiny dorsal-fin pterygiophores are laterally expanded in the regions between the spines. The first pterygiophore also

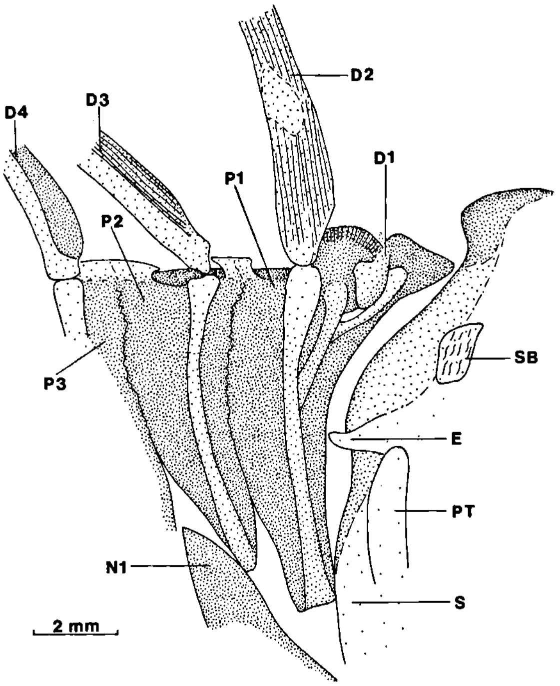

Fig. 4. Reconstruction of the more anterior dorsal-fin spines and their pterygiophores in the holotype of *Marosichthys huismani* (camera lucida). Abbreviations: D1-4, dorsal-fin spines one through four; E, epiotic and its posterior process; N1, neural spine of the first vertebra; P1-3, dorsal-fin pterygiophores one through three; PT, posttemporal; S, supracleithrum; SB, extrascapular scale bone.

is laterally expanded just in front of the deep indentation in which the cap-like first dorsal-fin spine is located. This lateral expansion is not fully preserved and it cannot be determined how far posterolaterally it formed a shield around the first spine. The first two pterygiophores have their ventral shaft-like portions situated in front of the upper half of the neural spine of the first vertebra, in the preneural space (Fig. 4). The third pterygiophore has its ventral shaft-like portion articulated in the first interneural space (between the neural spines of the first and second vertebrae). Posterior to the second vertebra, the neural spines are not well preserved. However, from the position of the centra and of the relatively well-preserved pterygiophores above them, there is every reason to believe that a ventral shaft of a pterygiophore is placed in each interneural space from the first to the sixth, and that the seventh space probably has two pterygiophores. Thus, it seems clear that there are no vacant interneural spaces.

Pleural ribs are preserved on the second to sixth vertebrae. There are remains of less well-preserved epineurals on several of these vertebrae (epineurals not shown in Fig. 2).

The supraoccipital has a low crest. There is a well-preserved lateral-line canal across the frontal in the region above the front of the eye. An extrascapular scale-bone is present on the surface of the posterior region of the frontal. The lateral ethmoid and nasal are well preserved and the latter has many canals and surface ornamentation. There is a large lachrymal below the lateral ethmoid and behind the nasal. An indeterminate number of more tubular infraorbitals are displaced posterodorsally from just behind the lachrymal. It cannot be determined whether a suborbital shelf was present. At the front of what appears to be the massive ethmoid is an oblong palatine, but just below this the fracture through the jaws prevents interpretation of other bony relationships. The bone that unnaturally projects out from the front of the snout just above the fracture is probably the upper jaw from the left side.

The upper part of the hyomandibular is clearly preserved where it articulates between the ventral flanges of the sphenotic and pterotic. There is no transverse crest on the upper lateral surface of the hyomandibular. The preopercle, opercle, and other opercular bones form a relatively narrow unit, at least as preserved, but not much detail can be determined for the individual bones. However, the posterior edge of the opercle is relatively straight.

The supracleithrum is a long shaft and connects dorsally with a posttemporal that appears to be broadly attached to the skull just below what is probably a posterior process of the epiotic (Fig. 4). The cleithrum and coracoid have wide flanges toward one another and the scapula has a large complete foramen (Fig. 5). The actinosts are not preserved and the pectoral-fin rays are too scattered to obtain a complete count. The postcleithrum is a single long shaft from the lower rear end of the supracleithrum to a level behind the base of the pelvic fin, but it is incomplete distally (the postcleithra from both

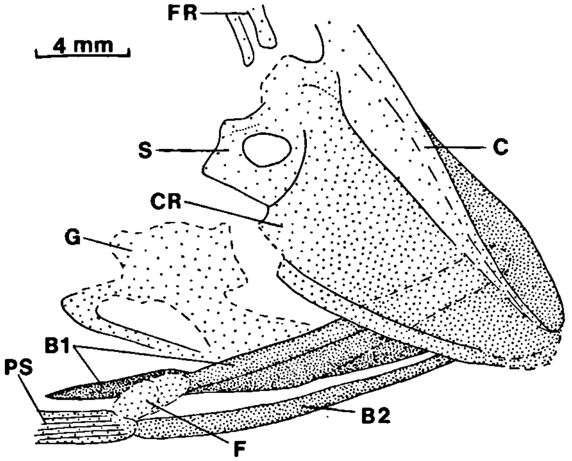

Fig. 5. Reconstruction of the pectoral-fin and pelvic-fin girdles in the holotype of *Marosichthys huismani* (camera lucida). Abbreviations: B1, basipterygium preserved in lateral view; B2, basipterygium from opposite side, probably only partially exposed in dorsoventral view; C, cleithrum; CR, coracoid; F, fragments of the pelvic-fin spine from the opposite side; FR, pectoral-fin rays; G, parts of the pelvic-fin girdle from the opposite side; PS, basal region of the better-preserved pelvic-fin spine.

sides are exposed).

The pelvis appears to be separated into its two halves, one side preserved above the other (Fig. 5). The upper-situated basipterygium is preserved in lateral view and appears to be of moderate depth in the region just behind the edge of the coracoid; its greatest vertical depth there is contained about 8.5 times (or 12%) in the length of the pelvis, but this measurement is not precise. There is no evidence of a distinct subpelvic keel with an anterior indentation. One of the pelvic-fin spines is represented only by a fractured base, behind which projects a short posterior process of the pelvis. The other pelvic-fin spine has a longer part of the basal region preserved, and this is deeply grooved longitudinally, but most of the length of the spine is lost beyond the fracture. Only one ray can be seen internal to the base of the better preserved pelvic-fin spine. It seems likely that there were a reduced number of pelvic-fin rays (i.e., several less than five).

Below the fracture through the jaws many teeth are scattered among what are probably mostly the broken pieces of the dentary bones, but with fragments from the opercular series as well. The scattered teeth clearly have relatively rounded bases at the sockets but are flattened distally, spatulate, and have minute emarginations or denticulations along the tapering, slightly rounded, darkened, distal ends (Fig. 6). These jaw teeth are up to 2.9 mm in length and 1.0 mm in width. The sockets of about ten of these teeth are exposed in one of the dentary bones, and these are in a linear arrangement indicative of being in a single series. In the middle of the fragmented lower jaw there is a single bone with three small, slender, conical teeth along one edge. By the size and shape of the bone and of the teeth it bears, this bone is probably a pharyngobranchial.

The body is covered with small (up to 0.4 mm diameter), more or less rounded, scale plates bearing three to five upright spinules.

PHYLOGENETICALLY INFORMATIVE FEATURES OF *MAROSICHTHYS*

The following discussion is based on the highly corroborated sequential phylogeny of the four families of acanthuroid fishes (siganids, luvarids, zanclids, acanthurids) and their sequential scatophagid and ephippidid outgroups documented by Tyler et al. (1989), Winterbottom (1993), and Winterbottom and McLennan (1993), and on the relationships of Recent acanthurid genera documented by Winterbottom (1993) and Guiasu and Winterbottom (1993). For Recent acanthurid genera, Tyler et al. (1989), Winterbottom (1993), and Guiasu and Winter-bottom (1993) have shown *Naso* to be the sister group of the other five genera, within which clade *Prionurus* is the sister group of the two clades composed of *Paracanthurus* + *Zebrasoma* and *Acanthurus* + *Ctenochaetus* (Winterbottom, 1993; Guiasu and Winterbottom, 1993).

In addition to the numerous genera of fossil acanthurids from the Eocene of Monte Bolca, Italy, reviewed by Blot and Tyler (1991), only two other fossil acanthurids need to be taken into consideration here in relation to the placement of *Marosichthys*. One of these is *Eonaso deani* (Hussakof), from the Antilles and of putatively Eocene but uncertain age, which Tyler and Sorbini (1997) redescribed and proposed as the sister group of the Recent *Naso*. The other is *Naso*

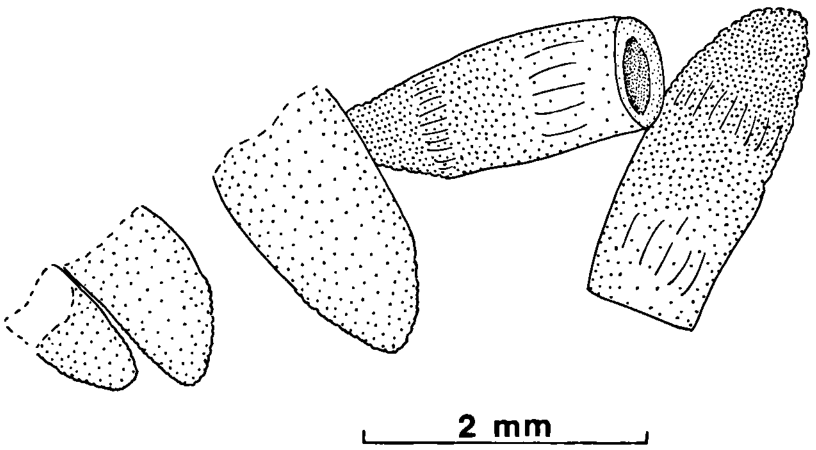

Fig. 6. Reconstruction of the better-preserved teeth in the holotype of *Marosichthys huismani* (camera lucida).

scombrurus Arambourg, from the Oligocene of Iran, which also is probably closely related to *Naso,* at least based on its described reduced number of dorsal-fin spines, caudal-peduncle fixed plates, and highly hypurostegic caudal-fin rays, but its relationships will not be better known until it is redescribed in comparison to the other fossil and Recent species. For present purposes, both *Eonaso deani* and *Naso scombrurus* are treated below as closely related to *Naso,* and their phylogenetically important features are mentioned parenthetically in relation to those of *Naso* and *Marosichthys*.

The proper placement of *Marosichthys* in the Acanthuridae is assured by its possession of a deep indentation in the distal end of the first dorsal-fin pterygiophore just in front of a grooved median flange around which the short first dorsal-fin spine rotates in a specialized locking mechanism between it and the much longer second dorsal-fin spine borne on the same pterygiophore (Tyler, 1970a, 1970b). This complex derived mechanism is found among all fishes only in the Acanthuridae. Other specializations unique to acanthurids among the acanthuroid fishes and present in *Marosichthys* are the long ethmoid, reduction of the subpelvic keel, postcleithrum a single piece, and spatulate teeth with denticulations.

The most obvious derived features of *Marosichthys* that also are found in some but not all other genera of acanthurids are: the reduction in the length of the first dorsal-fin spine to a cap of bone that does not protrude to the exterior; the lateral expansion of the distal end of the first pterygiophore around the first dorsal-fin spine; the reduction of the dorsal-fin spines to six; the loss of the supraneural bone; and, probably, the reduction in number of pelvic-fin rays.

In *Marosichthys* the first dorsal-fin spine is very short and does not protrude to the exterior, being a rounded cap of bone that represents only the base of the spine. This also is the specialized condition in all species of the Recent genus *Naso* (Tyler, 1970a) (and of *Eonaso* and probably also of *Naso scombrurus*). All other genera of acanthurids (both those of the Eocene and all Recent genera except *Naso*) have a longer first dorsal-fin spine that protrudes to the exterior, and this also is the generalized condition of the outgroups (Winterbottom, 1993).

In *Marosichthys* the distal end of the first dorsal-fin pterygiophore is laterally expanded just in front of the deep indentation into which the first dorsal-fin spine rotates. Even though the posterolateral extent of this shield cannot be determined in the single plate of the fossil, it is clear that a shield was present. This also is the specialized condition found in all species of the Recent genus *Naso* (with the exception of one species in which the expansion is secondarily lost; see Tyler, 1970b, and Guiasu and Winterbottom, 1993) (the structure of this region of the pterygiophore is unknown in *Eonaso* and *Naso scombrurus*). All other genera of acanthurids lack a posterolateral shield around the base of the first dorsal-fin spine, and this also is the generalized condition of the outgroups.

Other features of *Marosichthys* are at least concordant with a relationship with the Recent *Naso* based on the specialized reduction in the length of the first dorsal-fin spine and the lateral expansion of the distal end of the pterygiophore.

In *Marosichthys* the teeth are flattened, wider than deep toward the distal ends, and have only minute denticulations along the edges. In *Naso* the teeth are similarly minutely denticulate or smooth edged, whereas in all other Recent genera the teeth have far larger denticulations and lobes. Because the outgroups do not have denticulations or lobes (although they often are deeply notched), the minutely denticulate or smooth teeth in *Naso* (probably smooth in *Eonaso* and unknown in *Naso scombrurus*) are considered less specialized than the much more complexly lobed teeth in all the other Recent genera. Relatively smooth or only minutely denticulate teeth such as in *Marosichthys* and *Naso* also are found in several genera of Eocene acanthurids, but all of these have the primitive presence of a supraneural (predorsal bone) rather than the derived absence of it found in *Marosichthys* and *Naso.*

Marosichthys and *Naso* are similar in lacking a horizontal crest along the upper external surface of the hyomandibular, which also is the case in the Recent *Prionurus*, whereas all other Recent genera have such a specialized crest (Guiasu and Winterbottom, 1993). None of the Eocene genera are known to have a hyomandibular crest (condition unknown in *Eonaso* and *Naso scombrurus*) but, as discussed above for the teeth denticulations, *Marosichthys* and *Naso* differ from these Eocene genera by the specialized lost of the supraneural. However, the lack of a hyomandibular crest in *Marosichthys* is consistent with the condition in both *Naso* and *Prionurus.*

In *Marosichthys* the depth of the pelvis is about 12% of the length of the bone. Guiasu and Winterbottom (1993) give this percentage as 16% for *Naso* (generalized because outgroups are 17% or greater) and less than 11% for the other five genera of Recent acanthurids (between 10%-6%). This character is somewhat variable within the Eocene genera of acanthurids (Tyler and Sorbini, 1997) and measurements of it tend to be imprecise, but most of these fossil species have a ratio of about 12%-15% (up to about 30% in one species; unknown in *Naso scombrurus* but relatively slender at about 10% in *Eonaso*). Only a few Eocene species have a ratio of less than 11% and this is presumed to be derived independently of that in the five Recent genera (Sorbini and Tyler, 1997). However, there is so much variability in this feature in at least the fossil genera, that, at best, the pelvic depth in *Marosichthys* can be said to be relatively generalized and consistent with that in *Naso* and *Eonaso.*

Marosichthys probably has a specialized pelvic fin with a reduced number of rays, but this is uncertain. In any case, the reduction in the number of rays from the primitive condition of five (as found in four of the six Recent genera) to three has occurred independently in *Naso* and *Paracanthurus* (Guiasu and Winterbottom, 1993) and probably so in those few cases of Eocene species that seem to have fewer than five pelvic-fin rays. However, if the pelvic-fin rays are reduced in *Marosichthys*, this would relate it more to *Naso* (and to *Eonaso* and *Naso scombrurus*, in both of which the number of rays seems to be reduced) than to *Paracanthurus* because the latter genus is a member of a clade with several derived features (crest on hyomandibular, movable caudal-peduncle spine, highly lobed teeth) not found in *Naso* and *Marosichthys* (caudal-peduncle character unknown in the latter).

In *Marosichthys* the opercle has a relatively straight upper posterior edge, and this is the specialized condition also found in *Naso* (Guiasu and Winterbottom, 1993) (conditions unknown in *Eonaso* and *Naso scombrurus*). All other genera of acanthurids have a more convex posterior margin and this also is the generalized condition of the outgroups. However, the specialized condition in *Naso* includes a dorsally projecting dilator process and this process does not seem to be present in *Marosichthys*. Thus, *Marosichthys* may have only one aspect of this complex specialization.

Marosichthys has six dorsal-fin spines. The reduction in number of dorsal-fin spines to six or fewer among Recent genera has been documented (Guiasu and Winterbottom, 1993; Sorbini and Tyler, 1997) to be independent in *Zebrasoma* (whose species have four or five dorsal spines) and in *Naso* (whose species have five to seven dorsal spines) (*Eonaso* has five and *Naso scombrurus* probably has six). All of the other Recent genera have the more generalized condition of eight (*Ctenochaetus*) or nine (*Acanthurus*, *Prionurus*, *Paracanthurus*) dorsal-fin spines. Among the Eocene acanthurids, many genera have nine (*Proacanthurus* and probably *Metacanthurus*), eight (*Pesciarichthys*), or seven (*Eorandallius*, *Metaspisurus*, and *Lehmanichthys*) dorsal-fin spines. Only two of the Eocene genera have six or fewer dorsal-fin spines. The single species of *Acanthuroides* has six dorsal-fin spines, whereas in *Tylerichthys* one species, *T. milani*, has six and the other, *T. nuchalis*, has five. However, *Marosichthys* is like *Naso* (and *Eonaso* and probably *Naso scombrurus*) and the other Recent genera (with the exception of one of the species of *Prionurus*) in the derived absence of a supraneural. All of the Eocene genera, including those with six or fewer dorsal-fin spines, have the generalized condition of a supraneural being present. Nevertheless, the combination of a reduced number of dorsal-fin spines and the absence of a supraneural in *Marosichthys* relates it more to *Naso* than to *Zebrasoma* because, as with the pelvic fin-ray character above, the latter is a member of a clade with several derived features (hyomandibular crest, movable peduncular spine, highly lobed teeth) not found in *Naso* and *Marosichthys*.

Many of the derived features that characterize *Naso* (Tyler, 1970b; Tyler et al., 1989; Guiasu and Winterbottom, 1993; and Winterbottom, 1993) cannot be determined in *Marosichthys* because of the incomplete or poorly preserved skeleton. Thus, it remains unknown whether *Marosichthys* has *Naso*-like conditions of hypural fusion, reduction in the size of the uroneural, anal-fin spine and pterygiophore specializations comparable to those of the anterior dorsal-fin spines, and the reduction in the number of branchiostegal rays.

FEATURES UNIQUE TO *MAROSICHTHYS* AMONG ACANTHURIDS

Marosichthys has two features unique among acanthurids. The first two basal pterygiophores of the spiny dorsal fin are situated in front of the neural spine of the first vertebrae, in the preneural space. In all other acanthurids, from the Eocene to Recent, there is only a single pterygiophore anterior to the first neural spine (including in *Eonaso*; condition unknown in *Naso scombrurus*), and this is the ancestral condition for all acanthuroids (Tyler et al., 1989).

Marosichthys has no vacant interneural spaces. In all other acanthurids, from the Eocene to Recent, there is a single vacant interneural space, the third (including in *Eonaso*; condition unknown in *Naso scombrurus*), and this also is the case in the zanclid first outgroup. More distant outgroups have various arrangements but typically a single vacant space, although there are no vacant spaces in some species of one superfamilial clade, the luvaroids (Tyler and Bannikov, 1997).

CONCLUSION

Many derived features (especially the complex and innovative dorsal-spine locking mechanism) demonstrate that *Marosichthys* is a member of the perciform Acanthuridae rather than the tetraodontiform Triacanthidae. Two derived features (first dorsal-fin spine so shortened that it does not protrude to the exterior, and posterolateral expansion of the distal end of the first pterygiophore of the spiny dorsal fin around the first spine) indicate that the Miocene *Marosichthys* is closely related to the Recent *Naso* (along with *Eonaso* of uncertain age and the Oligocene *Naso scombrurus*). Many other features, some of which are derived, are concordant with this proposed relationship.

Marosichthys has two derived features that are unique within acanthurids (two pterygiophores in the preneural space and no vacant interneural spaces) and these are judged to be of sufficient magnitude to warrant the recognition of *Marosichthys* as generically distinctive within the family.

The sister group relationships within this clade of at least three genera (*Naso*, *Eonaso*, and *Marosichthys*) will not be able to be deciphered until more complete and better preserved specimens of *Marosichthys* and *Eonaso* become available and the holotype of *Naso scombrurus* is redescribed.

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