

***Arambourgthurus*, a new genus of hypurostegic surgeonfish (Acanthuridae) from the Oligocene of Iran, with a phylogeny of the Nasinae**

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ABSTRACT

The two specimens of an acanthurid fish from the Oligocene of Iran described by Arambourg (1967) as *Naseus scombrurus* are redescribed and illustrated. This species is unique among all acanthurid fishes, both fossil and Recent, in its scombroid-like extensive hypurostegy (bases of caudal-fin rays deeply overlapping the hypural plate) and in having three vacant interneural spaces. The new genus *Arambourgthurus* is established for this species. *Arambourgthurus* is shown to be a member of a clade (along with the Eocene *Sorbinithurus* and the Miocene *Marosichthys*) distinguished by the derived condition of having two dorsal-fin pterygiophores situated in the preneural space; this clade is shown to be the sister group of the clade composed of the Recent *Naso* and of *Eonaso* (the latter of unknown but probably less than Eocene age) on the basis of six synapomorphies defining the Nasinae.

KEY WORDS

Pisces,
Acanthuridae,
Nasinae phylogeny,
Oligocene,
Rupelian,
Iran.

RÉSUMÉ

Arambourgthurus, un nouveau genre d'Acanthuridae de l'Oligocène d'Iran, suivi d'une analyse phylogénétique des Nasinae.

Les deux spécimens d'acanthurides de l'Oligocène d'Iran décrits par Arambourg (1967) sous le nom de *Naseus scombrurus* sont redécrits et refigurés. Au sein des acanthurides, fossiles et actuels, ces espèces sont uniques par le développement de leur hypurostégie (base des rayons de la nageoire caudale recouvrant la plaque basale) ainsi que par la présence de trois espaces inter-neuraux. Ces espèces sont rapportées au nouveau nom de genre *Arambourgthurus* n. gen. *Arambourgthurus* appartient à un clade qui regroupe aussi *Sorbinithurus* de l'Éocène, et *Marosichthys* du Miocène. Ce clade est défini par la présence de deux ptérygiophores de la nageoire dorsale et lesquels se situent dans l'espace préneural. Sur la base de six synapomorphies définissant les Nasinae, il partage une relation de groupe-frère avec le clade composé des taxons actuels *Naso* et *Eonaso*, ce dernier est connu au moins depuis l'Éocène.

MOTS CLÉS

Pisces,
Acanthuridae,
phylogénie des Nasinae,
Oligocène,
Rupélien,
Iran.

INTRODUCTION

Arambourg (1967) described two specimens of an acanthurid fish from the lower Oligocene of Iran (Istehbanat locality, Rupelian) as *Naseus scombrurus*. *Naseus* Commerson in Lacepède (1801) is only a variant spelling and junior synonym of *Naso* Lacepède, 1801 (see Eschmeyer 1990), with *Naseus* having been used in the early 19th century for most fossil acanthurids. Arambourg compared his new species to what were then the two commonly recognized species of *Naseus*, both from the middle Eocene of Monte Bolca, Italy. He noted that the most distinctive feature of the Oligocene species was the scombroid-like deep overlapping by the caudal-fin rays almost to the midline of the hypural plate. However, this remarkable hypurostegy, unique among all acanthurids, both fossil and Recent, was not clearly shown in the photographs of the entire specimens accompanying the description, and it has not been mentioned subsequently. Other unusual or unique features of this species also have gone unnoted. The species is briefly redescribed and illustrated below.

An analysis of its features in comparison to those of all other fossil and Recent acanthurids warrants its recognition as the new genus *Arambourgthurus*. *Arambourgthurus* is shown to be a member of a clade with two other fossil genera (the Eocene

Sorbinithurus Tyler, 1999 and the Miocene *Marosichthys* Whitley, 1951) that uniquely share the derived condition of the ventral shafts of the first two dorsal-fin pterygiophores being swung forward and situated in the preneural space (*versus* only one pterygiophore in the preneural space in all other acanthurids). The sister group relationship of the *Arambourgthurus* + *Sorbinithurus* + *Marosichthys* clade with the clade composed of the Recent *Naso* and *Eonaso* Blot, 1984, of unknown age, is demonstrated by six synapomorphies for the Nasinae.

SYSTEMATICS

Family ACANTHURIDAE Rafinesque, 1810

Subfamily NASINAE Smith, 1955

Genus *Arambourgthurus* n. gen.

TYPE SPECIES. — *Naseus scombrurus* Arambourg, 1956.

ETYMOLOGY. — For Camille Arambourg, the distinguished paleontologist whose publications and arduous field work in many parts of the world greatly enriched our knowledge of Tertiary fossil fishes and the collections of the Muséum national d'Histoire naturelle, Paris. Prof. Arambourg first described the type species of the new genus and noted one of its most interesting and unique features. And “*thurus*”, a common ending for generic names among acanthurids.

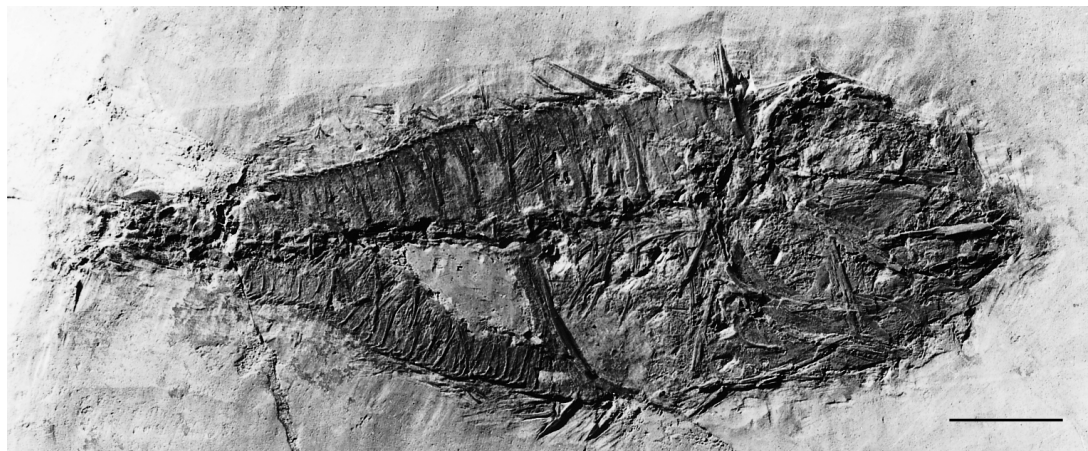


FIG. 1. — *Arambourgethurus scombrurus* (Arambourg), holotype, MNHN 1939-6-5 (EIP5), c. 85 mm SL, Oligocene of Iran. Scale bar: 10 mm.

DIAGNOSIS. — Unique among all acanthurids, both fossil and Recent, by two derived features: extensive hypurostegy, with the caudal-fin rays so broadly overlapping the hypural plate that their bases are separated by only a narrow horizontal space along the midline of the plate (*versus* hypurostegy absent or only very moderately developed); the first, second, and third interneural spaces vacant (*versus* only the second and third, or only the third, or none vacant).

Arambourgethurus scombrurus
(Arambourg, 1956)
(Figs 1-5)

MATERIAL EXAMINED. — Holotype, Muséum national d'Histoire naturelle (MNHN) 1939-6-5 (EIP5), single plate, head to right, c. 85 mm SL; the bones of the head are much displaced, and the last (urostylar) centrum and caudal fin are missing, the vertebral column ending with only an impression of the penultimate (12th) centrum and its posteriorly elongate neural and haemal spines. Paratype, MNHN 1939-6-7g (EIP7g) and 7d (EIP7d), 146 mm SL; 7g is a relatively complete specimen but 7d is only fragmentary; however, 7d has the best preserved remains of the bases of the hypurostegic caudal-fin rays.

TYPE LOCALITY AND HORIZON. — Both specimens are from the Istehbanat locality of Iran, of lower Oligocene age (Rupelian), about 35 My.

DIAGNOSIS. — That of the new genus, of which it is presently the only known representative.

RE-DESCRIPTION

Most of the bones of the head are poorly preserved and somewhat dislocated, and little of interest can be noted; no teeth are preserved in either specimen (the edges of the jaws are lost in the paratype and undistinguishable in the holotype). The hyomandibular is well-preserved and clearly exposed in the paratype; it has a relatively flat surface, without a horizontal crest along its upper lateral region below its articulation with the skull. The frontal, lateral ethmoid, ethmoid, and parasphenoid below and in front of the eye are clear in the paratype, and of normal acanthurid condition.

There are six dorsal-fin spines. The first spine is a short, non-protruding, cap of bone in both specimens, the remains of which are present over the median flange arising from the dorsal surface of the first dorsal-fin pterygiophore, around which the cap-like spine would rotate in a locking mechanism. The other dorsal-fin spines are best preserved in the holotype: the second spine is prominent and slightly longer than the third and fourth spines; the fifth spine is missing; the sixth spine is the longest in the series, being about one-third longer than the second spine. The first two dorsal spines are borne in supernumerary association on the first pterygiophore. In the paratype,

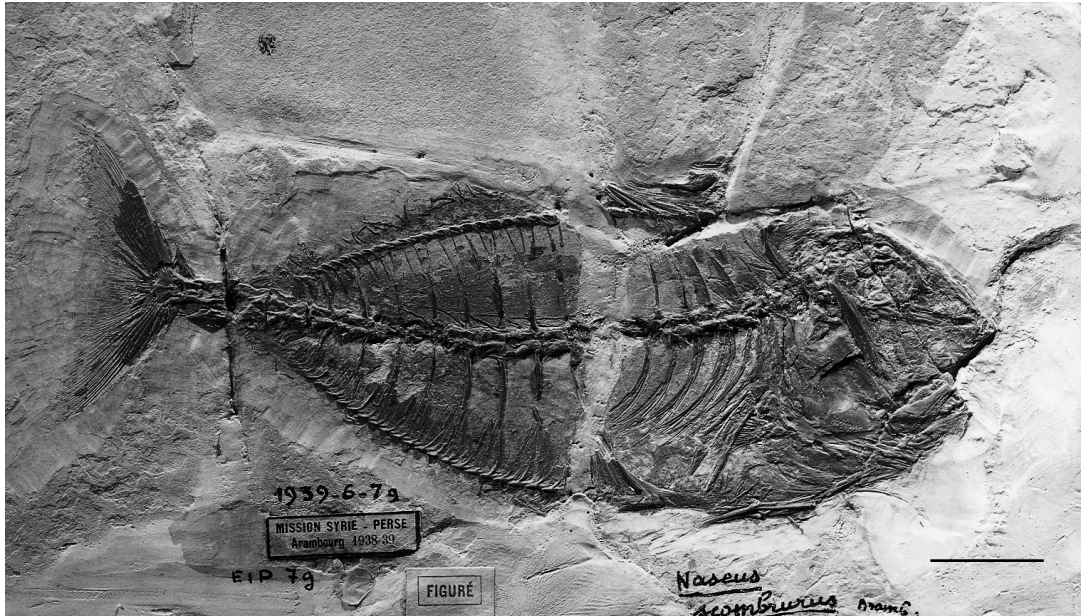


FIG. 2. — *Arambourthurus scombrurus* (Arambourg), paratype, MNHN 1939-6-7g (EIP7g), 146 mm SL, Oligocene of Iran. Scale bar: 20 mm.

the second and third dorsal spines are missing, but the distal end of the fourth spine and all of the fifth and sixth spines are present above a fracture through the pterygiophores. There is no evidence of any kind of posterolateral shielding flange from the first pterygiophore around the cap-like first spine. The dorsal-fin rays are fragmented and scattered, but there are about 24-26 pterygiophores behind those of the spiny dorsal fin and therefore about that many rays. There is no supraneural (predorsal) bone between the first dorsal pterygiophore and the skull.

The series of anal-fin spines are incomplete in both specimens. In the holotype, the third spine is fully preserved, situated in about the middle of the ventral surface of the second anal-fin pterygiophore. Only the distal end of the second anal spine is preserved in the holotype; the base of the spine and the region immediately in front of it where the first spine would be is missing. The base of the second spine is situated toward the posterior end of the ventral surface of a forward extension of the first anal-fin pterygiophore, but this extension is not well-preserved.

In the paratype, the third anal spine is missing but the second spine is completely preserved, and immediately in front of its base is a small cap of bone that is either the short, non-protruding, cap-like first anal spine or the rounded median flange of the pterygiophore around which the first spine would rotate in a locking mechanism. The bases of the first and second anal spines are situated just below lateral strengthening ridges toward the posterior end of the first anal-fin pterygiophore, and this pterygiophore has a long forward extension to a level in front of the ventral end of the postcleithrum. There is no evidence of any kind of posterolateral shielding flange from the first anal pterygiophore around the cap-like first spine. The anal-fin rays are fragmented and scattered, but there are about 24 pterygiophores in both specimens behind the two for the anal spines and therefore about that many rays.

In the pectoral-fin girdle, the scapular foramen is complete and the postcleithrum is a single bone. About 13-14 pectoral-fin rays are evident in the paratype.

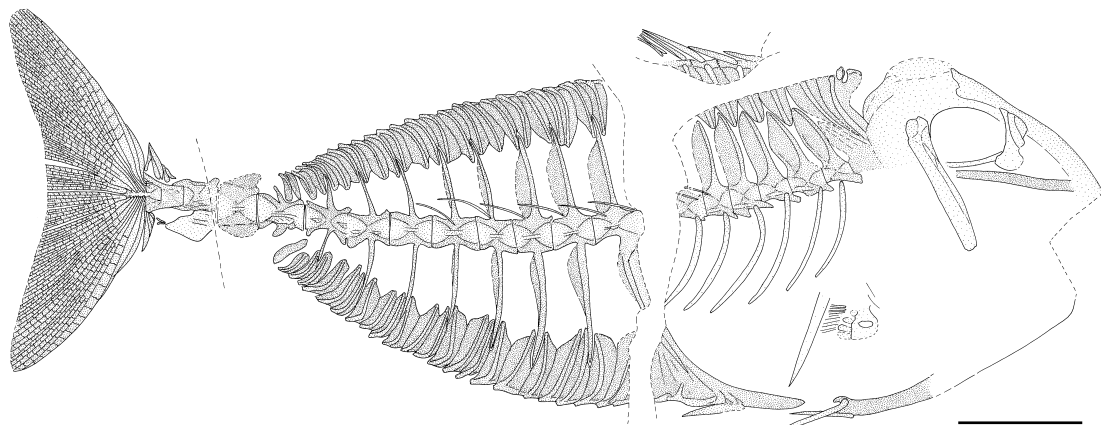


FIG. 3. — *Arambourthurus scombrurus* (Arambourg), reconstruction of the paratype, MNHN 1939-6-7g (EIP7g), 146 mm SL. Scale bar: 20 mm.

The pelvic fin has a stout spine; in the holotype there are either two or three rays internal to each spine, and in the paratype there seem to be two rays associated with each spine. It is clear that there are no more than three rays in each pelvic fin. The posterior process of the pelvis is short. The pelvis becomes relatively deep anteriorly at its articulation between the cleithra; the ratio of the length of the pelvis to its depth at the posterior edge of the cleithrum is 13%. There does not seem to be any significant anteroventral prong (subpelvic keel) from the lower anterior region of the pelvis below the cleithrum.

There are 16 principal caudal-fin rays and seven procurrent rays above and below; the innermost two principal caudal-fin rays, one from the upper lobe and one from the lower lobe, are deeply divided to the base (Arambourg interpreted these as four rays, accounting for his statement of 18 principal rays). Above and below the two innermost rays, the other principal rays more anteriorly increasingly overlap the hypural plate, and the proximal ends of the rays from the upper and lower lobes are only separated by a narrow space along the middle region of the plate, which middle region is slightly upraised as a crest. The hypural plate bears shallow grooves (visible in EIP7g because the fractured bases of the rays have adhered to EIP7d)

to accommodate the overlapping slender proximal ends of the rays.

There are 13 caudal vertebrae, as seen especially clearly in the paratype. The paratype has a fracture just in front of the centrum of the first caudal vertebra; this fracture continues into the middle region of the long haemal spine of the first caudal vertebra and of the dorsal shaft of the first anal-fin pterygiophore that this haemal spine supports along its anterior edge. The neural and haemal spines of the first to ninth caudal vertebrae are of decreasing length and support soft dorsal- and anal-fin pterygiophores. The neural and haemal spines of the tenth and eleventh caudal vertebrae are low but broad, whereas those of the twelfth caudal vertebra are elongated posteriorly above and below the urostylar thirteenth centrum. As exposed on EIP7g, it is clear that hypurals 1-4 are fully fused together into a single plate; hypural 5 cannot be distinguished as a separate element, perhaps because of the ray-accommodating grooves along the upper part as well as elsewhere on the fused plate. Most of the caudal vertebrae have prominent low crests for muscle attachment horizontally along the middle of the centra. There are two epurals and a small, short uroneural just below the bases of the epurals. There is a stout parhypural closely applied to the lower edge of

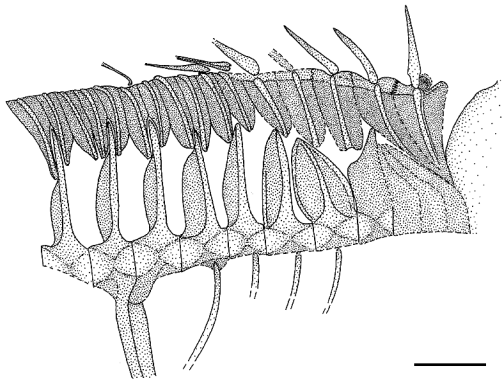


FIG. 4. — *Arambourghurus scombrurus* (Arambourg), reconstruction of the spiny dorsal fin and its pterygiophores, the abdominal vertebrae, and the first two caudal vertebrae of the holotype, MNHN 1939-6-5 (EIP5), c. 85 mm SL. Scale bar: 5 mm.

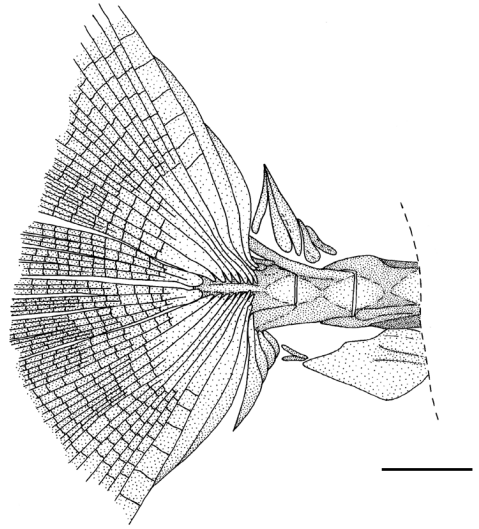


FIG. 5. — *Arambourghurus scombrurus* (Arambourg), reconstruction of the caudal fin and caudal skeleton of the paratype, MNHN 1939-6-7g (EIP7g), 146 mm SL. Scale bar: 5 mm.

the urostyle and hypural plate. The least depth estimated for the fleshy caudal peduncle, at the level of the eleventh caudal vertebra, is between 4.3–4.7% SL.

The six more posterior of the abdominal vertebrae are relatively well-preserved and individually distinct, but those more anteriorly are poorly preserved, fractured, and not individually distinct. Given that *Arambourghurus* has 13 vertebrae in the caudal series, like all other acanthurids, it is reasonable to presume that there were nine vertebrae in the even more conservative abdominal series, like all other acanthurids; moreover, there is space between the rear of the skull and the front of the clearly preserved sixth from last abdominal vertebra for about three more vertebrae.

The ventral shafts of the first two dorsal-fin pterygiophores are strongly curved anteriorly toward the lower region of the rear of the skull, and their lateral strengthening ridges converge just above the level of the centra and neural canal, with no neural spine in-between the two shafts. The neural spines of the first three abdominal vertebrae are closely applied to one another and squeezed in-between the rear of the strengthening

ridge of the second dorsal-fin pterygiophore and the front of the fourth neural spine.

The fourth and more posterior abdominal vertebrae in the paratype have well-developed ventral prezygapophyses; these are less clearly preserved in the holotype. Sturdy pleural ribs clearly are present on the fourth to ninth abdominal vertebrae, but whether pleurals were present more anteriorly is unclear. Slender epineurals are present from at least the fifth abdominal to the fifth caudal vertebrae.

In the paratype, there is a single dorsal pterygiophore between the neural spines of the fourth and fifth abdominal vertebrae but two pterygiophores here in the holotype. The next two interneural spaces (behind the fifth and sixth neural spines) have single pterygiophores present, posterior to which the interneural spaces have either one or two pterygiophores, or, far posteriorly, three pterygiophores.

The body is covered with minute scales bearing a central upright spinule or a tiny cluster of spinules, giving a shagreen-like appearance to the surface, with the limits of the individual scales not easily discernable. The lateral line is clear along

the middle region of much of the upper half of the body.

In the paratype there is a large (8.5 mm) caudal peduncular fixed-plate scale with a horizontal crest. This fixed plate is displaced ventrally below the eleventh (PU3) and twelfth (PU2) caudal centra. In the holotype, the single fixed plates from both sides are displaced just above and just below PU3; as in the paratype, each fixed plate has a horizontal crest.

ANALYSIS OF CHARACTERS

The following discussion of relationships is based on the highly corroborated sequential phylogeny of the five families of acanthuroid fishes (siganids, luvarids + †kushlukiiids, zancrids, acanthurids) and of their sequential scatophagid, ehippidid, and drepanid outgroups documented by Tyler *et al.* (1989), Winterbottom (1993), Winterbottom & McLennan (1993), Bannikov & Tyler (1995), Tyler & Bannikov (1997) and Tyler & Sorbini (1999), and on the relationships of Recent acanthurid genera documented by Winterbottom (1993) and Guiasu & Winterbottom (1993). All of these phylogenies are based on osteological and myological features, and for the most part these have been corroborated by Tang *et al.* (1999) in an analysis of molecular (mitochondrial DNA sequencing) data, with the possible exception that the drepanid, ehippidid, and scatophagid outgroups may not be sequential but, rather, form a sister group clade to the acanthuroids.

For Recent acanthurid genera, Tyler *et al.* (1989), Winterbottom (1993) and Guiasu & Winterbottom (1993) have shown that *Naso* (Nasinae) is the morphologically primitive sister group of the other five genera (Acanthurinae), with the latter considered below as the higher acanthurids. Within the clade of higher acanthurids, *Prionurus* Lacepède, 1804 is the sister group of the two clades composed of *Paracanthurus* Bleeker, 1863 + *Zebrasoma* Swainson, 1839 and of *Acanthurus* Forsskål, 1775 + *Ctenochaetus* Gill, 1885 (for these sister group relationships see Winterbottom 1993 and Guiasu & Winterbottom 1993; for the

phylogeny of the species of *Zebrasoma* see Guiasu & Winterbottom 1998, and for the phylogeny of the species of *Naso* see Borden 1998). The species of the (*Paracanthurus* + *Zebrasoma*) + (*Acanthurus* + *Ctenochaetus*) clade are considered below as the higher acanthurins.

Sorbini & Tyler (1998b) have shown that *Proacanthurus* Blot & Tyler, 1991, from the Eocene of Monte Bolca, is the morphologically primitive sister group of the higher acanthurid *Paracanthurus* + *Zebrasoma* and *Acanthurus* + *Ctenochaetus* clade on the basis of the uniquely innovative shared derived feature of a folding spine on the caudal peduncle.

For the specialized locking mechanism of the first dorsal- and anal-fin spines that is the most distinctively innovative derived feature of all acanthurids, and for other osteological data on the family, see Tyler (1970a, b).

There are three genera of fossil acanthurids that have derived morphological similarities to *Arambourghurus*, and all three of these have recently been redescribed (*Eonaso* by Tyler & Sorbini 1998a; *Marosichthys* by Tyler 1997) or described as new (*Sorbiniturus* by Tyler 1999a); see those papers for details of the anatomy of these three genera. For descriptions of the generically diverse acanthurids of the Eocene of Monte Bolca, Italy, see Blot & Tyler (1991), supplemented by the additional Monte Bolca genera described more recently by Sorbini & Tyler (1998a for *Protozebrasoma*) and Tyler (1999b for *Tauichthys*). The relationships between most of the Monte Bolca genera of acanthurids and the Recent genera are uncertain, with the exception of *Proacanthurus* discussed above.

Because the rear of the body is missing in the Eocene *Sorbiniturus* and the Miocene *Marosichthys*, several characters are unknown for them, and these are so stated and treated as unknown in the analysis, but this lack of information for a few features is not shown in the cladogram.

CHARACTERS SUPPORTING THE CLADOGRAM

The character numbers below correspond to those in the cladogram (Fig. 6).

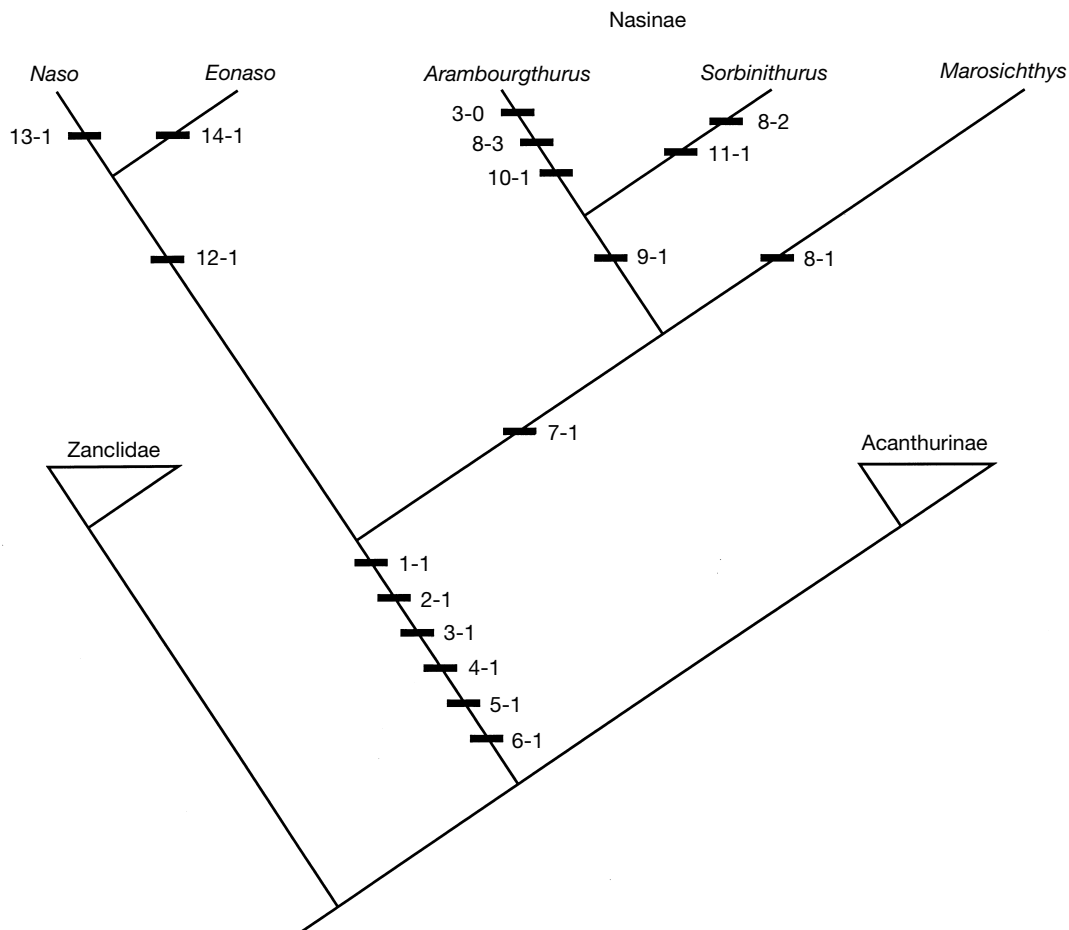


FIG. 6. — Cladogram of the relationships of the lower acanthurids (Nasinae), with numbers corresponding to those in the section "Analysis of characters": 1-1, short non-protruding first dorsal-fin spine; 2-1, three or fewer pelvic-fin rays; 3-1, dorsal pterygial shield (3-0, reversal to dorsal pterygial shield absent); 4-1, small uroneural; 5-1, hypurals one through four fused; 6-1, shallow caudal peduncle; 7-1, two dorsal pterygiophores in preneural space; 8-1, no vacant interneural spaces; 8-2, two vacant interneural spaces; 8-3, three vacant interneural spaces; 9-1, second interneural space vacant; 10-1, extensive hypurostegy; 11-1, supraneural present; 12-1, opercular dilator process; 13-1, anal pterygial shield; 14-1, narrow pelvis. Ages of genera: *Naso*, Recent; *Eonaso*, unknown but probably far more recent than Eocene; *Arambourghurus*, Oligocene; *Sorbinithurus*, Eocene; *Marosichthys*, Miocene.

1. Length of first dorsal-fin spine

The first dorsal-fin spine is of at least moderate length, clearly protruding to the exterior through the skin, and it is easily seen externally in most acanthurids and in the zanclid outgroup. By contrast, in the numerous species of *Naso* (Recent) and in the monotypic *Eonaso deani* (Hussakof, 1907; age unknown but probably far more recent than Eocene), *Arambourghurus scombrurus* (Arambourg, 1956;

Oligocene), *Sorbinithurus sorbinii* (Tyler, 1999; Eocene), and *Marosichthys huismani* (Beaufort, 1926; Miocene) the first dorsal spine is greatly reduced in size and does not protrude to the exterior. In these five genera, the first dorsal spine is represented only by a cap-like basal region that rotates over a median pterygial flange, in a locking mechanism with the base of the second dorsal spine as in all acanthurids irrespective of whether the first spine is a short cap

or a longer protruding element. Apomorphy: 1-1, reduced size and non-protrusion externally of the first dorsal-fin spine (*Naso*, *Eonaso*, *Arambourgthurus*, *Sorbinithurus*, *Marosichthys*).

2. Number of pelvic-fin rays

The pelvic fin has a spine and five rays in most acanthurids and in zancids. By contrast, among Recent species of acanthurids those of *Naso* and *Paracanthurus* have a spine and only three rays. Based on five synapomorphies uniting *Paracanthurus* with the higher acanthurids, Guiasu & Winterbottom (1993) document that the reduction in pelvic rays is independent in *Naso* and *Paracanthurus*. Among fossil species of acanthurids, the pelvic rays are reduced to three or less in *Eonaso*, *Arambourgthurus*, *Sorbinithurus*, *Marosichthys*, and *Tauichthys*. However, *Tauichthys* lacks five derived features (numbers 1, 3-6) shown herein to unite *Naso*, *Eonaso*, *Arambourgthurus*, *Sorbinithurus*, and *Marosichthys*, and the reduction in pelvic rays in *Tauichthys* is most parsimoniously interpreted as independent of that in the other five genera. Apomorphy: 2-1, reduction of the pelvic-fin rays to two or three (*Naso*, *Eonaso*, *Arambourgthurus*, *Sorbinithurus*, *Marosichthys*).

3. First dorsal-fin pterygiophore shield

The region of the first dorsal-fin pterygiophore just in front of the median flange around which the base of the first dorsal-fin spine rotates is deeply indented in all acanthurids, and in most acanthurids and in zancids the lateral surface of the pterygiophore around the indentation is relatively flat or has only a low strengthening ridge. By contrast, among Recent species of acanthurids, this region of the pterygiophore is expanded posterolaterally into a shield around the base of the first dorsal spine in all species of *Naso* except *N. thynnoides* Valenciennes, 1835 and in some species of *Zebrasoma*: in all specimens of *Z. xanthurum* (Blyth, 1852), and in some specimens of *Z. rostratum* (Gunther, 1873). However, because *N. thynnoides* is deeply nested within the phylogeny of *Naso*, and not basal to it (Borden 1998), and the sister taxa to *N. thynnoides* possess the pterygial shield, the lack of a shield in *N. thynnoides* is most parsimoniously interpreted

as a reversal (Guiasu & Winterbottom 1993). Based on five synapomorphies uniting *Zebrasoma* with the higher acanthurids (Guiasu & Winterbottom 1993), and that *Zebrasoma* lacks five derived features (numbers 1-2, 4-6) shown herein to unite *Naso*, *Eonaso*, *Arambourgthurus*, *Sorbinithurus*, and *Marosichthys*, the presence of a dorsal pterygial shield in *Zebrasoma* is most parsimoniously interpreted as independent of that in the other five genera. Among fossil species of acanthurids, a dorsal pterygial shield is present only in *Sorbinithurus* and *Marosichthys* (because of fracturing and loss of distal parts, only the more basal regions of the laterally flared shield are preserved); the condition is unknown in *Eonaso* but the shield is absent in *Arambourgthurus*. However, *Arambourgthurus* possesses five derived features (numbers 1-2, 4-6) uniting it with *Naso*, *Eonaso*, *Sorbinithurus*, and *Marosichthys*, and two others (numbers 7, 9) uniting it with the latter two genera, and the lack of the dorsal pterygial shield is most parsimoniously interpreted as a reversal. Apomorphy: 3-1, presence of a dorsal pterygial shield (*Naso*, *Sorbinithurus*, *Marosichthys*); absent by reversal, 3-0 (*Arambourgthurus*).

4. Uroneural size

The uroneural is well-developed and extends along all of the dorsal edge of the urostylar centrum and often posterodorsally to it in most acanthurids and in zancids. By contrast, the uroneural is much reduced in size to a small rounded bone situated mostly above the area of the centrum of the urostylar centrum and not extending far posteriorly to it in *Naso*, *Eonaso*, and *Arambourgthurus*; the condition is unknown in *Sorbinithurus* and *Marosichthys*. Apomorphy: 4-1, reduction in uroneural size (*Naso*, *Eonaso*, *Arambourgthurus*).

5. Hypural fusion

Hypurals 1-4 are separate from one another and from the urostylar centrum in most acanthurids and in zancids. By contrast, these hypurals and the urostylar centrum are fused together into a single plate in *Naso*, *Eonaso*, *Arambourgthurus*, and *Protozebrasoma*; the condition is unknown in *Sorbinithurus* and *Marosichthys*. Evidence about

the relationship of *Protozebrasoma* to *Zebrasoma* among the higher acanthurins versus to the lower acanthurids is equivocal (Sorbini & Tyler 1998a). However, *Protozebrasoma* lacks five derived features (numbers 1-4, 6) shown herein to unite *Naso*, *Eonaso*, *Arambourgthurus*, *Sorbiniithurus*, and *Marosichthys*, and the hypural fusion in *Protozebrasoma* is most parsimoniously interpreted as independent of that in the other five genera. In a few other Eocene of Monte Bolca acanthurids there may be partial fusion of hypurals 1-4 to one another but not to the centrum (e.g., in *Tauichthys* and probably in *Acanthuroides* Blot & Tyler, 1991, hypurals 1-2 are fused to one another and 3-4 also are fused to one another, but these two plates are not fused to the centrum) and this is not considered herein to be as derived a condition as the more fully fused hypural plate. Apomorphy: 5-1, hypurals 1-4 fused together and to the urostyle centrum (*Naso*, *Eonaso*, *Arambourgthurus*).

6. Caudal peduncle depth

The fleshy caudal peduncle is relatively deep in most acanthurids (least depth 7-15% SL) and in zanclyids (15-17% SL). By contrast, the caudal peduncle is more slender in *Naso* (3.0-5.5% SL), *Eonaso* (c. 4.5% SL), and *Arambourgthurus* (4.3-4.7% SL); the condition is unknown in *Sorbiniithurus* and *Marosichthys*. The caudal peduncle is somewhat slender in some species of *Prionurus* (ranging from 5-8% SL) and in both species of *Tylerichthys* Blot, 1980 (Eocene of Monte Bolca, 5.1-5.7% SL). However, both *Tylerichthys* and those species of *Prionurus* with a somewhat slender caudal peduncle lack five derived features (numbers 1-5) uniting *Naso*, *Eonaso*, *Arambourgthurus*, *Sorbiniithurus*, and *Marosichthys*, and the reduction in peduncle depth in *Tylerichthys* and *Prionurus* is most parsimoniously interpreted as independent of that in the other five genera. Apomorphy: 6-1, slender caudal peduncle (*Naso*, *Eonaso*, *Arambourgthurus*).

7. Number of dorsal-fin pterygiophores in preneural space

The ventral shaft of a single dorsal-fin pterygiophore, the first, is present in the preneural space

(between the rear of the skull and the neural spine of the first vertebra) in most acanthurids and in zanclyids. By contrast, the ventral shafts of the first two dorsal-fin pterygiophores are present in the preneural space in *Arambourgthurus*, *Sorbiniithurus*, and *Marosichthys*. Having two pterygiophores in the preneural space can be considered the culmination of a trend within the acanthurids for an anterior shift of the spiny dorsal-fin supports, as follows. The ancestral acanthuroid condition is for the ventral shaft of the first dorsal pterygiophore to be in the first interneural space (between the first and second neural spines), as in siganids and the first outgroup for acanthuroids, scatophagids (the first pterygiophore is in the second interneural space in the second outgroup, ehippidids). In luvarids the ventral shaft of the first dorsal pterygiophore is in the preneural space, either in the middle of the space or in contact with the skull (secondarily, the dorsal-fin shifts posteriorly in the fossil kushlukiid sister group of luvarids). In zanclyids and ancestrally for acanthurids the shaft of the first pterygiophore is in the preneural space in contact with the skull. Apomorphy: 7-1, ventral shafts of both the first and second dorsal-fin pterygiophores present in the preneural space (*Arambourgthurus*, *Sorbiniithurus*, *Marosichthys*).

8, 9. Number and position of vacant interneural spaces

The number and position of vacant interneural spaces (vacant in the sense of the absence of the ventral shaft of a dorsal-fin pterygiophore present between successive neural spines; the numbering of the space is based on that of the neural spine bordering the front of the space) are often phylogenetically informative among acanthurids and their outgroups. There is a single vacant interneural space, the third, in most acanthurids and in zanclyids. Among acanthurids, only in *Arambourgthurus*, *Sorbiniithurus*, and *Marosichthys* is the pattern different than this, each of these genera in its own way. In *Arambourgthurus* the first, second, and third interneural spaces are vacant; in *Sorbiniithurus* the second and third spaces are vacant; in *Marosichthys* no spaces are vacant. The *Marosichthys* condition is interpreted

as an interneural space specialization in the opposite direction to that in *Arambourgthurus* and *Sorbinithurus*, with the latter two sharing the derived condition of the second space being vacant as well as the plesiomorphic third space vacancy, and *Arambourgthurus* further specialized by the autapomorphic vacancy of the first space. Apomorphies: 8-1, no vacant interneural spaces (*Marosichthys*); 8-2, two vacant interneural spaces (*Sorbinithurus*); 8-3, three vacant interneural spaces (*Arambourgthurus*); 9-1, second interneural space vacant (*Arambourgthurus* and *Sorbinithurus*). An ordered transition series is not implied in the three divisions of character 8.

10. Hypurostegy

The bases of the caudal-fin rays only slightly overlap the hypurals in most acanthurids and in zanclics. In some species of *Naso* the bases of these rays have a somewhat greater overlap of the hypural plate posterodorsally and posteroventrally, but, nevertheless, they cover less than about one-fifth of the lateral surface of the plate (to about the extent illustrated for *N. thynnoides* and *N. sp.* in Tyler 1970b: figs 2; 3). By contrast, in *Arambourgthurus* the hypurostegy is extensive (just as much as in many scombroids, carangids, and lampridiforms), with the bases of the rays covering all but a narrow space along the middle of the hypural plate. The differences between the slight overlap of the ray bases in most acanthurids and the slight to moderate overlap among species of *Naso* are difficult to define and very subjective, but there is an enormous difference between these degrees of overlap and the extreme condition in *Arambourgthurus*. Apomorphy: 10-1, extensive hypurostegy (*Arambourgthurus*).

11. Supraneural

A single supraneural (predorsal bone) has been documented as the ancestral condition for the acanthurid + zanclic clade, with the *Naso* lineage (Nasinae) of acanthurids secondarily losing the bone (Sorbinini & Tyler 1998b). Among the five genera documented above to be united by six synapomorphies, the supraneural is absent in *Naso*, *Eonaso*, *Arambourgthurus*, and *Marosichthys*, whereas the supraneural is present in *Sorbinithurus* and this is most parsimoniously interpreted as a

reversal. Apomorphy: 11-1, independently regaining the supraneural (*Sorbinithurus*).

12. Dilator process of opercle

The dorsal region of the opercle is convex in most acanthurids and in zanclics. By contrast, Guiasu & Winterbottom (1993) document a dorsal process from the upper end of the opercle for the insertion of the dilator operculi muscle and an almost straight posterodorsal margin behind the process as present only in *Naso* among Recent acanthurids. There is evidence of the presence of this derived dilator process also in *Eonaso* (Tyler & Sorbinini 1998) but not in any of the other fossil taxa. Apomorphy: 12-1, presence of a dilator process (*Naso*, *Eonaso*). As described by Tyler (1997), *Marosichthys* has a relatively straight upper posterior opercular edge and, thus, one aspect of this character, but not the more functionally and morphologically important dilator process.

13. First anal-fin pterygiophore shield

Like the first dorsal-fin pterygiophore, the first anal-fin pterygiophore has a deep indentation into which the base of the first anal-fin spine rotates, and in most acanthurids and in zanclics the lateral surface of the pterygiophore around the indentation is relatively flat or has only a low strengthening ridge. By contrast, this region of the pterygiophore is expanded posterolaterally into a shield around the base of the short first anal spine in all species of *Naso* (including in *N. thynnoides* that has secondarily lost the dorsal pterygial shield) but not in any other acanthurids, fossil or Recent. Apomorphy: 13-1, presence of an anal pterygial shield (*Naso*).

14. Pelvic bone depth

Guiasu & Winterbottom (1993) document among Recent acanthurids that a relatively deep pelvis (basipterygium) like that in *Naso* with a length to depth ratio of substantially greater than 10% is plesiomorphic, with *Paracanthurus* having a 10% ratio and the four genera of higher Recent acanthurins having 6-8% ratios. Among the fossil species of acanthurids the depth ratios usually are plesiomorphic. For example, most Monte Bolca species have ratios of 12-15%, or even deeper in *Mataspisurus* Blot & Tyler, 1991 (18%) and

Acanthuroides (30%), but the pelvis is relatively more slender in *Metacanthus* Blot & Tyler, 1991 (11%) and especially in one of the four species of *Proacanthurus* (one species is 7% and the other three species are 10-15%; see Tyler & Sorbini 1998 for details). Among the five genera documented herein to be united by six synapomorphies, the ratios are *Naso* 16%, *Eonaso* 10%, *Arambourgthurus* 13%, *Sorbinithurus* 18%, and *Marosichthys* 12%. The relative narrowness of the pelvis in *Eonaso* within this clade is most parsimoniously interpreted as a reversal. Apomorphy: 14-1, independently reducing the pelvic depth (*Eonaso*).

CONCLUSION

Arambourgthurus is unique among all acanthurid fishes, both fossil and Recent, in having extensive hypurostegy and three vacant interneural spaces (first, second, and third). *Arambourgthurus* is the sister taxon to *Sorbinithurus* (which has two vacant interneural spaces, the second and third) based on the synapomorphy of the second interneural space being vacant. *Arambourgthurus* + *Sorbinithurus* is the sister group of *Marosichthys* (which has no vacant interneural spaces) based on the synapomorphy of two dorsal-fin pterygiophores present in the preneural space. The *Arambourgthurus* + *Sorbinithurus* + *Marosichthys* clade is the sister group of the clade composed of *Naso* + *Eonaso* (the latter two genera united by the opercular dilator process synapomorphy), with this Eocene to Recent clade of five genera of lower acanthurids (Nasinae) united by six synapomorphies, although several of these features are unknown for a few of the fossil taxa (especially *Sorbinithurus* and *Marosichthys*, in both of which the rear of the body is missing).

The minimal age of the Nasinae clade of five genera is that of its oldest member, *Sorbinithurus*, from the lower part of the middle Eocene (Lutetian, NP 14, *Discoaster subblodoensis* zone) of Monte Bolca, northern Italy, c. 52 My.

The Recent *Naso* is relatively widespread, being present in the Indo-western Pacific from South

Africa to Japan and from Hawaii to the Polynesian central Pacific island chains, but not in the eastern Pacific and Atlantic. One of the fossil genera of Nasinae, *Eonaso* of unknown age from Antigua in the Lesser Antilles of the Caribbean (and sister taxon to *Naso*), extends the former range of the subfamily into the western Atlantic. The two equally parsimonious biogeographic hypotheses about the distribution of the ancestor of the *Naso* + *Eonaso* clade have been discussed by Winterbottom & McLennan (1993): Indo-Pacific and Caribbean distribution after the emergence of the Panamanian isthmus with subsequent extinction in the eastern Pacific and Caribbean, *versus* a Tethyan distribution with extinction in the eastern Atlantic and Caribbean; in both cases *Eonaso* documents the Caribbean extinction. The other fossil Nasinae are known through the Tethys Sea in what is now Europe (*Sorbinithurus*) and the Near East (*Arambourgthurus*, Oligocene of Iran), and in the western Pacific (*Marosichthys*, Miocene of Celebes).

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