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MASSALONGIUS, GEN. & FAM. NOV., A NEW CLADE OF ACANTHUROID FISHES (PERCIFORMES, ACANTHUROIDEA) FROM THE EOCENE OF MONTE BOLCA, ITALY, RELATED TO THE ZANCLIDAE

ABSTRACT

Acanthurus gazolai Massalongo, 1859, was described based on a single specimen of a well-preserved fish in part and counterpart from the lower part of the Middle Eocene of Monte Bolca, Italy, and Massalongo thought it to be a species of Acanthuridae. This taxon has never been comprehensively redescribed in modern terms or reconstructed, and our knowledge of it is mostly based on the photograph of one of the counterparts in the original description. This poorly known taxon, with elongate sturdy upper and lower jaws and a high spiny dorsal fin, has been briefly speculated over the past century and a half to be either a chaetodontoid or an acanthuroid of indeterminate family. We herein redescribe this specimen, with its first reconstruction, and our cladistic analysis of its characteristics indicates that it represents a new genus (Massalongius) and family of Acanthuroidei that is the sister group of the Zanelidae.

Key words: Massalongius nov. gen., Massalongiidae nov. fam., Zanclidae, Acanthuroidea, Eocene, Monte Bolca, Italy.

RIASSUNTO

Acanthurus gazolai Massalongo, 1859, fu descritto basandosi su un unico esemplare, conservato nell'impronta e nella controimpronta, della base dell'Eocene medio di Bolca, da Massalongo, che lo attribuì alla famiglia Acanthuridae. Questo taxon non è mai stato ridescritto comprensibilmente con termini attuali o ricostruito, e la conoscenza di esso si basa principalmente sulla fotografia di una delle controimpronte della descrizione originale. Questo taxon poco conosciuto, con mandibola superiore e inferiore allungate e robuste e pinna caudale molto spinosa, durante la seconda metà del secolo scorso è stato considerato sia come chetodontide che acanturoide di un'indeterminata famiglia. Nel presente lavoro ridescriviamo l'esemplare, con la sua prima ricostruzione, e la nostra analisi cladistica delle caratteristiche indica che esso rappresenta un nuovo genere (Massalongius) e famiglia degli Acanthuroidei, il sister group degli Zanclidae.

Parole chiave: Massalongius nov. gen., Massalongiidae nov. fam., Zanclidae, Acanthuroidei, Eocene, Monte Bolca, Italia.

INTRODUCTION

Even among the ancient collections of fishes from the lower part of the Middle Eocene of Monte Bolca first described in the 19th century by a variety of mostly Italian naturalists, many remain poorly known and of uncertain classification in a contemporary sense of

systematics. One such case is the well-preserved specimen in part and counterpart at the Museo Civico di Storia Naturale di Verona that was described by Abramo Massalongo in 1859 as *Acanthurus gazolae*.

Woodward (1901) interpreted the original description as indicating that this species did not belong to Acanthurus but, rather, was probably a Chaetodontidae. Without examining the type specimen, Eastman (1904) and D'Erasmo (1922) agreed that it was related to Pygaeus sensu lato, which was at that time placed among the chaetodontids. In reviewing the status of his work on Monte Bolca fishes up to that date, Blot (1980) stated that this species could not be accommodated in Pygaeus, and that it represented a new genus, but that it remained to be seen whether it was an acanthuroid or a chaetodontid. Blot and Tyler (1991) revised all of the numerous taxa, many of them new, of Acanthuridae from Monte Bolca and in an addendum they gave a few notes on Acanthurus gazolai, including its acanthurid-like vertebral formula (Blot formula). They concluded that it should be placed incertae sedis among the basal chaetodontids. Bannikov (in press) reviewed the various Pygaeus-like taxa from Monte Bolca that had been referred to the Chaetodontidae, and concluded that they are not closely related to chaetodontids; he also excluded Acanthurus gazolai from the chaetodontids, with its acanthuroid affinities to be reported upon in the present paper.

We herein document the acanthuroid characters of *Acanthurus gazolai*, show it to be the sister group of the Zanclidae (the extant *Zanclus* and the Eocene of Monte Bolca *Eozanclus*), and place it in the new genus *Massalongius*, representing the new family Massalongiidae, in the new Zanclidae + Massalongiidae clade.

METHODS

Many features of the holotype were best seen when the part and counterpart were moistened with alcohol during microscopic examination. Abbreviations are as follows: MCSNV - Museo Civico di Storia Naturale di Verona; MYA - millions of years ago; PU - preural vertebra; SL - standard length; U - ural vertebra.

Interneural and interhaemal spaces are numbered based on the vertebra whose neural or haemal spine forms the anterior border of the space, with the first space being between the first and second neural or haemal spines, and the preneural and prehaemal spaces being those in front of the first neural and haemal spines (following Baldwin and Johnson, 1993; Bannikov and Tyler, 1995; Tyler and Bannikov, 1997; Tyler et al., 2002).

Genus Massalongius gen. nov.

Diagnosis. Body moderately deep (47% SL). Head large, only slightly less than body depth. Supraoccipital crest very high and posteriorly extended, to about vertical level of fourth vertebral centrum; sculpturing on lateral surface of crest indicating cancellous bone. Mouth terminal. Snout very long and tapering, its length about 3.5 times greater than orbit diameter. Ascending premaxillary process extremely long, but not reaching to anterior edge of orbit. Jaw teeth very small, villiform, in a narrow band. Lower jaw articulation distinctly in front of anterior edge of orbit. Preopercle slightly curved, without spines or serrations.

Vertebrae 22 (9+13); no parapophyses on abdominal vertebrae. Hypurals unconsolidated; probably three epurals and two uroneurals (broad stegural and elongate second uroneural). Pleural ribs from third to ninth vertebrae, short, slightly less than one-half depth of abdominal cavity. One supraneural, apparently a composite of two consolidated elements. Dorsal fin long-based, with nine spines (third longest, ninth longer than eighth) and 20 soft rays; spinous and soft parts continuous. Third interneural space vacant (no dorsal pterygiophore present between third and fourth neural spines). Anal fin with three spines and 20 soft rays. Pectoral fins situated relatively low, in about middle of abdominal region. Pelvic fin I, 5, with at least first ray greatly elongate. Caudal fin slightly rounded, almost truncate, with 16 principal rays, and 2-3 procurrent rays above and below.

Scales relatively small, with delicate ctenii and some upright spinules. Coloration with two or three vertically transverse bands, without ocelli.

Type species. Acanthurus gazolai Massalongo, 1859, by monotypy and designation herein.

ETYMOLOGY. Named in honor of the 19th century Italian geologist and paleobotanist Abramo Massalongo (1824-1860), who studied medicine in order to be a naturalist and later obtained a law degree, and who taught high school in Verona in the Ginnasio della Città (see Guidotti, 1985, for the diverse interests and career accomplishments of Dr. Massalongo). In addition to his botanical pursuits, he also catalogued and published photographs of many of the then-known fishes of the Eocene of Monte Bolca, and who first described and illustrated the type species of this unique acanthuroid genus.

Massalongius gazolai (Massalongo, 1859) Figures 1-3

Acanthurus Gazolae Massalongo, 1859, p. 26, pl. 7, fig. 1; description and photograph of one of the counterparts (MCSNV VIII D 200); mentions that a movable spine on the caudal peduncle distinguishes Acanthurus from Naseus (=Naso), and that A. Gazolae seems to have such a spine; however, we find nothing in the caudal region of the specimen (nor in Massalongo's photograph) that could be interpreted as a movable spine (nor a fixed plate).

Acanthurus Gazolae: De Zigno, 1874, p. 79 (of separate); holotype briefly redescribed, with some features more precisely so than in Massalongo.

Acanthurus gazolae: Woodward, 1901, p. 564; states that this species does not belong to Acanthurus and is probably a Chaetodontidae.

Pygaeus gazolae: Eastman, 1904, pp. 30-31; agrees with Woodward that this species is a Chaetodontidae, and that it can be accommodated in Pygaeus Agassiz sensu lato, which group of chaetodontids he believes also are related to Acanthuridae.

Pygaeus gazolai: D'Erasmo, 1922, p. 125; assigned to Pygaeus based on Eastman, and terminal letter in specific name changed to modern "i" masculine patronymic ending.

"Nov. gen.- nov. sp.": Blot, 1980, p. 375; states under listing of Chaetodontidae that this specimen (MCSNV VIII D 200-201) of *Acanthurus gazolai* cannot be accommodated in *Pygaeus* as proposed by Eastman, but, rather, that it represents a new genus and species (the latter a *lapsus calami* because this specimen is the type and only known specimen of *A. gazolai*, and therefore would not be a new species even if a new genus were proposed for it, and Blot [following reference] lists this specimen again a few pages later in the same publication, under Acanthuridae)

Acanthurus gazolai: Blot, 1980, p. 379; listed with holotype (D 200-201) in Acanthuridae, but with comment that it remains to be seen whether this is an acanthuroid or a chaetodontid.

Acanthurus gazolai: Blot & Tyler, 1991, p. 77; descriptive notes and Blot vertebral formula of holotype;

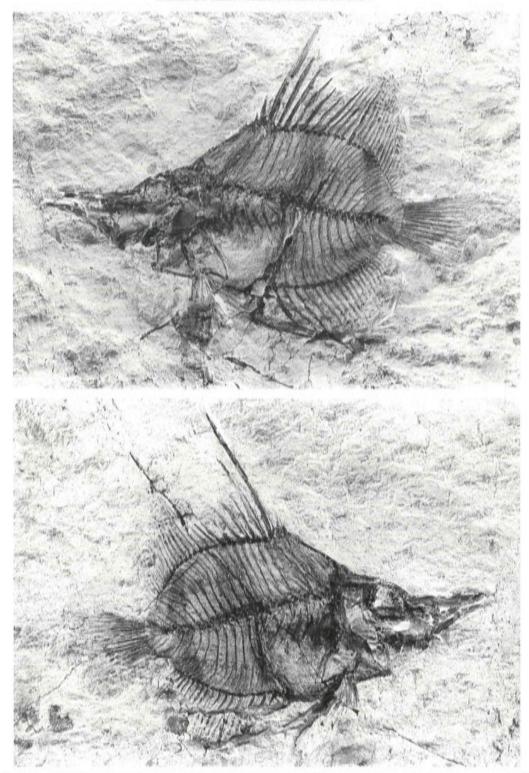


Figure 1 - Photographs of the counterparts of the holotype of *Massalongius gazolai* (Massalongo, 1859), Museo Civico di Storia Naturale di Verona, VIII 200 (head to left) and D 201, 63.0 mm SL, lower part of the Middle Eocene of the Pesciara site of the Monte Bolca locality, Italy (Veneto).

reviews all Monte Bolca taxa of Acanthuridae, and excludes Acanthurus gazolai, placing it incertae sedis among basal Chaetodontidae.

Pygaeus gazolai?: Frickhinger, 1991 and 1995, photograph of one of the holotypic counterparts (D 200) on p. 858 under Chaetodontidae.

Acanthurus gazolai: Bannikov, 2004, p. 56; states that it is not a Chaetodontidae but, rather, an acanthuroid under study by Tyler and Bannikov for this present paper.

HOLOTYPE. Museo Civico di Storia Naturale di Verona (MCSNV) VIII D 200-201 (head to left in D 200), part and counterpart, 63 mm SL; lower part of Middle Eocene, Lutetian, zone *Discoaster sublodoensis*; Monte Bolca locality (Veneto, northern Italy), Pesciara cave site; about 50 MYA. Only known specimen.

DIAGNOSIS. As for the genus.

Description. The body is rather deep, with a very short caudal peduncle, whose depth is about 0.27 of the body depth. The head is large; its length is about 0.91 of the body depth. The head length is contained 2.1 times in the SL. The dorsal profile of the body posteriorly is slightly more convex than the corresponding ventral profile.

 Head. The length of the head is greater than its depth. The rostro-frontal profile of the head is generally concave, with a slight convexity above the orbit. The orbit is relatively small; the diameter of the orbit is contained about 3.3 times in the snout length and contained 5.7 times in the head length. The orbit is situated high in the skull. The rostral part of the head is produced into a long, tapering snout, ending in a stout tube when the mouth is closed, as in the preserved specimen. The neurocranium is deep. The ethmoid region is relatively long. The supraoccipital crest is very high, thickened along its anterior or upper edge, and tapered to a blunt point posteriorly; as seen in D 200, the lateral surface of the crest has sculpturing consisting of narrow bands enclosing broader indented plains, which indicates cancellous bone conditions. The parasphenoid as exposed under the orbit is a slender slightly curved shaft with a ventral flange that is no deeper than the shaft-like part of the bone. The infraorbitals are too badly damaged to describe. The premaxilla has a long ascending process; the alveolar process is prominent but shorter than the ascending process, and there is no postmaxillary process. Short villiform teeth are poorly preserved in the premaxilla. An elongate narrow nasal is indistinctly preserved along the dorsal edge of the ascending premaxillary process. The mandible is long and very narrow at the symphysis; the dentary is about four times longer than the articular. There may be a few small serrations along the lower edge of the anterior region of the dentary. Short villiform teeth are clearly evident in a band along the upper edge of the dentary (teeth best seen in D 200). The lower jaw articulation is situated well anterior to the level of the anterior edge of the orbit. The axis of the hyomandibula is strongly inclined anteriorly. The quadrate is wide and triangular. The symplectic is small and narrow. The opercular region is relatively narrow, and these bones are badly damaged. The preopercle is very slightly curved along its anterior edge; no preopercular spines or serrations are evident. The lower edge of what we interpret as the interopercle, situated below the quadrate and anterior region of the preopercle, and behind the mandible, has low serrations. Neither branchial nor hyoid arches are evident.

Axial skeleton. There are what we interpret as 22 (9+13) vertebrae, including the
urostyle. The limits of many of the vertebrae in the regions of their centra are unclear, and

our determination of the vertebral count is based on the concordance of neural and haemal spines with the remains of the centra. After careful examination, we are confident in the count of 9+13, and this is also the count as determined by Blot and Tyler (1991) in their study focused on the vertebral column and pterygiophores of acanthuroids. The vertebral counts recorded by Massalongo (1859) of 24-25 (with 12 caudal) and by De Zigno (1874) of 25 are surely incorrect.

The vertebral column is very slightly sigmoid. The distal end of the slender first neural spine is situated between the lower ends of the supraneural and the first dorsal-fin pterygiophore; the distal end of the slender second neural spine is situated between the lower ends of the first and second dorsal pterygiophores; and the distal ends of the broader neural spines of both the third and fourth vertebrae are situated between the second and third dorsal pterygiophores, and thereby the third interneural space is vacant (this being the only vacant interneural space). The neural and haemal spines of the caudal vertebrae are relatively long and wide, becoming gradually shorter and more slender posteriorly in the series. The haemal spines of the anteriormost caudal vertebrae are almost vertically oriented; the distal regions of the first and second haemals are oriented anteroventrally, whereas the distal regions of all of the other haemal spines are either vertical (3rd) or inclined moderately posteroventrally (4th and more posterior). The haemal spines of the caudal vertebrae arise from the anterior to middle regions of their centra, and several of them (especially those of the 4th and 5th caudal vertebrae) are noticeably curved anteriorly in the basal to middle regions of their lengths. There are no parapophyses on the abdominal vertebrae. Relatively short and slender ribs (pleurals) are present on the third to ninth abdominal vertebrae; the ribs are slightly inclined posteriorly and they extend ventrally slightly less than one-half the depth of the abdominal cavity. No epineurals are evident.

- Paired fins and girdles. Neither the posttemporal nor supracleithrum are clearly distinguishable. The large cleithrum is gently and only slightly sigmoid and has a wide posterior expansion; its anterior edge below the level of the postcleithrum is relatively straight. The postcleithrum is a relatively strong shaft oriented obliquely posteroventrally; there is no evidence of a long oblique suture or space dividing the postcleithrum into separate upper and lower halves, and we think that the postcleithrum is probably a single bone, but because of fracturing in the middle region of the bone we cannot be sure of this. Although the coracoid is badly fractured, it seems to be relatively wide. The pectoral fin is not preserved, but based on the positions of the bones of the pectoral girdle, the fin is situated low on the body in about the middle region of the abdominal cavity.

The pelvis is large, and both its anterior (iliac) and posterior (ishiac) processes are well developed and long. Although the pelvic fin is incompletely preserved and many fractures are present where the pelvic fins from both sides are exposed, it is clear that there is a long, slender spine and five soft rays, and that at least the first ray is greatly elongate. Only the pelvic fin from one side is shown in the reconstruction, this being the pelvic fin in which the slender spine and the greatly elongate first ray are best exposed. The pelvic spine is 25% SL, and the first ray is 46% SL (as preserved, the basal region of the first ray overlays and obscures the lower region of the spine). The distal region of at least one branch of the elongate first ray is well preserved (more basally this ray is incomplete) and extends posteriorly beyond the level of the distal tips of the anal-fin spines and the first few anal soft rays. Because of fractures and poor preservation, the full lengths of the second to fifth pelvic rays cannot be determined, but fragments indicate that they were elongate and of decreasing length from the second to the fifth element. The pelvic fin is situated on what

we estimate to be the vertical level of the pectoral-fin base.

- Supraneural and dorsal fin. In our interpretation there is a single supraneural, but it is a compound element probably formed by the consolidation of two supraneurals, as best seen when the bony remains and impressions in the counterparts are moistened and closely compared. The anterior edge of this complex element is a relatively straight thickened shaft. The posterior edge of the element is a similar shaft, but this shaft dorsally has a prominent anterior curvature that crosses over the upper end of the anterior shaft (the anterior curved head of the posterior shaft best seen in D 200). From these distal ends, the two shafts gradually converge ventrally into a common single shaft. There is a thin bony lamina present between the divergent regions of the two rami of the unified shaft. We presume that a slightly shorter anterior supraneural has consolidated (and fused ventrally) with a slightly longer and anterodorsally curved posterior supraneural to form

the compound single element we recognize herein.

The dorsal fin is long-based and continuous, with a moderate indentation between the eighth and ninth spines. The spinous part of the dorsal fin consists of nine strong spines; the first spine is short but clearly protruding to the exterior, the third spine is much elongate, and the ninth spine is longer than the eighth. The distal tip of the third spine is fractured and displaced just behind and below the rest of the spine (in D 201); the length of the spine, with its displaced tip, is 27.8 mm, which is slightly more than twice as long as the base of the spiny dorsal fin. The fourth spine is complete in D 201 and 19.0 mm long; the fifth spine is incomplete at the tip in both counterparts. The lengths of the fourth to eighth spines gradually decrease, and the last spine (9th, 11.6 mm) is 1.3 times longer than the penultimate spine (8th, 8.7 mm). The first two spines are supernumerary on the first dorsalfin pterygiophore, and this pterygiophore extends anterodorsally as a prong just above the supraneural. The bases of the first three dorsal-fin spines are bifurcate and articulate (rotate in life) over rough-surfaced grooved flanges on the first two pterygiophores, as follows (see Fig. 3): the short first spine articulates to a high rounded flange demarked anteriorly by a deep indentation in the upper surface of the pterygiophore at the front of the spine, and an even deeper indentation at the rear of the spine; just behind the later indentation is a larger median flange on the first pterygiophore around which the broad base of the second spine articulates; the third spine articulates over a large flange similar to that for the second spine. Because of the rough grooved surfaces on the flanges around which these three spines articulate, we presume that these spines in life could be locked in various positions of erection.

The soft part of the dorsal fin consists of 20 segmented rays, with the last ray split to the base. The longest rays are in the anterior quarter of the fin. The length of the soft dorsal-fin base is about 1.2 times longer than the length of the spiny dorsal-fin base. The dorsal fin ends at the level above the anterior region of the hypurals; the last dorsal-fin pterygiophore is between the neural spines of the ninth and tenth caudal vertebrae. The pterygiophores of the dorsal fin penetrate down into the interneural spaces, with the interneural spaces below the spiny dorsal fin usually having the ventral shafts of one pterygiophore present (except for the third space, which is vacant, without a pterygiophore). The interneural spaces below the soft dorsal fin usually have the ventral shafts of two (anteriorly) or three (posteriorly) pterygiophores present. The pterygiophores of the dorsal-fin spines are wide in lateral aspect whereas the pterygiophores of the dorsal-fin soft rays are narrower; the pterygiophores decrease in length posteriorly in the series. Preservation is not sufficient to determine medial and distal pterygiophores.

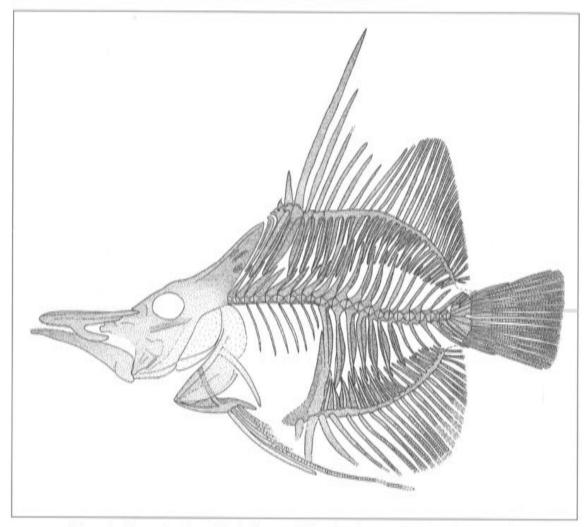


Figure 2 - Reconstruction of the holotype of Massalongius gazolai (Massalongo, 1859).

- Anal fin. The length of the anal-fin base is about 1.2 times shorter than the length of the dorsal-fin base. The anal fin has three spines and 20 soft rays. All three of the spines are incomplete distally; the first two spines are supernumerary on the first pterygiophore. The basal regions of the three spines and the immediately adjacent distal ends of the first two pterygiophores are badly fractured and incomplete; we cannot determine how the bases of the spines articulated with the pterygiophores (i.e., how similar the anal spines were to the arrangement of the first three dorsal-fin spines on their pterygiophores). The bases of the anal-fin soft rays are relatively widely spaced in the anterior part of the fin, but the bases become more closely spaced posteriorly in the series. The longest rays are in the middle of the fin. The anal fin ends at the level of about the middle of the centrum of the penultimate vertebra. The first pterygiophore of the anal fin is the longest and largest, with its distal region inclined obliquely anteriorly; its ventral end is poorly preserved but it is expanded anteriorly in front of the first anal-fin spine. The anal-fin pterygiophores decrease in length

posteriorly in the series. The interhaemal spaces above the anal fin have the dorsal shafts

of one to three pterygiophores present.

- Caudal fin and skeleton. The caudal skeleton is of the generalized perciform type, with fusion of PU1, U1, and U2 in the terminal centrum. The neural spine of PU2 is short and forms a low crest. All five hypurals, the parhypural, and the haemal spines of PU2 and PU3 are autogenous. Two epurals are clearly recognizable, and we believe that there are the remains and impression of a third epural just in front of the two more fully preserved ones. Our interpretation is that there are two uroneurals: a moderately long and broad first uroneural (i.e., stegural) over the region of the anterior half of the length of the fourth hypural; and a long, somewhat narrower second uroneural between the fifth hypural and third epural.

The caudal fin has 16 principal rays, with 14 branched (I,7+7,I). There are two procurrent rays above, while below two procurrent rays are clearly visible and there are the faint impressions of a third one at the beginning of the series. The caudal fin is moderately long

and very slightly rounded at the top and bottom.

- Squamation. Relatively small thin scales cover the entire body and bases of the unpaired fins. The scales have delicate ctenii, and some of them appear to bear upright spinules (type 4 spinoid scales of Roberts, 1993), as evidenced by faint indications on the matrix. Only a small part of the ascending region of the lateral line can be seen in the

anterior part of the body.

- Coloration. There are two prominent transverse bands of dark pigment on the body. One band extends from the end of the spiny dorsal fin to the beginning of the soft anal fin. The other band extends from the middle of the soft dorsal fin to the posterior part of the soft anal fin. Additionally, dark pigment is recognizable between the supraoccipital crest and the first dorsal-fin pterygiophore and this is probably the upper part of a less well-defined third, and anteriormost, band.

 Measurements of the holotype. The following measurements are given as a percent of the 63 mm SL.

Head length from tip of snout to posterior border of opercle: 43

Maximum depth of body, at anal-fin origin: 47

Length of snout: 26

Horizontal diameter of orbit: 8

Length of ascending process of premaxilla: 23

Length of lower jaw: 26

Distance between tip of snout and spiny dorsal-fin origin: 60

Distance between tip of snout and soft dorsal-fin origin: 80

Distance between tip of snout and anal-fin origin: ca. 65

Distance between tip of snout and posterior end of supraoccipital: 57

Distance between rear edge of base of pelvic fin and anal-fin origin; ca. 14

Length of base of spiny dorsal fin: 20

Length of base of soft dorsal fin: 26

Length of base of anal fin: 37

Length of first spine of dorsal fin: 3

Length of second spine of dorsal fin: 9

Length of longest (3rd) spine of dorsal fin: 44

Length of eighth spine of dorsal fin: 14

Length of ninth spine of dorsal fin: 18

Length of longest rays (4th-6th) of dorsal fin: 21 Length of longest rays (6th-8th) of anal fin: 18

Length of spine of pelvic fin: 25

Length of longest (1st) ray of pelvic fin: 46

Length of longest (middle) rays of caudal fin: 22

Least depth of caudal peduncle: 13

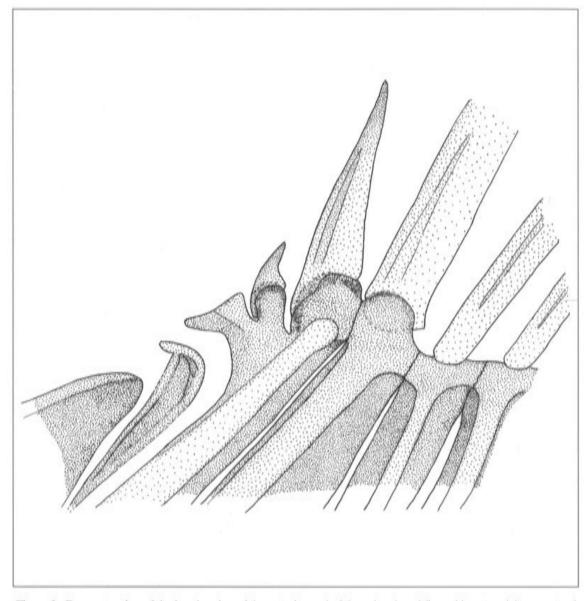


Figure 3 - Reconstruction of the basal region of the anterior end of the spiny dorsal fin and its pterygial supports of the holotype of *Massalongius gazolai* (Massalongo, 1859). From anterior (to the left) to posterior: the upper end of the supraoccipital crest; the compound single supraneural; the first dorsal-fin pterygiophore, with rounded ribbed flanges for locking articulation with the first two dorsal-fin spines; the second pterygiophore bearing the third spine; and the third and fourth pterygiophores bearing the fourth and fifth spines.

ANALYSIS OF ACANTHUROID CHARACTERS

The following analysis of characters to establish relationships is based on the highly corroborated sequential phylogeny of the five families of acanthuroid fishes (siganids, luvarids + †kushlukiids, zanclids, acanthurids) and of their sequential scatophagid and ephippidid outgroups documented by Tyler et al. (1989), Winterbottom (1993), Winterbottom and McLennan (1993), Bannikov and Tyler (1995), Tyler and Bannikov (1997), and Tyler and C. Sorbini (1999), and on the relationships of Recent acanthurid genera documented by Winterbottom (1993) and Guiasu and 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. A possible exception to this is that the molecular data suggest that the drepanid, ephippidid, and scatophagid outgroups (higher squamipinnes) may not be sequential but, rather, form a sister group clade to the acanthuroids. For different interpretations of the morphological evidence for the relationships of these higher squamipinne outgroups, see Mok and Shen (1983) and Blum (1988).

For Recent acanthurid genera, Tyler et al. (1989), Winterbottom (1993), and Guiasu and Winterbottom (1993) have shown *Naso* to be the morphologically primitive sister group of the other five genera, with the latter considered below as the higher acanthurids. Within the clade of higher acanthurids, *Prionurus* is the sister group of the two clades composed of *Paracanthurus* + *Zebrasoma* and *Acanthurus* + *Ctenochaetus* (Winterbottom 1993; Guiasu and Winterbottom, 1993; for the phylogeny of the species of *Zebrasoma* see Guiasu and

Winterbottom, 1998, and for that of the species of Naso see Borden, 1998).

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

the supraneural was present in the ancestral acanthurid.

For the *Naso*-like lower acanthurids (Nasinae), a phylogeny has recently been documented (Tyler, 2000), with the Recent *Naso* as the sister group to *Eonaso*, of uncertain but probably not Eocene age, and the *Naso* + *Eonaso* clade as the sister group to the Oligocene *Arambourgthurus* + the Eocene *Sorbinithurus* + the Miocene *Marosichthys*. Within the latter clade, *Arambourgthurus* + *Sorbinithurus* are sister taxa. See Tyler (1997, 1999, 2000) and Tyler and L. Sorbini (1998) for redescriptions of all of these *Naso*-like fossil genera.

For the specialized locking mechanism of the first dorsal- and anal-fin spines that are the most distinctively innovative derived features of all acanthurids, and for other

osteological data on the family, see Tyler (1970a, 1970b).

It is understandable that the new taxon *Massalongius* has been associated with the chaetodontids because it is similar in body form and jaw structure to some of the long-snouted genera of chaetodontids such as *Chelmon* and *Forcipiger*. However, the similarities are mostly superficial, and any close study of the specimen of *Massalongius* indicates that it lacks all of the derived features of chaetodontids that one could expect to be observed in Monte Bolca fossils. The synapomorphies of the Chaetodontidae have been well documented by Blum (1988), Ferry-Graham et al. (2001), and Smith et al. (2003). A large number of these derived diagnostic features of chaetodontids are soft tissue characters, including those made known during the last 15 years of the details of the laterophysic

connections between the swim bladder and the lateral line system. However, there are also many osteological features that are diagnostic of chaetodontids, and some of these are of

sorts that would be preserved and exposed in fossils.

For example, fossil chaetodontids could be expected to show at least the following synapomorphies: sequential articulation between the first dorsal-fin pterygiophore, the supraneurals, and the supraoccipital crest; the first dorsal-fin pterygiophore with a laterally expanded bony shelf to buttress the articulation with the base of the first dorsal-fin spine (the smaller first of the two supernumerary dorsal-fin spines); exceptionally long ribs, reaching nearly to the ventral mid-line; ribs with laminae extending forward from the medial edges of their ventral shafts; and one might sometimes be able to observe two others, the ethmoid placed posteriorly between the lateral ethmoids and anterior region of the orbit, and the anterior group of branchiostegal rays (two or reduced to one) not in contact with the ceratohyal; many other chaetodontid derived bony features might be difficult to determine in Monte Bolca fossils without special preparation, such as the perforate openings in the mesethmoid, the many specializations of the multiple bands of teeth in the jaws and of the pharyngeal teeth, the openings in the supracleithrum for the lateral line canal, etc.

Massalongius has none of these derived features of chaetodontids that might be seen in fossils, and thereby it cannot be a member of that family (note that while Massalongius has villiform teeth, these are in a single long narrow band along the length of the jaws and are not in a series of short multiple bands as in chaetodontids).

By contrast, *Massalongius* shares a wide variety of derived features with the higher squamipinnes (including ephippidids, scatophagids, acanthuroids) and, especially, of those that are diagnostic of the families of acanthuroids (the terminal sister group within the higher squamipinnes). These derived features of *Massalongius* include the easily determined reduction to 9+13 vertebrae, 16 caudal-fin rays, single supraneural, and anterior position of the first dorsal-fin pterygiophore in the first interneural space. Most instructive of all, *Massalongius* has the derived condition of a locking articulation of the first dorsal-fin spine rotating around a semicircular ribbed median pterygiophore flange that is an unique innovative feature found only in zanclids and acanthurids.

We discuss these higher squamipinne/acanthuroid features in the same order and numbering system as these features are given in their most extensive format, by Tyler et al.

(1989), with notation of a few modifications based on more recent work.

For the six characters of the Ephippididae + Scatophagidae + Acanthuroidei node, we cannot determine characters I (interarcual cartilage), II (interopercular shape), and V (gill membranes united at isthmus) in *Massalongius*, but *Massalongius* does possess character III (articular equal to or shorter than dentary) and VI (cancellous bone surface present on supraoccipital; cannot determine on frontal). Character IV (premaxillae non-protrusible or only slightly so, and premaxillae and maxillae with relatively little independent movement) is absent in *Massalongius* because one must assume that the long ascending process of the premaxilla and the posterior placement of the maxilla along the underside of the rear of the ascending process, as well as the long lower jaw, indicate that *Massalongius* had a significant gape and that the jaws were mobile, with the premaxilla protrusible along the maxillary articulation. This reversal to a lower squamipinne and perciform condition is a distinctive feature of *Massalongius* alone among all of the higher squamipinne fishes, including the acanthuroids.

For the four characters of the Scatophagidae + Acanthuroidei node, we cannot

determine character X (parietals absent) in Massalongius, but Massalongius does possess character VII (13 caudal vertebrae, in this case 9+13=22) and character IX (principal caudal-fin rays 8+8=16). Character VIII (only anterior uroneural pair present) is absent in Massalongius because the well-developed anterior uroneural (stegural) is followed by a long rod-like second uroneural, this being a reversal to the lower squamipinne condition. Tyler et al. (1989) stated that the position of the ventral shaft of the first dorsal-fin pterygiophore either directly over the first centrum (as in Siganus) or in front of the first neural arch, in the preneural space (the "first interneural space" in the now antiquated usage of Tyler et al., 1989), was a synapomorphy of the extant Acanthuroidei. However, the five genera of fossil siganids have the shaft of the first dorsal pterygiophore in the first interneural space (between the first and second neural spines; see Tyler and Bannikov, 1997; Bannikov and Tyler, 2002). Thereby, Tyler and C. Sorbini (1999) have shown that a synapomorphy of the Scatophagidae + Acanthuroidei node is to have the first dorsal pterygiophore shifted forward to the first interneural space (versus the second interneural space in the lower squamipinne outgroups), whereas the even further forward shifting of the first pterygiophore shaft to the preneural space (between the skull and first neural spine) is a synapomorphy of the higher acanthuroids (luvaroids + zanclids + acanthurids) independent of the lesser forward shift to just above the neural arch of the first vertebra in Siganus alone among siganids.

There are 11 adult characters for the Acanthuroidei node (i.e, the Siganidae + Luvaridae + Zanclidae + Acanthuridae node); there also are numerous larval characters given by Tyler et al. (1989) and myological characters given by Winterbottom (1993) for the various acanthuroid nodes that are not applicable to the fossil materials of acanthuroids. We cannot determine in Massalongius adult characters 2 (branchiostegal rays), 3 (second infraorbital articulation), 5 (supracleithral sensory canal), 8 (supraoccipital not contacting exoccipital), and 11 (narrow fourth pharyngeal toothplate), whereas character 4 (first dorsal pterygiophore placement) is now considered at a different level of universality, discussed above. Massalongius possesses character 1 (first neural spine fused to its centrum) and character 7 (angular much smaller than dentary, a more derived condition than character III previously discussed). Three other characters at this node are absent and interpreted as reversals for either Massalongius alone or for Massalongius + Zanclidae, as follows. Character 6 (maxillae and premaxillae closely bound together) is a further derived variation on character IV previously discussed, and the mobile premaxilla-maxilla articulation in Massalongius as evidenced by the size and position of the bones is a reversal to a lower squamipinne and perciform condition; this is one of the most distinctive features of Massalongius, uniquely so among all of the higher squamipinne and acanthuroid fishes. Character 9 (supraoccipital crest reduced) is a synapomorphy at this node, but the high supraoccipital in the two genera of Zanclidae (the Eocene Eozanclus and the Recent Zanclus) is considered as a reversal, and it is also here interpreted as a reversal in Massalongius; this is not unexpected given that Massalongius is proposed here as the sister group of the Zanclidae. Character 10 (supraneurals absent) is a synapomorphy at this node, but the presence of a single supraneural is an ancestral reversal by some acanthurids as well as by the two genera of zanclids and by Massalongius, once again not unexpectedly

for the proposed sister group of the Zanclidae.

Relative to the supraneural, we note here that Tyler and Bannikov (1997) have a detailed discussion on the importance of fossil taxa in determining the evolutionary history of supraneurals in acanthuroids. They demonstrate that the ancestral acanthuroid and

the ancestral siganid and luvarid + kushlukiid lacked a supraneural, but that it is equally parsimonious that the ancestor of the zanclid + acanthurid clade regained the supraneural and it was lost independently by Naso and four other Recent genera of acanthurids except Prionurus, or that this ancestor lacked the supraneural and it was regained independently by zanclids, Eocene fossil acanthurids, and Prionurus. Subsequently, L. Sorbini and Tyler (1998) found that the Eocene Proacanthurus, which has a supraneural, has a folding caudal peduncle spine and is the sister group of the four Recent genera with a folding caudal peduncle spine. Therefore, it became more parsimonious to propose that the ancestor of zanclids + acanthurids regained the supraneural, followed by the independent lost of the supraneural by Naso and by the four folding-spine Recent genera of acanthurids (three steps), rather than that this ancestor had the ancestral lower-acanthuroid condition of no supraneural, with independent regaining of the supraneural by zanclids, by Eocene genera of acanthurids other than Proacanthurus, by Prionurus, and by Proacanthurus (four steps).

The two phyletically basal families of acanthuroids, the Siganidae and Luvaridae (plus their fossil sister group Kushlukiidae) are remarkably specialized in many aspects of their anatomy, and Tyler et al. (1989) give 13 characters (numbers 12-24) that are synapomorphies of siganids and seven characters (33-39) that are synapomorphies of luvarids. The conditions of many of these siganid and luvarid specialized characters can be determined in *Massalongius*, and none are present in *Massalongius*, thereby excluding it from further consideration as a member of those two families.

There are eight adult characters that support the Luvaridae + Zanclidae + Acanthuridae node, and five adult characters that support the Zanclidae + Acanthuridae node, as follows.

For the eight characters of the Luvaridae + Zanclidae + Acanthuridae node, we cannot determine character 27 (infraorbital series curvature), 28 (palatine position), and 29 (spina occipitalis absence). *Massalongius* does possess character 31 (scales spinoid, with upright spinules) and probably character 32 (a single postcleithrum). We find no evidence of character 30 (small spinules laterally along length of soft fin rays) in *Massalongius*, but we are uncertain if these spinules are absent or simply not well preserved or exposed; if they are absent, it is a reversal also found in some acanthurids.

For the five characters that support the Zanclidae + Acanthuridae node, we cannot determine character 41 (orientation of fourth pharyngeal toothplate), 42 (ethmoid shape and relationship to vomer), and 44 (orientation of gut loops). *Massalongius* does possess both of the other two synapomorphies: character 40 (third interneural space vacant, with no dorsal pterygiophore between third and fourth neural spines; i.e., the "fourth interneural space" in the now antiquated usage of Tyler et al., 1989), and character 43 (first dorsal pterygiophore with ribbed median flange for locking first dorsal spine), the latter being a diagnostic innovative specialization of this clade, variously further derived within the group.

For the Zanclidae, Tyler et al. (1989) list seven adult characters that are autapomorphies of the Recent Zanclus cornutus, the only extant species of the family (they did not include fossil taxa in their acanthuroid phylogeny). Three of these seven derived characters apply only to Zanclus (character 45, adults with spiny protuberance on frontal at orbit; 46, most dorsal spines distally prolonged as filaments; 48, single supernumerary dorsal-fin spine), whereas the Eocene species, Eozanclus brevirostris (from Monte Bolca) has plesiomorphic conditions for these characters (no spiny frontal protuberance, dorsal spines not distally filamentous, two supernumerary dorsal spines). Massalongius is like Eozanclus in having

the plesiomorphic conditions of these three characters. Zanclus and Eozanclus do share the other four synapomorphies: character 47 (ribbed median locking flanges for first three dorsal spines); character 49 (increased numbers of soft dorsal- and anal-fin rays, with 38-42 dorsal and 31-35 anal); character 50 (single supraneural; which condition is now known to be an ancestral reversal for zanclids + acanthurids, as discussed above for character 10); character 51 (triangular peak-like supraoccipital crest). Massalongius shares three of these derived conditions: three ribbed median locking flanges; triangular peaked supraoccipital crest, even larger than in Zanclus and Eozanclus; single supraneural. Massalongius retains the plesiomorphic low numbers of 20 soft dorsal- and anal-fin rays rather than the increased numbers of Zanclus and Eozanclus.

For the Acanthuridae, Tyler et al. (1989) list three adult characters that are autapomorphies for all six extant genera (comprising two subfamilies, Nasinae and Acanthurinae). One of these (character 52, ethmoid cartilage size and position) cannot be determined in *Massalongius*, but the other two characters, both of which are innovative derived features for the Acanthuridae, are not present in *Massalongius*. Character 53 of acanthurids is a further elaboration on the dorsal and anal spine locking mechanism, with the development of a deep vertical groove to accommodate the short first spine as it rotates around the ribbed concentric flange of the first pterygiophore; such a deep vertical groove is absent in *Massalongius*. Character 54 of acanthurids is the presence on the caudal peduncle of either enlarged fixed plates (in *Naso* and *Prionurus*) or a single sharppointed folding spine (the other four genera); *Massalongius* has no such plates or folding spine. See L. Sorbini and Tyler (1998) for a discussion of the plates and folding spines in fossil acanthurids, in which only a minority of specimens of a particular species may have the spines or plates either preserved or exposed.

SYSTEMATIC CONCLUSION

From the above analysis of characters it is abundantly clear that *Massalongius* is not a chaetodontoid but, rather, an acanthuroid. *Massalongius* shares the majority of derived features with all of the major higher squamipinne and acanthuroid nodes, up to and including those of the Zanclidae + Acanthuridae terminal node, whereas *Massalongius* has no derived diagnostic features of the chaetodontoids. *Massalongius* exhibits many reversals of higher squamipinne and acanthuroid derived features, especially those associated with its long snout, sturdy jaws, and long ascending premaxillary process in a presumably protrusible upper jaw, and also of its caudal skeleton with two rather than only one uroneural. *Massalongius* shares other reversals with the Zanclidae (such as the high supraoccipital), or with zanclids and some acanthurids (one supraneural). One reversal of *Massalongius* (first dorsal pterygiophore in first interneural space) to the higher squamipinne condition is unique among the luvaroid + zanclid + acanthurid clade.

All of the characters analyzed herein indicate that *Massalongius* can be placed at the Zanclidae node in the phylogeny of the acanthuroids. More particularly, we believe the data support the recognition of *Massalongius* at the family level as the sister group to the Zanclidae, based on the following characters that define the involved clades. Characters are distinguished below by capitol letters to distinguish their usage in this new arrangement versus the numbers used in Tyler et al. (1989).

The Zanclidae + Massalongiidae clade is characterized by the following four unequivocal synapomorphies.

A, ribbed median pterygiophore locking flanges for first three dorsal spines: the concave bases of the first three dorsal-fin spines rotate around ribbed median flanges on the distal ends of the first two or three dorsal pterygiophores, there being a single ribbed flange on each of the first three pterygiophores in *Zanclus*, in which there is a single dorsal spine borne on each pterygiophore (this being the derived condition of a single supernumerary spine on the first pterygiophore), and two ribbed flanges on the first pterygiophore and one on the second pterygiophore in *Eozanclus* and *Massalongius* (this being the plesiomorphic condition for acanthuroids of two supernumerary dorsal spines); in the acanthurid sister group there is a single large ribbed flange on the first dorsal pterygiophore that supports the rotation of the first two spines, and there is a deep vertical groove in front of the flange, and the lower families of acanthuroids and the squamipinne outgroups have no such ribbed rotational flanges.

B, high supraoccipital crest: this crest is prominent in both Zanclus and Eozanclus, but it does not extend posteriorly very much beyond the level of the rear of the base of the skull, whereas in Massalongius it is larger, higher, and extends back well beyond the level of the base of the skull; in the acanthurid sister group and the lower families of acanthuroids the supraoccipital crest is reduced to a low ridge, and the condition in zanclids and Massalongius is a reversal to the high crest found in the lower squamipinnes.

C, slender, narrow teeth in a villiform (Massalongius) or setiform (Zanclus and Eozanclus) band: these delicate numerous slender teeth are in distinct contrast to the fewer and far large teeth (variously strong and conical to flattened, with or without lobes) in the basal genera of acanthurids (one genus, deeply nested in acanthurid phylogeny, secondarily with setiform teeth), and the basal genera of siganids also have a series of large strong teeth (one genus, deeply nested in siganid phylogeny, secondarily with more elongate teeth), whereas luvaroids (luvarids plus the fossil sister group kushlukiids) are autapomorphic in having small conical teeth, which may be lost with age, or are edentulous. All of these variations in dentition are documented in detail in Tyler and Bannikov (1997), with it being clear that the setiform and villiform teeth in zanclids and Massalongius are a reversal to conditions in many of the lower squamipinne outgroups.

D, high spiny dorsal fin, with the longest spine 44% SL in *Massalongius*, about 62% in *Eozanclus*, and more than 100% SL in the filamentous prolongation of the spine in *Zanclus*: in the acanthurid sister group the longest dorsal spines range from about 13% to 20% SL, in the luvarid + kushlukiid clade from about 12% SL or less (dorsal spines absent in some taxa), and in siganids from about 15% to 22% SL in most taxa and somewhat longer at 28% SL in one genus that is not basal in the phylogeny of the family (see Tyler and Bannikov, 1997).

When the Zanclidae clade is analyzed with the inclusion of the features of both the relatively plesiomorphic *Eozanclus* from the Eocene of Monte Bolca and the far more derived extant *Zanclus*, there are only two unequivocal synapomorphies for this family.

E, increased numbers of dorsal and anal soft rays, to 38-42 dorsal rays and 31-35 anal rays: all other acanthuroids have 33 or fewer dorsal rays and 32 or fewer anal rays.

F, anterior region of cleithrum below level of postcleithrum expanded and its front edge strongly convex, rounded: in all other acanthuroids the anterior region of the cleithrum is not much expanded and the anterior edge is relatively straight or only gently curved or sigmoid. By contrast, there is a longer series of derived features of *Massalongius* (Massalongiidae) that distinguishes it from its Zanclidae sister group, partially because it is a list of autapomorphies for the single included species. If other species of massalongiids are discovered in the future, surely many of the following derived features will no longer apply to the expanded higher taxon (much like the inclusion of the Eocene *Eozanclus* reduces the synapomorphy list for the Zanclidae based only on the extant *Zanclus*).

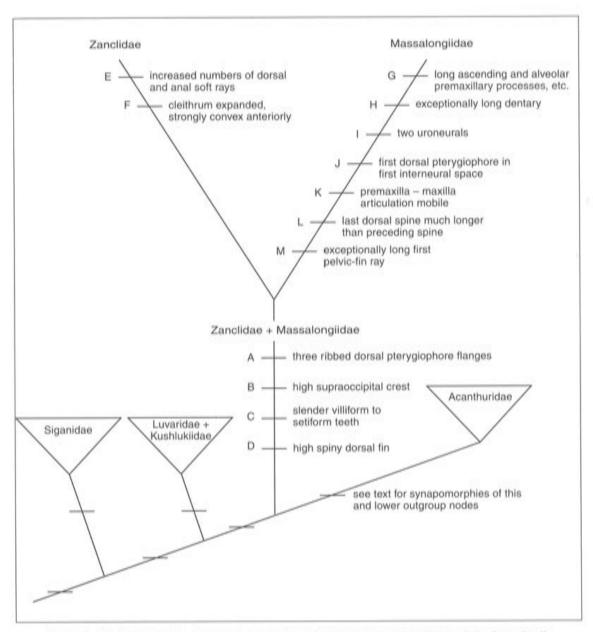


Figure 4 - Cladogram of the characters supporting the relationships of the fishes of the Superfamily Zancloidea (Zanclidae + Massalongiidae). Character letters (A - M) correspond to those discussed in the text. See text discussion of acanthuroid phylogeny for references giving characters that support the outgroup nodes.

The following are Massalongiidae autapomorphies.

G, long ascending process of premaxilla (23% SL), long alveolar process (17% SL from tip of snout to posterolateral end of process) extending far posterior to tooth bearing region, and posterior placement of maxilla along underside of rear region of ascending process, which together indicate significant gape and premaxilla protrusibility along maxillary articulation: this reversal (a complex that could be divided into several characters) to a lower squamipinne and perciform condition is unique among the higher

squamipinnes and acanthuroids.

H, exceptionally long dentary (21% SL), about four times longer than articular region: in zanclids, acanthurids, and siganids the dentary is no more than about twice as long as the articular region, and less than 8% SL, while in the luvarid + kushlukiid clade, with the largest dentary among acanthuroids, the dentary is no more than about 10% SL and no more than about two to two and a half times longer than the articular region; the elongate dentary of *Massalongius* is most parsimoniously interpreted as independent of that found in the long-snouted genera of chaetodontids (which have a relatively long articular versus relatively short in *Massalongius*).

I, well-developed anterior uroneural (stegural) followed by long rod-like second uroneural: this reversal to the lower squamipinne condition is unique among

acanthuroids.

J, shaft of first dorsal pterygiophore in first interneural space (between first and second neural spines) rather than in the preneural space as in luvaroids + zanclids + acanthurids: this is a reversal to the condition found in siganids and the lower squamipinnes.

K, premaxilla-maxilla articulation mobile rather than closely bound as in other acanthuroids: this is a reversal to the lower squamipinne condition, as an elaboration

associated with character G above.

L, rear region of upper edge of spiny dorsal fin with prominent concavity, the last spine (9th) much longer than the preceding spine: in all other acanthuroids the dorsal-fin spines either decrease gradually in length posteriorly in the series, or they are all of about the same length, and none have the last spine significantly longer than the preceding spine.

M, exceptionally long first pelvic-fin ray (46% SL): in zanclids the first pelvic ray ranges from about 22% to 28% SL, in acanthurids from about 12% to 21% SL, and in siganids from about 13% to 20% SL, while in luvarids + kushlukiids the pelvic fin is usually insignificant, and perhaps absent or resorbed in adults, with the exception of juveniles of the extant Luvarus imperialis in which the first ray is greatly elongate (about 55% SL), even more so than in Massalongius. In adult L. imperialis and in the related Eocene fossil Luvarus necopinatus, the rudimentary pelvic-fin rays are coalesced with the small spines into an operculum-like structure (see Bannikov and Tyler, 1995). Because only juveniles of Luvarus imperialis among all luvarids + kushlukiids have an elongate first pelvic ray, and this taxon is deeply nested within the phylogeny of that clade, the elongation of the first ray in juvenile L. imperialis is most parsimoniously interpreted as an independent acquisition to the elongation of the first pelvic ray found only in Massalongius among all members of the two terminal clades of acanthuroids (the zanclid + massalongiid and the acanthurid clades).

We do not belabor this list of derived features of *Massalongius* by documenting such relative length or proportional specializations as the especially elongate supraoccipital and the exceptionally small teeth relative to zanclids and other acanthuroids because it is abundantly evident from all of the characters above that *Massalongius* is a highly distinctive

acanthuroid, and equally distinctive even within the clade that includes zanclids.

Our recognition of the distinctive features of *Massalongius* at the family level is consistent with the treatment of another distinctive and entirely fossil clade within the acanthuroids, the Kushlukiidae, from the upper Paleocene to the lower Eocene of Turkmenistan and India. The Kushlukiidae are the sister group of the Luvaridae (together comprising the Luvaroidea clade), with luvarids known from several fossil taxa dating to the late Paleocene and Eocene as well as the single extant species. The specializations of the kushlukiids relative to luvarids and other acanthuroids involve the greatly increased number of vertebrae, the posterior placement of the origin of the dorsal fin and of the ventral shaft of the first dorsal pterygiophore, the postcleithrum expansion into a large plate, etc. (see Bannikov and Tyler, 1995). The derived differences between *Massalongius* and the zanclids are of a comparable order of magnitude to that between kushlukiids and luvarids, leading to our recognition of the family Massalongiidae as sister to the Zanclidae. We recognize the superfamily Zancloidea to accommodate the Zanclidae + Massalongiidae clade.

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