

# A new genus and species of surgeon fish (Perciformes, Acanthuridae) from the Oligocene of Kanton Glarus, Switzerland

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**Abstract** The new genus and species of surgeon fish, *Glarithurus friedmani* (Acanthuridae), from the Lower Oligocene (Rupelian) of Kanton Glarus, Switzerland, differs from all other acanthurid fishes, fossil and extant, by having a single anal-fin basal pterygiophore situated in the first interhaemal space, versus two or more such pterygiophores in all other taxa. The new taxon is based upon a 29-mm SL acronurus stage specimen that probably had already settled onto a benthic substrate from its pelagic larval stage and begun its transformation into a juvenile. It has a scalpel-like dermal spine on the caudal peduncle and a crest on the hyomandibular, which are derived characters that establish it as a member of the clade of higher acanthurins. Within that clade, it is unique because of the great depth of its basipterygium at the subpelvic keel.

**Keywords** Acanthuridae · *Glarithurus friedmani* · Scalpel scale · Acronurus · Oligocene · Kanton Glarus

## Introduction

Large schools of acanthurid surgeon fishes browsing on algae are a prominent component of modern coral reef ecosystems and their surrounding flats in tropical seas worldwide. Six genera and about 80 species of surgeon fishes are alive today (Randall 1955; Tyler 1970; Nelson

2006). Using the same level of morphological differentiation that has been used to distinguish the six Recent genera from one another, 15 genera of fossil acanthurids (in the Acanthurinae and Nasinae, which have both fossil and extant taxa) have been recognized from the Eocene to the Miocene (Tyler and Bannikov 2000), and two other genera represent distinct subfamilies of Eocene acanthurids (Padovathurinae and Gazolaichthyinae, Tyler 2005a, 2005b). Most of the fossil acanthurids are known from the Middle Eocene of the classic fossil locality of Monte Bolca in northern Italy, which is by far the richest coral-reef-associated ichthyofauna of Eocene age in the world. The 11 genera of acanthurin and nasin acanthurids known just from Monte Bolca are almost twice as morphologically diverse as is this dominant worldwide group of coral-reef fishes today, and the two taxa of padovathurin and gazolaichthyin acanthurids from Monte Bolca accentuate that disparity. The first appearance and great morphological diversification of surgeon fishes and of other acanthuroid families in the Middle Eocene also is suggested by molecular analyses (Clements et al. 2003; Klanten et al. 2004).

A review of the fossil Acanthuridae was given by Tyler and Bannikov (2000). Only four of the fossil genera of acanthurids are from localities other than Monte Bolca: *Caprovesposus* Danilchenko, 1960 (Early Eocene to Early Miocene of the northwestern Caucasus, Russia, and perhaps from Egypt, see below), *Arambourgthurus* Tyler, 2000 (Oligocene of Istehbanat, Iran), *Marosichthys* de Beaufort, 1926 (Miocene of Celebes, Indonesia), and *Eonaso* Blot, 1984 (unknown age; Antigua, Lesser Antilles). To these we add herein the new genus and species *Glarithurus friedmani* from the Oligocene of Kanton Glarus (Canton Glaris), Switzerland; it is the first acanthurid taxon known from the Glarus palaeofauna. The new taxon

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is based upon an acronurus settlement stage, as are several other genera of acanthurids, namely *Caprovesposus*, *Tau-ichthys* Tyler, 1999, and *Metacanthurus* Blot and Tyler, 1990. *Eorandallius* Blot and Tyler, 1990, has two species known from adult specimens and one acronurus specimen that has not been determined at the specific level (see Blot and Tyler 1990). Several acronurus specimens were described and referred to *Caprovesposus* sp. by Gaudant and Rouchy (1986) from the Miocene of Gebel Zeit, Egypt, but the state of their preservation makes the generic allocation uncertain. A very small acronurus specimen, 12.5 mm SL, of an undetermined genus and species, was described from the Miocene of Gavdos Island, Greece, by Gaudant et al. (2005).

## Materials and methods

The part and counterpart of the holotype (MB.f. 16519a, b) are kept in the palaeontological collection of the Museum für Naturkunde at the Humboldt-Universität Berlin (see below). They are part of an old collection that was purchased by the museum more than 200 years ago. The fine preparation was done with an HW airbrasive machine, using iron powder Cut 150 of less than 150 µm granularity.

### Anatomical terminology and abbreviations

Interneural and interhaemal spaces are numbered according to 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, respectively (e.g., Birdsong et al. 1988; Baldwin and Johnson 1993; Bannikov and Tyler 1995; Tyler and Bannikov 1997; Tyler et al. 2003).

For the radial elements supporting the median fins, we use the terms basal pterygiophore and distal pterygiophore, as has been used in most acanthurid osteological literature; these terms are equivalent to the more recent usage of proximal-middle radial and distal radial, respectively.

an, remains of angular; as, anal-fin spine; asr, anal-fin soft ray; bl, breakage lines of slab; br, branchiostegal rays; brr, remains of branchiostegal rays from other side; cl, cleithrum; ci, circumorbital elements; co, coracoid; de, dermethmoid; dmcr, dorsal marginal caudal ray (procurrent); dpcr, dorsal principal caudal ray; dppt, distal portion of pterygiophore; dr, remains of dentary and teeth; ds, dorsal-fin spine; dsr, dorsal-fin soft ray; ep, epural; fr, frontal; hac, haemaxanal complex; hs, haemal spine; hy,

hypural; hyo, hyomandibula; hydr, hyomandibular ridge/crest; le, lateral ethmoid; mx, maxilla; nc, neural crest; ns, neural spine; op, opercle; pcl, postcleithrum; pg, pelvic girdle; ph, parhypural; pl, remains of palatine; plr, pleural ribs; pop, preopercle; pot, posttemporal; ppsr, proximal portion of soft ray; pr, pectoral-fin rays; ps, pelvic-fin spine; pt, pterygiophore; pu, preural centrum; qu, quadrate; sc, scapula; sc, sensory canal; sca, scalpel-like dermal spine; scl, supracleithrum; soc, supraoccipital; sph, sphe-notic; sqr, remains of squamation; ssc, supraorbital sensory canal; u, ural centrum; un, uroneural; vmcr, ventral marginal caudal ray (procurrent); vpcr, ventral principal caudal ray; ?, ?? questionable/unidentified elements.

### Institutional abbreviations

MB.f.: Palaeontological (fish) collection of the Museum für Naturkunde, Leibnitz Institut für Evolutions- und Biodiversitätsforschung at the Humboldt-Universität Berlin; USNM: collections of the former United States National Museum, now in the National Museum of Natural History, Smithsonian Institution, Washington, DC.

## Systematic palaeontology

Family Acanthuridae Bleeker, 1859

Subfamily Acanthurinae

*Glarithurus*, new genus

Type species: *Glarithurus friedmani*, new species.

**Etymology:** *Glari*, in recognition of the importance of the palaeofauna from the Landesplattenberg Formation in Kanton Glarus; plus the suffix *thurus*, being the last two syllables in the type genus name *Acanthurus*, as also used in several other acanthurid generic names.

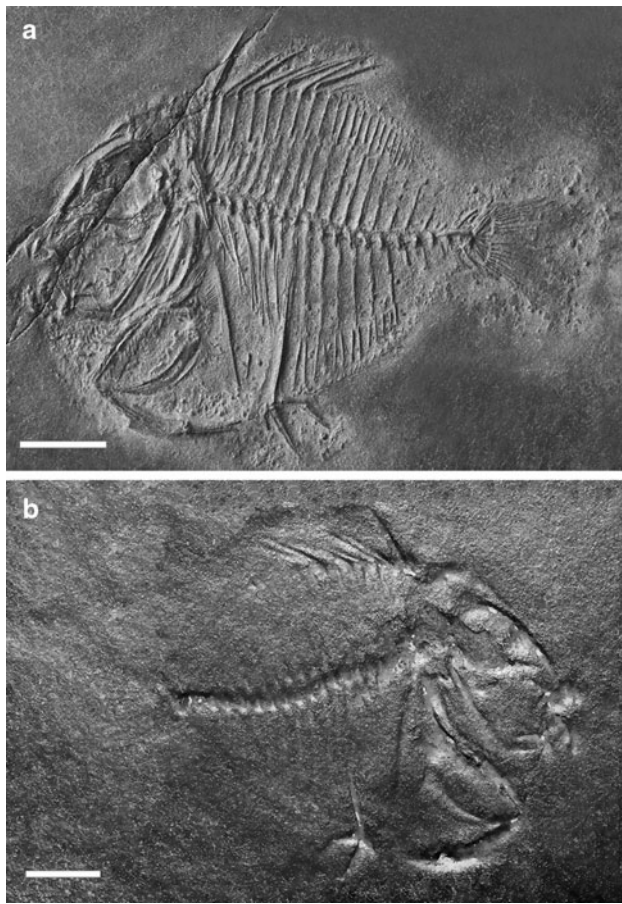
**Diagnosis:** Differs from all other acanthurid fishes by having only one anal-fin basal pterygiophore in the first interhaemal space (between the haemal spines of the first and second caudal vertebrae); differs from the other known members of the higher Acanthurinae by the very great depth of the basipterygium (pelvic bone) at the subpelvic keel.

**Composition:** Presently known only from the type species.

*Glarithurus friedmani*, new species (Figs. 1, 2, 3, 4)

**Etymology:** In honour of Matt Friedman, palaeoichthyologist at the University of Oxford, who perceptibly recognized an unprepared and misidentified (as the priacanthid *Acanus* Agassiz, 1838) little Kanton Glarus specimen in the Berlin museum collection as a probable acanthuroid and called it to our attention.

**Diagnosis:** That of the genus, of which it is the only known representative.



**Fig. 1** *Glarithurus friedmani*, holotype. Palaeontological collection, Museum für Naturkunde, Humboldt-Universität Berlin, 29.0 mm SL. **a** Main plate, MB.f. 16519a; **b** counterplate, MB.f. 16519b. Lower Oligocene (Rupelian), Landesplattenberg at Engi, near Glarus, Kanton Glarus, Switzerland. Each scale bar is 5 mm

*Type locality and horizon:* Lower Oligocene (Rupelian) of the Landesplattenberg slate quarry and mine at Engi, near Glarus, Kanton Glarus, Switzerland. Matt Formation, Early Oligocene; 30 MYA (according to Furrer and Leu 1998).

*Holotype (and only known specimen):* A 29-mm SL acronurus specimen, in the collections of the Museum für Naturkunde, Humboldt-Universität zu Berlin, MB.f. 16519a, b, in part and counterpart.

## Description

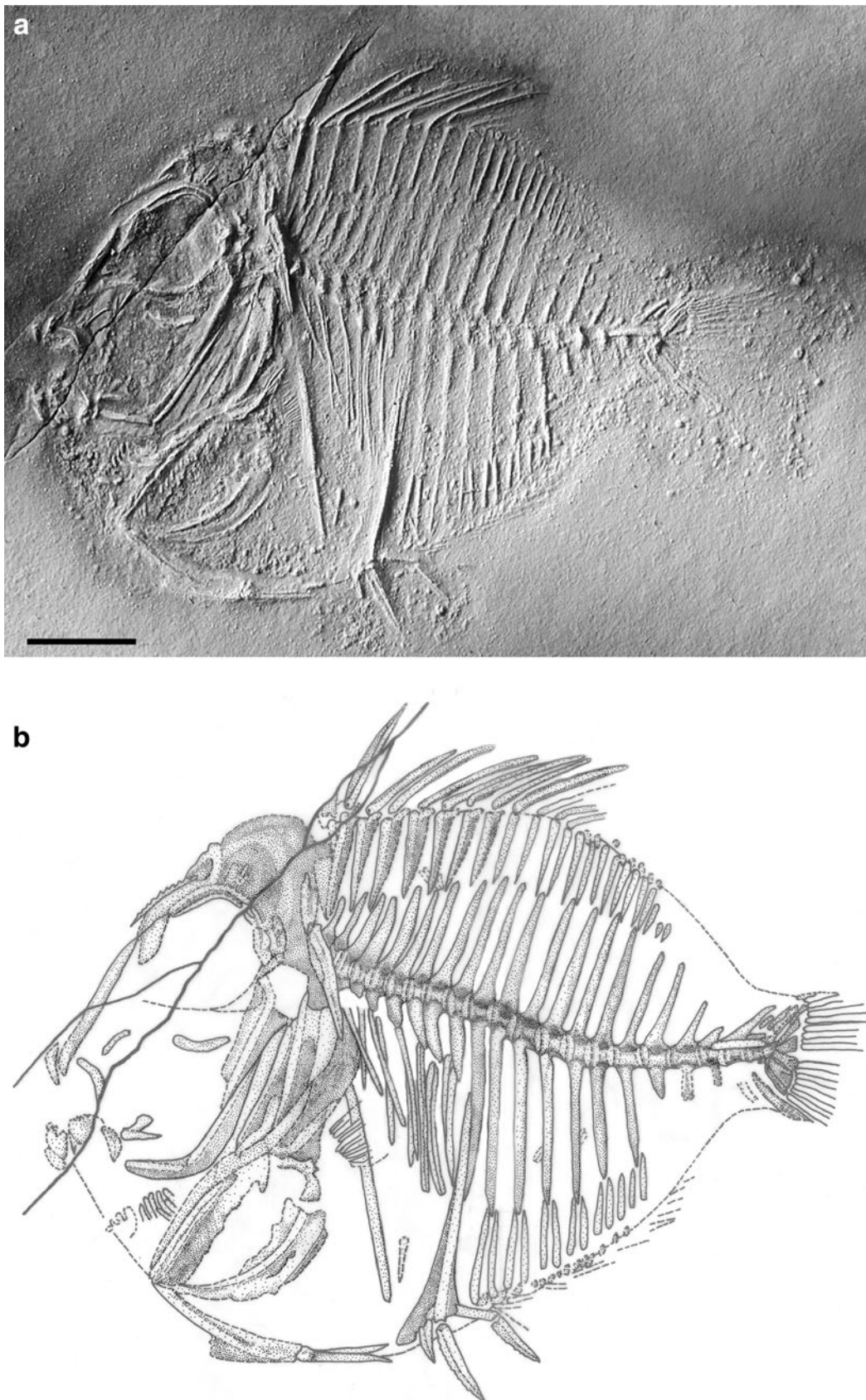
### Skull

The jaws and teeth are relatively poorly preserved, and it cannot be determined whether the edges of the teeth are lobed, denticulate, or smooth. There are indications that the dentary is much larger than the articular/angular.

The premaxilla is questionably identified in the upper jaw; below and behind this bone is the maxilla, which is probably detached. The quadrate, with a deep indentation posteriorly, is evident behind the lower jaw; the symplectic is not preserved. Behind the upper end of the maxilla is an elongate bone that probably represents the remains of the palatine and perhaps of the endopterygoid. Another prominent elongate bone in the upper region of the snout probably is composed of the dermethmoid and the nasal. In the suspensorium, the hyomandibula and the preopercle are well preserved. The hyomandibula is broad dorsally at its articulation with the skull and tapers ventrally along its contact with the anterodorsal edge of the preopercle. On the lateral surface of the anterodorsal region of the hyomandibula there is a curved and relatively horizontally oriented crest or ridge of bone (hyr, Fig. 3). The preopercle is moderately curved, and there is evidence of a sensory canal. The limits between the opercle and the subopercle are indistinct. Below the anterior end of the preopercle are the basal regions of a row of five branchiostegal rays, and just below them are the remains of a few other branchiostegal rays from the other side. In the lower region of the orbit, the upper edge of the parasphenoid is well preserved, whereas its ventral flange is less precisely indicated but appears to be of moderate depth. Below the parasphenoid is a somewhat upwardly curved arch of bone that is probably the remains of the infraorbital series of bones, and more anteriorly there is a vague indication of a large lachrymal. The upper region of the orbit is well defined by the remains of the lateral ethmoid and the relatively well-preserved frontal, which has some surface sculpturing and sensory canals. The upper anterior region of the frontal has a long prominent serrate ridge. Below the posteroventral region of the frontal there is evidence of the sphenotic, but the other otic bones are indistinct. The upper edge of the supraoccipital and the posterior curvature of the skull are well defined.

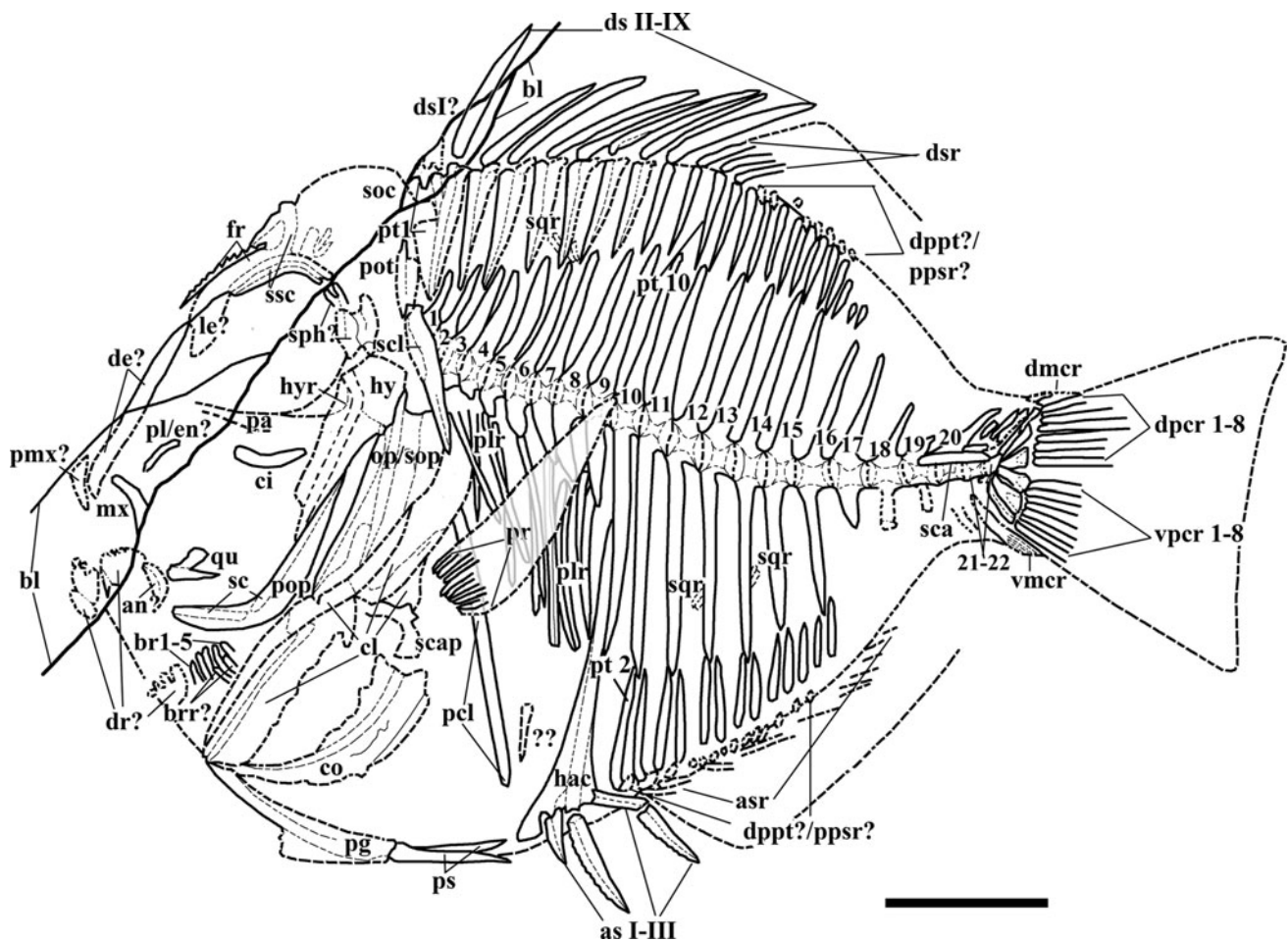
### Pectoral region

The vertically oriented posttemporal is clearly indicated at the rear of the skull just above and in front of the level of the most anterior centra of the vertebral column. Continuing below the posttemporal is the long, strong, vertically upright supracleithrum. The postcleithrum is a long shaft of bone from the rear edge of the cleithrum above the level of the pectoral-fin base to the lower region of the abdominal cavity; it appears to be a single bone. Just behind the lower region of the postcleithrum is a bone that may be the broken-off ventral end of the postcleithrum from the opposite side. The pectoral girdle is relatively well preserved, with a large, long, broad cleithrum and behind which is the large coracoid; just above the dorsal end of the



**Fig. 2** *Glarithurus friedmani*, holotype. **a** Main plate MB.f. 16519a, dusted with ammonium chloride (NH<sub>4</sub>Cl); **b** semi-schematic drawing, that emphasises the most important skeletal features. Scale bar is 5 mm





**Fig. 3** *Glarithurus friedmani*, reconstruction of holotype MB.f. 16519a, with labelling of most important skeletal features. See “Materials and methods” for abbreviations. Scale bar is 5 mm

coracoid is the scapula, which has evidence of a foramen and of a prominent knob for articulation with the uppermost pectoral-fin ray. The bases of the pectoral-fin rays are indicated; there are at least 12 rays, but perhaps a few others are not preserved ventrally; the rays become indistinct distally.

#### Pelvic region

The pelvis (basipterygium) is clearly outlined anterior to the pelvic fin, and it is relatively deep in the region of the subpelvic keel (pg, Fig. 3); the region of the posterior process of the pelvis is obscured by the pelvic fin. The pelvic-fin spine from each side is preserved, but the number of soft rays cannot be determined.

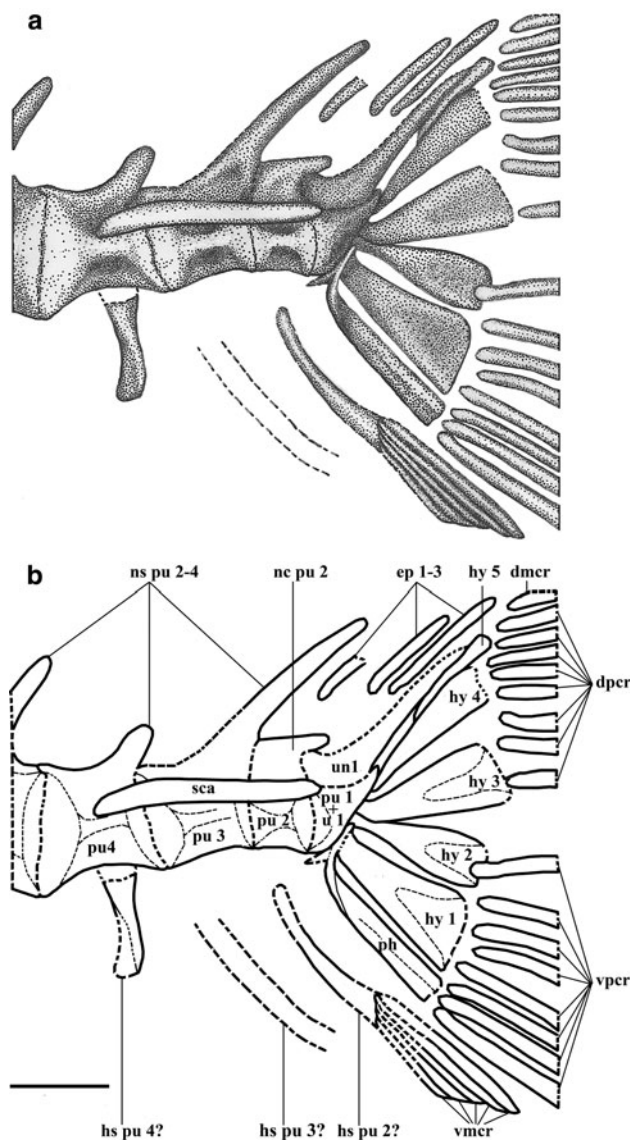
#### Axial skeleton

This is well preserved, and almost all of its elements are well exposed. There are nine abdominal and 13 caudal vertebrae. The lower regions of the first two abdominal

vertebrae are obscured behind the supracleithrum, but their neural spines have a normal position and arrangement. The neural spines of the abdominal vertebrae increase in length from the first to the ninth, and these vertebrae have parapophyses of increasing length from the third to the ninth, with each bearing a pleural rib; the longest ribs extend ventrally to about the middle of the abdominal cavity.

#### Dorsal fin and dorsal-fin supports

There are nine dorsal-fin spines; the first two are in supernumerary association on the first basal pterygiophore. Although the first spine (ds I, Fig. 3) is short, it clearly protrudes dorsally above the profile of the body; the anterior edge of the first spine is situated along the upper anterior bifurcation of a major fracture line in the matrix of the specimen. The third to the ninth spines are supported on individual basal pterygiophores. Only a few of the more anterior of the soft-dorsal-fin rays have much of their lengths preserved, but there are at least 14 fin rays and



**Fig. 4** *Glarithurus friedmani*, caudal fin supports of holotype MB.f. 16519a. **a** semi-schematic drawing that emphasizes the most important skeletal features; **b** same, labelled reconstruction. See “Materials and methods” for abbreviations. Scale bar is 1 mm

probably others that are not evident more posteriorly. There may be the remains of distal pterygiophores between the bases of some of the rays and their basal pterygiophores.

The first dorsal-fin basal pterygiophore is the largest of the series and is situated in the preneural space, with its lower region supported between the anterior edge of the first neural spine and the rear of the skull. The surface of the anterodorsal edge of the first dorsal pterygiophore has a deep indentation into which the base of the first dorsal-fin spine would have rotated in erection; there are two knob-like structures on the upper lateral surface of the pterygiophore that help support the first two spines (pt 1, Fig. 3). The first and second interneural spaces each accommodate

a single basal pterygiophore, the third interneural space is vacant (no ventral shaft of a dorsal-fin basal pterygiophore present), and each of the fourth to the tenth interneural spaces accommodates a single basal pterygiophore. More posteriorly, each interneural space accommodates initially two and then three basal pterygiophores before the last of the series of dorsal-fin basal pterygiophores becomes incomplete. The neural spines of the first six caudal vertebrae are about as long as that of the last (ninth) abdominal vertebra, whereas the neural spines of the seventh to the tenth caudal vertebrae are of progressively decreasing length. The neural spine of the 11th caudal vertebra (Pu3) is elongate, reaching dorsally to about the level of the distal ends of the epurals. The neural process of the 12th caudal vertebra (Pu2) is a very low crest, slightly lower even than the short neural spine of the 10th caudal vertebra (Pu4).

#### Haemal spines

Those of the caudal vertebrae are long and strong in the region supporting the anal fin; those of the first five caudal vertebrae are somewhat longer than their corresponding neural spines. The haemal spines of the sixth and seventh caudal vertebrae are of about the same size as the corresponding neural spines, whereas the haemal spines of the eighth and ninth caudal vertebrae are significantly shorter than their corresponding neural spines. This, however, may be an artefact, due to their incomplete preservation. The haemal spine of the 10th caudal vertebra (Pu4) is poorly preserved, but it is apparently somewhat longer than the corresponding neural spine. The haemal spines of the 11th and 12th caudal vertebrae (Pu3 and Pu2) are poorly preserved, but they clearly are very long, reaching distally to the level of the lower end of the hypural plate, and they are apparently autogenous.

#### Anal-fin and anal fin supports

There are three anal-fin spines, each with a serrate anterior edge and a serrate ridge along the lateral surface. The first two spines are in supernumerary association on the first basal pterygiophore. The first spine is short, but it clearly protrudes ventrally below the profile of the body. The second spine is sturdy and about twice as long as the first spine. The third spine is broken in about the middle of its length, and it is slightly longer than the second spine; the base of the third spine clearly articulates with the posteroventral end of the first basal pterygiophore. The full lengths of most of the soft-anal-fin rays are not exposed, but there are at least 13 fin rays and probably others that are not evident more posteriorly. There may be remains of distal pterygiophores between the bases of some of the rays and their basal pterygiophores.

The first anal-fin basal pterygiophore (hac, Fig. 3) is the largest of the series and is situated in the prehaemal space, with the posterodorsal edge of its shaft being supported along the anteroventral edge of the haemal spine of the first caudal vertebra. The surface of the anteroventral edge of the first anal pterygiophore has a deep indentation into which the base of the first anal-fin spine would have rotated in erection; there are two knob-like structures on the lower lateral surface of the pterygiophore that help support the first two spines (the more anterior of these, for the first spine, is less distinct than the other). There is a single anal-fin basal pterygiophore situated in the first interhaemal space, with its dorsal tip in contact with the anteroventral edge of the haemal spine of the second caudal vertebra. The second through fifth interhaemal spaces each accommodate two anal-fin basal pterygiophores, whereas the sixth space accommodates three basal pterygiophores; more posteriorly, the last of the series of anal-fin basal pterygiophores is incomplete.

### Caudal skeleton

This region (Fig. 4) is well preserved, with a terminal centrum (Pu1 + U1) bearing a long and broad uroneural, a parhypural and five separately articulated hypurals; the uppermost (fifth) hypural is a rod-like element situated between the distal regions of the uroneural and the fourth hypural. There are three long and rod-like epurals, except that the first element is incomplete distally. There are 16 principal caudal-fin rays, with five procurent rays along the ventral margin of the fin and at least one (and probably three) procurent ray(s) in the less-well-preserved dorsal margin of the fin. The distal ends of many of the branched principal rays are indistinct, but the fin appears to be slightly concave.

### Scales

The remains of more-or-less obliquely vertical elongate scales are preserved in many places on the flank of the body; however, the scales are relatively poorly preserved, and we can only estimate that their lengths are about five or six times their widths. The elongate, scalpel-like dermal spine (sca, Figs. 3, 4) on the caudal peduncle is situated along the upper half of the centra from the middle of the Pu4 centrum to the front of the terminal centrum (Pu1 + U1); in life, this folding spine would be erectable from its posterior region of attachment to the body, thus forming a formidable sharp piercing weapon.

### Measurements

Measurements as a per cent of the 29-mm SL are as follows: head (from premaxilla to estimated position of rear of

basioccipital) 38%; body depth at anal-fin origin 71%; caudal peduncle least depth 15%; depth of pelvis at sub-pelvic keel 22%; greatest width of pectoral girdle (obliquely across front of cleithrum to rear of coracoid) 18%; length of scalpel-like folding spine on caudal peduncle 8%; length of pelvic-fin spine 13%; length of first dorsal-fin spine 5%; length of second dorsal-fin spine 16%; length of ninth dorsal-fin spine 16%; length of first anal-fin spine 6%; length of second anal-fin spine 11%; length of third anal-fin spine 13%.

## Comments on diagnostic and other features of interest

### General information

In the following discussions, the term higher acanthurin refers to those genera with a slender, folding, scalpel-like dermal spine on the caudal peduncle and a crest anterodorsally on the hyomandibular (the latter character mostly unknown for fossils), comprising the (*Paracanthurus* Bleeker, 1863 + *Zebrasoma* Swainson, 1839) + (*Acanthurus* Forsskål, 1775 + *Ctenochaetus* Gill, 1885) clade among extant genera (Guiasu and Winterbottom 1993) and the Eocene of Monte Bolca *Proacanthurus* Blot and Tyler, 1990 (and probably also the Monte Bolca *Tauichthys*; see Sorbini and Tyler 1998b and Tyler and Bannikov 2000). By contrast, the lower acanthurins are the species of the extant *Prionurus* Lacépède, 1804, which have large fixed plates on the caudal peduncle (as also found in nasins) and no crest on the hyomandibular. The two clades of four extant genera within what we consider to be the higher acanthurins have been named as distinct tribes in the excellent, myologically based, phylogeny of Winterbottom (1993), but we do not utilize this formal nomenclature because the fossil taxa cannot be properly placed within such finely split categories of the derived clade of those acanthurids with a folding, scalpel-like, caudal peduncle spine and a hyomandibular crest. In fact, most fossil species of acanthurids are known from only one or very few specimens and the conditions of the caudal peduncle armature and of the anterodorsal region of the hyomandibula are unknown at present for many of them, so four monotypic genera cannot yet be assigned to either the higher or lower acanthurins. The phylogeny of the acanthuroids is documented in Tyler et al. 1989, Winterbottom 1993, Winterbottom and McLennan 1993, Guiasu and Winterbottom 1993, Tyler 2000, 2005a, b, and Tyler and Bannikov 2005.

Table 1 summarizes the character states of the six morphological features discussed below in all of the genera of the four subfamilies of Acanthuridae and in the two outgroup families.

**Table 1** Conditions of the six main morphological features discussed in the text for all genera of fossil and extant Acanthuridae and their two immediate outgroup families

Character	ZANCLIDAE		MASSALONGIIDAE		ACANTHURIDAE																											
	<i>Zanclus</i> <i>Eozanclus</i>		<i>Massalongius</i>	<i>Padovathurus</i>	<i>Gazolaiichthys</i>	Nasinae					lower						higher						unknown category within Acanthurinae									
						<i>Naso</i> <i>Eonaso</i> <i>Arambourghurus</i> <i>Sorbiniurus</i> <i>Marosichthys</i>					<i>Prionurus</i> <i>Eorandallius</i> <i>Lehmanichthys</i> <i>Pesciariichthys</i> <i>Protozebrasoma</i> <i>Tyleichthys</i>						<i>Proacanthurus</i> <i>Glarithurus</i> <i>Tauiichthys</i> <i>Paracanthurus</i> <i>Zebrasoma</i> <i>Acanthurus</i> <i>Ctenochaetus</i>						<i>Acanthuroides</i> <i>Caprovesposus</i> <i>Metacanthurus</i> <i>Metaspisurus</i>									
Number of pterygiophores in first interhaemal space	2	2	2	4	2	7	?	~4	~4,5	?	2	2	2	2	2,3	2	1	2	2	2	2	2	2,3	2	2	2	2	2	2	2	2	2
Number of pterygiophores in tenth interneural space	3	2	1	2	1	2	2	3	2	?	1,2	2	2	2	2	2	2	1	2	1	1	2	2,3	2	2	2	2	2	2	1	2	1
Depth of pelvis at subpelvic keel (% of pelvis length)	17–21	28	55	58	23–31	16	10	13	18	12	8	14–17	16	13	12–13	13	12	15	22	7–8	10	8	7	6	30	9	11	18				
Number of dorsal-fin spines	7	7	9	7	9	5–7	5	6	7	6	9	7	7	8	5	5,6	9	9	9	4	9	4,5	9	8	6	9	9	7				
Caudal peduncle armature	N	N	N	N	N	FP	FP	FP	?	?	FP	FP	FP	FP	?	FP	SS	SS	SS	SSp	SS	SS	SS	SS	?	SS?	?	?	?	?	?	?
Hyomandibular crest	—	?	?	?	?	—	?	—	?	—	—	?	?	?	—	?	?	?	+	+	+	+	+	+	+	?	?	?	?	?	?	?

FP, fixed plates; SS, folding scalpel spine; N, none; p, probably; ?, unknown; —, absent; +, present



the Eocene of Monte Bolca *Sorbinithurus* Tyler, 1999 and in the Oligocene of Iran *Arambourgthurus*, whereas the extreme forward positioning of the anal-fin origin in the many species of the extant *Naso* Lacépède, 1801 provides room for seven pterygiophores in this space. The anal-fin region in two other fossil genera of nasins is incomplete; therefore, the number of basal pterygiophores in the first interhaemal space is unknown in the Miocene of Celebes *Marosichthys* and in the Antilles *Eonaso*, which is of uncertain age but probably not Eocene. In the two exclusively fossil and probably basal subfamilies of Acanthuridae that comprise an unresolved trichotomy with the acanthurin + nasin clade, there are two anal basal pterygiophores in the first interhaemal space in *Gazolaichthys* Blot & Tyler, 1990 (*Gazolaichthyinae*), in which the anal-fin origin is not positioned far forward, but four pterygiophores in this space in *Padovathurus* Tyler, 2005 (*Padovathurinae*), in which the anal origin is far forward. As documented by Blot & Tyler (1990) for the extant taxa of acanthurids, in which numerous specimens were examined of many species, there is no known intraspecific variability in the number of pterygiophores in the first interhaemal space. Thus, it is evident that the condition of having a single pterygiophore in the first interhaemal space of *Glarithurus friedmani* is unique (Figs. 3, 5, 6, 7).

D1 → | ← D2

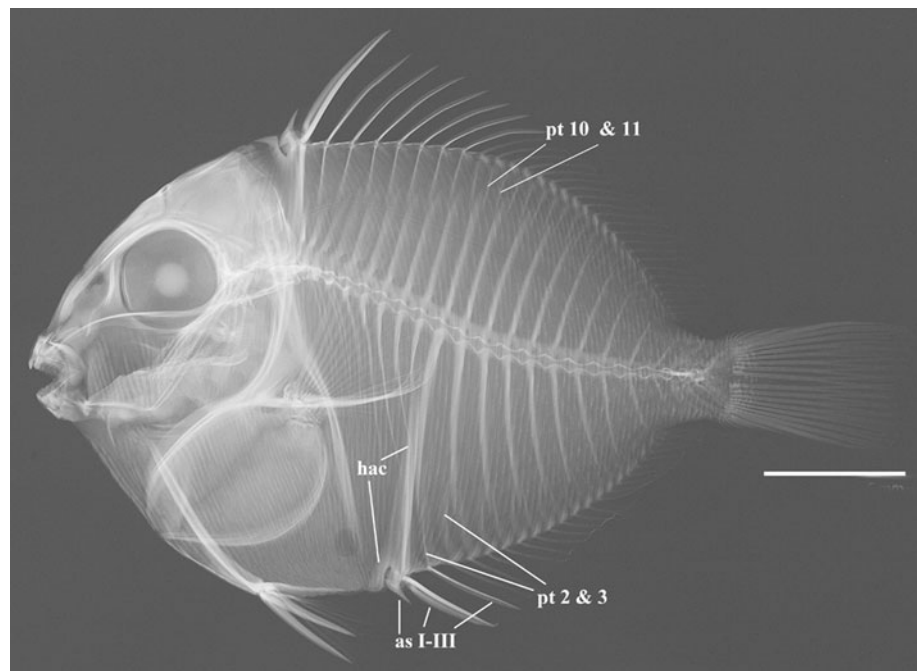
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3

Figure 1: Lateral view of the skeleton of a juvenile fish, showing various anatomical structures labeled with abbreviations. The fish is shown in profile, facing left. The skull is at the top left, with labels for the eye (le), operculum (pa), and various bones (mx, pmx, de, fr, ssc). The body is covered in scales, with labels for the dorsal fin (ds I-II, ds III-IX, dsr), pectoral fin (pr), pelvic fin (pcl), anal fin (as I-III, asr), and caudal fin (dper 1-8, vper 1-8, vmcr). The internal organs, including the heart (co) and liver (scap), are visible. A scale bar is present at the bottom right.

**Fig. 7** Radiograph of an alcohol preserved acronurus stage of an unidentified species of the genus *Acanthurus*. USNM 279390, 24.6 mm SL, Hawaii. Scale bar is 5 mm. The scalpel-like spine on the caudal peduncle is already moderately well developed. Note that there are two basal pterygiophores in the first interhaemal space; all other taxa of acanthurids have at least two basal pterygiophores (and up to seven) in this space, except *G. friedmani*, which has only one. Also note that two basal pterygiophores are present in the tenth interneural space, which is the majority condition among acanthurids; a minority of taxa, including *Glarithurus friedmani*, have only one basal pterygiophore in this space; a few taxa have three basal pterygiophores there



The Zancidae + Massalongiidae is the immediate outgroup of the Acanthuridae, and both the fossil and extant taxa of these two families have two basal pterygiophores in the first interhaemal space (see Blot and Voruz 1970, 1974 for the Eocene of Monte Bolca *Eozanclus* Blot & Voruz, 1970; Tyler et al. 1989 for the extant *Zanclus* Cuvier, 1831; and Tyler & Bannikov 2005 for the Eocene of Monte Bolca *Massalongius* Tyler & Bannikov, 2005). Because *Glarithurus friedmani* is a member of the higher acanthurins (by virtue of having a slender caudal peduncle spine rather than fixed plates and by having a crest on the anterodorsal surface of the hyomandibula), it is certain that the single pterygiophore in the first interhaemal space is a derived reduction.

In *Glarithurus friedmani* the dorsal end of the single basal pterygiophore in the first interhaemal space articulates with the anterior edge of the distal end of the haemal spine of the second caudal vertebra; thus, it corresponds in position to the more posterior of the two basal pterygiophores in this space in most other acanthurins (sequentially the third basal pterygiophore). *G. friedmani* does not have a basal pterygiophore that corresponds in position to the more anterior of the two pterygiophores (sequentially the second basal pterygiophore) in this space that is found in all other acanthurids. Among all other acanthurids, the dorsal end of the more anterior pterygiophore in the first interhaemal space articulates with the posterior edge of the distal end of the haemal spine of the first caudal vertebra.

#### Depth of pelvis

In an osteological analysis of the relationships of extant acanthurid genera, Guiasu & Winterbottom (1993)

documented that the depth of the pelvis (basipterygium), as measured more-or-less vertically at the subpelvic keel (the anteroventral, or iliac, process in front of the pelvic fin) and expressed as a percentage of the length of the pelvis, is relatively deep in the extant Nasinae (16%) and in the *Zanclus* (17–19%) and *Luvarus* Rafinesque, 1810 (53%) extant outgroups, and it represents the plesiomorphic condition. By contrast, the depth-to-length ratio is substantially lower in the extant Acanthurinae: it is 8% in the lower acanthurin *Prionurus*; and among the higher acanthurins it is 8–10% in *Paracanthurus* and *Zebrasoma*, 7% in *Acanthurus*, and 6% in *Ctenochaetus*. The far more numerous genera of fossil acanthurids are only partially in conformity with the Guiasu and Winterbottom (1993) hypothesis: of the four fossil genera of Nasinae, the subpelvic keel depth is 12% in *Marosichthys*, 13% in *Arambourgthurus*, and 18% in *Sorbinithurus*; but it is only 10% in *Eonaso*. Moreover, most of the numerous genera of fossil Acanthurinae (mostly from the Eocene of Monte Bolca) also have a relatively deep pelvis, with ratios ranging from 12 to 16%, or even deeper in *Metaspisurus* Blot & Tyler, 1990 (18%) and *Acanthuroides* Blot & Tyler, 1990 (30%), whereas some taxa have a relatively slender pelvis, such as *Tauichthys* (7–8%), *Caprovesposus* (9%), and *Metacanthurus* (11%). Furthermore, the higher acanthurin *Proacanthurus* from Monte Bolca is a genus with a relatively large number of species, and it has subpelvic keel depths ranging from shallow to deep: 7% in *P. elongatus* Blot & Tyler, 1990; 10% in *P. ovalis* (Agassiz, 1838); 12% in *P. tenuis* (Agassiz, 1835); and 15% in *P. bonatoi* Blot & Tyler, 1990. There obviously is

much homoplasy in the depth of the pelvis, and it remains to be seen whether the relatively slender pelvis in some fossil taxa is a derived condition obtained independently of that of the extant acanthurins (see Tyler & Sorbini 1998, and Tyler 1999, 2000, 2005b for additional data and analysis regarding pelvis depth).

In *G. friedmani* the pelvis has a relatively deep plesiomorphic condition of 22%. Based upon *G. friedmani* having a folding spine on the caudal peduncle and an anterodorsal crest on the hyomandibular, it is a member of the higher acanthurin clade that presently is known to include *Proacanthurus* and four extant genera (*Paracanthurus* + *Zebrasoma*) + (*Acanthurus* + *Ctenochaetus*). In *Proacanthurus* the pelvic depth is 7–15%, and in the four extant genera it is 6–10%. Thus, *G. friedmani* has a much deeper and more plesiomorphic pelvic depth than in any other taxon in its higher acanthurin clade, but it remains to be determined whether that greater depth is an ancestral feature of this clade or an independent reversal because of the considerable homoplasy of this feature.

We note that in the Monte Bolca *Tauichthys* there is evidence that a folding spine on the caudal peduncle may be present in *T. aspesae* Tyler & Bannikov, 2000, which indicates that *Tauichthys* is a probable member of the higher acanthurin clade (see discussion of hyomandibular crest, below). Both species of *Tauichthys* differ from *G. friedmani* by having very shallow pelvic depths (7–8%), which is the derived condition found in the extant taxa of the higher acanthurins, and in several other important features (e.g., dorsal-fin spines reduced to four).

Tenth interneural space with a single basal pterygiophore

In most acanthurids the 10th interneural space accommodates the ventral shafts of two, or rarely three, dorsal-fin basal pterygiophores. This position is often the place of transition between more anterior interneural spaces having a single basal pterygiophore present and those more posteriorly with two present (in *Naso* and a few related genera the transition between one versus two pterygiophores per interneural space is more anterior, as far forward as the sixth space; the same references given to support the preceding discussion of anal-fin pterygiophore placement are applicable here for dorsal-fin pterygiophore placement). But whether the transition to two pterygiophores per space occurs at the 10th space or more anteriorly, the following genera of fossil and extant acanthurids have two pterygiophores (or three as indicated) associated with the 10th space: among extant genera of acanthurins and nasins, all species of *Acanthurus* (*A. sohal* with three), *Naso*, and *Ctenochaetus*, and in *Prionurus* (*P. punctatus* Gill, 1862); among fossil genera, all species of *Proacanthurus*,

*Metacanthurus*, *Eorandallius*, *Acanthuroides*, *Lehmanichthys* Blot & Tyler, 1990, *Pesciarichthys*, *Tylerichthys*, *Eonaso*, *Tauichthys*, *Protozebrasoma* Sorbini & Tyler, 1998, and *Sorbinithurus*; there are three in the 10th space in *Arambourghthurus*; in the two more basal subfamilies of acanthurids, the fossil gazolaichthyins and padovathurins, there are two in the 10th space in *Padovathurus* and one in *Gazolaichthys*; and among the zancid + massalongiids outgroup to the acanthurids there are two in the 10th space in *Eozanclus*, three in *Zanclus*, and one in *Massalongius*.

By contrast, only a few acanthurid taxa (mostly extant) have a single basal pterygiophore accommodated in the 10th interneural space: among extant taxa all species of *Zebrasoma* and *Paracanthurus* and in *Prionurus scalprum* Cuvier & Valenciennes, 1835; and among fossils only *Metaspisurus*, *Caprovesposus*, and *Glarithurus*. In one fossil genus, *Marosichthys*, the 10th space is not preserved.

Because nasins, padovathurins, and the zancid outgroup have at least two pterygiophores in the 10th space, it is most parsimonious to interpret a single pterygiophore in this position as a derived condition in acanthurids and independent of that in *Massalongius* and *Gazolaichthys*. Among higher acanthurins, the derived condition is shared only by *Glarithurus* and the *Paracanthurus* + *Zebrasoma* clade, an indication that *G. friedmani* may be more closely related to that clade (and especially to *Paracanthurus*, with nine dorsal spines, rather than to *Zebrasoma*, with the greatly reduced number of four or five dorsal spines) than to the *Acanthurus* + *Ctenochaetus* clade. However, without knowing the dentition and many other features of the jaws and hyoid apparatus in *G. friedmani*, such assessment of its relationships within the higher acanthurins will remain speculative.

Number of dorsal-fin spines

Guiasu and Winterbottom (1993) documented that among extant acanthurids the lowest number of dorsal-fin spines, namely the four or five spines in *Zebrasoma* and the five of some species of *Naso*, are independently derived conditions. The derived condition of much reduced numbers of dorsal spines is also found in several taxa from the Eocene of Monte Bolca: four spines in *Tauichthys padremenini* Tyler 1999 and in *T. aspesae*; five spines in *Tylerichthys nuchalis* (Agassiz 1835); and five spines in *Protozebrasoma bloti* Sorbini & Tyler 1988a. There are also five spines in the Antillean *Eonaso* of uncertain age. Which number of dorsal spines between six and nine is the ancestral acanthurid plesiomorphic condition remains to be determined (Sorbini & Tyler 1998a, b; Tyler 1999). It is reasonable to assume, however, that *Glarithurus*, with nine dorsal spines, is probably more closely related to some of those genera with nine (among extant genera *Acanthurus*,



*Paracanthurus*, *Prionurus*; among fossil genera *Proacanthurus*, *Metacanthurus*, *Caprovesposus*, *Gazolaichthys*) or eight (the extant *Ctenochaetus* and the fossil *Pesciarichthys*) dorsal spines. Among these genera, only *Acanthurus*, *Paracanthurus*, *Ctenochaetus*, and *Proacanthurus* share with *Glarithurus* the derived folding, caudal peduncle spine and hyomandibular crest conditions that define the higher acanthurins, but within this clade the position of *Glarithurus* is not clarified by the number of dorsal-fin spines.

#### Folding, scalpel-like spine on caudal peduncle

It is fortunate that the long, scalpel-like, dermal spine on the caudal peduncle is preserved in the single specimen of *G. friedmani* because the caudal peduncle armature, whether fixed broad plates or a slender, scalpel-like, folding spine, is preserved in only a minority of the specimens of those fossil species known on the basis of numerous specimens (Sorbini and Tyler 1998b). A folding spine is the derived condition (see Winterbottom 1971 for mechanism), and its presence is sufficient to assure the proper placement of *G. friedmani* among the higher acanthurins; moreover, this conclusion is further supported by a feature of the hyomandibula discussed below.

#### Hyomandibular crest

Guiasu and Winterbottom (1993) documented two derived features that supported a terminal clade of four extant genera (*Paracanthurus* + *Zebbrasoma*) + (*Acanthurus* + *Ctenochaetus*): a folding, caudal peduncle spine and a crest or ridge along the anterodorsal region of the lateral surface of the hyomandibula. This crest is evident in *G. friedmani*; it is somewhat curvaceous but basically horizontally oriented.

We note that, with a few exceptions, there is no data regarding a hyomandibular crest or ridge in the descriptions and reconstructions of fossil acanthurids; in reconstructions the hyomandibula is mostly shown in peripheral outline with little or no indication of surface features.

One of the exceptions is the reconstruction of the only known specimen of *Tauichthys aspesae* in Tyler & Bannikov (2000). That reconstruction clearly shows a relatively horizontal crest in the anterodorsal region of the hyomandibula, even though this crest was not mentioned in the description. Based upon a pigmentation pattern on its caudal peduncle, Tyler and Bannikov (2000) proposed that *T. aspesae* probably has a slender, folding, caudal peduncle spine. We suggest herein that the definite presence of a hyomandibular crest in *T. aspesae* places the species within the higher acanthurin terminal clade of taxa, and because the other members of the higher acanthurin clade have a folding, caudal peduncle spine, it supports the interpretation that *T. aspesae* also probably has a folding spine. On

this basis, we list *Tauichthys* among the higher acanthurins in Table 1.

The others exceptions are that the original description of *Protozebrasoma bloti* by Sorbini & Tyler (1998a) and the redescription of *Marosichthys huismani* (de Beaufort, 1926) by Tyler (1997) both specifically mentioned that a hyomandibular crest is absent. The absence of this crest in *Marosichthys* is unremarkable because many derived features place it among the Nasinae (Tyler 2000), of which none are known to have a hyomandibular crest. However, it is the lack of this crest in *Protozebrasoma* that leads us to place it among the lower acanthurins in Table 1 based upon the rationale that it has at least one of the two features characteristic of this category even if its caudal peduncle armature is unknown; our placement predicts that *Protozebrasoma* will eventually be shown to have fixed plates rather than a scalpel spine.

#### Acronurus features

The width of the pectoral girdle, measured obliquely from the anterior edge of the cleithrum to the posterior edge of the coracoid, has been shown to be especially great in many acronurus stage specimens of both fossil and extant species (Tyler 1999). For example, the widths of the pectoral girdle in the acronurus stage holotypes of the two species of *Tauichthys* are 19–20%, whereas the widths in adults of both fossil and extant taxa are about 9–15%. The 18% width of this girdle in *G. friedmani* is one of several features indicating that the specimen is an acronurus stage. However, for some acronurus stage fossils of other taxa the pectoral width is not especially great, perhaps indicating that the specimen had already settled to the substrate and begun its transformation into a juvenile; examples of this are the 11% width in the acronurus stage of a specimen of *Eorandallius* sp. from Monte Bolca and the 13% width in a specimen of *Caprovesposus parvus* Danilchenko, 1960 from the Oligocene of Russia.

Prominent serrations are present on many of the head bones, the pelvic-fin spines, the second dorsal-fin spines and the anal-fin spines of acronurus stage specimens of extant species (see Johnson and Washington 1987). Serrations on numerous bones and spines have also been found on fossil acronurus specimens. They are best known on the many specimens of *Caprovesposus parvus* described by Bannikov & Tyler (1992), in which serrations are recorded on the dentary, frontal, mesethmoid, preopercle, pelvis, and the second dorsal-fin and anal-fin spines. All of the other fossil species with acronurus stage specimens also have at least some serrate bones. In the case of *G. friedmani*, the only skull bone with prominent serrations is the frontal, and this condition of relatively few bones being serrate may indicate that the specimen had already settled to the



substrate and was losing its acronurus features in the process of transformation into a juvenile. The anal spines in *G. friedmani* have serrate anterior edges and equally serrate lateral ridges along their lengths.

The scales of pelagic, acronurus stage larvae are more-or-less vertically oriented, narrow, and very elongate (e.g., Randall 1961; Johnson and Washington 1987; Frederich et al. 2010). In the 29-mm SL specimen of *Glarithurus friedmani*, the scales, although obliquely vertical in orientation, are not as long and slender as in fully acronurus stages of extant taxa, indicating that the scales of *G. friedmani* were in the process of being resorbed and replaced by the smaller and more rounded basal plates that are typical of juveniles.

The second dorsal-fin and second anal-fin spines in acanthurid larval stages are often very elongate (Leis and Rennis 1983; Leis and Richards 1984; Johnson and Washington 1987; Ozawa 1988; Tyler et al. 1989), and these two spines often remain elongate into at least the early acronurus stage. Among the known fossil acronurus stage specimens, the second dorsal and anal spines are elongate only in the single specimens (25.3 and 28.5 mm SL) representing the holotypes of *Tauichthys padremenini* and *T. aspesae*. These two spines are not elongate in any of the numerous specimens of *Caprovesposus parvus* (12.8–29.6 mm SL) (see Bannikov & Tyler 1992) nor in the single late acronurus specimens of *Metacanthurus veronensis* Blot & Tyler, 1990 (25.6 mm SL) and *Eorandallius* sp. (23.0 mm SL) (see Blot & Tyler 1990). The absence of elongation of the second dorsal and anal spines in *G. friedmani* is in conformity with the supposition that it is a very late acronurus stage that had already settled to the substrate and was well along in its transformation into a juvenile.

### Palaeoenvironment

All extant acronurus larvae originate from spawning on reefs; however, according to Furrer and Leu (1998:116–118), the marl slates from Landesplattenberg–Engi were deposited in the offshore section of a quiet bay that was not very deep, and there are no indications of coral reefs. There probably was a progressively more structured delta with a rocky coastline; therefore, it is difficult to reconcile the presence of acronurus larvae in such an area, even if such larvae are very rare. In extant habitats (e.g., the Hawaiian chain) it has been reported that these larvae become trapped by gyral and transported as far as 20–50 km away from the shoreline (Sale 1970). Nevertheless, although it is not known how they eventually escape from the gyral, they return to the reefs and shoreline before settlement, which is approximately the developmental state of the fossil acronurus specimen described herein.

### Conclusion

*Glarithurus friedmani*, from the Oligocene of Kanton Glarus, Switzerland, is shown to be unique among all other acanthurids, both fossil and extant, by having only one anal-fin basal pterygiophore situated in the first interhaemal space (versus two or more in all others). Because *G. friedmani* has a slender, folding spine on the caudal peduncle and a crest on the anterodorsal region of the hyomandibula, it is a member of the clade of higher acanthurins that includes *Proacanthurus* from the Eocene of Monte Bolca (and probably also *Tauichthys* from Monte Bolca) and four extant genera: (*Paracanthurus* + *Zebrosoma*) + (*Acanthurus* + *Ctenochaetus*). Within its higher acanthurin clade, *G. friedmani* is unique in the great depth of its pelvis at the subpelvic keel, which is a plesiomorphic condition. The holotype and only known specimen is a late acronurus stage that had already begun to lose some of the typical presettlement pelagic features and to transform into a benthic juvenile.

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