

Two New Genera and Species
of Oligocene Spikefishes
(Tetraodontiformes: Triacanthodidae),
the First Fossils of the
Hollardiinae and Triacanthodinae

*James C. Tyler, Anna Jerzmańska, Alexandre F. Bannikov,
and Jacek Świdnicki*



SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

1993

ABSTRACT

Tyler, James C., Anna Jerzmańska, Alexandre F. Bannikov, and Jacek Świdnicki. Two New Genera and Species of Oligocene Spikefishes (Tetraodontiformes: Triacanthodidae), the First Fossils of the Hollardiinae and Triacanthodinae. *Smithsonian Contributions to Paleobiology*, number 75, 27 pages, 20 figures, 3 tables, 1993.—Two new genera and species of spikefishes from the Menilitic Formation (late Tethys Sea) of the Upper Oligocene of Poland represent the first fossils of the two subfamilies of the tetraodontiform family Triacanthodidae. One of the new genera, *Prohollardia*, has a dome-like supraoccipital, the epiotics separated medially on the dorsal surface of the skull, the epiotics articulated anteriorly with the frontals, and a shaft-like posterior process of the pelvis, which are diagnostic features of the Hollardiinae. The other, *Carpathospinosus*, has a flattened supraoccipital with only a small crest anteromedially, the epiotics in contact medially on the dorsal surface of the skull, the epiotics separated from the frontals by the sphenotic, and a broad basin-like posterior process of the pelvis, which are diagnostic features of the Triacanthodinae. Some of these features of the Triacanthodinae are shown to be derived.

The separation of the two subfamilies of Triacanthodidae took place no less than about 29 to 24 MYA.

In an addendum, the Oligocene fish from Romania that was described in the dactylopteriform family Cephalacanthidae (Dactylopteridae) as *Cephalacanthus trispinosus* Ciobanu (1977) is referred to the Triacanthidae (the anatomically derived sistergroup of the Triacanthodidae) as a member of the triplespine genus *Acanthopleurus* Agassiz (1842). The single specimen is a juvenile and at least closely related to *A. serratus* Agassiz (1842) and *A. collettei* Tyler (1980), both from the Oligocene of Switzerland, and possibly identical to one or the other.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The trilobite *Phacops rana* Green.

Library of Congress Cataloging-in-Publication Data

Tyler, James C.

Two new genera and species of Oligocene spikefishes (Tetraodontiformes: Triacanthodidae), the first fossils of the Hollardiinae and Triacanthodinae / James C. Tyler...[et al.].

p. cm. — (Smithsonian contributions to paleobiology ; no. 75)

Includes bibliographical references.

1. *Prohollardia avita*—Poland. 2. *Carpathospinosus propheticus*—Poland. 3. Paleontology—Oligocene. 4. Paleontology—Poland. I. Tyler, James C., 1935— II. Series.

QE701.S56 no. 75 [QE852.T48] 560 s—dc20 [567'.5] 93-672

∞ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48—1984.

Contents

	<i>Page</i>
Introduction	1
Ichthyofaunal Associations	1
Methods and Documentation of Outgroup Data	2
Acknowledgments	2
Order TETRAODONTIFORMES Berg (1940)	3
Family TRIACANTHODIDAE sensu Tyler (1980)	3
Subfamily HOLLARDIINAE Tyler (1968)	3
<i>Prohollardia</i> , new genus	3
Diagnosis	3
<i>Prohollardia avita</i> , new species	3
Description	3
Head	3
Vertebral Column	8
Pectoral Fin and Girdle	8
Pelvic Fin and Girdle	8
Spiny Dorsal Fin	9
Soft Dorsal Fin	10
Anal Fin	11
Caudal Fin and Skeleton	11
Scales	11
Subfamily TRIACANTHODINAE Tyler (1968)	11
<i>Carpathospinosus</i> , new genus	11
Diagnosis	11
<i>Carpathospinosus propheticus</i> , new species	12
Description	12
Head	13
Vertebral Column	14
Pectoral Fin and Girdle	14
Pelvic Fin and Girdle	14
Spiny Dorsal Fin	16
Soft Dorsal Fin	17
Anal Fin	17
Caudal Fin and Skeleton	17
Scales	17
Other Relevant Fossil Taxa	17
Discussion of Subfamilial Defining Characters	18
Pelvis	21
Position of Epiotics on Dorsal Surface of Skull	22
Epiotic Anterior Articulation	22
Supraoccipital	22
First Basal Pterygiophore of Anal Fin	23
Summary of Subfamilial Characters of New Taxa	23
Relationships of <i>Prohollardia</i> in Hollardiinae	23
Synapomorphies of <i>Prohollardia</i> and <i>Hollardia</i>	24
Similarities between <i>Prohollardia</i> and Other Genera	24
Summary of Relationships of <i>Prohollardia</i>	25

Relationships of <i>Carpathospinosus</i> in Triacanthodinae	25
Referral of <i>Cephalacanthus trispinosus</i> Ciobanu to Triacanthidae	25
Conclusion	26
Literature Cited	27

Two New Genera and Species of Oligocene Spikefishes (Tetraodontiformes: Triacanthodidae), the First Fossils of the Hollardiinae and Triacanthodinae

*James C. Tyler, Anna Jerzmańska, Alexandre F. Bannikov,
and Jacek Świdnicki*

Introduction

Continuing annual explorations since 1954 by the Department of Paleozoology of Wrocław University to document the Oligocene ichthyofauna of the portion of the Carpathian Mountains in southern Poland have obtained thousands of specimens of marine fishes within the Menilite Formation (Menilite Beds) of the late Tethys Sea. These collections contain fishes from all six IPM (Ichthyofauna, Paleogene, Menilite) zones (Kotlarczyk and Jerzmańska, 1976). The zones range in age from about 36 MYA for the beginning of IPM 1 to about 24 MYA for the end of IPM 6 (Kotlarczyk and Jerzmańska, 1988), and in habitat from epi- through meso- to bathypelagic and benthic to neritic (Jerzmańska and Kotlarczyk, 1976).

Some of these specimens are the first fossil records for families otherwise known only from Recent species (such as Alepocephalidae; Jerzmańska, 1979). Many of them are judged to be anatomically distinctive at the generic level from their Recent relatives (Jerzmańska, 1968, 1974), such as the two new genera of triacanthodids described herein. Others are only specifically distinct (such as the caproids *Capros radobojanus* (Kramberger) and *C. medianus* Świdnicki and the zeid *Zenopsis clarus* Daniltshenko), while some appear to be identical with Recent species (such as the zeid *Zeus faber* Linnaeus) (Świdnicki, 1986).

James C. Tyler, Office of the Director, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Anna Jerzmańska and Jacek Świdnicki, Zoological Institute, Wrocław University, Sienkiewicza 21, 50-335 Wrocław, Poland. Alexandre F. Bannikov, Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, 117647 Moscow, Russia.

Among the materials collected between 1981–1990 at Błażowa in IPM 6 (range about 27–24 MYA) and in 1983–1987 at Przysietnica in IPM 4 (range about 29–28 MYA) are specimens of two new genera and species of spikefishes that are the first fossil records of the triacanthodid subfamilies Hollardiinae and Triacanthodinae. The descriptions of the hollardiin *Prohollardia avita*, new genus and species, and the triacanthodin *Carpathospinosus propheticus*, new genus and species, are based on well-preserved and complete holotypes and, respectively, three and nine paratypes. Although the paratypes are not as well preserved overall as the holotypes, they have certain anatomical features well exposed and have substantially expanded our knowledge of the new taxa.

These two new taxa of the Triacanthodidae are especially interesting systematically because they represent both of the subfamilies of triacanthodids, which until now were known only from Recent species. This establishes that the division of the family into two subfamilial lineages (the Hollardiinae with *Prohollardia* and two Recent genera, and the Triacanthodinae with *Carpathospinosus* and nine Recent genera) took place no less than about 29 to 24 MYA.

ICHTHYOFAUNAL ASSOCIATIONS

In five of the six IPM zones the predominant fishes are mesopelagic, with a lesser number of epipelagic and benthic forms, whereas IPM 2 contains only neritic and sublittoral species. IPM zones 6 and 4 in which *Prohollardia* and *Carpathospinosus* have been found, respectively, are both dominated by mesopelagic fishes such as the myctophid *Eomyctophum*, the photichthyid *Vinciguerria*, and the ster-

noptychids *Polyipnus* (IPM 4 only) and *Argyropelecus* (IPM 6 only). Less frequent are the epipelagic clupeids *Alosa* and *Clupea*, the trichiurid *Lepidopus*, and the scombrid *Scomber* (IPM 6 only). Least common in zones 4 and 6 are benthic species such as Pleuronectiformes (genera undetermined), the caproid *Capros*, and the zeid *Zeus* (for the biostratigraphy of the Menilite Beds see Kotlarczyk and Jerzmańska, 1976, 1988; Jerzmańska and Kotlarczyk, 1981).

The two new genera of Triacanthodidae significantly increase the known benthic component of zones IPM 4 and 6 because they presumably were bottom dwelling like Recent triacanthodids, which occur benthically at depths of 38 to over 900 m (usually 180 to 500 m), with one specialized bathypelagic species found at over 1000 m depth (Tyler, 1968:62, 174). The smallest specimens of one of the new species, *Carpathospinosus propheticus*, are 12–18 mm SL and could be either epipelagic postlarval stages or recently settled benthic juveniles.

METHODS AND DOCUMENTATION OF OUTGROUP DATA

Standard length (SL) is from the tip of the upper jaw to the end of the hypural plate. Most measurements of the fossils are given with confidence to the nearest 0.1 mm, but those of which we are less sure are given as “about” or, with the least precision, “estimated.” Drawings were prepared with the use of a camera lucida on a Olympus stereomicroscope.

Measurement definitions, bone terminology, and comparative data for the Recent species follow Tyler (1968). Of particular interest here is the process of the pelvis behind the bases of the pelvic spines (posterior process). Its length is measured along the midline from the level of the middle of the bases of the spines to the distal end of the pelvis; its width is measured across both halves of the pelvis between the locking flanges of the pelvic spines (estimated if necessary in the fossils). In text discussions of the pelvis, the term “process” when unmodified refers to the posterior process and not to the ascending process. In the fossil specimens, head length is from the tip of the upper jaw to the place estimated to be the upper end of the gill opening between the anterior edge of the cleithrum and the posterior edge of the opercle.

Abbreviations for the names of bones in the illustrations are: Art = articular; Bpt = basal pterygiophore; Br = branchiostegal ray; Chy = ceratohyal; Cl = cleithrum; Den = dentary; Ecp = ectopterygoid; Ep = epiotic; Epu = epural; Eth = ethmoid; Fr = frontal; Hhy = dorsal and ventral hypohyals; Hyo = hyomandibula; Hyp = hypurals; Iop = interopercle; Mpt = metapterygoid; Msp = mesopterygoid; Mx = maxilla; Ns = neural spine; Op = opercle; Pal = palatine; Pas = parasphenoid; Pcl = postcleithrum; Pel = pelvis; Pf = prefrontal (lateral ethmoid); Phyp = parhypural; Pmx = premaxilla; Pop = preopercle; Pot = prootic; Ptot = pterotic; Pts = pterosphenoïd; Ptt = posttemporal; Pu = preural centra; Qu = quadrate; Scl = supracleithrum; Soc = supraoccipital; Sop = subopercle; Sph = sphenotic; Sym = symplectic; Uh = urohyal; V = vomer.

Documentation of the osteological features of tetraodontiform outgroups is from Tyler (1968, 1980). Data on the osteology of caproids and zeiforms are from the descriptions of *Zeus* by Starks (1898), Norman (1934), and Gregory (1933); the description of *Grammicolepis* by Shufeldt (1888); the comparisons between the Upper Cretaceous *Palaeocyttus* and the Recent *Cyttus*, *Neocyttus*, and *Zeus* by Gaudant (1978); the comparisons between the Oligocene *Zeus faber* and the Recent *Zeus* and *Zenopsis* by Świdnicki (1986); the comparisons between caproids and zeiforms by Gaudant (1977), Rosen (1984), and Zehren (1987); the review of zeiform characteristics by Heemstra (1980); and the works on fossil caproids by Sorbini (1983), Sorbini and Bottura (1987), Świdnicki (1988), and Bannikov (1991). We believe the upper Cretaceous specimen described by Gayet (1980a,b) as *Microcapros* to be a beryciform (Bannikov, 1991:55).

We examined cleared and stained specimens at the National Museum of Natural History and dry skeletal materials at the American Museum of Natural History of the zeids *Zeus*, *Zenopsis*, *Capromimus*, *Cyttus*, *Cytopsopsis*, and *Stethopristes*, the macruricyttid *Zenion*, the grammicolepidids *Grammicolepis* and *Xenolepidichthys*, the parazenid *Parazen*, the oreosomatids *Neocyttus*, *Alloocyttus*, and *Pseudocyttus*, and the caproids *Capros* and *Antigonia*. Additionally, Steven Zehren has provided us data on zeiform osteology used for outgroup analysis in his study of caproids.

The familial relationships of the Tetraodontiformes adopted here are essentially those determined by Winterbottom's (1974) phylogenetic analysis, as modified for fossil groups by Tyler and Bannikov (1992).

Abbreviations used in parenthetical expressions identifying outgroups in the text are: 1 o.g. and 2 o.g. for the first and second successive outgroups.

ACKNOWLEDGMENTS

We appreciate the support provided by the Polish Academy of Sciences and Wrocław University for travel accommodations for the participants from Russia and the United States that facilitated the research with their Polish colleagues. Ewa Świdnicka of the Department of Paleozoology, Wrocław University, greatly assisted the research during the entire study. Steven Zehren, University of Alabama, generously provided us with literature and osteological data on zeiforms. Hans-Dieter Sues, Royal Ontario Museum, Toronto, carefully searched the collections at the Institut für Palaeontologie, Bonn, for specimens of *Cryptobalistes* and prepared one of those he found to enhance its exposure. Richard Vari, Smithsonian Institution, spent much time giving us good advice on our cladistic analyses, and the manuscript greatly benefited from his constructive suggestions and from those of Richard Winterbottom, Royal Ontario Museum, Toronto, and C.L. Smith, American Museum of Natural History, New York, elicited during the preacceptance review process. At the Smithsonian Institution Press we thank Craig Warren for the

careful copy editing and typesetting of the paper and Diane M. Tyler for the preparation of the tables.

This research was supported in part by Polish grant CPBP 04.03.III/5.3 to A. Jerzmańska.

Order TETRAODONTIFORMES Berg (1940)

Family TRIACANTHODIDAE sensu Tyler (1980)

Subfamily HOLLARDIINAE Tyler (1968)

This subfamily includes five species in the Recent genera *Hollardia* and *Parahollardia* of the western Atlantic and central Pacific oceans and the new Oligocene genus *Prohollardia* from the Polish Carpathian Mountains.

Prohollardia has a dome-like supraoccipital with a convex posterior surface, the epiotics separated from one another medially on the dorsal surface of the skull, the epiotics articulated anteriorly with the frontals, and a shaft-like posterior process of the pelvis. These are diagnostic characteristics of the subfamily Hollardiinae. While these features are used to define the subfamily, our analysis indicates that none of them are unequivocally derived and consequently we cannot demonstrate that the Hollardiinae is monophyletic (see "Discussion of Subfamilial Defining Characters").

Prohollardia, new genus

TYPE SPECIES.—*Prohollardia avita*, new species, by monotypy and present designation.

ETYMOLOGY.—From the Greek, *pro* (early or ancestral) plus *hollardia*, for both the subfamily Hollardiinae of which the new genus is the earliest known member and its proposed sistergroup relationship with *Hollardia* Poey (1861). That name honors Henri Hollard, the pioneer mid-19th century monographer of the anatomy and classification of the plecognath (tetraodontiform) fishes; feminine.

DIAGNOSIS

Prohollardia differs from all other Triacanthodidae by the presence of an enlarged scale plate with a prominent thorn-like spine projecting dorsally over each eye (versus no such scale); the almost vertical orientation of the hyomandibula (versus oriented obliquely anteroventrally); the last basal pterygiophore of the spiny dorsal fin and the first two basal pterygiophores of the soft dorsal fin oriented approximately vertically (versus inclined anteroventrally); the spiny dorsal-fin base slightly shorter than the soft dorsal-fin base (versus spiny dorsal-fin base significantly longer than soft dorsal-fin base); a longer soft dorsal-fin base, higher soft dorsal fin, longer head, and more extensive covering of the spiny dorsal fin and its membranes by spinulose scales.

Prohollardia differs from all other Hollardiinae by the more pronounced difference in the relative lengths of the first and

second dorsal spines; the more pronounced difference in the relative lengths of the pelvic spine and posterior process of the pelvis; and the more anterior origin of the spiny dorsal fin in relation to the gill opening (see description for quantification of these diagnostic features).

Prohollardia avita, new species

FIGURES 1-10; TABLE 1

MATERIAL.—Holotype, Zoological Institute, Department of Paleozoology, Wrocław University (ZPALWr.) A/2096, an almost complete specimen in part and counterpart, except for the posterior part of the caudal fin and the anterior part of the anal fin, 44.4 mm SL. Three paratypes: ZPALWr. A/2097, in part and partial counterpart, estimated 25.0 mm SL; ZPALWr. A/2098, in part and counterpart, about 29.0 mm SL; ZPALWr. A/2099, single plate, about 26.0 mm SL. All of the materials are impressions in siliceous-argillaceous shales from the same horizon and locality, see below.

TYPE HORIZON.—Upper Oligocene, zone IPM 6 of the Menilite Beds.

TYPE LOCALITY.—Błażowa, south of Rzeszów, Rzeszów Province, the Carpathians, southeast Poland (49°53'N, 22°06'E).

DIAGNOSIS.—As for the genus.

ETYMOLOGY.—From the Latin *avitus* (very old or ancient), in reference to the Oligocene age of the type material; feminine.

DESCRIPTION

Judging from the body sizes of the various life history stages of the Recent species of the family, the holotype (Figures 1, 2) is probably a young adult and the paratypes are probably juveniles. Measurements for the specimens are given in Table 1. A summary of the differences between *Prohollardia*, *Carpathospinosus*, and the Recent genera of the two subfamilies is given in Table 3.

The maximum proportional depth of the body is relatively great in *Prohollardia*, 70.0%–72.0% SL (average 71.2), compared to other triacanthodids, although, like allometry in head size discussed below, this is at least partially a function of the small size of the type specimens. The only other triacanthodids with comparably great body depths at this size are hollardiins: two of the three species of the Recent *Hollardia*, *H. meadi* Tyler and *H. hollardi* Poey and one of the two species of the Recent *Parahollardia*, *P. lineata* (Longley), in which the depth is 65%–73% SL at about 30–50 mm SL. Among triacanthodins body depths as great as even about 57%–67% SL at small specimen sizes are found only in *Johnsonina eriomma* Myers.

HEAD.—The head (Figure 3) is exceptionally long (48.0%–52.4% SL, average 49.5). In other triacanthodids the head is 33%–45% SL (longest in juveniles), with average values of 35%–40% SL in all Recent species with head shapes comparable to that of the new species (the notably elongate

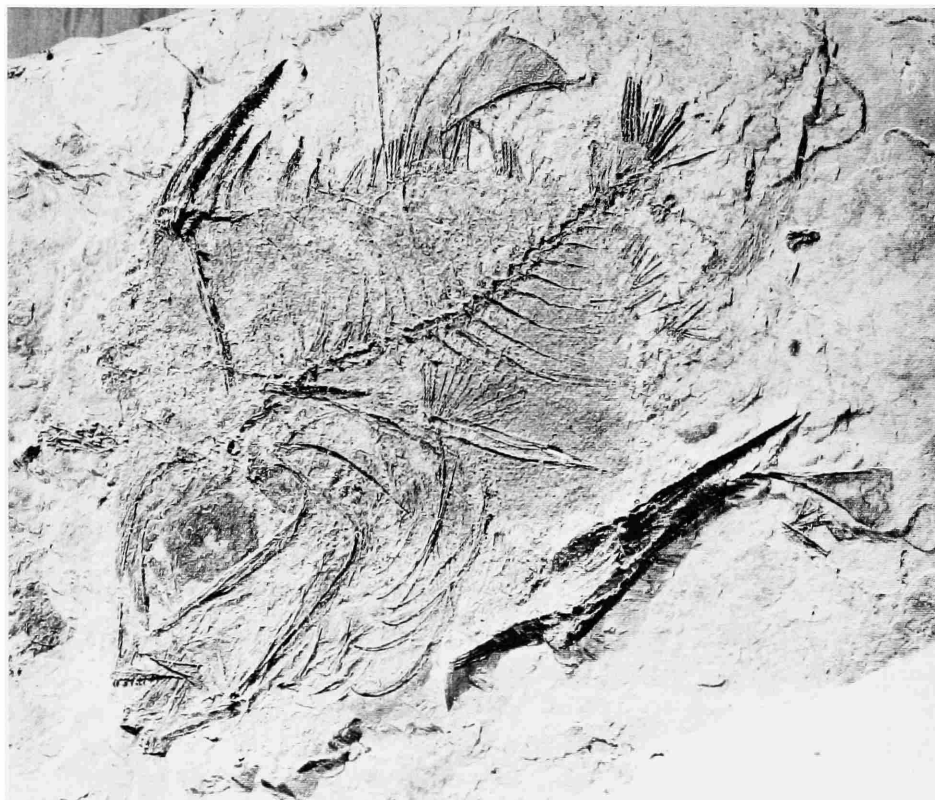


FIGURE 1.—*Prohollardia avita*, new genus and species, photograph of holotype, ZPALWr. A/2096, 44.4 mm SL, Menilite Beds, IPM 6, Błażowa, southern Poland, Carpathian Mountains, Upper Oligocene.

TABLE 1.—Measurements of *Prohollardia avita*, new genus and species.

Character	Holotype		Paratypes					
	ZPALWr.A/2096 mm	%SL	ZPALWr.A/2099 mm	%SL	ZPALWr.A/2097 mm	%SL	ZPALWr.A/2098 mm	%SL
Standard length	44.4		26.0*		25.0†	–	29.0*	–
Head length	22.0	49.5	12.5*	48.0*	12.0†	48.0†	15.2*	52.4*
Body depth	32.0*	72.0*	18.5*	71.5*	17.5†	70.0†		
Predorsal length	27.0	60.0	14.5	55.7*	14.2*	56.8†		
First dorsal spine	12.5	28.1	5.4	20.7*	6.1	24.4†		
Second dorsal spine	6.3	14.1	3.4	13.0*	3.3	13.2†	–	–
Third dorsal spine	5.6	12.6	2.2	8.4*	3.0	12.0†	–	–
Pelvic spine	13.4	30.1			–		5.5	19.0*
Pelvis width	3.0*	6.7*			–		–	–
Pelvis length	9.5	21.4			–		4.2	14.5*
Spiny-dorsal base	10.5*	23.6*	5.0*	19.2*	–		–	–
Soft-dorsal base	11.6	26.1	6.0*	23.0*	–		–	–
Anal base	8.2	18.0	4.3*	16.5*	–			
Soft-dorsal height	10.2	23.0			–			

*Value is approximate.

†Value is an estimate (less precise than approximate).

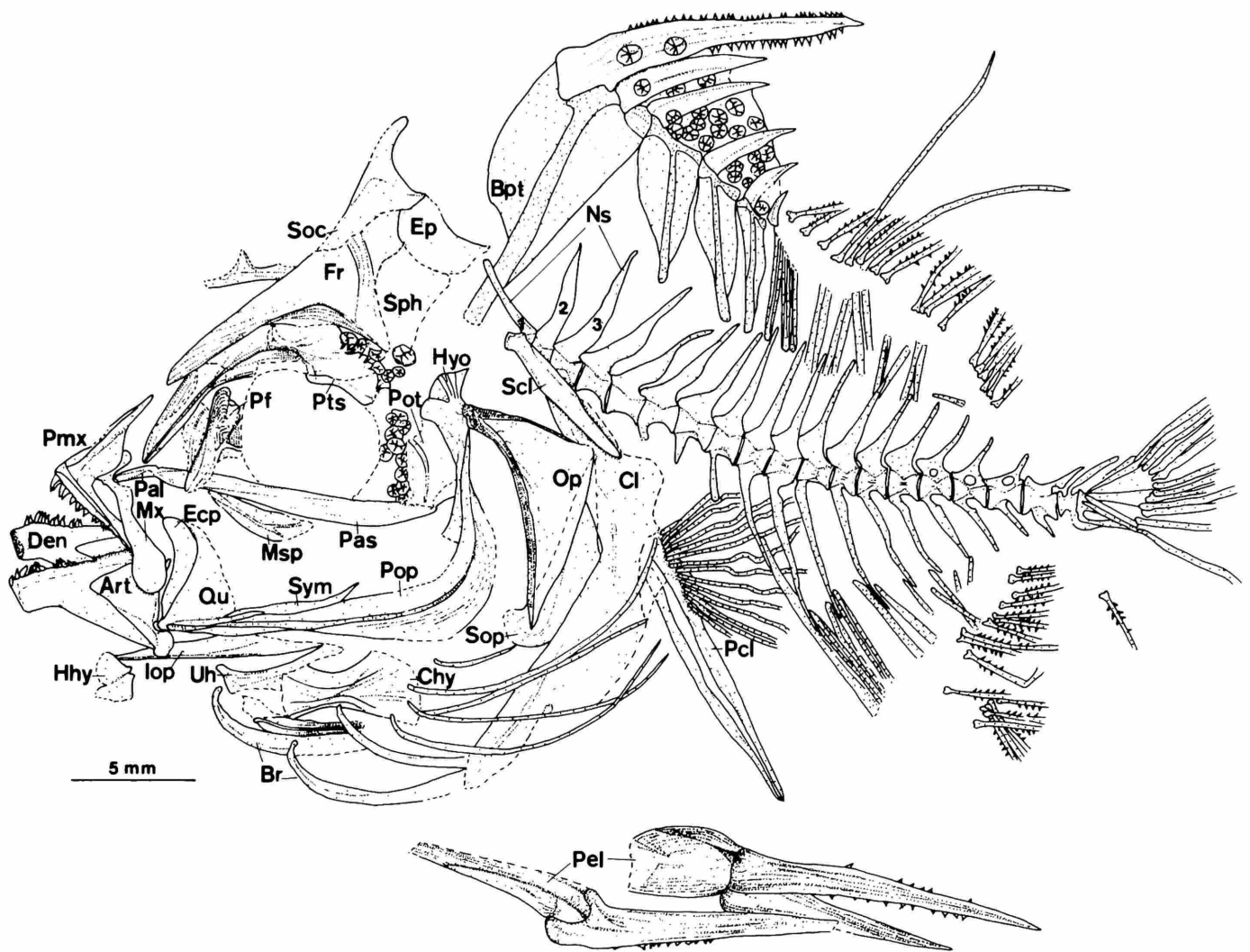


FIGURE 2.—*Prohollardia avita*, new genus and species, reconstruction based on holotype.

tubular snout in two highly specialized genera, *Halimochirus* and *Macrorhamphosodes*, results in head lengths of 50%–62% SL). The relative head size of the type materials of *Prohollardia* is significantly longer, even in comparison to head size in equally small specimens of Recent triacanthodids. The head in the other new Oligocene genus, *Carpathospinosus*, also is relatively long, 45.5% SL, somewhat shorter than in *Prohollardia* but only slightly longer than in small specimens of some other species of triacanthodids.

The supraoccipital (Figures 2, 3) is entirely dome-like, as in other hollardiins, with a concave posterior profile in lateral view and what would be a convex or rounded posterior surface in posterior view. The supraoccipital articulates anteriorly with the posterior part of the frontals and laterally with the epiotics, separating the epiotics on the dorsal surface of the skull. The epiotics articulate anteriorly with the frontals. There are traces

of the sphenotic below the posterior region of the frontal and anterior to the epiotic. The long frontals are wide posteriorly and taper to points anteriorly. Closely applied to each frontal in the region over the orbit is a greatly enlarged scale plate bearing a prominent dorsally oriented thorn-like process (preserved in the holotype and ZPALWr. A/2097) (Figures 3, 4). Because the enlarged supraocular spiny scale is visible in both the largest (44.4 mm SL) and in one of the smaller (25.0 mm SL) specimens, we assume that this unique feature among triacanthodids is diagnostic of the new species at all sizes and not just a juvenile character. However, we would not be surprised if the spine on the supraocular scale is relatively smaller in adults larger than our present materials. The prefrontals are well preserved on the holotype and border the anterior wall of the orbit. The indistinct remains of the ethmoid can be seen on the anterior regions of the left frontal (Figures 2,

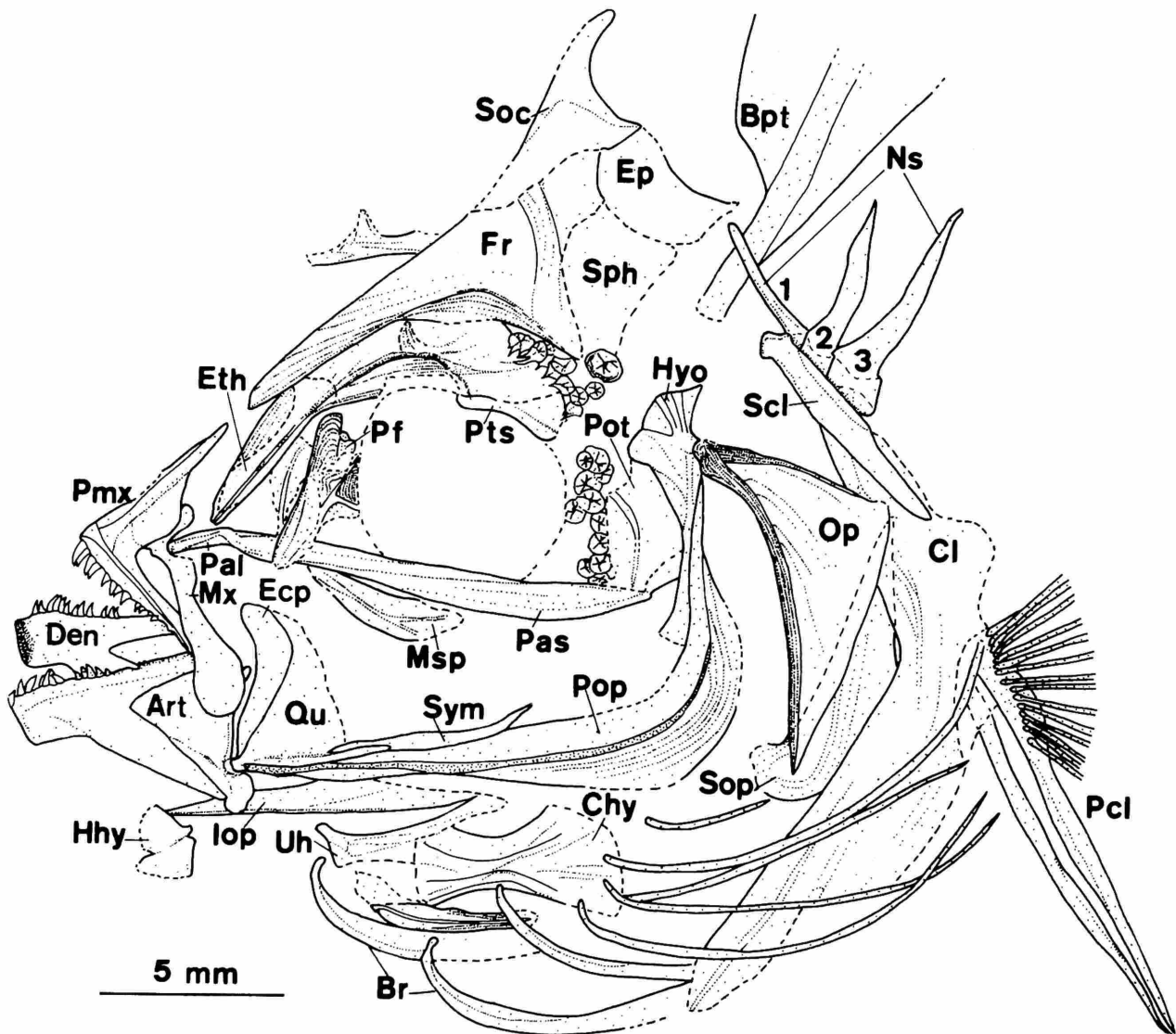


FIGURE 3.—*Prohollardia avita*, new genus and species, reconstruction of lateral view of skull of holotype.

3). The parasphenoid is relatively straight in the orbital region and has a moderately developed ventral flange (Figure 3). Close to the skull of one of the paratypes (ZPALWr. A/2097) are three thin unidentifiable isolated bones that we think are disarticulated pieces of the specimen (Figure 5 A–C).

The jaws are well preserved. The L-shaped premaxilla has a sturdy ascending process and a narrow alveolar process. The maxilla is broadest posteriorly, constricted in the middle, and expanded into an articular facet anteriorly where it meets the palatine and premaxilla in what apparently was a moveable articulation allowing for slight protrusion of the upper jaw. The dentary is broad and concave posteriorly to accommodate its articulation with the articular. The teeth are mostly represented by impressions but were obviously stout, conical, in a single series, and slightly curved posteriorly. There are about 12 to 14

teeth to each side of the upper and lower jaws, based on a combination of the impressions and the space available for missing teeth along the alveolar edge of the bones. We are confident that the teeth are in a single series without additional internal teeth because the left dentary is displaced upward in the holotype and exposed in medial view. The lack of inner series teeth is similar among hollardiids to the condition of *Hollardia* and in contrast to that of *Parahollardia*, in which inner series teeth are present.

The hyomandibula is expanded dorsally and tapers to a shaft ventrally. It is oriented almost vertically (Figure 3), unlike the distinctly oblique orientation in all Recent triacanthodids (orientation questionable in the other new Oligocene genus, *Carpathospinosus*, but probably oblique).

The opercle is a large, thin, almost triangular bone with

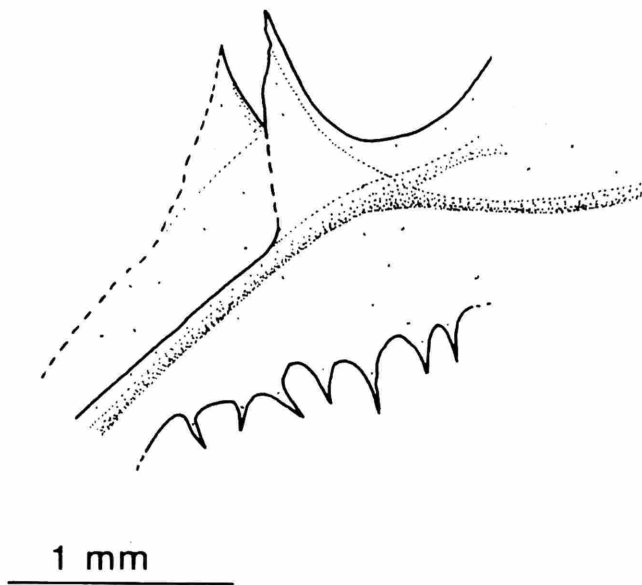


FIGURE 4.—*Prohollardia avita*, new genus and species, enlarged right and left supraocular scale plates with thorn-like spines, paratype ZPALWr. A/2097, estimated 25.0 mm SL (same locality as holotype, see Figure 1).

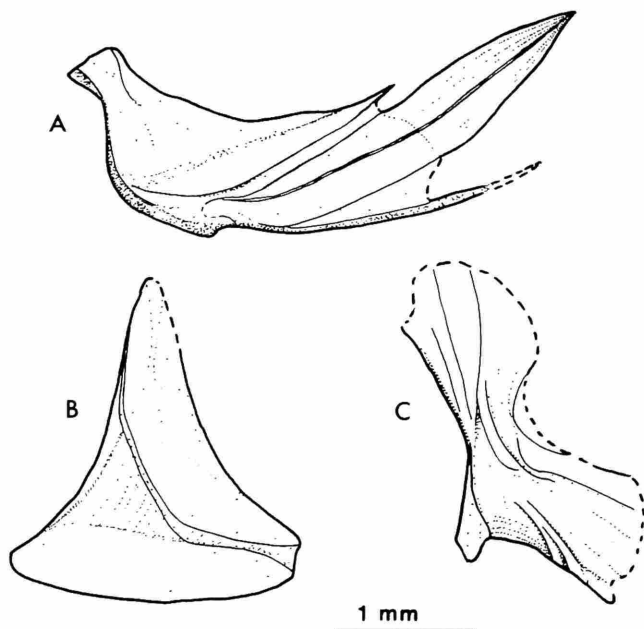


FIGURE 5.—*Prohollardia avita*, new genus and species, three unidentifiable, isolated bones on plate with paratype ZPALWr. A/2097, all to same scale.

heavy ossification along its anterior and dorsal margins (Figures 3, 6). The subopercle is rounded anteroventrally and tapers to a point posterodorsally (Figure 7). The preopercle is strongly curved, with the lower arm about twice as long as the upper and at about a 90° angle to it. The broad curved regions of the preopercle and subopercle bear fine grooves and ridges

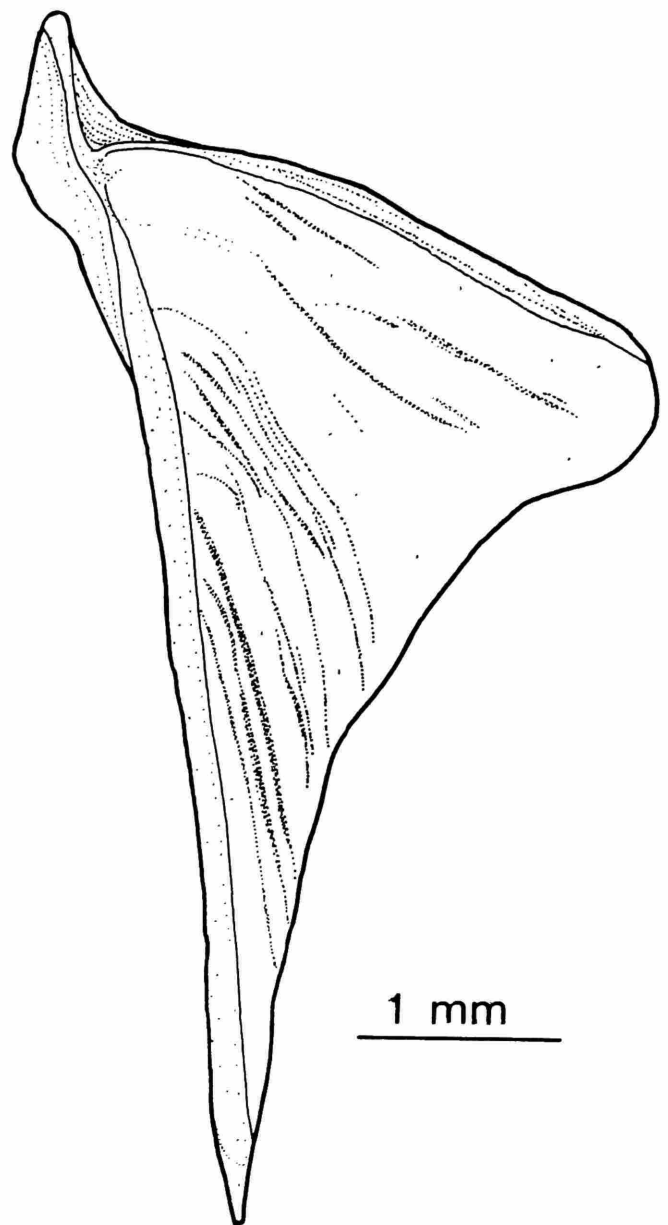


FIGURE 6.—*Prohollardia avita*, new genus and species, isolated opercle in lateral view, paratype ZPALWr. A/2097.

on their lateral surfaces, approximately parallel to their longest edges (Figures 3, 7). The interopercle is visible anteriorly where it is displaced forward beyond the articulation of the lower jaw with the quadrate.

The long ceratohyal is constricted in the middle and broadened posteriorly. The epihyal is not evident. The branchiostegal rays from both sides are somewhat intermixed, but our interpretation of them is that there are six rays of increasing length posteriorly on each side, two in a forward group articulated to the ventral surface of the middle of the ceratohyal and four placed more posteriorly along the side of

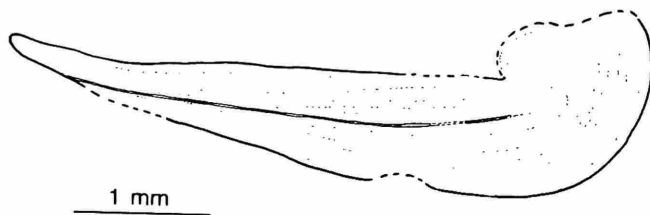


FIGURE 7.—*Prohollardia avita*, new genus and species, isolated subopercle in lateral view, holotype.

the rear of the ceratohyal and, presumably, the epihyal. The two anterior rays are slightly expanded and flattened while the posterior group are rod-like. In the area below the posterior region of the lower jaw and the anterior end of the interopercle are traces of two bones which we interpret as displaced dorsal and ventral hypohyals (Figure 3).

VERTEBRAL COLUMN.—There are eight abdominal and 12 caudal vertebrae (Figure 2). The neural spine of the first vertebra is directed anteriorly and closely applied to the rear of the neurocranium. This neural spine is presumed to have been bifid (i.e., the two halves not meeting over the neural canal) just as in Recent triacanthodids because the ventral end of the first basal pterygiophore of the spiny dorsal fin passes through it medially to articulate in a cavity in the rear of the skull. All of the other neural spines are non-bifid and posterodorsally oriented. The neural spines of the second and third vertebrae are relatively more vertical than the others, while those of the fourth to seventh vertebrae are more oblique than those that follow. The bases of the neural spines are expanded anteroposteriorly from the second abdominal vertebra to Pu_3 . Neural foramina are visible on the lateral surfaces of the neural arches on the seventh to ninth caudal vertebrae (Figure 9).

Traces of parapophyses are visible on the last three abdominal vertebrae in the holotype and ZPALWr. A/2097; those on the first two of these vertebrae are shorter and broader than that on the last one (Figure 2). There is no evidence of either pleural or epipleural ribs. Because all Recent triacanthodids and the other new Oligocene genus have epipleurals but

lack pleural ribs, we believe that epipleurals were present in *Prohollardia* but were not preserved. Haemal arches and spines are well developed on the caudal vertebrae. The caudal skeleton is described below.

PECTORAL FIN AND GIRDLE.—Only the elongate supracleithrum and ventral postcleithrum are well preserved. Both are placed obliquely to the axis of the skull, and the latter ends in the region above the posterior half of the pelvis (Figure 2). The cleithrum is only poorly indicated except along its anterior edge.

The pectoral fin has 15 well-preserved intact rays. The short uppermost ray is sturdy, unbranched, and about one-third the length of the second ray, which also appears to be unbranched. The third to 13th rays are branched.

PELVIC FIN AND GIRDLE.—The pelvis is large, sturdy, and relatively short, with a broad oblique ascending process extending anteriorly from the level of the pelvic spines to what would be the posterior edge of the cleithrum if the pelvis were in its normal position (it is fractured and one part is displaced slightly anteroventrally, Figure 8). The pelvis has a stout shaft-like posterior process. The length of the process is 21.4% SL in the holotype but distinctly shorter, about 14.5% SL, in the one paratype in which it can be measured (ZPALWr. A/2098). The length of this process in the paratype is much shorter than in other species of triacanthodids, in which the length averages 24%–34% SL (except in the two long-snouted genera, which have a similarly long process relative to the body but lower averages of 19%–24% SL because of the exceptionally long head). The length of the process in the holotype, while relatively short, is, however, comparable to that in some specimens of the hollardiin *Hollardia hollardi*. In *H. hollardi* the length of the process is more variable than in any other triacanthodid, ranging from 16.3%–29.1% SL (average 24.7), with most specimens having a length of 22% SL or greater. Specimens of *H. hollardi* in which the process is 16%–21% SL range widely in size, from 53–132 mm SL, with no correlation between the length of the process and standard length (see fig. 145 in Tyler, 1968:335). The relative shortness (20% SL or less) in the length of the

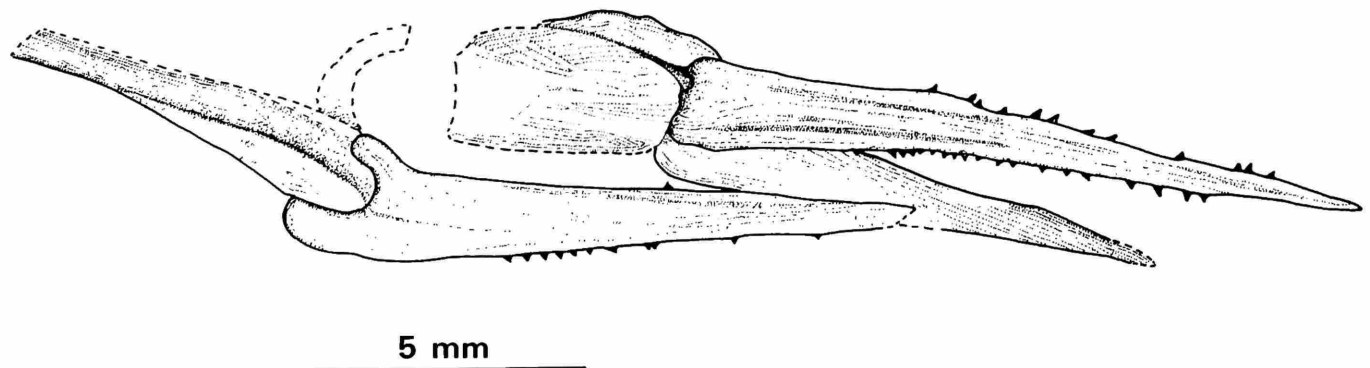


FIGURE 8.—*Prohollardia avita*, new genus and species, pelvis and pelvic fin in approximately ventral view to right of fracturing indicated by dashed lines and in approximately lateral view to left of fracturing, holotype.

process is peculiar to *Prohollardia avita* and to some specimens of *H. hollardi*, and the great variability in its length also is found only in those two species. While longer than in *P. avita* and some specimens of *H. hollardi*, the process in the other new Oligocene genus, *Carpathospinosus*, is relative shorter (25.4% SL) than in most specimens of other species of triacanthodids.

The width of the pelvis between the spines in *Prohollardia* is 6.7% SL in the holotype, the only specimen in which it can be measured. This is relatively broad in comparison to other hollardiins, in which the averages for the five Recent species are 3.6%–6.2% SL. However, the pelvic width, like its length, is highly variable in the Recent hollardiin with the widest pelvis, *H. hollardi*, in which the width ranges from 4.5%–8.4% SL (average 6.2), encompassing the width measurement in *Prohollardia*. In *Prohollardia* the pelvic width is contained 3.2 times in the length of the process, while in Recent hollardiins the average values are 4.0–6.7 (with only *H. hollardi* among hollardiins having some specimens with a value as low as 3.2 like that of the single specimen of *Prohollardia* in which this can be measured).

The two halves of the pelvis apparently are medially fused or consolidated with one another in the largest specimen (the 44.4 mm SL holotype) but clearly are separate in one of the three smaller specimens (ZPALWr. A/2098, 29.0 mm SL). Fusion of the halves of the pelvis with increasing specimen size also occurs in Recent triacanthodids. In the holotype the pelvic spines and the posterior process are exposed mostly in dorsoventral view, but the ascending process is seen in lateral view.

The length of the strong pelvic-fin spine (30.1% SL in the holotype and 19.0% SL in the only paratype in which it can be measured, ZPALWr. A/2098) is 1.3–1.4 times (average 1.4) longer than the length of the relatively short posterior process (see measurements above). In Recent triacanthodids the pelvic spines are usually about the same length as the process but sometimes slightly longer (1.1 times) or shorter (0.8–0.9 times). In the other new Oligocene genus, *Carpathospinosus*, the pelvic spines are exceptionally long and the process exceptionally short, the spine 1.5 times longer than the process.

The pelvic spines bear deep longitudinal grooves and are covered with spinulose scales except at the naked extreme distal tips. There is no evidence of fin rays, but fossil material in this type of shale matrix is unlikely to reveal one or two short or rudimentary rays just behind the base of the pelvic spine such as are found in all Recent triacanthodids.

SPINY DORSAL FIN.—The origin of the spiny dorsal fin (Figure 2) is distinctly anterior to the vertical line through the level of the gill opening, as determined by the well-preserved posterior edge of the opercle and the anterior edge of the cleithrum. In most other triacanthodids the spiny dorsal-fin origin is over or slightly behind the vertical through the level of the gill opening, but it is distinctly posterior to it in the hollardiin *Hollardia*, over or slightly in front of it in the

hollardiin *Parahollardia*, and distinctly in front of it in the triacanthodid *Mephisto* (as much so as in *Prohollardia*). The relative position of the spiny dorsal-fin origin relative to the gill opening in *Prohollardia* is mostly a function of the longer head and associated more posteriorly located gill opening rather than reflective of a forward migration of the spiny dorsal fin. For example, the predorsal distance (snout to base of first dorsal-fin spine) in *Prohollardia* averages 57.5% SL, which is relatively great in comparison to most other triacanthodids (averages 40%–50% SL). However, it is similar to that in two of the three species of *Hollardia* (averages 55.8% SL in *meadi* and 58.8% SL in *hollardi*), in which the spiny dorsal-fin origin is slightly to distinctly behind the gill opening. The relatively great predorsal length in these species of *Hollardia* and in *Prohollardia* is also partially a function of their greater body depth relative to most other triacanthodids. The spiny dorsal-fin origin is placed over the second centrum in *Prohollardia* but over the posterior end of the basioccipital or the anterior end of the first vertebra in all other triacanthodids with moderate to great body depths (i.e., exclusive of the somewhat elongate *Atrophacanthus* and *Tydemanina*, and the much elongate, long-snouted *Halimochirurgus* and *Macrorhamphosodes*).

The base of the spiny dorsal fin in *Prohollardia* (Table 1) is slightly shorter than the base of the soft dorsal fin, whereas in all of the Recent triacanthodids and the Oligocene *Carpathospinosus* (Table 2) the spiny dorsal-fin base is distinctly longer than the soft dorsal-fin base. The spiny dorsal-fin base is 23.6% and 19.2% SL in the holotype and ZPALWr. A/2099 respectively, versus 26.1% and 23.0% SL for the soft dorsal-fin base (Table 1). Comparable measurements for the soft dorsal-fin base (but not the spiny dorsal-fin base) in all Recent triacanthodids are given in Tyler (1968). The lengths of the spiny dorsal-fin base of representative species of most of the Recent genera can be determined from the illustrations of the skeletons in that work. The spiny dorsal-fin base ranges from 26%–32% SL and the soft dorsal-fin base from 16%–22% SL in triacanthodids with typical snouts (Table 3; 20%–21% SL and 10%–12% SL respectively in the two long-snouted genera), with the spiny dorsal-fin base longer.

Prohollardia has six dorsal-fin spines, with all but the short last element bearing deep longitudinal grooves along their lengths. The first spine is strongest, longest, curved posteriorly, and covered with spinulose scales except at the extreme distal tip. The first spine in the holotype is somewhat longer (28.1% SL) than the spiny dorsal-fin base (23.6% SL), but in the one paratype (ZPALWr. A/2099) in which both measurements can be made the first spine is only marginally longer (20.7% SL) than the base (19.2% SL). If depressed the first dorsal spine in *Prohollardia* would reach only slightly beyond the origin of the soft dorsal fin. In Recent triacanthodids the first dorsal spine is either shorter or only slightly longer than the spiny dorsal-fin base, reaching posteriorly no more than to the level of the base of about the third to fourth soft dorsal-fin ray. In the other new Oligocene genus, *Carpathospinosus*, the first dorsal spine is

especially long (Table 2), of much greater length than the spiny dorsal-fin base.

The length of the second spine is contained 1.6–2.0 times (average 1.8) in that of the first spine (see description of spiny dorsal fin in *Carpathospinosus* for comparisons with other triacanthodids). The remaining spines decrease gradually in length posteriorly.

The interspinous membranes of *Prohollardia* are extensively covered with spinulose scales, contrary to conditions in the Oligocene *Carpathospinosus* and Recent triacanthodids, most of which have no scales on the interspinous membranes. Only the three species of *Hollardia* among the hollardiins and *Johnsonina* among the triacanthodins have some scales along the basal part of the interspinous membranes. Even when best developed, as found in *H. hollardi*, the scaly sheath is confined to the basal portions of the fin.

There are five basal pterygiophores, of which the first is the largest and bears the first two spines. The first pterygiophore has well-developed anterior and posterior flanges and a strong columnar central shaft that reaches to what is apparently a concavity on the lower posterior surface of the skull between the exoccipitals and the bifid neural spine of the first vertebra. The second pterygiophore is similar to the first except shorter, narrower, and with a posteroventrally directed shaft reaching to between the neural spines of the third and fourth abdominal

vertebrae. The three remaining pterygiophores are progressively smaller and articulate in the interneural spaces of the fifth and sixth to the seventh and eighth vertebrae. No pterygiophore articulates between the neural spines of the fourth and fifth vertebrae. The last pterygiophore is oriented approximately vertically, while in all other triacanthodids the inclination of this pterygiophore is anteroventral.

SOFT DORSAL FIN.—The soft dorsal-fin base is the longest among triacanthodids (Table 3). There are 19 dorsal-fin rays (visible only in holotype), most of which are well preserved only basally. The rays bear spinules laterally, as do those of Recent triacanthodids. Two of the rays in the holotype are complete enough to measure: the fourth is 23% SL, higher than in any Recent triacanthodid (range 11.4%–20.4% SL, averages 13–19, excluding the long-snouted genera which have lesser values) or the Oligocene *Carpathospinosus* (about 16% SL), while the seventh ray is slightly shorter.

There are 13 soft dorsal-fin basal pterygiophores visible (best preserved in the holotype, especially anteriorly). The first and second are oriented approximately vertically and reach ventrally to between the neural spines of the eighth abdominal and first caudal vertebrae. The next 10 basal pterygiophores are variously displaced but overall are relatively less vertical than the first two, while the last is displaced horizontally over the neural spine of the sixth caudal vertebra in the holotype (Figure

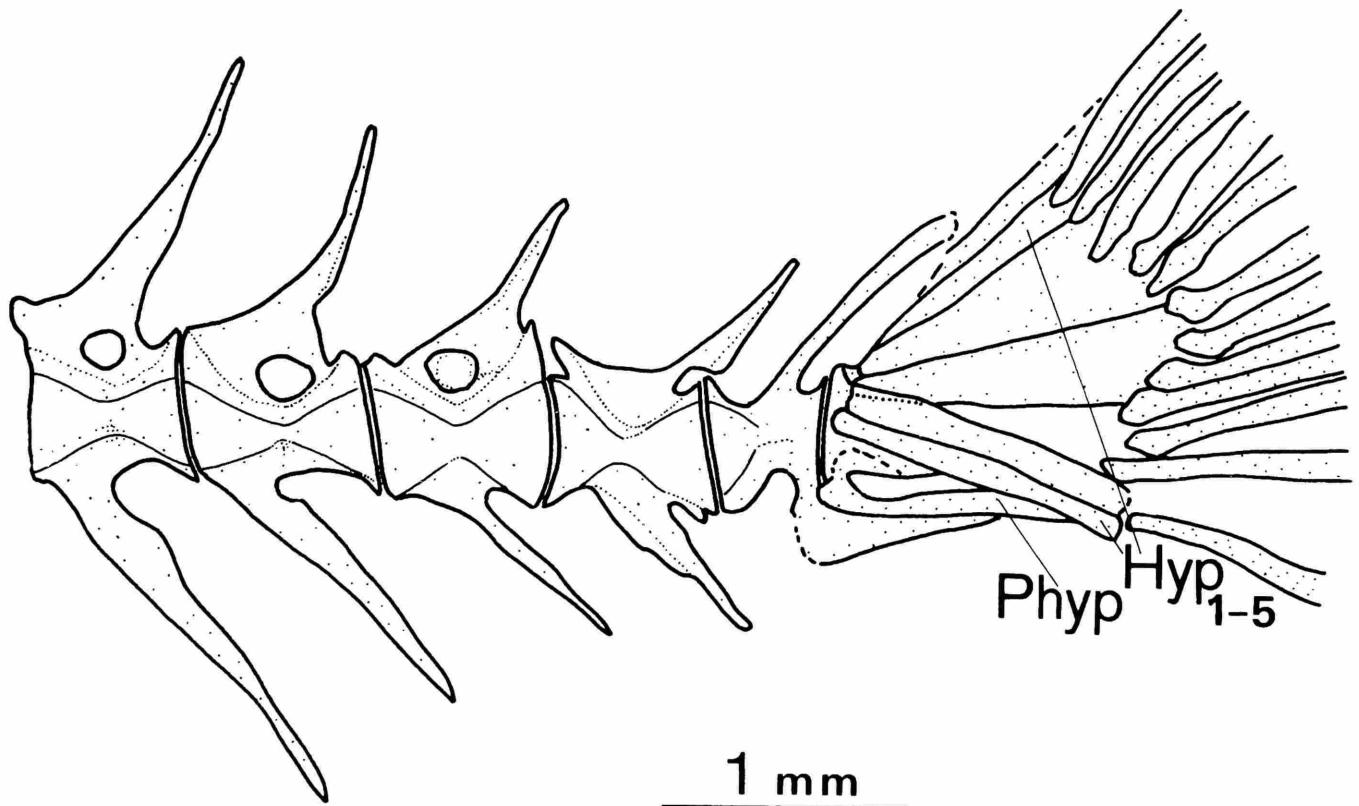


FIGURE 9.—*Prohollardia avita*, new genus and species, caudal fin and skeleton, holotype.

2). The vertical orientation of the first two pterygiophores in *Prohollardia* is unique among triacanthodids, which otherwise have all of the pterygiophores inclined anteroventrally.

ANAL FIN.—There are 15 anal-fin rays (holotype and ZPALWr. A/2098), incomplete distally (it remains to be seen whether the anal fin in *Prohollardia* is as uniquely high as the soft dorsal fin). The bases of the rays are spinulose. The first basal pterygiophore is the largest in the series. None of the basal pterygiophores has the distal region preserved and it therefore is impossible to determine whether an anteromedial flange was present, as in Recent hollardiins and in *Carpathospinosus* alone among the triacanthodids.

CAUDAL FIN AND SKELETON.—There are 12 caudal-fin rays, with only the basal parts preserved. The details of the caudal skeleton are poorly preserved but a parhypural and at least five separate hypurals are evident in the holotype (Figure 9). The element above the fifth hypural may be either a sixth hypural, an epural, or a uroneural. The third and fourth hypurals are the largest, and the first and second are displaced and partially cover the distal end of the parhypural. In the holotype the neural spine on Pu_2 is longer than that on Pu_3 .

SCALES.—Spinulose scales completely cover the head, body, spiny dorsal-fin membranes, and all but the extreme distal tips of the dorsal and pelvic spines (Figure 2).

The rounded basal plates of most of the scales in the holotype (Figure 10A–C) bear a single upright spinule, but a few have three spinules, with the central one the largest. A single spinule is present on the scale plates in the smaller specimens. There are star-like radiations around the bases of the spinules. These are typical numbers and shapes of the spinules for small specimens of triacanthodids.

Subfamily TRIACANTHODINAE Tyler (1968)

This subfamily includes 15 species in nine Recent genera from the Indo-western Pacific (8 of the 9) and western Atlantic oceans and the new Oligocene genus *Carpathospinosus* from the Polish Carpathian Mountains.

Carpathospinosus has a flat supraoccipital bearing a small crest anteromedially, the epiotics meeting medially on the dorsal surface of the skull, the epiotics separated from the frontals by the sphenotics, and a broad basin-like posterior process of the pelvis. These are diagnostic characteristics of the subfamily Triacanthodinae. Three of the defining characteristics of the triacanthodids are here hypothesized to be derived and establish the monophyly of the subfamily (see "Discussion of Subfamilial Defining Characters").

Carpathospinosus, new genus

TYPE SPECIES.—*Carpathospinosus propheticus*, new species, by monotypy and present designation.

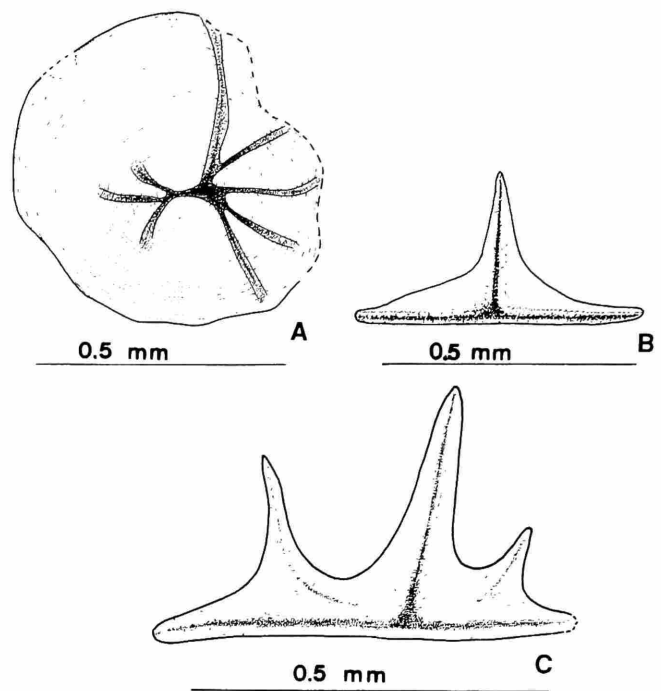


FIGURE 10.—*Prohollardia avita*, new genus and species, scales, holotype: A, basal plate in dorsoventral view; B, C, scales with one and three upright spinules in lateral view.

ETYMOLOGY.—*Carpatho*, found in the Carpathian Mountains; and the Latin *spinosus* for the large size of the first dorsal spine and for the pelvic spine; masculine.

DIAGNOSIS

Carpathospinosus differs from all other Triacanthodidae by the first dorsal spine with a longer average relative length (37% SL versus 24%–34%) and the second dorsal spine considerably shorter, with an average relative length at the low end of the range of length in other triacanthodids (15% SL versus 13%–29% SL), its length contained an average of 2.4 times in the length of the first spine (versus length of second spine contained an average of 1.1–1.4 times in length of first spine in Recent triacanthodids and 1.8 times in the Oligocene *Prohollardia*).

Carpathospinosus differs from all other Triacanthodinae by the presence of an anteromedial flange on the first basal pterygiophore of the anal fin (versus flange absent); the pelvic spine much longer than the length of the posterior process of the pelvis, the process contained about 1.5 times in the length of the spine (versus pelvic spine usually shorter but sometimes as long as or very slightly longer than the process, the process contained about 0.8 to 1.1, usually 1.0, times in the length of the spine); the head especially long, about 45% SL (versus averages of 35%–41% SL except in the two long-snouted genera). The relative width of the pelvis in *Carpathospinosus* is

greater than in any other triacanthodin except the Recent *Bathyphylax*.

Carpathospinosus propheticus, new species

FIGURES 11-19; TABLE 2

MATERIAL.—Holotype, ZPALWr.A/3000, an almost complete specimen in part and counterpart, with only the anterior part of the lower jaw missing, 33.4 mm SL. Nine paratypes, ZPALWr.A/3001–A/3009, about 12.0–33.0 mm SL, less complete and less well preserved than the holotype, all in part and counterpart (some fragmentary): ZPALWr. A/3001, about 25.0 mm SL, incomplete; ZPALWr. A/3002, about 29.0 mm SL, without anterior part of spiny dorsal fin; ZPALWr. A/3003, about 16.0 mm SL, without caudal fin; ZPALWr. A/3004, about 25.0 mm SL, without anterior part of head and first dorsal spine; ZPALWr. A/3005, about 30.0 mm SL, part of postcranial skeleton without dorsal and caudal fins; ZPALWr. A/3006, about 25.0 mm SL, without anterior part of head and posterior end of body; ZPALWr. A/3007, about 12.0 mm SL, parts of head, vertebral column, and spiny dorsal fin; ZPALWr. A/3008, 33.0 mm SL, mostly isolated bones; ZPALWr. A/3009, about 18.0 mm SL, nearly complete.

There are 10 other highly fragmentary or poorly preserved specimens from the same formation of what are probably *Carpathospinosus* but since we cannot be absolutely certain of their specific identity we do not designate them as paratypes.

All but one of the specimens are impressions in siliceous-argillaceous shales; the exception is ZPALWr. A/3002, which is in laminated limestones as partially preserved bones, spines, and fin rays in both plates.

TYPE HORIZON.—Upper Oligocene, zone IPM 4 of the Menilite Beds.

TYPE LOCALITY.—Przysietnica, northwest of Sanok, Krosno Province, the Carpathians, southeast Poland (49°44'N, 22°03'E).

DIAGNOSIS.—As for the genus.

ETYMOLOGY.—From the Greek *prophetes*, in allusion to the first known occurrence of the wide basin-like posterior process of the pelvis that is characteristic of the triacanthodin lineage of triacanthodid evolution; masculine.

DESCRIPTION

Judging from the sizes of the various life history stages of the Recent species of the family, the holotype (Figures 11, 12) is

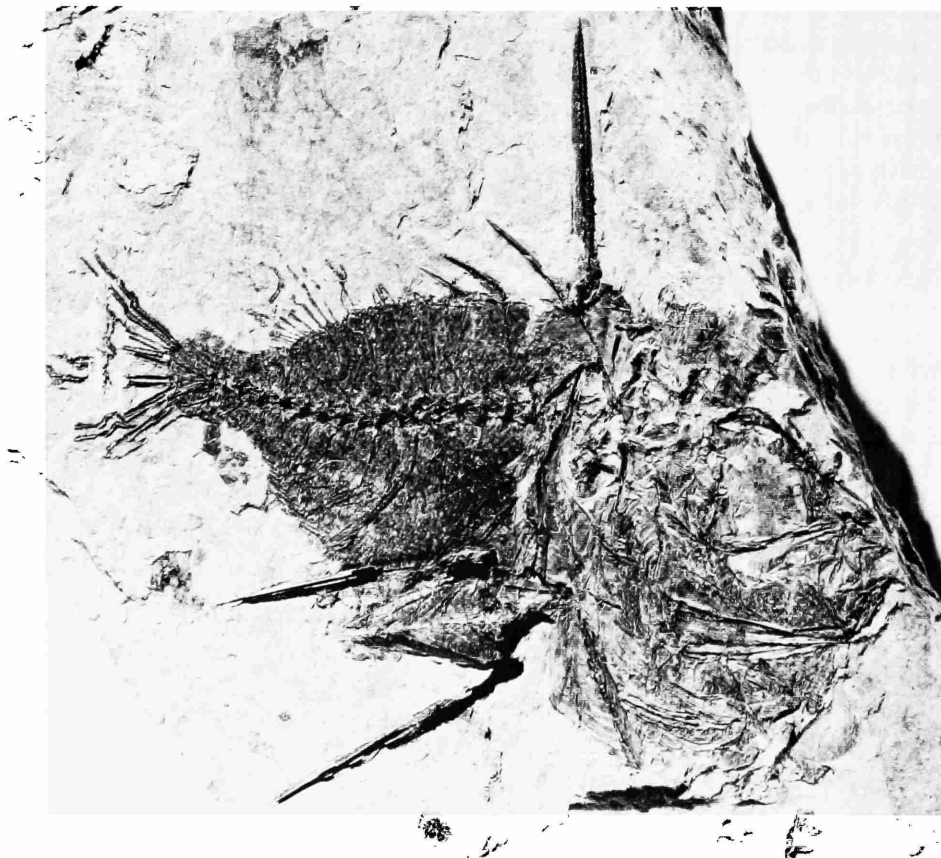


FIGURE 11.—*Carpathospinosus propheticus*, new genus and species, photograph of holotype, ZPALWr. A/3000, 33.4 mm SL, Menilite Beds, IPM 4, Przysietnica, southern Poland, Carpathian Mountains, Upper Oligocene.

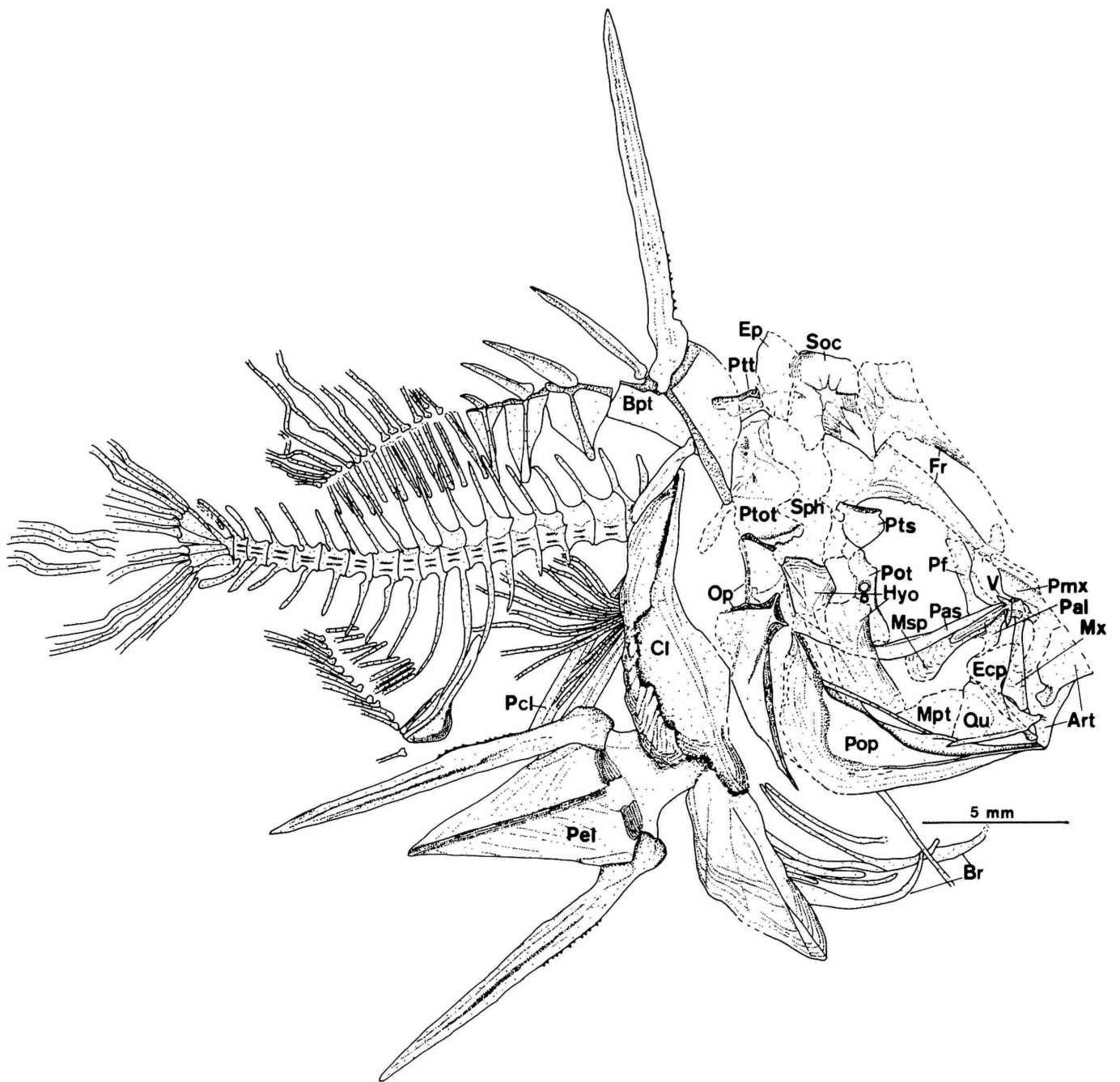


FIGURE 12.—*Carpathospinosus propheticus*, new genus and species, reconstruction based on holotype.

probably a young adult and the seven larger paratypes are probably juveniles. The three smallest paratypes, ZPALWr. A/3007, ZPALWr. A/3003, and ZPALWr. A/3009, respectively about 12, 16, and 18 mm SL, could be postlarvae or recently settled juveniles. Measurements for two of the specimens are given in Table 2.

The maximum depth of the body is 50.0% SL in the holotype, the only specimen in which it can be accurately measured, comparable to that in small specimens of several

other triacanthodins (e.g., *Triacanthodes* and *Johnsonina*, see Tyler, 1968:126, figs. 152, 166).

HEAD.—The head (Figure 13) is relatively long, 45.5% SL in the holotype, the only specimen in which it can be accurately measured. The Oligocene hollardiin *Prohollardia* has a longer head (average 49.5% SL) than *Carpathospinosus* but among Recent triacanthodins with typical heads (i.e., excluding the two genera with elongate snouts) the head length averages 35%–41% SL. In triacanthodids the head is proportionally

TABLE 2.—Measurements of *Carpathospinosus propheticus*, new genus and species.

Character	Holotype		Paratype	
	ZPALWr. A/3000 mm	%SL	ZPALWr. A/3001 mm	%SL
Standard length	33.4		25.0*	
Head length	15.2	45.5	—	
Body depth	16.7	50.0	—	
Predorsal length	17.5	52.3	12.5	50.0*
First dorsal spine	13.0	38.9	8.7	34.8*
Second dorsal spine	5.3	15.8	3.7	14.8*
Third dorsal spine	3.6	10.7	—	—
Pelvic spine	13.0	38.9	—	—
Pelvis width	4.4	13.1	—	—
Pelvis length	8.5	25.4	—	—
Spiny-dorsal base	9.0	26.9	—	—
Soft-dorsal base	5.1	15.2	—	—
Anal base	5.0	14.9	—	—

*Value is approximate.

longest in juveniles and the greatest lengths recorded for those with typical snouts are 44.7% SL in both a 23.7 mm SL specimen of the hollardiin *Hollardia hollardi* and a 18.1 mm SL specimen of the triacanthodin *Johnsonina eriomma*. Because the holotype of *Carpathospinosus* is relatively small and has an only marginally longer head than in these two small specimens of other triacanthodids, we do not consider this difference significant.

The supraoccipital is flat and bears a small crest anteromedially, as seen in dorsal view on the holotype (Figure 13) and ZPALWr. A/3001. The epiotics meet medially on the dorsal surface of the skull and are separated anteriorly from the frontals by the sphenotics. The well-preserved prootic in the holotype is displaced slightly into the orbit, and bears two neural foramina of the trigemino-facialis chamber. The long frontals are wide posteriorly and taper to points anteriorly. Only the straight middle part of the parasphenoid in the lower region of the orbit is preserved. There is a faint trace of the prefrontal at the front of the orbit.

The jaws are typical for triacanthodids, with the L-shaped premaxilla having a long ascending process (best seen in ZPALWr. A/3009). The lower jaw is much deeper posteriorly than anteriorly and has a slightly concave ventral edge. There are at least 12 and perhaps a few more small conical teeth to each side of the upper and lower jaws (best seen in ZPALWr. A/3009).

None of the specimens have the upper and lower jaws well-enough preserved and appropriately exposed for it to be determined whether inner series teeth were present.

The hyomandibula is only exposed in the holotype, and only as two large fragments, the dorsal head from the left side and the ventral shaft from the right side. The dorsal head may be slightly displaced anteriorly because it appears to articulate mainly with the sphenotic rather than about equally with the

pteroitic and sphenotic. The piece representing the ventral shaft of the hyomandibula is oriented obliquely but displaced significantly anteriorly. It is impossible to determine whether the hyomandibula in its natural position had an oblique orientation as in all Recent triacanthodids, but we have no reason to believe that it was oriented vertically as in *Prohollardia*.

The opercle is triangular and it and the anterior part of the subopercle bear a series of ridges and furrows parallel to their margins (best seen in ZPALWr. A/3004). The long preopercle (Figure 14) is bent slightly more than 90°; on the isolated preopercle of ZPALWr. A/3008 a large lamina dorsalis is visible. The ceratohyal and the branchiostegal rays are not well preserved.

VERTEBRAL COLUMN.—There are eight abdominal and 12 caudal vertebrae (Figure 12). In ZPALWr. A/3006 the first abdominal vertebra is displaced and exposed in posterior view (Figure 15). The right and left halves of its neural spine are separate, without a roof over the neural canal. This bifid neural arch and spine presumably attached to the rear of the skull and enclosed the ventral shaft of the first basal pterygiophore of the spiny dorsal fin, as in all other triacanthodids. The remaining neural spines are fused in the midline and inclined posterodorsally. Wide parapophyses and enlarged bases of the neural spines on the last three abdominal vertebrae are apparent in ZPALWr. A/3007 and, to a lesser extent, ZPALWr. A/3006. Traces of epipleurals are preserved in the latter specimen. Haemal arches and spines are well developed on the caudal vertebrae, with those on Pu₂ being longer and stronger than the others in the caudal peduncle. The caudal skeleton is described below.

PECTORAL FIN AND GIRDLE.—The large cleithrum is expanded posteroventrally, bluntly rounded anteriorly, and tapered to a point dorsally (Figure 16). Like the opercular bones, the cleithrum bears a series of fine ridges and furrows parallel to its edges and has an anterior crest along its midportion. The narrow supracleithrum is placed distinctly obliquely to the axis of the skull. The postcleithra are represented by only the poorly preserved right and left halves of the ventral postcleithrum. Traces of 14 pectoral-fin rays and of three actinosts are visible in ZPALWr. A/3002.

PELVIC FIN AND GIRDLE.—The halves of the basin-like posterior process of the pelvis have a flat ventral expanse with upturned lateral edges; their medial edges are in close contact but unfused in the midline (Figure 17). The process can be measured only in the holotype. It is exceptionally wide, its width contained 1.9 times in its length. In all other triacanthodins except the genus *Bathyphylax* the process is substantially narrower, with width into length averages in the species with typical snouts of 2.8 to 5.2. In the two species of *Bathyphylax* the process is as wide as in *Carpathospinosus*, having average width into length ratios of 1.9 and 2.3. In the two long-snouted genera of triacanthodins the process is narrow (average ratios of 4.2 to 6.1).

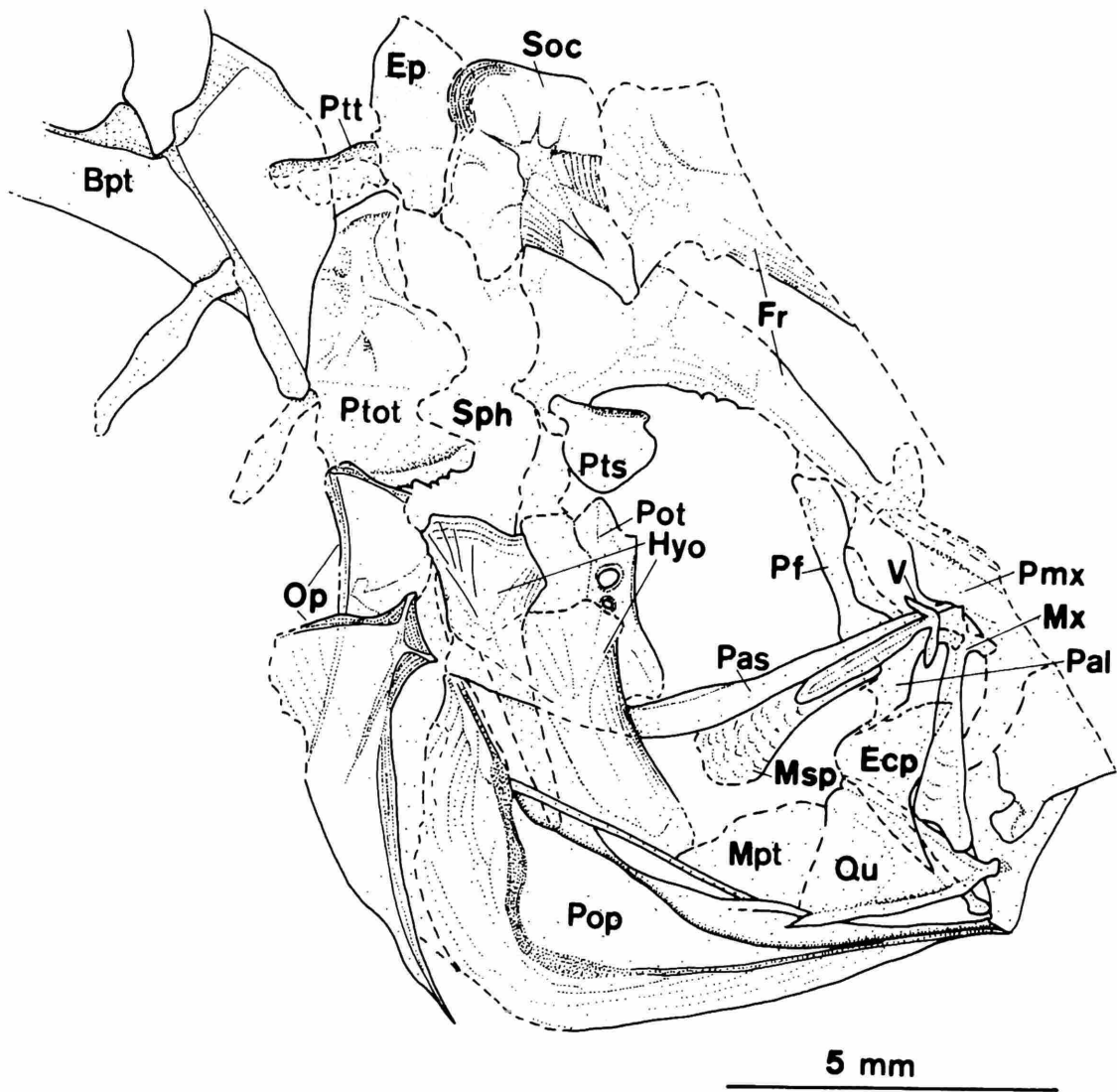


FIGURE 13.—*Carpathospinosus propheticus*, new genus and species, reconstruction of lateral view of skull of holotype.

The pelvic fin consists of a long strong spine, the basal one-half to two-thirds of which is covered with spinulose scales. There is no evidence of fin rays. The length of the spine (only fully preserved in the holotype) is much greater, about 1.5 times, than that of the relatively short posterior process of the pelvis. In all Recent triacanthodids the pelvic spine is approximately the same length as the process, with average ratios of 0.8 to 1.1, and usually 1.0. The Oligocene *hollardi* *Prohollardia*, with a moderate pelvic spine length but a short process, has a process into spine ratio of 1.3–1.4, intermediate between that of Recent triacanthodids and *Carpathospinosus*. However, we doubt that the situation in *Carpathospinosus*, with a basin-like process and exceptionally long pelvic spines, is comparable to that in *Prohollardia*, with a shaft-like process

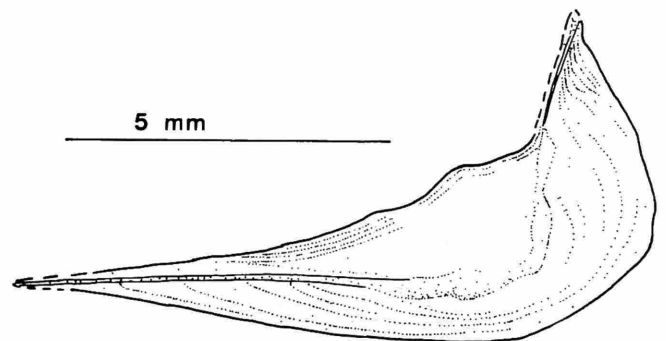


FIGURE 14.—*Carpathospinosus propheticus*, new genus and species, isolated preopercle in lateral view, paratype ZPALWr. A/3008, 33.0 mm SL (same locality as holotype, see Figure 11).

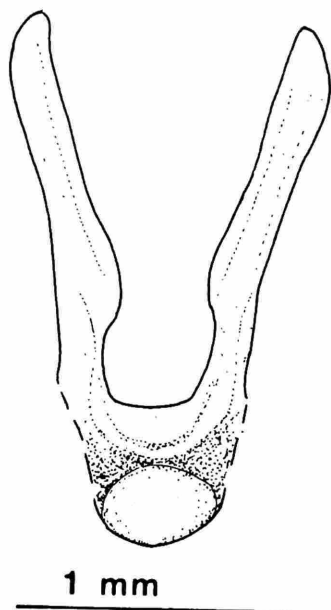


FIGURE 15.—*Carpathospinosus propheticus*, new genus and species, isolated first abdominal vertebra in posterior view, paratype ZPALWr. A/3006, about 25.0 mm SL (same locality as holotype, see Figure 11).

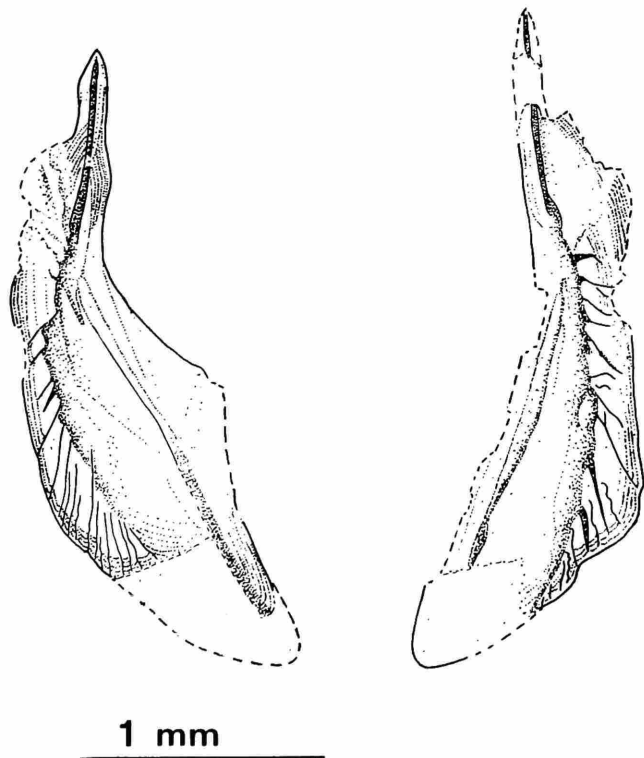


FIGURE 16.—*Carpathospinosus propheticus*, new genus and species, left and right cleithra in lateral view, holotype.

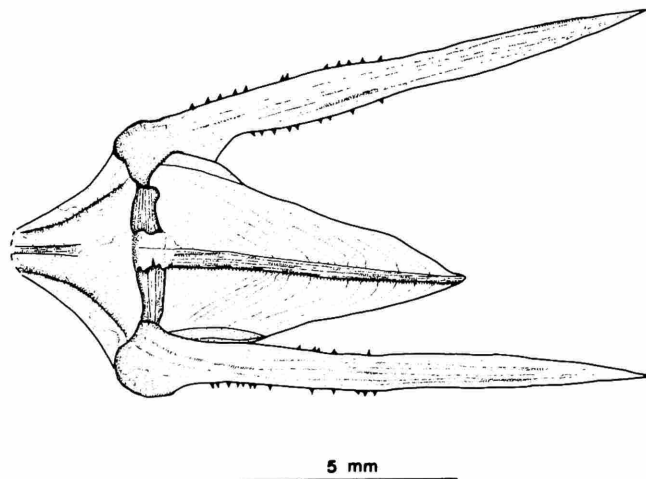


FIGURE 17.—*Carpathospinosus propheticus*, new genus and species, pelvis and pelvic fin in ventral view, holotype.

of highly variable length and more typical pelvic spine relative length.

SPINY DORSAL FIN.—The spiny dorsal-fin base is much longer than the soft dorsal-fin base, typical of all other triacanthodids except the Oligocene hollardiin *Prohollardia*, which has a shorter spiny dorsal-fin base. The origin of the spiny dorsal fin is distinctly behind the vertical through the posterior margin of the gill opening. Five dorsal spines are visible on the holotype, with a sixth probably present based on faint traces of a basal pterygiophore (sequentially fifth) that would have supported it (Figure 12). When depressed the long first spine (Table 2) would have reached approximately to the vertical through the base of the eleventh soft dorsal-fin ray, far more posteriorly than in any other triacanthodid. The first spine has longitudinal grooves and spinulose scales (bearing a single upright process) that cover the basal one-third to one-half of its length.

The first spine is much longer (38.9% and 34.8% SL, average 36.9, holotype and ZPALWr. A/3001, respectively) than the second spine (15.8% and 14.8% SL, average 15.3), with the length of the second spine contained an average of 2.4 times in the length of the first spine (Table 3). In Recent triacanthodids the second spine is only slightly shorter than the first. Average values for all species with typical heads are 20.9%–33.8% SL for the first spine, 15.4%–28.8% SL for the second spine (the long-snouted genera have lesser values), and 1.1–1.4 for the second spine into the first. In the Oligocene *Prohollardia* the length of the first spine is at the low end of the range of values in most other triacanthodids of comparable size, while the length of the second spine is slightly less than in other species. The ratio of the length of the second spine into that of the first in *Prohollardia* is 1.8, intermediate between that of *Carpathospinosus* and Recent triacanthodids, just as is the case with the pelvic process into pelvic spine ratio. In neither case,

however, are the intermediacy of these values in *Prohollardia* achieved in a comparable manner to those in *Carpathospinosus*.

The second to fifth (and presumably sixth) dorsal spines in *Carpathospinosus* decrease gradually in length posteriorly. The spiny dorsal-fin membrane is scaleless, except for a single series of scales along its base that is continuous with those of the body.

The five basal pterygiophores of the spiny dorsal fin decrease gradually in anteroposterior width posteriorly. The first basal pterygiophore bears the first two spines. It is inclined anteroventrally, extends between the bifid neural spine of the first vertebra, and articulates closely with the rear of the skull. The second pterygiophore is oriented slightly anteroventrally in the space between and above the neural spines of the third and fourth vertebrae, while the space between the neural spines of the fourth and fifth vertebrae is vacant. The third and fourth pterygiophores are oriented, respectively, vertically and slightly anteroventrally and insert between the neural spines of the fifth and sixth and sixth and seventh vertebrae. The narrow anteroventrally inclined fifth pterygiophore inserts between the neural spines of the seventh and eighth vertebrae.

SOFT DORSAL FIN.—There are about 15 dorsal-fin rays, which are only well preserved basally. Traces of the distal regions of some of the rays in the holotype indicate that the greatest fin height was about 16% SL, like other triacanthodids except the Oligocene *Prohollardia*, in which the fin is much higher. All of the basal pterygiophores of the soft dorsal fin are narrow and inclined anteroventrally.

ANAL FIN.—The basal regions of 12 fin rays are visible but the distal regions are essentially absent. The first basal pterygiophore is the largest, and bears a prominent anteromedial crest or flange along most of the ventral half of its length. Such a flange is absent in Recent triacanthodins but present in Recent hollardiins (condition unknown in the Oligocene *Prohollardia*).

CAUDAL FIN AND SKELETON.—There are 12 caudal-fin rays, which are only well preserved basally. The caudal skeleton (Figure 18) is poorly preserved, especially dorsally where only one, incomplete, epural is visible. In the holotype the neural spine of Pu_2 is longer than that of Pu_3 (Figure 12). Five separate hypurals are evident, with the uppermost rod-like and the fourth the deepest. The parhypural is autogenous.

SCALES.—Spinulose scales completely cover the head, body, and distal one-half to two-thirds of the first dorsal and pelvic spines. Each of the rounded basal plates has a single upright spinule from whose base there are star-like radiations (Figure 19).

Other Relevant Fossil Taxa

The status of fossils previously referred to the triacanthodids and triacanthids needs to be clarified to assist the discussion of the placement of the two new Oligocene genera. In his phenetic

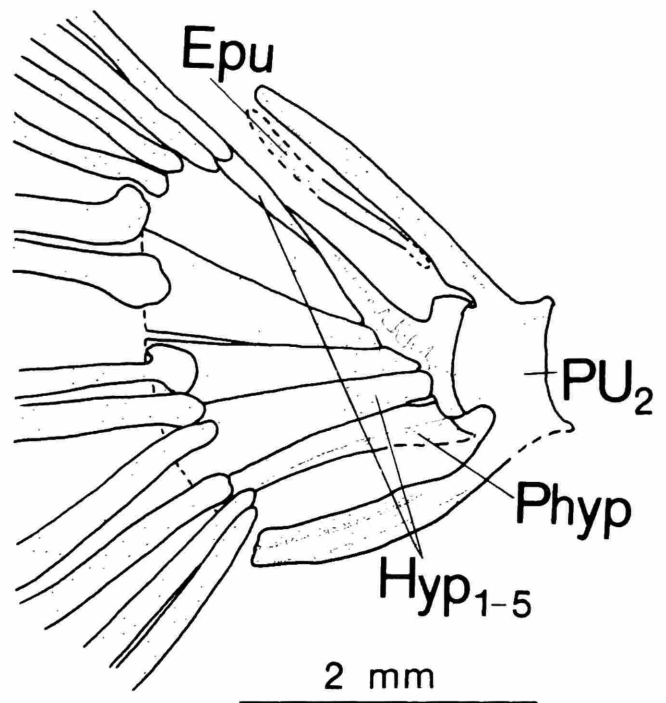


FIGURE 18.—*Carpathospinosus propheticus*, new genus and species, caudal fin and skeleton, holotype.

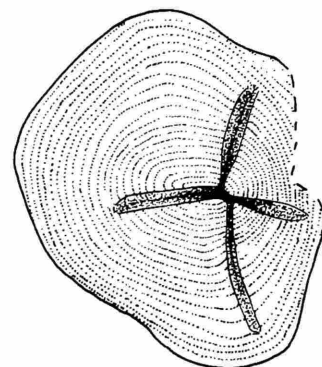


FIGURE 19.—*Carpathospinosus propheticus*, new genus and species, basal plate of scale in dorsolateral view, holotype.

or evolutionary classification (i.e., non-cladistic) of the triacanthoids and other tetraodontiforms, Tyler (1980) placed the Eocene *Eoplectus* and *Zignoichthys* as one subfamily (Eoplectinae) and the Eocene *Spinacanthus* and *Protobalistum* as another subfamily (Spinacanthinae) of the triacanthodids along with the Recent hollardiins and triacanthodins.

Eoplectus and *Zignoichthys* were referred to the triacanthodids by Tyler (1973, 1980) because of their overall general similarity to that family based on the presence of what are now

recognized to be numerous plesiomorphic features such as well-developed spiny dorsal and pelvic fins (condition of these uncertain in *Zignoichthys*). Tyler emphasized that *Eoplectus* and *Zignoichthys* represented the ancestral line of tetraodontoids because both genera possess the single most impressive specialized feature of tetraodontoids, the complex and innovative incorporation of the individual tooth elements into the jaw bones of a crushing beak. In Winterbottom's (1974) cladistic analysis of tetraodontiform relationships *Eoplectus* and *Zignoichthys* were removed from the triacanthodids and recognized (we believe correctly) as distinct families of tetraodontoids, with the Eoplectidae as the sister group of all other tetraodontoids and the Zignoichthyidae as the sister group at the next higher node on the cladogram (on the presumption that the spiny dorsal fin and pelvis were of reduced size in *Zignoichthys*).

Spinacanthus and *Protobalistum* were referred by Tyler (1968, 1980) to the triacanthodids mostly on the basis of the enormous spiny dorsal fin and short-based soft dorsal and anal fins. Winterbottom (1974) interpreted the presence of the spiny dorsal fin and the short-based soft fins in these two genera as plesiomorphic features and removed them from the triacanthodids. He placed them as the Spinacanthidae among the balistoids because of the proposed derived nature of an elongate ethmoid region, small eye high in the head, and forward position of the spiny dorsal-fin origin. The spinacanthids (both genera based on single specimens) are known almost exclusively on the basis of external features, with the condition of the pelvis and pelvic fin unknown. Until more specimens of these two genera with some of their osteology exposed become available, we accept their placement among the balistoids on the basis of the few derived external features of similarity between the groups. The poorly resolved familial relationships of spinacanthids are discussed by Tyler and Bannikov (1992) in relation to the enigmatic Eocene balistoid *Eospinus*.

The Oligocene *Cryptobalistes* is poorly known (the single species based on three impressions, a holotype in counterpart and a single plate paratype). The general external countenance and osteological features are in many ways intermediate between triacanthids and balistids. For these reasons they were placed by Tyler (1968, 1980) as a subfamily (Cryptobalistinae) of the triacanthids. Winterbottom (1974), however, pointed out that one clearly apomorphic feature of *Cryptobalistes* was its basin-like pelvis, similar to that of triacanthodins. Therefore, he removed *Cryptobalistes* from the triacanthids and placed it questionably as a subfamily of the triacanthodids. A more definitive phylogenetic placement of *Cryptobalistes* awaits additional specimens with well-exposed internal characters.

The better-preserved holotypic counterpart plate on which most of the original description and illustrations of *Cryptobalistes* are based cannot be located despite many efforts by Winterbottom (1974:96), Tyler (1980:98), and us more recently. It was probably destroyed during World War II after having been transferred from Bonn to the Cologne Natural

History Museum. Hans-Dieter Sues (pers. comm.) searched the Bonn collections for us and found two single plates of the species, both faint impressions, one of which may be the paratype, and the other probably not a type specimen. Dr. Sues prepared the latter specimen for us by powered glass air abrasion but it does not show any of the critically important osteological features (e.g., the shapes of the pelvis and supraoccipital) that would permit us to resolve its relationships. Thus, *Cryptobalistes* as presently known cannot shed light on the analysis of the relationships of the two new Oligocene genera of triacanthodids.

The earliest known tetraodontiform, *Plectocretacicus* (Sorbini, 1979), from the upper Cretaceous of Lebanon, has not yet had its familial relationship thoroughly analyzed but it was tentatively placed among the aracanid-ostraciid clade of balistoids and its relationships do not seem to be germane to the present work.

DISCUSSION OF SUBFAMILIAL DEFINING CHARACTERS

The description of a new Oligocene genus in each of the two subfamilies of triacanthodids that otherwise consist of Recent species calls for the determination of which of the five major differential features that have been used (Tyler, 1968, 1980) to phenetically define the subfamilies are primitive versus derived. Establishment of the polarity of the shaft-like versus basin-like posterior process of the pelvis, the meeting of the epiotics medially on the dorsal surface of the skull versus their being excluded from the dorsal surface by the supraoccipital, the articulation anteriorly of the epiotics with the frontals versus the sphenotics, the dome-shaped versus flat supraoccipital, and the presence versus absence of an anteromedial flange on the first basal pterygiophore of the anal fin is critical to an understanding not only of the phylogeny of the triacanthodids but also of the triacanthids that together form the sistergroup of all other tetraodontiforms.

To polarize these features we accept the Triacanthodidae (and its two subfamilies, the Hollardiinae and Triacanthodinae) as the sistergroup of the Triacanthidae, those two families (the triacanthoids) as the sistergroup of all other Tetraodontiformes (the balistoids and tetraodontoids) as proposed in the ordinal phylogeny of Winterbottom (1974, but recognizing the familial systematic levels of Tyler, 1980). We likewise accept the Zeiformes (excluding caproids) as the extraordinary outgroup for the Tetraodontiformes (Rosen, 1984).

Thus, in our analyses of relationships we treat hollardiins and triacanthodins as sistergroups for which triacanthids are the first outgroup (1 o.g.). All other tetraodontiforms are the sister group of the triacanthoids and therefore the second outgroup (2 o.g.). However, because the balistoid and tetraodontoid lineages among the second outgroup are so anatomically distinctive, we frequently discuss the conditions in balistoids (balistids and monacanthids, and their sister group composed of aracanids and ostraciids) separately (as 2a o.g.) from those of tetraodontoids (as 2b o.g., the clade based on the anatomically

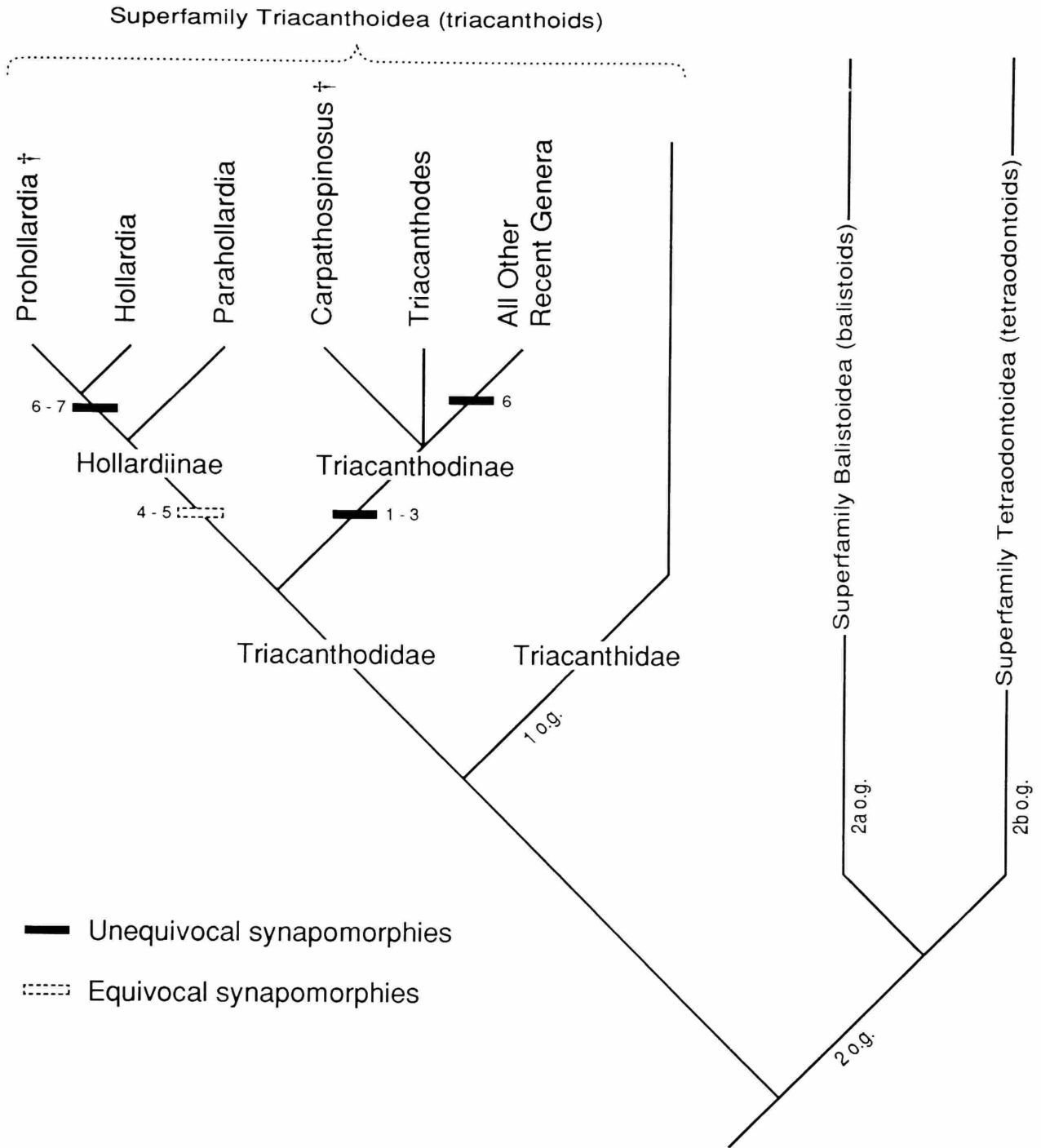


FIGURE 20.—Cladogram of relationships of the two new Oligocene genera of Triacanthodidae (relationships of other families based largely on Winterbottom, 1974). Unequivocal synapomorphies are: 1, posterior process of pelvis basin-like; 2, epiotics meeting medially on dorsal surface of skull; 3, epiotics separated from frontals by sphenotics; 6, inner series teeth absent; 7, scales present on spiny dorsal-fin membranes. Equivocal synapomorphies are: 4, supraoccipital dome-like; 5, first anal-fin basal pterygiophore flange present. See text for discussion of each of these features used to establish relationships of the fossils within the family.

generalized Eocene eoplectids, which also includes triodontids, zignoichthyids, tetraodontids, diodontids, and molids). These relationships are summarized in Figure 20.

In the following analysis it is necessary to keep in mind the distinction between the names of the triacanthodids (Triacanthodidae) and its subfamilies, the triacanthodins (Triacantho-

TABLE 3.—Major differences and similarities of *Prohollardia*, *Carpathospinosus*, the Recent Hollardiinae, and the Recent Triacanthodinae with typical snout lengths (i.e., excluding the two genera with extremely elongate tubular snouts, *Macrorhamphosodes* and *Halimochirurgus*); data for Recent species from Tyler (1968).

Character	<i>Prohollardia</i>	Recent Hollardiinae	<i>Carpathospinosus</i>	Recent Triacanthodinae with typical snouts
Shape of posterior process of pelvis	shaft-like	shaft-like	basin-like	basin-like
Relationship of epiotics to one another	do not meet one another medially on dorsal surface of skull, separated by supraoccipital	do not meet one another medially on dorsal surface of skull, separated by supraoccipital	meet one another medially on dorsal surface of skull, not separated there by supraoccipital	meet one another medially on dorsal surface of skull, not separated there by supraoccipital
Relationship of epiotics to frontals	articulate anteriorly with frontals	articulate anteriorly with frontals	separated from frontals by sphenotics	separated from frontals by sphenotics
Shape of supraoccipital	dome-like	dome-like	broad and flat, with medial crest	broad and flat, with medial crest
Anteromedial flange on distal region of first anal-fin basal pterygiophore	unknown	present	present	absent
Teeth internal to major outer series	absent	present (<i>Parahollardia</i>) or absent (<i>Hollardia</i>)	unknown	present (<i>Triacanthodes</i>) or absent (all other genera)
Scales on spiny dorsal-fin membranes	many, with extensive coverage	some to many, with moderate coverage (<i>Hollardia</i>) or absent (<i>Parahollardia</i>)	absent	absent (except some in <i>Johnsonina</i>)
Origin of spiny dorsal fin in relation to gill opening	distinctly in front	over or slightly in front (<i>Parahollardia</i>) or distinctly behind (<i>Hollardia</i>)	distinctly behind	usually over, sometimes slightly behind, but distinctly in front in <i>Mephisto</i>
Inclination of last basal pterygiophore of spiny dorsal fin	vertically	anteroventrally	anteroventrally	anteroventrally
Inclination of basal pterygiophores of soft dorsal fin	first two vertically	all anteroventrally	all anteroventrally	all anteroventrally
Enlarged scale plate with spine over eye	present	absent	absent	absent
Inclination of hyomandibular	almost vertical	oblique	probably oblique	oblique
Coverage of first dorsal-fin and pelvic spines with spinulose scales	only extreme distal tip naked	distal $1/10$ to only extreme distal tip naked	distal $2/3-1/2$ naked	distal $1/2-1/10$ naked
Length of spiny dorsal-fin base relative to soft dorsal-fin base	slightly shorter	longer than	longer than	longer than
First dorsal-fin spine when un-erected reaching posteriorly to:	slightly beyond soft dorsal-fin origin to level of about third ray	in front of or to origin or slightly beyond origin of soft dorsal fin (to level of about second or third ray)	well beyond soft dorsal-fin origin to level of about eleventh ray	in front of or to origin, or moderately beyond origin of soft dorsal fin (to level of about third or fourth ray)
Number of dorsal-fin rays	19	15-18 (\bar{x} = 16-17)	15	13-16 (\bar{x} = 14-16)
Number of anal-fin rays	15	13-16 (\bar{x} = 14-15)	12	11-14 (\bar{x} = 12-14)
Head length as % SL	48.0%-52.4% (\bar{x} = 49.5)	33.7%-44.7% (\bar{x} = 38-40)	45.5%	33.1%-44.7% (\bar{x} = 35-41)
Body depth as % SL	70.0%-72.0% (\bar{x} = 71.2)	40.0%-73.4% (\bar{x} = 51-66)	50.0%	28.9%-66.8% (\bar{x} = 31-53)

TABLE 3.—Continued.

Character	<i>Prohollardia</i>	Recent Hollardiinae	<i>Carpathospinosus</i>	Recent Triacanthodinae with typical snouts
Predorsal length as % SL	55.7%–60.0% (\bar{x} = 57.5)	44.9%–65.1% (\bar{x} = 46–59)	50.0%–52.3% (\bar{x} = 51.2)	33.7%–54.1% (\bar{x} = 36–48)
Length of first dorsal spine as % SL	20.7%–28.1% (\bar{x} = 24.4)	17.2%–37.9% (\bar{x} = 24–32)	34.8%–38.9% (\bar{x} = 36.9)	18.6%–37.3% (\bar{x} = 21–34)
Length of second dorsal spine as % SL	13.0%–14.1% (\bar{x} = 13.4)	12.9%–33.6% (\bar{x} = 18–29)	14.8%–15.8% (\bar{x} = 15.3)	13.1%–31.5% (\bar{x} = 15–29)
Length of second dorsal spine into that of first dorsal spine	1.6–2.0× (\bar{x} = 1.8)	1.0–1.3× (\bar{x} = 1.1–1.3)	2.4–2.5× (\bar{x} = 2.4)	1.0–1.4× (\bar{x} = 1.2–1.4)
Soft dorsal-fin height as % SL	23.0%	12.1%–20.4% (\bar{x} = 14–18)	~16%	11.4%–19.8% (\bar{x} = 13–19)
Spiny dorsal-fin base as % SL	19.2%–23.6% (\bar{x} = 21.4)	27%–30%	26.9%	26%–32%
Soft dorsal-fin base as % SL	23.0%–26.1% (\bar{x} = 24.6)	18%–22%	15.2%	16%–21%
Spiny dorsal-fin base in relation to soft dorsal-fin base	shorter by 2.5%–3.8% SL (\bar{x} = 3.2%)	longer by 5%–12% SL	longer by 11.7% SL	longer by 10%–14% SL
Length of posterior process of pelvis as % SL	14.5%–21.4% (\bar{x} = 18.0)	16.3%–32.2% (\bar{x} = 24–30)	25.4%	21.7%–39.4% (\bar{x} = 28–34)
Width of posterior process of pelvis as % SL	6.7%	2.6%–8.4% (\bar{x} = 4–6)	13.1%	5.3%–17.8% (\bar{x} = 6–18)
Posterior process of pelvis width into length	3.2×	3.2–9.3× (\bar{x} = 4–7)	1.9×	1.9–5.8× (\bar{x} = 2–5)
Length of pelvic spine as % SL	19.0%–30.1% (\bar{x} = 24.6)	14.7%–34.3% (\bar{x} = 23–30)	38.9%	18.8%–42.4% (\bar{x} = 25–36)
Length of posterior process of pelvis into length of pelvic spine	1.3–1.4× (\bar{x} = 1.4)	0.9–1.0× (\bar{x} = 1.0)	1.5×	0.8–1.1× (\bar{x} = 1.0)

dinae) and hollardiins (Hollardiinae), and the triacanthids (Triacanthidae).

PELVIS (*Character 1*).—The posterior process is shaft-like in hollardiins, with the halves from either side closely articulated or fully consolidated with one another along their medial edges to form a stout rod, flattish to slightly concave dorsally and rounded to ridged (U- to V-shaped in cross-section) ventrally. In triacanthodins the two halves of the process are dorsoventrally flattened, situated in the horizontal plane, and articulated with one another medially, while their lateral portions are upturned, thus forming a broad basin of varying widths (for widths see section on “Relationships of *Carpathospinosus* in Triacanthodinae” and Table 3).

In triacanthids (1 o.g.) the process is a sturdy shaft, with the two halves fused or extensively sutured together to form a solid bone like a railroad rail in cross-section, in what we interpret as a more solidified version of the shaft-like process of hollardiins.

In balistoids (2a o.g.) the entire pelvis usually (i.e., in all but a few highly specialized monacanthids in which the pelvis is secondarily somewhat reduced; pelvis absent in aracanids and

ostraciids) is a long strong shaft in which the two halves are indistinguishably fused together in the midline. The balistoid condition differs from that of hollardiins and triacanthids mainly in having rudimentary pelvic spine elements at its posterior end rather than large spines with a locking mechanism midway along its length. The balistoid pelvis has some additional specializations, including a posterodorsal lobe and concave anterolateral surfaces associated with the rotation of the pelvis around its cleithral attachment which permits balistoids to flare a dewlap between the end of the pelvis and the anus.

In tetraodontoids (2b o.g.) a pelvis is present only in the two most morphologically primitive families. In the Eocene eoplectids there is a pelvic fin but the structure of the pelvis is unknown. In triodontids there is a pelvis but no pelvic fin. The posterior half of the pelvis is shaft-like, with the two halves closely articulated to one another medially and, in larger specimens, partially fused. The ascending process is deeply concave to accommodate the muscles that rotate the pelvis in flaring a huge dewlap of abdominal skin (comparable to that of balistoids).

Because the posterior process is basin-like only in triacanthodins and shaft-like in its sistergroup (hollardiins) and in all of the tetraodontiform outgroups, it is hypothesized that the shaft-like condition is plesiomorphic and that the basin-like condition is a synapomorphy of triacanthodins.

It is noteworthy that some zeids among the zeiform extraordinary outgroup have a pelvis with a posterior process comparable to the shaft-like plesiomorphic condition of the bone in tetraodontiforms. In *Zeus* and *Zenopsis* each half of the pelvis has a sturdy shaft-like process which is rounded in cross-section and slightly separated from its opposite member along the midline of the belly. The average length of the process is 11% SL in *Zeus faber* (including the Oligocene specimen illustrated by Świdnicki, 1986:111, fig. 1) and 16%–22% in the three examined species of *Zenopsis*. If these paired processes were closely articulated to one another in the midline the combined sturdy shaft would be similar to that of hollardiins, and, in the case of *Zenopsis*, almost as long as that in hollardiins (averages 24%–30% SL). Some other zeids (*Cyttus* and *Capromimus*) have paired processes that are more or less shaft-like while others (*Cytopsopsis* and *Stethopristes*) have processes that are short, flat, paired plates oriented obliquely dorsolaterally to ventromedially, a very different configuration than that of *Zeus* and *Zenopsis*.

In other zeiform families (parazenids, grammicollepidids, oreosomatids, and macrurocyttids) there is much variation in the shape of the posterior processes but they are basically flattened and oblique rather than shaft-like.

The tapering posterior paired processes of some zeids apparently are homoplastic to the thicker consolidated shaft-like structures in hollardiins, given the large number of derived features uniting the tetraodontiforms.

POSITION OF EPIOTICS ON DORSAL SURFACE OF SKULL (Character 2).—The epiotics do not meet medially on the dorsal surface of the skull in hollardiins, being separated there by the supraoccipital. In triacanthodins, by contrast, the medial edges of the epiotics are broadly in contact on the dorsal surface of the skull behind the supraoccipital (Tyler, 1968, fig. 4). In triacanthids, balistoids, tetraodontoids (1–2 o.g.), and the zeiform extraordinary outgroup the epiotics are separated by the supraoccipital on the dorsal surface of the skull as in hollardiins. Such separation therefore is hypothesized to be the plesiomorphic condition for tetraodontiforms. The triacanthodid condition of the epiotics meeting medially on the dorsal surface behind the supraoccipital consequently is considered derived.

EPIOTIC ANTERIOR ARTICULATION (Character 3).—In hollardiins the epiotics articulate anteriorly with the frontals while in triacanthodins the epiotics and frontals are separated by the sphenotics. In triacanthids and balistoids (1–2a o.g.) the epiotics contact the frontals. Among tetraodontoids (2b o.g.) the epiotics articulate with the frontals in the morphologically primitive triodontids and in molids and nearly all tetraodontids. However, in a few specialized tetraodontids (e.g., *Chonerhinos*,

Xenopterus, *Carinotetraodon*) and in all diodontids the epiotics are separated from the frontals by the sphenotics, somewhat comparably to the condition in triacanthodins.

In the zeiform extraordinary outgroup the epiotics are separated from the frontals by the parietals, a bone not present in tetraodontiforms. Thus, the separation of the epiotics and frontals in zeiforms by the parietals is not homologous with the condition in triacanthodins, diodontids, and some tetraodontids in which the two bones are separated by the sphenotics.

Based on outgroup comparisons the separation of the frontals and epiotics in triacanthodins is derived. A hypothesis that the condition of the epiotics articulating with the frontals is plesiomorphic for tetraodontiforms requires three steps to account for the independent acquisition of separation of the epiotic and frontal in triacanthodins, diodontids and some tetraodontids. The contrasting hypothesis of the separation of the epiotics by the sphenotics being plesiomorphic would require six steps (independent acquisition by hollardiins, triacanthids, balistids–ostraciids, triodontids, some tetraodontids, and molids) to account for the distribution of the epiotic-frontal articulation character in the majority of groups of tetraodontiforms. Likewise, epiotic articulation with the frontal is primitive for the triacanthoid clade, requiring only one step for acquisition of epiotic separation by the sphenotics (versus two if epiotic separation were hypothesized as primitive) and this is evidence of triacanthodid monophyly.

SUPRAOCCIPITAL (Character 4).—The supraoccipital in hollardiins is dome-like, without a broad flat expanse. In triacanthodins the supraoccipital is flat, with a broad flat expanse and a small crest or dome anteromedially.

In triacanthids (1 o.g.) the structure of the posterodorsal region of the skull is similar to that of hollardiins, for the supraoccipital is dome-like, without a broad flat expanse. The main difference between the dome-like structure in hollardiins and triacanthids is that the posterior surface of the dome is convex in the former and concave in the latter.

In balistoids (2a o.g.) the supraoccipital in the balistid–monacanthid clade is flat, with a high medial crest and posterior buttress in balistids for support of the highly specialized, enlarged, and forward migrated first basal pterygiophore of the spiny dorsal fin (the carina). In the aracanid–ostraciid clade of balistoids the supraoccipital is similarly flat, but without any buttressing since the spiny dorsal fin is absent.

In tetraodontoids (2b o.g.) the supraoccipital is relatively flat and has a well-developed low flange projecting posteriorly in triodontids, tetraodontids, and diodontids. In molids, however, the supraoccipital is more dome-like. Nevertheless, numerous specialized features unite the molids with the other tetraodontoids (Winterbottom, 1974; Tyler, 1980). Thus, the dome-like supraoccipital in molids must be considered to have been acquired independently of that in triacanthoids under the overall most parsimonious scheme of relationships.

The hypothesis of a flat supraoccipital being primitive for tetraodontiforms is in accord with the condition in the zeiform

extraordinary outgroup, in which the supraoccipital is always relatively broad and flat, with a low to high medial crest.

While a flat supraoccipital is hypothesized to be primitive for tetraodontiforms, there are two equally parsimonious explanations for the distribution of the dome-like supraoccipital in triacanthoids. Either the flat supraoccipital is the ancestral condition for the triacanthoid clade and the dome-like condition has been acquired independently by hollardiins and triacanthids, or the apomorphic dome-like condition arose in the ancestor of the triacanthoid clade and was lost secondarily by triacanthodins (two steps in either case).

Thus, if the ancestral triacanthoid had a flat supraoccipital like zeiforms and balistoids (and most tetraodontoids) then the dome-like supraoccipital would be a synapomorphy of hollardiins. Although equivocal, we favor this hypothesis and consider the dome-like supraoccipital as an ambiguous synapomorphy of hollardiins. Conversely, if the ancestral triacanthoid had a dome-like supraoccipital then the simpler dome with a convex posterior surface as found in hollardiins could be considered primitive because the central elevation of the relatively round, flat plate of the ancestral tetraodontiform supraoccipital presumably would result in a conical structure rather than one with a triacanthid-like concave posterior surface. The condition of the triacanthid supraoccipital is therefore hypothesized to be derived under this scenario.

Another hypothesis, that the configuration of the supraoccipital-epiotic region is a synapomorphy that indicates triacanthodins are the sistergroup of hollardiins and triacanthids is not parsimonious when other evidence is considered. The seven myological synapomorphies given in Winterbottom (1974), and presumably many of the specialized osteological character states for triacanthoids given in Tyler (1980), support the hypothesis of a sistergroup relationship between triacanthodins and triacanthids rather than between hollardiins and triacanthids.

FIRST BASAL PTERYGIOPHORE OF ANAL FIN (*Character 5*).—The first anal-fin basal pterygiophore in hollardiins has a prominent anteromedial flange along the lower portion of its length in *Hollardia* and, to a lesser extent, in *Parahollardia*. As a consequence, the pterygiophore is "+" shaped in cross-section. In Recent triacanthodins and in triacanthids, balistoids, and tetraodontoids (1–2 o.g.) this anteromedial flange is absent and the pterygiophore is T-shaped in cross-section. The absence of the flange is therefore judged to be the plesiomorphic condition for tetraodontiforms.

As with supraoccipital shape, we can only note that, given the distribution of the presence of the flange, the possession of the flange is a possible synapomorphy of hollardiins under one of the two equally parsimonious hypotheses. Under that scenario the absence of the flange also is a possible synapomorphy of all Recent triacanthodins to the exclusion of *Carpathospinosus*.

It is noteworthy that in the zeiform extraordinary outgroup the first anal-fin basal pterygiophore sometimes has a low thick

crest along its lower anterior edge, especially in zeids. Under the overall most parsimonious scheme of higher level relationships noted above, this crest in some zeiforms is hypothesized as homoplastic to the thinner flange on the first anal-fin basal pterygiophore in triacanthodins.

The presence of an anteromedial flange in one of the new Oligocene genera, *Carpathospinosus* (which has three synapomorphies uniting it with triacanthodins), requires reassessment of its significance. Rather than being a potentially unequivocal diagnostic synapomorphy of hollardiins, the presence of the flange also in *Carpathospinosus* can be explained equally parsimoniously by the flange having arisen in the ancestor of the triacanthoid clade and been lost by the ancestor of Recent triacanthodins or that the ancestral triacanthoid lacked the flange which was acquired independently by hollardiins and *Carpathospinosus* (two steps in either case).

SUMMARY OF SUBFAMILIAL CHARACTERS OF NEW TAXA.—Three of the five contrasting character states (shape of posterior process of pelvis, position of epiotic on posterodorsal region of skull, and anterior articulation of epiotic) that are used to diagnose the two subfamilies of triacanthodins can be unequivocally polarized and for all three the derived condition (basin-like process, epiotics meeting medially on dorsal surface of skull, and epiotics separated from frontals by sphenotic) is found in triacanthodins (including the Oligocene *Carpathospinosus*). The other two characteristics (supraoccipital shape and form of anteromedial edge of first basal pterygiophore of anal fin) are equivocal but the conditions (supraoccipital dome-like and anteromedial flange on pterygiophore present) found in hollardiins (including the Oligocene *Prohollardia*) could be derived under one of two alternate scenarios for each feature.

Thus, we have been able to establish the monophyly of triacanthodins but not unequivocally so that of hollardiins.

RELATIONSHIPS OF *Prohollardia* IN HOLLARDIINAE

The two Recent genera of hollardiins are distinguished by several features (Tyler, 1968:68, 73, 93). *Parahollardia* has one to ten (usually two to four) teeth internal to the outer series in each jaw, the origin of the spiny dorsal fin usually slightly in front of the vertical through a line along the upper edge of the gill opening, and the scales of large adults with numerous, finely branched upright spinules. *Hollardia* has no inner series teeth, the spiny dorsal origin slightly to distinctly behind the level of the gill opening, and the scales of large adults with relatively few and coarse branches of the spinules.

Prohollardia lacks inner series teeth and the position of the origin of the spiny dorsal fin is distinctly anterior to the level of the gill opening. All of the specimens of *Prohollardia* are relatively small and comparison cannot be made to the differential spinule conditions that develop only in large specimens of the other two genera, small specimens of which have spinules like those of *Prohollardia*.

Of the tooth and spiny dorsal-fin origin differences of the two Recent genera, for which there are comparable data for *Prohollardia*, the former is phylogenetically informative but the latter is difficult to polarize because of pronounced variability in the position of fin origin in the sister group and outgroups.

For example, in triacanthodins the spiny dorsal-fin origin varies from over or only slightly in front of or behind the gill opening to substantially behind it (e.g., *Macrorhamphosodes*) or substantially in front of it (*Mephisto*). In triacanthids (1 o.g.) the origin is slightly to distinctly behind the gill opening, while in balistoids (2a o.g.) the origin is over or distinctly behind the gill opening in balistids but over to well in front of it in the derived monacanthids (spiny dorsal fin absent in the derived aracanid–ostraciid clade). In tetraodontoids (2b o.g.) the spiny dorsal fin usually is absent but when present in the Eocene eoplectids its origin is well behind the gill opening and when present as a rudiment in triodontids its origin is far behind the gill opening. In the zeiform extraordinary outgroup the spiny dorsal-fin origin is well behind the gill opening (i.e., anterior edge of cleithrum).

Because the spiny dorsal-fin origin is slightly to well behind the gill opening in triacanthids, morphologically primitive balistoids, eoplectids, and triodontids, we consider this the plesiomorphic condition. Therefore, the far anterior position of the origin in *Prohollardia* is hypothesized simply as an autapomorphy within hollardiins, and independent of that found in *Mephisto* alone among triacanthodins.

SYNAPOMORPHIES OF *Prohollardia* AND *Hollardia*.—Among triacanthodids inner series teeth are present only in one Recent genus (*Parahollardia*) of hollardiins and in one Recent genus (*Triacanthodes*) of triacanthodins. All triacanthids (1 o.g.) have inner series teeth in both the upper and lower jaw. Among balistoids (2a o.g.), the more morphologically primitive members (balistids and monacanthids) have inner series teeth in the upper jaw but these are absent in the lower jaw, while in the more derived members (the aracanid–ostraciid clade) inner teeth are absent in both jaws. Most tetraodontoids (2b o.g.) have inner series teeth in the form of a specialized trituration apparatus of a few molariform or laterally elongate teeth or of a massive plate of consolidated teeth. In the zeiform extraordinary outgroup, the dentition usually forms a narrow band several teeth wide. We interpret the zeiform condition as ancestral to that of a major outer row with fewer teeth internal to it. The presence of inner series teeth in the first outgroup and in at least the morphologically primitive members of the second tetraodontiform outgroup, and the ancestral conditions in the zeiform outgroup, leads us to hypothesize that the presence of inner series teeth is plesiomorphic. Therefore, the absence of inner series teeth (*Character 6*) is hypothesized as a synapomorphy of *Prohollardia* and *Hollardia* in the Hollardiinae, and homoplastic to the loss of inner series teeth in all triacanthodins except *Triacanthodes*.

Only one other character has been found that differs between

the three genera of hollardiins which can be polarized with confidence. This feature, involving the scales on the spiny dorsal fin, also indicates a sistergroup relationship between *Prohollardia* and *Hollardia*.

The membrane of the spiny dorsal fin is essentially scaleless in all triacanthodins, with the exception of a few scales basally between the second to fourth spines in *Johnsonina* (Tyler, 1968:158, fig. 53). This membrane is scaleless in triacanthids (1 o.g.), in balistoids (2a o.g.) with spiny dorsal fins (balistids and monacanthids), in eoplectids and triodontids that alone among tetraodontoids (2b o.g.) have a spiny dorsal fin, and in the zeiform extraordinary outgroup. A scaleless interspinous membrane thus is clearly plesiomorphic for tetraodontiforms.

Among hollardiins the interspinous membrane is scaleless in *Parahollardia*, while in *Hollardia* there are either a few (*H. meadi* and *H. goslinei* Tyler) to many (*H. hollardi*) spinulose scales basally on the membranes and in *Prohollardia* an even more extensive covering of the membranes with scales. Therefore, among hollardiins we consider the presence of interspinous membrane scales (*Character 7*) as a synapomorphy of *Hollardia* and *Prohollardia*, with the extensive covering in *Prohollardia* autapomorphic. The few interspinous scales present in *Johnsonina* among the triacanthodins is most parsimoniously interpreted as homoplastic to that in hollardiins.

SIMILARITIES BETWEEN *Prohollardia* AND OTHER GENERA.—There are a number of other similarities between *Prohollardia* and one or more species of *Hollardia* that are suggestive of a relationship between them. For example, there are 19 dorsal-fin rays in *Prohollardia* and modally 17, but often 18 in *Hollardia hollardi*, while *Hollardia goslinei* and *H. meadi* and *Parahollardia lineata* and *P. schmidtii* Woods have only 16 rays modally. There are 15 anal-fin rays in *Prohollardia* and *H. hollardi* (modally) but only 14 modally in the other two species of *Hollardia* and both species of *Parahollardia*. However, these fin-ray differences are difficult to polarize because of pronounced variability in the outgroups (see Tyler, 1968, 1980 for meristic data).

We note that increased body depth in hollardiins is as variable as the position of the spiny dorsal-fin origin. In triacanthodins the average body depth is 31%–53% SL in the species with typical body shapes (i.e., exclusive of the two long-snouted derived genera with depths of only 16%–22% SL). In triacanthids (1 o.g.) the average body depth is 31%–45% SL, and in balistoids (2a o.g.) about 40%–50% SL in most species (but with depth especially wide ranging in the derived monacanthids, from about 12%–86% SL in such genera as, respectively, *Psilocephalus* and *Brachaluteres*). Body depth is moderate in most tetraodontoids (2b o.g.), usually 25%–45% SL (but great in the Eocene eoplectids, 93% SL). In the zeiform extraordinary outgroup the depth ranges from about 50%–55% SL in at least the more anatomically generalized members (i.e., zeids).

Therefore, we hypothesize body depths of about 30% to 55%

SL as plesiomorphic for tetraodontiforms. Among hollardiins only *Parahollardia schmidti* has comparable body depths, 50%–60% SL in specimens of 30 to 50 mm SL, versus greater average depths of 65%–73% SL in similarly small specimens of *Parahollardia lineata*, *Hollardia hollardi*, and *H. meadi* (no specimens of *H. goslinei* this small are available, but it has as deep a body as in the adults of the other two species of *Hollardia*) and *Prohollardia*. It is equally parsimonious to hypothesize that the ancestral hollardiin had moderate body depth like *Parahollardia schmidti* and increased depth is an independent acquisition of the *Prohollardia*–*Hollardia* clade and of *Parahollardia lineata*, or that the ancestral hollardiin had increased body depth followed by reduction of depth in *P. schmidti* (two steps in either case).

The relatively short length (average 17.9% SL) and great width (6.7% SL) of the posterior process of the pelvis in *Prohollardia* is more similar to the conditions in *Hollardia hollardi* (average length 24.7% SL and width 6.2% SL) (and in *H. meadi* for length, average 23.7% SL; and in *H. goslinei* for width, average 5.9% SL) than to other hollardiins, in which the average length is 27.0%–29.8% SL and width 3.6%–4.6% SL. These proportional differences, however, are difficult to polarize, primarily because neither the triacanthodins nor the zeiform extraordinary outgroup has a comparably solid, medially placed, shaft-like process.

SUMMARY OF RELATIONSHIPS OF *Prohollardia*.—We are confident that two synapomorphies show the sistergroup relationship within the hollardiins between *Prohollardia* and *Hollardia*; the absence of inner series teeth and the presence of scales on the membranes of the spiny dorsal fin. The other numerous similarities between the two genera are either equivocal or not phylogenetically useful.

RELATIONSHIPS OF *Carpathospinosus* IN TRIACANTHODINAE

While its many autapomorphies easily distinguish *Carpathospinosus* from all other triacanthodins, any effort to establish its relationships therein is severely hampered by not knowing whether it possesses inner series teeth and uncertainty about whether the presence of an anteromedial flange on the first anal-fin basal pterygiophore is primitive or derived (see “Discussion of Subfamilial Defining Characters”). We are aware of only one feature that sheds light on its relationships within the subfamily.

The width of the basin-like posterior process of the pelvis is especially great in *Carpathospinosus* and in one of the Recent genera, *Bathyphylax*. The basin-like condition is considered a derived feature because it is unique to triacanthodins among tetraodontiforms (except also present in the enigmatic Oligocene *Cryptobalistes*, previously discussed).

The width of the shaft-like posterior process in hollardiins and in triacanthids (1 o.g.) varies from about 2%–6% SL (average values, here and below). Pelvic widths range from about 6%–12% SL in most triacanthodins with typical heads

(3%–7% SL in the two long-snouted genera because of the long head, but pelvic widths not narrow in comparison to at least some of the more generalized triacanthodins). The one exception is *Bathyphylax*, in which the pelvis is exceptionally wide (about 14% SL in *B. bombifrons* Myers and 18% SL in *B. omen* Tyler), as wide as or wider than in *Carpathospinosus* (13% SL). The pelvic width into pelvic length ratio is correspondingly lower in *Carpathospinosus* (1.9) and *Bathyphylax* (1.9–2.3) than in other triacanthodins (2.8–5.2 in those with typical snouts; as great as 6.1 in the long-snouted genera).

In triacanthodins pelvic widths greater than the 6% SL greatest average found in hollardiins and triacanthids must be considered apomorphic, increasingly so with increasing width in an ordered transformation series. The great pelvic width could be interpreted as a synapomorphy of *Carpathospinosus* and *Bathyphylax* indicating their sistergroup relationship. However, this argument is somewhat weakened by the fact that two other triacanthodins have pelvises that are only slightly less wide than in *Carpathospinosus*; the width is between 11%–12% SL and the ratio 2.8–3.0 in the monotypic *Mephisto* and in one of the two species of *Paratriacanthodes*, *P. retrospinis* Fowler. Since the differences in pelvic width and the width into length ratio in these various genera, or of one of the species of the genus, are slight, we prefer to simply postulate that *Carpathospinosus* is probably most closely related among the triacanthodins to the genera with relatively wide pelvises (*Bathyphylax*, *Mephisto*, and *Paratriacanthodes*).

Given the unknown condition of inner dentition in *Carpathospinosus*, the uncertainty of the interpretation of the anteromedial flange on the first anal-fin basal pterygiophore, and the close approach by several other genera to the great pelvic width in *Carpathospinosus* and *Bathyphylax*, we prefer to place *Carpathospinosus* in an unresolved trichotomy with, on the one hand, *Triacanthodes* (inner series teeth present and flange absent), and on the other with the clade composed of all of the other Recent triacanthodin genera (inner series teeth and flange absent).

REFERRAL OF *Cephalacanthus trispinosus* CIOBANU TO TRIACANTHIDAE

Ciobanu (1977) briefly described a small (29 mm SL) Oligocene fish from Romania in the dactylopteriform family Cephalacanthidae = Dactylopteridae as *Cephalacanthus trispinosus*. This allocation apparently was based on the resemblance of the large first dorsal and pelvic spines to the massive occipital and preopercular spines in dactylopterids, and perhaps to their elongate but slender dorsal spines. However, the single specimen is described as having numerous soft dorsal (20–22) and anal (16) rays, far more than in dactylopterids, and a pectoral fin of normal size, whereas the pectoral is always enormously elongate in dactylopterids. There is no mention in the description or evidence in the illustration of enlarged scales

and bony plates such as those that cover the body of dactylopterids.

The illustration of *Cephalacanthus trispinosus* shows a fish that is strikingly similar to a young triplespine of the tetraodontiform family Triacanthidae, and especially to the two species of *Acanthopleurus* Agassiz (1842, 1844): *A. serratus* Agassiz (1842, 1844) and *A. collettei* Tyler (1980), both from the Oligocene of Canton Glarus, Switzerland. The first dorsal spine is far larger than the second spine (only two spines are shown and described but the three or four smaller more posterior ones probably were not as well preserved or observable), the left and right pelvic spines are also prominent and there is a long and probably shaft-like posterior process of the pelvis between them, the caudal peduncle tapers posteriorly, and the spiny dorsal-fin base is much shorter than the soft dorsal-fin base, all typical features of triacanthids. As with *Acanthopleurus*, most of the internal osteological features are poorly exposed, but all features evident in the illustration of *Cephalacanthus trispinosus* are consistent with its being referable to *Acanthopleurus*.

There is no explanation for the listing in the description of *Cephalacanthus trispinosus* of four pelvic fin elements, 20 caudal fin rays, and 23–24 vertebrae, and the illustration does not clarify the matter; presumably these meristics are misinterpretations of the difficult to decipher impressions in black shales that are typical of all other specimens of the Oligocene *Acanthopleurus*.

While the species described by Ciobanu as *Cephalacanthus trispinosus* is surely a species of *Acanthopleurus*, it is impossible on the basis of its description and illustration to determine whether it is a valid third species of that genus or a synonym of one of the two presently recognized species. The type specimen will have to be re-examined before that determination can be made. For the moment we simply note

that the 29 mm SL holotype of *Acanthopleurus trispinosus* has a relatively deep body of 35% SL, a depth more like that of *A. collettei* than that of the more shallow bodied *A. serratus*. However, the available specimens of both *A. serratus* (11 specimens, 78–153 mm SL) and *A. collettei* (7 specimens, 82–120 mm SL) are much larger than that of *trispinosus* and body depth in triacanthids is greatest in small specimens and decreases with increasing specimen size to such an extent that the small holotype of *trispinosus* cannot be placed with confidence on extrapolations of the ontogenetic body depth curves given by Tyler (1980:97, fig. 46) for either of the two species of *Acanthopleurus*.

Conclusion

The data discussed herein allow us to assign the two new Oligocene genera within each of the two subfamilies of triacanthodids as their first fossil representatives. The data also support the hypothesized sistergroup relationship of one of the fossil taxa (*Prohollardia*) to a particular Recent genus (*Hollardia*) of Hollardiinae, and of the other (*Carpathospinosus*) to a group of several Recent genera of Triacanthodinae characterized by especially broad pelvises. It also establishes that the separation of the two subfamilial lineages of triacanthodids took place no less than about 29 to 24 MYA.

The information in this study makes it obvious that all of the osteological differences between the two subfamilies of triacanthodids and their triacanthid and other outgroups need to be re-analyzed cladistically to expand the data base of polarized characteristics. That will be necessary in interpreting the phylogenetic relationships of the subfamilies beyond the presently recognized differences in the shapes and articulations of the bones in the supraoccipital–epiotic region, the shape of the posterior process of the pelvis, and the shape of the first anal-fin basal pterygiophore.

Literature Cited

- Agassiz, Louis
 1842. *Recherches sur les poissons fossiles*. Volume 2, plate 75. Neuchâtel.
 1844. *Recherches sur les poissons fossiles*. Volume 2, part 2: pages 73–336. Neuchâtel.
- Bannikov, Alexandre F.
 1991. On the Systematic Position of the Family Caproidae with Reference to the Eocene Genus *Acanthonemus*. *Journal of Ichthyology* (translation of *Voprosy Ikhtiologii*), 31(5):47–58.
- Berg, Leo S.
 1940. Classification of Fishes, Both Recent and Fossil. *Travaux de l'Institut Zoologique de l'Académie des Sciences de l'USSR*, 5:87–517.
- Ciobanu, Mihai
 1977. *Fauna fosila din Oligocenul de la Piatra Neamt*. 159 pages. Bucuresti: Editura Academiei Republicii Socialiste Romania.
- Gaudant, Mireille
 1977. Sur la découverte dans le Crétacé de Laveiras (Portugal) du plus ancien zeiforme connu. *Geobios*, 10(3):487–488.
 1978. Contribution à l'étude anatomique et systématique de l'ichthyofaune cénomaniennne du Portugal, Première partie: les "Acanthopterygiens." *Comunicações dos Serviços Geológicos de Portugal*, 63:105–149.
- Gayet, Mireille
 1980a. Sur la découverte dans le Crétacé de Hadjula (Liban) du plus ancien Caproidae connu. *Comptes Rendus de l'Académie des Sciences* (Paris), series D, 290:447–448.
 1980b. Découverte dans le Crétacé de Hadjula (Liban) du plus ancien Caproidae connu. -Étude anatomique et phylogénétique. *Bulletin du Muséum National d'Histoire Naturelle* (Paris), series 4, section C, 2(3):259–269.
- Gregory, William K.
 1933. Fish Skulls: A Study of the Evolution of Natural Mechanisms. *Transactions of the American Philosophical Society*, 23(2):1–481.
- Heemstra, Phillip C.
 1980. A Revision of the Zeid Fishes (Zeiformes: Zeidae) of South Africa. *Ichthyological Bulletin of the Institute of Ichthyology, Rhodes University, Grahamstown*, 41:1–18.
- Jerzmańska, Anna
 1968. Ichthyofaune des couches à ménilite (flysch des Karpathes). *Acta Palaeontologica Polonica*, 13(3):379–488.
 1974. *Kotlarczykia bathybia* gen. n., sp. n. (Teleostei) from the Oligocene of the Carpathians. *Acta Palaeontologica Polonica*, 19(2):281–289.
 1979. Oligocene Alepocephaloid Fishes from the Polish Carpathians. *Acta Palaeontologica Polonica*, 24(1):65–76.
- Jerzmańska, Anna, and Janusz Kotlarczyk
 1976. The Beginnings of the Sargasso Assemblage in the Tethys? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 20:297–306.
 1981. Fish Fauna Evolutionary Changes as the Basis of the Stratigraphy of the Menilite Beds and Krosno Beds. *Zemni Plyn a Nafta*, 26(1): 63–74.
- Kotlarczyk, Janusz, and Anna Jerzmańska
 1976. Biostratigraphy of the Menilite Beds of Skole Unit from the Polish Flysch Carpathians. *Bulletin de l'Académie Polonaise des Sciences, Serie des Sciences de la Terre*, 24(1):55–61.
 1988. Ichthyofauna w stratygrafii Karpat. *Przegląd Geologiczny*, 6: 346–352.
- Norman, John R.
 1934. *A Systematic Monograph of the Flatfishes (Heterosomata), Volume 1: Psettodidae, Bothidae, Pleuronectidae*. 459 pages. London: British Museum (Natural History).
- Poey, Felipe
 1861. Poissons de Cuba, especes nouvelles, Part 3. *Memorias sobre la Historia Natural de la Isla de Cuba*, 2:337–356.
- Rosen, Donn E.
 1984. Zeiforms as Primitive Plectognath Fishes. *American Museum Novitates*, 2782:1–45.
- Shufeldt, Robert W.
 1888. Further Studies on *Grammicolepis brachiusculus*, Poey. *Journal of Morphology*, 2(2):271–295.
- Sorbini, Lorenzo
 1979. Segnalazione di un plectognato Cretacico *Plectocretacicus* nov. gen. *Bollettino del Museo Civico di Storia Naturale di Verona*, 6:1–4.
 1983. *La collezione Baja di pesci e piante fossili di Bolca*. 117 pages. Verona: Museo Civico di Storia Naturale di Verona.
- Sorbini, Lorenzo, and Cristina Bottura
 1987. *Antigonia veronensis*, an Eocene Caproid from Bolca (Italy). *Bollettino del Museo Civico di Storia Naturale di Verona*, 14:255–269.
- Starks, Edwin C.
 1898. The Osteology and Relationships of the Family Zeidae. *Proceedings of the United States National Museum*, 21:469–476.
- Świdnicki, Jacek
 1986. Oligocene Zeiformes (Teleostei) from the Polish Carpathians. *Acta Palaeontologica Polonica*, 31(1–2):111–135.
 1988. Juveniles of Some Oligocene *Antigonia* (Caproidae, Teleostei) from the Polish Carpathians. *Acta Palaeontologica Polonica*, 33(3): 249–259.
- Tyler, James C.
 1968. A Monograph on Plectognath Fishes of the Superfamily Triacanthoidea. *Academy of Natural Sciences of Philadelphia Monograph*, 16:1–364.
 1973. A New Species of Triacanthodid Fish (Plectognathi) from the Eocene of Monte Bolca, Italy, Representing a New Subfamily Ancestral to the Triodontidae and to the Other Gymnodonts. *Museo Civico di Storia Naturale di Verona, Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2:128–156.
 1980. Osteology, Phylogeny, and Higher Classification of the Fishes of the Order Plectognathi (Tetraodontiformes). *National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service Circular*, 434:1–422.
- Tyler, James C., and Alexandre F. Bannikov
 1992. A Remarkable New Genus of Tetraodontiform Fish with Features of Both Balistids and Ostraciids from the Eocene of Turkmenistan. *Smithsonian Contributions to Paleobiology*, 72:1–14.
- Winterbottom, Richard
 1974. The Familial Phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as Evidenced by Their Comparative Myology. *Smithsonian Contributions to Zoology*, 155:1–201.
- Zehren, Steven J.
 1987. Osteology and Evolutionary Relationships of the Boarfish Genus *Antigonia* (Teleostei: Caproidae). *Copeia*, 1987(3):564–592.