

# The Miocene gadid fish *Palimphemus anceps* Kner, 1862: a reappraisal

**Giorgio CARNEVALE**

Dipartimento di Scienze della Terra, Università degli Studi di Torino  
Via Valperga Caluso, 35, I-10125 Torino (Italia)  
[giorgio.carnevale@unito.it](mailto:giorgio.carnevale@unito.it)

**Mathias HARZHAUSER  
Ortwin SCHULTZ**

Geologisch-Paläontologische Abteilung,  
Naturhistorisches Museum in Wien,  
Burgring 7 A-1010 Vienna (Austria)

Carnevale G., Harzhauser M. & Schultz O. 2012. — The Miocene gadid fish *Palimphemus anceps* Kner, 1862: a reappraisal. *Geodiversitas* 34 (3): 625-643. <http://dx.doi.org/10.5252/g2012n3a9>

## ABSTRACT

The gadid fish *Palimphemus anceps* Kner, 1862 is redescribed in detail based on 43 specimens from the Miocene deposits of St. Margarethen, in the Eisenstadt-Sopron Basin, Burgenland, Austria. The morphoanatomical analysis of the material referred to *Palimphemus anceps* revealed that it can be distinguished from other members of the family Gadidae Rafinesque, 1810 by a unique combination of characters, including: elongated and laterally compressed body, head length about  $\frac{1}{3}$  of SL, large massive neurocranium with outer margins of the frontals thickened and ornamented by longitudinal pits and ridges along the ventral surface, hyomandibula with large ventrally directed preopercular process, opercle with a thick horizontal rib arising from the articular condyle, anal-fin insertion well behind the first dorsal-fin origin; preanal distance exceeding the base length of the first anal fin, length of the first anal-fin base reduced, 45-46 (18 + 27/28) vertebrae, third dorsal fin with 17-21 rays, first anal fin with 18-21 rays, second anal fin with 18-19 rays, caudal fin with 41-43 rays, and pectoral fin with 15-18 rays. *Palimphemus anceps* appears to be a basal gadine closely related to the genus *Micromesistius* Gill, 1867. Like other basal gadine genera – *Gadiculus* Guichenot, 1850, *Micromesistius* and *Trisopterus* Rafinesque, 1814 – *Palimphemus anceps* possibly was a thermophilous gadid that inhabited the shallow waters of the central Paratethys during the Middle Miocene.

## KEY WORDS

Teleostei,  
Gadiformes,  
Gadidae,  
*Palimphemus anceps*,  
Miocene,  
Paratethys,  
St. Margarethen,  
Austria.

## RÉSUMÉ

*Redescription du poisson gadine miocène Palimphemus anceps Kner, 1862.*

Le poisson gadide *Palimphemus anceps* Kner, 1862 est redécrit en détail, sur la base de 43 spécimens provenant des dépôts du Miocène de St. Margarethen, dans le bassin d'Eisenstadt-Sopron, Burgenland, Autriche. L'analyse morphoanatomique du matériel attribué à *Palimphemus anceps* a révélé qu'il se distinguait des autres membres de la famille des Gadidae Rafinesque, 1810 par une combinaison unique de caractères, à savoir : le corps allongé et comprimé latéralement, la longueur de la tête représentant environ  $\frac{1}{3}$  de la longueur standard, le neurocrâne massif avec les marges extérieures des frontaux épaissies et ornées par des fosses et des nervures longitudinales le long de la surface ventrale, l'hyomandibulaire avec de grands processus préoperculaires dirigés ventralement, l'opercule avec une épaisse nervure horizontale découlant du condyle articulaire, l'insertion de la première nageoire anale largement en arrière de l'origine de la première nageoire dorsale, la distance préanale dépassant la longueur de base de la première nageoire anale, la longueur de la base de la première nageoire anale réduite, 45-46 (18+27/28) vertèbres, 17-21 rayons sur la troisième nageoire dorsale, 18-21 rayons sur la première nageoire anale, 18-19 rayons sur la deuxième nageoire anale, 41-43 rayons sur la nageoire caudale et 15-18 rayons sur la nageoire pectorale. *Palimphemus anceps* semble être un gadine basal étroitement lié au genre *Micromesistius* Gill, 1867. Comme d'autres genres de gadine basal – *Gadiculus* Guichenot, 1850, *Micromesistius*, et *Trisopterus* Rafinesque, 1814 – *Palimphemus anceps* était probablement un taxon thermophile qui occupait les eaux peu profondes de la Paratéthys centrale au cours du Miocène moyen.

## MOTS CLÉS

Teleostei,  
Gadiformes,  
Gadidae,  
*Palimphemus anceps*,  
Miocène,  
Paratéthys,  
St. Margarethen,  
Autriche.

## INTRODUCTION

Exquisitely preserved articulated skeletons of teleost fishes from the Miocene corallinacean limestone in Austria are known since the first half of the 19<sup>th</sup> century. During the first decade of the second half of that century, brilliant Austrian naturalists such as Johann Jakob Heckel and Rudolf Kner, described several specimens collected in a few outcrops in the vicinity of the village of St. Margarethen, in the Eisenstadt-Sopron Basin, Burgenland (Heckel 1850, 1856; Heckel & Kner 1861; Kner 1862). After a long scientific gap (see Gorjanović-Kramberger 1902), a new series of studies has been realized in the last 30 years, mostly based on new material collected in the course of two large excavation campaigns, which resulted in the production of a vast collec-

tion of finely preserved fishes and invertebrates now housed in the Naturhistorisches Museum, Wien (Bachmayer 1980; Bellwood & Schultz 1991; Schultz 1993, 2006a, b; Chanet & Schultz 1994). However, a comprehensive analysis of the biodiversity of this extraordinary ichthyofauna remains elusive.

In his 1862s study, Kner created a new taxon, *Palimphemus anceps*, in order to allocate a single moderately well-preserved specimen from St. Margarethen (Fig. 1). The relationships of this taxon were not clarified, even though it was compared to several percomorph groups, including the agonids, bembroids, callionymids, platycephalids, and the Paleogene euzaphlegid *Palimphytes* Agassiz, 1844; more recently, without any reasonable argument, this taxon has been considered to be related to the lanternfishes of the family

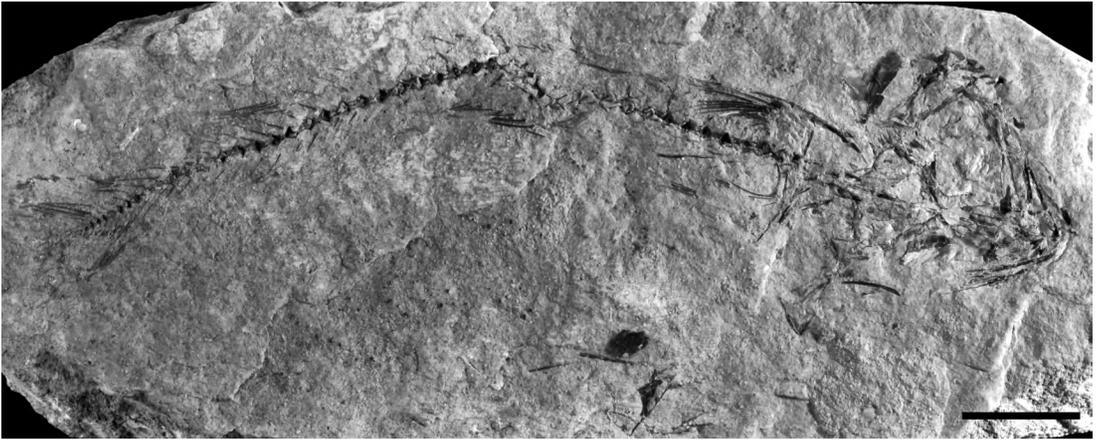


FIG. 1. — *Palimphemus anceps* Kner, 1862. Holotype, PIWU uncatalogued. Scale bar: 20 mm.

Myctophidae Gill, 1893 (see e.g., Bellwood & Schultz 1991). A detailed osteological analysis of the type specimen and additional material in the collection of the Naturhistorisches Museum in Vienna unequivocally indicates that *Palimphemus anceps* is a representative of the family Gadidae Rafinesque, 1810.

Members of the family Gadidae are benthopelagic fishes that primarily inhabit the shallow waters, outer shelves and slopes of the Northern Hemisphere. The family Gadidae consists of more than 30 extant species (Nelson 2006), many of which support relevant commercial fisheries, comprising over  $\frac{1}{4}$  of the world marine fish catch (see Cohen *et al.* 1990).

The earliest members of the family Gadidae apparently date back to the Paleocene (see e.g., Rosen & Patterson 1969; Cohen 1984; Fedotov & Bannikov 1989; Nolf & Steurbaut 1989). The skeletal record of the family has not been investigated in great detail, whereas the extremely rich otolith-based record has been extensively explored (see Gaemers 1976, 1978; Nolf & Steurbaut 1989), primarily in the North Sea Basin, a region historically characterized by rich populations of gadid fishes.

Because of the largely incomplete knowledge of the fossil history of gadid fishes, the revision of *Palimphemus anceps* certainly represents a fur-

ther step to a better understanding of the morphological and biogeographical evolution of this economically relevant group of fishes. Therefore, the purpose of this paper is to present a detailed osteological description of this long time neglected Miocene taxon, and to discuss its affinities within the family Gadidae.

#### STRATIGRAPHY AND PALEOENVIRONMENT

The fossils were collected at the Kummer quarry at St. Margarethen in Burgenland (Austria) in Middle Miocene coralline limestone which are usually referred to as Leitha Limestone in the regional literature (Keferstein 1828; Riegl & Piller 2000). The Leitha Limestone is characterized by the occurrence of coralline algae in various growth forms, representing rhodolite facies or a maerl-type sediment (calcarene consisting mainly of fragments of branching red algae). It formed especially along the margins of the Leitha Mountains and Rust Hills, which formed a small carbonate platform during the Middle Miocene (Schmid *et al.* 2001).

The Kummer quarry is a well-known fossil collecting site in the Neogene Eisenstadt-Sopron Basin. The quarry exposes strata along the Rust

Hills and is situated at the main road about 2 km E of St. Margarethen village (47°48'01.76"N, 16°37'59.12"E). A detailed sedimentological description and facies analysis of the Kummer quarry is provided by Schmid *et al.* (2001). According to that study, the section is dominated by thick units of corallinacean debris. It is characterized by corallinacean debris, rhodoliths, oysters, pectinids and fragmented echinoids deposited in a well aerated, shallow sublittoral environment with coarse, mobile carbonate sands. These sands were deposited as large channels which were produced during storm-triggered debris flows. Thin layers of greenish-whitish calcarenitic maerls, within the channels represent the background-sedimentation during calm phases. Reduced water energy, low oxygen conditions and occasional hypoxic events established in these depressions on the platform and gave rise to fossil accumulations. The lack of scavenging and deterioration caused an extraordinary preservation of the fauna, which consists of a large number of different fishes.

The dating of the konservat-lagerstätte is based on calcareous nannoplankton, which indicates zone NN5b (Schmid *et al.* 2001). Therefore, the deposition of the strata is supposed to have occurred around the Langhian/Serravallian boundary roughly between *c.* 14.0–13.5 Ma.

## MATERIAL AND METHODS

The holotype of *Palimphemus anceps* Kner, 1862 (Fig. 1) is deposited in the Palaeontologisches Institut der Wiener Universität (PIWU), while all the other 42 specimens referred to this species are deposited in the Geologisch-Palaeontologische Abteilung of the Naturhistorisches Museum, Wien (NHMW). The fossils are preserved on greenish-whitish laminated calcarenitic marls with bones that appear dark orange or brown. Some specimens required matrix removal before examination in order to allow investigations of their skeletal structures in as much detail as possible; these were prepared using thin entomological needles. The specimens were examined using a Leica MZ6 stereomicroscope equipped with a

camera lucida drawing arm. Measurements were taken with a dial caliper, to the nearest 0.1 mm. Comparative information was derived mainly from the literature (e.g., Svetovidov 1948; Inada & Nakamura 1975; Fahay & Markle 1984; Dunn 1989; Cohen *et al.* 1990).

## ABBREVIATIONS

boc	basioccipital;
ep	epural;
f	frontal;
hyp	hypural;
in	intercalar;
le	lateral ethmoid;
mx	maxilla;
pas	parasphenoid;
phy	parhypural;
pmx	premaxilla;
pro	prootic;
pto	pteric;
spo	sphenotic;
v	vomer.

## SYSTEMATICS

### Subdivision TELEOSTEI

*sensu* Patterson & Rosen, 1977

Order GADIFORMES Goodrich, 1909

Suborder GADOIDEI *sensu* Endo, 2002

Family GADIDAE Rafinesque, 1810

### Genus *Palimphemus* Kner, 1862

DIAGNOSIS. — Gadine fish with elongate and laterally compressed body; head length about one third of SL; gape of the mouth wide, extending posteriorly up the half of the orbit; anal-fin insertion well behind the first dorsal-fin origin; preanal distance about 46% SL, exceeding the base length of the first anal fin; length of the first anal-fin base reduced, measuring slightly less than one fourth of SL; 45–46 (18 + 27/28) vertebrae; third dorsal fin with 17–21 rays; first anal fin with 18–21 rays; second anal fin with 18–19 rays; caudal fin with 41–43 rays; pectoral fin with 15–18 rays; large massive neurocranium, its maximum width measured in the postorbital sector contained less than two times in its length; outer margins of the frontals thickened and ornamented by longitudinal pits and ridges along the ventral surface; hyomandibula with a relatively large ventrally directed preopercular process; opercle with a thick horizontal rib arising from the articular condyle.

REFERRED SPECIES. — Type species only.

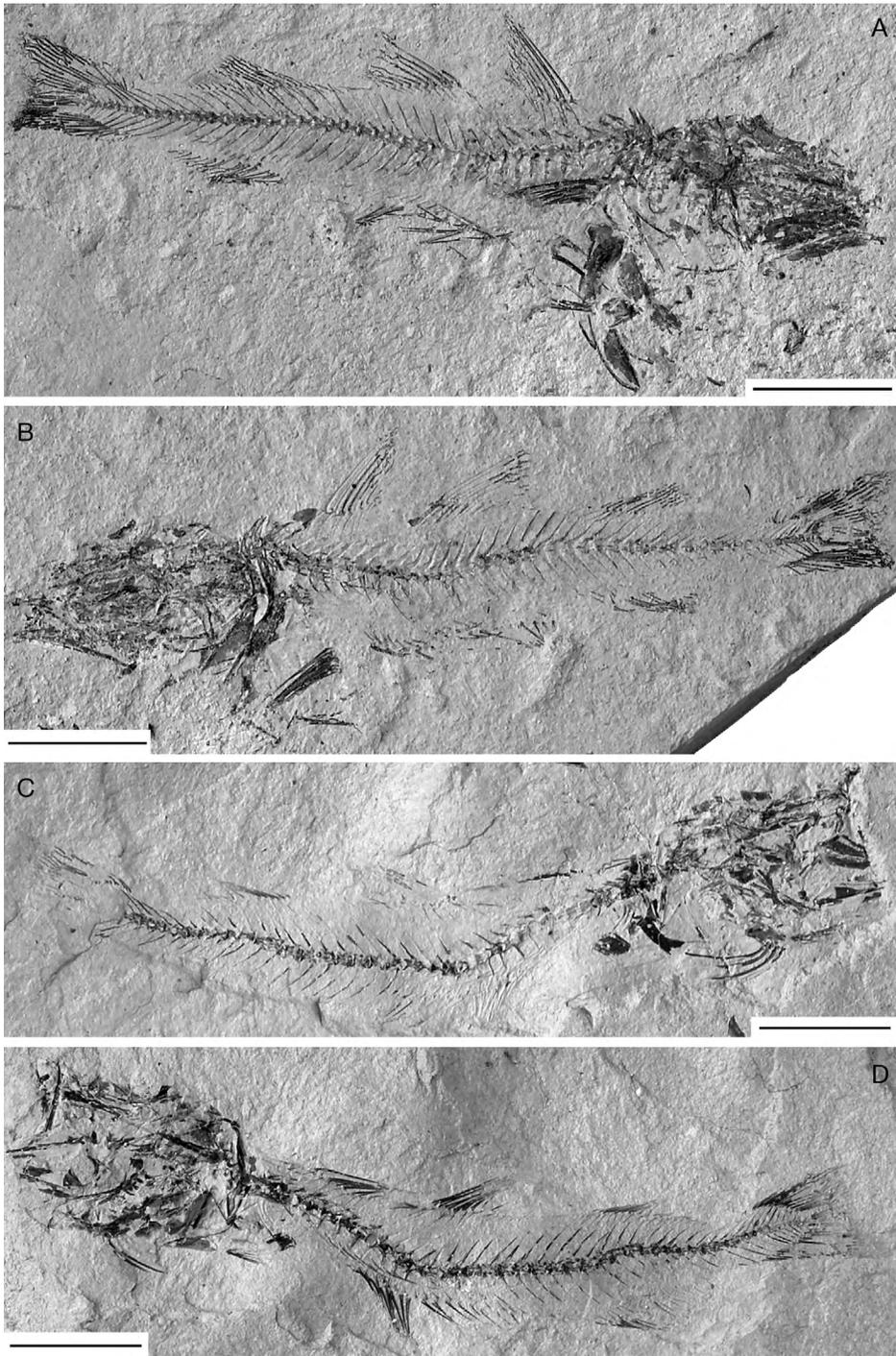


FIG. 2. — *Palimphemus anceps* Kner, 1862: A, NHMW 1975/1752/248; B, NHMW 1975/1752/247; C, NHMW 1988/149/48a; D, NHMW 1988/140/48b. Scale bars: 20 mm.

*Palimphemus anceps* Kner, 1862  
(Figs 1-8; 9A, D, F)

*Palimphemus anceps* Kner, 1862: 490-495; pl. 1, fig. 2; 1863: 148. — Woodward 1901: 270. — Schubert 1906: 697. — Schultz *in* Brzobohatý & Schultz 1978: 444. — Hofmann 2001: 221. — Schultz *in* Schmid, Harzhauser & Kroh 2001: 22.

HOLOTYPE. — PIWU, without catalogue number.

REFERRED SPECIMENS. — NHMW 1975/1752/248 and 247, complete well-preserved articulated skeleton in part and counterpart, 114.7 mm SL (Figs 2A-B); NHMW 1988/140/48a and b, nearly complete articulated skeleton (Fig. 2C, D); NHMW 1976/1812/38, partially complete articulated skeleton lacking the caudal portion (Fig. 3A); NHMW 1976/1812/51a and b, nearly complete articulated skeleton in part and counterpart (Fig. 3B, C); NHMW 2002z0181/0087a and b, nearly complete articulated skeleton in part and counterpart (Fig. 4A, B); NHMW 1975/1691/28a and b, complete articulated skeleton, 195 mm SL; NHMW 1974/1650/5, partially complete articulated skeleton; NHMW 1986/138/13a and b; NHMW 1975/1691/81, moderately well-preserved neurocranium exposed in ventral view; NHMW 1975/1691/27, largely incomplete articulated skeleton; NHMW 1975/1752/42, incomplete partially disarticulated skeleton; NHMW 1975/1752/50, partially complete articulated skeleton; NHMW 1975/1752/246, partially complete articulated skeleton; NHMW 1988/140/80a and b, nearly complete skeleton in part and counterpart; NHMW 1975/1691/89, largely incomplete poorly preserved articulated skeleton; NHMW 1975/1696/68, largely incomplete poorly preserved articulated skeleton; NHMW 1975/1752/220, incomplete articulated axial skeleton in part and counterpart; NHMW 1976/1812/62, incomplete articulated axial skeleton; NHMW 1976/1812/138, incomplete articulated axial skeleton; NHMW 1975/1696/53, largely incomplete articulated skeleton; NHMW 1975/1735/8, largely incomplete, partially disarticulated skeleton; NHMW 1975/1691/18, largely incomplete articulated skeleton; NHMW 1975/1696/52, moderately well-preserved articulated caudal portion of the skeleton; NHMW 1975/1812/69, largely incomplete partially disarticulated skeleton; NHMW 1975/1752/29, moderately well-preserved articulated caudal portion of the skeleton; NHMW 1975/1752/202, moderately well-preserved articulated caudal portion of the skeleton; NHMW 1976/1837/98, nearly complete poorly preserved articulated skeleton; NHMW 1988/140/142, incomplete articulated skeleton; NHMW 1975/1691/22, incomplete articulated skeleton lacking the head; NHMW 1976/1837/53, incomplete articulated skeleton; NHMW 1976/1837/185, largely incomplete poorly preserved articulated skeleton;

NHMW 1986/138/27, incomplete poorly preserved articulated skeleton; NHMW 1976/1837/189, poorly preserved articulated skeleton; NHMW 1992/151/11a and b, partially preserved head in part and counterpart; NHMW 1986/138/8, nearly complete poorly preserved articulated skeleton; NHMW 1986/138/31, incomplete articulated skeleton, lacking part of the head and the middle part of the body; NHMW 1975/1752/217, incomplete poorly preserved articulated skeleton; NHMW 1976/1812/40, slightly incomplete articulated skeleton; NHMW 2000z0135/0078, poorly preserved articulated skeleton in part and counterpart; NHMW 2002z0181/0088 + 0089, nearly complete neurocranium in part and counterpart; NHMW 2006z0220/0005, poorly preserved largely incomplete anterior part of the body; NHMW 2006z0220/0007, largely incomplete disarticulated anterior portion of the body.

TYPE LOCALITY AND HORIZON. — St. Margarethen locality, Kummer quarry; Middle Miocene, Late Badenian, *Bulimina-Bolivina* Zone, NN5b zone (see Schmid *et al.* 2001).

DIAGNOSIS. — As for the genus.

MEASUREMENTS. — (based on specimen NHMW 1975/1752/248; total length: 123.9 mm; standard length [SL]: 114.7 mm) as percentage of SL: maximum body depth: 20.3; head length: 29.3; head depth: 16.7; snout length: 11.0; caudal peduncle length: 6.3; caudal peduncle depth: 8.0; predorsal (1<sup>st</sup> fin) distance: 37.5; predorsal (2<sup>nd</sup> fin) distance: 52.1; predorsal (3<sup>rd</sup> fin) distance: 71.7; preanal (1<sup>st</sup> fin) distance: 46.0; preanal (2<sup>nd</sup> fin) distance: 74.1; distance between 1<sup>st</sup> and 2<sup>nd</sup> dorsal fins: 7.5; distance between 2<sup>nd</sup> and 3<sup>rd</sup> dorsal fins: 9.0; distance between 1<sup>st</sup> and 2<sup>nd</sup> anal fin: 5.4; mouth gape extension: 12.9; 1<sup>st</sup> dorsal-fin base length: 7.5; 2<sup>nd</sup> dorsal-fin base length: 10.3; 3<sup>rd</sup> dorsal-fin base length: 14.2; 1<sup>st</sup> anal-fin base length: 23.7; 2<sup>nd</sup> anal-fin base length: 14.2; pectoral-fin length: 14.1.

#### DESCRIPTION

The body is elongate and laterally compressed. The head is well-developed and slender, contained slightly more than three times in SL. The snout is elongate. The diameter of the orbit cannot be measured in the examined material because of inadequate preservation; however, the orbit was probably rather large in origin. The caudal peduncle is moderately developed.

The head skeleton is disarticulated, at least partially, in all the specimens examined; the bones are always displaced from their original position and are often extensively fragmented, so that is somewhat difficult to recognize the original morphology of the various elements.

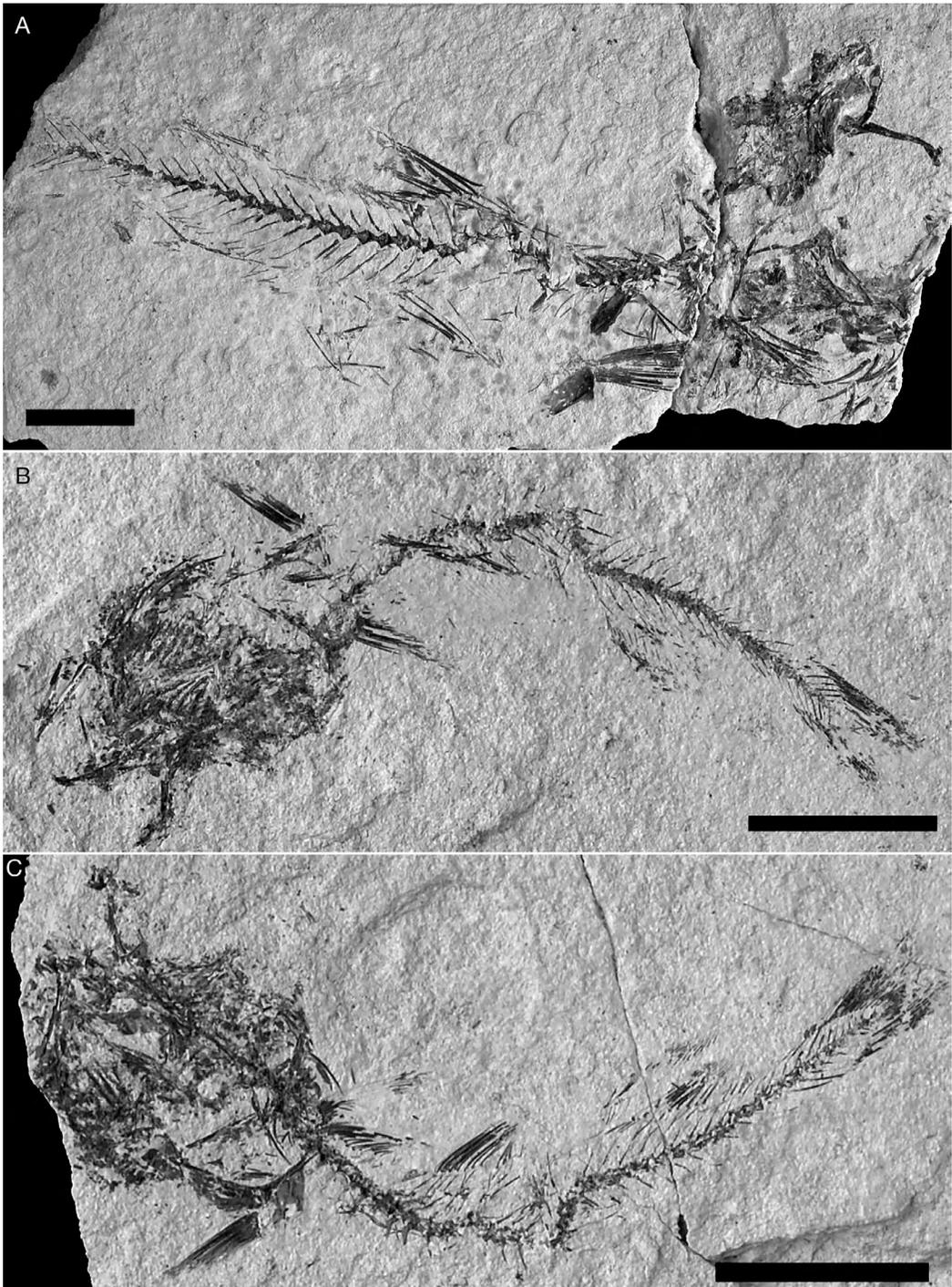


FIG. 3. — *Palimphemus anceps* Kner, 1862: **A**, NHMW 1976/1812/38; **B**, NHMW 1976/1812/51a; **C**, NHMW 1976/1812/51b. Scale bars: 20 mm.

### *Neurocranium*

The neurocranium is often exposed in ventral view (see Fig. 5). It appears to be moderately depressed dorsoventrally, with a straight upper profile. The neurocranium is quite large; its maximum width measured in the postorbital sector is contained less than two times in the length of its base. In general, the neurocranium is nearly ovoid, with the length of its orbitorostral portion, measured at the level of the frontal sphenotic notch, slightly greater than the length of the posterior portion. The ethmoid bloc is strongly ossified. The vomer is large, massive and ventrally flattened, with a curved anterior margin; vomerine teeth are not preserved in the material examined. The lateral ethmoids have wide triangular lateral wings. The posterior process of the lateral ethmoid appears to be absent. The (fused) frontals are the largest bones of the skull roof. The ventral surface of these bones (see Fig. 5) is strongly thickened and ornamented by longitudinal ridges and pits. The parasphenoid is robust, apparently straight, with a flat ventral surface. The basioccipital forms the floor of the posterior portion of the neurocranium. The topographic relationships between sphenotics, prootics, pterotics, and intercalars are identical to those of other gadine fishes (see e.g., Svetovidov 1948). The external surface of the prootics and intercalars is convex. The posterior corner of the pterotics consists of a thick and remarkably pointed spinous process.

Nasal and infraorbital bones are inadequately preserved in the specimens examined.

### *Jaws*

The gape of the mouth is rather wide; it probably reached the half of the orbit. The anterior tip of the dentary projects beyond the premaxilla. The premaxilla has robust and stout articular and ascending processes and an elongate and laminar postmaxillary process with gently rounded profile (Fig. 6A). There are two rows of teeth, the outer with few elongate and medially curved teeth, while the inner row is characterized by densely spaced minute pointed teeth. The maxilla is a robust and elongate bone, with a strong articular head (Fig. 6A). The lower jaw is long and shallow. The dentary has a long cavity (adductor chamber) that housed in origin the mandibularis section of the adductor mandibulae

muscle. There is a short symphyseal process. The angulo-articular has a steep and irregular posterior slope and a large articular condyle (Fig. 6B). The mandibular teeth are similar to those of the upper jaw.

### *Suspensorium*

The bones of the suspensorium are extensively crushed and difficult to recognize, except for the fan-shaped quadrate and the hyomandibula; the hyomandibula (Fig. 6C) is relatively elongate and possesses a long and straight opercular process and a ventrally directed and sharply pointed preopercular process; the lower process of the hyomandibula is absent.

### *Opercular series*

Opercular bones are badly damaged in most of the specimens examined, including NHMW 1974/1650/5, NHMW 1976/1812/69 and NHMW 1988/140/48. On the contrary, these are well preserved in the specimen NHMW 1975/1691/27. The preopercle is crescent-shaped with a regularly convex posterior margin. The interopercle and subopercle are laminar thin bones with a reduced thickening along their dorsal margin. The opercle has a subtriangular outline with rounded dorsal angles and shows a thick horizontal rib arising from its articular condyle (Fig. 6D).

### *Visceral arches*

Of the branchial skeleton, fragments of elongate and slender bones, possibly the ceratobranchials, can be recognised in some specimens; curved and pointed (pharyngo) branchial teeth are also present and what appears to be a pharyngobranchial plate (2<sup>nd</sup> or 3<sup>rd</sup>) is preserved in NHMW 1976/1812/51b and NHMW 1986/138/13a, whereas the dentigerous subtriangular fifth ceratobranchials are exposed in NHMW 1976/1812/51 (Fig. 6E). The hyoid bar bears seven sabre-like brachioistegal rays, all articulating with the anterior ceratohyal.

### *Axial skeleton*

The vertebral column comprises 45 to 46 vertebrae, of which 18 are abdominal. The vertebral centra are rectangular, longer than high, and characterized by lateral ridges. The anterior four vertebrae are shorter than the others. The abdominal vertebrae

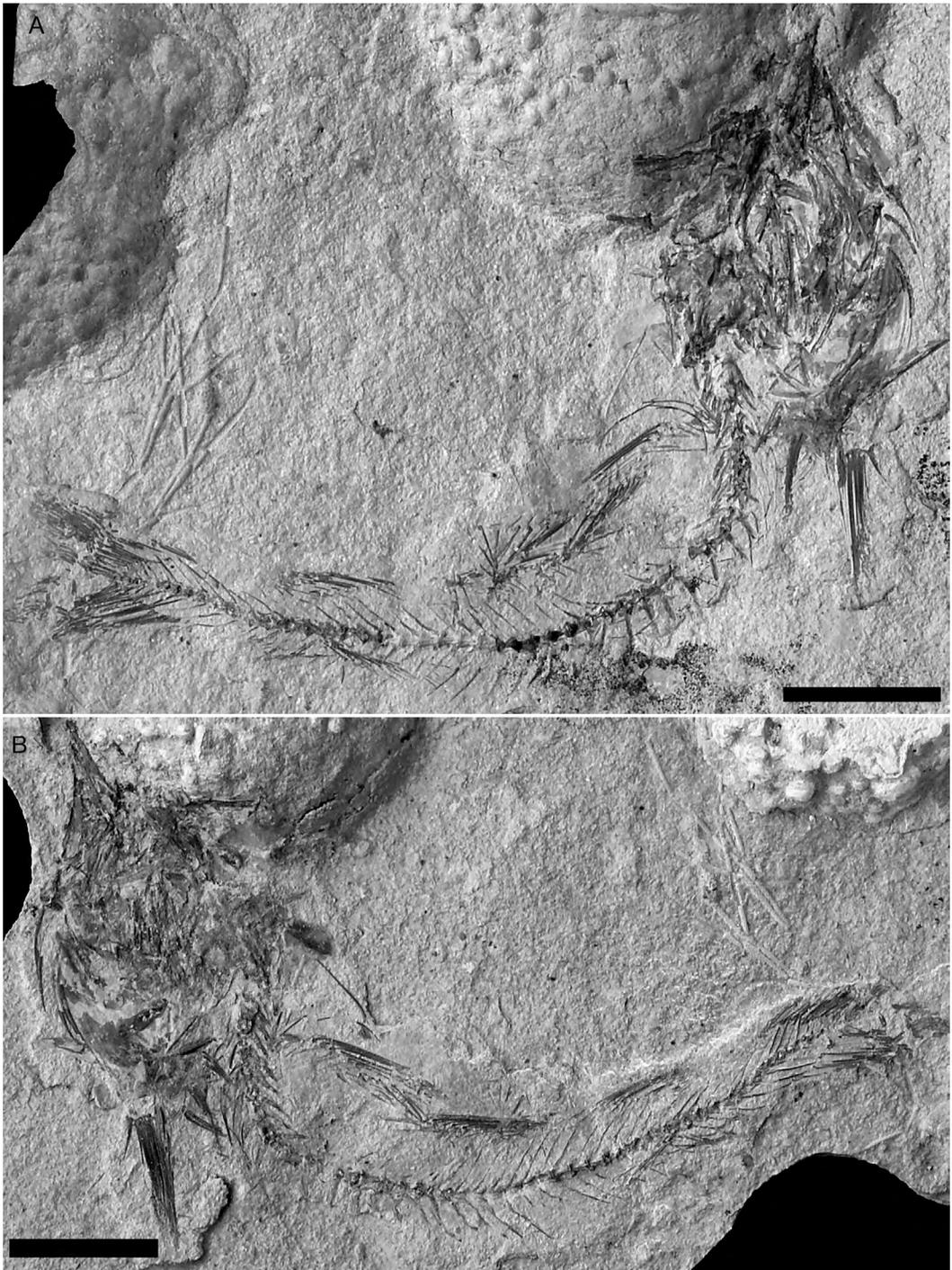


FIG. 4. — *Palimphemus anceps* Kner, 1862: **A**, NHMW 2002z0181/0087b; **B**, NHMW 2002z0181/0087a. Scale bars: 20 mm.

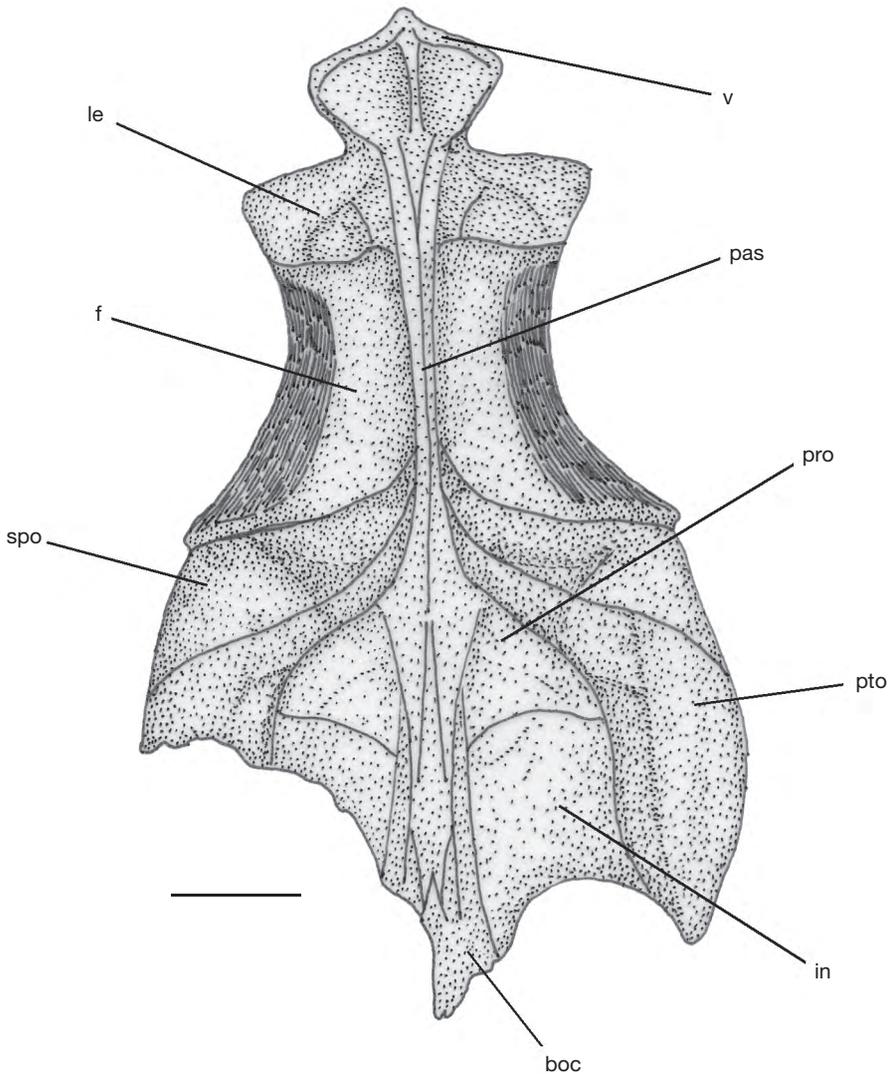


FIG. 5. — *Palimphemus anceps* Kner, 1862 (NHMW 1976/1812/38), neurocranium, ventral view. Abbreviations: see Material and methods. Scale bar: 5 mm.

bear well-developed, nearly vertical parapophyses, characterized by broad bases and pointed tips. The neural spines of vertebrae two to 14 are thickened, antero-posteriorly enlarged, and strongly bent backward. Slender pleural ribs articulate with the abdominal vertebrae; the anterior ribs originate ventrally on the vertebral centra, while the posterior ones insert on the posteroventral margin of the parapophyses. Thin epineural bones are also

present. The caudal skeleton (Fig. 7) is consistent with that of other gadids, and is characterized by two hypurals, a parhypural, two epurals, and absence of X and Y bones (see Barrington 1935a, b; Rosen & Patterson 1969; Marshall & Cohen 1973; Matarese *et al.* 1981; Patterson & Rosen 1989). The caudal fin is forked. The total number of caudal-fin rays ranges from 41 to 43, with seven upper and eight lower procurent elements.

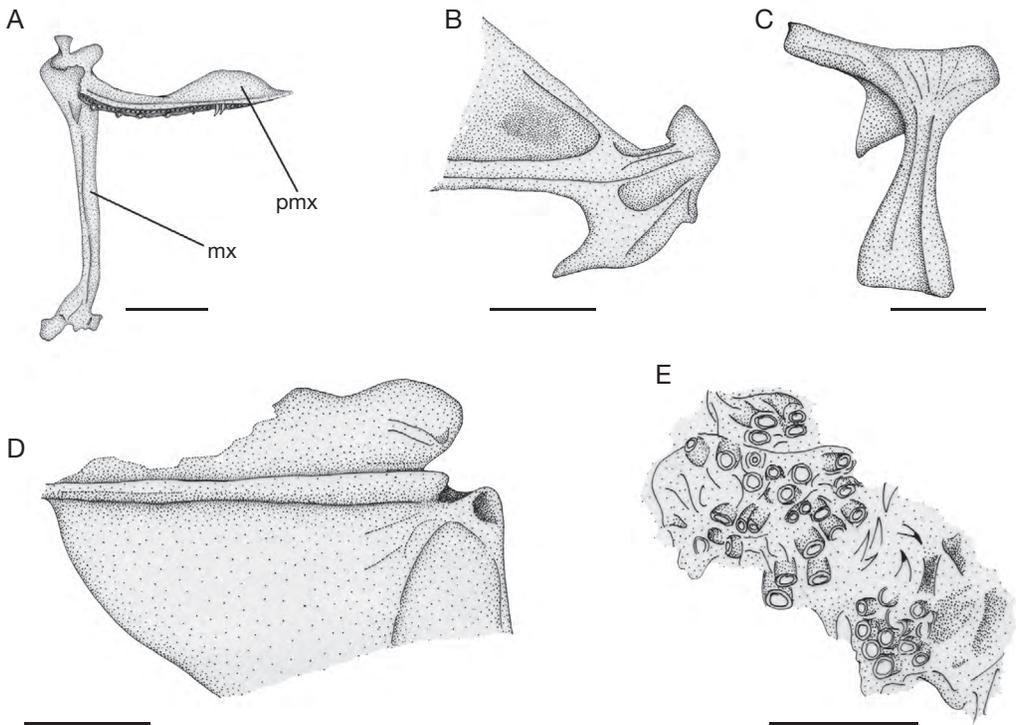


FIG. 6. — *Palimphemus anceps* Kner, 1862: **A**, NHMW 1976/1812/38, upper jaw, right medial view; **B**, NHMW 1986/138/13a, angulo-articular, right medial view; **C**, NHMW 1976/1812/38, hyomandibula, right lateral view; **D**, NHMW 1976/1812/38, opercle, left medial view; **E**, NHMW 1976/1812/51, 5<sup>th</sup> ceratobranchial. Abbreviations: see Material and methods. Scale bars: A, C, D, 5 mm; B, 2 mm; E, 1 mm.

### Median fins

There are three dorsal fins. The first dorsal fin inserts at the level of the 7<sup>th</sup> vertebra and contains 10–12 rays. The second dorsal fin inserts at the level of the 14<sup>th</sup> vertebra and contains 10–12 rays of progressively decreasing size. The first pterygiophore of the two anterior dorsal fins are large, roughly triangular in shape. The third dorsal fin originates at the level of the 26<sup>th</sup> vertebra and comprises 17–21 rays. The dorsal fins are separated from each other by large gaps, of which that between the second and third fins is greater than the length of the first dorsal-fin base. There is an indeterminate number of rayless pterygiophores (interneural bones in the sense of Dunn & Matarese 1984) between the second and third dorsal fins.

There are two anal fins. The first anal fin originates well behind the first dorsal-fin origin, approximately at the level of the 12<sup>th</sup> vertebra, and

apparently consists of 18–21 rays, but the original number was probably higher. The length of the base of the first anal fin is widely shorter than the distance between the tip of the snout and the origin of the first anal fin. The second anal fin is approximately opposite to the third dorsal fin, inserting at the level of the 27<sup>th</sup> vertebra; this fin contains 18–19 rays. The first and second anal fins are separated by a short distance, which reaches about 5% SL. Despite their external separation, the two anal fins are internally continuous, connected by rayless pterygiophores.

### Paired fins

The pectoral fin contains 15–18 rays. Of the girdle, the posttemporal, supracleithrum, cleithrum, postcleithrum, and parts of the scapula and coracoid are preserved in some specimens. The posttemporal is widely forked (Fig. 8C), with the two arms form-

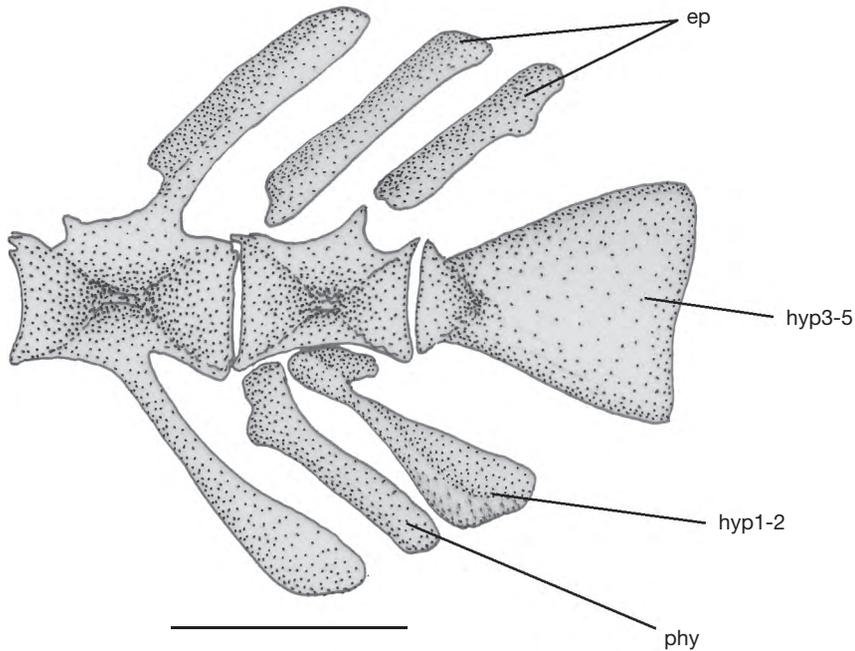


FIG. 7. — *Palimphemus anceps* Kner, 1862 (NHMW 1975/1691/28a+b), reconstruction of the caudal skeleton, left lateral view. Abbreviations: see Material and methods. Scale bar: 2 mm.

ing an acute angle that measures about 30°, very similar to that of *Micromesistius australis* Norman, 1937 (see Svetovidov 1948); the lateral flop (in the sense of Endo 2002) of the posttemporal is absent. The supracleithrum is a robust elongate bone with a gently rounded anterior profile. The cleithrum is large (Fig. 8A), with a prominent lower arm, similar to that of other gadids (see e.g., Dunn 1989; Endo 2002). The postcleithrum is moderately elongate, slender and remarkably curved and possesses a laminar spatulate proximal head (Fig. 8B); it greatly resembles that of *M. australis* (see Svetovidov 1948).

The pelvic fin consists of six rays. The basipterygium (Fig. 8D) is narrow and tubular distally and broadly expanded proximally; the proximal portion of the bone is roughly triangular with a thick central ridge, and a pointed and nearly triangular median process.

#### *Squamation*

The body is covered by small cycloid scales.

#### DISCUSSION

The limits, composition and intrarelationships of the family Gadidae have been extensively debated in the last 150 years. Gill (1863, 1884) recognized five subfamily-level groups (brosmines, ciliatines [= gaidropsarines], gadines, lotines and phycines) within this family. The separation between these groups was primarily supported by characters related to the structure of the median fins. In their monumental “Fishes of North and Middle America”, Jordan & Evermann (1898) recognized the same five groups exclusively based on the configuration of the dorsal fin. Regan (1903) did not discuss the intrafamilial relationships of the gadids. A few years later, Williamson (1909) discussed the phylogenetic relationships of the gadines on the basis of a large array of morphological characters. However, in all of these studies, the limits and composition of this family were widely different from those recognized today since members of many gadiform families (Bregmacerotidae Gill, 1872; Merlucciidae Gill,

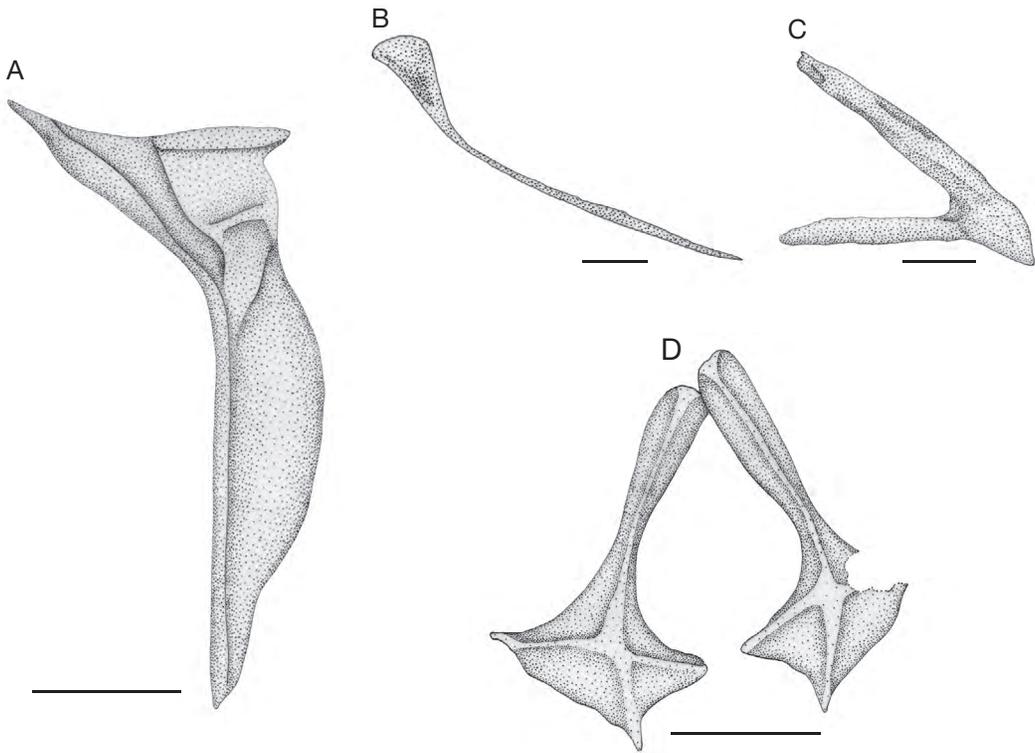


FIG. 8. — *Palimphemus anceps* Kner, 1862: **A**, NHMW 1986/138/13b, cleithrum, right medial view; **B**, NHMW 2002z0181/0087a, postcleithrum, right medial view; **C**, NHMW 1976/1812/69, posttemporal, left lateral view; **D**, NHMW 1986/138/13b, basipterygia, ventral view. Scale bars: A, 5 mm; B-D, 2 mm.

1884; Moridae Moreau, 1881) were considered as belonging to the Gadidae. Svetovidov (1948) based on a detailed morphological study concluded that the classification of this family must be based on functionally related features, the median fins, and recognized a graded series of more than 20 genera separated into three subfamilies, Gadinae, Lotinae Bonaparte, 1838 and Merlucciinae. Except for Gae-mers (1976) that recognized six subfamilies based on otolith characters, the classification proposed by Svetovidov (1948) remained nearly unmodified for more than 30 years when Markle (1982), using a cladistic approach, presented a new classification of the family based on meristic and developmental data. Markle (1982) also documented the anatomical basis for the exclusion of the hakes (merlucciids) from the Gadidae. The classification proposed by Markle (1982) was discussed by Fahay & Markle

(1984) and Dunn & Matarese (1984), who provided additional diagnostic characters for each subfamily and attempted to establish the relationships of these groups based on early life history stages. Dunn (1989) provided the first cladistic analysis of the family. Unfortunately, his cladogram was weakly supported leading him to consider it as highly tentative. Primarily based on arthrology and myology, Howes (1991a) proposed a totally different classification of the family. More recently, Endo (2002), also based on morphological data, recognized two intrafamilial groups, each constituted by two subfamilies. However, except for the monophyletic status of the family Gadidae and subfamily Gadinae, there is no agreement between the different classifications proposed. This is mostly due to the troublesome nature of character polarity and homology in these fishes, in turn related to the

high level of homoplasy and the number of reversals and losses in character states (see Dunn 1989). In the last decade, several molecular phylogenies focusing on gadid intrarelationships appeared (Carr *et al.* 1999; Møller *et al.* 2002; Pogson & Mesa 2004; Bakke & Johansen 2005; Coulson *et al.* 2006; Teletchea *et al.* 2006; von der Heyden & Matthee 2008; Roa-Varón & Ortí 2009). Teletchea *et al.* (2006) based on the combined morphological-molecular approach recognized four subfamilies within the Gadidae, namely the Gadinae, Gaidropsarinae, Lotinae and Phycinae.

The morphoanatomical analysis of the specimens of *Palimphemus anceps* has revealed several apomorphic gadine characters, such as the general physiognomy of the body, the possession of three dorsal and two anal fins, and absence of X and Y bones in the caudal skeleton (Svetovidov 1948; Markle 1982, 1989; Dunn & Matarese 1984; Fahay & Markle 1984; Dunn 1989; Howes 1991a; Endo 2002; Teletchea *et al.* 2006). Within the gadine fishes, the general appearance of *Palimphemus* is in many ways reminiscent of that of *Micromesistius* Gill, 1863 to which it appears to be related; such a possible phylogenetic relationship is supported by a number of shared derived features, including: lower jaw projecting beyond the upper one, wide separation between the first and second and the second and third dorsal fins, absence of the posterior process of the basipterygium, absence of the lower process of the hyomandibula, possession of a moderately elongate postcleithrum (see Dunn 1989), and absence of the lateral flap of the posttemporal (see Endo 2002). However, despite the remarkable affinity between *Palimphemus* and *Micromesistius* as evidenced by the comparative analysis, these two genera distinctly differ from each other in many morphometric, meristic and anatomical characters (Fig. 9A, B).

Morphometric characters, such as the deeper body (20.3 vs 16.5-18% SL), longer head (29.3 vs 22-24% SL), massive and wider neurocranium (maximum width 54.3 vs 45-46.5% of cranial length) (Fig. 9C, D), insertion of the anal fin well behind the first dorsal-fin origin (preanal distance 46 vs 31-34% SL), preanal distance exceeding the base length of the anal fin, wider separation

between first and second dorsal fins (7.5 vs 5-6% SL), reduced separation between second and third dorsal fins (9 vs 10.5-12% SL), wider separation between first and second anal fins (5.4 vs 1.2-3.5% SL), reduced first dorsal-fin base length (7.5 vs 9.5-10.5% SL), reduced first anal-fin base length (23.7 vs 36-38% SL), and reduced second anal-fin base length (14.2 vs 17-18.5% SL) clearly evidence the taxonomic identity of the genus *Palimphemus*.

As far as the meristic features are concerned, the comparison between the two genera evidenced the reductive nature of several parameters in *Palimphemus*, which is characterized by fewer vertebrae (45-46 vs 54-60), third dorsal-fin rays (17-21 vs 21-27), first (18-21 vs 33-41) and second (18-19 vs 22-30) anal-fin rays, and pectoral-fin rays (15-18 vs 18-23).

Moreover, *Palimphemus* and *Micromesistius* also exhibit different character states of phylogenetically relevant features (see Dunn 1989).

As described above, the hyomandibula of *Palimphemus anceps* bears a ventrally directed and sharply pointed preopercular process (Fig. 9E), whereas those of both species of *Micromesistius* possess a short and horizontally oriented preopercular processes (Fig. 9F, G). Therefore, according to the interpretation provided by Dunn (1989), *Micromesistius* exhibits the derived condition also observed in gaidropsarines and *Raniceps* Cuvier *in* Oken, 1817; *Palimphemus* is characterized by the plesiomorphic condition, typical of most gadid fishes.

The possession of the horizontal opercular rib is a remarkable diagnostic feature of *Palimphemus anceps*; because of the relatively large size of the specimen, it is possible to hypothesize that the opercular rib was retained during the ontogeny in this Middle Miocene gadid, likewise in the extant gadid genera *Gadiculus* Guichenot, 1850, *Melanogrammus* Gill, 1862, *Merlangius* Geoffroy, 1767, *Microgadus* Gill, 1865 and *Pollachius* Nilsson *in* Bonaparte, 1846 (see Dunn 1989).

The vertebral column of *Palimphemus anceps* contains 18 abdominal vertebrae. Basal gadines such as *Gadiculus* and *Trisopterus* Rafinesque, 1814 are characterized by a similar low number of abdominal vertebrae (13-19). This appears to be the primitive condition within gadids (Dunn 1989).

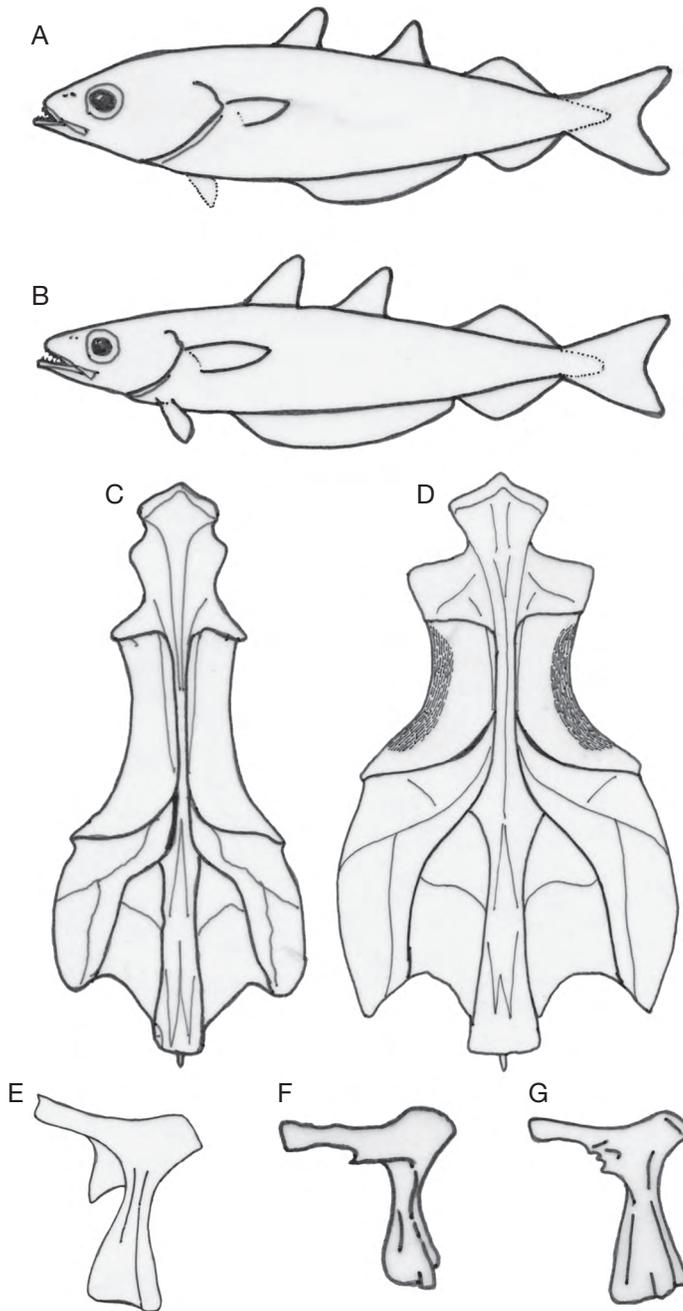


FIG. 9. — **A, B**, reconstruction of *Palimphemus anceps* Kner, 1862 (**A**) and *Micromesistius poutassou* (Risso, 1827) (**B**), modified from Cohen *et al.* (1990); **C, D**, ventral aspect of the neurocranium of *Micromesistius poutassou* (**C**) and *Palimphemus anceps* (**D**); **E-G**, hyomandibula of *Palimphemus anceps* (**E**), *Micromesistius poutassou* (**F**) and *Micromesistius australis* (**G**); **C, F, G**, modified from Svetovidov (1948).

*Micromesistius* shows the derived condition with a very high number of abdominal vertebrae that ranges from 24 to 26 elements.

An additional remarkable difference between *Palimphemus* and *Micromesistius* concerns the total number of caudal-fin rays. *Palimphemus anceps* has a reduced total number of caudal-fin rays (41-43), similar to those characteristic of *Gadiculus* and *Trisopterus* (< 45). The total number of caudal-fin rays is moderately high (50) in *Micromesistius*. According to Dunn (1989), the condition of *Gadiculus*, *Palimphemus* and *Trisopterus* must be interpreted as primitive.

The apparent affinities with the genus *Micromesistius* allowed us to infer about the phylogenetic position of *Palimphemus* within the gadine fishes. Recent phylogenetic analyses (Teletchea *et al.* 2006; von der Heyden & Matthee 2008; Roa-Varón & Ortí 2009) include *Micromesistius* in a well-defined clade together with the genera *Gadiculus* and *Trisopterus*. All of these molecular studies concur to suggest that the clade formed *Gadiculus*, *Micromesistius* and *Trisopterus* is sister to a clade comprising all the other gadine genera. As described above, a large set of morphological and meristic features evidence the existence of close relationships between *Palimphemus* and *Micromesistius*, thereby suggesting that *Palimphemus* may be the fourth member of the clade of basal gadine genera recurrently hypothesized by molecular phylogenetic analyses. The plausibility of such a clade appears to be supported by both the fossil record and biogeography. Based on the stratigraphic ranges of fossil gadine fishes provided by Nolf & Steurbaut (1989), the genera *Gadiculus*, *Micromesistius* and *Trisopterus* appeared in the Oligocene and were remarkably diverse and abundant in the Miocene, whereas the remaining gadine genera mostly appeared in the record during the Pliocene. This distributional pattern fits well with the results of the phylogenetic analyses, evidencing the congruence between the order of events in the evolution of gadine fishes and the appearance of the two main clades. The existence in the Miocene of a genus – *Palimphemus* – related to *Micromesistius* is therefore perfectly consistent with the general trends of the fossil record of the

Gadidae. The three basal gadine genera, *Gadiculus*, *Micromesistius* and *Trisopterus*, are the only members of the Gadidae, together with *Merlangius*, which extend to the warm temperate continental shelves of the eastern Atlantic and the Mediterranean (Svetovidov 1948; Howes 1991b). Fossil otoliths document the presence of these thermophilous genera in the Mediterranean and Paratethys during the Miocene (e.g., Nolf & Steurbaut 1983; Radwańska 1992). In Central Paratethys, these genera possibly were sympatric with *Palimphemus anceps*. Therefore, it is reasonable to hypothesize that the thermophilous affinity of the members of the group of basal gadines (including *Palimphemus*) possibly represents a further distinctive ecological character of this clade.

#### Acknowledgements

We are grateful to Walter Landini (Dipartimento di Scienze della Terra, Università di Pisa, Pisa) for its suggestions and critical review of an early draft of the text. We are particularly grateful to Alice Schumacher (NHMW) for the photographs. Thanks are also due to Federica Giudice for improvement of the English. Many thanks go to Alexandre F. Bannikov (Paleontological Institute, Russian Academy of Sciences, Moscow), Francesco Santini (Department of Ecology and Evolutionary Biology, University of California at Los Angeles, Los Angeles) and Annemarie Ohler (Muséum national d'Histoire naturelle, Paris) for constructive advice on improving the manuscript. The research of the senior author was supported by the SYNTHESYS grants of the Naturhistorisches Museum, Wien.

#### REFERENCES

- BACHMAYER F. 1980. — Eine fossile Schalgennadel (Syngnathidae) aus dem Leithakalk (Badenien) von St. Margarethen, Burgenland (Österreich). *Annalen des Naturhistorischen Museums in Wien* 83: 29-33.
- BAKKE I. & JOHANSEN S. D. 2005. — Molecular phylogenetics of Gadidae and related Gadiformes based on mitochondrial DNA sequences. *Marine Biotechnology* 7: 61-69.

- BARRINGTON E. J. 1935a. — Structure of the caudal fin of the cod. *Nature* 135: 270.
- BARRINGTON E. J. 1935b. — The structure and development of the tail in the plaice (*Pleuronectes platessa*) and the cod (*Gadus morhua*). *Quarterly Journal of the Microscopical Society* 79: 447-469.
- BELLWOOD D. R. & SCHULTZ O. 1991. — A review of the fossil record of the parrotfishes (Labroidae: Scaridae), with a description of a new *Calotomus* species from the Middle Miocene (Badenian) of Austria. *Annalen des Naturhistorischen Museums in Wien* 92 A: 55-71.
- BRZOBOHATÝ R. & SCHULTZ O. 1978. — Die Fischfauna des Badeniens, in PAPP A., CÍCHA I., SENES J. & STEININGER F. (eds), *M<sub>4</sub> Badenien (Moravien, Wielicien, Kosovien)*. *Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys* 6: 441-465.
- CARR S. M., KIVLICHAN D. S., PEPIN P. & CRUTCHER D. C. 1999. — Molecular systematic of gadid fishes: implications for the biogeographic origins of Pacific species. *Canadian Journal of Zoology* 77: 19-26.
- CHANET B. & SCHULTZ O. 1994. — Pleuronectiform fishes from the Upper Badenian (Middle Miocene) of St. Margarethen (Austria). *Annalen des Naturhistorischen Museums in Wien* 96 A: 95-115.
- COHEN D. M. 1984. — Gadiformes: overview, in MOSER H. G., RICHARDS W. J., COHEN D. M., FAHAY M. P., KENDALL A. W. JR. & RICHARDSON S. L. (eds), *Ontogeny and systematics of fishes*. American Society of Ichthyologists and Herpetologists, Special Publication 1: 259-265.
- COHEN D. M., INADA T., IWAMOTO T. & SCIALABBA N. 1990. — Gadiform fishes of the world. *FAO Fisheries Synopsis* 10: 1-442.
- COULSON M. W., MARSHALL H. D., PEPIN P. & CARR S. M. 2006. — Mitochondrial genomics of gadine fishes: implications for taxonomy and biogeographic origins for whole-genome data sets. *Genome* 49: 1115-1130.
- DUNN J. R. 1989. — A provisional phylogeny of gadid fishes based on adult and early life-history characters, in COHEN D. M. (ed.), *Papers on the Systematics of Gadiform Fishes*. *Science Series, Natural History Museum of the Los Angeles County* 32: 209-236.
- DUNN J. R. & MATARESE A. C. 1984. — Gadidae: development and relationships, in MOSER H. G., RICHARDS W. J., COHEN D. M., FAHAY M. P., KENDALL A. W. JR. & RICHARDSON S. L. (eds), *Ontogeny and Systematics of Fishes*. American Society of Ichthyologists and Herpetologists, Special Publication 1: 283-299.
- ENDO H. 2002. — Phylogeny of the order Gadiformes. *Memoirs of the Graduate School of Fisheries Sciences, Hokkaido University* 49: 75-149.
- FAHAY M. P. & MARKLE D. F. 1984. — Gadiformes: development and relationships, in MOSER H. G., RICHARDS W. J., COHEN D. M., FAHAY M. P., KENDALL A. W. JR. & RICHARDSON S. L. (eds), *Ontogeny and Systematics of Fishes*. American Society of Ichthyologists and Herpetologists, Special Publication 1: 265-283.
- FEDOTOV V. F. & BANNIKOV A. F. 1989. — On the phylogenetic relationships of fossil Gadidae, in COHEN D. M. (ed.), *Papers on the systematics of gadiform fishes*. *Science Series, Natural History Museum of the Los Angeles County* 32: 187-196.
- GAEMERS P. A. M. 1976. — New concepts in the evolution of the Gadidae (Vertebrata, Pisces), based on their otoliths. *Mededelingen van der Werkgroep voor Tertiaire en Kwartaire Geologie* 13: 3-22.
- GAEMERS P. A. M. 1978. — A biozonation based on Gadidae otoliths for the northwest European younger Cenozoic, with description of some new species and genera. *Mededelingen van der Werkgroep voor Tertiaire en Kwartaire Geologie* 15: 141-161.
- GILL T. N. 1863. — Synopsis of the North American gadoid fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia* 15: 229-242.
- GILL T. N. 1884. — On the anacanthine fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1884: 167-183.
- GOODRICH E. S. 1909. — Vertebrata Craniata. Fascicule I. Cyclostomes and fishes, in LANKASTER E. R. (ed.), *A Treatise on Zoology. Part 9*. Adam & Charles Black, London, 518 p.
- GORJANOVIC-KRAMBERGER D. 1902. — Palaeoichthyologische Beiträge. *Mitteilungen aus dem Jahrbuche der Kaiserlichen Ungarischen Geologischen Anstalt* 14: 1-21.
- HECKEL J. J. 1850. — Beiträge zur Kenntniss der fossilen Fische Oesterreichs. I. *Denkschriften der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 1: 201-242.
- HECKEL J. J. 1856. — Beiträge zur Kenntniss der fossilen Fische Oesterreichs. *Denkschriften der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 11: 187-274.
- HECKEL J. J. & KNER R. 1861. — Neue Beiträge zur Kenntnis der fossile Fische Oesterreichs. *Denkschriften der Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 19: 49-76.
- HOFMANN T. 2001. — Der Leithakalk, in WEIDERT W. K. (ed.), *Klassische Fundstellen der Paläontologie, Band 4*. Goldschneck-Verlag, Korb: 215-221.
- HOWES G. J. 1991a. — Anatomy, phylogeny and taxonomy of the gadoid fish genus *Macruronus* Günther, 1873, with a revised hypothesis of gadoid phylogeny. *Bulletin of the British Museum of Natural History (Zoology)* 51: 77-110.
- HOWES G. J. 1991b. — Biogeography of gadoid fishes. *Journal of Biogeography* 18: 595-622.
- INADA T. & NAKAMURA I. 1975. — A comparative study of two populations of the gadoid fish *Micromesistius australis* from the New Zealand and Patagonian-Falkland regions. *Bulletin of the Far Seas Fisheries Research Laboratory* 13: 1-26.
- JORDAN D. S. & EVERMANN B. W. 1898. — Fishes of

- North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in waters of North America north of Isthmus of Panama. Part III. *Bulletin of the United States National Museum* 47: 2183-3136.
- KEFERSTEIN C. 1828. — Beobachtungen und Ansichten über die geognostischen Verhältnisse der nördlichen Kalk-Alpenkette in Österreich-Bayern. *Teutschland geognostisch-geologisch dargestellt* 513: 1-425.
- KNER R. 1862. — Kleinere Beiträge zur Kenntnis der fossilen Fische Österreichs. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Abteilung I* 45: 485-498.
- KNER R. 1863. — Über einige fossile Fische aus den Kreide- und Tertiärschichten von Comen und Pod-sused. *Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe, Abteilung I* 48: 126-148.
- MARKLE D. F. 1982. — Identification of larval and juvenile Canadian Atlantic gadoid with comments on the systematics of gadid subfamilies. *Canadian Journal of Zoology* 60: 3420-3438.
- MARKLE D. F. 1989. — Aspects of character homology and phylogeny of the Gadiformes, in COHEN D. M. (ed.), Papers on the systematics of gadiform fishes. *Science Series, Natural History Museum of the Los Angeles County* 32: 59-88.
- MARSHALL N. B. & COHEN D. M. 1973. — Order Anacanthini (Gadiformes): characters and synopsis of families, in COHEN D. M. (ed.), Fishes of the Western North Atlantic. *Memoirs of the Sears Foundation for Marine Research* 6: 479-495.
- MATARESE A. C., RICHARDSON S. L. & DUNN J. R. 1981. — Larval development of Pacific tomcod, *Microgadus proximus*, in the Northeast Pacific Ocean with comparative notes on larvae of walleye Pollock, *Theragra chalcogramma*, and Pacific cod, *Gadus macrocephalus* (Gadidae). *Fishery Bulletin* 78: 923-940.
- MØLLER P. R., JORDAN A. D., GRAVLUND P. & STEFFENSEN J. F. 2002. — Phylogenetic position of the cryope-lagic codfish genus *Arctogadus* Drjagin, 1932 based on partial mitochondrial cytochrome b sequences. *Polar Biology* 25: 342-349.
- NELSON J. S. 2006. — *Fishes of the World*. John Wiley & Sons Inc., Hoboken, 601 p.
- NOLF D. & STEURBAUT E. 1983. — Revision des otolithes de téléostéens du Tortonien stratotypique et de Montegibbio (Miocène supérieur d'Italie septentrionale). *Mededeelingen van de werkgroep voor Tertiaire en Kwartaire Geologie* 20: 143-197.
- NOLF D. & STEURBAUT E. 1989. — Importance and restrictions of the otolith-based fossil record of gadiform and ophidiiform fishes, in COHEN D. M. (ed.), Papers on the systematics of gadiform fishes. *Science Series, Natural History Museum of the Los Angeles County* 32: 47-58.
- PATTERSON C. & ROSEN D. E. 1977. — Review of ichtthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* 158: 81-172.
- PATTERSON C. & ROSEN D. E. 1989. — The Paracanthopterygii revisited: order and disorder in COHEN D. M. (ed.), Papers on the Systematics of Gadiform Fishes. *Science Series, Natural History Museum of the Los Angeles County* 32: 5-36.
- POGSON G. H. & MESA K. A. 2004. — Positive Darwinian selection at the Pantophysin (*Pan I*) Locus in marine gadid fishes. *Molecular Biology and Evolution* 21: 65-75.
- RADWAŃSKA U. 1992. — Fish otoliths in the Middle Miocene deposits of southern Poland. *Acta Geologica Polonica* 42: 141-328.
- RAFINESQUE C. S. 1810. — *Indice d'ittologia siciliana; ossia, catalogo metodico dei nomi latini, italiani e siciliani dei pesci, che si rinvencono in Sicilia disposti second un metodo natural e seguito da un'appendice che contiene la descrizione di alcuni nuovi pesci siciliani*. Messina.
- REGAN C. T. 1903. — On the systematic position of the gadoid or anacanthine fishes. *Annals and Magazine of Natural History* 11: 459-466.
- RIEGL B. & PILLER W. E. 2000. — Biostromal coral facies - a Miocene example from the Leitha Limestone (Austria) and its actualistic interpretation. *Palaios* 15: 399-413.
- ROA-VARÓN A. & ORTÍ G. 2009. — Phylogenetic relationships among families of Gadiformes (Teleostei, Paracanthopterygii) based on nuclear and mitochondrial data. *Molecular Phylogenetics and Evolution* 52: 688-704.
- ROSEN D. E. & PATTERSON C. 1969. — The structure and relationships of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History* 141: 357-474.
- SCHMID H. P., HARZHAUSER M. & KROH A. 2001. — Hypoxic Events on a Middle Miocene Carbonate Platform of the Central Paratethys (Austria, Badenian, 14 Ma), with contributions by Coric S., Rögl F. & Schultz O. *Annalen des Naturhistorischen Museums in Wien* 102 A: 1-50.
- SCHUBERT R. J. 1906. — Die Fischotolithen des Österreich-Ungarn Tertiärs. III. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt* 56: 623-706.
- SCHULTZ O. 1993. — Der Nachweis von *Scorpaena* s.s. (Pisces, Teleostei) im Badenien von St. Margarethen, Burgenland, Österreich. Revision von *Scorpaena prior* Heckel in Heckel & Kner, 1861. *Annalen des Naturhistorischen Museums in Wien* 95 A: 127-177.
- SCHULTZ O. 2006a. — Rasiermesserfische (Aeoliscus: Centriscidae: Osteichthyes) aus dem Badenien (Mittel-Miozän) von St. Margarethen im Burgenland, Österreich (Zentrale Paratethys). *Annalen des Naturhistorischen Museums in Wien* 107 A: 71-85.

- SCHULTZ O. 2006b. — An Anglerfish, *Lophius* (Osteichthyes, Euteleostei, Lophiidae), from the Leitha Limestone (Badenian, Middle Miocene) of the Vienna Basin, Austria (Central Paratethys). *Beiträge zur Paläontologie* 30: 427-435.
- SVETOVIDOV A. N. 1948. — Treskoobraznye [Gadiformes], in Fauna SSSR, *Zoologicheskii Institut Akademii Nauk SSSR* 34, Ryby [Fishes], IX 4: 1-222. [in Russian; English translation, 1962, Jerusalem: Israel Program for Scientific Translation].
- TELETCHEA F., LAUDET V. & HÄNNI C. 2006. — Phylogeny of the Gadidae (sensu Svetovidov, 1948) based on their morphology and two mitochondrial genes. *Molecular Phylogenetics and Evolution* 38: 189-199.
- VON DER HEYDEN S. & MATTHEE C. A. 2008. — Towards resolving familial relationships within the Gadiformes, and the resurrection of the Lyconidae. *Molecular Phylogenetics and Evolution* 48: 764-769.
- WILLIAMSON H. C. 1909. — On the specific characters of the haddock (*Gadus aeglefinus*, Linn.); whiting (*Gadus merlangus*, Linn.); *Gadus poutassou*, Risso; *Gadus argenteus*, Guichenot; *Gadus saida*, Lepechin; *Gadus ogac*, Richardson; *Gadus navaga*, Köheuter; with a key to the species of *Gadus* found in northern waters. *Annual Report of the Fisheries Board of Scotland* 27: 97-134.
- WOODWARD A. S. 1901. — *Catalogue of the Fossil Fishes in the British Museum (Natural History), Vol. IV: Actinopterygian Teleostomi of the Suborders Isospondyli (in part), Ostariophysi, Apodes, Percosoces, Hemibranchii, Acanthopterygii, and Anacanthini*. Trustees of the British Museum (Natural History), London, 636 p.

Submitted on 1<sup>st</sup> February 2011;  
accepted on 31 March 2011.