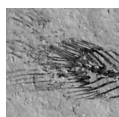# Middle Miocene rockling (Teleostei, Gadidae) from the Paratethys (St. Margarethen in Burgenland, Austria)

GIORGIO CARNEVALE & MATHIAS HARZHAUSER

Fishes of the subfamily Gaidropsarinae, commonly known as rocklings, are anatomically unique within the family Gadidae (Teleostei, Gadiformes), mostly because of their possession of a highly specialized chemosensory and vibratile first dorsal fin. The genus *Gaidropsarus* contains 13 extant species occurring from subtropical to temperate waters in the North Atlantic, Mediterranean, South Africa, New Zealand, Tasmania, Japan and southeastern Pacific, plus a single fossil species from the Miocene of Algeria. A new species of rockling, *Gaidropsarus pilleri* sp. nov., is described from the Middle Miocene (Late Badenian) corallinacean limestone of St. Margarethen in Burgenland, Eisenstadt-Sopron Basin, Austria based on seven articulated skeletons. The new species is based on a unique combination of features, including: possession of a wide neurocranium (neurocranial width contained less than two times in its length); well-developed sphenotic spine; epibranchials 2 and 3 characterized by massive uncinate processes; presence of 44 (13 + 31) vertebrae; five posterior parapophyses enlarged, the posterior three wing-like; 2nd dorsal fin contains about 50 rays; anal fin with 43 rays; caudal peduncle very short (2.4% SL). *Gaidropsarus pilleri* sp. nov. is the earliest known occurrence of the rocklings based on skeletal remains. The vibratile and chemosensory first dorsal fin of gaidropsarines may have arisen by co-option of the first dorsal-fin module. • Key words: Teleostei, Gadiformes, Gadidae, *Gaidropsarus pilleri*, Middle Miocene, Badenian, St. Margarethen in Burgenland, Eisenstadt-Sopron Basin, Austria.

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The gaidropsarines, commonly known as rocklings, constitute a monophyletic assemblage of bottom-living gadid fishes that occur from the intertidal zone to the deep-sea. This small group includes three genera, among which *Gaidropsarus* is by far the most diverse with 14 recognized species (see Svetovidov 1986, Carnevale 2007). The genus *Gaidropsarus* is the only member of the group characterized by a bipolar distribution (Howes 1991), with species that occur in subtropical to temperate waters in the North Atlantic, Mediterranean, South Africa, New Zealand, Tasmania, Japan and southeastern Pacific. More than half of the known species occur in the northern hemisphere, mostly in the north-eastern Atlantic and the Mediterranean. Articulated skeletal remains of gaidropsarines are extremely rare in the fossil record, apparently represented by a single partially complete individual from the Messinian of the Chelif Basin, Algeria (Carnevale 2007). The goal of this paper is to describe a new species of the genus *Gaidropsarus* from the Middle Miocene corallinacean limestone of St. Margarethen in Burgenland, Eisenstadt-Sopron Basin, Austria.

Fossil fishes from the corallinacean limestone cropping out in the surroundings of the St. Margarethen in Burgenland village are known since the first half of the 19th century (see Münster 1846) and several specimens were described at that time by celebrated Austrian naturalists such as J.J. Heckel and R. Kner (Heckel 1950, 1856; Heckel & Kner 1861; Kner 1862). A very large collection of these finely preserved fossil fishes is currently housed in the Naturhistorisches Museum in Vienna and only a small part has been studied (Bachmayer 1980; Bellwood & Schultz 1991; Schultz 1993, 2006a, 2006b; Chanet & Schultz 1994; Carnevale *et al.* 2012). A comprehensive analysis of the diversity and paleoenvironmental significance of this ichthyofauna is currently in progress.

The Middle Miocene corallinacean limestone exposed in the Neogene Eisenstadt-Sopron Basin is usually referred

to as Leitha Limestone (Keferstein 1828, Riegl & Piller 2000). Fossil fishes were collected at the Kummer Quarry, along the Rust Hills, about 2 km E of St. Margarethen in Burgenland village (47° 48´ 01.76˝ N, 16° 37´ 59.12˝ E). A detailed analysis of the stratigraphy and sedimentology of the Kummer Quarry was carried out by Schmid *et al.* (2001). The ichthyolitiferous layers consist of greenish-whitish calcarenitic marls that originated in a general regime of reduced water energy and hypoxic conditions. The age of these deposits has been established based on the calcareous nannoplankton content, which indicates zone NN5b, around the Langhian/Serravallian boundary, approximately between 14.0 and 13.5 Ma, corresponding to the Late Badenian of the Paratethyan stratigraphy (*Bulimina-Bolivina* Zone of Papp *et al.* 1978).

Materials and methods

The specimens are deposited in the Geological-Palaeontological Department of the Natural History Museum, Vienna (NHMW). The available material consists of seven articulated skeletons with bones that appear brown or dark orange, preserved on greenish-whitish laminated calcarenitic marls.

The fossils were examined using a Leica MZ6 stereomicroscope equipped with a camera lucida drawing arm. Measurements were taken with a dial calliper, to the nearest 0.1 mm. Some skeletons required matrix removal before examination; this was achieved using thin entomological needles.

Comparative information was derived mainly from the literature (*e.g.*, Svetovidov 1948, 1986; Shcherbachev 1995; Carnevale 2007; Balushkin 2009).

Systematic palaeontology

Subdivision Teleostei *sensu* Patterson & Rosen, 1977
Order Gadiformes Goodrich, 1909
Suborder Gadoidei *sensu* Endo, 2002
Family Gadidae Rafinesque, 1810

Genus *Gaidropsarus* Rafinesque, 1810

***Gaidropsarus pilleri* sp. nov.**
Figures 1–7, Table 1

Holotype. – NHMW 1988/140/137a+b, nearly complete and well-preserved articulated skeleton in part and counterpart (Fig. 1).

Paratypes. – NHMW 1988/0140/0090a+b, partially complete articulated skeleton in part and counterpart (Fig. 2A, B); NHMW 1976/1812/0141, incomplete articulated skeleton

lacking the head and anterior portion of the axial skeleton (Fig. 2C); NHMW 1986/0138/0020a+b, partially complete articulated skeleton in part and counterpart (Fig. 2F, G); NHMW 2000z0135/0113, partially complete articulated skeleton in part and counterpart (Fig. 2J, K).

Type locality and horizon. – St. Margarethen in Burgenland locality; Kummer Quarry; Middle Miocene, Late Badenian (around the Langhian/Serravallian boundary), *Bulimina-Bolivina* Zone, NN5b zone (see Schmid *et al.* 2001).

Referred material. – NHMW 1976/1812/0127a+b, partially complete articulated skeleton in part and counterpart (Fig. 2D, E); NHMW 1988/0140/0017a+b, partially complete articulated skeleton in part and counterpart (Fig. 2H, I).

Diagnosis. – A *Gaidropsarus* with wide neurocranium (neurocranial width contained less than two times in its length); well-developed sphenotic spine; epibranchials 2 and 3 with massive uncinate processes; 44 (13 + 31) vertebrae; five posterior parapophyses enlarged; three posterior parapophyses wing-like; 2nd dorsal fin with about 50 rays; anal fin with 43 rays; caudal peduncle very short (2.4% SL).

Etymology. – It is our pleasure to name this species in honour to the celebrated Austrian palaeontologist Werner E. Piller in recognition of his outstanding contribution to the Mesozoic and Cenozoic palaeontology.

Measurements. – [Based on the holotype NHMW 1988/140/137a+b; standard length (SL): 88.8 mm.] As percentage of SL: maximum body depth: 19.2%; head length: 21.6%; snout length: 7.3%; mouth gape extension: 12.9%; caudal peduncle length: 2.4%; caudal peduncle depth: 4.8%; predorsal (2nd fin) distance: 37%; preanal distance: 50.4%; 2nd dorsal-fin base length: 56.4%; anal-fin base length: 43.8%.

Description. – The body is elongate and relatively slender (Figs 1, 2). The maximum body depth is contained more than five times in SL. The head is large and dorsoventrally compressed, its length is contained less than five times in SL. The snout is elongate and nearly tubular. The diameter of the orbit cannot be properly defined because of inadequate preservation. The caudal peduncle is extremely reduced (2.4% SL), its length is contained slightly less than two times in its depth.

The head skeleton exhibits various degrees of disarticulation in the examined specimens, with the bones displaced from their original position and often extensively fragmented and inadequately preserved. The neurocranium is clearly recognizable in most of the available specimens,
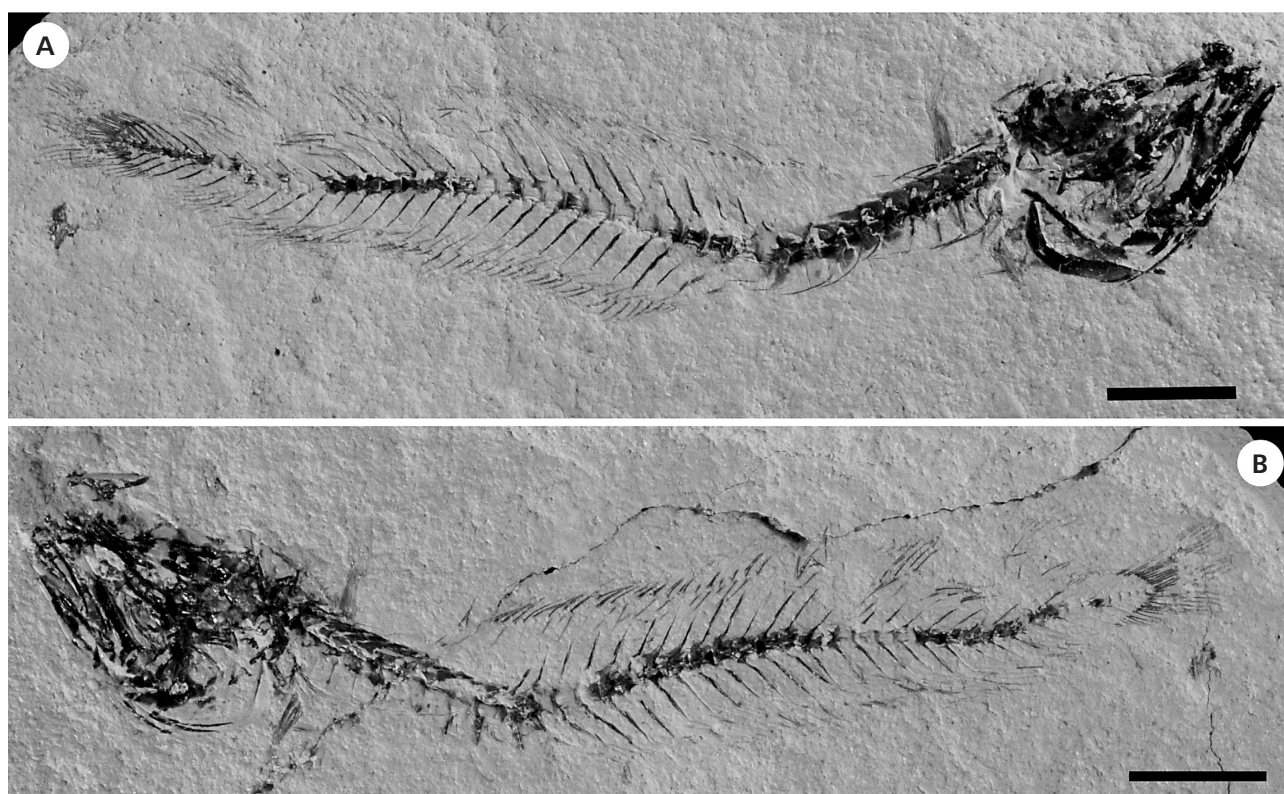
Figure 1. *Gaidropsarus pilleri* sp. nov. Holotype. • A – NHMW 1988/140/137a; B – NHMW 1988/140/137b. Scale bars 10 mm.

Table 1. Counts for *Gaidropsarus pilleri* sp. nov.

	vertebrae	2nd dorsal-fin rays	anal-fin rays	caudal-fin rays	pectoral-fin rays
NHMW 1988/140/137a+b	44 (13+31)	?50	43	34	17 (18)
NHMW 1976/1812/0127a+b	44 (13+31)	?	?	?	?17
NHMW 1988/0140/0090a+b	? (13+?)	?	?	?	?
NHMW 2000z0135/0113	?	?	?	?	?
NHMW 1976/1812/0141	? (?+31)	?	43	36	?
NHMW 1988/0140/0017a+b	44 (13+31)	?	?	(33) 34	?
NHMW 1986/0138/0020a+b	?	?	41+?	33	17

often exposed in dorsal view (Fig. 3). It is low, with nearly straight dorsal and ventral profiles. The neurocranium is relatively broad; its maximum width measured in the postorbital sector is contained less than two times in the length of its base. The length of the orbitorostral portion of the neurocranium, measured at the level of the sphenotic spine, is slightly shorter than that of the posterior portion. The ethmoid bloc is wide and heavily ossified. The osteological configuration of the neurocranium and the topographic relationships between the bones are identical to those of other congeners (see Svetovidov 1948). The vomer has an angular anterior profile; small recurved vomerine teeth can be observed along the ventral surface of this bone. The anterodorsal portion of the mesethmoid is slightly inflated. The lateral ethmoids bear large lateral processes with a distal end characterized by a rounded profile. The frontals are by far the largest bones of the skull roof; the lateral margins of these bones are notably rounded in the orbital region. The supratemporal lateral line canal is clearly exposed in the paratype NHMW 1988/0140/0090b due to collapse of the overlying frontal crests. The parietals are irregular in shape. The outer surface of the supra-occipital appears to be nearly flat; the supraoccipital crest is reduced (see Howes 1990) and extends posteriorly slightly behind the posterior margin of the neurocranium. Both the sphenotics bear a strong tubular anterolaterally protruding spine. The parasphenoid is a robust straight bone. What appear to be the prootic and intercalar are characterized by a notably convex outer surface. The basioccipital is downcurved posteriorly.

The gape of the mouth is rather large, apparently reaching the posterior edge of the orbit. The upper jaw projects beyond the anterior tip of the lower jaw. The premaxilla has stout and very robust articular and ascending processes separated from each other by a deep notch, and a thin and pointed postmaxillary process (Fig. 4A); the alveolar process bears a number of small conical teeth with slightly recurved tips arranged in several rows, and a short labial row of six to eight relatively large conical teeth. The maxilla is an elongate bone with a robust and heavily ossified articular head. The dentary is slender and characterized by a short symphyseal process. The teeth of the lower jaw are identical to those of the upper jaw; some of the teeth of the lingual row are considerably larger than the others.

The suspensorium is clearly traceable in the holotype NHMW 1988/140/137 (Fig. 4B, C). The hyomandibula has a single articular head, very long and laminar opercular process and reduced preopercular process (Fig. 4B). The symplectic is large and nearly triangular in outline. The ectopterygoid and endopterygoid are greatly elongate. As in other gaidropsarines, the ventral margins of ectopterygoid and palatine are not continuous along the same line (see Stainier *et al*. 1986, Endo 2002).

Except for a left preopercle partially exposed in the holotype NHMW 1988/140/137 (see Fig. 4C), the bones of the opercular series are extensively damaged and difficult to interpret. There is a relatively large hyomandibular-preopercle interosseus space (*sensu* Endo 2002).

The hyoid bar is thick and gently curved. There are six or seven branchiostegal rays all articulating with the anterior ceratohyal.

The branchial skeleton is always disarticulated. The ceratobranchials are elongate and slender. Partially complete dorsal gill arches are recognizable in the holotype NHMW 1988/140/137 (Fig. 5). What appear to be the first, second and third epibranchials possess large and robust uncinate processes. There is no evidence of the first pharyngobranchial. The second, third and fourth pharyngobranchials bear numerous small conical teeth.

The vertebral column comprises 44 vertebrae, of which 13 are abdominal (Table 1). The first abdominal vertebra is closely articulated with the basioccipital. The vertebral centra are thick, subrectangular and longer than high (Figs 1, 2). Strong longitudinal ridges and struts are present along the lateral surface of each centrum. Dorsal and ventral prezygapophyses are well-developed along the entire vertebral column, while dorsal postzygapophyses mostly occur in caudal vertebrae. The neural spines of the abdominal vertebrae are anteroposteriorly expanded, strongly thickened and considerably bent backward; their lateral surface is extensively sculptured with shallow irregular pits. The neural spines of caudal centra are slender and nearly straight. The parapophyses of the five posterior abdominal vertebrae are broadly expanded anteroposteriorly

and gradually increasing in size; of these, the three posterior are wing-like, each characterized by a central thickened ridge, a straight posterior margin, and pointed distal tip. Abdominal vertebrae four to eight bear short and relatively strong pleural ribs that insert along the ventral margin of the centra through thick and rounded articular heads. Epineurals appear to be exclusive of the abdominal region of the axial skeleton starting from the third vertebra; the first of these slender, elongate and delicate bones appear to be articulated with the ventro-lateral portion of the third vertebra while the following elements originate along the posterior margin of the pleural ribs and, subsequently, of the enlarged parapophyses.

The caudal skeleton is consistent with that of other rocklings (see Monod 1968, Patterson & Rosen 1989), characterized by two hypural plates (hypurals 1–2 and hypurals 3–5), a parhypural, two epurals and X and Y bones (Fig. 6). The caudal fin is rounded and contains 33 to 36 caudal-fin rays. Five caudal-fin rays are supported by the upper hypural plate (hypurals 3–5), and two rays are supported by the lower hypural plate.

The first dorsal fin is not preserved in the available specimens. The second dorsal fin inserts at the level of the 10th vertebra and contains about 50 rays supported by slender pterygiophores.

There is a single anal fin. This originates well behind the second dorsal-fin origin, at the level of the 16th vertebra and consists of 43 rays supported by thin and slender pterygiophores.

The pectoral fin comprises 17 to 18 long rays. Some bones of the pectoral girdle, including the posttemporal and supracleithrum are scarcely preserved in the examined specimens. The cleithrum is a large crescent-shaped bone with a prominent lower limb and a remarkably thickened anterior edge. Scapula and coracoids are partially exposed in the holotype NHMW 1988/140/137 (Fig. 7); the morphology of these bones is consistent with that of extant gaidropsarines (see Stainier *et al*. 1986, Balushkin 2009); the scapular foramen is located between scapula and coracoids. The postcleithrum is rod-like and slightly curved.

The pelvic fin and girdle cannot be properly recognized due to inadequate preservation.

The body is covered by thin, deciduous cycloid scales.

Taxonomic discussion. – The remarkable quality of the preservation of most of the osteological features in the specimens documented in this paper allowed a well-supported clarification of their taxonomic status.

The descriptive analysis clearly evidenced the gadiform affinity of the seven examined articulated skeletons. The physiognomy of the body and the overall architecture of the skeleton unquestionably indicate that these fossils belong to the order Gadiformes. Moreover, these fossils exhibit some of the gadiform synapomorphies recognized
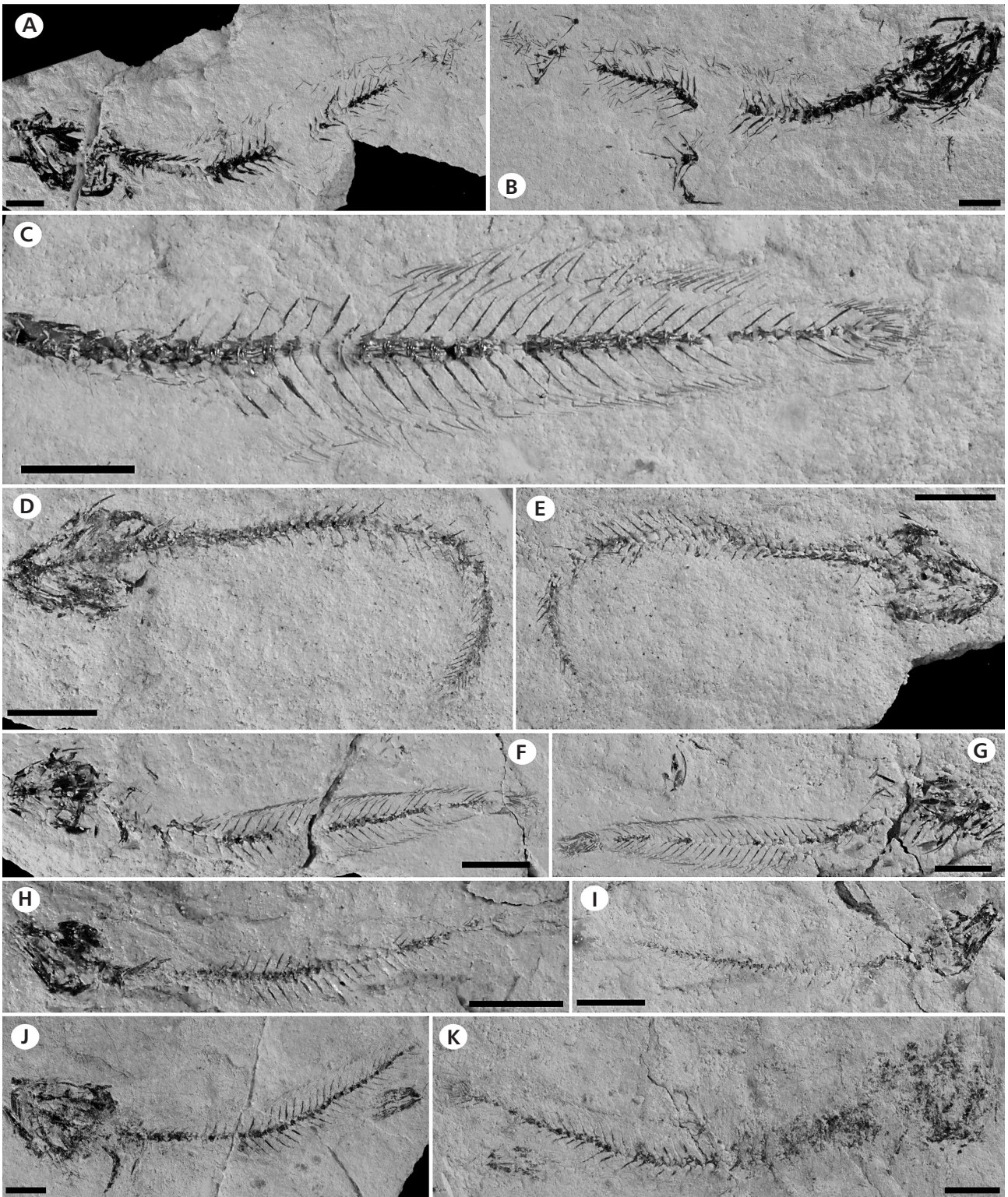
Figure 2. *Gaidropsarus pilleri* sp. nov. • A – NHMW 1988/0140/0090a, paratype; B – NHMW 1988/0140/0090b, paratype; C – NHMW 1976/1812/0141, paratype; D – NHMW 1976/1812/0127a; E – NHMW 1976/1812/0127b; F – NHMW 1986/0138/0020a, paratype; G – NHMW 1986/0138/0020b, paratype; H – NHMW 1988/0140/0017a; I – NHMW 1988/0140/0017b; J – NHMW 2000z0135/0113a, paratype; K – NHMW 2000z0135/0113b, paratype. Scale bars 10 mm.
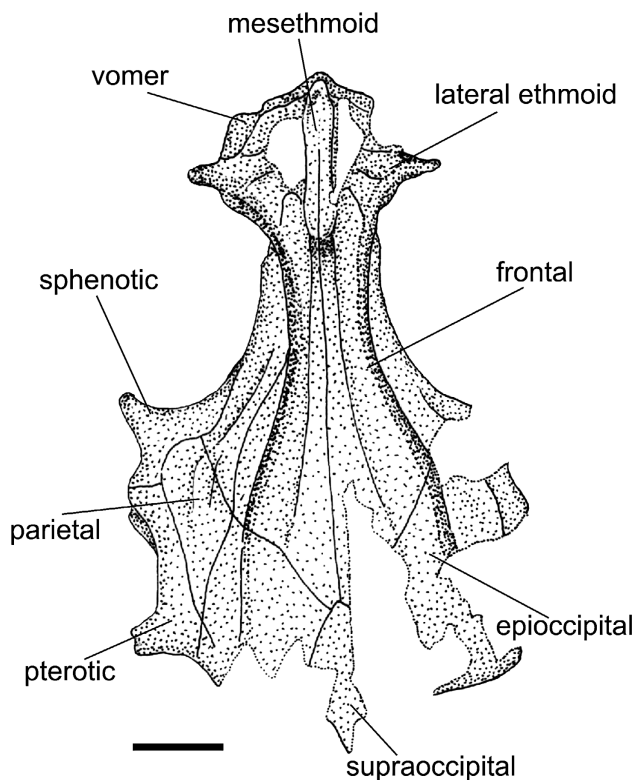
Figure 3. *Gaidropsarus pilleri* sp. nov. NHMW 1988/0140/0090b, paratype, neurocranium, dorsal view. Scale bar 2 mm.

by several comprehensive studies (*e.g.*, Marshall & Cohen 1973, Patterson & Rosen 1989), including the possession of X and Y bones (Markle 1982, Cohen 1984, Fahay & Markle 1984, Patterson & Rosen 1989), absence of epineurals on the two anterior abdominal vertebrae (Patterson & Rosen 1989), scapular foramen located between scapula and coracoids (Endo 2002), and possession of a large hyomandibular-preopercular interosseous space (Okamura 1989, Endo 2002).

Within the Gadiformes, the possession of a large hyomandibular-preopercle interosseous space as well as the presence of two hypural bones in the caudal skeleton clearly indicate that the fossils are members of the suborder Gadoidei (see Markle 1989, Endo 2002, Teletchea *et al.* 2006). As far as the placement at the family level is concerned, the possession of a rounded caudal fin and the absence of branchiostegal rays on the posterior ceratohyal are clearly indicative of the Gadidae (Endo 2002, Teletchea *et al.* 2006).

The family Gadidae includes about 30 extant species belonging to 16 genera arranged in four subfamilies, namely the Gadinae, Gaidropsarinae, Lotinae and Phycinae (see Endo 2002, Teletchea *et al.* 2006). The classification of this group has been traditionally based on the structure of the median fins (see Svetovidov 1948) and subsequently also on meristics and developmental data (see, *e.g.*, Markle 1982, Dunn & Matarese 1984, Fahay &

Markle 1984). More recently, Endo (2002) proposed a classification with four subfamilies based on morphological data and Teletchea *et al.* (2006) reached similar results based on a combined morphological-molecular approach. None of the osteological features recognized by Endo (2002) and Teletchea *et al.* (2006) as diagnostic of the Gadinae (dorsal shelf of the lachrymal concave; posterior process of the lateral ethmoid secondarily reduced; anterior frontal crests fused; postcleithrum with an expanded proximal end; possession of three dorsal and two anal fins), Lotinae (anterior shift of the palate-vomerine ligament V origin; vomerine head posterolaterally enlarged; absence of process on epibranchial 1) or Phycinae (a single branchiostegal ray articulating on the posterior ceratohyal; basipterygia transversely arrayed; dorsal supernumerary fin rays lost; presence of a ligamentary connection between supracleithrum and anterior appendage of swimbladder) subfamilies can be recognized in the gadid specimens from St. Margarethen in Burgenland documented herein. On the contrary, the specimens clearly exhibit at least one of the gaidropsarine synapomorphies recognized by Teletchea *et al.* (2006), five and two caudal-fin rays articulating with the upper and lower hypural plates, respectively. Moreover, at least the holotype NHMW 1988/140/137 shows a unique palatopterygoid configuration, with the ventral margin of palatine and ectopterygoid not continuous (*e.g.*, Stainier *et al.* 1986), a condition exclusive of gaidropsarines and phycines (Endo 2002). Therefore, on the basis of the osteological evidence, it is possible to assign the seven articulated skeletons described in this paper to the subfamily Gaidropsarinae. The three extant genera belonging to this subfamily share the possession of the muscle anterior rectus ventralis, a peculiar condition of the muscle trasversus ventralis anterior, possession of two to four snout barbels and, more important, the possession of a vibratile first dorsal fin consisting of an elongate pseudospine followed by small unsegmented rays forming a fleshy ridge that rises within a shallow median groove (see Endo 2002, Teletchea *et al.* 2006). Three of these four characters refer to soft anatomical features that are not prone to fossilization and, as a consequence, not commonly preserved and observable in fossils. The remaining synapomorphic gaidropsarine character, possession of a vibratile first dorsal fin, is not recognizable in the fossils due to inadequate preservation. This structure is extremely delicate and only occasionally has been documented in fossil remains (Carnevale 2007). The thin pterygiophores that support the short unsegmented rays that form most of the first dorsal fin and their associated musculature are unique in being surrounded by a firm capsule of myoseptal collagen (Kotrschal *et al.* 1984) and are not membraneously connected to each other (Vandewalle *et al.* 1987); the collagen capsule provides a sort of structural separation from the rest of the axial skeleton that likely favoured a rapid
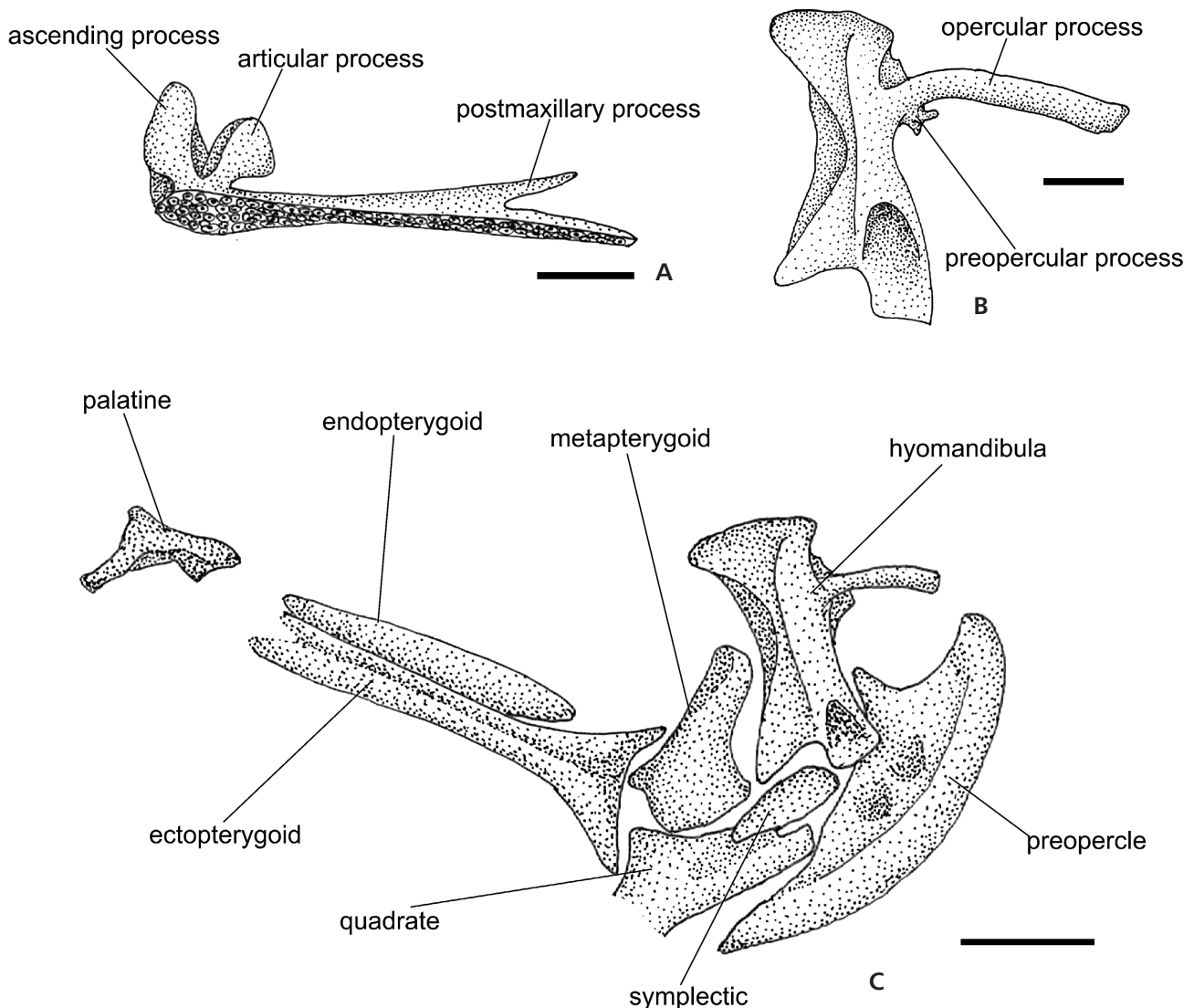
Figure 4. *Gaidropsarus pilleri* sp. nov. • A – NHMW 2000z0135/0113, paratype, premaxilla, right medial view, scale bar 2 mm; B – NHMW 1986/0138/0020a, paratype, hyomandibula, left lateral view, scale bar 1 mm; C – NHMW 1988/0140/0137b, holotype, suspensorium, left lateral view, scale bar 2 mm.

disarticulation during the early stages of decay after the death of the fish. Such tendency to a precocious disarticulation of the first dorsal fin during the early phases of the fossilization process apparently led to the misidentification of fossil rocklings, which, on the basis of the number of exposed dorsal fins, have been erroneously assigned to certain genera of the Lotinae, such as *Brosme* (see Kramberger-Gorjanovic 1884, Arambourg 1927), even though the fossil skeletal remains exhibit several osteological and meristic (*e.g.*, fin and vertebral formulae) features clearly indicative of the Gaidropsarinae (see Carnevale 2007).

The subfamily Gaidropsarinae includes 17 species arranged in the three genera *Ciliata*, *Enchelyopus* and *Gaidropsarus*. Wheeler (1969) recognized two additional genera, *Antonogadus* and *Onogadus*, which are currently

considered as junior synonyms of *Gaidropsarus* (see Cohen & Russo 1979). Diagnostic features for the genera of the Gaidropsarinae were defined by Svetovidov (1948), who separated them based on number of barbels and supratemporal pores, and neurocranial and vomerine tooth shape. Cohen & Russo (1979) claimed that the number of barbels is the only feature that provides unquestionable evidence for the separation of the three genera. Anyway, the number of barbels and supratemporal pores and the shape of the vomerine tooth patch are clearly not recognizable in the fossils documented herein. The neurocranial width appears in some ways similar to that characteristic of the species *Ciliata mustela*; however, as reported by Cohen & Russo (1979), the proper evaluation of the diagnostic value of this character will require further examination.
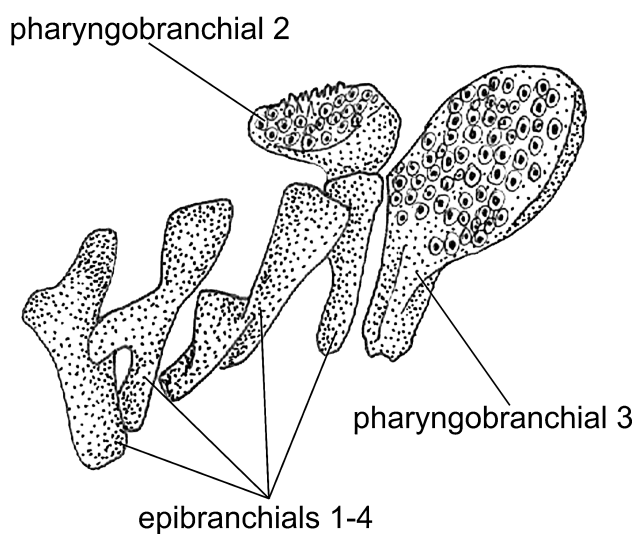
pharyngobranchial 2

pharyngobranchial 3

epibranchials 1-4

Figure 5. *Gaidropsarus pilleri* sp. nov. NHMW 1988/140/137a, holotype, partially complete dorsal gill arches, right series, ventral view. Scale bar 2 mm.

The fossil gaidropsarines described in this paper are assigned to the genus *Gaidropsarus* because of the possession of greatly enlarged parapophyses and broad and angular vomerine head. According to Svetovidov (1948), the possession of enlarged parapophyses is characteristic of *Gaidropsarus* species while the genera *Ciliata* and *Enchelyopus* have narrow and short parapophyses.

With 14 known species, the genus *Gaidropsarus* is the most speciose of the subfamily Gaidropsarinae (see Svetovidov 1986, Shcherbachev 1995, Carnevale 2007, Balushkin 2009). The Miocene *Gaidropsarus pilleri* sp. nov. from St. Margarethen in Burgenland described in this paper differs from all the species of the genus, except *G. biscayensis* and *G. capensis*, by its vertebral, dorsal-, anal-, and pectoral-fin complements (see Table 2). It differs from both *G. biscayensis* and *G. capensis* by having a shorter caudal peduncle (2.4% SL vs 6.4–7.5% SL in *G. capensis* and 3.9–6.0% SL in *G. biscayensis*; Svetovidov 1986). Moreover, the Miocene species from St. Margarethen in Burgenland is unique within the genus *Gaidropsarus* by having a wider neurocranium with well developed anterolaterally directed sphenotic spines. Additional peculiar features observed in *Gaidropsarus pilleri* sp. nov. include the presence of massive uncinate processes in the epibranchials 2 and 3, and the possession of enlarged parapophyses on the five posteriormost abdominal vertebrae, of which the posterior three are wing-like.

Concluding remarks

Gaidropsarus pilleri sp. nov. from the Middle Miocene calcarenitic laminated marls outcropping in the surroundings of St. Margarethen in Burgenland constitutes the earliest skeletal record of the genus *Gaidropsarus* and, more generally, of the whole subfamily Gaidropsarinae. The earliest stages of the evolutionary history of this group of gadid fishes, however, are better documented in the otolith record, which documents the occurrence of *Gaidropsarus* since the Rupelian (Nolf & Steurbaut 1989). The Early Oligocene existence of gaidropsarines is consistent with that of its sister, the Phycinae, which also appeared in the Rupelian (see Nolf & Steurbaut 1989). Therefore, the gaidropsarine body plan dates back at least to the lower part of the Oligocene, a time interval characterized by a conspicuous radiation of gadid fishes, with the appearance of several

Table 2. Synopsis of meristic values of fossil and extant species of the genus *Gaidropsarus*. Data from Svetovidov (1986) and Carnevale (2007).

	vertebrae	2nd dorsal-fin rays	anal-fin rays	caudal-fin rays	pectoral-fin rays
Gaidropsarus pilleri sp. nov.	44	50	43	33–36	17–18
Gaidropsarus argentatus	51–53	54–62	43–51	?	22–24
Gaidropsarus biscayensis	44–47	48–52	40–45	?	18–20
Gaidropsarus capensis	41–43	46–49	39–43	?	18–20
Gaidropsarus ensis	52	53–62	41–48	?	22–25
Gaidropsarus granti	?	60	48	?	21
Gaidropsarus guttatus	49–50	53–57	48–50	?	17–19
Gaidropsarus insularum	47–49	66–70	57	?	19–22
Gaidropsarus macrophthalmus	45–47	53–58	45–49	?	17–19
Gaidropsarus mediterraneus	47–50	54–58	44–49	?	16–19
Gaidropsarus murdjadjensis	?	?	?	?	16
Gaidropsarus novaezelandiae	46–49	55–69	50–59	?	20–21
Gaidropsarus pakhorukovi	46–47	62	51	38	25
Gaidropsarus parini	47	60–63	53	35–37	23–25
Gaidropsarus vulgaris	48–49	59–62	48–53	?	21–22

Figure 6. *Gaidropsarus pilleri* sp. nov. NHMW 1976/1812/0141, paratype, caudal skeleton, left lateral view. Scale bar 1 mm.
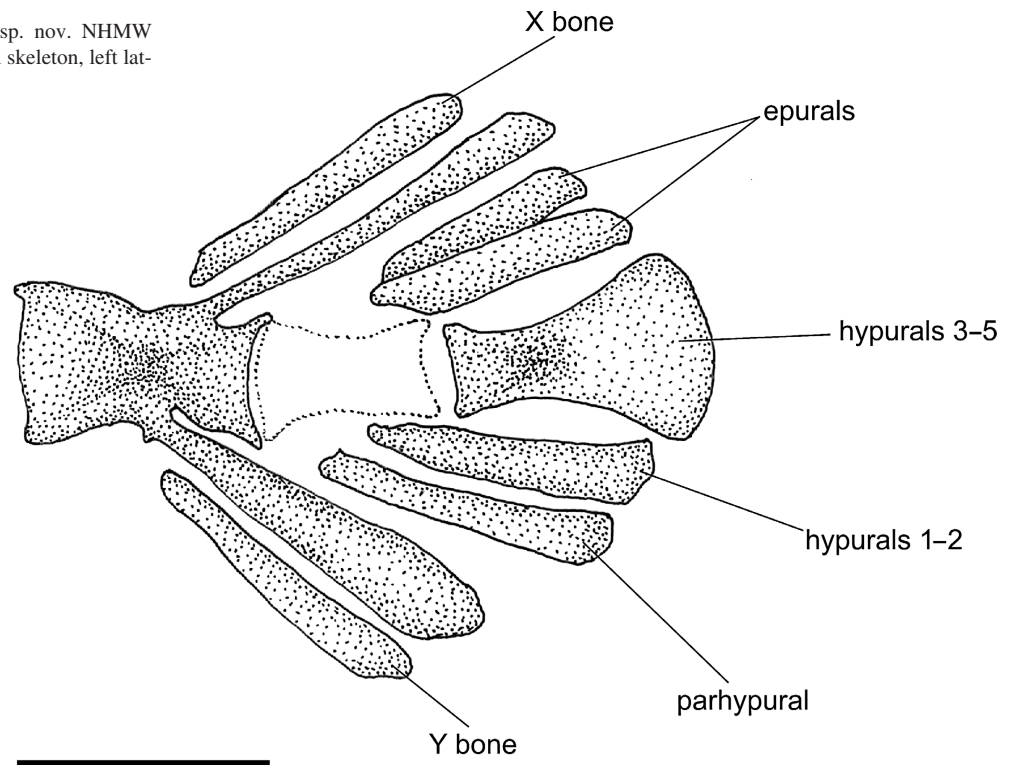
lineages (see Fedotov & Bannikov 1989, Nolf & Steurbaut 1989).

Despite its problematic observation in fossil specimens, the vibratile first dorsal fin certainly represents the most salient feature of the gaidropsarine body plan (see Endo 2002). This structure is a highly modified version of the plesiomorphic gadiform first dorsal fin and is characterized by a prominent anterior pseudospine behind which several soft rays project from a strongly reduced fin web as a fringe of short thin filaments. Cohen & Russo (1979) considered the prominent pseudospine and the subsequent series of delicate filaments as homologues of the first and second dorsal fins of other gadine fishes, respectively. Such hypothesis is not supported by anatomical and ontogenetic evidence. The second and third dorsal fins of gadines are separated only externally, characterized by a continuous pterygiophore series between them (see Markle 1982); such an internal structural continuity of these fins suggests that they should be regarded as the product of an external fragmentation of the second dorsal fin, thereby implying that the second and third dorsal fins of gadines are homologous of the continuous second dorsal fin of other gadids and, more generally, of other gadiform fishes. Therefore, the entire first dorsal fin of gaidropsarines should be considered as homologous of the first dorsal fin of the other gadiforms.

The anatomical structure of the peculiar anterior dorsal fin of gaidropsarines has been described by several authors (*e.g.*, Bateson 1890; Bogoljubsky 1908; Thomson 1912; Crisp *et al*. 1975; Kotrschal *et al*. 1984, 1985, 1993; Peters *et al*. 1987; Vandewalle *et al*. 1987; Kotrschal & Whitear 1988; Whitear & Kotrschal 1988; Kotrschal & Finger 1996). The pseudospine bears a number of taste buds and the epidermis of the thin and short filamentous rays contains millions of solitary chemosensory cells. The entire first dorsal fin is innervated by branches of the recurrent facial nerve and by spinal nerves. The nervus recurrens facialis sends branches to the pectoral, pelvic and dorsal fins. The branches that innervate the first dorsal fin are joined by branches from the dorsal ramuli of spinale nerves and pass through the wall of the capsule of collagenous connective tissue that encloses the supporting elements of the fin and their associated muscles (Kotrschal *et al*. 1985). Overall, the first dorsal fin of gaidropsarines constitutes specific sensory organ, a sort of water sampler, representing a unique novelty (in the sense of Hall & Kerney 2012) within the Teleostei. Each ray is moved by two pairs of muscles, the erectores and depressores. The lateral movements of the rays are allowed by the erectores muscles and maintain the fin in a constant undulation that draws sea water towards and through the fin rays and backwards as a slightly perceptible current (see Kotrschal *et al*. 1984, Vandewalle *et al*. 1987). According to Kotrschal *et al*. (1985), the selective advantage acting during the evolution of this chemosensory organ was the ability to detect prey among the animals living on the area surrounding the fish in its living habitat.

The origin of such a spectacular morphological innovation is really difficult to interpret. According to Mabee
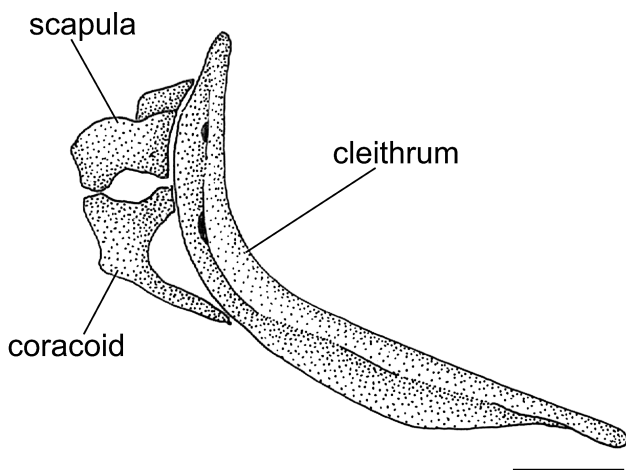
Figure 7. *Gaidropsarus pilleri* sp. nov. NHMW 1988/0140/137a, holotype, pectoral girdle, right lateral view. Scale bar 2 mm.

et al. (2002), the dorsal fins can be regarded as discrete developmental modules. Mabee *et al.* (2002) hypothesized that the spinous first dorsal fin of acanthomorph fishes (including gadiforms) essentially represents an anterior duplication of the posterior soft-rayed dorsal fin. Modular organization enhances the possibility of duplication and divergence of discrete and anatomically regionalized structures (see Gilbert 2010), since duplication may result in the origin of redundant structures and divergence allows them to assume new anatomical or functional roles. As evidenced by Mabee *et al.* (2002), the regionally specialized spinous dorsal fin may revert secondarily to a spine-less condition in some acanthomorph lineages, including flatfishes and dolphinfishes. The Gadiformes possibly represents a further group characterized by such a secondary reversion, even considering that the first dorsal fin of the basal gadiform *Melanonus* exclusively comprises soft rays (see Howes 1993). From a structural point of view, the first and second dorsal fins of most gadiforms are nearly identical to each other, suggesting that their respective modules usually do not follow divergent evolutionary trajectories. On the other hand, the vibratile first dorsal fin of gaidropsarines possibly represents a case of decoupled developmental modularity. However, considering the unspecialized first dorsal fin that occurs in most gadiform lineages, it is difficult to believe that the highly specialized, chemosensory and vibratile first dorsal fin of gaidropsarines solely represents the evolutionary product of duplication and divergence of a single dorsal fin module. Instead, like the first dorsal fin of actinistians, chimaeroids and symmoriform sharks (see Maisey 2009), that of gaidropsarines possibly constitutes an example of co-option (in the sense of Raff 1996), which involves both morphological and functional transformation of a pre-existing first dorsal fin module (Maisey 2009).

Acknowledgements

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