A primitive megalichthyid fish (Sarcopterygii, Tetrapodomorpha) from the Upper Devonian of Turkey and its biogeographical implications

Philippe JANVIER
UMR 5143 du CNRS, Département Histoire de la Terre,
Muséum national d'Histoire naturelle, case postale 38,
57 rue Cuvier, F-75231 Paris cedex 05 (France)
janvier@mnhn.fr
and Department of Palaeontology, The Natural History Museum,
Cromwell Road, London SW7 5BD (United Kingdom)

Gaël CLÉMENT
UMR 5143 du CNRS, Département Histoire de la Terre,
Muséum national d'Histoire naturelle, case postale 38,
57 rue Cuvier, F-75231 Paris cedex 05 (France)
gclement@mnhn.fr

Richard CLOUTIER
Département de Biologie, Université du Québec à Rimouski,
300 allée des Ursulines, Rimouski, Québec, G5L 3A1 (Canada)
richard.cloutier@uquar.qc.ca

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KEY WORDS
Sarcopterygii,
Tetrapodomorpha,
Megalichthyidae,
"Osteolepiformes",
Devonian,
Turkey,
biogeography,
new genus,
new species.

ABSTRACT

The vertebrate fauna of the red sandstone of Pamucak-Sapan Dere Unit of the Upper Antalya Nappe (Frasnian?, Turkey) is reviewed on the basis of new material. The association of the phyllolepid *Placolepis* with the arthrodire *Holonema* in this fauna strongly suggests a Frasnian age or, at any rate, older than the Famennian. The unique osteolepiform sarcopterygian of this fauna is here described in detail and referred to *Sengoerichthys ottoman* n. gen., n. sp., which is considered as the most generalized megalichthyid known to date.

MOTS CLÉS
Sarcopterygii,
Tetrapodomorpha,
Megalichthyidae,
"Ostéolépiformes",
Dévonien,
Turquie,
biogéographie,
nouveau genre,
nouvelle espèce.

RÉSUMÉ
Un mégalichthyide primitif (Sarcopterygii, Tetrapodomorpha) du Dévonien supérieur de Turquie et ses implications biogéographiques.
La faune de vertébrés des grès rouges de l'unité de Pamucak-Sapan Dere (Frasnien ?) de la Nappe supérieure d'Antalya (Turquie) est révisée sur la base de nouveau matériel. L'association du phyllolépide *Placolepis* et de l'arthrodire *Holonema* dans cette faune suggère un âge Frasnien, en tout cas antérieur au Famennien. L'unique sarcoptérygien ostéolépiforme de cette faune est décrit en détail et attribué à *Sengoerichthys ottoman* n. gen., n. sp. Ce genre est ici considéré comme le plus primitif des Megalichthyidae connus.

INTRODUCTION

The red sandstone of the Armutgözlek Tepe is exposed in the Sarcinar Dağ, 17 km north-northwest of Kemer, in the Antalya Bay, Turkey (Antalya map, 1/25 000^e, 30°29'00"E, 36°43'16"N; Fig. 1). It belongs to the Pamucak-Sapan Dere Unit of the Upper Antalya Nappe (Janvier & Marcoux 1976, 1977; Janvier & Ritchie 1977; Janvier 1977, 1980, 1983). The vertebrate fauna found in this sandstone layer suggests a Frasnian age. Moreover, this fauna is the richest vertebrate fauna from an "Old Red Sandstone" facies from the Near East (Seilacher 1963; Janvier & Marcoux 1977). A preliminary faunal list and the paleobiogeographical implications of this Late Devonian vertebrate fauna from Turkey were discussed by Janvier (1983) and Lelièvre *et al.* (1993; see also review in Young 1993a).

The Armutgözlek Tepe material was collected in 1976 and belongs to the Museum of the Maden Tetkik ve Arama collection (MTA, Ankara, Turkey) and is registered with the prefix AT. Casts of the specimens are housed in the collection of the Muséum national d'Histoire naturelle (MNHN), Paris, France. New material from Armutgözlek Tepe was collected in 1994 and 2003 by J. Marcoux and one of us (PJ) and belongs to the MNHN. It is registered with the prefix VDT.

ABBREVIATIONS

ac.qu	articular condyles of the quadrate;
am.f	anterior mandibular fossa;
Brf	fossa bridgei;
da.co	denticulate area on the vertical lamina of the coronoids;
en	external nostril;
Ent	entopterygoid;
f.co	coronoid fangs;
in.pad	insertion area of the posterior adductor muscle of the mandible;
ioc	opening for the infraorbital sensory canal;
m.sym	mandibular symphysis;
nca	nasal capsule;
oa.It	overlap area for the intertemporal;
oa.Ju	overlap area for the jugal;
oa.La	overlap area for the lacrimal;
oa.Pa	overlap area for the parietal;
oa.Po/It	overlap area for the postorbital or intertemporal;
onc	canal for the olfactory nerve;
pac	parotic crest;
paf	parasymphysial fangs on the interpremaxillary posterior process of the premaxilla;
pdn	posterodorsal notch of the entopterygoid;
Prart	prearticular;
pref	prenasal fossa;
psym.f	parasymphysial fang;
psym.p	parasymphysial plate;
spc.g	groove for the spiracular canal;
sph.re	spiraculo-hyomandibular recess;
tfc	trigemino-facialis chamber.

LOCALITY AND FAUNA

The geological setting of the Armutgözlek Tepe locality (Fig. 1) was described by Janvier & Marcoux (1977). The vertebrate remains are restricted to a unique lens within the red sandstones, the latter overlying a thick series of unfossiliferous evaporites that is bracketed by the Upper Silurian and the Frasnian (the latter being dated by the vertebrate occurrence). The bone is generally well preserved, pinkish in colour, and does not show traces of thermal alteration (i.e. the bone is weakly recrystallized, with preservation of cell lacunae and tubules of the dentine). However, in some outcrops that are close to, or even within Permian and Mesozoic dykes, the bones are black in colour and histological features are obliterated.

The faunal list of the Armutgözlek Tepe locality given by Janvier (1983) is modified and updated here:

- Placodermi
  - Antiarcha
    - *Bothriolepis* sp.
  - Arthrodira
    - Phyllolepida
      - *Placolepis* sp. indet.
    - Phlyctaeniida
      - *Groenlandaspis seni* Janvier & Ritchie, 1977
      - *Groenlandaspis* sp. indet.
    - Brachythoraci
      - *Holonema* sp. cf. *H. radiatum* Obruchev, 1932
  - Ptyctodontida
    - Ptyctodontida gen. et sp. indet.
- Acanthodii
  - Ischnacanthiforme gen. et sp. indet. (probably two species, judging from the ornamentation of isolated spines associated with characteristic jaw bones)
- Osteichthyes
  - Dipnoi
    - *Oervigia* sp.
    - Dipteridae gen. et sp. indet.
  - Tetrapodomorpha
    - *Sengoerichthys ottoman* n. gen., n. sp.

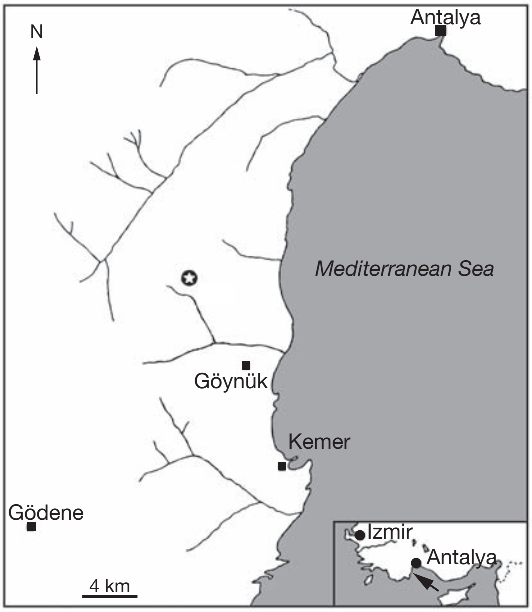

FIG. 1. — Location of the Armutgözlek Tepe locality (✪). Arrow in the framed map of southern Turkey indicates the Kemer area. Modified after Janvier & Marcoux 1977.

The unique chondrichthyan tooth mentioned by Janvier (1983: 2) is now determined as an osteichthyan pharyngeal tooth, quite similar to that of the osteolepiform *Medoevia* (Lebedev 1995: fig. 15) and most probably belongs to the megalichthyid described herein. New material collected during the 1994 field work also allows the record of a second *Groenlandaspis* species and of *Placolepis* material, both currently under description.

Cosmine-covered dermal bones of an "osteolepiform" are abundant in the Armutgözlek Tepe locality. Some of these remains have been described, such as the pectoral girdle (Janvier & Marcoux 1976; Janvier 1980), the parieto-ethmoidal division of the skull and the lower jaw (Janvier 1983). These remains have been considered as belonging to a primitive "Megalichthyinae". New material and recent progress in our understanding of tetrapodomorph phylogeny allow us to provide a more precise assessment of the systematic position of this form, referred here to a new genus and species.

SYSTEMATICS

OSTEICHTHYES Huxley, 1880
SARCOPTERYGII Romer, 1955
RHIPIDISTIA Cope, 1887
TETRAPODOMORPHA Ahlberg, 1991

Family MEGALICHTHYIDAE Hay, 1902

REMARKS

The family Megalichthyidae was considered as a subfamily (Megalichthyinae Hay, 1902) of the Osteolepididae Cope, 1889 by Vorobyeva (1977) and Schultze (1988) on the basis of the cosmine covering, which is in fact a plesiomorphic feature for the Rhipidistia, and possibly all Sarcopterygii (Cloutier & Ahlberg 1996). Later on, Ahlberg & Johanson (1998) recognized a megalichthyid clade within the "Osteolepididae", but did not assign it to a subfamily rank. They considered the Osteolepididae as a paraphyletic group of basal "osteolepiforms" (also paraphyletic).

The Megalichthyidae include the type genus *Megalichthys* Agassiz, 1835 (*M. hibberti* Agassiz, 1843, *M.* cf. *hibberti* of Schultze 1974, *M. agassizianus* Lohest, 1889, *M. coccolepis* Young, 1870, *M. intermedius* Woodward, 1891, *M. laticeps* Traquair, 1884, *M. macropomus* Cope, 1892; Carboniferous-Lower Permian), *Ectosteorhachis* Cope, 1880 (*E. nitidus* Cope, 1880; Carboniferous-Lower Permian), and *Cladarosymblema* Fox, Campbell, Barwick & Long, 1995 (*C. narrienense* Fox, Campbell, Barwick & Long, 1995; Lower Carboniferous).

Schultze (1988) included the poorly known genus *Lohsania* Thomson & Vaughn, 1968, from the Lower Permian of Utah, USA, within the Megalichthyidae. Young *et al.* (1992) also added *Megistolepis* Obruchev, 1955 (Upper Devonian of Siberia; Vorobyeva 1977) and *Mahalalepis* Young, Long & Ritchie, 1992 (Middle Devonian of Antarctica; Young *et al.* 1992) in this family, but the latter forms do not display the most diagnostic features of the group (i.e. the least homoplasic ones; see discussion in Fox *et al.* 1995). Long (1995) suggested that the genus *Megapomus* Vorobyeva, 1977 (Upper Devonian of Russia) could also be a megalichthyid.

A large indetermined Megalichthyidae (probably a new taxon; Daeschler *et al.* 2003) from the Famennian tetrapod locality of Red Hill, Pennsylvania, is currently under study.

Some other occurrences, referred with doubt to megalichthyids, could be added here: a lower jaw from the Upper Pennsylvanian of Hamilton, Kansas (Schultze 1988), and vertebrae and scales from the Lower Carboniferous of Morocco (Janvier *et al.* 1979). The occurrence of a megalichthyid in the Late Devonian of Colombia (Janvier & Villarroel 1998; Janvier *et al.* 2004) still needs to be confirmed, although the Late Frasnian fauna of the Cuche Formation does yield a large "osteolepidid". An isolated postparietal shield from the Early Famennian of Iran could also belong to the Megalichthyidae (Vachik Hairapetian pers. comm. May 2005).

Young *et al.* (1992) defined seven synapomorphies for the Megalichthyidae (including *Megalichthys* Agassiz, 1835, *Ectosteorhachis* Cope, 1880, *Mahalalepis* Young, Long & Ritchie, 1992 and *Megistolepis* Obruchev, 1955): 1) external nostril elongate or slit-like; 2) external nostril partly enclosed by a posterior tectal bone; 3) posterior interpremaxillary process of premaxillary bearing tusks; 4) vomers short and broad, sometimes with a strong mesial process; 5) closed pineal foramen; 6) parietal bones (frontal bones of Young *et al.* [1992]) notched to receive the posterior nasals; and 7) lacrimal notch well developed.

Fox *et al.* (1995) redefined the diagnosis of the Megalichthyidae on the basis of the detailed study of *Cladarosymblema narrienense* Fox, Campbell, Barwick & Long, 1995, from the Lower Carboniferous of Queensland, Australia. They included in the Megalichthyidae the genera *Megalichthys*, *Ectosteorhachis*, *Cladarosymblema*, a new genus from the Permian of Norway (to be described by Ulf Borgen, Stockholm, on the basis of more complete material than the lower jaw and isolated scales of *Megalichthys* sp. figured by Heintz [1935]), and the megalichthyid from Turkey described herein. These authors accepted the monophyly of the Megalichthyidae, as supported by the characters provided by Young *et al.* (1992), apart from the notch of the parietal to accommodate the posterior nasal, which is a variable character, but they considered that this list was too incomplete to accurately diagnose the Megalichthyidae. In addition, they provided a more detailed diagnosis to differentiate the Megalichthyidae from the other "osteolepiform" families, although it includes some characters found in other "osteolepiforms". However, this diagnosis provides unique combination of characters.

Genus *Sengoerichthys* n. gen.

TYPE SPECIES. — *Sengoerichthys ottoman* n. gen., n. sp.

ETYMOLOGY. — Named after Professor Celal Sengör, Istanbul Teknik Üniversitesi, Istanbul, Turkey.

DIAGNOSIS. — Same as for the type species, by monotypy.

REMARKS

Considering the presence of parasymphysial fangs on the premaxilla and the dentary (paf, Fig. 3) and the absence of pineal foramen (Fig. 2A), *Sengoerichthys* n. gen. fits the family diagnosis of Fox *et al.* (1995). However this new species also shows other megalichthyid characters in a plesiomorphic state, compared to the three Carboniferous and Permian genera (i.e. *Megalichthys*, *Ectosteorhachis* and *Cladarosymblema*) assigned to this family by Fox *et al.* (1995). Notably, the external nostril is still in a lateral position in *Sengoerichthys* n. gen. (Fig. 2B) whereas it is situated more dorsally and posteriorly in *Megalichthys* and *Ectosteorhachis*, and, to a lesser extent, in *Cladarosymblema*; and the scapulocoracoid is rather small (Fig. 8D1), as in most other "osteolepiforms".

The other features of *Sengoerichthys* n. gen. are plesiomorphic "osteolepiform" characters or plesiomorphic megalichthyid characters. It is impossible to define the new genus *Sengoerichthys* n. gen. by an autapomorphy. It is a megalichthyid that only presents general features, or symplesiomorphies, of this group. Nevertheless its unique combination of characters allows us to erect a new genus.

This Frasnian "osteolepiform" is in many respects quite similar to the Lower Carboniferous *Cladarosymblema narrienense* from Queensland, Australia (Fox *et al.* 1995), but differs from the latter in showing: 1) a parietal that is shorter, relative to the parieto-ethmoidal length; 2) a reduced or closed pineal foramen; 3) a laterally situated external nostril; 4) marginal rounded teeth on the coronoids, arranged in numerous rows in front of the coronoid fangs; and 5) a smaller scapulocoracoid. These conditions are all plesiomorphic for the Megalichthyidae. Therefore, *Sengoerichthys* n. gen. is considered here as the most generalized megalichthyid known to date.

Sengoerichthys ottoman n. sp.
(Figs 2-12)

Ostéolépiforme indet. – Janvier & Marcoux 1976: figs 1, 2.

Ostéolépiformes – Janvier & Marcoux 1977: 187.

Osteolepidae gen. et sp. indet. – Janvier 1977: fig. 1.

Osteolepididae gen. et sp. indet. – Janvier *et al.* 1979: fig. 5A. — Janvier 1980: figs 5A, B, 6A-E.

Indetermined osteolepiform – Rosen *et al.* 1981: 193.

Megalichthyinae gen. et sp. indet. – Janvier 1983: figs 7A-C, 8A-G, 9A, B.

Megalichthyinae gen. et sp. indet. – Lelièvre *et al.* 1993: fig. 7E.

Janvier's Turkish specimen – Fox *et al.* 1995: 109.

Primitive megalichthyid – Clément *et al.* 2005: 6.

HOLOTYPE. — Anterior portion of an isolated right lower jaw (AT058, Fig. 10B1, B2).

ETYMOLOGY. — From Ottoman.

DIAGNOSIS. — Megalichthyidae with a relatively elongated and slender skull compared to other megalichthyids; ethmoidal part of the skull roof longer than the parietal length; external nostril in lateral position and more oval in shape than slit-like; weakly developed posterior interpremaxillary processes which do not divide the prenasal fossa; large parasymphysial plate covered with numerous rounded denticles; vertical laminae of coronoids bearing numerous small denticles with enlarged denticle-covered areas anteriorly to the coronoid fangs; anterior mandibular fossa relatively small and laterally covered by the adjacent dermal bones; posterior lamina of the maxilla moderately deep for a Megalichthyidae; and scapulocoracoid relatively small for a Megalichthyidae.

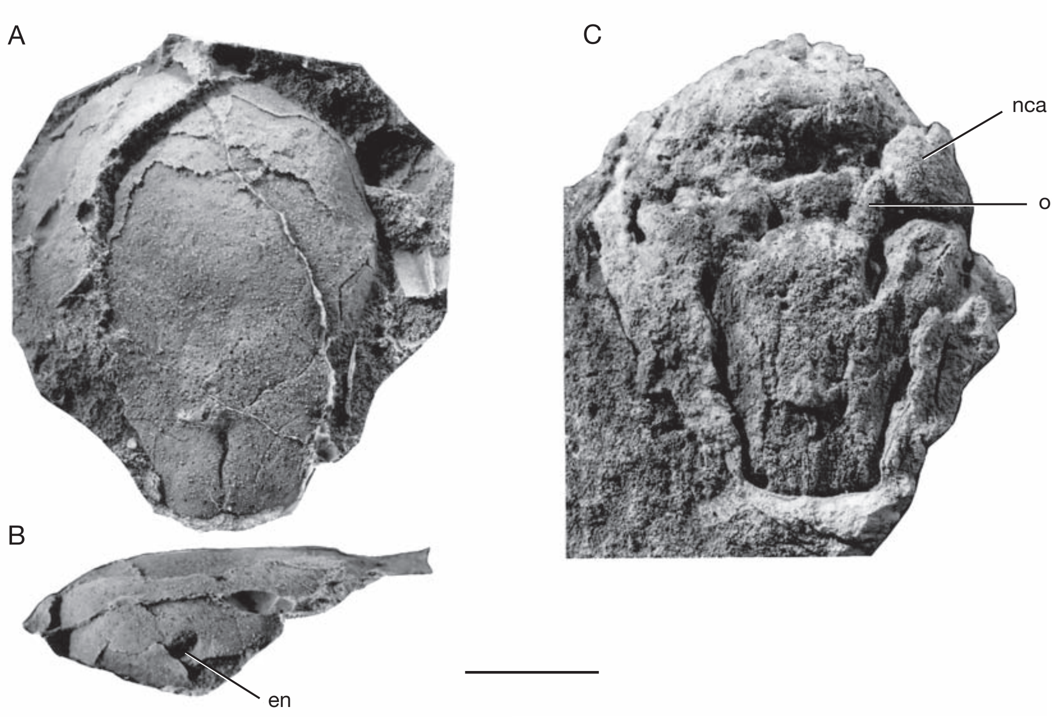

FIG. 2. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of the Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; parieto-ethmoidal shield (AT050) in dorsal (**A**) and lateral (**B**) views, and internal mould of the sphenethmoid of the same specimen showing part of the palate and of the nasal capsules in dorsal view (**C**). Abbreviations: **en**, external nostril; **nca**, nasal capsule; **onc**, canal for the olfactory nerve. Scale bar: 10 mm.

TYPE LOCALITY. — Armutgözlek Tepe, Kemer, Turkey.

TYPE UNIT. — Upper Devonian, ?Frasnian, Red Sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe.

MATERIAL EXAMINED. — Two sphenethmoids: AT050 (Fig. 2), AT051 (Fig. 3); three otoccipitals: AT063 (Fig. 4A), AT062 (Fig. 4B), VDT09 (Fig. 5); isolated maxilla VDT10 (Fig. 7); incomplete right mandible AT055 (Fig. 10A); right mandible fragment VDT11 (Fig. 10C); incomplete palatoquadrate AT064 (Figs 8A; 9); two entopterygoids: AT065 (Fig. 8B), AT071 (Fig. 8C); gular plate AT075 (Fig. 12); two cleithra with associated scapulocoracoid: AT01 (Fig. 8D), AT078; incomplete cleithrum AT02 (Fig. 8E); ?anocleithrum AT066 (Fig. 8F); scale or bone fragment AT070 (Fig. 8G).

DESCRIPTION

Janvier (1980: figs 5A, B, 6; 1983: figs 7-9) and Janvier & Marcoux (1976) described the parieto-ethmoidal shield (as well as part of the sphenethmoid internal anatomy), the lower jaw, and the pectoral girdle of *S. ottoman* n. gen., n. sp. New material consists of three otoccipitals with the postparietal shields, two entopterygoids, a posterior part of the palatoquadrate, a maxilla, as well as other fragments of dermal bones.

Skull roof

As a whole, the skull of *Sengoerichthys* n. gen. resembles that of *Cladarosymblema*. The skull roof is relatively elongated and narrow, compared to the broad and short skulls of *Megalichthys* and *Ectosteorhachis*. The parieto-ethmoidal shield and internal structures of the sphenethmoid (Figs 2; 3) were briefly described by Janvier (1983). Most of the anterior dermal bone pattern is hidden by the cosmine covering, and the only suture that is clearly visible externally is the interparietal suture. This sinuous suture runs from the posterior limit of the pineal bump to the posterior margin of the parietals. However, immersion of the counterpart of specimen AT050 in alcohol, before it was cleaned with hydrochloric acid, showed some sutures delimiting the parietals, posterior nasals and possibly supraorbitotectals (Janvier 1983: fig. 8B; Fig. 6). The length of the parietal is about half of that of the entire ethmoidal region, and this condition separates *S. ottoman* n. gen., n. sp. from all other megalichthyids. The anterior part of the parietal is broader than its posterior part. Contrary to the condition in *Cladarosymblema* and *Megalichthys*, the anterior margin of the parietal does not show any notch for the posterior nasal. There is no pineal foramen (Fig. 2A), although the suture between the two parietals ("frontaux" in Janvier 1983) seems to widen anteriorly, as in *Cladarosymblema* (Fox *et al.* 1995: fig. 7B, D). The lack of a pineal foramen is one of the synapomorphies of the Megalichthyidae, however this condition is largely homoplastic among osteichthyans. The posterolateral part of the internal surface of the parietal displays a descending process (AT050, Fig. 2C), which most likely contacted the anterior process of the supratemporal, as seen in the anterior region of a large postparietal shield referred here to *Sengoerichthys* n. gen. (Fig. 5). The anterior pit-lines are entirely situated on the parietals, and are slightly curved and asymmetrical in AT050 (Figs 2A; 6). Their position is similar to that in *Cladarosymblema* (Fox *et al.* 1995).

Contrary to the condition in *Cladarosymblema*, which presents some large and more or less aligned sensory pores, it is not possible to distinguish the larger pores that indicate the trajectory of the ethmoidal, infraorbital and supraobital sensory line canals. Furthermore, groups of pores ("Paul's organ" in Vorobyeva & Lebedev 1986), which are obvious in some specimens of *Cladarosymblema* (Fox *et al.* 1995: fig. 8A, B), *Megalichthys* (Jarvik 1966: figs 12, 14C, 15A), and some "Osteolepididae" (e.g., *Osteolepis*, *Gyroptychius*, *Medoevia*), cannot be confirmed in *Sengoerichthys* n. gen.

The postparietal shield is only known by a large specimen (Fig. 5). Its general shape is similar to that of *Megalichthys* and *Cladarosymblema*. The anterolateral margin of the supratemporal presents an anterior process showing a complex articular structure for the parietal and the intertemporal, which seems to be characteristic of the Megalichthyidae (Bjerring 1972). The ventral surface of this anterior process of the supratemporal presents a large bulge, as in *Cladarosymblema* (Fox *et al.* 1995: fig. 29B). A large overlap area is present posteriorly to the anterior process of the supratemporal (oa.Po/It, Fig. 5C). This overlap area would have been covered by the postorbital in a *Megalichthys*-like pattern, and by the intertemporal in a *Cladarosymblema*-like pattern. The available material of *Sengoerichthys* n. gen. does not allow to decide which pattern was present in this taxon.

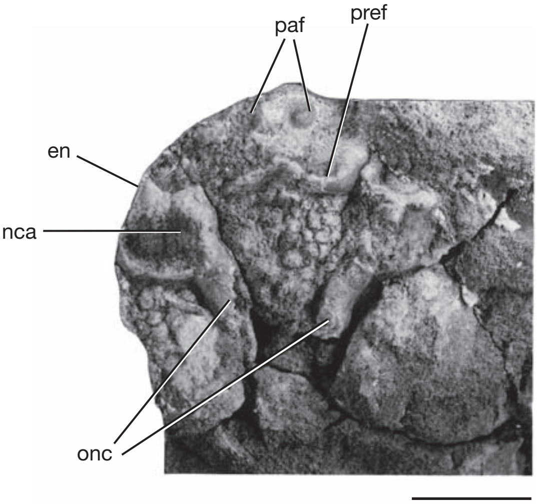

FIG. 3. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; internal mould of an incomplete sphenethmoid in dorsal view (AT051). Abbreviations: **en**, external nostril; **nca**, nasal capsule; **onc**, canal for the olfactory nerve; **paf**, parasymphysial fangs on the interpremaxillary posterior process of the premaxilla; **pref**, prenasal fossa. Scale bar: 10 mm.

External nostril

The external nostril of megalichthyids is delimitated by anterior and posterior dermal bones (either the "prenarial" and "postnarial" [Thomson 1964], or the "lateral rostral" and "anterior tectal" [Fox *et al.* 1995], respectively).

The position of the lateral rostral relative to the anterior tectal is not clear in *Sengoerichthys* n. gen., because the cosmine layer hides the sutures (Fig. 2B). In contrast to all other megalichthyids, except for

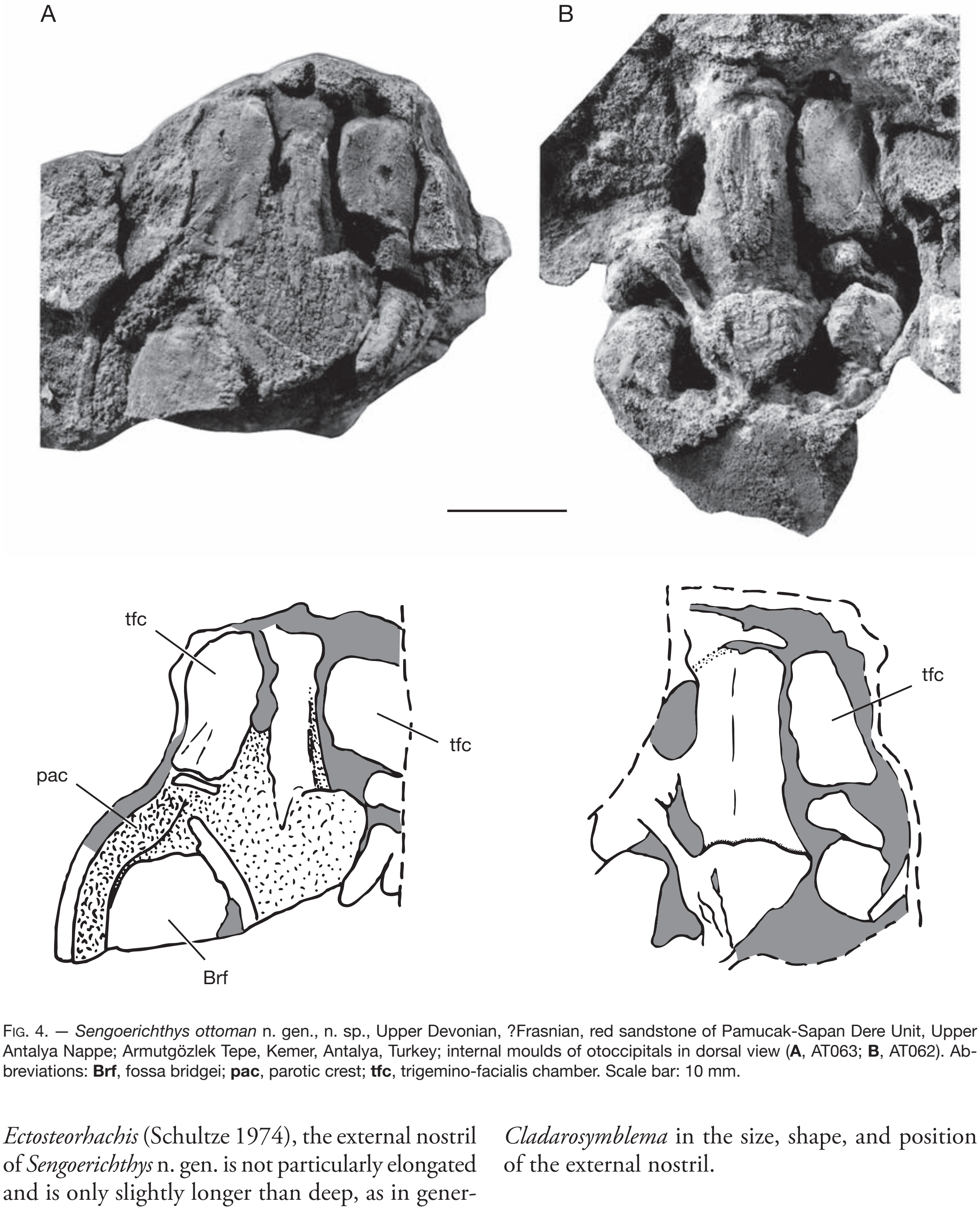

FIG. 4. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; internal moulds of otoccipitals in dorsal view (**A**, AT063; **B**, AT062). Abbreviations: **Brf**, fossa bridgei; **pac**, parotic crest; **tfc**, trigemino-facialis chamber. Scale bar: 10 mm.

Ectosteorhachis (Schultze 1974), the external nostril of *Sengoerichthys* n. gen. is not particularly elongated and is only slightly longer than deep, as in generalized "Osteolepididae". Its position is also clearly lateral and close to the oral margin (en, Fig. 2B) compared to that of *Megalichthys* and *Ectosteorhachis*. In contrast *Sengoerichthys* n. gen. closely resembles *Cladarosymblema* in the size, shape, and position of the external nostril.

Neurocranium

The ventral view of the sphenethmoid presents a large prenasal fossa (pref, Fig. 3) divided into two pits by a median endoskeletal crest. The nasal capsules (nca, Figs 2C; 3) are situated postero-laterally to this fossa. The canals for the olfactory tracts diverge from each other at the level of the median portion of the sphenethmoid (onc, Figs 2C; 3).

Two otoccipitals, whose size agrees with those of the isolated sphenethmoids from the same locality, show some internal structures (Fig. 4A, B), such as the encephalic cavity and part of the labyrinth cavity with part of its semicircular canals. Although these structures are poorly preserved, their proportions agree with those described in *Megalichthys* (Romer 1937) and *Gogonasus* (Long *et al.* 1997).

The dorsal impression of the parotic crest (pac, Fig. 4A), well visible on the left side of AT063, shows that the fossa bridgei (Brf, Fig. 4A) was proportionally large. The general shape of the fossa bridgei seems to be very similar to that in *Cladarosymblema* and *Ectosteorhachis*.

Maxilla

An isolated maxilla is the only cheek bone of *Sengoerichthys* n. gen. known so far. This maxilla (Fig. 7) presents a deep posterior lamina, a feature shared by all Megalichthyidae and some "osteolepidids" (e.g., *Gogonasus*, *Latvius* and *Medoevia*). However this lamina is not as deep as that of *Megalichthys* or *Ectosteorhachis* and, in this respect, very similar to that of *Cladarosymblema*. In external view the dorsal margin of the bone shows two overlap areas, a posterior one for the jugal and an anterior one for the lacrimal (oa.Ju, oa.La, Fig. 7).

Palate

An interpremaxillary process bearing fangs, a synapomorphy of megalichthyids, is produced by the posteromedial extension of a palatal process of the premaxillae. This condition is present in *Sengoerichthys* n. gen. (Fig. 3) although the interpremaxillary process is less developed than in *Megalichthys hibberti* (Jarvik 1966: fig. 17) or *Ectosteorhachis* (Thomson 1964: fig. 3A). Because of its weak development, the interpremaxillary process does not contribute to the division of the prenasal fossa (pref, Fig. 3; "fossa apicalis" in Jarvik 1966, 1980). This condition is quite similar to that of *Cladarosymblema* (Fox *et al.* 1995: figs 20-22).

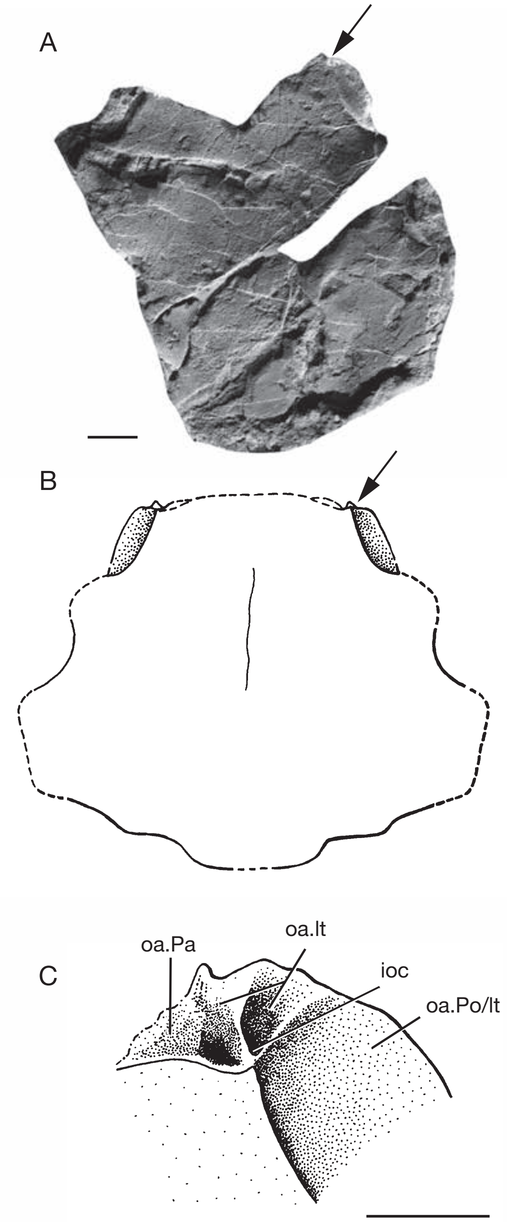

FIG. 5. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; large postparietal shield (VDT09): **A**, imprint of the external surface; **B**, reconstruction in dorsal view; **C**, detail of the anterior process of the supratemporal in dorsal view. Abbreviations: **oa.It**, overlap area for the intertemporal; **oa.Pa**, overlap area for the parietal; **oa.Po/It**, overlap area for the postorbital or intertemporal; **ioc**, opening for the infraorbital sensory canal. Scale bars: 10 mm.

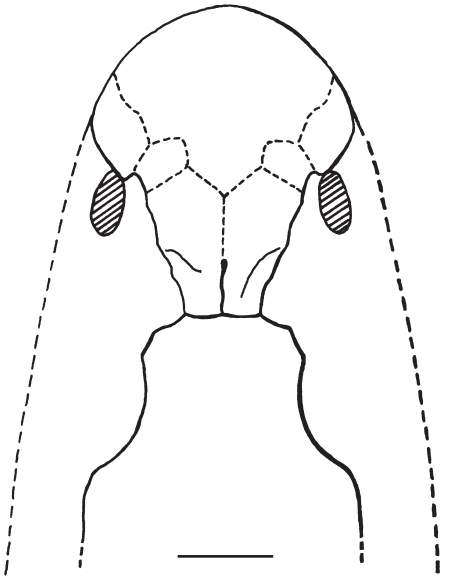

FIG. 6. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; reconstruction of the skull roof in dorsal view; sutures on the parieto-ethmoidal shield based on the specimen AT050 before acid preparation (see Janvier 1983: fig. 7B) and outline of the postparietal shield based on the specimen AT063 (see Fig. 4A). Scale bar: 10 mm.

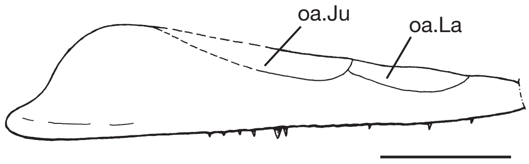

FIG. 7. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; isolated maxilla (VDT10) in external view. Abbreviations: **oa.Ju**, overlap area for the jugal; **oa.La**, overlap area for the lacrimal. Scale bar: 10 mm.

An almost complete isolated entopterygoid (Fig. 8B) is closely similar to that of *Medoevia* (Lebedev 1995: fig. 9) and *Gogonasus* (Long *et al.* 1997: fig. 30A) and, like the latter, shows a posterodorsal notch. This notch is also clearly visible on a fragment of the posterior part of the entopterygoid (pdn, Figs 8A2; 9B). The oblique crest of the entopterygoid is well marked (Fig. 8B), also as in *Gogonasus* and *Medoevia*. The entopterygoid of *Cladarosymblema* is unknown.

An isolated posterior part of a palatoquadrate (Figs 8A; 9), whose size agrees with that of the sphenethmoids and otoccipitals described above, shows a rounded posterior margin. Such a shape of the palatoquadrate is known in generalized "osteolepiforms", in contrast to that of the Tristichopteridae (= Eusthenopteridae; Cloutier 1996) which presents a much straighter margin. As a whole, this palatoquadrate portion is very similar to that of *Megalichthys* (Watson 1926: fig. 33), *Gogonasus* (Long *et al.* 1997: fig. 29) and *Medoevia* (Lebedev 1995: fig. 9). Its internal surface is covered by the entopterygoid, dorsally and posterodorsally to which is a deep spiraculo-hyomandibular recess (sph.re, Fig. 9B, C). This recess is continued anteriorly by a narrow spiracular groove (spc.g, Fig. 9B). The articular condyle of the quadrate is large and shows a constriction in its median part (ac.qu, Fig. 9A).

Lower jaw

Four isolated lower jaws have been found, although only one provides information on the symphysial region, which is most diagnostic (Fig. 10B1, B2; Janvier 1983: fig. 9B). The internal side of the lower jaw presents a parasymphysial plate (psym.p, Figs 10B2; 11), three coronoids and an elongated prearticular (Figs 10A2; 11). The dentary bears anteriorly a pair of parasymphysial fangs (psym.f, Fig. 11). The size of these fangs is approximately the same as that of the coronoid fangs (f.co, Fig. 11). Such large parasymphysial fangs of the dentary are known in the Rhizodontida (Andrews 1985; Long 1989; Johanson & Ahlberg 2001), the derived Tristichopteridae (Jarvik 1952, 1972; Vorobyeva 1977; Johanson & Ahlberg 1997), *Panderichthys* (Gross 1941), as well as in most of the early tetrapods (Ahlberg *et al.* 1994; Jarvik 1996; Ahlberg & Clack 1998).

The paired parasymphysial plates ("adsymphysial plates" in Schultze 1988 and Lebedev 1995; "crista dentalis" in Thomson 1964) of *Sengoerichthys* n. gen. are jointed medially and their denticulated posterior expansions contact the anterior margin of the denticulated area of the anterior coronoid

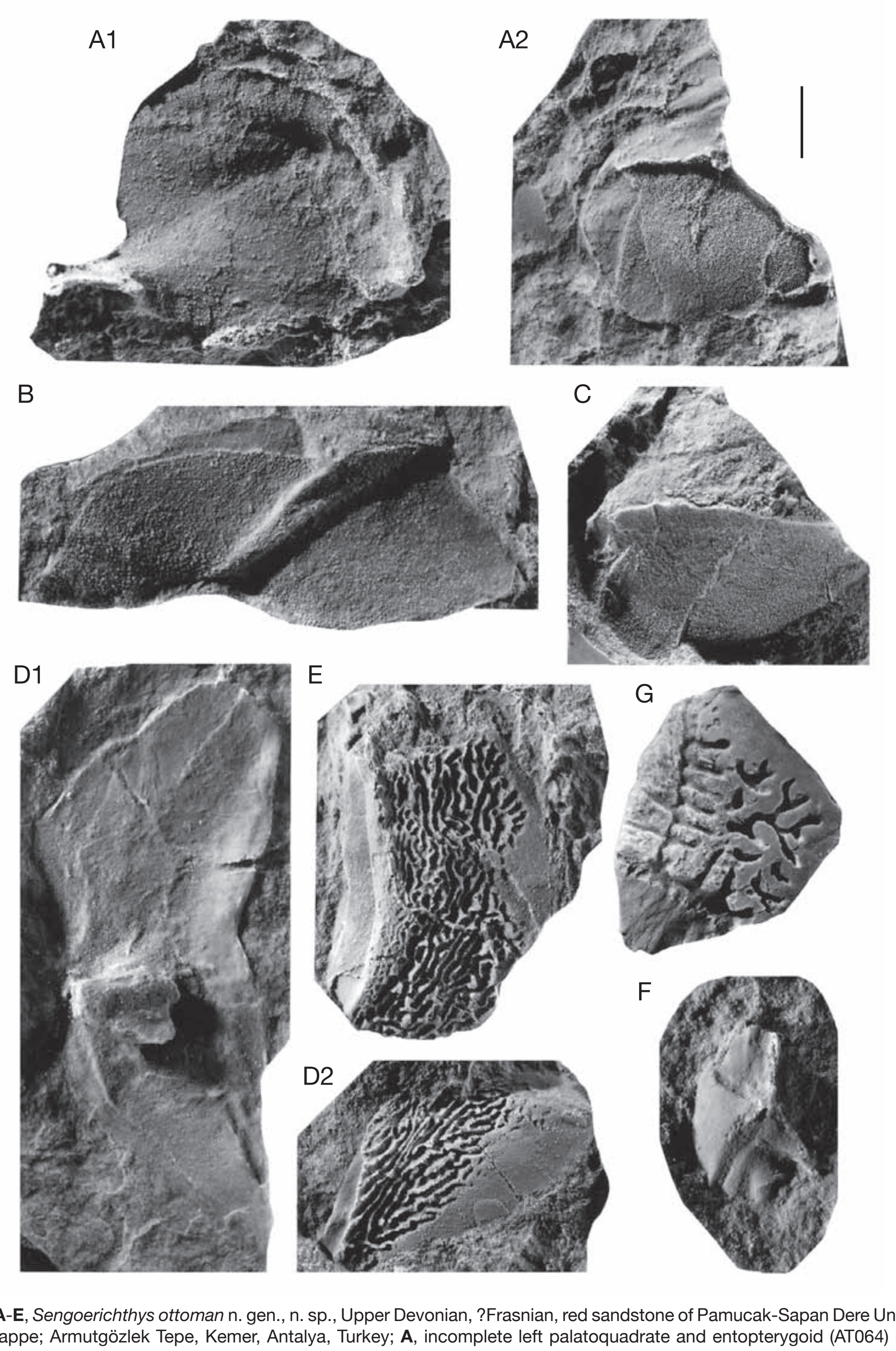

FIG. 8. — **A**-**E**, *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; **A**, incomplete left palatoquadrate and entopterygoid (AT064) in lateral (**A1**) and medial (**A2**) views; **B**, right entopterygoid in medial view (AT065); **C**, incomplete left entopterygoid in medial view (AT071); **D**, left cleithrum and scapulocoracoid (AT01) in medial (**D1**) and lateral (**D2**) views; **E**, incomplete left cleithrum in lateral view (AT02); **F**, **G**, cosmine covered elements assigned to *Sengoerichthys* n. gen. with some doubt; **F**, ?anocleithrum in lateral view (AT066); **G**, scale or dermal bone fragment showing traces of cosmine resorption (AT070). Scale bar: 10 mm.

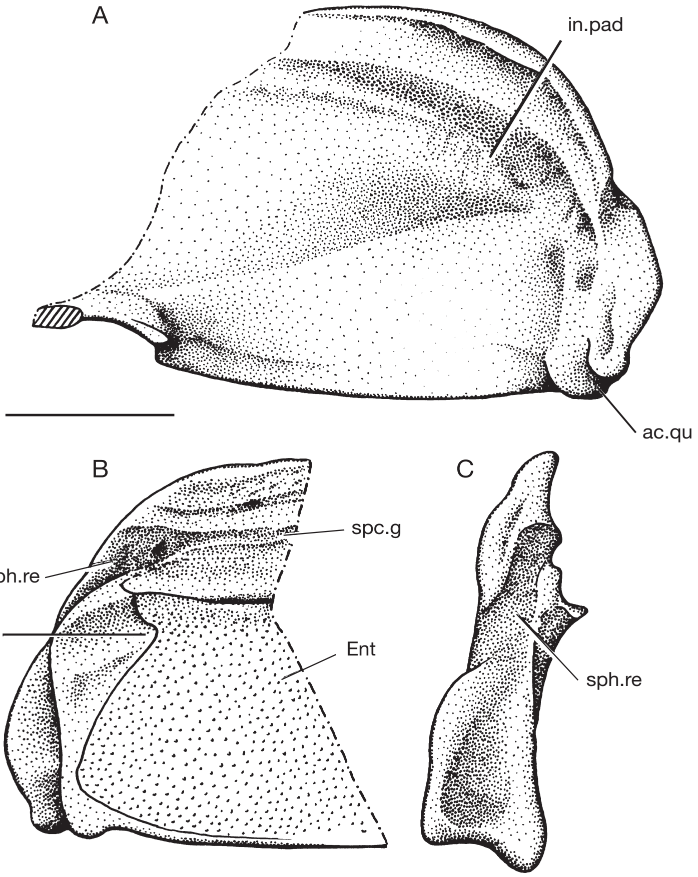

FIG. 9. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; reconstruction of the palatoquadrate in lateral (**A**), medial (**B**), and posterior (**C**) views based on the specimen AT064 (Fig. 7A). Abbreviations: **ac.qu**, articular condyles of the quadrate; **Ent**, entopterygoid; **in.pad**, insertion area of the posterior adductor muscle of the mandible; **pdn**, posterodorsal notch of the entopterygoid; **spc.g**, groove for the spiracular canal; **sph.re**, spiraculo-hyomandibular recess. Scale bar: 10 mm.

(Figs 10B2; 11). Some other megalichthyids also possess a denticulated posterior expansion of the parasymphysial plate contacting the anterior coronoid, notably *Ectosteorhachis*, *Cladarosymblema*, and an indeterminate megalichthyid from the Carboniferous of Kansas (Thomson 1964; Schultze 1974, 1988; Fox *et al.* 1995). This condition is also known in some other "osteolepiforms" (e.g., *Gogonasus*, *Lamprotolepis*, *Litoptychius*, *Gyroptychius*, and *Medoevia* [Vorobyeva 1977; Long 1987; Lebedev 1995; Long *et al.* 1997]).

On the contrary, parasymphysial plates were supposed to be absent in *Megalichthys* (Thomson 1964: 295), but the recent revision of the material referred to *Megalichthys intermedius* has provided evidence for a very small parasymphysial plate on two lower jaws (Mohun 2003). These plates are restricted to the mesial margin of the jaw, and bear few well developed teeth (Mohun 2003: fig. 6). The parasymphysial plates are also known to be reduced in *Eusthenopteron* (Jarvik 1980), *Megistolepis* (Vorobyeva 1977: pl. 7:6), *Platycephalichthys* (Vorobyeva 1977: fig. 15C, pl. 13:1), and *Panderichthys* (Ahlberg 1991; Ahlberg & Clack 1998).

In *Sengoerichthys* n. gen., the parasymphysial plates are club-shaped and larger anteriorly than posteriorly. Their dorsal surfaces are covered with numerous small denticles, as in *Ectosteorhachis* (Thomson 1964: fig. 4B, C; Fox *et al.* 1995: fig. 53) and *Cladarosymblema* (Fox *et al.* 1995: figs 46B, 49C, 50D, E, 57). The denticles on the parasymphysial plates and on the anterior part of the prearticular of *Sengoerichthys* n. gen. are similar in size to those of *Cladarosymblema*, and smaller than those in *Ectosteorhachis* (Fox *et al.* 1995: figs 46B, C, 49C, 50D, E, 53A, B).

The sutures between the coronoids are not clearly visible in *Sengoerichthys* n. gen. However, a number of three coronoids is suggested by the presence of three pairs of coronoid fangs (Figs 10A2; 11). Judging from the space between the coronoid fangs, it seems that the anterior coronoid is longer than the middle and posterior ones, as in *Cladarosymblema*, *Gogonasus*, and *Medoevia* (Long 1985; Fox *et al.* 1995; Lebedev 1995; Long *et al.* 1997).

A remarkable feature is the presence of numerous small rounded denticles on the vertical lamina of the coronoids (da.co, Figs 10B2; 11). These denticles are more or less aligned on the narrow vertical lamina of the coronoids, except anteriorly to the coronoid fangs where the vertical lamina displays enlarged areas covered with irregularly scattered denticles. Among megalichthyids, *Ectosteorhachis* also presents more than one row of denticles on the vertical lamina of the coronoids (Fox *et al.* 1995: fig. 53C). In *Cladarosymblema*, the vertical lamina of the coronoids is reduced and devoid of denticles, without enlarged areas anteriorly to the coronoid fangs (Fox *et al.* 1995: fig. 50D, E). However, Fox *et al.* (1995: 167) noticed that clusters of few small teeth (not denticles, since they have folded bases) are present on the vertical lamina of two specimens of *Cladarosymblema*. This condition is also known in *Medoevia* (Lebedev 1995: fig. 11), *Gogonasus* (Fox *et al.* 1995: fig. 52B-E; Long *et al.* 1997: fig. 36), and *Kenichthys* (Chang & Zhu 1993), and is supposed to be a primitive condition for "osteolepiforms" (Vorobyeva 1977: 63). However, this condition is most likely plesiomorphic for rhipidistians as a whole, since it is also known in the porolepidids *Porolepis* and *Heimenia* (Kulczycki 1960; Jarvik 1972; Clément 2001), in *Powichthys* (Jessen 1980) and in *Youngolepis* (Chang 1991). It could also be plesiomorphic for all sarcopterygians, since it is known in *Psarolepis* (Yu 1998). Quite a similar condition is encountered, though less developed, in the early tetrapods *Obruchevichthys*, *Elginerpeton*, *Acanthostega*, *Crassigyrinus* and *Gephyrostegus* (Ahlberg & Clack 1998).

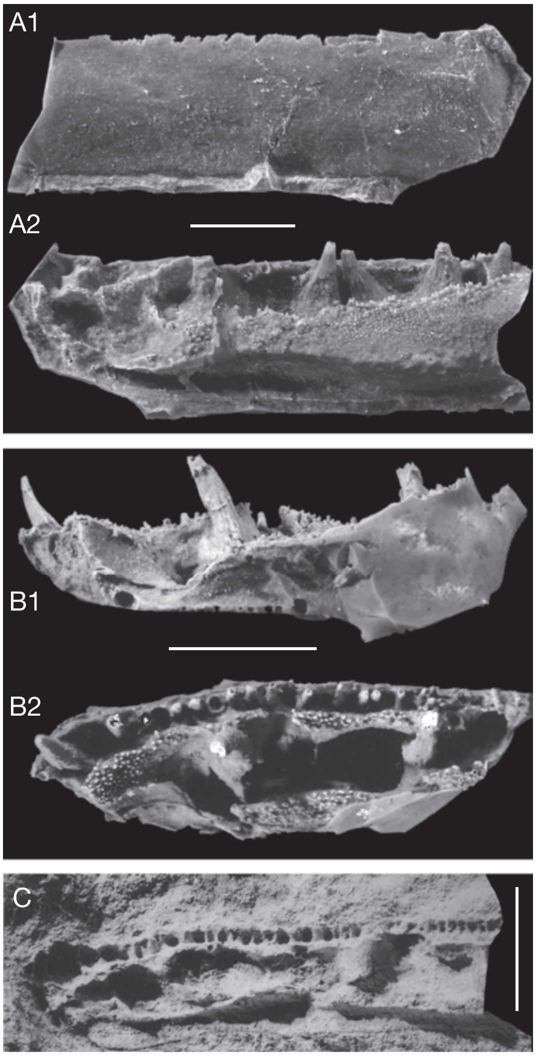

FIG. 10. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; incomplete lower jaws: **A**, right lower jaw (AT055) in lateral (**A1**) and medial (**A2**) views; **B**, right lower jaw (holotype AT058) in medial (**B1**) and dorsal (**B2**) views; **C**, right lower jaw in medial view (VDT11). Scale bars: 10 mm.

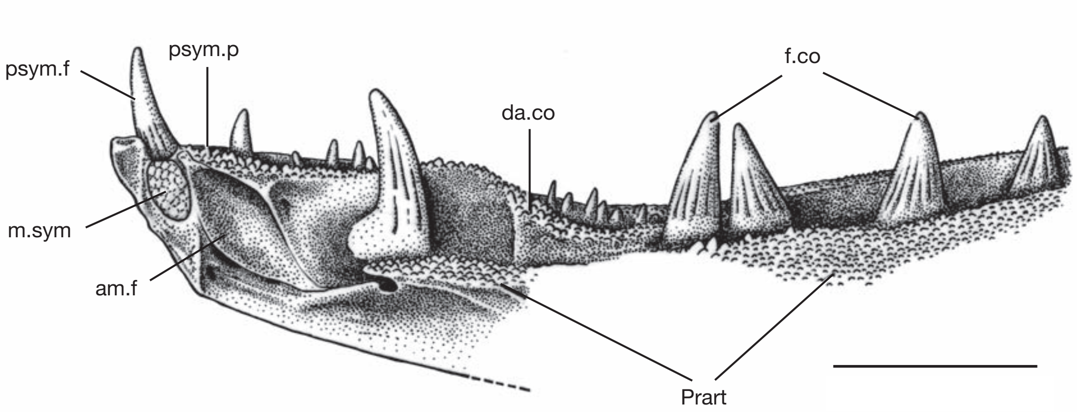

FIG. 11. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; right lower jaw in medial view based on the specimens AT055 and AT058 (Fig. 10A, B). Abbreviations: **am.f**, anterior mandibular fossa; **da.co**, denticulate area on the vertical lamina of the coronoids; **f.co**, coronoid fangs; **m.sym**, mandibular symphysis; **Prart**, prearticular; **psym.f**, parasymphysial fang; **psym.p**, parasymphysial plate. Scale bar: 10 mm.

The anterior limit of the denticulated area of the prearticular is situated at the level of the anterior coronoid fang, as in *Cladarosymblema* (Fox *et al.* 1995: fig. 51A, B).

The medial surface of the parasymphysial plate, coronoids, and prearticular are thus covered with numerous small rounded denticles. A similar extensive denticulated covering of the medial side of the lower jaw is known in the osteolepidids *Gogonasus* (Fox *et al.* 1995: fig. 52; Long *et al.* 1997: fig. 36D) and *Medoevia* (Lebedev 1995: fig. 11), but also in the other megalichthyids *Cladarosymblema*, *Megalichthys*, and *Ectosteorhachis*. As suggested above, this condition is nevertheless most likely plesiomorphic for "osteolepiforms", and even for rhipidistians.

Sengoerichthys n. gen. shows a deep groove between the dentary and the coronoids (Fig. 10B2), as in the megalichthyids *Cladarosymblema* and *Ectosteorhachis* (Fox *et al.* 1995), but also *Medoevia* (Lebedev 1995: fig. 11) and *Gogonasus* (Long *et al.* 1997: fig. 36). This feature is also known in other groups, such as the Rhizodontida.

An anterior mandibular fossa is present in *Sengoerichthys* n. gen. between the symphysial region and the anterior tip of the prearticular (am.f, Fig. 11). It most likely accommodated the vomerine fang. It is floored by the Meckelian bone and laterally delimited by dermal bones (i.e. the anterior part of the anterior coronoid and the posterior part of the parasymphysial plate). *Sengoerichthys* n. gen. and *Cladarosymblema* are very similar in this respect, and different from *Megalichthys* and *Ectosteorhachis* where the anterior mandibular fossa is larger and uncluttered (Mohun 2003).

Gular plate

The gular is more elongated than that of other megalichthyids (Fig. 12). This elongation is linked to the more elongate shape of the entire head of *Sengoerichthys* n. gen.

Pectoral girdle

The pectoral girdle is mainly known by a well preserved cleithrum and associated scapulocoracoid (Fig. 8D1) previously described in detail by Janvier & Marcoux (1976) and Janvier (1980). The triradiate scapulocoracoid is less extensive on the internal surface of the cleithrum than in other megalichthyids (Andrews & Westoll 1970: fig. 2; Thomson & Rackoff 1974: fig. 1; Fox *et al.* 1995: fig. 63), but it is nevertheless larger than in most other "osteolepiforms" (e.g., *Eusthenopteron*), with the exception of *Medoevia* (Lebedev 1995: fig. 21). In *Medoevia*, the internal surface of the scapulocoracoid presents a very similar triangular shape to that of *Sengoerichthys* n. gen. A strikingly similar morphology of the scapulocoracoid (i.e. a subtriangular shape with an enlarged anterior region) also occurs in the tristichopterid *Cabonnichthys* (Ahlberg & Johanson 1997: fig. 13A).

An anocleithrum (Fig. 8F) presents a cosmine-covered triangular area and two overlap areas for the cleithrum and the supracleithrum, respectively. This anocleithrum is assigned to *Sengoerichthys* n. gen. with some doubt since the other megalichthyids do not have a cosmine-covered anocleithrum. Furthermore its shape is different from that of the anocleithrum of *Cladarosymblema* (Fox *et al.* 1995: fig. 59C, D) and its anterodorsal process seems bifid, as in the dipnoans *Andreyevichthys* (Krupina 1997), *Scaumenacia* (Jarvik 1980) and *Chirodipterus* (Campbell & Barwick 1987). Therefore, it is not ruled out that this anocleithrum may belong to a dipnoan rather than to *Sengoerichthys* n. gen.

DERMAL ORNAMENTATION AND SCALES

Most of the dermal bones and isolated scales referred to *Sengoerichthys* n. gen. are covered with a continuous cosmine sheet. However some thick elements (Fig. 8D2, E, G) show evidence of major cosmine resorption as in the Carboniferous and Permian megalichthyids (Thomson 1975). We rule out dipnoan derivation for these isolated remains, because of the absence of Westoll-lines on all cosmine covered elements found at the Armutgözlek Tepe locality.

The vermiculate ornamentation of the cleithrum of *Sengoerichthys* n. gen. (Fig. 8D2, E) is known in numerous "osteolepiforms" but well marked in megalichthyids. This ornamentation is almost identical to that of the cleithrum of *Cladarosymblema* (Fox *et al.* 1995: fig. 60A).

BIOSTRATIGRAPHICAL AND PALEOBIOGEOGRAPHICAL CONSIDERATIONS

The Gondwanan affinities of the Armutgözlek Tepe fauna are mainly indicated by the presence of the phyllolepid placoderm *Placolepis* sp. (Dupret *et al.* 2005) and, to some extent, by the presence of two species of the arthrodire *Groenlandaspis*. The latter genus is widely distributed in Gondwana (Australia, Antarctica, South Africa, Falkland Islands) from the ?upper Pragian-Eifelian of the Dulcie Sandstone and Cravens Peak Beds of Australia (Young & Goujet 2003) to the uppermost Famennian of eastern Turkey (Janvier *et al.* 1984), Australia and South Africa, but is restricted to the Famennian in Euramerica (see review in Janvier & Clément 2005) with one possible occurrence in the uppermost Frasnian of Scatt Craig, Scotland (Newman 2005).

FIG. 12. — *Sengoerichthys ottoman* n. gen., n. sp., Upper Devonian, ?Frasnian, red sandstone of Pamucak-Sapan Dere Unit, Upper Antalya Nappe; Armutgözlek Tepe, Kemer, Antalya, Turkey; right gular plate (AT075) in internal view. Scale bar: 10 mm.

The Armutgözlek Tepe locality was first referred to the Frasnian by Janvier & Marcoux (1977), but later to the Famennian by Janvier (1983), based on the presence of phyllolepids, and despite the presence of the arthrodire *Holonema*, which is not recorded with certainty above the Frasnian-Famennian boundary. Since then, phyllolepids have been shown to occur in Gondwana well before the Famennian, in the Frasnian and Givetian (Long 1984; Ritchie 1984; Young 1993a, 2005a, b), although the group remains unknown before the Famennian outside Gondwana. Knowing that southern Turkey was, in Devonian times, part of the Gondwanan margin, the presence of phyllolepids and *Holonema* in the Armutgözlek Tepe fauna made a Frasnian age plausible. Moreover, new findings suggest that at least one phyllolepid in this fauna can be referred to the genus *Placolepis* (Dupret *et al.* 2005). The latter is known in the Givetian and Frasnian of Australia (Young 2005a) and the arthrodire *Holonema* is known from the late Emsian to the late Frasnian. The *Holonema* species found in the Armutgözlek Tepe locality is very similar to *H. radiatum* from the Frasnian of Russia and Iran (Lelièvre *et al.* 1981) and close to *H. westolli* from the Frasnian of Australia.

If the Frasnian age for this locality is correct, then the presence of a megalichthyid in Turkey would support the hypothesis of an earlier Gondwanan occurrence for this group (Janvier *et al.* 1979). No megalichthyid remains have yet been recorded in Euramerica before the Famennian. In contrast *Mahalalepis* from the Givetian of Antarctica (Young *et al.* 1992), if eventually identified as a megalichthyid, provides evidence for earlier occurrence of this group in Gondwana, well before the Famennian. It should be pointed out, however, that the Famennian of Russia and Siberia also yields a number of cosmine-covered "osteolepiforms", notably *Megistolepis* (Vorobyeva 1977) and *Cryptolepis* (Vorobyeva 1975; Lebedev 1995), whose affinities are still unclear, and it is not ruled out that they turn out to be primitive megalichthyids.

The Armutgözlek Tepe fauna is the westernmost Late Devonian vertebrate fauna of Gondwanan type associated to an "Old Red Sandstone" facies, with the exception of the ?Givetian-Frasnian faunas in the red sandstones of Colombia (Janvier & Villarroel 2000) and Venezuela (Young & Moody 2002).

The composition of the vertebrate fauna of the Armutgözlek Tepe locality is consistent with the hypothesis that phyllolepids, and probably megalichthyids, had a broad distribution in Gondwana by the Frasnian, but had not yet dispersed into Euramerica (Laurentia + Baltica). A similar case can be made for other fishes, probably restricted to marginal or freshwater environments, such as the placoderm *Groenlandaspis*, the lungfish *Soederberghia*, the rhizodontid tetrapodomorphs, and the gyracanthid acanthodians. The genus *Groenlandaspis* is known in Gondwana since the ?Pragian-Emsian but only in the Famennian of Euramerica. The rhynchodipterid lungfish *Soederberghia* is known in the Frasnian and Famennian of Australia, but only in the Famennian of Pennsylvania, East Greenland and Belgium (Lehman 1959; Ahlberg *et al.* 2001; Clément & Boisvert 2006). Rhizodontids are known from the Givetian-Frasnian of Gondwana (Janvier & Villarroel 2000; Johanson & Ahlberg 2001) but the earliest Euramerican occurrences are so far only in the late Famennian of Pennsylvania (Davis *et al.* 2001, 2004) and the Middle Famennian of Belgium (Clément *et al.* 2004).

The apparently rapid dispersal of these organisms into Euramerica during the Famennian provides evidence for some kind of continental link; i.e. a continuity of the marginal deposits, between Euramerica and Gondwana (Young 1993b). Most early paleogeographical reconstructions for the Late Devonian (Van der Voo 1988; Kent & Van der Voo 1990; Scotese & McKerrow 1990; Li *et al.* 1993, 1995) showed a major discrepancy with the paleontological data, notably an increasingly large oceanic space between Euramerica and Gondwana from the Early to the Late Devonian, although a contact between these two supercontinents by the Early Carboniferous is widely accepted. However, it is likely that the Euramerica-Gondwana contact had occurred by the Famennian, but the precise location of this contact is still uncertain. According to Dalziel *et al.* (1994) it could have taken place either between the southern margin of Euramerica (present-day eastern Europe) and the central region of the northern margin of the Gondwana (present-day Near or Middle East), or between the southwestern margin of Euramerica (present-day western North America) and the northeastern margin of Gondwana (present-day northwestern South America). The recent findings of Frasnian vertebrate-bearing "Old Red Sandstone" facies in Colombia and Venezuela (Janvier & Villarroel 2000; Young *et al.* 2000) possibly support the latter possibility. The Frasnian fauna of the Cuche Formation (Colombia) yields two taxa, the antiarch *Asterolepis* and the porolepiform *Holoptychius* (or, at any rate a holoptychiid), which commonly occur as early as the Middle Devonian in Euramerica, but have hitherto never been recorded from Gondwana, with the exception of a holoptychiid in the upper Famennian of Australia. The Colombian occurrences are the only instance of Euramerican vertebrate taxa that may have dispersed into Gondwana before the Famennian, and it may hint at an early Gondwana-Euramerica connection at the level of northwestern South America.

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