A new *Crossognathus* (Actinopterygii, Teleostei) from the Lower Cretaceous of Romania with comments on Crossognathidae relationships

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Cavin L. & Grigorescu D. 2005. — A new *Crossognathus* (Actinopterygii, Teleostei) from the Lower Cretaceous of Romania with comments on Crossognathidae relationships. *Geodiversitas* 27 (1) : 5-16.

ABSTRACT

Crossognathus danubiensis n. sp., known by a single specimen from the middle Albian of the vicinity of Giurgiu, south Romania, is described. The new species differs from other *Crossognathus* by the very elongated posterior infraorbitals covering the vertical limb of the preopercle and part of the opercle and by the bones of the opercular series with fine posterior radiating ridges. Some of its characters, such as the presence of numerous well developed branchiostegal rays, are unusual for crossognathids and are discussed. We discuss the phylogenetic relationships of crossognathids and we point out several characters indicating possible relationships with the Late Jurassic Varasichthyidae. This possible sister-group relationship is regarded as a working hypothesis for further studies on basal teleosts phylogeny.

KEY WORDS
Actinopterygii,
Teleostei,
Crossognathus,
Lower Cretaceous,
Romania,
basal teleosts,
phylogeny,
new species.

RÉSUMÉ

Un nouveau Crossognathus *(Actinopterygii, Teleostei) du Crétacé inférieur de Roumanie et remarques sur les relations des Crossognathidae.*

Crossognathus danubiensis n. sp. est décrit sur la base d'un unique exemplaire en provenance de l'Albien moyen des environs de Giurgiu dans le sud de la Roumanie. La nouvelle espèce se distingue des autres *Crossognathus* par des infraorbitaires postérieurs très allongés couvrant entièrement la branche verticale du préopercule et une partie de l'opercule, ainsi que par les ossifications de la série operculaire portant de fines crêtes rayonnantes. Certains de ses caractères, telle la présence de rayons branchiostèges bien développés, sont inhabituels chez les Crossognathidae et sont discutés. Les relations phylogénétiques des Crossognathidae sont abordées et nous soulignons plusieurs caractères indiquant de possibles relations avec les Varasichthyidae du Jurassique supérieur. Ce résultat doit servir d'hypothèse de travail pour de futures études sur la phylogénie des téléostéens basaux.

MOTS CLÉS
Actinopterygii,
Teleostei,
Crossognathus,
Crétacé inférieur,
Roumanie,
téléostéens basaux,
phylogénie,
nouvelle espèce.

INTRODUCTION

The Cretaceous actinopterygian fossil record of Romania is poor. The only documented occurrence is *Osmeroides dobrogensis* Grigorescu & Marin, 1971 from the Turonian of the Babadag Basin (Grigorescu & Marin 1971). We describe here a new species based on a single isolated specimen from the middle Albian found in the vicinity of Giurgiu, about 100 km south of Bucharest (Fig. 1).

Rich Albian fish assemblages are known from various localities around the world, such as in North America (Paluxy Formation in US, Tepexi de Rodriguez in Mexico), South America (Santana Formation in Brazil), and Australia (Toolebuc Formation). The only rich Albian fish fauna in Europe is from the British Gault. No comparable fish assemblages are known in Central Europe and Asia. Thus, every single discovery outside the main fish localities is important for our understanding of Early Cretaceous teleost distribution and phylogeny.

The objective of this paper is to describe the new species and to discuss its possible relationships. We also comment some characters relevant to assessing relationships among basal teleosts, and we discuss the possible sister-group relationship with Varasichthyidae as already proposed by Cavin (2001). The goal of the present paper, however, is not to provide a comprehensive analysis of the phylogenetic relationships of basal teleosts.

ANATOMICAL AND INSTITUTIONAL ABBREVIATIONS

An	angular;
Axp	axillary process;
Bop	branchiopercle;
br	branchiostegal ray;
Cl	cleithrum;
D	dentary;
Dpt	dermopterotic;
Dsp	dermosphenotic;
Ecpt	ectopterygoid;
Enpt	entopterygoid;
Ext	extrascapular;
ext.com	extrascapular commissure;
Fr	frontal;
G	gular;
Io	infraorbital bone;
md	median depression;
Mx	maxilla;
Op	opercle;
Pa	parietal;
Pal	palatine;
Pop	preopercle;
Psp	parasphenoid;

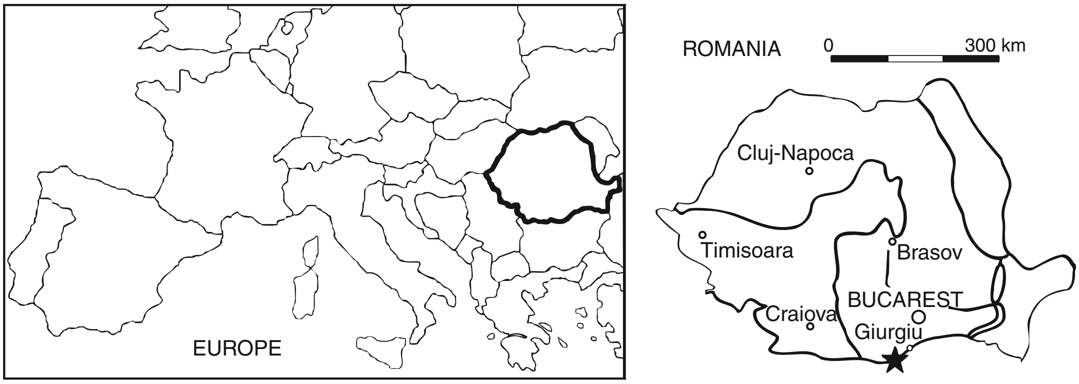

FIG. 1. — Location map of Romania showing the position of the type locality (★).

Ptt	posttemporal;
Q	quadrate;
Scl	supracleithrum;
Smx	supramaxilla;
Sob	supraorbital;
Sop	subopercle;
sr	sclerotic ring;
BMNH	The Natural History Museum, London;
FGGUB	Faculty of Geology and Geophysics, University of Bucharest.

GEOLOGICAL SETTING

The fossil was found on the Romanian bank of the Danube in a shallow drill core made in the 1950's during the building of a railway and road bridge crossing the Danube from Giurgiu in Romania to Russe in Bulgaria. The locality is now flooded by the Danube waters. The rock in which the bridge pillars were embedded and which provided the fossil fish specimen is a fine gray marl with glauconite, that filled the body after the death and bury. The matrix, visible in the posterodorsal part of the specimen where the squamation is eroded, resembles the British Gault. The gray marls represent the uppermost (youngest) deposit that outcrops at the lowest level of the river under the Quaternary terraces.

The place of the discovery belongs to the Moesian Platform, the geotectonic unit that separates the Southern Carpathians from the Stara Planina Mountains in northern Bulgaria.

For more than 40 years the specimen was kept in a private collection, without being described. It eventually reached Prof. Theodor Neagu from the Laboratory of Paleontology of the University of Bucharest, who gave it for study to the second author of this paper.

The circumstances of the discovery – accidentally, by a non-specialist – did not leave information on the depth and consequently, on the precise stratigraphic level of the specimen. According to Prof. T. Neagu who studied the ammonites and foraminifera from the drillings near Giurgiu (Neagu 1959), the marl deposits that yielded the specimen is middle Albian in age with the ammonite *Hoplites dentatus* (Sowerby, 1821) and the belemnite *Neohibolites minimus* (Miller, 1826) as index-species.

MATERIAL EXAMINED

Apsopelix (= "*Syllaemus*") *anglicus* (Dixon, 1850): BMNH P.611, holotype (Lower Chalk), BMNH P.49055 (Lower Chalk), BMNH P.9890 (Gault), BMNH P.9053 (Gault), BMNH P.47196 (Gault). Wenz (1965: 21) suggested that the specimens from the Gault and from the Chalk show different body ratios and constitute two groups. But she did not create a new taxon for the Gault specimens.

Osmeroides lewesiensis (Mantell, 1822): BMNH P.4296 (Chalk).
Osmeroides levis Woodward, 1901: BMNH P.1854 (Chalk).
Crossognathus danubiensis n. sp.: FGGUB.V.210.

SYSTEMATICS

Subclass ACTINOPTERYGII Cope, 1887
Division TELEOSTEI
sensu Patterson & Rosen, 1977
Family CROSSOGNATHIDAE
Patterson & Rosen, 1977

Genus *Crossognathus* Pictet, 1858

TYPE SPECIES. — *Crossognathus sabaudianus* Pictet, 1858: 18-28, pls 2, 4, figs 1-6.

Crossognathus danubiensis n. sp.

HOLOTYPE AND ONLY KNOWN SPECIMEN. — FGGUB.V.210.

TYPE LOCALITY. — On the bank of the Danube, vicinity of Giurgiu, Romania.

TYPE LEVEL. — Middle Albian.

ETYMOLOGY. — From the Latin *Danubius*, the name of the Danube River.

DIAGNOSIS. — *Crossognathus* with elongated posterior infraorbitals covering the vertical limb of the preopercle and part of the opercle, opercular bones with fine posterior radiating ridges, small teeth on the ectopterygoid and palatine, numerous and well developed branchiostegal rays, scales small, numerous, with radii on the posterior exposed area.

DESCRIPTION (FIGS 2-4)

The single-known specimen is incomplete. The head is preserved, but the anterior extremity of the skull roof, the ethmoid region and the tips of mandibles are missing. The ventral part of the squamation is preserved back to the level of the pelvic fins, whilst dorsally the squamation is preserved up to the level of the midline between the pectoral and the pelvic fins. The specimen is slightly dorso-ventrally flattened. The head is tapered ventrally at the level of the mandibles, but broadens posteriorly at the levels of the opercular apparatus.

Skull roof

Only the posterior part of the skull roof is preserved. The anterior tips of both frontals (Fr) are missing. The preserved posterior parts show that the frontal is broader posteriorly than anteriorly, giving a roughly triangular outline in dorsal view. The surface of both frontals is not well preserved, but ridges and weak reticulated networks of ridges radiate from each centre of ossification. A stronger ridge runs posteromedially from each centre of ossification and meets its counterpart in the midline, defining the posterior margin of a median shallow depression (md). Such a median depression is present in crossognathids (Taverne 1989) and pachyrhizodontids (Forey 1977) among other teleosts. The suture between frontals is smooth and forms a sigmoid line in the half of the length of preserved bones. Most of the posterior part of the skull roof is covered by the hypertrophied extrascapulars (Ext) and only reduced surfaces of both parietals (Pa) are visible. They contact the frontals with interdigitate sutures. Because of the size of extrascapulars, we cannot determine if both parietals are in contact in the midline (the medioparietal condition versus the lateroparietal condition). Posterolaterally to the frontals and laterally to the parietals is a pair of badly preserved ossifications, regarded as dermopterotics (Dpt). The general shape of these ossifications show that they protrude posterolaterally and extend the lateral margins of the wide frontals posteriorly. The posterior lateral development of the dermopterotics corresponds to the maximum width of the skull roof. Such a shape of the posterior skull roof in dorsal view is reminiscent of crossognathids (Wenz 1965; Teller-Marshall & Bardack 1978; Taverne 1989). A piece of the anterior part of the parasphenoid (Psp), exposed in dorsal view because the anterior part of the skull roof is lacking, and a piece of the right lateral ethmoid, are visible. Pieces of thin curved bones inside the orbit indicate the presence of sclerotic rings (sr). Other elements of the

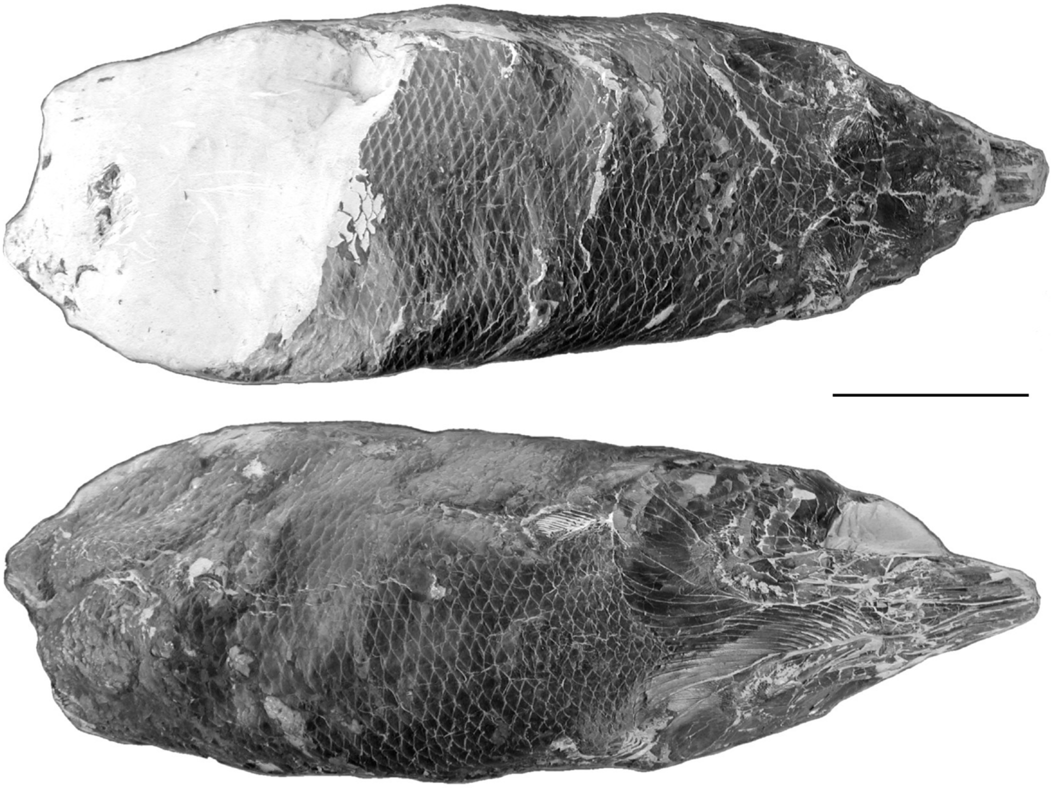

FIG. 2. — *Crossognathus danubiensis* n. sp., photographs of the specimen in dorsal (top) and ventral (bottom) views. Scale bar: 50 mm.

skull roof and of the braincase, as well as the path of sensory canals, are either not preserved, or not visible on the specimen.

Circumorbital bones

Only the posterior half of the ring formed by the circumorbital bones is preserved, and we cannot determine if the circumorbital ring was complete. All the bones forming the circumorbital ring are very thin and fractured, making difficult the observation of limits between the ossifications. The dermosphenotic (Dsp) is located in the posterodorsal edge of the orbit and shows a sinusoidal contact with the last infraorbital. The posterior margin of the orbit is formed by two large infraorbitals (Io) that extend posteriorly over the vertical limb of the preopercle and the anterior part of the opercle. Ventrally, the margin of the orbit is formed by an elongated infraorbital that covers part of the dorsal border of the horizontal limb of the preopercle. The three visible infraorbitals are ornamented on their posterior half with fine radiating shallow grooves. From the infraorbital sensory canal, portions of canals are visible parallel to the posteroventral margin of the orbit, as well as some posteriorly orientated short bone-enclosed branches that seem to radiate from two points located dorsally and ventrally along the posterior section of the canal. A relatively similar pattern is visible on the reconstruction of the cheek of *Crossognathus sabaudianus* Pictet, 1858 proposed by Taverne (1989: fig. 2).

Suspensorium

Only a small part of the suspensorium is visible. The quadrate (Q) is antero-posteriorly elongated, its posterior margin being almost horizontal in lateral view. The posteroventral process of the quadrate is well developed and forms a thickened body of bone by comparison with thin plate-like remaining part of the quadrate. The anterior extremity of the posteroventral process forms a broad concave articular facet that receives the postarticular process of the mandible as described in *Apsopelix* (Teller-Marshall & Bardack 1978). Ventrally, the posteroventral process of the quadrate bears a groove in which rested the symplectic. Only a piece of the latter bone is still visible on the left side of the specimen. Suturing with the anterior margin of the quadrate is the ectopterygoid (Ecpt), which shows a concave ventral edentulous margin. The rest of the suspensorium is not visible, except the dorsal face of the entopterygoid (Enpt) and of the elongated palatines (Pal) that extend horizontally from the lateral margins of the suspensorium to the parasphenoid. Two patches of minute alveoli are visible medially on the right ectopterygoid and on the ventral side of the right palatine, the latter one still bearing a few small rounded teeth.

Upper jaw

From the upper jaw, only fragments of the right maxilla (Mx) and parts of both supramaxillae (Smx) are preserved; no teeth are visible. The posterior supramaxilla bears on the posterior half of the bone a pattern of radiating grooves extending from a longitudinal axis and the anterior supramaxilla bears trace of a similar pattern on its dorsalmost margin. Such ornamentation has been described in *Apsopelix anglicus* (Teller-Marshall & Bardack 1978) and figured in *Crossognathus sabaudianus* (Taverne 1989). In

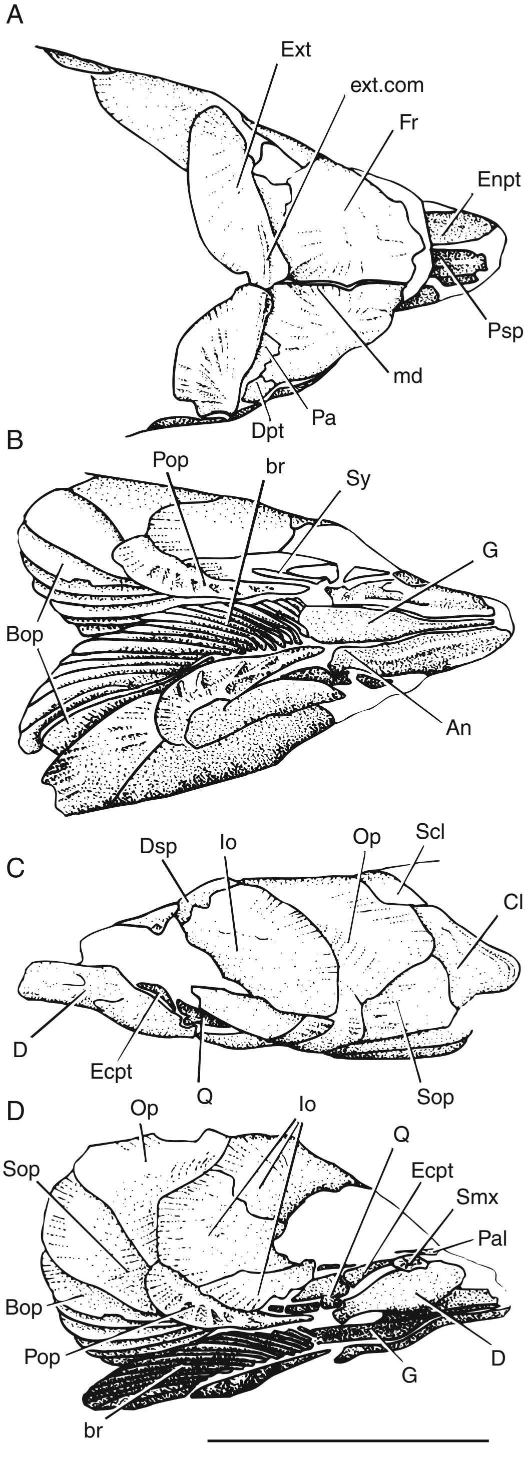

FIG. 3. — *Crossognathus danubiensis* n. sp., holotype (FGGUB.V.210), drawings of the head in dorsal (**A**), ventral (**B**), left lateral (**C**) and right ventrolateral (**D**) views. Abbreviations: **An**, angular; **Bop**, branchiopercle; **br**, branchiostegal ray; **Cl**, cleithrum; **D**, dentary; **Dpt**, dermopterotic; **Dsp**, dermosphenotic; **Ecpt**, ectopterygoid; **Enpt**, entopterygoid; **Ext**, extrascapular; **ext.com**, extrascapular commissure; **Fr**, frontal; **G**, gular; **Io**, infraorbital bone; **md**, median depression; **Op**, opercle; **Pa**, parietal; **Pal**, palatine; **Pop**, preopercle; **Psp**, parasphenoid; **Q**, quadrate; **Scl**, supracleithrum; **Smx**, supramaxilla; **Sop**, subopercle; **Sy**, symplectic. Scale bar: 50 mm.

"*Syllaemus albiensis*", regarded as a synonym of *Apsopelix anglicus* by Patterson & Rosen (1977) and Teller-Marshall & Bardack (1978), and as a synonym of *Crossognathus sabaudianus* by Taverne (1989: fig. 2), Wenz (1965) described a shallow longitudinal groove running along both ossifications.

Lower jaw

Both lower jaws are preserved, but only their posterior part show any details. The general shape of the hemi-mandibles is apparently proportionally longer and shallower than in *Apsopelix anglicus* and *Crossognathus sabaudianus*, in which it is described as leptolepid-like (Taverne 1989). We should, however, point out that the posterior oral margin of the mandible is reconstructed in *Crossognathus sabaudianus* (Taverne 1981: fig. 20; 1989: fig. 5) and in "*Syllaemus albiensis*" (Wenz 1965: fig. 5). No teeth are visible on the holotype, but the oral margin of the dentary is not well preserved. The dentary (D) has a concave ventral outline in lateral view and forms ventrally a sharp edge extending medially as a horizontal shelf, as in *Apsopelix anglicus* (Teller-Marshall & Bardack 1978). The medial margins of these shelves are ornamented with fringes. The angular (An) extends anteroventral into a thin process on the edge of the mandible. The ventral part of the retroarticular process and of the facet bears a reticulate ornamentation. As the hemi-mandibles are visible in lateral view only, we cannot distinguish the sutures between the bones of the posterior extremity of the mandible (angular, articular, retroarticular).

Opercular series, branchiostegal rays, and gular

The preopercle (Pop) is crescent in shape with a rounded and regular posterior angle. Its dorsal extremity is hidden by the infraorbitals. The posterior and posteroventral margins of the bone are ornamented with very fine grooves, reminiscent of the ornamentation observed on the infraorbitals. At least seven bone-enclosed canals extend radially from the main sensory canal in the posteroventral and ventral parts of the ossification. The anterior tip of the preopercle is tapered. The opercle (Op) is a well developed bone. Its dorsal and posterior margins are rounded, and its ventral margin is obliquely orientated and slightly concave. The subopercle (Sop) is also well developed, with a regular rounded posterior margin and a straight ventral margin. Only a small part of the interopercle is visible on the right side of the skull, the main body of the bone being hidden under the horizontal limb of the preopercle. This condition is common in crossognathids, since Wenz (1965) regarded the interopercle in "*Syllaemus albiensis*" as absent, because the ossification was hidden under the preopercle. The dorsalmost branchiostegal ray differs from the other ones by its stronger ornamentation and by its anterior extremity that disappears below the horizontal limb of the preopercle with a different angle that the mean angle formed by the bases of the more anterior branchiostegal rays. This ossification is specific enough to deserve the designation of branchiopercle (Bop), as described in *Amia calva* (Grande & Bemis 1998). Apart from the branchiopercle, 21 left, elongated and plate-like branchiostegal rays (br) are visible. The bases of the anteriormost rays are covered by the thin gular plate. The left series of rays covers the right series (a sinistral individual). The gular plate is an elongated bone that extends anteriorly from the symphysis to a level situated at the anterior extremities of the preopercles posteriorly. The ossification is tapered and very thin at the symphysis, then broadens in the middle length of the mandible and reaches a constant width posteriorly. A few minute teeth similar to those borne by the palate are visible of the floor of the buccal cavity. They are probably borne by the basihyal and/or basibranchial, although the latter bones are not visible on the specimen.

Pectoral girdle and fins

The extrascapulars are very large, meet together in the middline, and cover most of the parietals. The canal for the extrascapular commissure runs parallel and close to the straight anterior margin of the extrascapular. The posterior margin is rounded and the surface of the bone is ornamented with fine radiating ridges. The postemporal is also very

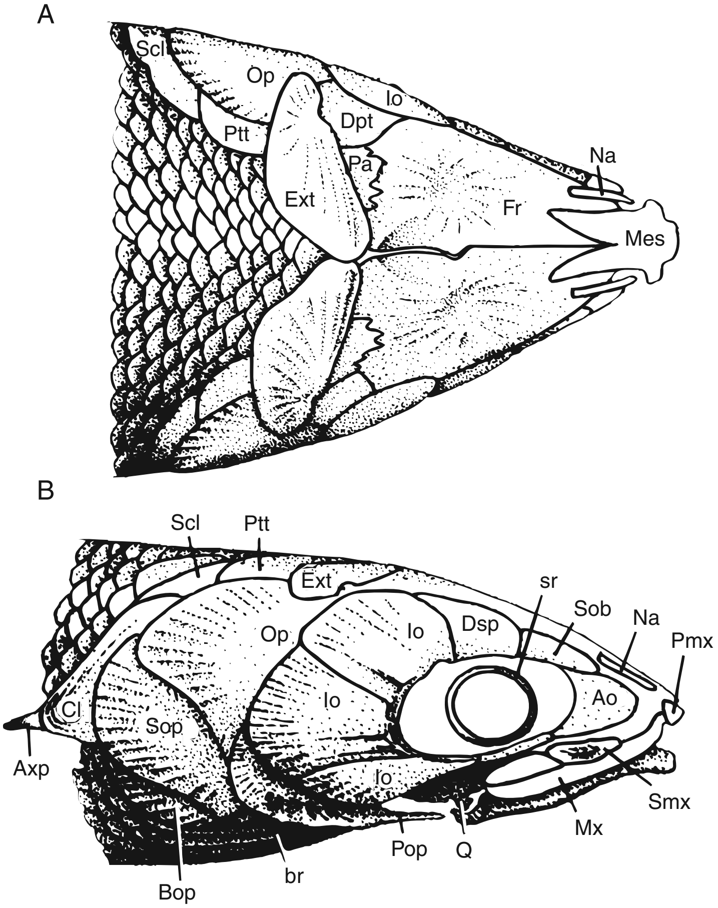

FIG. 4. — Reconstruction of the head of *Crossognathus danubiensis* n. sp. in dorsal (**A**) and lateral (**B**) views. Abbreviations: **Ao**, antorbital; **Axp**, axillary process; **Bop**, branchiopercle; **br**, branchiostegal ray; **Cl**, cleithrum; **Dpt**, dermopterotic; **Dsp**, dermosphenotic; **Ext**, extrascapular; **Fr**, frontal; **Io**, infraorbital bone; **Mes**, mesethmoid; **Mx**, maxilla; **Na**, nasal; **Op**, opercle; **Pa**, parietal; **Pmx**, premaxilla; **Pop**, preopercle; **Ptt**, posttemporal; **Q**, quadrate; **Scl**, supracleithrum; **Smx**, supramaxilla; **Sob**, supraorbital; **Sop**, subopercle; **sr**, sclerotic ring.

large, but badly preserved on the specimen. The cleithrum has a well developed posteroventral edge, that expands above the pectoral fin as in *Apsopelix anglicus* (Teller-Marshall & Bardack 1978). An elongated axillary process is visible on the left side of the specimen, the surface of which is marked by pittings as in *Apsopelix anglicus* (Woodward 1903). The number of postcleithra cannot be determined. The bases of fin rays and their traces on the squamation visible on both sides of the specimen indicate that the pectoral fins were elongated and contained at least 12 rays.

Scales

The scales broadly overlapped each other. They are small, cycloid, with numerous fine circuli and radii in the exposed posterior area. We estimate that 30 horizontal scale rows are present on each side of the body just behind the pectoral girdle. The general scale morphology corresponds to the description made by Taverne (1989) for *Crossognathus sabaudianus*, but differ from the scales observed in *Apsopelix anglicus* from the English Gault and Chalk (pers. obs.) and from North America (Dunkle 1958). Moreover, the relative size of the scales is much smaller in *C. danubiensis* n. sp., since 10-12 horizontal rows only are present on each side at midbody in *Apsopelix* (Woodward 1903; Teller-Marshall & Bardack 1978).

DISCUSSION

Of the characters used by Taverne (1989) to define the Crossognathidae, *C. danubiensis* n. sp. possesses the following (slightly modified from Taverne 1989, with a * for the probable derived characters for basal teleosts): the palatine bone is apparently elongated*, there are few broad infraorbitals* and a median frontal depression*, the skull roof is wide in its posterior part due to the lateral development of the dermopterotic*, the posttemporal is hypertrophied*. A very large extrascapular, anteriorly situated and covering part of the parietal*, is another character present in all crossognathids. *C. danubiensis* n. sp. has teeth on the suspensorium, in opposition with the Taverne's list of diagnostic characters for crossognathids. However, this character has not been directly observed by Taverne (1989: fig. 2) in *Crossognathus sabaudianus* Pictet, 1858, and Teller-Marshall & Bardack (1978: 14) claimed with caution that the pterygoid elements are edentulous in *Apsopelix anglicus* (Dixon, 1850).

Apsopelix Cope, 1871 and *Crossognathus* Pictet, 1858 are closely related, and Taverne (1989) proposed some characters to distinguish both genera, with the following ones visible on *C. danubiensis* n. sp.: the extrascapular covers the pterotics and the parietals more completely in *Crossognathus* than in *Apsopelix*; the dermosphenotic is very large in both genera, but in *Crossognathus* it extends more posteriorly than the infraorbitals on the posterior margin of the orbit and covers the anterodorsal edge of the opercle, while it is not the case in *Apsopelix*. In *C. danubiensis* n. sp. the pattern is slightly different, since we interpret the broad ossification covering the anterodorsal edge of the opercle as an infraorbital, with a smaller dermosphenotic located more anteriorly, above the orbit. Our interpretation should be regarded with caution, because it rests on a single specimen and the bones are damaged in that region, which renders difficult the delimitation of sutures. The opercular series is proportionally larger in *Crossognathus* than in *Apsopelix*; the subopercle is narrower and deeper in *Apsopelix* than in *Crossognathus*. Accordingly, *C. danubiensis* n. sp. is closer to *Crossognathus sabaudianus* than to *Apsopelix anglicus* and is here included in the genus *Crossognathus*, waiting for more abundant material to assess this assignment. *C. danubiensis* n. sp., however, differs from both *Crossognathus* and *Apsopelix* by its proportionally much smaller scales.

It is worth noting than two characters of *C. danubiensis* n. sp. are shared with Osmeroididae Forey, 1973: the presence of small teeth on the palatine and ectopterygoid and the numerous and well developed branchiostegal rays. However, as mentioned above, the absence of teeth on the palatine and ectopterygoid is not definitively proven in other crossognathids (the available material in The Natural History Museum collection do not allow us to see this character). Moreover, this character seems to be highly homoplasic when its distribution is observed on a cladogram of basal teleosts (Cavin 2001: fig. 16). The second character, numerous branchiostegal rays, deserved comments. The skull of crossognathids is generally described as compressed to a sharp edge ventrally (Woodward 1903; Wenz 1965; Teller-Marshall & Bardack 1978). We effectively found that most specimens of *Apsopelix anglicus* from the English Gault and Chalk housed in the BMNH, especially those from the Gault, show a tapered ventral edge. In BMNH P.9890, the ventral margin of both hemi-mandibles bears a deep groove, the medial margin of which is in contact with its counterpart. A narrow gular plate is visible at the level of the articulation of the lower jaw, but is hidden more anteriorly. Posteriorly to the lower jaw, the paired preopercles are in contact with each other along their ventral margins. This structure, also visible in BMNH P.9053 and BMNH P.47196a, is quite unusual in teleosts. No traces of branchiostegal rays are visible in all the available specimens, which led Wenz (1965) to suggest that branchiostegal rays and interopercles are absent in this taxon. We hypothesise that the spread branchiostegal rays are exposed in the specimen of *C. danubiensis* n. sp. for taphonomical reasons, in particular because of the slight dorsoventral crushing of the body and head. Such a set of branchiostegal rays should also be present in other crossognathids, but are rarely visible because of the different modes of preservation. Woodward (1903) and Teller-Marshall & Bardack (1978) mentioned the impressions of respectively 10 and 12 rays in specimens of *Apsopelix anglicus*, but the three authors suspected that the number of rays was originally higher. Accordingly, the apparent similarities between the Romanian fish and *Osmeroides* species are here regarded as due to the mode of preservation.

PHYLOGENETIC RELATIONSHIPS

The systematic affinities of crossognathids are unclear. They have been placed with caution in the family Mugilidae Cuvier & Valenciennes, 1836 by Stewart (1900: 383), within the clupeids (Woodward 1903) or ranged in their own family, the Crossognathidae, in the Percesoces (Woodward 1901). Patterson & Rosen (1977) placed the Crossognathidae in a very basal position among the teleosts, as the sister group of Osteoglossomorpha-Elopocephala. Then, Taverne (1989) gathered the Crossognathidae with the Pachyrhizodontidae in the Crossognathiformes, resolved as the sister-group of the Clupeomorpha-Euteleostei. Patterson (1993) accepted this view without discussing it. Cavin (2001) again placed the Crossognathidae before the node Elopomorpha-Clupeocephala (Osteoglossomorpha were not included in this analysis) and suggested, but did not demonstrate, possible affinities with the Varasichthyidae Arratia, 1981, which are basal teleosts known from the Late Jurassic of Chile and Cuba (Arratia 1981, 1984, 1986, 1994, 1997; Arratia & Schultze 1985). This hypothesis of relationships rests on the similar evolutionary level among the basal teleosts of characters from the skull, such as the foramen for the vagus nerve placed in the posterolateral face of exoccipital alone (Arratia 1999), the edentulous parasphenoid, the trigeminal foramen opening into orbit, as well as in characters from the caudal skeleton, such as the presence of six uroneurals with the anteriormost ones reaching PU3 and *c.* 10 hypurals. Other characters, which are potential synapomorphies of crossognathids and varasichthyids, are a parasphenoid extending posterior to the basioccipital (in some of the taxa at least), premaxillae and intercalars atrophied, the articular and angular are fused together (independently acquired in clupeocephalans according to Cavin's analysis), the ventroposterior region of preopercle broadly expanded (Cavin 2001). According to the discussion above, we can add one new character to the list of potential synapomorphies: the presence in the preopercular canal of numerous tubules or grooves in ventral limb reaching ventral and ventroposterior margin of the preopercle. Recently, Arratia (1996) found a sister-group relationship between varasichthyids and *Ascalabos* von Münster, 1839 from the Late Jurassic of Germany. This clade is defined by a unique synapomorhy, the presence of cycloid scales with circuli crossed by transverse lines in the middle field, and a homoplasy, the middle pitline groove crossing the parietal and extending onto the pterotic. Scales with circuli crossed by transverse lines in the middle field are apparently present on one specimen of *Crossognathus anglicus* from the Chalk (BMNH P.49055) but it is unclear if the transverse lines really cross the circuli or simply extends them after forming a sharp edge. The second character, the middle pitline groove crossing the parietal and extending onto the pterotic, has not been observed on the available crossognathids material.

None of the characters mentioned above are unique among teleosts, and it is only their most-parsimonious distributions, which will provide clues of affinities. A thorough survey of these characters among basal teleosts is now necessary to test the hypothesis of the monophyly of a group containing the two crossognathids genera (*Crossognathus* and *Apsopelix*) and some or all varasichthyids (*Varasichthys* Arratia, 1981; *Domeykos* Arratia & Schultze, 1985; *Protoclupea* Arratia & Schultze, 1985; *Luisichthys* White, 1941) or encompassing a still larger set of taxa (varasichthyids + *Ascalabos*), but this is not the topic of the present paper.

CONCLUSION

The combination of characters observed in *Crossognathus danubiensis* n. sp. justifies the establishment of a new species. Osteological comparisons are made herein with published descriptions of *Crossognathus* and *Apsopelix* from Taverne (1989) and Teller-Marshall & Bardack (1978) respectively, plus information from Patterson & Rosen (1977) on both genera, and from direct observations of *Apsopelix* material housed in the BMNH collection. The specimens of *Crossognathus* described by Taverne and by Patterson & Rosen have been discovered in two sites in Germany (lower Aptian of Helgoland and Neocomian of Hildesheim near Hanover). However, in these papers and in the study herein, the type specimen of *Crossognathus sabaudianus* from the Neocomian of Voirons, Switzerland, kept in the Natural history Museum of the City of Geneva, has not been examined. The type specimen has not been re-studied since the work of Pictet (1858) and its re-description, together with a precise description of the material from Hildesheim, is now desirable to verify if all the German material really belongs to *C. sabaudianus*.

Although based on a single specimen, the new species described here is important because it has implications on phylogenetic relationships of crossognathids as well as extending the known geographical area of crossognathids. Before the discovery of these specimen crossognathids were known from North America and Western Europe.

Acknowledgements

We thank Prof. Theodor Neagu (Laboratory of Paleontology of the University of Bucharest) for providing the specimen and for the information regarding the stratigraphy of the Albian deposits from Giurgiu. We thank Peter Forey (London) and the referees, Gloria Arratia (Berlin) and Louis Taverne (Bruxelles), for their help and comments on the manuscript. LC's research was supported by a Marie Curie Individual Fellowship funded by the Swiss Federal Office for Education and Science (grant No. 02.0335).

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Submitted on 29 March 2004;
accepted on 11 August 2004.