†*Gonostoma dracula* sp. nov. (Teleostei, Gonostomatidae) from the Oligocene deposits of the Central Paratethys (Romania): earliest occurrence of the modern bristlemouths

Ionuţ Grădianu, Tomáš Přikryl, Růžena Gregorová & Antony S. Harold

The Gonostomatidae comprise bioluminescent, meso- to bathypelagic fishes which occur from temperate to tropical climates. The members of this family, most notably *Cyclothone* spp., represent the most abundant vertebrates on Earth. In the present day fauna, the Gonostomatidae consist of six genera: *Bonapartia*, *Cyclothone, Diplophos*, *Gonostoma*, *Margrethia*, *Triplophos*. Although the earliest known gonostomatid, †*Primaevistomias weitzmani,* is from the middle Eocene of the Caucasus, the most significant increase in number of individual specimens occurred in the Early Oligocene of the Central and Eastern Paratethys. †*Scopeloides glarisianus* represents the most abundant Oligocene gonostomatid species and has been recorded from Switzerland, the Czech Republic, Poland, Romania, Caucasus, and Iran, while specimens of †*Kotlarczykia bathybia* are rare, isolated and reported only from Poland and the Czech Republic. In this paper we describe †*Gonostoma dracula* sp. nov., which seems to be the earliest fossil species of *Gonostoma*. The specimens were discovered in the Dysodilic Shale intercalations of the Kliwa Sandstone Formation from Piatra Pinului in the Gura Humorului area, Eastern Carpathians (Romania). †*Gonostoma dracula* sp. nov., differs from all extinct and extant representatives of the genus and seems to exhibit a sequence of characters that are problematic among *Gonostoma* species and that show varying affinities with living representatives, although with some important similarities with *G. bathyphilum*. †*Gonostoma dracula* sp. nov., represents the oldest species to date and the first record of the genus from the Oligocene deposits of the entire Paratethys area. Relevant aspects of paleogeography and paleoecology are discussed. • Key words: Stomiiformes, Gonostomatidae, †*Gonostoma dracula* sp. nov., Paratethys, Oligocene, Romania.

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The Gonostomatidae (bristlemouths) are relatively small oceanic bioluminescent fishes, usually not exceeding 400 mm standard length, which occur from temperate to tropical areas in mesopelagic and bathypelagic depths (Weitzman 1997, Miya & Nishida 2000, Harold 2002). In the present day fauna, the Gonostomatidae include six genera, namely *Bonapartia* Goode & Bean, 1896; *Cyclothone* Goode & Bean, 1883; *Diplophos* Günther, 1873; *Gonostoma* Rafinesque, 1810; *Margrethia* Jespersen & Tåning, 1919; and *Triplophos* Brauer, 1902 (Ahlstrom *et al.* 1984, Weitzman 1997, Harold 1998). According to Miya & Nishida (2000), some species of *Gonostoma* should be treated as members of the resurrected genus *Sigmops* Gill, 1883, although we are of the opinion that the evidence upon which the resurrection of that genus is based is not as strong as it should be. Despite the fact that some members of this family are the most abundant vertebrates on Earth (*i.e. Cyclothone* spp.; Nelson 2006), it is very surprising that the family does not have an enormously rich fossil record. Although historic literature dates the oldest

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gonostomatids to the Cretaceous (†*Paravinciguerria* Arambourg, 1954), the oldest recognized member of the family is represented by †*Primaevistomias weitzmani* from the middle Eocene formations of the northern Caucasus (Prokofiev & Bannikov 2002). Oligocene gonostomatids, such as †*Scopeloides glarisianus,* have been described from different parts of the Paratethys realm, such as Switzerland (Agassiz 1833–1844, Wettstein 1886), Romania (Paucă 1931, Ciobanu 1977, Baciu 2001, Grădianu 2010), Czech Republic (Kalabis 1948, Gregorová 1997, Přikryl *et al.* 2012), Caucasus (Daniltchenko 1960, Prokofiev 2005), Iran (Arambourg 1967) and Poland (Jerzmańska 1968, Kotlarczyk *et al*. 2006). During continuing research on the Paratethys fish fauna, another species of the Gonostomatidae, †*Kotlarczykia bathybia* Jerzmańska, 1974, was described from the 'upper bathypelagic horizon' of the Oligocene Menilitic Beds from the Polish Carpathians (Jerzmańska 1974), and later †*Kotlarczykia* sp. from the Moravian part of the Carpathians (Gregorová 1989). The Miocene record of the family is more diversified and includes specimens from Japan, attributed to the extinct gonostomatid genus †*Ohuus* Sato, 1962, while species from other parts of the world are classified with the recent genera *Gonostoma, Sigmops* and *Cyclothone* (*e.g.* Arambourg 1925, 1927; David 1943; Carnevale 2007; Nazarkin 2015, Přikryl & Carnevale 2017). The first appearance of members of the nominal genus *Gonostoma* has been reported to be from the middle Miocene deposits of Italy and Algeria (Arambourg 1925, 1927). On the other hand, even these specimens, classified as †*G. albyi* (Sauvage, 1873), have problematic characters (see discussion below) and its possible relationships to other gonostomatid taxa are unknown. †*Gonostoma dracula* sp. nov., from Piatra Pinului (Romania), is described herein from the Oligocene and represents the oldest known record of the genus. Detailed osteological and morphological analysis of the species is provided as well as comparisons with selected extant and extinct representatives of the family, and a discussion of its affinities.

Geological setting

Hypoxic to anoxic conditions which dominated the entire Oligocene and part of the Early Miocene in the Paratethys Sea influenced sedimentation within the basins and resulted in the formation of bituminous rocks (for details see, *e.g.* Baldi 1980; Rögl & Steininger 1983; Nagymarosy 1990; Popov *et al*. 2002, 2004). The presence of extremely well-preserved Oligocene fish fossils in the Dysodilic Shales Formation from the Moldova Valley region (Piatra Pinului outcrop) were noted for the first time by Athanasiu (1910). The potential represented by this fossiliferous outcrop, from the Marginal Folds Nappe (Eastern Carpathians, Romania), has caught the attention of many palaeontologists (Paucă 1934; Brustur & Grigorescu 1973; Trelea *et al.* 1973, 1974, 1977), which through these papers have highlighted Oligocene ichthyofaunal biodiversity. However, the taxonomy of that fish fauna is in need of revision. From a stratigraphic point of view, the geological formation from the Piatra Pinului outcrop is of Oligocene age (Ionesi 1971) from the Poiana-Făget-Isachia syncline, Humor demi-window (Marginal Folds Nappe, Eastern Carpathians). The Marginal Folds Nappe (Vrancea Nappe) is covered by the Tarcău Nappe (Fig. 1A) and appears at the surface only as a tectonic window, demi-window or rabotage outliers (Ionesi 1971, Mutihac & Ionesi 1974, Săndulescu 1984, Bădescu 2005). The following geological formations have been identified from the lithological column of the Marginal Folds Nappe: Lower Menilites, Bituminous Marls, Lower Dysodilic Shales, Kliwa Sandstones, and the Upper Dysodilic Shales and Menilites (Ionesi 1971, Grasu *et al.* 1988). Geological formation from which the *Gonostoma* fossils were collected is the Dysodilic Shale intercalation from the upper part of the Kliwa Sandstone Formation (Fig. 1B).

Material and methods

The main material reported herein was collected in September 2008 and 2009 by the senior author (I.G.) and is housed in the Paleontological Collection of the Piatra Neamț Natural Sciences Museum. Body size standard length (SL) is given in mm. The GPS coordinates of the outcrop are: 47° 32' 26.7" N, 25° 52' 46.1" E (WGS 84). The fossil specimens were studied using Zeiss, Jena, Olympus, and Leica stereomicroscopes. One of the specimens required removal of the matrix from a few vertebrae using a scalpel. For comparison we used extinct and extant specimens of gonostomatids. Extinct material: †*Scopeloides glarisianus* (Agassiz, 1844) MSNPN-PC Nos 113, 114, 201, 219, 267, 496–499, 612, 615 (A + B) Oligocene age, Bituminous Marls, Marginal Folds Nappe (Pietricica Mountain, Piatra Neamț, Romania); MMB Nos Ge 29524, Ge 23978/19/15, Ge 23978/19/9, Ge 23978/19/13, Ge 31594–31610, Ge 29543 from the Dynów Marlstone of the Menilitic Formation, Oligocene age (Litenčice, Moravia, Czech Republic); NMP Pc 10050a, b from the Dynów Marlstone of the Menilitic Formation, Oligocene age (Kelč, Moravia, Czech Republic); 11 unnumbered specimens (some of them with counterpart) from the Dynów Marlstone of the Menilitic Formation, Oligocene age (Litenčice, Moravia, Czech Republic); and Pc 02862, 02863 (part and counterpart), from the Dynów Marlstone of the Menilitic Formation, Oligocene age (Loučka u Valašského Meziříčí, Moravia, Czech Republic). Extant material: *Gonostoma elongatum* Günther, 1878, cleared and stained specimen GLI TP No. 92 [modification of Potthoff (1984) method]. Other comparative data regarding both fossil and extant

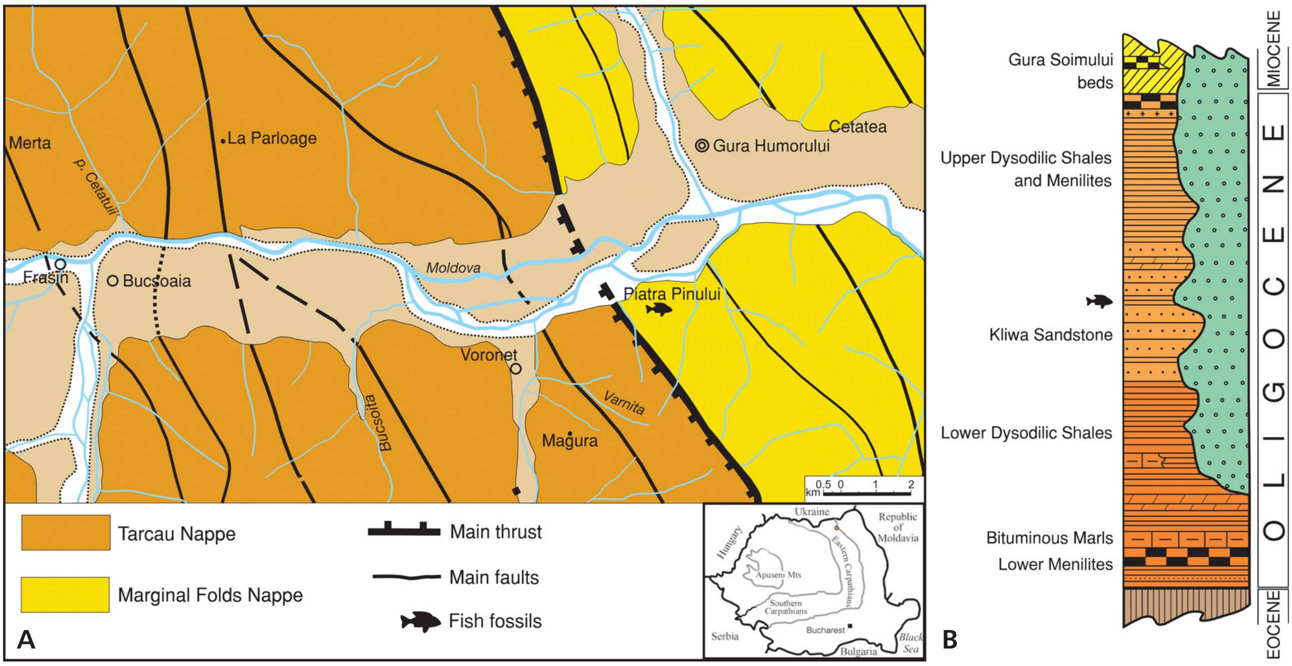

Figure 1. A – geological sketch map of the Gura Humorului region (based on Ionesi 1971). • B – lithostratigraphic column of the Marginal Folds Nappe from the central-northern part of the Eastern Carpathians (based on Grasu *et al.* 2007).

material are from the literature (Arambourg 1927, 1967; Daniltchenko 1960; Grey 1960; Jerzmańska 1968; Kusaka 1969, 1977; Weitzman 1974; Ahlstrom *et al.* 1984; Harold & Weitzman 1996; Harold 1998, 2002; Prokofiev & Bannikov 2002; Prokofiev 2005).We include the ural vertebra and urostyle in vertebral counts, counting the caudal complex as one vertebra. Descriptive terminology, including qualitative characters and standardized counts and measurements, are based on Grey (1960) and Harold (1998). Features and terminology of the photophores are based on Harold (2002). In the comments on phylogenetic relationships we follow the list of characters and nomenclature for the Gonostomatidae in Harold (1998).

Anatomical abbreviations. – AfR – anal fin ray; Cle – cleithrum; Cor – coracoid; Cv1 – first caudal vertebra; De – dentary; DfR – dorsal fin ray; Ect – ectopteygoid; Epn – epineural; Epp – epipleural; Fr – frontal; Hsp – haemal spine; Hym – hyomandibula; Iop – interopercle; Max – maxilla; Mes – mesopterygoid; Met – metapterygoid; Nsp – neural spine; Op – opercle; Pfr – pectoral fin ray; Pg – pterygiphores; Pmx – premaxilla; Pop – preopercle; Psp – parasphenoid; Pt – posttemporal; Q – quadrate; Pr – pleural rib; Scl – supracleithrum; Smax – supramaxilla; Sop – subopercle; Spn – supraneural; Sy – symplectic; T – teeth; Unsp – unfused neural spine; Vf – ventral fin.

Dagger symbol. – We use the dagger symbol (†) for the fossil representatives.

Institutional abbreviations. – MSNPN-PC – Paleontological Collection of the Natural Sciences Museum Piatra Neamţ; MMB – Moravian Museum Brno, Department of Geology and Paleontology; NMP – Paleontological collection of National Museum Prague; GLI TP – comparative collection of Tomáš Přikryl.

Systematic Palaeontology

Subdivision Teleostei Müller, 1845
sensu Patterson & Rosen (1977)
Order Stomiiformes Fink & Weitzman, 1982
Infraorder Gonostomata Weitzman, 1974
Family Gonostomatidae Gill, 1893 *sensu* Weitzman (1974)

Genus *Gonostoma* Rafinesque, 1810

†*Gonostoma dracula* sp. nov.

Figures 2, 3A, B, 5A, B, 6, 7

Holotype. – MSNPN-PC No. 820, about 60 mm SL, almost complete specimen (Fig. 2).

Paratype. – MSNPN-PC No. 889, about 65 mm SL, almost complete specimen, head slightly disarticulated (Fig. 7, 8A, B).

Type horizon and locality. – Dysodilic Shale intercalation from the Kliwa Sandstone Formation, Poiana-Făget-Isachia

Figure 2. †*Gonostoma dracula* sp. nov. from the Oligocene of Gura Humorului, Romania. Holotype MSNPN-PC No. 820, about 60 mm SL, anterior left. Scale bar 10 mm.

syncline, Humor demi-window (Marginal Folds Nappe, Eastern Carpathians), Piatra Pinului outcrop.

Material. – Except types, MSNPN-PC No. 821, incomplete specimen; No. 840A, B (part and counterpart), incomplete specimen; No. 841A, B (part and counterpart), incomplete specimen; No. 842, incomplete specimen; No. 890, 891 incomplete specimens.

Etymology. – The species was named after the Romanian famous fictional character from the Bram Stoker novel; the teeth of the new species resemble vampire fangs.

Diagnosis. – The head is longer than the depth of the body, head length about 4.6 in SL. Small orbit, about 2.4 in body depth. The maxilla bears eight conical teeth, with two different lengths: elongate, fang-like, with the interspaces occupied by small acicular teeth. The urohyal has an almost straight posterior margin. Vertebrae 40 (19 + 21). The left and right parts of the neural arches from the first 18 vertebrae are not fused in the midline. The epineurals from the first 21 vertebrae are attached to the base of the neural arches/spines. A single robust supraneural is present and inserted between the neural arches of the fourth and fifth vertebrae. Epipleurals are thin and inserted at the bases of the first three haemal spines. Dorsal fin rays 12 or 13. Anal fin with about 28 rays. Pectoral-fin rays very long (28% SL).

Description. – Elongated thin body; the maximum depth is in the head region. The head is relatively large, its length greater than its depth. The orbit is small and it is positioned well anterior to the quadrate joint with the mandible. The caudal peduncle is very narrow (18.7 in SL).

Neurocranium: The supraoccipital is comparatively small relative to the frontal. The state of preservation of the parietal does not allow us to observe its general shape. The frontals have an almost triangular shape; they are relatively short and present few radial ridges posterodorsally. The parasphenoid is straight and slender and passes through the median portion of the orbit. The nasal bone is relatively robust.

Oral jaws and dentition: The premaxilla is short, its length is about $^1/_4$ that of the maxilla (Fig. 3A, B); the ascending process of the premaxilla is very small, acute, triangular shaped and much shorter than the descending process. The ventral portion of the premaxilla is straight and possesses two conical fang-like teeth, with small acicular teeth in the interspace. The maxilla is elongate and widened posteriorly; eight conical teeth, with two different lengths, fang-like, with the interspaces occupied by small acicular teeth. The supramaxilla is small, shaft-like, and located posterodorsally to the maxilla. The lower jaw is robust; the alveolar portion bearing about five conical teeth, with a similar arrangement to those of the maxilla; the interspace teeth are comparable with those of the maxilla.

Suspensorium: The quadrate is elongated and triangular; the joint with the mandible is positioned well posterior to the orbit. The symplectic is short and thin by comparison to the quadrate. The hyomandibula is elongate, flexed anterodorsally and almost oblique, and with a slightly flared

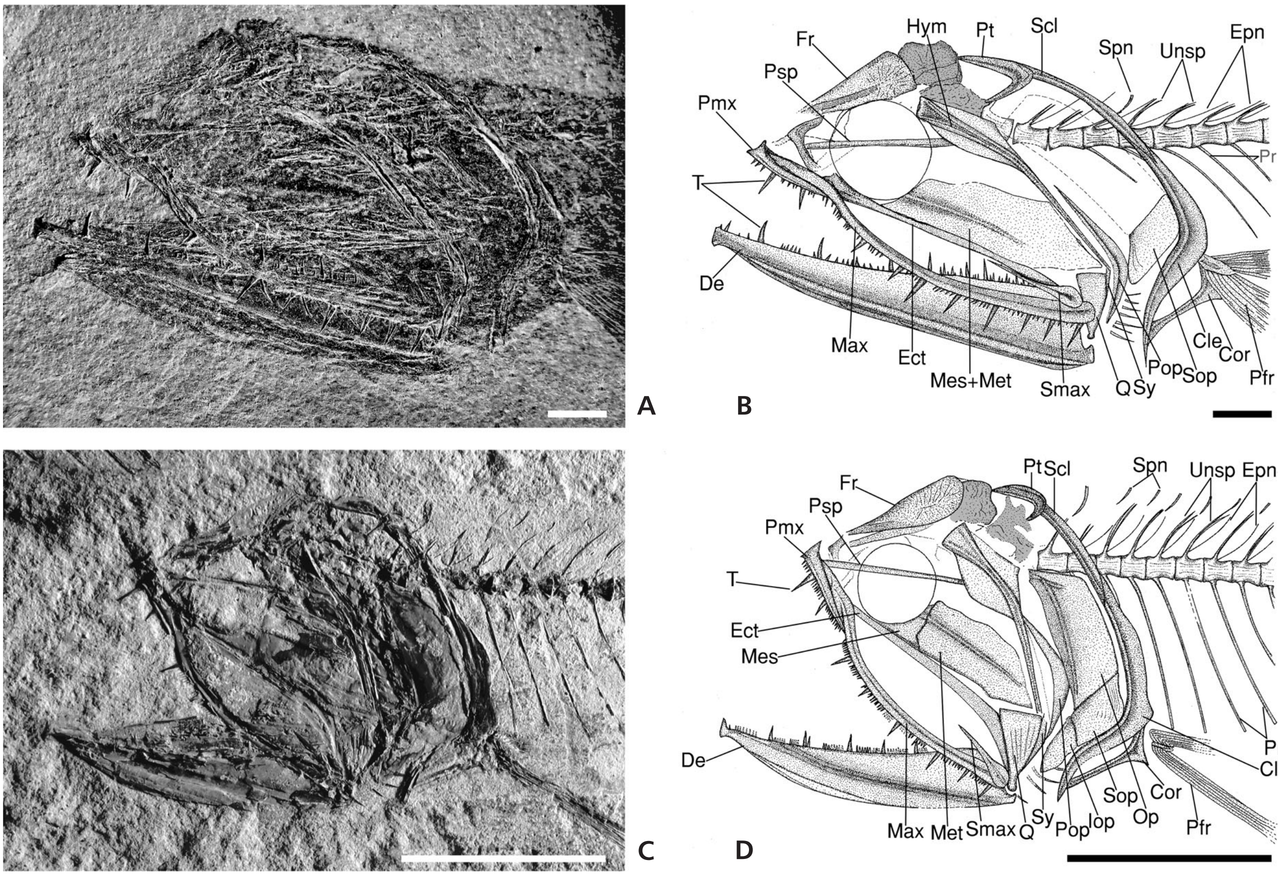

Figure 3. A, B – †*Gonostoma dracula* sp. nov. from the Oligocene of Gura Humorului, Romania, MSNPN-PC No. 890, anterior left; A – specimen photograph; B – reconstruction of the head skeleton, pectoral fin girdle, anterior vertebral centra and associated structures. Scale bar 2 mm. • C, D – †*Scopeloides glarisianus* from the Oligocene of Piatra Neamţ, Romania, MSNPN-PC No. 113, anterior left; C – specimen photograph; D – reconstruction of the head skeleton, pectoral fin girdle, anterior vertebral centra and associated structures. Scale bar 10 mm. Translucent grey colour in B, D indicates the areas that could not be interpreted.

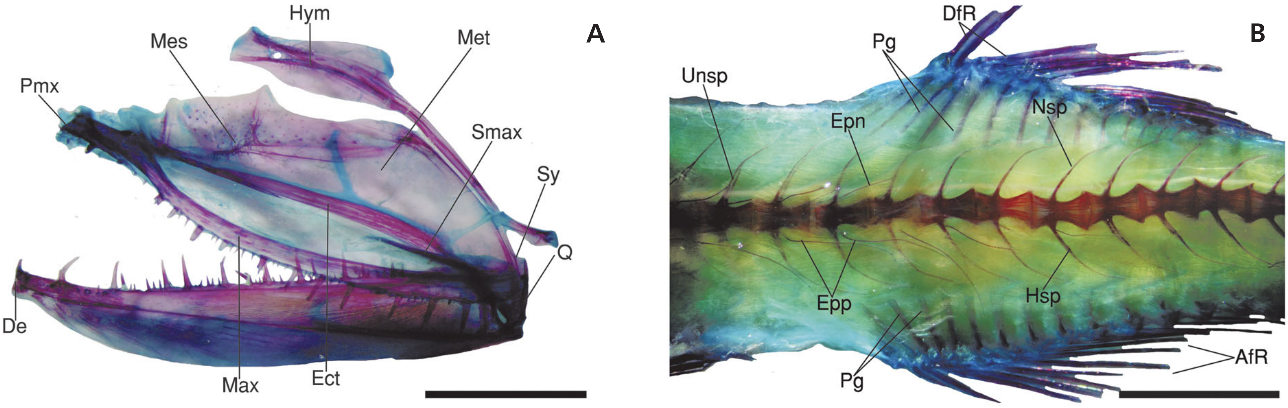

Figure 4. *Gonostoma elongatum*, extant fauna (cleared and stained specimen), GLI TP No. 92, anterior left. • A – jaws and suspensorium, right side, lateral view. • B – vertebral column, dorsal fin, anal fin and associated structures, left side, lateral view. Scale bar 5 mm.

termination at the capsular joint; the articulation with the neurocranium is located posterodorsally of the orbit; the ventral portion is slightly tapered ventrally and overall much narrower than the dorsal portion (Fig. 3A, B). The ectopterygoid is long, thin and almost straight; its posterior portion is in contact with the anterior part of the quadrate and partly covered by the supramaxilla. The mesopterygoid and metapterygoid are partially visible but their general shape cannot be established due the state of preservation.

Opercular region: The opercle is narrow, vertically elongate and slightly inclined at about a 45 degree angle; it bears a small oblique ridge originating in the hyomandibular-opercular joint region. The preopercle is small and broadly curved. The subopercle is approximately parallelogram-shaped with rounded corners and exhibits very thin growth lines anteriorly.

Hyoid and branchial arches: The gill arches are poorly preserved. The branchiostegal rays are visible in one specimen, MSNPN-PC No. 889 (Fig. 7); however, it is not possible to count the precise number of rays. The urohyal (Figs 7; 8A, B) is clearly visible on the paratype; it is triangular in shape, with the lateral edges thickened, with an almost straight posterior margin and very thin growth lines on the lateral surface.

Vertebral column: There are 19 abdominal and 21 caudal vertebrae. The first vertebra is visible in the holotype. The vertebral centra are highly elongate, as is characteristic of *Gonostoma* and *Cyclothone* species (see Harold 1998); the length of the third caudal vertebrae is about 1.3 mm. The neural spines of the abdominal vertebrae are short, thin, slightly curved posteriorly and extended dorsally to the profile of the body; the first 18 abdominal vertebrae have unfused left and right side of the neural arches in the midline. The most anterior fused neural arch (forming a neural spine) is on the 19th vertebra. Epineurals are associated with the bases of the neural arches/neural spines and are present in a continuous series from the second abdominal vertebra posteriorly through the second caudal vertebra (Figs 3A, B; 5A, B). The neural spines of the caudal vertebrae are robust and become shorter towards the caudal fin. The first haemal spine is slightly curved and contacts the dorsal tip of the first pterygiophore of the anal fin. The haemal spines of the 17th and 18th vertebrae are longer. Epipleurals are attached at the base of the haemal spines for the first three caudal vertebrae (Fig. 5A, B). All the neural and haemal spines are posteriorly inclined. The 4th through 19th vertebrae bear small, thin, pleural ribs that do not contact the ventral profile of the body. The ribs become shorter towards the last abdominal vertebra. Small parapophyses are present on the last three abdominal vertebrae.

Pectoral fin and girdle: The general shape of the pectoral girdle is crescent like (Fig. 3A, B). The posttemporal is a well-preserved bone with two anterior processes articulated with the neurocranium; posteroventrally it is articulated with the supracleithrum. The supracleithrum is an elongated, almost obliquely oriented bone that overlaps the dorsal part of the cleithrum. The cleithrum is a robust, sigmoid bone, slightly expanded in the mid-ventral region; the distal tip of the ventral limb of the cleithrum is pointed. The coracoid projects anteroventrally as a slightly thin process which ends at the ventral termination of the cleithrum; its dorsal portion is short, slightly widened and projects anterodorsally, reaching the cleithrum close to the pectoral fin insertion. The pectoral fin is very long and narrow, extending posteriorly to near the pelvic fin insertion. There are about 10–11 pectoral-fin rays. The insertion of the pectoral fin is close to the ventral body profile, near a vertical through the sixth vertebra.

Pelvic girdle: The pelvic girdle is approximately wedge-shaped; it is relatively short and anterodorsally oriented; the pelvic fin insertion is on the ventral profile of the body, ventral to the 16th abdominal vertebra. The pelvic-fin rays are long, extending close to the anal fin origin. It is not possible to count the exact number of rays.

Supraneural bones and dorsal fin: One robust, rather anteriorly curved, supraneural is inserted between the fourth and fifth abdominal vertebrae (Fig. 3A, B). On the subsequent neural arches some extremely thin supraneurals are visible but their precise number is difficult to establish; at least six supraneurals are visible starting with the fifth vertebra. The dorsal fin insertion is above the second caudal vertebra. There are 12 or 13 soft rays. The first two rays are shorter, possibly unsegmented, and pointed (*i.e.* rudimentary soft rays); the third ray is segmented and much longer. The first three branched rays are longest and form relatively elongate anterior fin lobe. The next rays are branched and decrease in length posteriorly, with the last one being the shortest. The proximal pterygiophores are slightly expanded ventrally and anteroventrally-posterodorsally inclined. The first two rays are supported by a process formed by three or four fused slender proximal pterygiophores. The anteriormost of these pterygiophores is longest and seems to be almost aligned with the dorsal body profile; posteriorly, the pterygiophores are decreasing in length and inclination.

Anal fin: There are at least 28 soft rays. The first two rays are much shorter, possibly unsegmented and pointed. The third ray is much longer and segmented; the next rays are branched and decrease in length posteriorly through caudal fin. The anal fin has an overall shape that is similar to that described for the dorsal fin, and is situated directly below it. The first two pterygiophores are anteriorly inclined and each supports a fin ray; in the interval between the fourth and tenth pterygiophores the inclination shifts from anteriorly to posteriorly. The first pterygiophore is aligned with the ventral body profile; the second one is in contact with the haemal spine from the first caudal vertebrae. The dorsal (proximal) part of the first 12 or 13 proximal pterygiophores is slightly widened while the others appear to be slender and decrease in length toward the caudal fin.

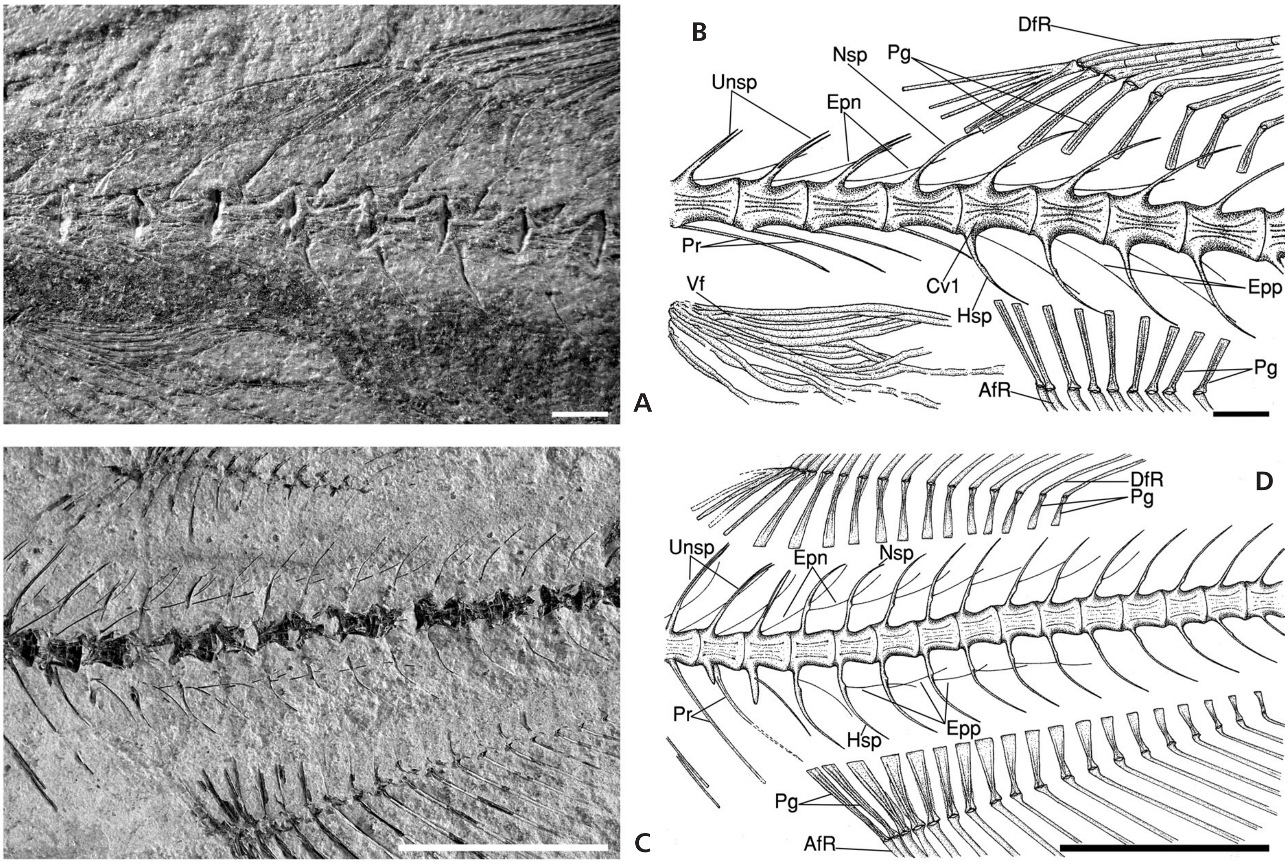

Figure 5. A, B – †*Gonostoma dracula* sp. nov. from the Oligocene of Gura Humorului, Romania, MSNPN-PC No. 890, left side, lateral view, anterior left; A – specimen photograph; B – reconstruction of the vertebral column, dorsal fin, anal fin and associated structures. Scale bar 1 mm. • C, D – †*Scopeloides glarisianus* from the Oligocene of Piatra Neamţ, Romania, MSNPN-PC No. 113, left side, lateral view; C – specimen photograph; D – reconstruction of the vertebral column, dorsal fin, anal fin and associated structures. Scale bar 10 mm.

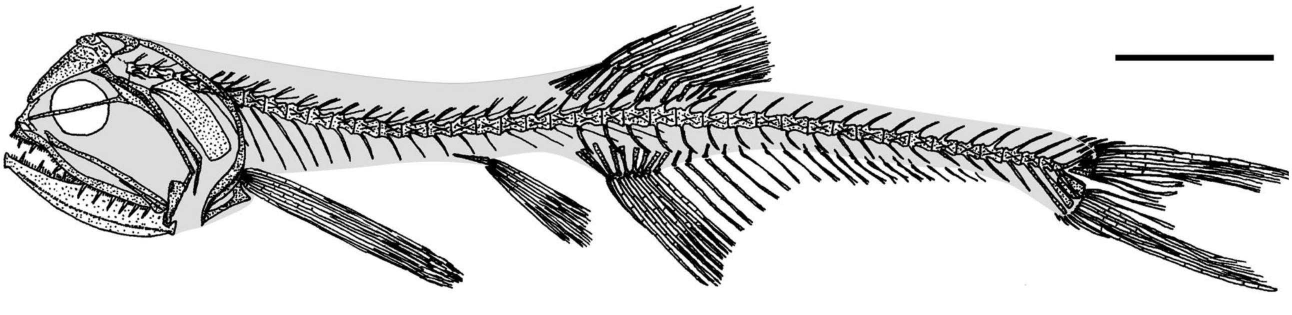

Figure 6. †*Gonostoma dracula* sp. nov. from the Oligocene of Gura Humorului, Romania. Holotype, anterior left. Composite reconstruction of the skeleton. Scale bar 10 mm.

Caudal fin and skeleton: The haemal spines from PU_3 and PU_2 are longer than those immediately anterior; the haemal spine from PU_2 is slightly expanded and robust. The parhypural is expanded and wedge-like. There are six hypurals and they appear to be autogenous. Two epurals are clearly visible. The caudal fin is forked; there are 19 principal rays and 12 procurrent rays (7, i, 9 + 8, i, 5).

Squamation: There are no scales visible.

Photophores: The photophores are poorly preserved and difficult to observe. However, we distinguish 10–11 photophores of the AC series on the left side of the holotype and 13 photophores of the same series on the right side of MSNPN-PC No. 841B specimen.

Measurements: Morphometric characters were taken from two specimens (MSNPN-PC No. 820, holotype, and MSNPN-PC No. 889, paratype) and presented as percent SL in Table 1.

Figure 7. †*Gonostoma dracula* sp. nov. from the Oligocene of Gura Humorului, Romania. Paratype MSNPN-PC No. 889, about 65 mm SL, anterior right. Scale bar 10 mm.

Table 1. Proportional measurements (% SL) of †*Gonostoma dracula* sp. nov.

†*G. dracula* sp. nov.	No. 820	No. 889
Standard length (mm)	60	65
Maximum body depth	11.6	15.3
Caudal peduncle depth	4.6	5.3
Length of the head	21.6	23.0
Predorsal length	57.3	58.4
Preanal length	56.6	61.5
Preventral length	45.0	49.2
Pelvic to anal fin	11.1	12.7
Pectoral to pelvic fin origin	20.0	21.0
Dorsal fin base	9.6	11.6

Discussion and Comparisons

The composition of the family Gonostomatidae is a persisting question and cannot be adequately addressed here. According to Harold (1998), there are seven extant species in the genus *Gonostoma*, although some of these have been placed relatively recently in another genus: *G. denudatum* Rafinesque, 1810; *G. elongatum* Günther, 1878; *G. gracile* Günther, 1878; *G. bathyphillum* (Vaillant, 1884) *in* Filhol (1884), *G. atlanticum* Norman, 1930; *G. ebelingi* Grey, 1960; *G. longipinnis* Mukhacheva, 1972. Miya & Nishida (2000) recognized two monophyletic groups in their revised classification of *Gonostoma*, retaining *G. denudatum* and *G. atlanticum* in that genus and placing *G. ebelingi*, *G. elongatum*, *G. longipinnis*, *G. gracile*, *and G. bathyphillum* in the ressurected genus *Sigmops* Gill, 1883. Until a more robust phylogeny for *Gonostoma* and the Gonostomatidae is available, we prefer to continue recognizing all seven species in *Gonostoma*.

Although gonostomatid fossils are relatively well known, especially from the Early Oligocene of the Paratethys and Miocene of the Mediterranean Basin, some of them are poorly preserved, and for this reason not all critical character states are observable. The most abundant fossil species of gonostomatid is †*Scopeloides glarisianus*; it was initially described by Agassiz (1844) as †*Osmerus glarisianus* from the Oligocene of Glarus (Switzerland), and was revisited by Wettstein (1886) who considered that this species belongs to the genus †*Scopeloides*. Further, Paucă (1934), Daniltchenko (1946), Arambourg (1967), Jerzmańska (1968), Gregorová (1997), Baciu (2001) and Prokofiev (2005) re-described and compared †*Scopeloides glarisianus* with the extant species of *Gonostoma*. †*Scopeloides* is unanimously considered a separate genus of the Gonostomatidae but with many similarities with *Gonostoma*. Those results were based mainly on meristic and morphometric characters, and without phylogenetic considerations, and are provided herein (Tab. 2).

The first fossil records of the genus *Gonostoma* are known only from the Miocene of the Mediterranean Basin. Sauvage (1873) described †*Pseudoeleginus albyi* on the basis of poorly preserved material from the Late Miocene formation of Licata (Italy); Arambourg (1925) considered that the specimens belonged to *Gonostoma* and later described in 1927 the same species from Oran (Raz-el-Aïn, Algeria); further, Gaudant (2002, 2008) reported †*Gonostoma albyi* (Sauvage, 1873) also from the Messinian of the Mediterranean Basin. The meristic char-

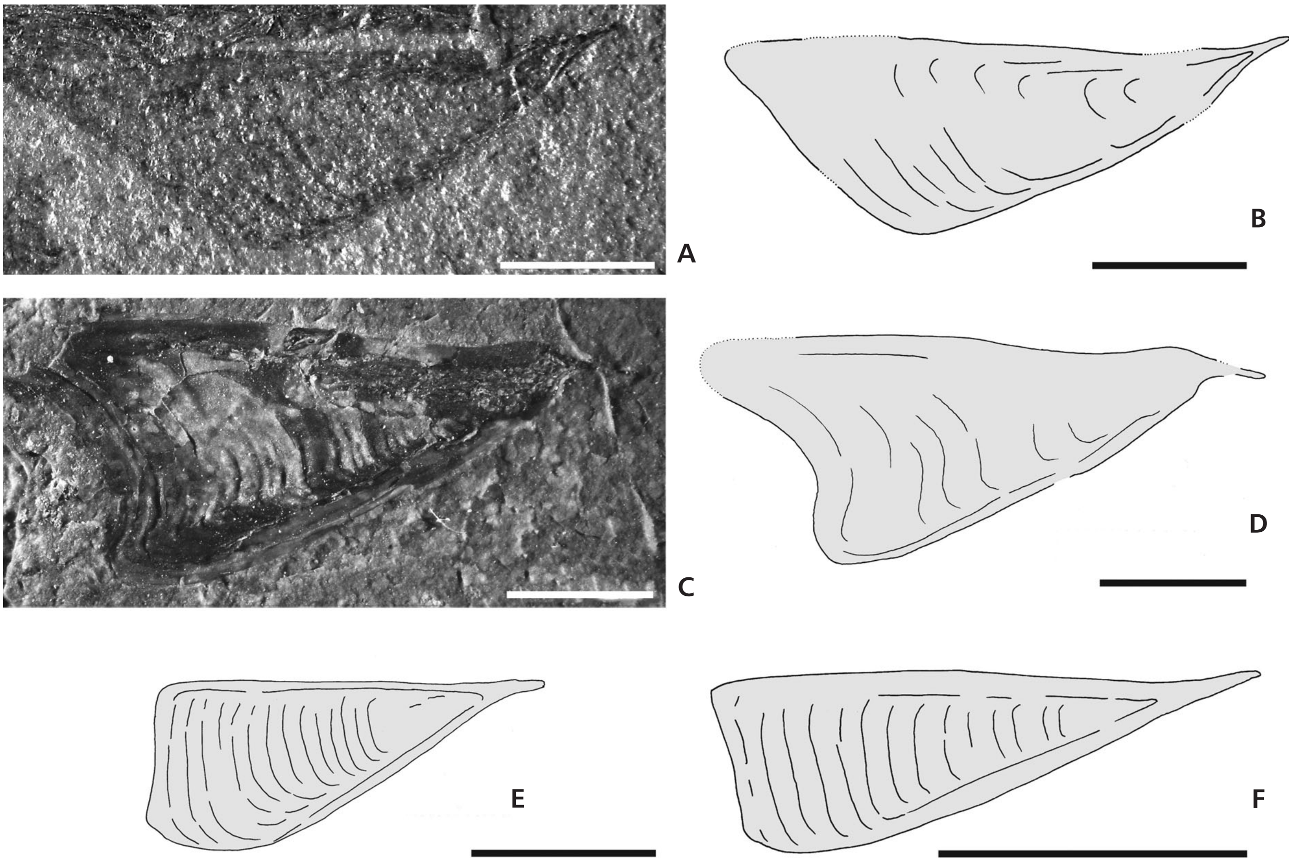

Figure 8. A, B – †*Gonostoma dracula* sp. nov. from the Oligocene of Gura Humorului, Romania, Paratype MSNPN-PC No. 889, anterior right; A – urohyal photography; B – interpretative drawing. Scale bar 2 mm. • C, D – †*Scopeloides glarisianus* from the Oligocene of Kelč, Czech Republic, NMP Pc 10050a, anterior right; C – urohyal photography; D – interpretative drawing. Scale bar 2 mm. • E – *Gonostoma elongatum*, urohyal sketch after Kusaka (1977). Scale bar 5mm. • F – *Gonostoma gracile*, urohyal sketch after Kusaka (1969). Scale bar 10 mm.

acters (vertebrae: 16 + 30; dorsal fin: 10 rays; anal fin: 32 rays; pectoral fin: 12 rays; pelvic fin: 7 rays; caudal fin: 7, i, 9 + 9, i, 4 rays), together with no observations of the photophores or other diagnostic characters, lead us to believe that this species needs taxonomic revision and a complete re-description. Unfortunately, neither of these specimens was available for study during the current research and preparation of the manuscript.

Morphological comparisons among extinct and extant members of the Gonostomatidae allow us to identify a variety of characters that definitely support the validity of the new species, †*G. dracula* sp. nov. Harold (1998) proposed that the monophyly of the Gonostomatidae is supported by ten synapomorphies, of which in †*G. dracula* sp. nov. are clearly visible only three, including the loss of IP photophores (character [10] from Harold, 1998), pattern of maxillary dentition [12], and short premaxilla [13]. One additional feature which should be considered is the elongate parapophysis of the first vertebral centrum [19]. However, because of the preservational state this character is partly visible only in one of our specimens (MSNPN-PC No. 842).

From the list of the characters used by Harold (1998) that relate to *Gonostoma sensu lato* and *Cyclothone* (clades F, G, H, J), the following are observed in our specimens: the vertebral centra are highly elongate [31], the opercular condyle of the hyomandibula is reduced, not extending posteriorly beyond the posterior margin of the hyomandibula [34], the hyomandibula is flexed anterodorsally, producing a long oblique limb leading to the articulation with the pterotic [36], epineural and epipleural bones associated with the caudal vertebrae are attached to the bases of, respectively, the neural or haemal spine or to the centra [50], the neural spines are reduced, represented by the unfused, open arches only throughout the postcranial skeleton [40c], the dorsal and anal fin origins are in or close to a vertical passing through first caudal vertebrae [49], the third and fourth hypurals are fused into a single plate-like element [44c], and there are only three sets of epipleurals [48(1)].

As documented above, †*Gonostoma dracula* sp. nov., is characterized by a peculiar combination of features which are present in all the extant species of *Gonostoma* and *Cyclothone*: [31], [34], [36] plus characters from

Table 2. Comparison of selected meristics of *Gonostoma* species group and †*Scopeloides glarisianus.* Extant species data are from Grey (1960) and Mukhacheva (1972).

		Fin rays			
Species	Vertebrae	Dorsal	Anal	Pectoral	Pelvic
†*S. glarisianus*	39–41 (18–19 + 21–22)	14–15	28–29	11–12	8–9
†*G. dracula* sp. nov.	40 (19 + 21)	12–13	28	11–12	7–8
G. elongatum	39–41	12–15	28–32	10–13	7–8
G. ebelingi	43–46	12–13	28	9	8
G. gracile	40–42	10–14	26–29	9–10	7–8
G. bathyphillum	37–40	11–15	22–26	10–14	7–9
G. atlanticum	38–39	16–18	27–31	9–11	6–8
G. denudatum	39	14–15	28–31	11–12	8
G. longipinnis	40	13–14	26–29	11–13	7–8

clades G, H, J (for details see Harold 1998); the new species shares character [50] with *Gonostoma elongatum* (see Fig. 4B), *G. ebelingi*, *G. longipinnis*, *G. gracile*, *G. bathyphilum* and characters [40c], [49] with *G. ebelingi*, *G. longipinnis*, *G. gracile*, *G. bathyphilum*. Moreover, †*G. dracula* sp. nov., does not share character [44c] with *G. bathyphilum* but shares character [48(1)], reduction of the epipleural series to just three sets, only with that species.

Comparatively, in †*S. glarisianus* the vertebrae are shorter and slightly deepened; there are 7 or 8 epineurals and 6 or 7 epipleurals associated with the caudal vertebrae and which are attached at $^{1}/_{3}$ length from the base of the neural/haemal spine (Fig. 5C, D); the neural arches are almost twice long (Fig. 3C, D) and the first fused neural spine is on the last abdominal or first caudal vertebra (Fig. 5C, D); the anal fin insertion is slightly posterior to the vertical through the dorsal-fin origin.

Apart from these characters, we identified one additional osteological feature that supports our conclusions as to the affinities of the new taxon: the morphology of the urohyal. The urohyal is an unpaired ossification of the sternohyoideus muscle in teleosts (Arratia & Schultze 1990). Kusaka (1969, 1977) reviewed urohyals of selected teleost genera and families, including several representatives of the genus *Gonostoma*. In the †*G. dracula* sp. nov. paratype specimen MSNPN-PC No. 889, the urohyal is visible (Figs 7, 8A, B) and shows a typical almost straight posterior margin (see description), similarly as in *G. elongatum* and *G. gracile* (Kusaka 1969, 1977; Fig. 8E, F). In †*Scopeloides glarisianus* (MMB No. Ge 29543 and NMP Pv 10050a/b), the urohyal, which was originally interpreted as a postcleithrum by one of us (Gregorová 1997; tab. 2, fig. 4), is completely different, with concave posterior margin (Fig. 8C, D) and thus can be used as one of features for separation of these two Oligocene gonostomatid taxa. The features presented herein confirm that †*Gonostoma dracula* sp. nov. is a new species of gonostomatid which is phylogenetically close to *G. bathyphillum.* It is the first record of a species of *Gonostoma* from the Parathethys area. †*Gonostoma dracula* sp. nov. seems to exhibit a sequence of characters which indicate either a close relationship with the *G. bathyphillum* plus *Cyclothone* clade [based on the phylogeny of Harold (1998)] or among the five species recognized as *Sigmops* by Miya & Nishida (2000) thought to be the sister group of a clade containing *G. denudatum*, *G. atlanticum* and *Cyclothone* spp. However, for the moment we are not in a position to provide a more detailed, parsimony-based analysis of its precise phylogenetic position; such a work requires further study of extant species and better preserved fossil specimens.

Palaeogeography and palaeoecology of the Gonostomatidae from the Oligocene of the Carpathian Basin

Hypoxic to anoxic conditions which dominated throughout the Oligocene and part of the Early Miocene in the Paratethys Sea influenced sedimentation within the basins and resulted in the formation of bituminous rocks (for details see, *e.g.* Baldi 1980; Rögl & Steininger 1983; Nagymarosy 1990; Popov *et al.* 2002, 2004). Almost unanimously, the beginning of the Oligocene age is correlated with sea level drop (Haq *et al.* 1988) and a cooling climate (Zachos *et al.* 2001 *in* Melinte-Dobrinescu & Brustur 2008). During a strong global eustatic regression, the first isolation of the Paratethys emerges in the Early Oligocene, through the end of the NP 22 nannoplankton zone (Nagymarosy 1990). In the Eastern Carpathians (Romania, Piatra Neamţ area) †*Scopeloides glarisianus* is exclusively found in the Bituminous Marls Formation which corresponds to the nannoplankton zone NP 22 (Melinte-Dobrinescu & Brustur 2008).

In the northern part of the Eastern Carpathians (Gura Humorului area), specimens of †*Scopeloides* are unknown; this could be a taphonomical phenomenon rather than to a peculiar palaeodistribution within the Carpathian Basin. In Poland and Czech Republic, †*S. glarisianus* is found in the Dynów Marls and Chert Beds, which are within the nannoplankton NP 22 zone (Kotlarczyk *et al.* 2006). Above these layers no †*S. glarisianus* specimens are reported. The presence of †*S. glarisianus* in the Bituminous Marls Formation (Piatra Neamţ area) together with *Vinciguerria* Jordan & Evermann, 1896 and †*Oligophus* Gregorová, 2004 species could suggest a considerable water depth for this part of the basin, as Kotlarczyk *et al.* (2006) also proposed for similar observations in Poland. Evidence of †*S. glarisianus* in the Early Oligocene coeval deposits of Russia, Switzerland and Iran lead us to hypothesize the presence of connections within the basin. On the other hand, the age of the Iran deposits is problematic; based on fish taxa, Arambourg (1967) proposed for the aforementioned deposits the Rupelian age which seems to be invalidated by further microfaunal analyses that indicate Middle to Late Eocene age (Afsari *et al.* 2014). †*Kotlarczykia bathybia* Jerzmańska, 1974 was described from the 'upper bathypelagic horizon' of the Oligocene Menilitic Beds from the Polish Carpathians (Jerzmańska 1974) which correspond to the nannoplankton NP 23 zone (Kotlarczyk *et al.* 2006); later †*Kotlarczykia* sp. was described from the Moravian part of the Carpathians (Gregorová 1989, 1997) from the Šitbořice Member in the Cieszyn Silesia region. In other areas of the Paratethys no specimens of †*Kotlarczykia* have been reported.

During the Late Oligocene, connection of the Paratethys with the world ocean was established again; the Central Paratethys was connected with Mediterranean through the Slovenian corridor (Popov *et al.* 2004). Furthermore, this is also confirmed by the presence of coccolithic limestone (Jaslo Limestone) throughout the Carpathian Basin area, including the Romanian territory, in the NP 24 Calcareous Nannoplankton zone (Melinte-Dobrinescu & Brustur 2008). The explosive diversification of sphenoliths and discoasters are indicative of an open marine situation and higher inferred water temperature (Aubry 1992, Fornaciari & Rio 1996) and could regionally express the global Late Oligocene Warming event (Zachos *et al.* 2001 *in* Melinte-Dobrinescu & Brustur 2008) simultaneous with a sea-level rise. Olaru (1989) consider, based on a nannofloral fluctuation pattern, that the Late Oligocene was marked by an increase in sea temperature.

†*Gonostoma dracula* sp. nov. is found in the lower part of the Late Oligocene deposits from Eastern Carpathians, Romania (Fig. 1B); in the Piatra Pinului outcrop, where this species was discovered, the massive Kliwa Sandstone deposits are interlayered with thin Dysodilic Shale intercalations and correspond to the Nannoplankton Zone NP 24–NP 25 (Melinte-Dobrinescu & Brustur 2008). At the same level, several specimens of a species of *Polyipnus* Günther, 1887 were identified together with †*Anenchelum* de Blainville, 1818 and †*Palaeorhynchus* de Blainville, 1818. The presence of these species could indicate a warm environment and a considerable depth for this area, probably more than 200 m. The appearance of *Gonostoma* species in this part of the Carpathian Basin may be related to the beginning of climate warming and the restoration of connections with the Mediterranean.

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