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Deep-water chondrichthyans from the Early Miocene of the Vienna Basin (Central Paratethys, Slovakia)

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Sampling of latest Burdigalian (Miocene) silty clays from the Malé Karpaty Mountains in the Slovakia revealed a deep-water, low diversity shark fauna. The fauna is dominated by teeth of very small squaliform sharks, including two new species, *Eosqualiolus skrovinai* sp. nov. and *Paraetmopterus horvathi* sp. nov. The generic composition of the squaliform fauna is more similar to that known from the Eocene than that of today, suggesting a post–early Miocene faunal turnover within this clade, at least locally. Nectobenthic, non squaliform sharks are rare, but include the new sawshark species *Pristiophorus striatus* sp. nov., while minute teeth of an enigmatic taxon described here as *Nanocetorhinus tuberculatus* gen. et sp. nov. probably indicate the presence of a previously unrecorded planktivore. The unusual composition of the fauna, with the complete absence of taxa known to be of medium to large size, suggests an unusual, and probably very stressed, palaeoenvironment.

Key words: Squaliformes, Dalatidae, Etmopteridae, *Pristiophorus*, sharks, Miocene, Slovakia, Paratethys.

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Introduction

The fossil record of deep-water sharks is generally poor, and much of it comes from a very small number of sites. As a result, little is known about the evolution of deep marine shark clades and the development of deep-water ecosystems through time. The most diverse clade of sharks in modern deep marine environments is the Squaliformes. These are known to have been diverse since the Late Cretaceous (e.g., Adnet et al. 2008; Siverson 1993), with many species being small to very small and possessing highly specialized dentitions. While the known fossil record of squaliforms comprises a large number of genera (e.g., Adnet and Cappetta 2001; Kriwet and Klug 2009; Straube et al. 2010), many of these are known from a very limited number of records, so that radiations and turnovers within the clade are very poorly known (e.g., Straube et al. 2010). Deep-water members of other shark clades are, if anything, even less well known. Here we present a new fauna of deep-water squaliforms and associated taxa, which adds significantly to our knowledge of the development of deep-water ecosystems.

Institutional abbreviations.—SNM Z, Slovak National Museum in Bratislava.

Geological setting

The shark fauna were collected at the Cerová-Lieskové locality in the Slovak Republic. The outcrop is situated on the western slope of the Malé Karpaty Mountains, which form the eastern margin of the central Vienna Basin (Fig. 1A). During the Miocene, this basin formed part of the Central Paratethys Sea, which has long been known to yield the remains of deep-water sharks (e.g., Pfeil 1983). Upper Burdigalian ("Karpatian") sediments, assigned to the Lakšárska Nová Ves Formation (Špička and Zapletalová 1964), are well exposed in a former claypit (Fig. 1B), represented by massive, locally laminated calcareous clay and clayey silt with thin tempestites (up to 10 mm thick) and several thin sandstone layers in the uppermost part of the section (Fig. 1C). The total thickness of the section exposed amounts to more than 15 m, but the lower 5 m are currently covered by scree. Macrofossil assemblages comprise vertebrates (teleosts, chondrichthyans) and a wide spectrum of invertebrates (bivalves, gastropods, cephalopods, scaphopods, decapods, isopods, regular and irregular echinoids, ophiuroids, siliceous sponges, and rare corals). Microfossil suites include both benthic and planktonic foraminifera, radiolarians, sponge spicules, ostracods, crinoid ossicles, fish otoliths and, in places, extremely abundant Bacillariophyta.

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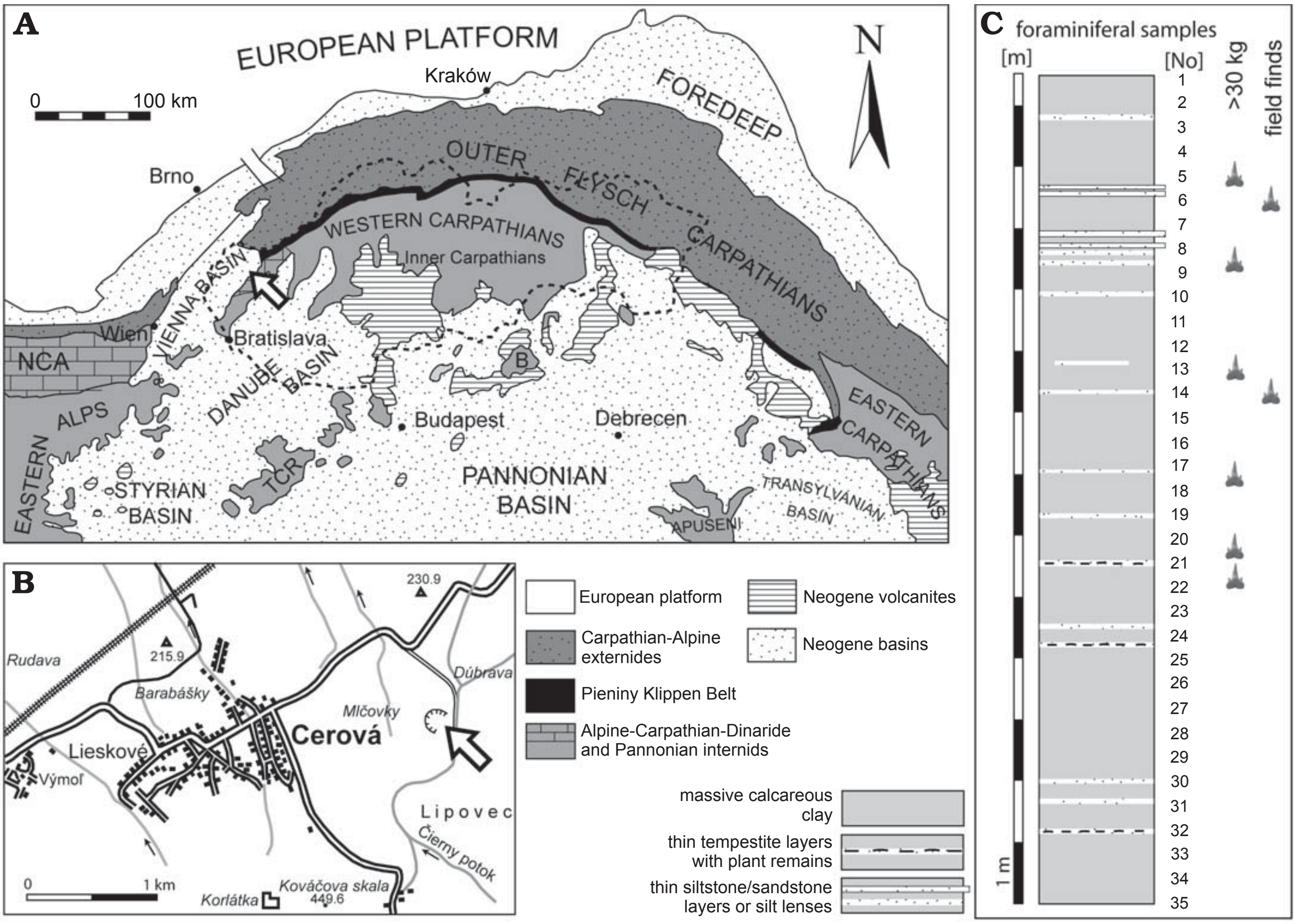

Fig. 1. **A**, **B**. Geographic position of the Cerová section at the eastern border of the Vienna Basin. Abbreviations: B, Bükk; NCA, Northern Calcareous Alps; TCR, Transdanubian Central Range. **C**. Lithology of the section; numbers indicate the position of the foraminiferal samples as mentioned in the text.

Dating of these deposits relies on the co-occurrence of the foraminifera *Uvigerina graciliformis* Papp and Turnovsky, 1953 and *Globigerinoides bisphericus* Todd in Todd et al., 1954 and the absence of the genus *Praeorbulina* Olsson, 1964. The first appearance datum (FAD) of *Uvigerina graciliformis* marks the base of the Karpatian stage (Cicha and Rögl 2003), while that of *G. bisphericus* is within Zone M4b of Berggren et al. (1995), correlating with the upper Karpatian. The appearance of *Praeorbulina* marks the start of the middle Miocene; there is no evidence for a significant range of ages present in the pit. The regional Paratethyan Karpatian stage has consistently been considered to be the time-equivalent of the latest Burdigalian (Rögl et al. 2003; Piller et al. 2007).

Material and methods

During the initial sampling for foraminifera and fish otoliths, several horizons containing abundant shark teeth were observed (Figs. 1C, 2). Some 30–70 kg were taken per sample, except for sample 2, which is represented by 5 kg. Each sample was wetted in a solution of hydrogen peroxide, washed through 0.2 mm, 0.5 mm, and 1 mm meshes and dried. This process was repeated several times. Finally the residue was wetted in a solution of sodium pyrophosphate and cleaned by ultrasound. This method completely removed sediment, and each sample was reduced to 0.15–0.2% of its original weight. Shark teeth were recovered at a rate higher than two specimens per kg of sediment.

The teeth show no signs of abrasion, and the only wear observed is consistent with in-life damage. There is, however, a considerable amount of damage caused by hyphate microborings, typically limited to the root and internal dentine of the teeth but rarely penetrating the enameloid (Fig. 3). In many cases the borings are concentrated in the root of the teeth, and they may be so intense that the root is wholly or partially destroyed. Where the boring is less intense, it can be seen to comprise several distinct morphologies. The most common microborings are the rather irregular tubular borings *Mycelites ossifragus* Roux, 1887. While the overall morphology of these networks is not easy to recognize (Underwood and Mitchell 2004), in some specimens it is possible to see irregular bifurcation and mutual avoidance of the borings (Fig. 3B). Less

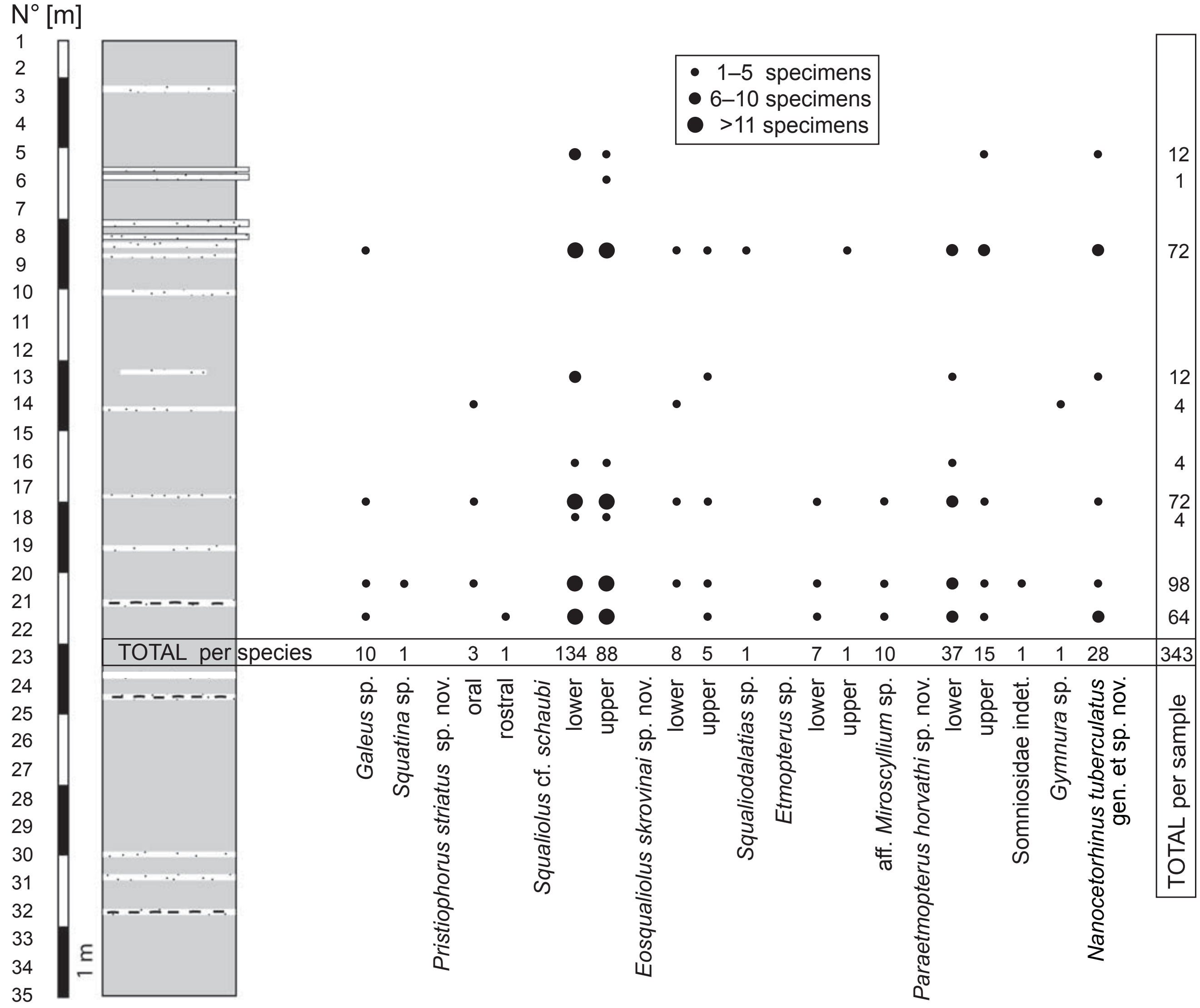

Fig. 2. Distributions of chondrichthyan teeth within the sampled section.

common are the radial and regularly bifurcating microborings of *Abeliella riccioides* Mägdefrau, 1937 (Underwood et al. 1999). Networks of *A. riccioides* may have different boring diameters from each other, but the boring size within a particular network remains constant (Fig. 3A$_1$). A single specimen of a boring comprising multiple branches originating from poorly defined nodes along its length (Fig. 3A$_2$) was also recognized. This does not appear to conform to any named ichnotaxon.

The tooth terminology largely follows Cappetta (1987); generic terms have been used where possible to avoid implication of homology.

Systematic palaeontology

Cohort Euselachii Hay, 1902

Subcohort Neoselachii Compagno, 1977

Order Carcharhiniformes Compagno, 1977

Family Scyliorhinidae Gill, 1862

Genus *Galeus* Rafinesque, 1810

Type species: *Galeus melastomus* Rafinesque, 1810; Recent, Sicily, Italy.

Galeus sp.

Fig. 4A–F.

Material.—Ten incomplete teeth including SNM Z 27432 to SNM Z 27437.

Description.—All teeth of this species are very small, being below 0.7 mm in width or height and represent four low-crowned lateral teeth and one high-crowned anterior tooth. The lateral teeth are either a similar height to width, or slightly wider than high, while the anterior tooth is higher than wide. The teeth are highly cuspate, with between 5 and 10 cusps. The degree of symmetry of the lateral teeth is very variable, with teeth ranging from close to bilaterally symmetrical to strongly asymmetrical, with the main cusp flanked by three cusplets on the mesial side and only one on the distal side; the

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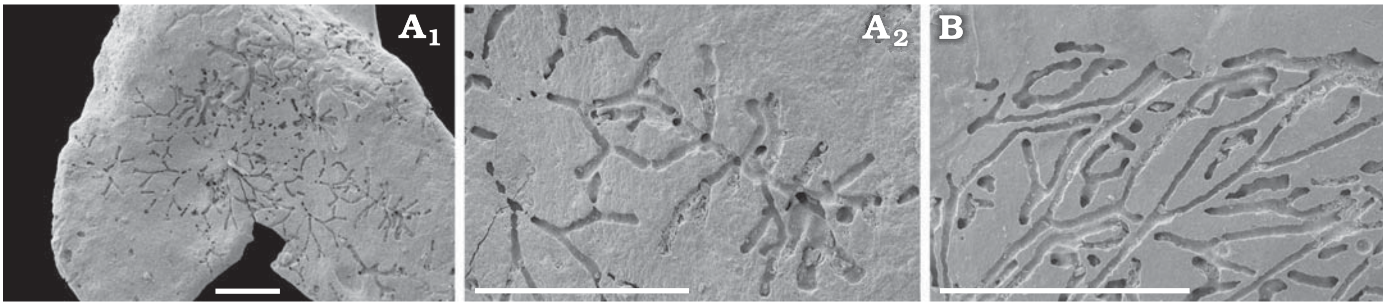

Fig. 3. Microborings in the Miocene shark teeth from Cerová section in Malé Karpaty, Slovakia. **A**. SNM Z 27430, bed 20–21. Two different sizes of *Abeliella riccioides* Mägdefrau, 1937 and an unnamed boring in a tooth root (*Squaliolus*) (A_1). Detail of unnamed boring from A_1 (A_2). **B**. SNM Z 27431, bed 8–9. *Mycelites ossifragus* Roux, 1887 at a tooth crown-root junction (*Paraetmopterus*). Scale bars 0.1 mm.

anterior tooth is strongly angled mesially, with the main cusp angled in that direction. The main cusp is, where preserved, less than twice the height of the innermost lateral cusps in the lateral teeth, but is proportionally very large and high in the anterior tooth. The labial face of the cusps of lateral teeth is smooth and almost flat, being separated from the lingual face by a very well developed cutting edge, while below the cusps on the labial face of the crown, short and sharp-edged folds are present, that expand into small swellings at the base of the crown basal face. In the anterior tooth, widely spaced and strong folds extend most of the height of the main cusp, with some bifurcating near the crown base. Close to the base of the crown, a fine polygonal ornament is present both on and between the folds of all teeth. The lingual face of the cusps is convex and ornamented by several weak but sharp edged folds, which reach almost to the cusp apex but do not reach the base of the crown. Where preserved, the root is low and "V" shaped, without a nutritive groove. The lateral and labial faces of the root are concave, and flare towards the basal face, from which they are separated by a sharp angle. A major foramen is present in the centre of the root labial face, with rare, smaller foramina also present. The root basal face is weakly convex and has a number of foramina, which are variable in size and shape and irregularly distributed.

Remarks.—These teeth all appear to belong to a single species of highly heterodont syliorhinid. The heterodonty, highly cuspate lateral teeth and pattern of ornament is seen in two extant genera, *Galeus* and *Apristurus* Garman, 1913. The differentiation of these genera by their dentition is discussed by Herman et al. (1990) and Adnet (2006). Despite the poor quality of material available here, the degree of heterodonty, lack of a nutritive groove in the root and asymmetry of the anterior tooth suggest that these specimens should be assigned to *Galeus*.

Order Squatiniformes de Buen, 1926

Family Squatinidae Bonaparte, 1838

Genus *Squatina* Duméril, 1806

Type species: *Squalus squatina* Linnaeus, 1758; Recent, probably North Sea, Europe.

Squatina sp.

Fig. 4G.

Material.—Single partial tooth, SNM Z 27438.

Description.—The single broken tooth is very small, with an estimated crown height of about 2.2 mm. Only the cusp and a portion of the lateral blade are preserved. The cusp is triangular and higher than wide with biconvex faces separated by a very well developed cutting edge. The preserved portion of the lateral blade is of a similar length to the cusp height, and joins to the cusp with a low degree of curvature, suggesting that the tooth would have been high and narrow when intact.

Remarks.—The tooth is assignable to the genus *Squatina*, and the high form suggests that is an anterior tooth. The lack of well preserved material prevents a more detailed assignment.

Order Pristiophoriformes Compagno, 1973

Family Pristiophoridae Bleeker, 1859

Genus *Pristiophorus* Müller and Henle, 1837

Type species: *Pristis cirratus* Latham, 1794; Recent, New South Wales, Australia.

Pristiophorus striatus sp. nov.

Fig. 4H–K.

Holotype: SNM Z 27441, anterior oral tooth.

Etymology: From the striated ornament on the oral teeth.

Type locality: Cerová-Lieskové, Vienna Basin, Slovakia.

Type horizon: Lakšárska Nová Ves Formation, late Karpatian (equivalent to latest Burdigalian), Miocene.

Material.—Two additional oral teeth and an incomplete rostral tooth; SNM Z 27439, SNM Z 27440, SNM Z 27442.

Diagnosis (based on oral teeth).—Teeth considerably wider than high. Cusp well developed relative to other members of the genus but forms less than half of height of crown and less than quarter of width of crown. Bases of cusp form sharp angle with linguo-occlusal edge of crown. Labial crown face with widely spaced and irregular vertical folds, some reaching close to base of cusp or linguo-occlusal edge, others very short and limited to labial crown edge.

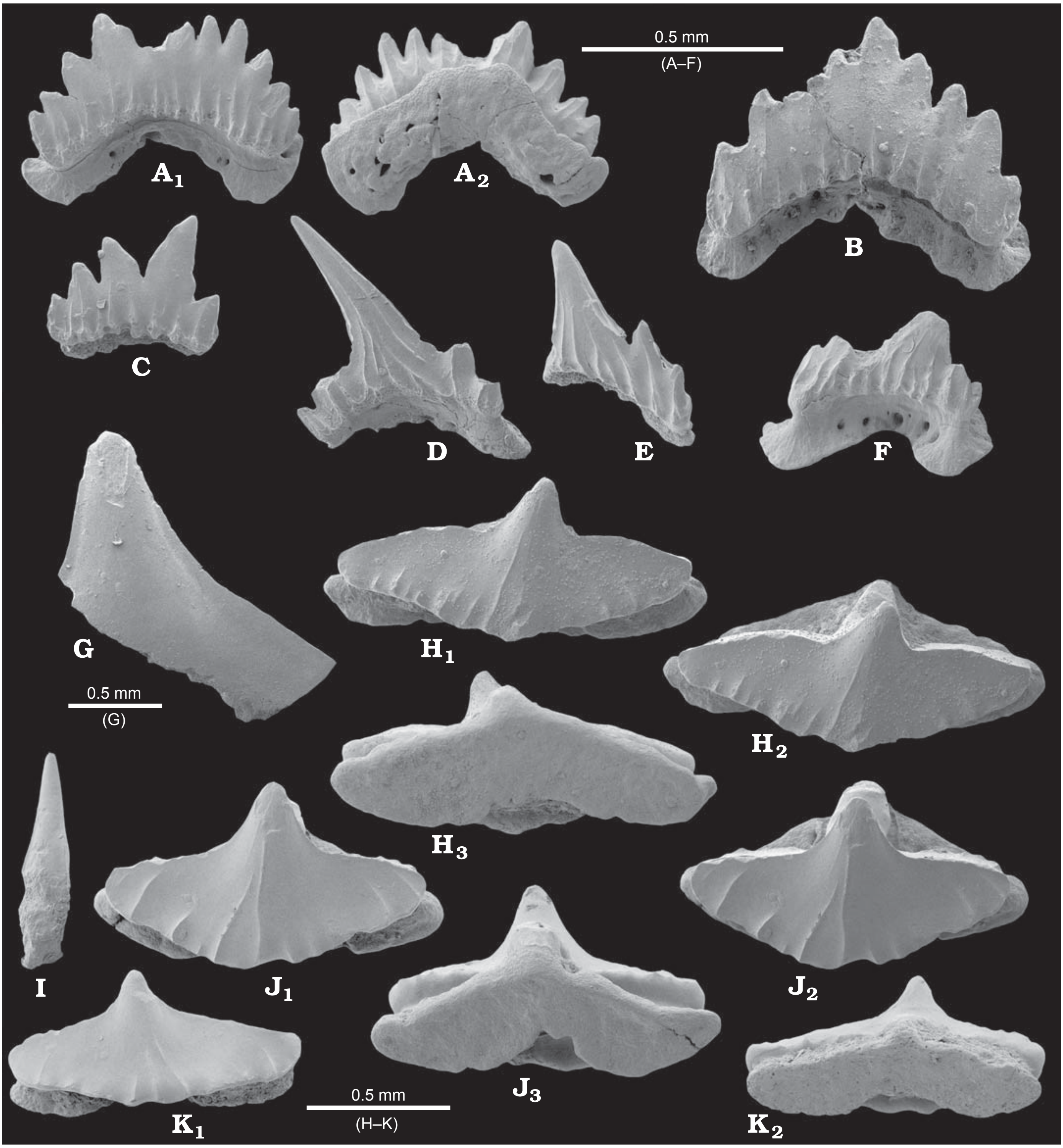

Fig. 4. Miocene non-squaliform shark teeth from Cerová section in Malé Karpaty, Slovakia. **A**–**F**. *Galeus* sp. **A**. SNM Z 27432, bed 17–18, anterolateral tooth in labial (A_1) and lingual (A_2) views. **B**. SNM Z 27433, bed 17–18, anterolateral tooth in labial view. **C**. SNM Z 27434, bed 17–18, posterior tooth in labial view. **D**. SNM Z 27435, bed 20–21, anterior tooth in labial view. **E**. SNM Z 27436, bed 21–22, anterolateral tooth in labial view. **F**. SNM Z 27437, bed 21–22, anterolateral tooth in labial view. **G**. *Squatina* sp., SNM Z 27438, bed 20–21, partial tooth in labial view. **H**–**K**. *Pristiophorus striatus* sp. nov. **H**. SNM Z 27439, bed 20–21, lateral tooth in labial (H_1), occlusal (H_2), and basal (H_3) views. **I**. SNM Z 27440, bed 21–22, partial rostral tooth in lateral view **J**. Holotype, SNM Z 27441, bed 17–18, anterior tooth in labial (J_1), occlusal (J_2), and basal (J_3) views. **K**. SNM Z 27442, bed 14, lateral tooth in labial (K_1) and basal (K_2) views.

Folds do not bifurcate and all reach crown labial edge. Labial edge of crown slightly crenulated with no differentiated labial protuberance.

Description.—The oral teeth of this species are small, being up to 1.3 mm wide. In all cases the tooth was far wider than high, being more than twice as wide as high when viewed labi-

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ally. The labial face of the crown is weakly rhombic, being widest in the centre and tapering towards the lateral extremities which are somewhat rounded. A short but sharp and very clearly demarcated cusp is present at the centre of the occlusal crown edge. The cusp is about as high as wide and is less than half the height of the crown. The crown labial face is flat to very weakly convex, with the labial face of the cusp being weakly convex. The labial face of the crown is ornamented by weak but sharp edged folds. These folds originate from the basal edge of the crown and extend vertically across the crown to various degrees, with some folds reaching the base of the cusp or close to the occlusal edge, but others being limited to the immediate vicinity of the basal edge. The folds are irregularly spaced and do not appear to form any systematic pattern, and do not bifurcate. There are weak crenulations where the folds meet the basal face of the crown. The labial and lingual crown faces are separated by a well developed cutting edge, and form an angle of less than 90°. The lingual crown face is flat, but is expanded below the cusp to form a well developed but narrow uvula. Short, weak and irregular folds are seen on the lingual crown face and weak crenulations are present at its base. The crown overhangs the root on all sides, with the labial and lingual faces of the root being low and concave. The root is hemiaulacorhize and typically weakly "V" shaped when viewed basally. The basal face of the root is flat, and flared laterally, with the root being slightly wider than the crown. Several large foramina are present near the centre of the lingual face of the root, and a single large foramen is present to one side of the uvula on the labial root face.

The rostral tooth is very small and incomplete. The blade is oval in cross section and has a weak cutting edge on one side but is otherwise smooth. The root is not preserved. This is probably a secondary rostral tooth or one of the reduced teeth from the ventral surface of the rostrum.

Remarks.—*Pristiophorus* has been recorded from a number of Cenozoic chondrichthyan assemblages, including from the Miocene of Europe. However, these records are based predominantly on rostral teeth (e.g., Barthelt et al. 1991, and referrences therein; Vialle et al. 2011). Many of these fossil rostral teeth of *Pristiophorus* are not distinguishable from those of extant species and for that reason we suggest that *Pristiophorus* species based on rostral teeth should be considered as nomina dubia unless they can be shown to have autapomorphic characters. As a result, although it is possible that the species present here is conspecific with the type material of *Pristiophorus suevicus* Jaekel, 1890, this cannot be demonstrated, as the holotype of *P. suevicus* cannot be regarded as diagnostic.

Pristiophorus striatus sp. nov. differs from most other species of *Pristiophorus* in possessing wide and low teeth with a well defined cusp and a labial ornament. The ornamented labial face is shared with *Pristiophorus lacipidinensis* Adnet, 2006 from the Eocene of France, but this species differs in having fewer folds that frequently do not reach the basal edge of the crown, as well as a larger and less clearly differentiated crown. *Pristiophorus rupeliensis* Steurbaut and Herman, 1978 from the Oligocene of Belgium (as figured in Hovestadt and Hovestadt-Euler 1995) has incipient ornamentation along the labial basal crown face but this never forms elongate folds; in addition the teeth are high and typically possess a well developed labial protuberance.

Order Squaliformes Compagno, 1973

Family Dalatiidae Gray, 1851

Genus *Squaliolus* Smith and Radcliffe, 1912

Type species: *Squaliolus laticaudus* Smith and Radcliffe, 1912; Recent, Luzon, Philippines.

Squaliolus cf. *schaubi* (Casier, 1958)

Fig. 5.

1958 *Centroscymnus schaubi* Casier; Casier 1958: pl. 1: 11.
1972 *Squaliolus schaubi* Casier, 1958; Ledoux 1972: fig. 11b, c, f, h–l.
2004 *Squaliolus schaubi* Casier, 1958; Underwood and Mitchell 2004: pl. 1: 3–8.
2006 ?*Squaliolus* sp.; Takakuwa 2006: fig. 4.6.
2011 *Squaliolus schaubi* (Casier, 1958); Vialle et al. 2011: fig. 2.6.

Material.—137 lower and 89 upper partial and complete teeth including SNM Z 27443 to SNM Z 27454.

Description.—There is extreme dignathic heterodonty with slender and pointed upper teeth and blade-like lower teeth.

The lower teeth are small, being less than 2 mm high. They show very little monognathic heterodonty, with the exception of the rather wide posterior tooth. There is strong labio-lingual compression of the teeth and a well developed cutting edge is present on the cusp and distal heel. There is a single cusp that is strongly inclined distally and comprises less than a quarter of the total height of the tooth. The cusp reaches almost to the distal edge of the tooth, and has weakly convex mesial and distal cutting edges that lack serrations. Rare specimens have a slightly sigmoidal curvature to the mesial cutting edge. Distally, the cusp overhangs a low and rounded distal heel. The tooth below the cusp is roughly rectangular and higher than wide, with a slightly convex distal edge and concave mesial edge. There is a weak notch on the basal edge of the tooth. The labial tooth face is largely covered by enameloid, which reaches at least three quarters of the way to the base of the tooth. There is a major concavity on the mesial side of the tooth that reaches as far distally as level with the middle of the base of the cusp. This lacks enameloid and has a semicircular upper edge. Several small foramina are present along the edge of this concavity. A very well developed foramen is present at the base of the enameloid, creating a narrow ridge between this hole and the mesial concavity. One of two smaller foramina is present behind the main foramen along the weakly curved enameloid base. The lingual side of the tooth is largely flat, but tapers occlusally and basally from a slight horizontal ridge on the upper part of the tooth. There is a deeply indented region below the distal heel, which is the surface that would articulate with the mesial indentation on the labial face of the adjacent tooth. The basal edge of the enameloid is gently curved with a ma-

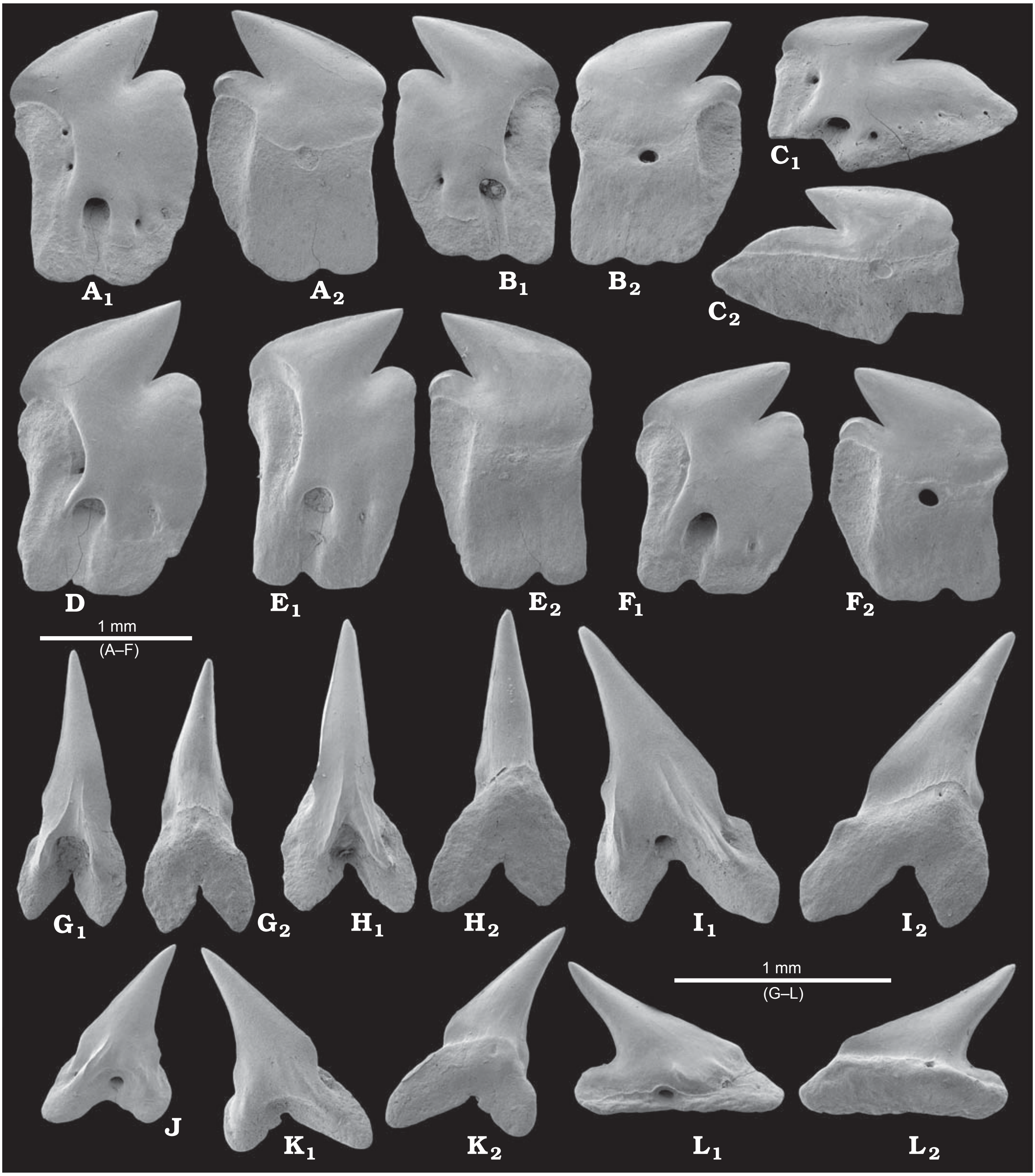

Fig. 5. Miocene squaliform shark *Squaliolus* cf. *schaubi* (Casier, 1958) teeth from Cerová section in Malé Karpaty, Slovakia. **A**. SNM Z 27443, bed 20–21, lower tooth in labial (A_1) and lingual (A_2) views. **B**. SNM Z 27444, bed 13, lower tooth in labial (B_1) and lingual (B_2) views. **C**. SNM Z 27465a, bed 20–21, lower posterior tooth in labial (C_1) and lingual (C_2) views. **D**. SNM Z 27465b, bed 5, ?male lower tooth in labial view. **E**. SNM Z 27447, bed 5, lower symphyseal tooth in labial (E_1) and lingual (E_2) views. **F**. SNM Z 27448, bed 8–9, lower tooth in labial (F_1) and lingual (F_2) views. **G**. SNM Z 27449, bed 20–21, upper toot in labial (G_1) and lingual (G_2) views. **H**. SNM Z 27450, bed 20–21, upper tooth in labial (H_1) and lingual (H_2) views. **I**. SNM Z 27451, bed 20–21, upper tooth in labial (I_1) and lingual (I_2) views. **J**. SNM Z 27452, bed 17–18, upper tooth in labial view. **K**. SNM Z 27453, bed 8–9, upper tooth in labial (K_1) and lingual (K_2) views. **L**. SNM Z 27454, bed 21–22, upper posterior tooth in labial (L_1) and lingual (L_2) views.

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jor foramen just below the basal edge of the enameloid at its lowermost point. No other foramina are evident on the lingual tooth face. The posterior tooth is similar to the other lower teeth, but the distal portion of the tooth is highly expanded, with the distal heel forming a long, horizontal blade below which the root is similarly expanded.

The upper teeth are slender and typically between 1 and 1.5 mm high and show a low degree of heterodonty, largely seen as increasing asymmetry of the teeth with distal inclination of the cusp in teeth from more posterior jaw positions. Teeth are higher than wide and comprise a single cusp above a clearly bilobed root. The cusp has straight to slightly concave mesial and distal edges and comprises about half of the height of the tooth. There is a continuous but weak cutting edge separating weakly convex labial and lingual faces. A poorly developed projection is present on the mesial and distal edges of most teeth and forms a slight overhang of the root. At the base of the labial side of the cusp are a pair of weak vertical ridges that pass downwards into sharp-edged extensions of the crown on the labial faces of the root lobes, reaching at least half the height of the root. The root is quite robust and comprises two very well differentiated root lobes forming an internal angle of 90° or less. In lateral teeth, the mesial root lobe is longer and has a more rounded termination than the distal lobe. The basal face of the root is flat, but there is not the strongly demarked edge between the basal and labial faces as seen in some squaliform teeth. There is a very large foramen at the base of the crown between the two crown lobes on the labial side, and a small foramen at the sharply angled lingual projection at the top of the root. One or more small lateral foramina may also be present.

Remarks.—While morphologically very similar to specimens from elsewhere referred to *Squaliolus schaubi*, the teeth recorded here are consistently smaller. It is unclear whether this size difference arises from intraspecific regional variation, as recorded in extant *Etmopterus* (see Yano 1997) and the Cretaceous squaliform *Protosqualus* (see Underwood and Mitchell 1999), or if separate but dentally similar taxa are represented. The presence of teeth with a slightly sigmoidal cusp, a character seen in mature males (Herman et al. 1989), suggests that the teeth are not from juveniles. Specimens of lower teeth with a rather more elongate cusp with more strongly sigmoidal leading edge have been recognized in the Miocene of Germany (Barthelt et al. 1991, as *Squaliolus* sp. 1) and southern France (Ledoux 1972: fig. 11a, d, e, g). Lower teeth of this morphology were not recorded during this study and therefore may not be conspecific with *Squaliolus schaubi* and may instead represent a species of *Euprotomicrus* Gill, 1862 (see Herman et al. 1989). Two lower teeth figured from the Miocene of Japan by Takakuwa (2006) may represent different species; while the specimen in their fig. 4 may be referable to *Squaliolus schaubi*, the specimen in fig. 3 differs from *S. schaubi* in having a higher and more erect cusp, higher tooth shape overall and larger labial foramina.

Genus *Eosqualiolus* Adnet, 2006

Type species: *Eosqualiolus aturensis* Adnet, 2006, Middle Eocene of France.

Eosqualiolus skrovinai sp. nov.

Fig. 6A–G.

Holotype: SNM Z 27456, lower tooth.

Etymology: In honour of Michal Škrovina, who was the first person who encouraged one of us (JS) with our palaeontological interests.

Type locality: Cerová-Lieskové, Vienna Basin, Slovakia.

Type horizon: Lakšárska Nová Ves Formation, late Karpatian (equivalent to latest Burdigalian), Miocene.

Material.—Nine lower and five upper partial and complete teeth including SNM Z 27455 to SNM Z 27461.

Diagnosis.—Extreme dignathic heterodonty present. Lower teeth with high cusp comprising nearly half of total tooth height. Cusp triangular with straight edges, inclined distally but not extending distally of short but well differentiated and semicircular distal heel. Tooth below cusp of similar height and width. Enameloid on labial face extends at least three quarters of distance to basal edge. A major labial foramen is present just above base of enameloid in centre of tooth, with a vertical groove below extending to root basal edge, forming a distinct notch on basal edge. A single smaller foramen is present behind main one. Major curved concavity marks mesial edge of enameloid below anterior part of cusp. Mesial profile of root with concavity below mesial end of cusp with swelling immediately below that. Tooth thickest at swollen horizontal ridge at base of enameloid on lingual face. Well developed concavity present below distal heel on lingual face. Upper teeth slender with single elongate cusp comprising over half of tooth height. Cusp weakly inclined distally and faintly sigmoidal. Cusp biconvex with continuous cutting edges that reach base of cusp. On labial face, base of cusp bifurcates into two short ridges on top of root lobes. These lobes have an acute edge and several short but sharp-edged ridges are present. Root low and flat-based, slightly asymmetrical, with short and rounded root lobes giving "heart-shaped" basal profile. Weak lingual protuberance is present with a large terminal foramen.

Description.—There is extreme dignathic heterodonty with slender upper teeth and triangular and blade-like lower teeth.

The lower teeth are only one well preserved tooth and several damaged teeth. These are larger than those of co-occurring squaliforms, reaching 3 mm in height. Despite the small number of specimens, there appears to be limited monognathic heterodonty. There is a strong labio-lingual compression and a well developed cutting edge is present along the occlusal edge of the tooth. The single cusp comprises nearly half the total tooth height and is somewhat erect, with the distal edge being only slightly distally inclined. Both mesial and distal edges of the cusp nearly straight, other than near the base of the mesial edge where a small concavity may be present in some teeth. The cusp does not overhang the distal edge of the tooth, and there is a strongly convex distal heel below it. The

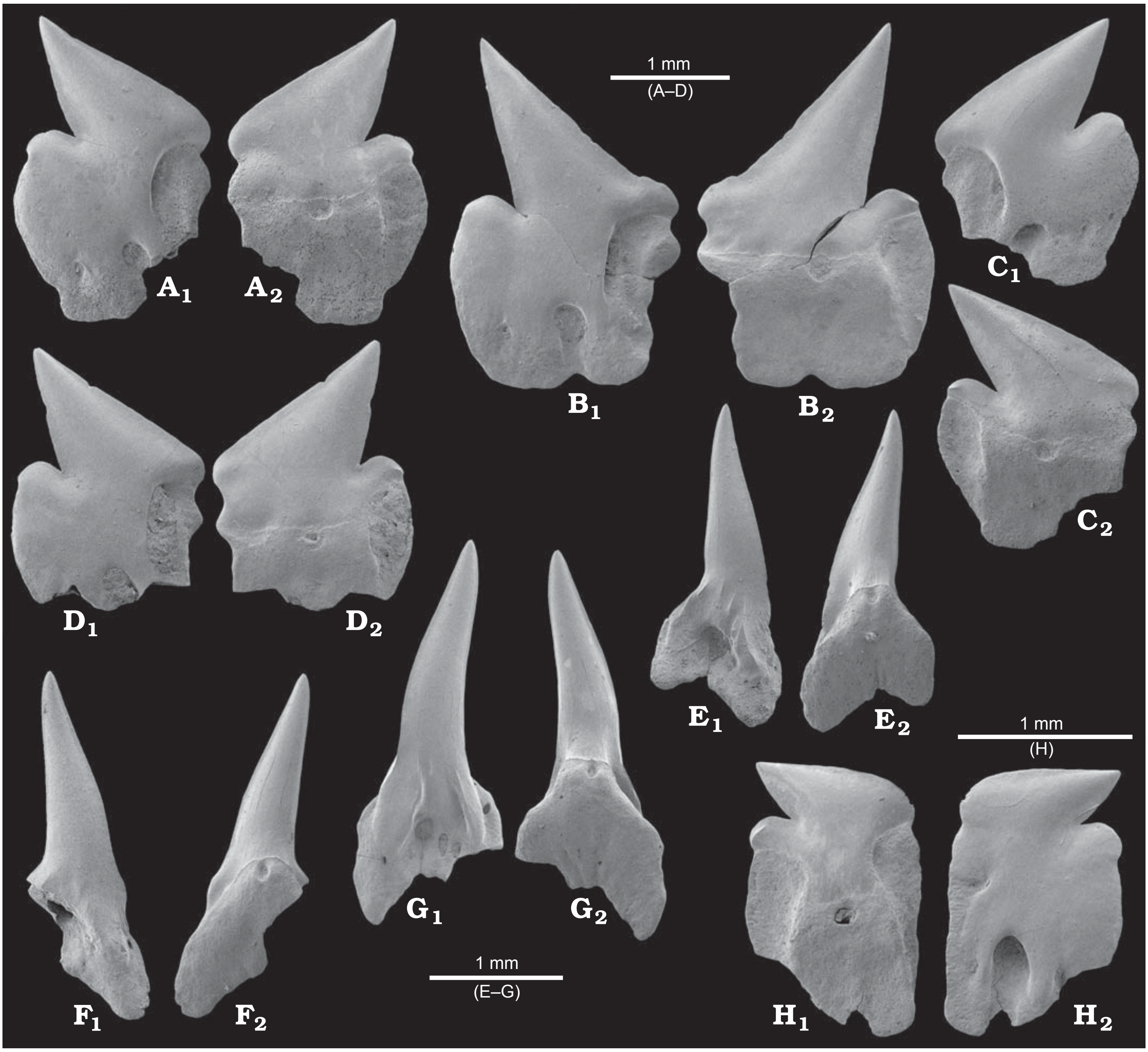

Fig. 6. Miocene squaliform sharks *Eosqualiolus* and *Squaliodalatias* teeth from Cerová section in Malé Karpaty, Slovakia. **A**–**G**. *Eosqualiolus skrovinai* sp. nov. **A**. SNM Z 27455, bed 8–9, lower tooth in labial (A_1) and lingual (A_2) views. **B**. Holotype, SNM Z 27456, bed 14, lower tooth in labial (B_1) and lingual (B_2) views. **C**. SNM Z 27457, bed 8–9, lower tooth in labial (C_1) and lingual (C_2) views. **D**. SNM Z 27458, bed 14, lower tooth in labial (D_1) and lingual (D_2) views. **E**. SNM Z 27459, bed 20–21, upper tooth in labial (E_1) and lingual (E_2) views. **F**. SNM Z 27460, bed 17–18, upper tooth in labial (F_1) and lingual (F_2) views. **G**. SNM Z 27461, bed 8–9, upper tooth in labial (G_1) and lingual (G_2) views. **H**. *Squaliodalatias* sp., SNM Z 27462, bed 8–9, lower tooth in labial (H_1) and lingual (H_2) views.

tooth below the cusp is roughly square, with a weakly convex distal edge and irregularly concave mesial edge. There is a weak notch on the basal edge of the tooth below the main labial foramen. The mesial edge of the root is rather lobate, with a small swollen region about a third of the way down the root edge. Enameloid, reaches close to the base of the tooth on the labial side. There is a major concavity on the mesial side of the tooth, the distal edge of which is strongly indented and weakly overhung by enameloid. This concavity lacks enameloid and has a semicircular upper edge. Several small foramina are present along the upper part of the edge of this concavity. A very well developed foramen is present at the base of the enameloid, with a shallow vertical groove being present between this and the notch on the tooth basal edge. Up to three small foramina are present distally. The lingual side of the tooth is largely flat, but thickens slightly to form a faint horizontal ridge on the upper part of the tooth. There is a deeply indented region below the distal heel. The basal edge of the enameloid is straight with a major foramen just below the basal edge of the enameloid in the central part of the tooth

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face; a small foramina may also be present to the anterior of this.

The upper teeth are slender and about 2 mm in height and show a low degree of heterodonty. Teeth are considerably higher than wide and comprise a single cusp and a weakly bilobed root. The cusp is straight to very faintly sigmoidal and rather inclined distally and is well over twice as high as wide. There is a continuous cutting edge separating the weakly convex labial face and more strongly convex lingual face. At the base of the labial side of the cusp is a bifurcating ridge that extends along at least half of the length of the root lobes. There are a number of rather short and irregular enameloid folds present both on these ridges and on the base of the crown between them. The root is quite robust and possesses two root lobes that are short but clearly differentiated, with a sharp internal angle and have rather angular terminations. The base of the root is flat but there is no sharp division between this and the labial face. There is a very large foramen at the base of the crown between the two crown lobes on the labial side, and a small foramen at the weak lingual protuberence at the top of the root. One or more small lateral foramina may also be present.

Remarks.—*Eosqualiolus aturensis* Adnet, 2006 from the Eocene of France is very similar to *E. skrovinai* sp. nov., especially as regards the lower teeth. Lower teeth of *E. aturensis* differ from those of *E. skrovinai* in having a weakly concave mesial edge to the cusp and a straighter mesial edge to the root. The upper teeth of *E. aturensis* are more slender than those of *E. skrovinai*, and lack a complete cutting edge and the ridged ornament on the labial face of the crown as well as having a less "heart-shaped" basal face. Specimens of lower and upper teeth from the Miocene of Jamaica, figured as *Squaliolus* sp. and *Scymnodon* aff. *obscurus* (Vaillant, 1888) respectively by Underwood and Mitchell (2004), represent a different, but possibly closely related species, as does the material described as "Symnorhinidae indet" by Ledoux (1972); see also Adnet et al. (2006b). In addition to being far larger, the lower teeth of these species have a higher and more angular root that is mesially displaced. It is unclear whether these would be referable to *Eosqualiolus* or an additional related genus.

Stratigraphic and geographic range.—Eocene to Miocene, Tethyan Atlantic.

Genus *Squaliodalatias* Adnet, Cappetta, and Reynders, 2006b

Type species: *Squaliodalatias weltoni* Adnet, Cappetta, and Reynders 2006b; Middle Eocene, southern France.

Squaliodalatias sp.

Fig. 6H.

Material.—One rather damaged lower tooth, SNM Z 27462.

Description.—The only recorded tooth is 1.6 mm high and strongly labio-lingually compressed. The tooth is about 1.5 times as high as wide and, damage to the distal part notwithstanding, rather rectangular in profile. There is a single cusp that is very strongly inclined distally with the mesial edge of the cusp being close to 90° to the mesial edge of the tooth. The cusp reaches almost to the distal edge of the tooth, and has weakly convex mesial and distal cutting edges that lack serrations. Distally, the cusp overhangs a semicircular distal heel. There is a well developed cutting edge on the cusp and a distal heel. The tooth below the cusp has a weakly convex distal edge (as far as can be seen) and very straight mesial edge. The labial tooth face is largely covered by enameloid, which reaches at least three quarters of the way to the base of the tooth. There is a rather subtle concavity on the mesial side of the tooth, with the upper part of the concavity having an enameloid cover. There is a foramen at the base of the enameloid within this concavity. A very large and prominent foramen is present on the lower part of the tooth labial face, forming the top of a wide and deep vertical groove. Smaller foramina are present both mesial and distal to the main foramen. On the lingual face of the tooth, a broad ridge is present from the base of the crown to the base of the root, comprising the central third of the tooth width at the top and widening downwards. Somewhat symmetrical concavities are present on the mesial and distal sides of this ridge. The basal edge of the enameloid is at the top of the mesial and distal concavities and extends about a third of the way down the central ridge. A major foramina is present close to the centre of the root lingual face.

Remarks.—The single tooth of this species is not dissimilar to the anterior teeth of *Squaliolus schaubi*, but can be separated from them by the greater overall height of the tooth, lower cusp, larger main labial foramen and weaker and partly enameloid-covered mesial concavity. There are strong resemblances with the anterior teeth of *Squaliodalatias weltoni* Adnet, Cappetta, and Reynders, 2006b from the Eocene of France, which shares the same overall tooth proportions and the very large labial foramen, and as such this tooth is assigned to the same genus. Our specimen differs from *Squaliodalatias weltoni* in having a lower cusp without a concave mesial edge and a less well defined mesial concavity. This genus possibly occurs in the Oligocene of California (Welton 1979) and Langhian of France (Cappetta 1970: 76, fig. 9; Ledoux 1972: 161, fig. 12; Adnet et al. 2006b: 64).

Family Etmopteridae Fowler, 1941

Genus *Etmopterus* Rafinesque, 1810

Type species: *Etmopterus aculeatus* Rafinesque, 1810 (= *Squalus spinax* Linnaeus, 1758 by monotypy); Recent, probably North Sea, Europe.

Etmopterus sp.

Fig. 7A–G.

Material.—Seven lower and one upper partial and complete teeth including SNM Z 27463 to SNM Z 27468.

Description.—There is extreme dignathic heterodonty in this species, with multicuspate upper teeth and more blade-like lower teeth.

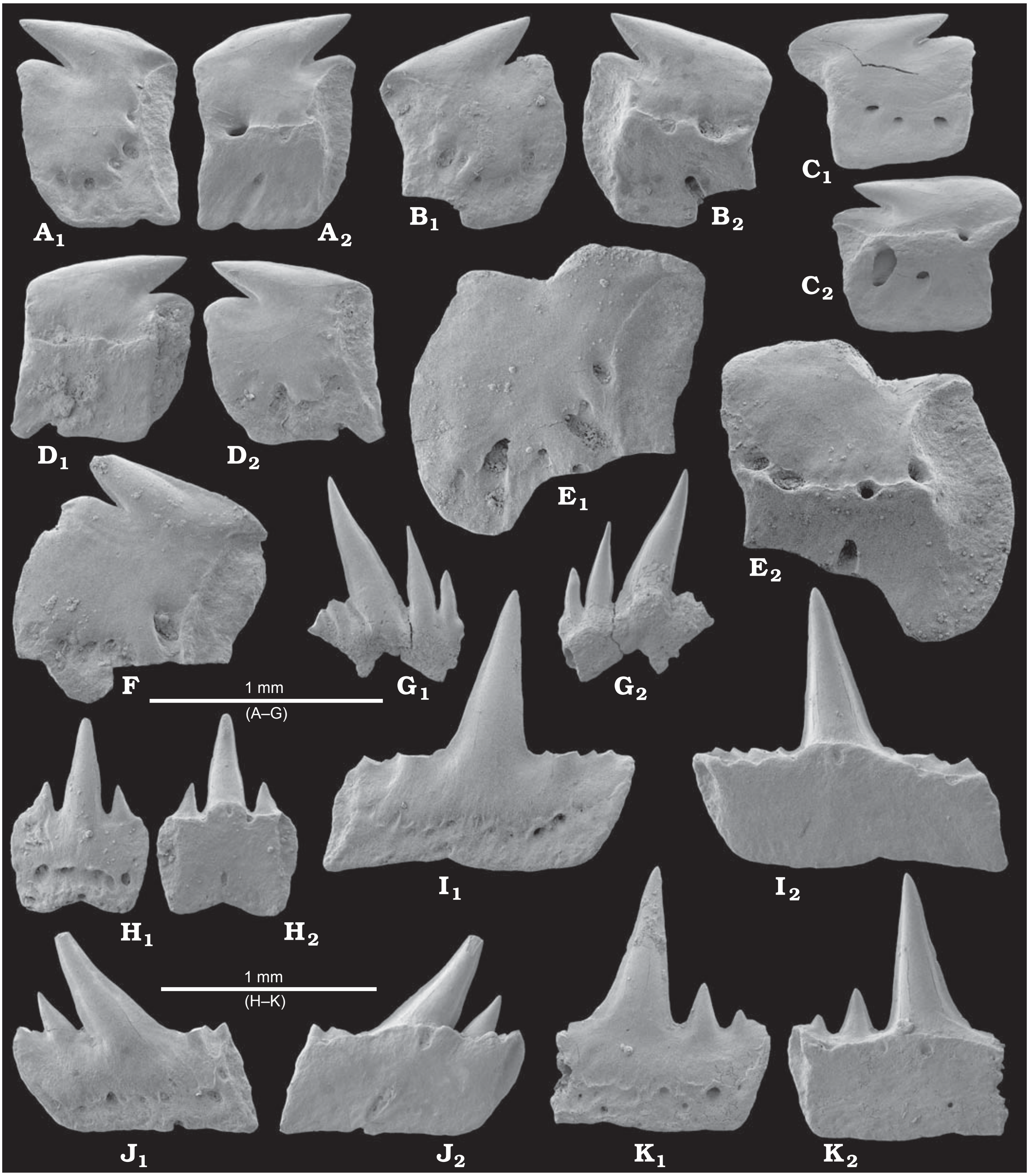

Fig. 7. Miocene squaliform sharks *Etmopterus* and aff. *Miroscyllium* teeth from Cerová section in Malé Karpaty, Slovakia. **A**–**G**. *Etmopterus* sp. **A**. SNM Z 27463, bed 17–18, lower tooth in labial (A$_1$) and lingual (A$_2$) views. **B**. SNM Z 27464, bed 17–18, lower tooth in labial (B$_1$) and lingual (B$_2$) views. **C**. SNM Z 27465, bed 17–18, lower posterior tooth in labial (C$_1$) and lingual (C$_2$) views. **D**. SNM Z 27465, bed 21–22, lower tooth in labial (A$_1$) and lingual (A$_2$) views. **E**. SNM Z 27466, bed 17–18, lower tooth in labial (E$_1$) and lingual (E$_2$) views. **F**. SNM Z 27467, bed 17–18, lower tooth in labial view. **G**. SNM Z 27468, bed 8–9, upper tooth in labial (G$_1$) and lingual (G$_2$) views. **H**–**K**. aff. *Miroscyllium* sp. **H**. SNM Z 27469, bed 17–18, lower symphyseal tooth in labial (H$_1$) and lingual (H$_2$) views. **I**. SNM Z 27470, bed 17–18, lower tooth in labial (I$_1$) and lingual (I$_2$) views. **J**. SNM Z 27471, bed 21–22, lower lateral tooth in labial (J$_1$) and lingual (J$_2$) views. **K**. SNM Z 27472, bed 17–18, lower tooth in labial (K$_1$) and lingual (K$_2$) views.

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The lower teeth are very small, being typically about 1 mm high, with rare larger specimens. They appear to show moderate monognathic heterodonty, with the exception of the rather wide posterior tooth, and possibly some degree of ontogenetic heterodonty. Teeth vary from rather higher than wide to slightly wider than high and all teeth show strong labio-lingual compression. The single cusp is very strongly inclined distally and comprises less than a quarter of the total height of the tooth. The cusp reaches to the distal edge of the tooth in all but the posterior tooth, and has weakly convex to straight mesial and distal cutting edges. Distally, the cusp overhangs a weakly developed and convex distal heel. The tooth below the cusp is roughly rectangular where preserved, but is rather variable in profile, with smaller, and presumably juvenile, teeth having a more angular profile. The mesial edge of the tooth is almost straight in the smallest teeth to faintly concave, but is very strongly so in a posterior tooth where a sharply angled notch is present. The distal edge of the tooth is variably convex in all teeth, being less so in smaller teeth. The basal edge of the tooth is straight or has a weak notch towards the distal end. A vertical concavity is present on the mesial side of the tooth labial face and a similar one on the distal side of the lingual tooth face. Other than in the concavity, enameloid covers large parts of the tooth labial face, where it has a convex lower edge that is deepest near the central part of the tooth. Three to six foramina are present along the lower edge of the labial enameloid covering, and these are rather irregular in their size, distribution and as to whether there is a short groove extending basally from the foramen. The lingual side of the tooth is largely flat, but is slightly swollen close to the base of the crown. The basal edge of the enameloid is straight and horizontal, terminating at a faint horizontal ledge. Two to four large foramina are present along this ledge, one of which appears to connect with a foramen about half way down the root face.

Only one broken upper tooth was recorded. This comprises a slender main cusp and at least two pairs of very long and slender lateral cusplets (as preserved). All three preserved cusps are at least three times as high as wide, and are nearly straight. The labial face of the cusps is faintly convex, and is separated from the strongly convex lingual face by a continuous cutting edge. The preserved root is bilobed and has root lobes that are roughly parallel sided. There is a poorly developed lingual protuberance.

Remarks.—This species differs from the *Etmopterus* sp. figured by Ledoux (1972) from the Miocene of France, in having lower teeth with a more rounded profile of the distal edge, a more rounded basal edge of the crown labial face which has more evenly spaced foramina, and a rather lower profile overall. Teeth have been figured from relatively few extant species of *Etmopterus*, but these, and specimens observed by one of us (CJU), cover examples of most of the species groups defined by Straube et al. (2010). Teeth of the species recorded here are very similar to those of the *E. pusillus* species group (of Shirai and Tachikawa 1993), with the relatively low root and rounded and symmetrical labial enameloid covering being apparently restricted to this species group. The low numbers of well preserved teeth are here considered insufficient for a species diagnosis, while there is the possibility that the material present here represents an extant species from which the dentition is currently unrecorded.

Genus *Miroscyllium* Shirai and Nakaya, 1990

Type species: *Centroscyllium sheikoi* Dolganov, 1986; Recent, Kyushi-Palau Ridge, Pacific.

aff. *Miroscyllium* sp.

Fig. 7H–K.

1972 *Centroscyllium* sp.; Ledoux 1972: fig. 10.

2006 *Miroscyllium* sp.; Adnet et al. 2006a: fig. 3 (refiguring of specimens from Ledoux 1972).

Material.—Ten lower partial and near complete teeth including SNM Z 27469 to SNM Z 27472.

Description.—As no upper teeth of this taxon were recovered, the degree of dignathic heterodonty cannot be assessed.

The lower lateral teeth are very small, less than 1.5 mm wide, and show extreme labio-lingual compression, rendering the teeth highly fragile. There is a slender and erect or distally inclined main cusp flanked by (where preserved) one or two pairs of lateral cusplets. The main cusp is at least twice as high as wide and has straight to faintly concave edges, while the lateral cusplets are proportionally lower and wider. The cusps are clearly separated but a continuous cutting edge is present across all cusps. The root is considerably wider than high and rhombic in profile, with the upper edge being distally displaced. On the labial face, enameloid extends over half way to the base of the tooth, and has a convex and weakly pectinate lower edge. There are numerous foramina irregularly spread along, and below, the base of the enameloid. In some teeth there is a fine wrinkled surface texture on the lowermost part of the enameloid. The lingual face of the root is flat and smooth, with a slight shelf at the base of the cusps. There is a foramen at the top of the root below the main cusp, and several smaller foramina along the transverse bulge at the top of the root, some within small pits. In one tooth (Fig. 7J) a region of open groove on the lingual root face suggests that the main foramina at the top and bottom of the root are connected. There are vertical notches on the mesial and distal edges of the tooth, with the mesial notch displaced labially and the distal notch displaced lingually.

A lower symphyseal tooth (Fig. 7H) is higher than wide. It is in many ways similar to the lateral teeth, but differs in a number of respects. The main cusp is flanked by a single pair of lateral cusplets, and overlies a root that has a concave basal face, giving rise to poorly developed root lobes. At the base of the enameloid on the labial tooth face, a row of foramina is partly merged to form an irregular slot. Foramina are also present at the base of the labial root face and lower part of the lingual root face where they are not present in the lateral teeth. On the lateral parts of the lingual face there are vertical concavities, with the presence of these concavities on both sides of the same root face being indicative of a symmetrically positioned, and thus symphyseal tooth.

Remarks.—These teeth are extremely fragile and the majority are severely damaged. Despite that, there is sufficient material to have a good idea of the overall morphology of the teeth. While the lower lateral teeth are very distinctive, the symphyseal tooth is somewhat similar to the upper anterior teeth of *Paraetmopterus horvathi* sp. nov. Despite this, it differs in being more labio-lingually compressed and having a deeper root without well defined root lobes in addition to having the vertical concavities that form part of the locking mechanism of lower teeth. The teeth agree very closely with two teeth figured by Ledoux (1972) from the Miocene of France as *Centroscyllium* sp. These teeth were subsequently placed within *Miroscyllium*, following a study of the dentition of extant material by Adnet et al. (2006a). While our specimens are similar to the lower teeth of adult *Miroscyllium sheikoi*, they are more mesio-distally expanded. It is therefore possible that while the species seen here is strongly reminiscent of *Miroscyllium*, and possibly very closely related to it, it represents a taxon with lesser degrees of ontogenetic heterodonty and rather wider lower teeth.

Genus *Paraetmopterus* Adnet, 2006

Type species: *Paraetmopterus nolfi* Adnet, 2006; Middle Eocene, France.

Paraetmopterus horvathi sp. nov.

Fig. 8A–J.

1991 *Centroscymnus* sp.; Barthelt et al. 1991: pl. 1.9.
2006 *Centroscymnus* sp. B.; Takakuwa 2006: figs. 3.5, 4.4.

Etymology: In honour of Juraj and Tereza Horvath and their children Josef, Tobias, Lia, Benda, Mia, Johanka, and...

Holotype: SNM Z 27473, lower tooth.

Type locality: Cerová-Lieskové, Vienna Basin, Slovakia.

Type horizon: Lakšárska Nová Ves Formation, late Karpatian (equivalent to latest Burdigalian).

Material.—38 additional lower and 15 upper partial and complete teeth including SNM Z 27474 to SNM Z 27482.

Diagnosis.—Extreme dignathic heterodonty and weak monognathic heterodonty. Lower teeth rectangular in profile, at least twice as high as wide. Mesial edge of tooth smoothly concave, with distal edge almost straight. Cusp small and very strongly distally inclined with apex not reaching distal edge of tooth. Crown enameloid extends about half way down labial face of tooth with semicircular termination. Base of enameloid extends one third of way down lingual face of tooth. Labial face typically with three large foramina, two at base of enameloid towards mesial and distal sides of tooth and a central foramen below the limit of enameloid. Weak horizontal transverse shelf with two foramina at base of enameloid on lingual face. Upper teeth symmetrical with elongate main cusp and single, or rarely double, pair of small lateral cusplets. Cusplets short and robust and closely attached to the main cusp with a continuous cutting edge. Outer edges of cusplets typically overhang lateral part of root. Root labio-lingually compressed and variable in height. Flat to faintly concave basal root face with gentle notch on linguo-basal edge giving the basal face a "heart-shaped" profile in all teeth.

Description.—The lower teeth are close to homodont, while some degree of monognathic heterodonty is present in the upper teeth. The lower teeth are up to 1.4 mm high and 0.75 mm wide. The teeth are somewhat rectangular in labial profile, but have a concave mesial and convex distal edge giving the tooth a general curved profile. The crown and lower half of the root are strongly labiolingually compressed, but the upper part of the root is rather thicker, being expanded lingually. The single cusp is small and very low, with a very strong distal inclination, with the mesial edge being less than 10 degrees from the horizontal (taken as the basal edge of the root). The majority of the cusp mesial edge is straight, but it is convex towards the mesial end of the crown. The cusp reaches almost to the distal end of the crown, and overhangs a small and gently convex distal heel. There is a continuous cutting edge with no serrations. The base of the enameloid on the labial face of the tooth is smoothly curved and often semicircular and reaches to about half the total tooth height. The base of the enameloid on the lingual side of the tooth is also convex, but does not expand as far down the tooth. There is a well developed concavity below the mesial end of the crown on the labial side of the tooth, with a corresponding concavity below the distal heel on the lingual face. The mesial edge of the root is concave, and this is especially pronounced immediately below the base of the crown. The distal edge of the root is typically rather straighter than the mesial edge, and typically comprises a concavity towards the upper and lower ends of the root and a convex region in the centre. The basal edge of the root is straight to weakly convex. The labial face of the root is flat and penetrated by three extremely well developed foramina in most teeth. There are two foramina close to the base of the enameloid to the mesial and distal sides of the tooth midpoint, and a smaller foramen rather lower on the root labial face at a position close to the tooth midline. The lingual face of the root is smooth and thickens upwards from a very compressed region close to the root basal edge to a thickened area just below the base of the crown, the upper edge of which forms a weak shelf. Two large foramina are present on this shelf at the top of the root.

Upper teeth are slightly higher than wide and typically close to symmetrical. There is a well developed main cusp that comprises over half of the height of the tooth, flanked by one or two pairs of small but well developed lateral cusplets. The outermost cusplets are very weakly divergent and slightly overhang the root. The root is weakly bilobed and strongly labiolingually compressed. Viewed lingually, the root has a weakly developed lingual protuberance, below which the rounded to weakly angular root lobes diverge. The root lobes are short and only weakly separated by an obtuse internal angle. The face of the root is flat. There is a well developed foramen close to the apex of the lingual protuberance, and another on the root lingual face close to, or at, the basal edge. A pair of foramina are present below the lateral cusplets on the lingual root face, and additional small foram-

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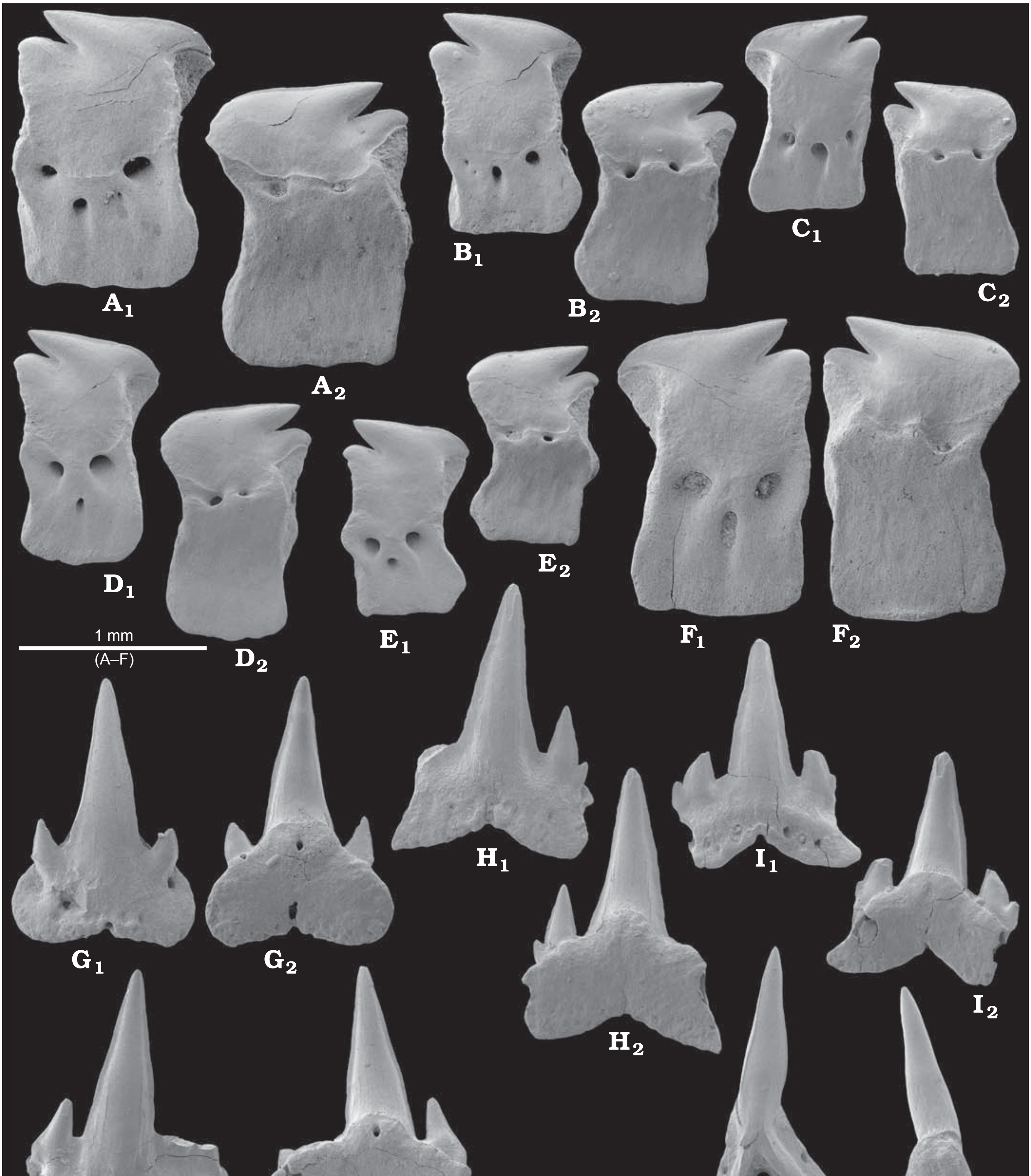
A1
A2
B1
B2
C1
C2
D1
D2
E1
E2
F1
F2
1 mm
(A–F)
G1
G2
H1
H2
I1
I2
J1
J2
1 mm
(G–J)
K1
K2
1 mm
(K)

ina are present just below the base of the enameloid on the labial face.

Remarks.—*Paraetmopterus* has previously only been recorded from the Eocene of France where it is represented by abundant specimens of *P. nolfi* Adnet, 2006. Although very similar overall, *P. horvathi* differs in a number of ways. The lower teeth show far less heterodonty than those of *P. nolfi*, being consistently higher and more rectangular. The mesial edge of *P. nolfi* teeth is very strongly and irregularly concave, unlike the smoother and less extreme concavity in *P. horvathi,* with the positioning of the labial foramina being far more consistent and regular. The upper teeth of *P. horvathi* differ from those of *P. nolfi* in having a more "heart-shaped" root basal face in most teeth and having more robust lateral cusplets that are more closely attached to the main cusp.

Although not previously recorded outside the Eocene, *Paraetmopterus* appears to be present, but unrecorded, in other of Miocene faunas, having been identified as *Centroscymnus*. *Paraetmopterus* therefore appears to be present in the Miocene of Germany (Barthelt et al. 1991, as *Centroscymnus* sp.) and Japan (Takakuwa 2006, as *Centroscymnus* sp. B). The similarity between the lower teeth of *Paraetmopterus* and *Centroscymnus* Bocage and Capello, 1864 was noted by Adnet (2006). The two genera can, however, be readily distinguished by the form of the upper teeth as described above, and by the presence of an enameloid-covered vertical ridge on the labial face of the root of lower teeth, as well as the presence of a nutritive groove on the lingual root face.

Stratigraphic and geographic range.—Eocene to Miocene; Tethyan Europe.

Family Somniosidae Jordan, 1888

Somniosidae indet.

Fig. 8K.

Material.—One upper tooth from sample 17–18, SNM Z 27483.

Description.—This small tooth, about 1.2 mm high, is extremely gracile and comprises a slender cusp above a strongly bilobed root. The cusp is straight and slightly inclined relative to the root, and is over three times as high as wide. The labial face of the cusp is weakly convex, but becomes more strongly convex towards the base. At the base of the cusp, the labial face of the crown forms a bifurcating ridge than continues for half the length of the labial side of the root lobes. A weak crest is present on each of these basal lobes of the crown. A weak cutting edge separates the labial from lingual faces of the cusp, but does not reach the cusp base. The lingual face of the cusp is strongly convex and unornamented. The root lobes are parallel sided and form an acute angle to each other. The distal lobe is slightly longer and wider than the mesial lobe. The root is labio-lingually compressed with a flat basal face. A weakly developed lingual protuberance is present which bears a (poorly preserved) terminal foramen. There are large foramina on the mid part of the lateral faces of the root, and in the notch between the root lobes on the lingual side.

Remarks.—Although well preserved, this tooth cannot be readily assigned to a taxon. The overall shape of the tooth is very similar to that of species of the somniosid genera *Centroscymnus* and *Scymnodalatias* Garrick, 1956 (as figured by Herman et al. 1989). Despite this, more material would be needed for a more definite taxonomic assignment.

Order Myliobatiformes Compagno, 1973

Family Gymnuridae Fowler, 1934

Genus *Gymnura* van Hasselt, 1823

Type species: *Raja micrura* Bloch and Schneider, 1801; Recent, Suriname.

Gymnura sp.

Fig. 9I.

Material.—Single imperfect tooth, SNM Z 27484.

Description.—The single tooth is small, being about 1 mm wide, and wider than high or deep. The crown is strongly curved, with a concave labial face and rather sharply angled lateral extremities, with a faintly convex region below the cusp. The cusp is broken, but projects lingually. There is a cutting edge between the cusp and the lateral ends of the crown, but this fades and becomes less sharp laterally. The crown is smooth on both labial and lingual face. The crown overhangs the root on all sides, and there is no uvula or labial protuberance although the base of the crown on the lingual side is weakly flared. The root is low and smaller than the crown, being rather lingo-labially compressed. The basal part of the root is damaged by bioerosion, but a wide nutritive groove is present.

Remarks.—Teeth of *Gymnura* are present in a large proportion of Cenozoic chondrichthyan-bearing rocks (CJU personal observations; David Ward, personal communication 2011), with Neogene specimens having been figured on several occasions (e.g., Cappetta 1970) but are commonly overlooked because of their small size. In addition, the tooth mor-

← Fig. 8. Miocene squaliform sharks *Paraetmopterus* and Somniosidae teeth from Cerová section in Malé Karpaty, Slovakia. **A**–**J**. *Paraetmopterus horvathi* sp. nov. **A**. Holotype, SNM Z 27473, bed 17–18, lower tooth in labial (A_1) and lingual (A_2) views. **B**. SNM Z 27474, bed 17–18, lower tooth in labial (B_1) and lingual (B_2) views. **C**. SNM Z 27475, bed 8–9, lower tooth in labial (C_1) and lingual (C_2) views. **D**. SNM Z 27476, bed 20–21, lower tooth in labial (D_1) and lingual (D_2) views. **E**. SNM Z 27477, bed 20–21, lower tooth in labial (E_1) and lingual (E_2) views. **F**. SNM Z 27478, bed 8–9, lower tooth in labial (F_1) and lingual (F_2) views. **G**. SNM Z 27479, bed 17–18, upper anterior tooth in labial (G_1) and lingual (G_2) views. **H**. SNM Z 27480, bed 8–9, upper tooth in labial (H_1) and lingual (H_2) views. **I**. SNM Z 27481, bed 21–22, upper tooth in labial (I_1) and lingual (I_2) views. **J**. SNM Z 27482, bed 8–9, upper tooth in labial (J_1) and lingual (J_2) views. **K**. Somniosidae indet., SNM Z 27483, bed 20–21, upper tooth in labial (K_1) and lingual (K_2) views.

phology appears to be very conservative within the genus, and the dentitions of extant species are poorly known.

Neoselachii incertae sedis

Genus *Nanocetorhinus* nov.

Type species: *Nanocetorhinus tuberculatus* gen. et sp. nov.; see below.

Etymology: From the overall resemblance to the teeth of the planktivorous shark *Cetorhinus* de Blainville, 1816, but differ in their vastly smaller size.

Diagnosis.—Teeth minute, rarely exceeding 1 mm high, with a single cusp overlying an irregular to bilobed root. Weak heterodonty other than compressed symphyseal teeth. Cusp slender, over three time as long as wide, straight or faintly curved. Cusp faces strongly convex with very well developed cutting edge bearing weak and very irregular serrations. Labial face of cusp with well developed granulae or irregular granulate ridges. Flared collar at base of cusp with fine pitted ornament. Root rather irregular with two lobes present to a greater or lesser degree. Basal face of root with irregular foramina or often incompletely closed over resulting in single very large basal foramen.

Remarks.—The teeth of *Nanocetorhinus* gen. nov. do not closely resemble those of any other neoselachian genus, so their affinity is uncertain. While the overall shape of the teeth is similar to that of *Cetorhinus*, there are many differences in the ornamentation, presence of the "collar", and form of the root and its vascularisation, while the characteristic gill rakers of *Cetorhinus* were not recorded associated with teeth *Nanocetorhinus* gen. nov. Indeed, the simple crown and rather irregular root is reminiscent of that seen in many, unrelated, planktivorous chondrichthyans. The small size of these teeth, presence of a "collar" and frequent open base of the root may suggest that these are dermal denticles, and not oral teeth. Despite this, the irregular shape of the root with discrete root lobes and lack of a flat basal face are not seen in any denticles of extant chondrichthyans that have been figured or observed (CJU personal obserwations); and lack of denticles of this overall morphology amongst extant chondrichthyans all suggest that *Nanocetorhinus* does not represent denticles but represents oral teeth of an enigmatic taxon.

Nanocetorhinus tuberculatus sp. nov.

Fig. 9A–H.

2005 Elasmobranch dermal denticle or possible tooth, Form I, Johns et al. 2005: fig. 37.

Etymology: From the tuberculate surface ornament of the teeth.

Holotype: SNM Z 27485.

Type locality: Cerová-Lieskové, Vienna Basin, Slovakia.

Type horizon: Lakšárska Nová Ves Formation, late Karpatian (equivalent to latest Burdigalian).

Material.—28 additional partial and complete teeth including SNM Z 27486 to SNM Z 27492.

Diagnosis.—As for genus.

Description.—The teeth comprise a single cusp above a rather irregular root, with the cusp comprising at least half of the total tooth height. They are very small, typically less than 1 mm high, and more than twice as high as wide. There is low degree of heterodonty, other than a single symphyseal tooth (Fig. 9F) that is extremely mesio-distally compressed compared to the other teeth. The cusp is elongate and roughly circular in cross section, being straight or having a slight curvature. The base of the cusp is marked by a pronounced and slightly constricted "collar", the base of which expands slightly onto the upper surface of the root. Broken cusps reveal that no pulp cavity is present within the tooth crown. The labial face of the cusp is strongly ornamented with irregular tubercles, some of which are sharp-edged, which are on occasion connected to form irregular longitudinal ridges. The ornament extends from the top of the "collar" and reaches close to the cusp apex. The lingual face is smooth or ornamented by one to three weak longitudinal enameloid folds. The "collar" is constricted at the top where it joins the cusp, and rather flared at the base where it meets the root. There is a fine granulate ornament over the entire "collar". The root is wider than the cusp, and the cusp stands proud of the root labial surface. Although rather variable in form, the root is quite bulky and has two, variably well developed, root lobes that project basally. The root lobes are round or oval in cross section, and have pointed apices. The basal face of the root is typically at least partly open to reveal a pulp cavity within the root. In some specimens this is not the case, and the central part of a convex lingual root face is penetrated by several, rather irregular, foramina. Smaller foramina are present on the lingual face of the root lobes, and a weak groove may be present between these and the main opening. The symphyseal tooth is generally similar to the other teeth, especially in side view, but is very strongly compressed, resulting in the depth of the tooth being at least three times the width.

Remarks.—The teeth of this taxon have a very distinct morphology that is rather different from that of any other known chondrichthyan, so the affinity is uncertain. The morphology is simple, comprising a single cusp and rather irregular root, and is of a general type shared with many planktivorous sharks and rays. The teeth of juvenile specimens of *Cetorhinus* have a complex rugose ornament and irregular cutting edge, similar to that seen in *Nanocetorhinus tuberculatus* (see Herman et al. 1993), although most of this ornament is lost in the teeth of adults. Teeth of *Cetorhinus*, however, differ from those of *N. tuberculatus* in having a globular, anaulacorhize root and lacking a distinct collar at the base of the cusp, in addition to being far larger. Furthermore, symphyseal teeth are absent in lamniform sharks including *Cetorhinus*. As a result, the similarities between the teeth of *Cetorhinus* and *N. tuberculatus* are here considered to be superficial and not indicative of taxonomic affinity. Teeth of the some planktivorous batoids resemble those of *N. tuberculatus* (see Herman et al. 2000) in possessing an irregular reticulate ornament, but have a very different morphology to both the root and crown. In addition, there is some resemblance between teeth of *N. tuberculatus* and those of some Squaliformes. Teeth of *Aculeola nigra* de

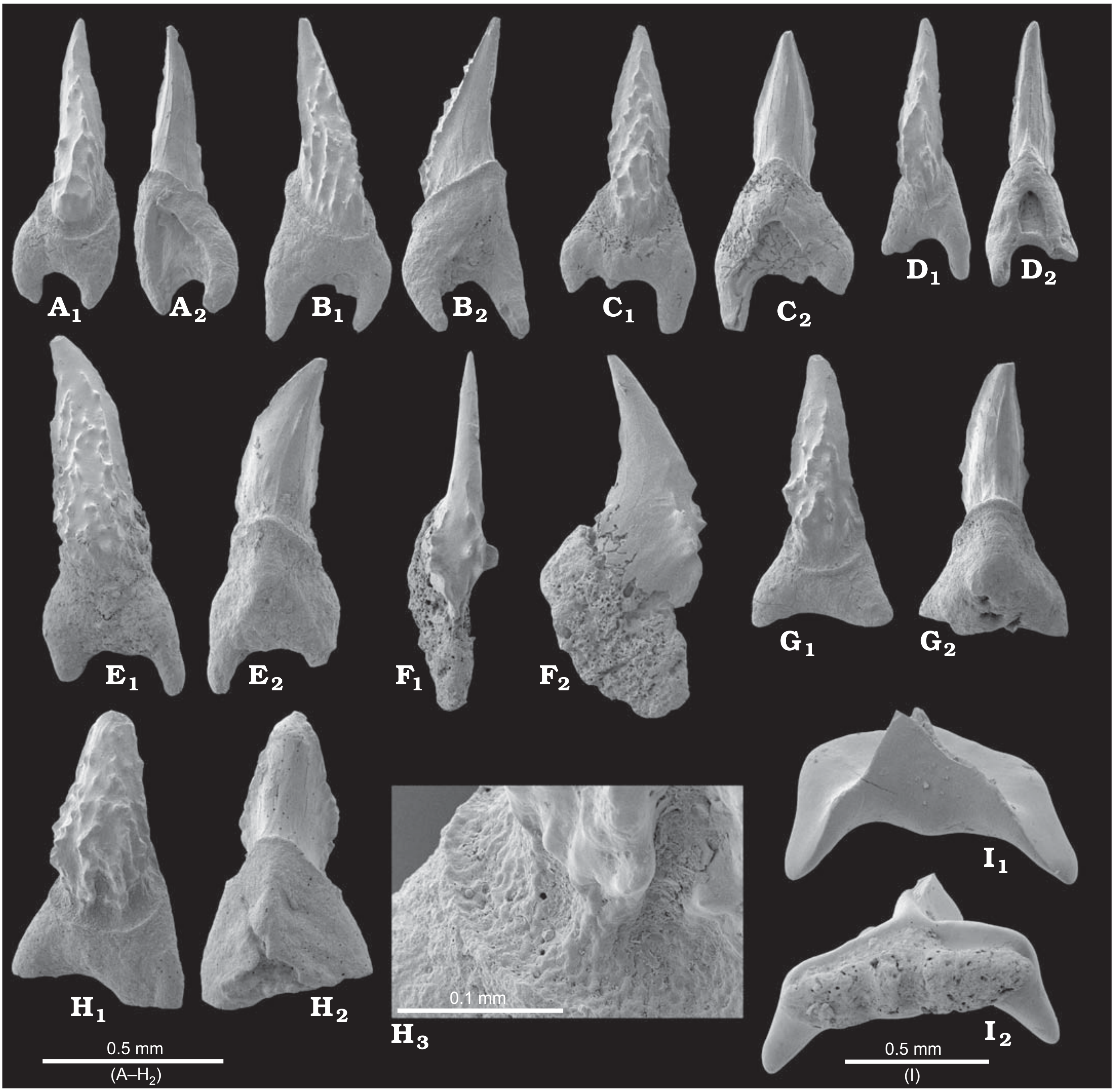

Fig. 9. Miocene neoselachian and myliobatiform sharks of *Nannocetorhinus* and *Gymnura* teeth respectively, from Cerová section in Malé Karpaty, Slovakia. **A**–**H**. *Nannocetorhinus tuberculatus* gen. et sp. nov. **A**. Holotype, SNM Z 27485, bed 21–22, in labial (A_1) and lingual (A_2) views. **B**. SNM Z 27486, bed 8–9, in labial (B_1) and lingual (B_2) views. **C**. SNM Z 27487, bed 17–18, in labial (C_1) and lingual (C_2) views. **D**. SNM Z 27488, bed 8–9, in labial (D_1) and lingual (D_2) views. **E**. SNM Z 27489, bed 13, in labial (E_1) and lingual (E_2) views. **F**. SNM Z 27490, bed 17–18, in labial (F_1) and lateral (F_2) views. **G**. SNM Z 27491, bed 20–21, in labial (G_1) and lingual (G_2) views. **H**. SNM Z 27492, bed 20–21, in labial (H_1) and lingual (H_2) views, detail (H_3). **I**. *Gymnura* sp., SNM Z 27484, bed 14, in occlusal (I_1) and basal (I_2) views.

Buen, 1959 also possess a single cusp with some ornamentation at its base and a bilobed root that commonly has a large basal opening (see Herman et al. 1989). Despite this, the crown and root of *A. nigra* and other similar squaliform teeth, are much more regular, and the roots have a well defined morphology with a flat basal face.

The simple and rather irregular form of the teeth of *Nanocetorhinus tuberculatus* is typical of the non-functional teeth of planktivorous taxa. In addition, there is no evidence for wear on the apex or cutting edges of the teeth, and the irregular ornament is inconsistent with the teeth having been used to penetrate food items. It is therefore probable that this taxon was a planktivore, or possibly microphageous suction feeder, where the teeth played little or no direct role in food

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manipulation. While the teeth of *N. tuberculatus* are very small, this is not necessarily indicative of a small body size, as teeth of planktivores do not scale with body size; Herman et al. (2000) figures teeth of a 4.8 m width *Manta* that are all below 1.5 mm in high. Johns et al. (2005) figure imperfect specimens of this taxon from the Late Oligocene or Early Miocene of western Canada. It is also present in Miocene of France (Sylvain Adnet, personal communication 2010).

Neoselachii incertae sedis: denticles

Denticle Type 1

Fig. 10A, B.

Material.—Frequent denticles including SNM Z 27493, SNM Z 27494.

Description.—Denticles of this type are somewhat rhomboid in form, but follow a similar basic morphology. The denticle crown is flat and thin and overlies narrow and short neck and root region; the neck and root are typically poorly preserved. The crown is biconvex and "lozenge-shaped" in surface view, with a number of sharp and continuous longitudinal ridges. In some denticles, there are small lateral points along the distal edge either side of the main central projection. The crown surface between the ridges is weakly concave. Typically three or six ridges are present, in the case of the latter these appear to be arranged in parallel pairs. At the anterior margin of the denticle crown, some of the ridges widen. Wear is not seen on the upper surface, although damage to the denticle edges may be present.

Remarks.—Denticles of this general morphology are not diagnostic to taxonomic group, and are present within many pelagic, and some benthic, shark taxa. The lack of wear due to contact with the substrate suggests that these denticles were not present on the underside of a benthic species.

Denticle Type 2

Fig. 10C–E.

Material.—Very common denticles including SNM Z 27495 to SNM Z 27497.

Description.—Denticles of this type are abundant and range in form from short and very robust to high and gracile, but intermediate forms are also present. In all cases there is a strong and continuous curvature of the crown neck and crown, with a flat surface of the crown being absent unless it has been formed by wear. The anterior part of the crown has four to seven (most commonly five) ridges that continue across the upper surface unless they are removed by wear. Where these reach the distal edge of the denticle, they form a variable pectinate edge. The stem and crown is typically completely covered by a fine reticulate ornamentation. This comprises irregular and anastomosing ridges, each with a weak anterior edge and sharp posterior edge. The stem is variably constricted, but is always robust, and expands basally into a rhombic root what is commonly of a similar width to the crown. Wear is commonly present and often severe, with the surface both polished and bearing abundant longitudinal scratches.

Remarks.—The degree of wear typically present on these denticles is indicative of abrasion by the substrate on the skin of a benthic taxon. It is unclear whether all denticles of this type relate to a single taxon, but the characteristic fine-scale ornamentation would suggest that this is likely. These denticles are very similar to those of some extant deep-water scyliorhinids, and it is therefore likely that these also relate to this group, and may be conspecific with the *Galeus* species recognized from dental remains.

Denticle Type 3

Fig. 10F.

Material.—Single denticle, SNM Z 27498.

Description.—The single denticle of this morphology is superficially like Type 2, but is far more robust, lacks a well defined neck and a fine surface ornament. The denticle is about as wide as long, and has a flat and smooth, roughly triangular, crown surface. Several short but strong ridges are present along the anterior edge of the crown. The neck is very short and only weakly constricted and originates from a root of similar overall dimensions to the crown.

Remarks.—The robust form of the denticle is similar to that of several groups of benthic chondrichthyans, and as a result the affinity is uncertain.

Denticle Type 4

Fig. 10G–H.

Material.—Rare denticles including SNM Z 27499, SNM Z 27500.

Description.—These uncommon denticles have a very characteristic "arrowhead" crown which is longer than wide and comprises a pointed distal apex which widens proximally into rounded "wings". Anterior to these is a roughly parallel-sided projection which forms about half of the length of the crown. A single or pair of very robust ridges run along the projection to close to the apex. There is a constricted and short neck over a wide root that is commonly roughly "T" shaped in basal view.

Remarks.—Denticles similar to this are present on the dorsal surfaces of a range of slow swimming chondrichthyans, including species of *Heterodontus*, *Squatina*, and some rhinobatid rays. As a result, the affinities of this denticle are uncertain.

Denticle Type 5

Fig. 10I.

Material.—Single denticle, SNM Z 27501.

Description.—This denticle is damaged, but the general morphology is clear. It is irregularly oval, with a rather conical root capped by a smaller crown, with no obvious constricted neck. The crown is irregular and has a number of short conical projections extending from its upper surface

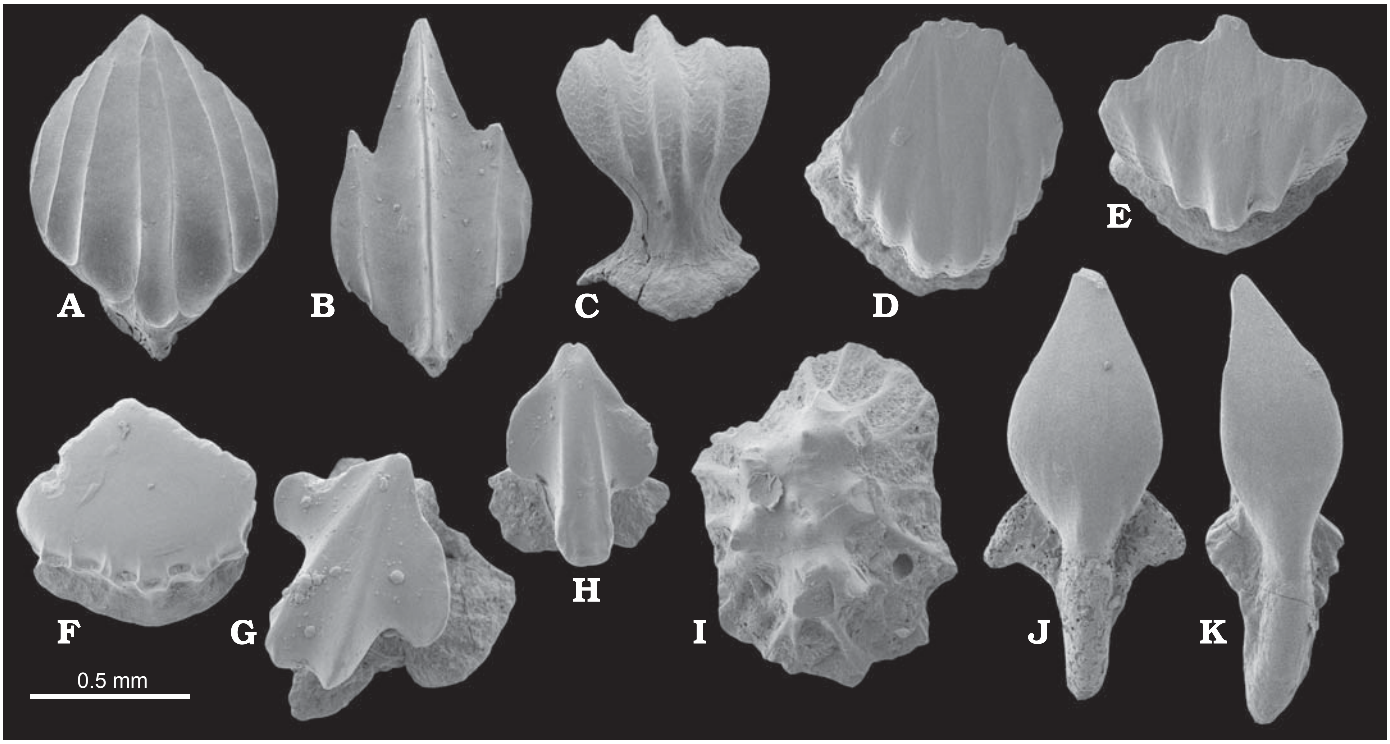

Fig. 10. Miocene neoselachian shark denticles from Cerová section in Malé Karpaty, Slovakia. All from bed 20–21 (except I, bed 17–18), all surface view. **A**, **B**. Denticle Type 1. **A**. SNM Z 27493. **B**. SNM Z 27494. **C**–**E**. Denticle Type 2. **C**. SNM Z 27495. **D**. SNM Z 27496. **E**. SNM Z 27497. **F**. Denticle Type 3. SNM Z 27498. **G**, **H**. Denticle Type 4. **G**. SNM Z 27499. **H**. SNM Z 27500. **I**. Denticle Type 5. SNM Z 27501. **J**, **K**. Denticle Type 6. **J**. SNM Z 27502. **K**. SNM Z 27503.

and edges. Below this, the sides of the root have a series of string vertical ridges, some bifurcating towards the base.

Remarks.—The overall form of this denticle is similar to that present on the dorsal surface of a number of batoid taxa, but the detailed form of the crown does not appear to closely resemble that of any examples that have been figured or observed by us so the generic affinity is unclear.

Denticle Type 6

Fig. 10J, K.

Material.—Frequent denticles including SNM Z 27502, SNM Z 27503.

Description.—These extremely characteristic denticles are quite abundant. They are far longer than wide and are symmetrical or slightly curved. The crown is slender and leaf-shaped, with a pointed apex. This has a smooth surface and lacks sharp edges. The crown is strongly displaced to the posterior relative to the root. The anterior end of the crown passes downwards into the short neck that forms a robust ridge on the anterior end of the root. The root is smaller than the crown and has an elongate rhombic profile.

Remarks.—This form of denticle does not appear to relate well to any figured or observed in modern chondrichthyans, and therefore is likely to belong to an extinct genus. The overall shape of the denticle is very similar to that of many extant etmopterids, but these all appear to differ in possessing a single or multiple sharp ridges along the length of the denticle and having as more star-shaped root. It is therefore likely that these specimens belong to an extinct etmopterid genus, with their relative abundance suggesting that one of the commoner tooth taxa would be likely. This denticle morphology is therefore tentatively considered as conspecific with *Paraetmopterus horvathi* sp. nov.

Palaeoecology

The chondrichthyan and associated faunas all suggest that deposition occurred within deep-water. Virtually all the taxa are related to forms that are either restricted to, or commonly present in, deep-water environments, and a depth of several hundred metres is likely. Squaliforms dominate both the numbers and diversity of the assemblage and contain members of all three of the families of strongly heterodont squaliforms that are today almost entirely limited to deep or open waters. *Squaliolus* and the closely related *Eosqualiolus* are both present, with the former being the dominant genus in this assemblage. While *Squaliolus* and related taxa are widely recorded and often common in deep-water assemblages in the Eocene (Adnet 2006) and Miocene (Casier 1958; Ledoux 1972; Underwood and Mitchell 2004; Takakuwa 2007; Vialle et al. 2011), they are relatively uncommon if widely distributed today (e.g., Seigel 1978). Extant *Squaliolus* are mesopelagic predators, feeding on teleosts and cephalopods, and show diurnal vertical migration between about 200 and 500 m depth (Seigel 1978). While *Etmopterus* is a relatively minor component of the assemblage, the extinct etmopterid *Paraetmopterus* is common. Living *Etmopterus* are nectobenthic in deep-waters, with most species occupying depths of between 200 and 800 m, although some species also venture into shallower or deeper-waters (e.g., Compagno et al. 2005). While species of *Pristiophorus* living in temperate waters are often found at shallow depths, tropical species are typically present at depths of 200 m or more. This association of *Pristiophorus* with other deep-water faunas is recorded in many fossil assemblages (e.g., Barthelt et al. 1991; Adnet 2006; Cappetta and Cavallo 2006; Marsili and Tabanelli 2007; Vialle et al. 2011) and it appears to have been a dominantly deep-water genus through the Cenozoic. While many scyliorhinids are present in deep-water environments, *Galeus* is a speciose and widespread deep-water genus in modern seas (e.g., Compagno et al. 2005) and is known from deep-water fossil assemblages (e.g., Cappetta 1987, Marsili 2007). Other sharks and rays are rare and there are no specimens of facultative shallow-water taxa, with *Gymnura* being highly active and will cross open water despite feeding largely in shallow water. Virtually all previous records of deep-water chondrichthyan assemblages from the Cenozoic have recorded specimens of *Isistius* and teeth from Centrophoridae and Hexanchidae, as well as pelagic lamniforms (e.g., Ledoux 1972; Adnet 2006; Vialle et al. 2011). While our collection mode may have excluded larger, but rare, teeth of hexanchids and lamniforms, their absence in extensive surface-collected samples of macrofossils must suggest they were essentially absent from the assemblage. The absence of *Isistius* and Centrophoridae must also be regarded as unusual, with the former sometimes being especially abundant in Miocene deep-water assemblages (e.g., Vialle et al. 2011).

Overall, the fauna described here is remarkable in the small adult size of almost all of the chondrichthyans. Comparison with extant relatives suggests that all the squaliform sharks are likely to have had an adult size of less than 0.4 m, with many probably half that length. It is possible that the fauna was composed of taxa specialized for conditions where either oxygen or nutrients were very limited. Low nutrient levels would explain the absence of larger sharks and taxa with a high metabolic rate, while the absence of larger host organisms would explain the absence of the parasitic shark *Isistius*.

Despite the small number of Miocene deep-water chondrichthyan assemblages known, it is evident than some species had extremely wide distributions. *Paraetmopterus horvathi* sp. nov. is present, if previously unrecognised, from Germany (Barthelt et al. 1991) and Japan (Takakuwa 2006), while *Squaliolus schaubi* (Casier 1958) is known from the tropical West Atlantic (Casier 1958; Underwood and Mitchell 2004) as well as Europe. The enigmatic *Nanocetorhinus tuberculatus* gen. et sp. nov. is recorded from the Canadian Pacific (Johns et al. 2005) and is present in the Miocene of France (Sylvain Adnet, personal communication 2010).

Palaeoecological conditions based on associated benthic micro and macrofossil groups also suggest rather deep and poorly oxygenated water. Palaeodepths were estimated following the two-step equations for benthic foraminifera (Hohenegger 2005). Analyses (evaluated for sample interval 14 to 20) suggest water depths of 240–330 m with extreme values ranging from 149 to 498 m. Based on Murray plots (1973, 1991), most of the shelf and deep-sea foraminiferan assemblages have Fisher α diversity values ranging from 5 to 15, and Shannon H values from 1.5 to 3.5. Evaluated samples show Fisher α values ranging from 5.5 to 8 and Shannon H values from 1.9 to 2.6. A ternary plot for representation of wall type structures confirms that the assemblages characterize shelf and deep marine environments (for details see Schlögl et al. 2011). A deep-water environment (around 300 m) for similar foraminiferan associations was proposed by Spezzaferi et al. (2002) for the Styrian Basin.

Among associated molluscs, more than 85% of the benthic gastropods are carnivores, scavengers or parasites (Harzhauser et al. 2011). In total numbers, the carnivorous tonnoideans, naticids, and conaceans predominate along with nassariids, which are scavengers and/or predators. Herbivores are extremely rare. Among the bivalves, two carnivores, four chemosymbionts, four detritivores and four suspension feeders are represented. Such a composition indicates deposition in the aphytal zone and a low contribution by transported taxa from shallower settings (Schlögl et al. 2011). An ecologically highly significant taxon is the scaphopod *Gadilina taurogracilis*. Its descendent *Gadilina triquetra* (Brocchi, 1814) is widespread in Pliocene deposits of Italy where, according to Ceregato et al. (2007), it is strictly bathyal and indicative of unstable deep marine environments. The crustacean assemblage is predominantly composed of deep-water genera such as *Callianopsis*, *Agononida*, *Munidopsis*, and *Mursia* (Hyžný and Schlögl 2011).

Benthic foraminiferal assemblages are dominated by infauna to deep infauna composed mainly of dysoxic–suboxic index species. Only some samples contain oxyphilic genera. Analysed samples of the studied interval (samples 14–20) yield BFOI (benthic foraminiferal oxygen indices; Kaiho 1994, 1999) values corresponding to dysoxic or low oxic conditions (Schlögl et al. 2011). This is consistent with the shark fauna in suggesting that a restricted and low oxygen palaeoenvironment was present.

While squaliform sharks have been abundant and diverse in many deep-water environments from the Cretaceous to the present (e.g., Klug and Kriwet 2010; Straube et al. 2010) their fossil record is highly biased by the rarity of suitable deep-water facies for their collection and to some extent their small size and fragility. While diverse faunas of fossil squaliforms are known from the Cretaceous (Müller 1989; Siverson 1993), Eocene (Adnet 2006), Miocene (Ledoux 1972) and Pliocene (e.g., Cigala Fulgosi 1996; Marsili and Tabanelli 2007), many records come from small and incompletely described faunas or as rare specimens within shelf assemblages. As a result, while very diverse squaliform faunas appear to have been present in deep-seas throughout the Cenozoic, knowledge of them is generally poor. While many extant squaliform genera are present in the Eocene (Adnet 2006), there are also several genera present in the Eocene that are now extinct. The Miocene fauna described here contains three extinct genera that are known from the Eocene, whereas there is only one possible example of an extant genus that is known from the Miocene but not the Eocene (*Miroscyllium*). It therefore appears that the loss of squaliform diversity since the Miocene, in the Tethyan region at least, may have exceeded the origination of new genera since the Eocene. The timing of this diversity loss suggests that it postdates the initiation of Antarctic glaciation in the Oligocene, but may coincide with the onset of extensive Arctic glaciations during the late Neogene and/or the dramatic changes to the seas of the Mediterranean region in the late Miocene. Unfortunately, little is known of Cenozoic squaliform diversities outside southern Europe and so it is unclear if these changes are regional or global.

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