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RESEARCH PAPER

Bathyal sponges from the late Early Miocene of the Vienna Basin (central Paratethys, Slovakia)

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Abstract Here we report, for the first time, a very rich and diversified sponge assemblage from late Early Miocene deposits of a central part of the Vienna Basin (Paratethys) in Slovakia. Bodily preserved sponges are described as a new genus and species *Paracinachyrella fossilis* (Tetiliidae, Demospongiae). Dissociated spicules reveal the presence of the "soft" demosponges that belong to families Tetillidae, Theneidae, Geodiidae, Samidae, Thrombidae, Thoosidae, Agelasidae, Myxillidae, Bubaridae, and Tedaniidae, the lithistid family Pleromidae, and an undetermined rhizoclone-bearing lithistid. Fragments of dictyonal skeleton indicate the presence of hexactinellid sponges that belong to the families Farreidae and Euretidae, and lychniscosan sponges. We estimate that at least 16–19 different species of siliceous sponges inhabited this region of the Central Paratethys during the latest Burdigalian. Most of these sponges are reported for the first time from the Miocene of the Paratethys. This sponge fauna has clear Tethyan affinities and indicates the existence of connection between Paratethys and Tethys during the latest Burdigalian, as well as the presence of open marine, deep-water, bathyal conditions in this part of the Vienna Basin.

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Keywords Porifera · Spicules · Demospongiae · Lithistida · Hexactinellida · Burdigalian · New species

Kurzfassung Wir beschreiben eine neue, sehr reiche und diverse Schwamm-Assoziation aus Ablagerungen des späten Unter-Miozän des zentralen Teils des Wiener Beckens (Paratethys) in der Slowakei. Körperlich Schwämme werden als neue Gattung und Art Paracinachyrella fossilis (Tetiliidae, Demospongiae) beschrieben. Disassoziierte Nadeln belegen die Anwesenheit von "weichen" bzw. skelettlosen Demospongiern, die zu den Familien Tetillidae, Theneidae, Geodiidae, Samidae, Thrombidae, Thoosidae, Agelasidae, Myxillidae, Bubaridae und Tedaniidae sowie zu den lithistiden Familien Pleromidae und einem unbestimmten Rhizoclon-tragenden Lithistiden gehören. Bruchstücke dictyonaler Skelette sprechen für die Anwesenheit hexactinellider Schwämme, die zur Familie Euretidae und lychniscosen Schwämmen gehören. Wir schätzen, dass mindestens 16-19 verschiedene Arten von kieseligen Schwämmen diese Region der zentralen Paratethys während des jüngsten Burdigal besiedelten. Die meisten dieser Schwämme werden zum ersten Mal aus dem Miozän der Paratethys beschrieben. Diese Schwamm-Fauna zeigt klare Affinitäten und spricht für eine offene Verbindung zwischen Paratethys und Tethys während des jüngsten Burdigal und impliziert, dass offen marine, tiefe, bathyale Bedingungen in diesem Teil des Wiener Beckens vorherrschten.

Schlüsselwörter Porifera · Spiculae · Demospongiae · Lithistida · Hexactinellida · Burdigal · neue Art

Introduction

Sponges are rarely reported from the Miocene of the Paratethys, and usually only as loose (dissociated) spicules (Alexandrowicz and Tomaś 1975; Alexandrowicz 1978; Riha 1982, 1983; Hurcewicz 1991; Pisera and Hladilová 2003). This rarity is not real but caused rather by lack of studies and nonpreservation (in shallow-water carbonate deposits). Here we report a rich assemblage of siliceous sponges from the Lower Miocene deposits of the Slovakian sector of the Vienna Basin. The material is mainly composed of dissociated spicules, but several completely preserved specimens have also been found, allowing for precise determination and description. The fauna of sponges described here is the first from the Miocene of the Paratethys which is so well preserved and diversified, allowing for ecological and biogeographical interpretations.

Geographical and geological setting

Sponges and rock samples for micropaleontological studies were collected at the Cerová–Lieskové locality in the western part of the Slovak Republic. The outcrop is situated at the foothills of the Malé Karpaty Mountains forming the actual eastern margin of the central Vienna Basin (Fig. 1). During the Miocene, this basin was part of the Central Paratethys Sea. Upper Burdigalian ("Karpatian" in the Paratethys scale) sediments, assigned to the Lakšárska Nová Ves Formation (Špička and Zapletalová 1964), are well exposed in a former clay pit, represented by massive, locally laminated, calcareous clays and clayey silts with thin tempestite intercalations (up to 10 mm thick) and several thin sandstone/siltstone layers. The studied section is more than 15 m thick. Macrofossil assemblages comprise vertebrates, mainly teleosts, and a wide spectrum of invertebrates—bivalves, gastropods, scaphopods

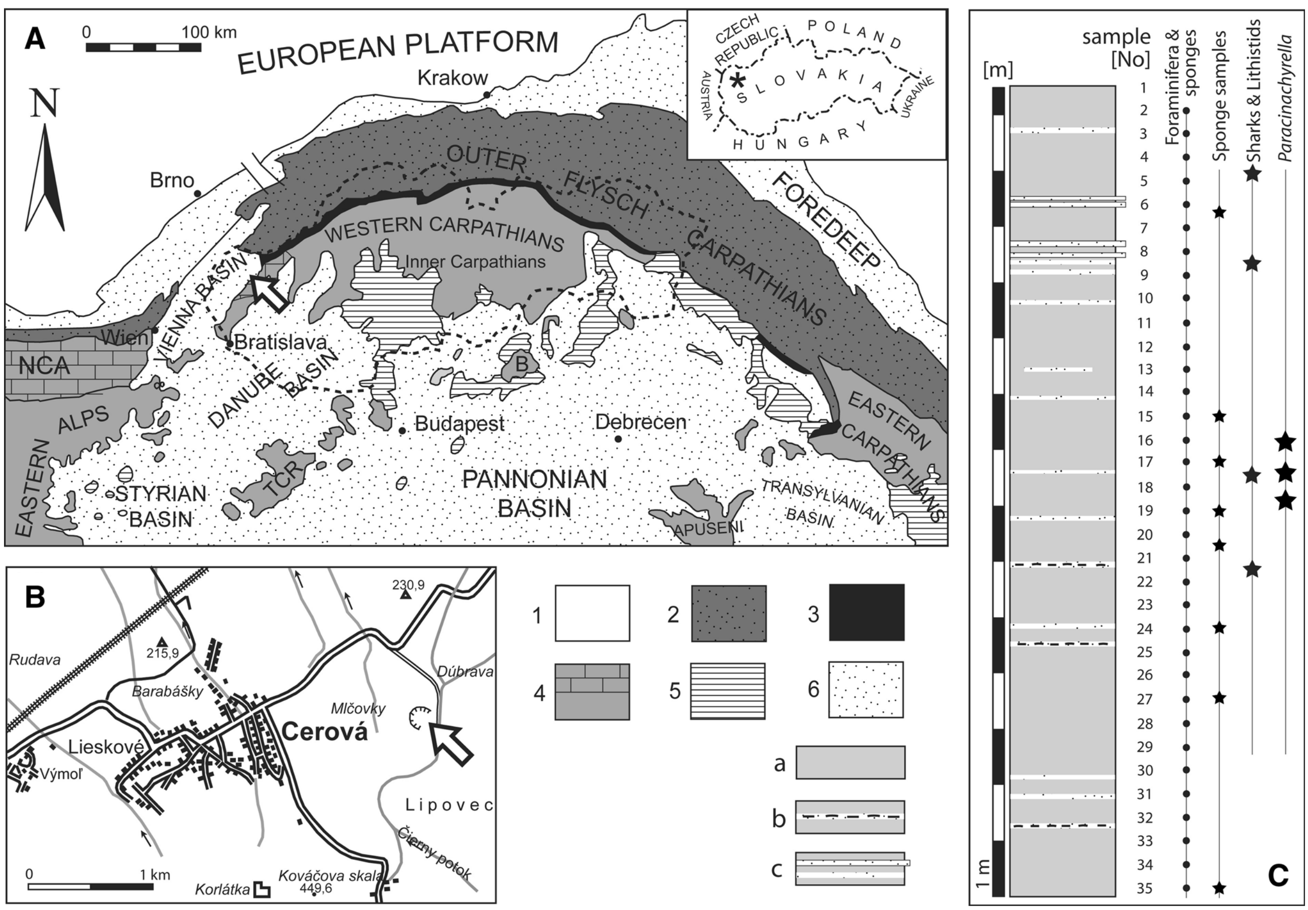

Fig. 1 *A* Position of the Vienna Basin in the Carpathian–Pannonian system. *B* Location of the Cerová–Lieskové clay pit, indicated by *arrow*: *1* European platform units. *2* Carpathian–Alpine externides. *3* Pieniny Klippen Belt. *4* Alpian–Carpathian–Dinaride and Pannonian internides. *5* Neogene volcanics. *6* Neogene basins. *B* Bükk, *NCA* Northern Calcareous Alps, *TCR* Transdanubian Central Range. *C* Simplified section through the Cerová–Lieskové clay pit. *a* Massive calcareous clay. *b* Thin tempestite layers with plant debris. *c* Thin siltstone/sandstone layers or silt lenses. *Small circles* indicate presence of sponge spicules within the samples taken for foraminiferal analyses. *Small asterisks* localize samples taken for sponge assemblages (400–1,000 g), *medium asterisk* presence of lithistid sponges in "shark samples" (more than 30 kg), *large asterisks* articulated *Paracinachyrella* specimens (map and section based on Schlögl et al. 2011, modified)

(Harzhauser et al. 2011), cephalopods (Schlögl et al. 2011a), decapods (Hyžný and Schlögl 2011), isopods (Hyžný et al. 2013), barnacles (Harzhauser and Schlögl 2012), regular and irregular echinoids, asteroids, ophiuroids, siliceous sponges, and solitary corals. Microfossil suites include benthic and planktonic foraminifera, radiolarians, sponge spicules, ostracods, crinoid ossicles, coleoid statoliths, fish otoliths, shark teeth (Underwood and Schlögl, in press), and extremely abundant diatoms.

Age assignment of these deposits relies on the co-occurrence of the foraminifera *Uvigerina graciliformis* Papp and Turnovsky, 1953 and *Globigerinoides bisphericus* Todd *in* Todd, Cloud, Low and Schmidt, 1954 and the absence of the genus *Praeorbulina* Olsson, 1964. The first appearance datum of *U. 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 beginning of the Middle Miocene. 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).

Materials and methods

Most of the sponges investigated here are represented by loose spicules only, but several specimens (at least one demosponge species) are preserved intact but flattened. After being photographed, a small part of the specimens was treated in HCl to obtain clean spicules for study under scanning electron microscopy (SEM, Institute of Paleobiology). To search for microscleres, the surface of the specimens was scratched with a brush, and the material was deposited directly on a SEM stub for further investigation.

Dissociated spicules occurring in the sediment were obtained from samples containing 400–1,000 g of sediment. Each sample was dissolved in a 10 % solution of hydrochloric acid, with the residue subsequently dried. In the next step, the residue was treated with hydrogen peroxide, washed through 0.063-mm mesh, and dried. This part of the process was repeated several times. Finally, the residuum was cleaned in an ultrasonic bath. As a result of this method, each sample could be reduced to 0.15–0.2 % of its original weight. Such residue was screened under a binocular microscope, and all the morphological types of spicules collected were subsequently attached to a stub and investigated by SEM.

All the investigated material is stored in the Slovak National Museum in Bratislava, acronym SNM Z.

Systematic paleontology

Both hexactinellid and demosponge spicules were common in the investigated residue, but demosponges dominated and were more diversified. Apart from dissociated spicules, several completely preserved demosponge specimens were also collected, and some of them could be confidently determined. These are formally described below, followed by a taxonomic interpretation of loose spicules.

Phylum Porifera Grant, 1836
Class Demospongiae Sollas, 1885
Order Spirophorida Bergquist and Hogg, 1969
Family Tetillidae Sollas, 1886
Genus *Paracinachyrella* gen. nov.

Derivation of the name: referring to the affinity to the Recent genus *Cinachyrella* Wilson, 1925

Diagnosis: tetillid sponges with protriaenes, anatriaenes, and strongyloxeas as megascleres and raphides as microscleres

Paracinachyrella fossilis sp. nov. (Fig. 2)

Derivation of the name: referring to the fact that it is a fossil sponge

Holotype: specimen SNM Z21 here illustrated (Fig. 2A, C)

Type locality and horizon: Cerová-Lieskové section (Slovakian part of the Vienna Basin, central Paratethys), Karpatian (late Early Miocene), layer 16

Material: two specimens and several fragments, all flattened and/or cross-sections with spicules preserved in original radial arrangement (layers 16–19)

Diagnosis: as for the genus

Description: Sponge with globular/ovoid morphology (about 5 cm × 3 cm) of the body and radially arranged spicules (Fig. 2A). The megascleres are protriaenes, anatriaenes (always broken), and long oxeas with one end blunt (strongyloxeas) that are 550 μm (Fig. 2B–D) radiating outwards from the center of the sponge, the triaenes with long and slender rhabdom (always broken) and cladi of about 150 μm in diameter. Microsclere spicules are bundles of small, slender raphides (trichodragmas) up to 80 μm. Apart from these typical tetillid spicules, we found fusiform oxeas that may or not belong to this sponge.

Remarks: This very well-preserved, articulated, flattened sponge body possessing such a set of spicules (raphid microscleres and triaene megascleres), as well as the ovoid morphology and radial arrangement of spicules, allow us to assign the studied sponges to the family Tetillidae Sollas, 1886. The presence of ana-, protriaenes, and strongyloxeas, as well as raphides as microscleres, suggests close affinity

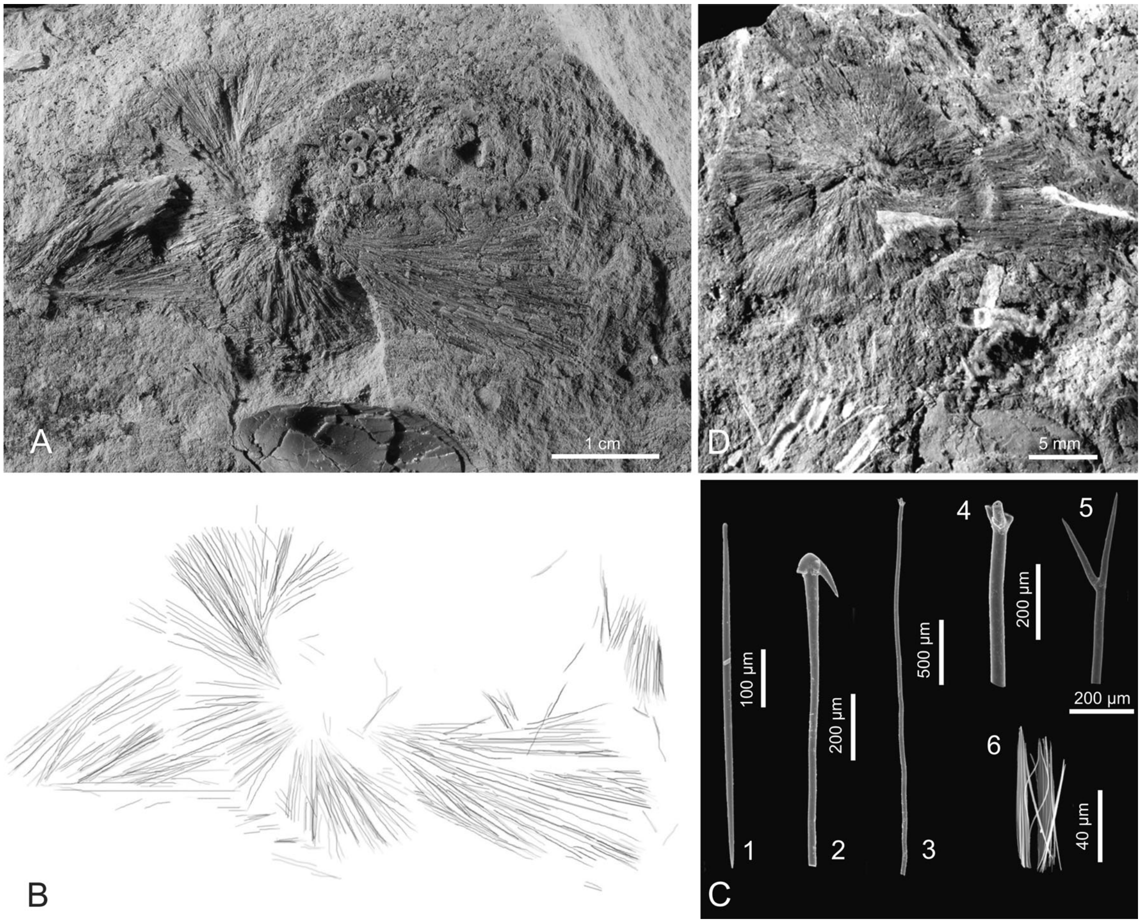

Fig. 2 *Paracinachyrella fossilis* gen. et sp. nov. *A* Articulated sponge body, holotype specimen SNM Z21. *B* Diagram of arrangement of spicules in the holotype. *C* Spiculation of the holotype: *C1*, strongyloxea; *C2*, anatriaenes; *C3–C5*, protriaenes; *C6*, raphides (trichodragmas) microscleres; *D* Articulated sponge body, specimen SNM Z22

with the genus *Cinachyrella* Wilson, 1925. We also noted numerous sigma microscleres, but they must clearly be a contamination. The thick, fusiform oxeas may also be a contamination or belong to a specialized cortical zone known in *Cinachyrella*, but we were unable to prove this. Only the lack of oxeas and sigmaspires (that may be simply not found) differentiate the studied sponge from the genus *Cinachyrella*. Taking into consideration these differences in spiculation, as well as the Miocene age of the studied material, we decided to propose a new genus and species for the studied sponges. Earlier, the first fossil representatives of Tetillidae were reported by Schrammen (1910) from the Upper Cretaceous of Germany. He described a new genus *Tetilliopsis* (with two new species) that are spherical sponges with a radial arrangement of long oxeas and protriaenes, but without observed microscleres.

Dissociated demosponge spicules

Loose nonlithistid demosponge spicules were moderately frequent, constituting about half of the investigated sponge spicules in the studied assemblage. They occurred in all studied samples. The spicules produced by Demospongiae are characterized by monaxial and/or tetraxial symmetry (Hooper and Soest 2002).

The most abundant spicule types were monaxons, including oxeas and styles (Fig. 3A–E), but simple triaenes (Fig. 3F, G) were also frequent. Unfortunately, precise taxonomic assignment of these morphologically simple spicules is difficult or even impossible because they can appear in many different demosponge groups. Such spicules, with low diagnostic value, are here only illustrated but without precise taxonomic assignment.

This is also the case of the spheraster (Fig. 3L–N, R) and triods (Fig. 3H, I), because they can appear in a wide array of demosponges. Sigma microscleres (Fig. 3P, Q) may belong to many distinct taxa within the Poecilosclerida, and the short-shafted dichotriaenes (Fig. 3K) belong, most probably, to the order Astrophorida. The calthrops (Fig. 3O) may belong to the Calthropellidae Lendenfeld, 1907 but also appear in other taxa, e.g., Pachastrellidae Carter, 1875. Anthasters (Fig. 3S, T) appear, e.g., in the

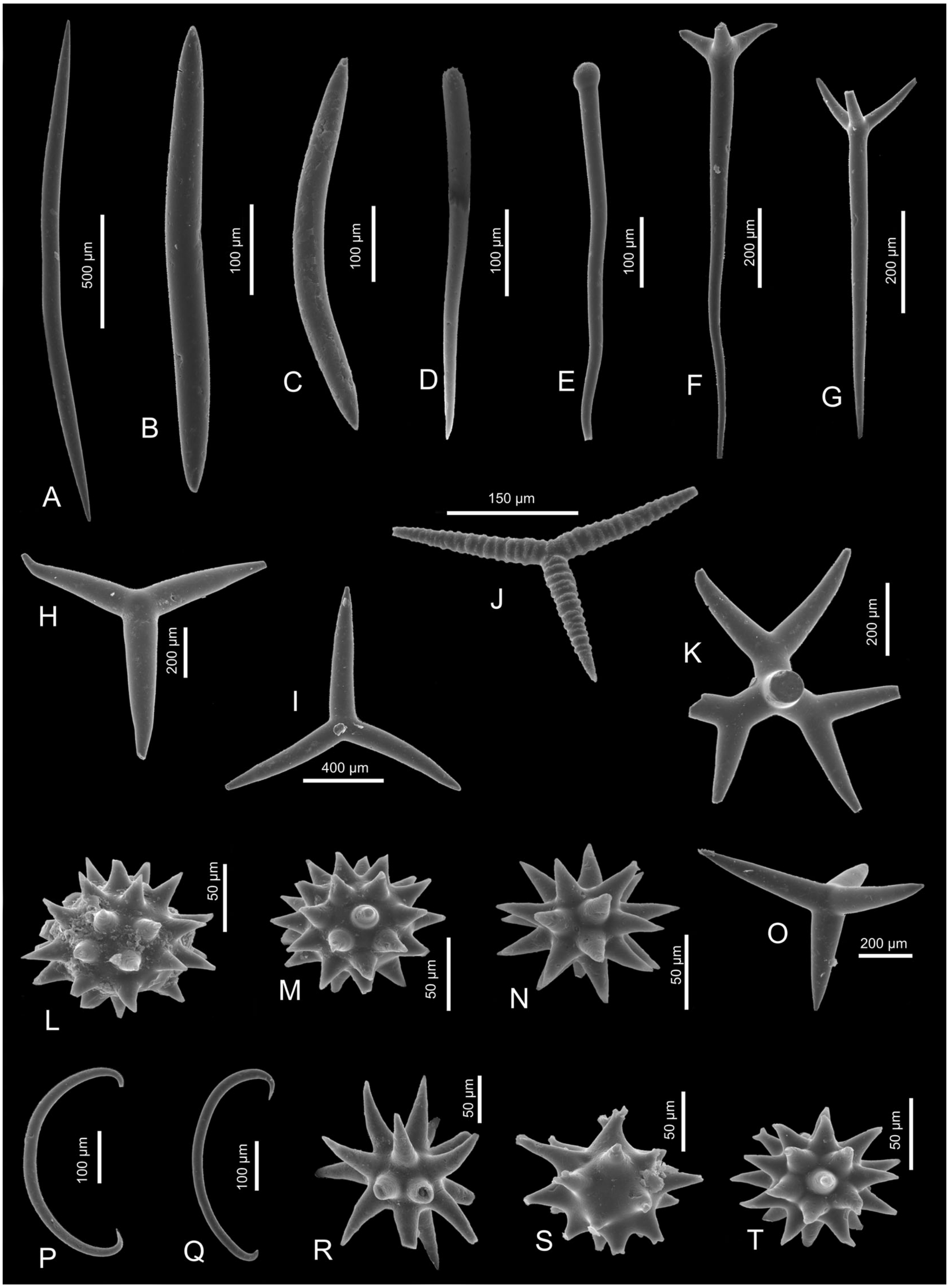

Fig. 3 Loose demosponge spicules: *A–C* different types of oxeas; *D*, *E* styles; *F*, *G* triaenes; *H*, *I* triods; *J* cricotriod of *Annulastrella* Sollas, 1886; *K* dichotriaene; *L–N*, *R* spheraster; *O* calthrop; *P*, *Q* microsclere sigmas; *S*, *T* anthasters

Hadromerida. On the other hand, there are also some very characteristic morphological types of spicules in the studied material that allow assignation to a particular taxon, and these are discussed below.

Theneids

The triactinal, annulate spicules (cricotriods) closely resemble those of astrophorid *Annulastrella* Sollas, 1886

(Fig. 3J) (Theneidae Carter, 1883). The spicule is particularly similar to those of *Annulastrella ornata* (Sollas, 1888) (previously described as *Vulcanella*). Today, this species is noted from eastern Atlantic waters (the Azores and Cape Verde) (Boury-Esnault 2012). Similar fossil spicules were already described from the Miocene of Bahamas by Bukry (1978, pl. 13, figs. 17, 20). There are also some Triassic and Cretaceous spicules (annulate microxeas and plesiasters) of *Monilites* Carter, 1871b (family unknown) that resemble *Vulcanella* spicules (see Wiedenmayer 1994).

Tetillids

In the studied samples, apart from wholly preserved sponges belonging to Tetillidae, described above, there were also loose spicules that may be assigned to tetillids. These are numerous anatriaenes with cladome up to 100 µm in diameter (Fig. 4A–C), and slender protriaenes with cladome up to 200–300 µm long (Fig. 4D, E) closely resembling those of Recent tetillids. Also sigmaspire microscleres (up to 400 µm) (Fig. 4G, H) were found, but they may belong to other sponges. There were also some heavily spined, about 300-µm-long, oxeas called acanthoxeas (Fig. 4F), which resemble those of the genus *Acanthotetilla* Burton, 1959, but similar forms may occur also in the poecilosclerid *Histodermella* Lundbeck, 1910 (family Coelosphaeridae Dendy, 1922). Today, tetillids are cosmopolitan in all oceans and all depths (Hooper and Soest 2002). Spicules that may be undoubtedly assigned to tetillids are known since the Cretaceous (Wiedenmayer 1994).

Geodiids

Ovoid spicules called sterrasters, with numerous fused rays, their endings with the characteristic stellate terminations (Fig. 4M, N, Q), also appeared in the studied material. These spherical microscleres were over 100 µm in size. Additionally, the studied sample contained triaenes up to about 900 µm long (Fig. 4K, L), and various spherasters up to 100 µm in diameter (Fig. 4I, J). Such a set of spicules is characteristic for the astrophorid family Geodiidae, Gray 1867. Additionally, some astrose spicules (130–150 µm in diameter) (Fig. 4O, P) were found that also belong to the order Astrophorida. Sponges belonging to the Geodiidae bear also various styles, but if isolated, they are not characteristic enough to be assigned as geodiid's. Unfortunately, in this case, more precise taxonomic assignment of all the above geodiid spicules to a particular lower taxon is not possible due to the fact that present-day taxonomy of this family is based not only on spicule morphology but also on the disposition of spicules in the sponge body (Uriz 2002a). Today, geodiid sponges occur worldwide and inhabit a wide bathymetric range, from very shallow to bathyal depths. They live on soft bottoms, as well as in caves and overhangs in the sublittoral zone (Uriz 2002a). Undoubted geodiid sterrasters are common in the fossil record since the Cretaceous (Wiedenmayer 1994). Bodily preserved specimens of *Geodia* were described by Finks et al. (2011) from the Eocene of North Carolina, USA.

Samids

Numerous amphitriaenes–double triaenes with short rhabds bearing two opposed cladomes (Fig. 5A–D)–were also found among the Slovakian spicules. These spicules are over 200 µm in largest dimensions, and closely resemble those of the cosmopolitan, excavating, Holocene samid species *Samus anonymus* Gray, 1867 (Sollas 1888). Today, sponges of this monotypic spirophorid taxon are reported from submarine caves at shallow depths, and excavate limestone substrates, from many parts of the world (for more details see Hooper and Soest 2002). They have been noted recently in the Miocene of Portugal (Pisera et al. 2006), but are known at least since the Eocene (Wiedenmayer 1994).

Thrombids

The astrophorid family Thrombidae Sollas, 1888 includes only two genera and six species (Uriz 2002b; Gomez 2006). They are characterized by having spiny trichotriaenes with dimensions intermediate between those of megascleres and microscleres, often with clads divided dichotomously or trichotomously, and streptaster microscleres that are not always present (Uriz 2002b). Only acanthotrichotriaenes (Fig. 5E, F) were found in our material, with cladomes up to 80–100 µm in diameter, that closely resemble those of the Recent species *Thrombus abyssi* Carter, 1873. No streptaster microscleres were found among the Slovakian spicules. Today, thrombids inhabit a wide range of depths but are mostly found in the bathyal zone of the Atlantic, Mediterranean, and Pacific (Hooper and Soest 2002), while the species *T. abyssi* inhabits the Atlantic and Indo-Pacific Oceans (Uriz 2002b). The oldest fossil occurrence of the genus is from the Late Eocene of New Zealand by Hinde and Holmes (1892), who described such spicules without any taxonomical attribution.

Thoosids

Thoosidae Cockerell, 1925 is characterized by the presence of oxeas, styles, or strongyles as megascleres, and microrhabds and/or amphiasters, or both, as microscleres (Rützler 2002). In the studied sample, there were rare,

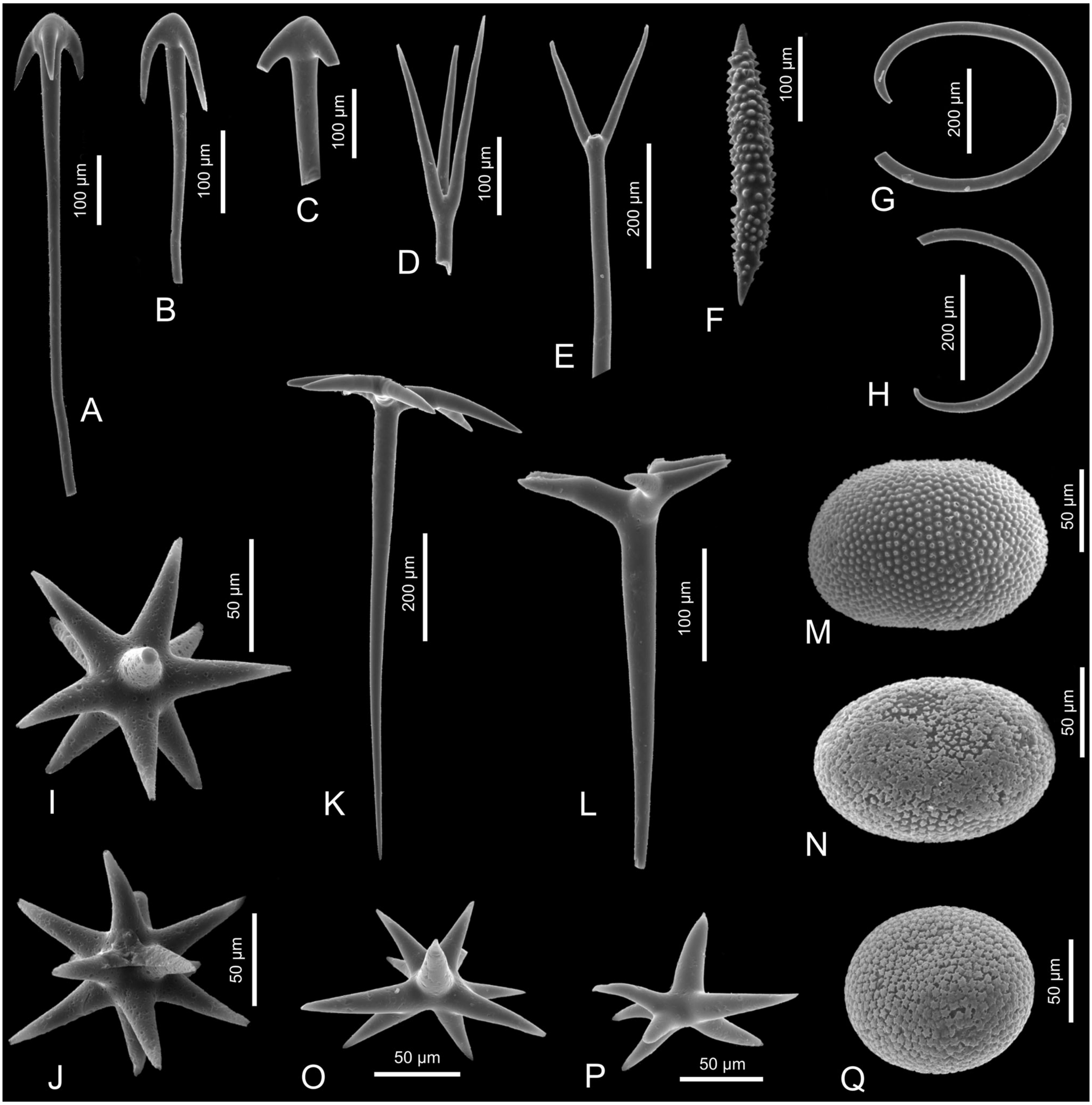

Fig. 4 Loose demosponge spicules: *A–C* anatriaenes of the spirophorid family Tetillidae; *D*, *E* protriaenes of the spirophorid family Tetillidae; *F* acanthoxea of the spirophorid *Acanthotetilla* Burton, 1959 (family Tetillidae) or poecilosclerid *Histodermella* Lundbeck, 1910 (family Coelosphaeridae); *G*, *H* sigma microscleres, probably of the spirophorid family Tetillidae; *I*, *J*, *O*, *P* oxyasters of the family Geodiidae (order Astrophorida); *K*, *L* triaenes of the family Geodiidae (order Astrophorida); *M*, *N*, *Q* sterraster microscleres of the family Geodiidae (order Astrophorida)

tuberculated, about 500-µm-long oxeas (Fig. 5G) that closely resemble those of Recent species *Alectona wallichii* Carter, 1874. Sponges belonging to this species are rare and rather small, and live cryptically inside calcareous substrates (Rützler 2002). They were noted from Hawaii (Vacelet 1999) and southern coasts of the African Continent (Van Soest et al. 2012). The spicules are almost identical to those described from the Recent by Vacelet (1999). Pisera et al. (2006) described identical spicules from Miocene deposits of Portugal and assigned them also to *A. wallichii*. A situation such as that described, where there is a worldwide distribution of a species today, with apparent long geological history, suggests that we are dealing with a species complex.

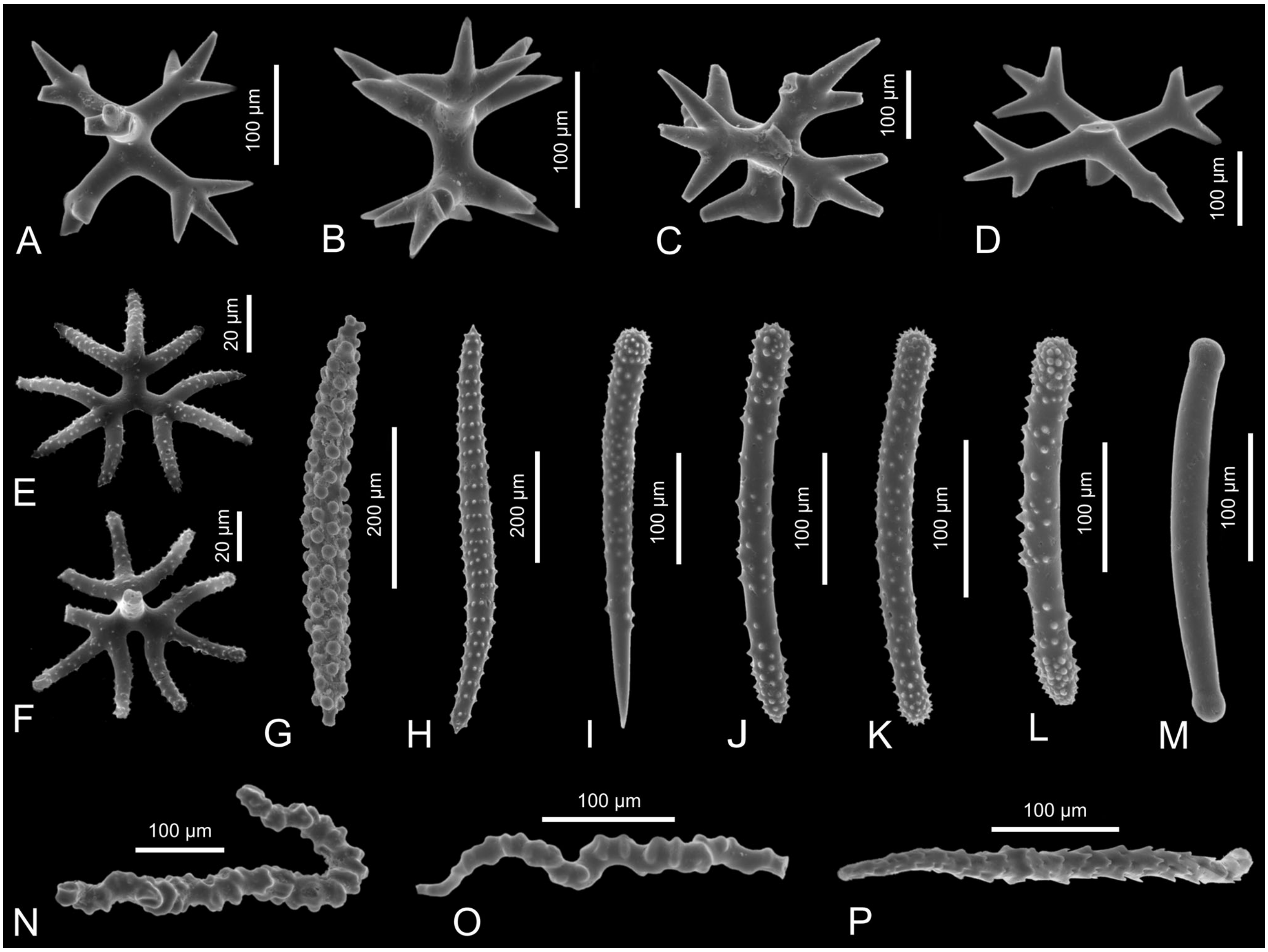

Fig. 5 Other demosponge spicules: *A–D* amphitriaenes of *Samus* cf. *anonymus* Gray, 1867, family Samidae (order Spirophorida); *E*, *F* acanthotrichotriaenes of *Thrombus* Sollas, 1886, family Thrombidae (order Astrophorida); *G* tuberculated oxea of *Alectona* Carter, 1879, family Thoosidae (order Astrophorida); *H* verticillate oxea of *Agelas* Duchassaing and Michelotti, 1864, family Agelasidae (order Agelasida); *I–K* acanthostyles (*I*, *J*) and acanthostrongyle (*K*) of *Ectyonopsis* Carter, 1883, family Myxillidae (order Poecilosclerida); *L* acanthostrongyle of *Ectyonopsis* Carter, 1883, family Myxillidae (order Poecilosclerida); *M* tylote of the family Tedaniidae (order Poecilosclerida); *N*, *O* tuberculated monaxons of *Monocrepidium* Topsent, 1898, family Bubaridae (order Halichondrida); *P* diactine (broken) ?hexactinellid (Amphidiscosida) spicule

Agelasids

Other soft demosponge spicules that occurred sporadically in the studied material belong to the family Agelasidae Verrill, 1907. Although the most common morphotype in this family are acanthostyles, in some species there are verticillate oxeas present (Fig. 5H) with concentric whorls of the tubercles, like those of Recent *Agelas axifera* Hentschel, 1911. So far, agelasids have been described from tropical Atlantic and Indo-West Pacific waters, with a single Australian and a single Mediterranean species, with the deepest occurrence at 150 m (Van Soest 2002a). Agelasid spicules are known since the Cretaceous (Wiedenmayer 1994).

Myxyllids

The family Myxillidae Dendy, 1922 was represented among the studied spicules by rare acanthostyles and acanthostrongyles. Both the acanthostrongyles and acanthostyles possess echinated surface, becoming more densely sculptured at the ends of the spicule (Fig. 5I–L). These spicules with mucronate ends are identical to those of Recent myxillid *Ectyonopsis* Carter 1883. Today, this genus is reported from rather shallow, temperate and cold waters (Van Soest 2002b) from the Southern Ocean (Van Soest et al. 2012), with one exception only. Similar spicules were described by Schrammen (1924) from the Cretaceous of Germany, and Mostler (1990) from the Jurassic of Austrian Alps.

Bubarids

Other "soft" demosponge spicules found in the studied material were rare tuberculated, meandering, diactinal spicules (monaxons) of 300 µm in length (Fig. 5N, O). They are almost identical to those of the halichondrid family Bubaridae Topsent, 1894. Despite the fact that there were no other spicules characteristic of bubarids noted (such as long, smooth, slightly curved styles and/or slightly curved subtylostyles or tylostyles), the presence of these tuberculated diactinal spicules clearly indicates the presence of the genus *Monocrepidium* Topsent, 1898 in the studied material. Most genera of these encrusting sponges with hispid surface are found today in the east Atlantic, Mediterranean, and Indian Ocean, and are restricted to rather deep waters (Alvarez and Soest 2002). Spicules that resemble those here described and that may belong to the same taxonomical group were reported from the uppermost Triassic by Mostler (1986), and from the Cretaceous by Schrammen (1924).

Tedaniids

In our material, spicules that may belong to the poecilosclerid family Tedaniidae Ridley and Dendy, 1886 were also found. These are tylotes (350 µm in length) (Fig. 5M). Tedaniids are encrusting, massive or digitate sponges found predominantly in tropical and warm-temperate waters of the Atlantic, Indian, and Pacific Oceans on rocks and stones in shallow, littoral waters up to 100 m deep (Van Soest 2002a, b).

Lithistids

In paleontological literature, this group of sponges is treated as the formal order Lithistida Schmidt, (1870), but it is, in fact, a highly polyphyletic group of sponges characterized by the occurrence of articulated choanosomal spicules of various shapes and geometries, called desmas (Pisera and Lévi 2002a). For this reason, lithistids are treated in the zoological literature as a useful but informal group, and their formal rank should be abandoned. Various lithistids are very common in the fossil record since the Ordovician (Pisera 2006).

Lithistid spicules are very rare at Cerová and have been found in only two larger samples of sediment (samples 8–9 and 21–22, more than 50 kg of washed sediment). Moreover, they were very rarely observed also in samples 4–5 and 17–18 (a few small fragments for more than 50 kg of sediment). One rhizoclone desma (Fig. 6F) and several typical megaclone desmas (Fig. 6G, I) have been found. These are the first occurrences of lithistid sponges in the Miocene of the Paratethys. Rhizoclones occur in various families of lithistid sponges (Pisera and Lévi 2002a), thus offering no precise taxonomic information. On the contrary, megaclones are very characteristic (Pisera and Lévi 2002b) and indicate the presence of *Pleroma* Sollas, 1888. Today, this genus is common in the SW Pacific, very rare in the tropical western Atlantic, and recently has also been found in the Indian Ocean, off Western Australia (Pisera, unpublished data). Fossil pleromids are very common in the Late Cretaceous deposits of Europe, and have been also noted (Pisera, unpublished data) in the Eocene of Spain and the Pliocene of Sardinia, but interestingly, appear to be absent from the Mediterranean Sea today. Both lithistids with rhizoclones and those that represent the genus *Pleroma* are today deep-water dwellers, usually at several hundred meters depth in tropical areas (Pisera and Lévi 2002b). They prefer hard substrates, which are missing in the investigated sediment, what may suggest that these spicules were transported.

Disassociated hexactinellid spicules

The hexactinellid (Hexactinellida Schmidt, 1870) spicules found and that occur in all studied samples are mostly pentactines and hexactines that are interpreted as dermal and/or gastral spicules of the order Hexasterophora. Based on their morphology and sculpture, there are at least two different species represented. Smooth pentactines with slender rays (Fig. 7A, B) are less common. Relatively heavily tuberculated pentactines and hexactines (Fig. 7C–I) are the most common hexactinellid spicules, clearly belonging to a different species. Apart from these spicules, larger samples of sediment contained fragments that belong to hexasterephoran hexactinellids with fused (dictyonal) skeletons. Those that are smooth, and clearly composed of one layer bearing tuberculated spines on one side (Fig. 6A, B), belong clearly to one species, representing family Farreidae Gray, 1872, most of *Farrea* Bowerbank, 1862. This genus is cosmopolitan today and has a very wide (82 to over 5,000 m) bathymetric distribution (Reiswig 2002a; Lopes et al. 2011), but it is typical of bathyal depths. More common are stout and irregular dictyonal skeletons with swollen and tuberculated nodes (Fig. 6C, J, K) that belong to one species of Euretidae Zittel, 1877, possibly in *Pararete* Ijima, 1927. This genus possesses a choanosomal skeleton with similarly swollen and tuberculated nodes (see Reiswig and Wheeler 2002) and occurs today in the Japan–Indonesian region at depths between 100 and 800 m (Reiswig and Wheeler 2002).

Fragments of a sculptured lychniscosan skeleton (Fig. 6D, E) representing one species are very rare. Today, lychniscosan sponges are very rare and occur mostly in deep water (however, as shallow as 82 m is also possible) in the West Indies, Red Sea, Indonesia, and Philippines (Reiswig 2002b). This is the first record of lychniscosan sponges from the Miocene of the Paratethys.

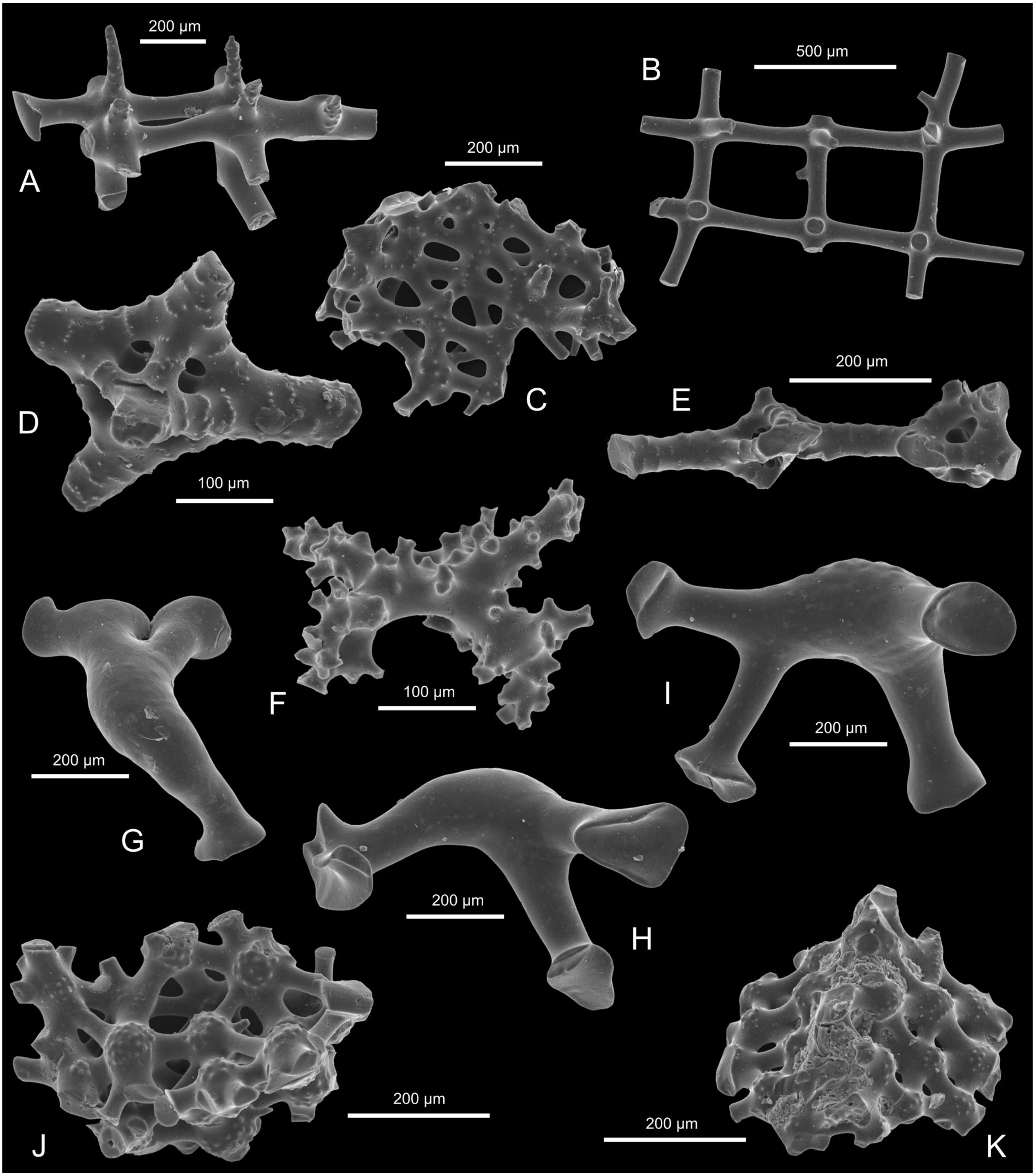

Fig. 6 Hexactinosid, lychniscosid, and lithistid spicules: *A*, *B* fragment of dictyonal skeleton of hexactinosid species I; *C*, *J*, *K* fragments of dictyonal hexactinosid skeleton II; *D*, *E* fragment of dictyonal skeleton of lychniscosid sponge; *F* lithistid rhizoclone desma; *G*–*I* megaclone desmas of the lithistid *Pleroma*

A strange, 300 µm long (partly broken) and thin spicule (Fig. 5P), which is finely acanthose, resembling some hexactinellid (Amphidiscosida) diactines has also been found. Amphidiscosid sponges are typical bathyal dwellers (Tabachnick and Menshenina 2002a, b).

All together, at least two species of Hexactinosa, and one species of Lychniscosa were found at Cerová. It is

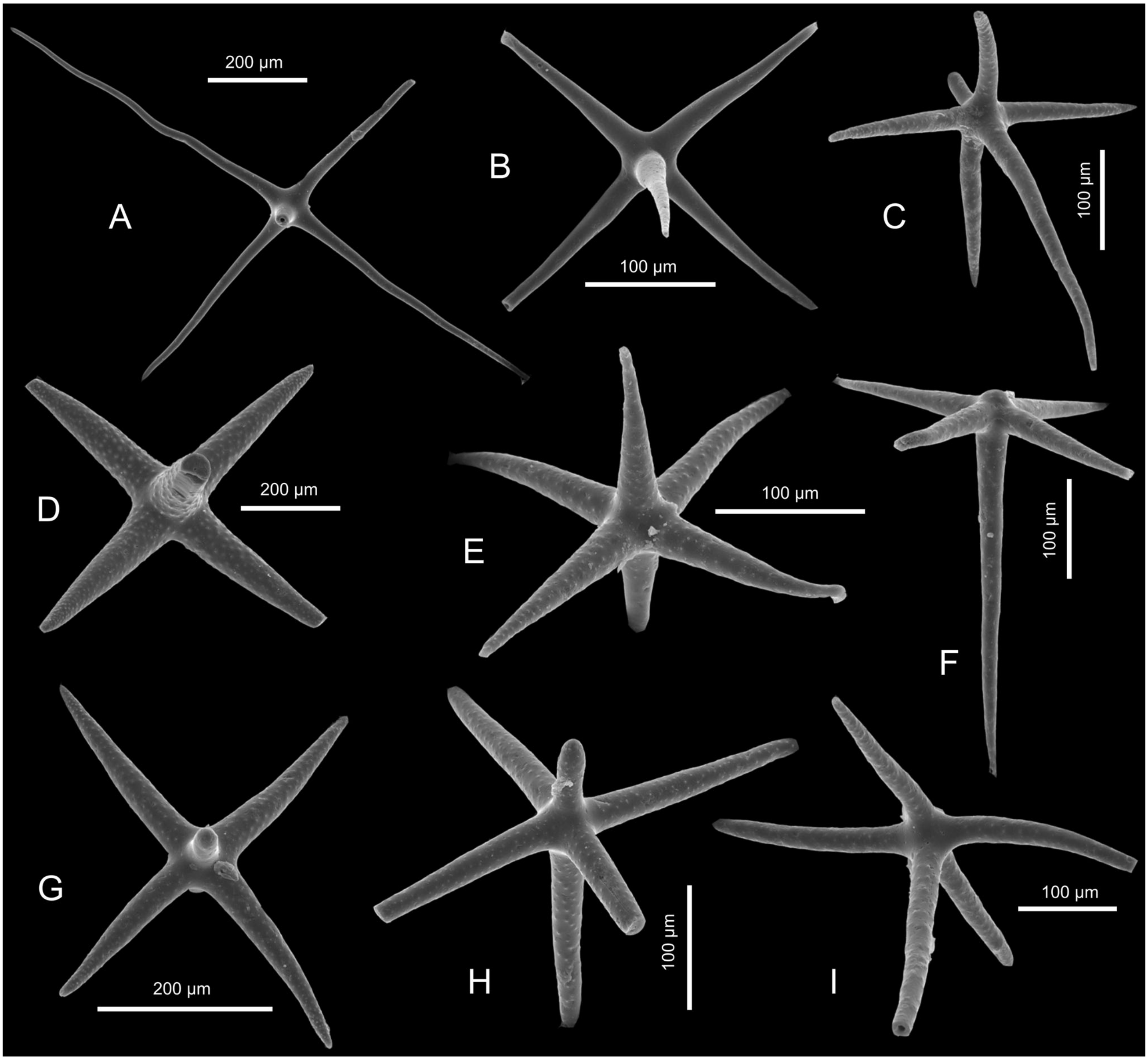

Fig. 7 Loose hexactinellid spicules: *A*, *B* smooth pentactines that most probably belong to one species; *C–I* tuberculated penta- and hexactines that most probably belong to one species

impossible to say if loose hexactines and pentactines belong to these species, or some other hexactinellids with unfused choanosomal skeleton, thus making it difficult to decide how many species of hexactinellid species occur at Cerová.

Paleoecology and biogeography

Sponge taxa above species level that occurred at Cerová during the terminal Early Miocene may occur today in both deep and relatively shallow waters. Most of them, however, are characteristic of relatively deep water today. Hexasterophoran hexactinellid sponges, for example, are characteristic of bathyal depths, with the exception of special habitats such as submarine caves and/or fjords (Vacelet 1988; Vacelet et al. 1994), which is clearly not the present case. Some demosponges found at Cerová may have inhabited shallow waters, i.e., *Geodia*, but this genus has a very wide bathymetric range and is also common in bathyal waters, where it forms dense aggregations in so-called Ostur bottoms (Klitgaard and Tendal 2001). Lithistids, while very rare, also show this bathymetric range. On the other hand, the fact that they usually require hard (rocky) substrate, which was clearly absent in the visible section, suggests that also lithistids may be transported from shallower settings where such substrate was available for their colonization. Similarly, this may also be the case for myxillid, tedaniid, and agelasid sponges, which today inhabit shallow waters, but at Cerová co-occur with bathyal species. These sponges may also have been transported from shallower surrounding areas. One has also to note that the myxillid, tedaniid, and agelasid spicules are rare or even very rare, as are lithistid spicules.

Paleoecological interpretation of the sponge assemblage is supported by the other co-occurring groups of fossils. We can refer to the published results on benthic foraminifera, which were carefully evaluated for the sample interval 14–20 (Fig. 1, for methods applied see Schlögl et al. 2011a). Paleodepth estimations range between 240 and 330 m, which is also in good accordance with coeval foraminiferal associations from the same lithofacies from the Styrian Basin in Austria (Spezzaferri et al. 2002). These upper bathyal conditions were tested on the composition of associated macrofaunal communities. Benthic gastropods are dominated by carnivores, scavengers (and/or predators) or parasites (more than 85 %, Harzhauser et al. 2011). Herbivores are extremely rare. Among the bivalves, the association consists of carnivores, chemosymbiotic, detritivores, and suspension feeders (Harzhauser et al. 2011). Such benthic mollusc composition indicates deposition in the aphytal zone and a very low contribution of transported taxa from shallower settings. Scaphopod *Gadilina taurogracilis* is considered as ancestor of *Gadilina triquetra* (Brocchi, 1814), which is widespread in Pliocene deposits of Italy. According to Ceregato et al. (2007), it is strictly bathyal and indicative of unstable deep marine environments. Even more significant is the crustacean assemblage, which is predominantly composed of deep-water genera such as *Callianopsis*, *Agononida*, *Munidopsis*, and *Mursia* (Hyžný and Schlögl 2011). Moreover, the calculated paleodepth range is in accordance with the optimal conditions of Recent nautiloid cephalopods, ancestors of which occur in great numbers in the Cerová section (Schlögl et al. 2011a). In addition to invertebrates, further support for deposition within a considerable depth of water can be provided by chondrichthyans (Underwood and Schlögl, accepted). Virtually all of the chondrichthyan taxa present in the studied deposits are related to forms that are either restricted to, or commonly present in, deep-water environments. Squaliforms dominate the assemblage in both number and diversity, and contain members of all three families of strongly heterodont squaliforms, today almost entirely limited to deep or open waters.

Most of the sponge genera found at Cerová have rather wide geographical distributions and occur in both Atlantic and Indo-West Pacific regions, with the notable exception of the myxillid *Ectyonopsis*, which occurs almost exclusively around Australia and in the Southern Ocean. The taxa with Miocene record are known from the Tethyan area. This pattern suggests Tethyan affinities of the studied sponge fauna, as well as the existence of good connections between Paratethys and Tethys during the Karpatian. Another known Karpatian assemblage of siliceous sponge spicules from Moravia (Pisera and Hladilová 2003) is dominated by astrophorid demosponges, while hexactinellids are very rare, which suggests that it characterizes shallower (although still deeper littoral) environment. On the other hand, the Badenian assemblage of spicules from Moravia, where amphidoscophoran hexactinellid spicules are common (Riha 1982, 1983), absent at Cerová, suggests even deeper water conditions during their deposition.

Conclusions

1. Well-preserved, intact specimens of "soft" siliceous demosponges were found in the Karpatian (Lower Miocene) deposits of the Cerová section (Slovakian part of the Vienna Basin, Paratethys), which are described here as a new genus and species, *Paracinachyrella fossilis* (Tetillidae, Demospongiae).
2. Dissociated spicules/skeleton fragments occurring in the same rocks witness that a rich assemblage of siliceous sponges inhabited the investigated region. Representatives of at least 13–15 demosponge species (including two species of lithistids that are reported for the first time from the Paratethys Miocene), belonging to 10 demosponge families have been recognized. Hexactinellids are represented by at least 3–4 species that belong to Hexactinosida and Lychniscosida, the latter reported for the first time from the Lower Miocene of the Paratethys.
3. Most investigated sponges characterize rather deep, most probably bathyal environment, an interpretation supported by the ecological character of the associated fauna. The presence of likely shallow-water elements as agelasids, myxillids, and tedaniids may indicate their transport from surrounding shallower environments. The likelihood of such transport is also supported by the presence of clearly allochthonous lithistid demosponge spicules, which require a hard substrate for attachment. Such environmental setting is absent at the Cerová section.
4. The majority of the sponges identified in the Cerová Karpatian deposits at genus/family level are widely distributed today and occur in Atlantic and Indo-West Pacific provinces. Those known from the Miocene occur in the Tethyan area. This indicates Tethyan

affinities of the Cerová sponge fauna and confirms a good connection between Paratethys and Tethys during the latest Burdigalian (Karpatian).

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