New species of lithistid sponges from the Paleogene of the Ukraine

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ABSTRACT
Four new species of lithistid sponges, *Lerouxia digitata* n. sp., *Theonella ukrainica* n. sp. (Theonellidae, Tetracladina), *Chenendopora piaskovskii* n. sp. (Chenendoporidae, Tetracladina) and *Plinthosella magna* n. sp. (Plinthosellidae, suborder *incertae sedis*), are described from the Paleogene (most probably Oligocene) of the Ukraine. It is the largest lithistid fauna of that age known. In a preliminary report by Oakley (1942) these sponges were erroneously attributed to *Corallistes* (one species), *Discodermia* (three species) and *Jereica clavaeformis* Pomel. The species *Lerouxia digitata* n. sp., *Chenedopora piaskovskii* n. sp. and *Plinthosella magna* n. sp. represent genera which were known so far only from the Cretaceous. The species *Theonella ukrainica* n. sp. belongs to the still living genus. Such long stratigraphical ranges of the genera of the investigated sponges is more general feature known also among other lithistids. These sponges are extraordinarily preserved, showing even flexibility of the skeleton and have in most cases dermalia preserved *in situ*. A curious feature of this fauna is very heavy silification of most described sponges, unknown among Recent lithistids.

KEY WORDS
Porifera,
Lithistida,
taxonomy,
Paleogene,
Ukraine,
new species.

RÉSUMÉ

Nouvelles espèces d'éponges lithistides du Paléogène d'Ukraine.

Quatre nouvelles espèces d'éponges lithistides, *Lerouxia digitata* n. sp., *Theonella ukrainica* n. sp. (Theonellidae, Tetracladina), *Chenendopora piaskovskii* n. sp. (Chenendoporidae, Tetracladina) et *Plinthosella magna* n. sp. (Plinthosellidae, sous-ordre *incertae sedis*), sont décrites du Paléogène (probablement Oligocène) d'Ukraine, représentant la plus importante faune de lithistides connue de cet âge. Ces éponges avaient été attribuées de façon erronée à *Corallistes* (une espèce), à *Discodermia* (trois espèces) et à *Jereica clavaeformis* Pomel dans un travail préliminaire par Oakley (1942). Les espèces *Lerouxia digitata* n. sp., *Chenendopora piaskovskii* n. sp. et *Plinthosella magna* n. sp. représentent des genres qui étaient connus seulement du Crétacé. L'espèce *Theonella ukrainica* n. sp. appartient à un genre actuel. La longue représentation stratigraphique de ces genres est un caractère général qui est connu chez d'autres lithistides. Ces éponges sont extrêmement bien préservées, montrant même une certaine flexibilité du squelette, avec, dans la plupart des cas, les dermalia conservés *in situ*. Un caractère surprenant de cette faune est une forte silicification de la plupart des spécimens, inconnue chez les lithistides actuelles.

MOTS CLÉS
Porifera,
lithistides,
taxonomie,
Paléogène,
Ukraine,
nouvelles espèces.

INTRODUCTION

The Tertiary lithistid faunas, especially well-preserved, are rare and poorly known (Wiedenmayer 1994; Pisera 1999), thus any new well-preserved fauna of that age is of crucial importance. The siliceous sponges reported in this paper are of Paleogene, most probably Oligocene age. The only other known to me, yet undescribed, lithistid fauna of Oligocene is that reported by Wiedenmayer (1994) from Antigua (West Indies). The Eocene siliceous sponges, including lithistids are common and relatively well-preserved in the Castle Hayne Limestone (North Carolina, USA) and were partly described by Rigby (1981) who reported tetracladine lithistids. Finks (1986 and pers. comm.) reports, without description, abundant plinthosellid lithistids from the same formation. The Eocene sponge faunas from the Vic Basin (NE Spain) contain mostly hexactinellids, but lithistids are rare (Serra-Kiel & Reguant 1991; Busquets *et al*. 1997); among them one rhizomorine and two indeterminable nonrhizomorine lithistids have been recognized (Pisera unpubl.). The Eocene lithistid fauna reported from southwestern Australia (Chapman & Crespin 1934; Laubenfels 1953; Pickett 1983) is more diversified and contains numerous tetracladine and megamorine sponges, but still poorly known, and under investigation now (Pisera, in prep.).

Far more common are Miocene siliceous sponge faunas which, apart from hexactinellids, usually contain numerous lithistid species. They are known from Algeria where lithistids are represented mostly by rhizomorines accompanied by some dicranocladine and tetracladine species (Pomel 1872; Moret 1925; Moissette *et al*. 1984). The Miocene sponge faunas from southern Spain contain over 20 species of lithistids, mostly rhizomorines, but tetracladines, dicranocladines and megamorines are also present (Ott d'Estevou & Termier 1978; Ott d'Estevou *et al*. 1981; Brimaud & Vachard 1986). Siliceous sponges have also been reported from the Tertiary of Italy (Mazzetti & Manzoni 1879; Malfatti 1900; Menin 1972) but they are mostly hexactinellids; these faunas were never systematically investigated and taxonomic determinations offered in the literature are rather doubtful.

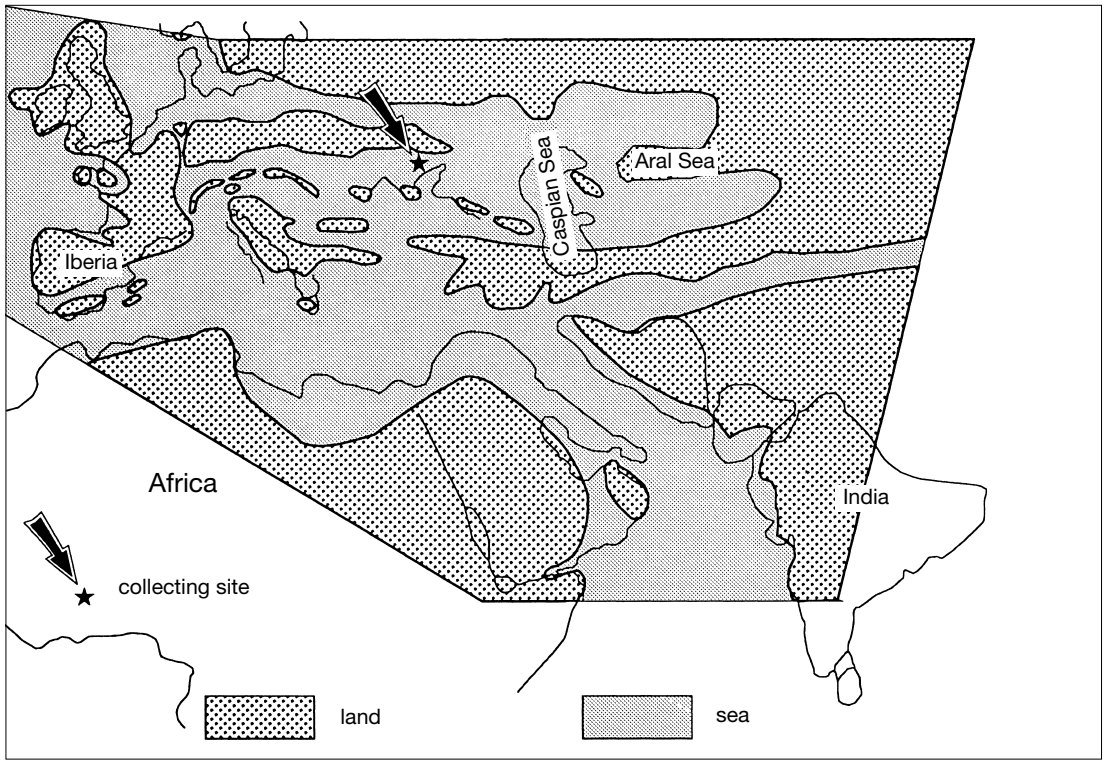

FIG. 1. — Paleogeographical map for the Early Oligocene time of the Mediterranean and Paratethys Seaways with the collecting site of sponges marked by an asterisk (paleogeography after Rögl 1998, modified).

ABBREVIATION USED
NHM Natural History Museum, London.

MATERIAL

Lithistid sponges under investigations are extraordinarily preserved and in most cases have the original siliceous skeleton still flexible. It means that desmas are only articulated and not fused by diagenetic silica. In other known Tertiary faunas, desmas are often substituted by calcium carbonate and/or embedded into hard calcareous material (so called "mummies", see Pisera 1997). This very good preservation of skeleton, in the present investigated material, is most probably due to protection by clay sediments. These discussed sponges were discovered in 1927 by the Soviet geologist B. V. Piaskovsky, but were never described taxonomically, except for short notes referring to the geological situation and their preservation (Piaskovsky 1929, 1952; Oakley 1942). Piaskovsky (1929) recognized them correctly as lithistid sponges, while Oakley (1942) after preliminary examination, reported one *Corallistes* species, three species of *Discodermia* and *Jereica clavaeformis* Pomel. Bodily preserved lithistids are accompanied by common loose spicules of other demosponges and rare fragments of Hexactinosa.

The investigated sponges were discovered during hydrogeological investigations about 25 km north of the Ukrainian town of Zaprozhnoye, in the village on the left bank of the Dniepr River. The age of the sponge-bearing deposits was first determined as early Oligocene, and later more conservatively as Paleogene (Piaskovsky 1952). During the Paleogene, this region of the Ukraine was a part of the Paratethys sea and had then been connected both with the Mediterranean and

Boreal Atlantic regions (Fig. 1). The sponges occur in clayey-sandy rock infilling local depression in crystalline basement (Piaskovsky 1929). The sponge-bearing rocks were first discovered in wells by villagers, and then in specially dug, geological shafts up to 16 metres deep. According to Piaskovsky (1929), the sponges have in places been the dominant constituent of the rock but clearly only some of them have been collected, as they are not numerous in the collection housed in the NHM in London and in St. Petersburg. The studied collection is housed in the NHM in London under the collection number NHM ZN1 to 11.

SYSTEMATICS

Suborder TETRACLADINA Zittel, 1878

Family THEONELLIDAE Lendenfeld, 1903

REMARKS

Fossil sponges with tetracladine desmas and phyllotriaene dermalia have been traditionally included by paleontologists in the family Discodermiidae Schrammen, 1910. The scope of this family (apart from microscleres which are absent in fossils) seems to be the same as the family Theonellidae Lendenfeld, 1903 of zoologists, which has priority (Brimaud & Vachard 1986). Also the family Lerouxidae Moret, 1926 differs neither in choanosomal nor dermal skeleton from Theonellidae Lendenfeld, and is here included in Theonellidae.

Genus *Theonella* Gray, 1867

Theonella ukrainica n. sp.
(Figs 2A-D; 3)

MATERIAL. — 24 fragmentary specimens (NHM ZN5, ZN10). Holotype, specimen NHM ZN5A; paratype, NHM ZN10A.

ETYMOLOGY. — The species name refers to the Ukraine where the material was discovered.

DIAGNOSIS. — These are small branching *Theonella* with one to several longitudinal canals in the centre. Choanosomal desmas as smooth regular tetraclones. Dermalia as phyllotriaenes with slender clads and pointed tips, or small irregular discotriaenes.

DESCRIPTION

Numerous fragments of small, up to 5 cm long, branching sponges with branches 6-8 mm thick. One to several vertical, 0.5 to 1.0 mm wide, round canals run along the sponge in the centre. Sometimes these canals approach the lateral surface and then may be partly open. In the main trunk several canals always occur, in branches less or only one. These canals usually do not open at the tips of the branches. Branches usually rounded more rarely laterally flattened with rounded tips, when preserved. Skeleton consists of smooth, regular tetraclones, with moderately branched terminal articulations; they are 255-430 μm in size. Dermal skeleton developed mostly as phyllotriaenes with slender pointed clads, which are 250-580 μm in size. In some areas, however, small discotriaenes that are irregular in outline also occur, and are 220-280 μm in size. Choanosomal tetraclones are very regular in the upper and inner part of branches and measure 255-430 μm in size, while in lower (older) parts, close to the surface, and around canals they are very densely packed and irregular. The space between dermal phyllotriaenes is often infilled in the older part of branches with very densely packed and tightly interlocking small, flat, irregular spicules resembling rhizoclones.

REMARKS

The specimens included by me into *T. ukrainica* were most probably one of those included into *Discodermia* by Oakley (1942). The genus *Theonella*, to my knowledge, has never been found as fossil before, except for an indication by Laubenfels (1955) which I was unable to resolve. Assignment of my material to *Theonella* is based on the type of desmas and their articulation and accompanying dermal phyllotriaenes. No microscleres have been found. Most theonellas have a spongocoel developed, but my specimens are tiny-branching in habit, and thus lack of spongocoel, instead several vertical canals are developed.

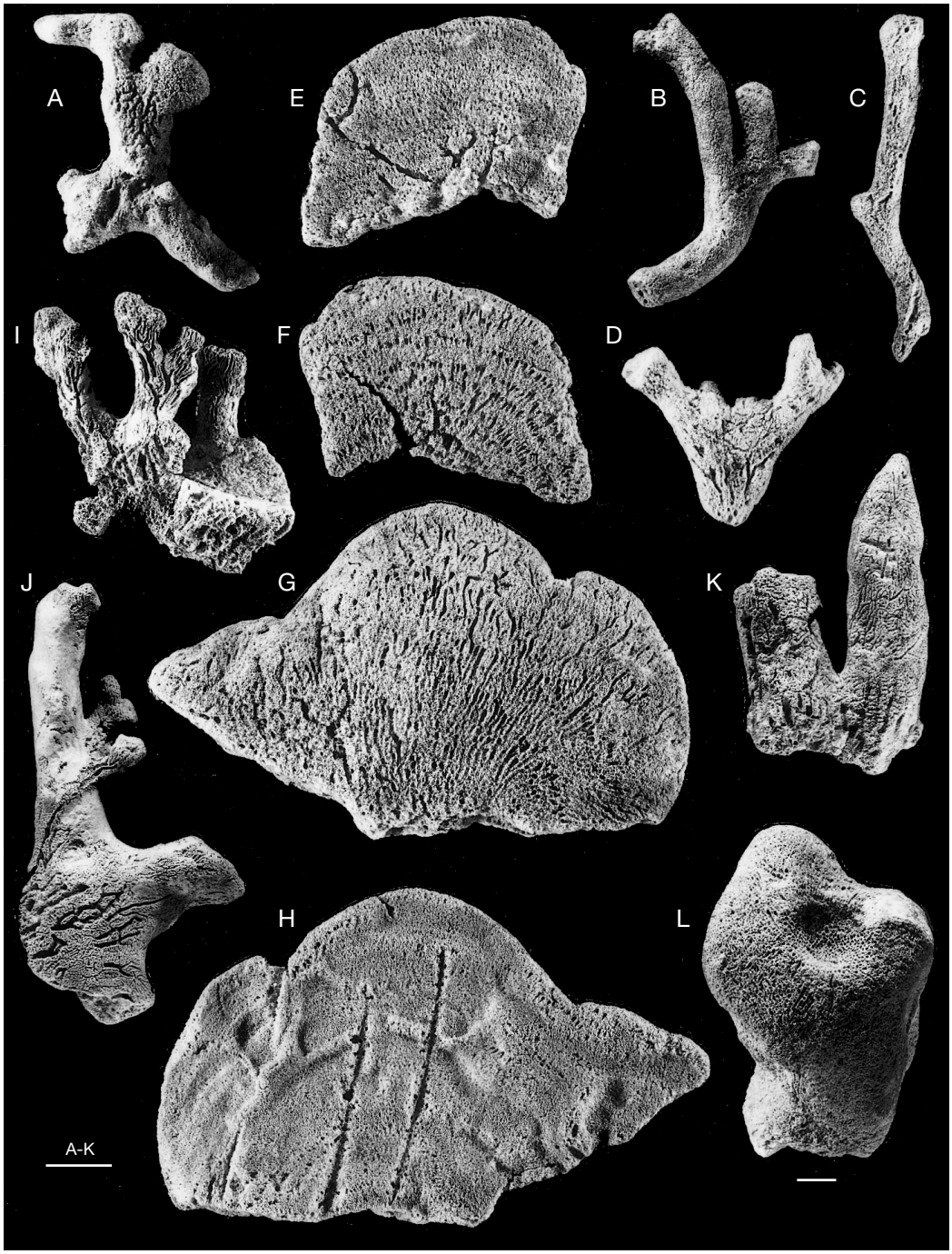

FIG. 2. — Habit of the investigated sponges; **A**-**D**, *Theonella ukrainica* n. sp.; **A**, NHM ZN10D; **B**, holotype NHM ZN5A; **C**, NHM ZN5E; **D**, NHM ZN5F; **E**-**H**, *Chenendopora piaskovskii* n. sp.; **E**, **F**, paratype NHM ZN11 in lower side (E) and upper side (F) views; **G**, **H**, holotype NHM ZN1 in upper (G) and lower side (H) views; **I**-**K**, *Lerouxia digitata* n. sp.; **I**, NHM ZN4; **J**, holotype, NHM ZN7; **K**, paratype, NHM ZN8; **L**, *Plinthosella magna* n. sp., holotype NHM ZN3, oblique view. Scale bars: A-D, G, H, L, 1 cm; E, F, I-K, 2 cm.

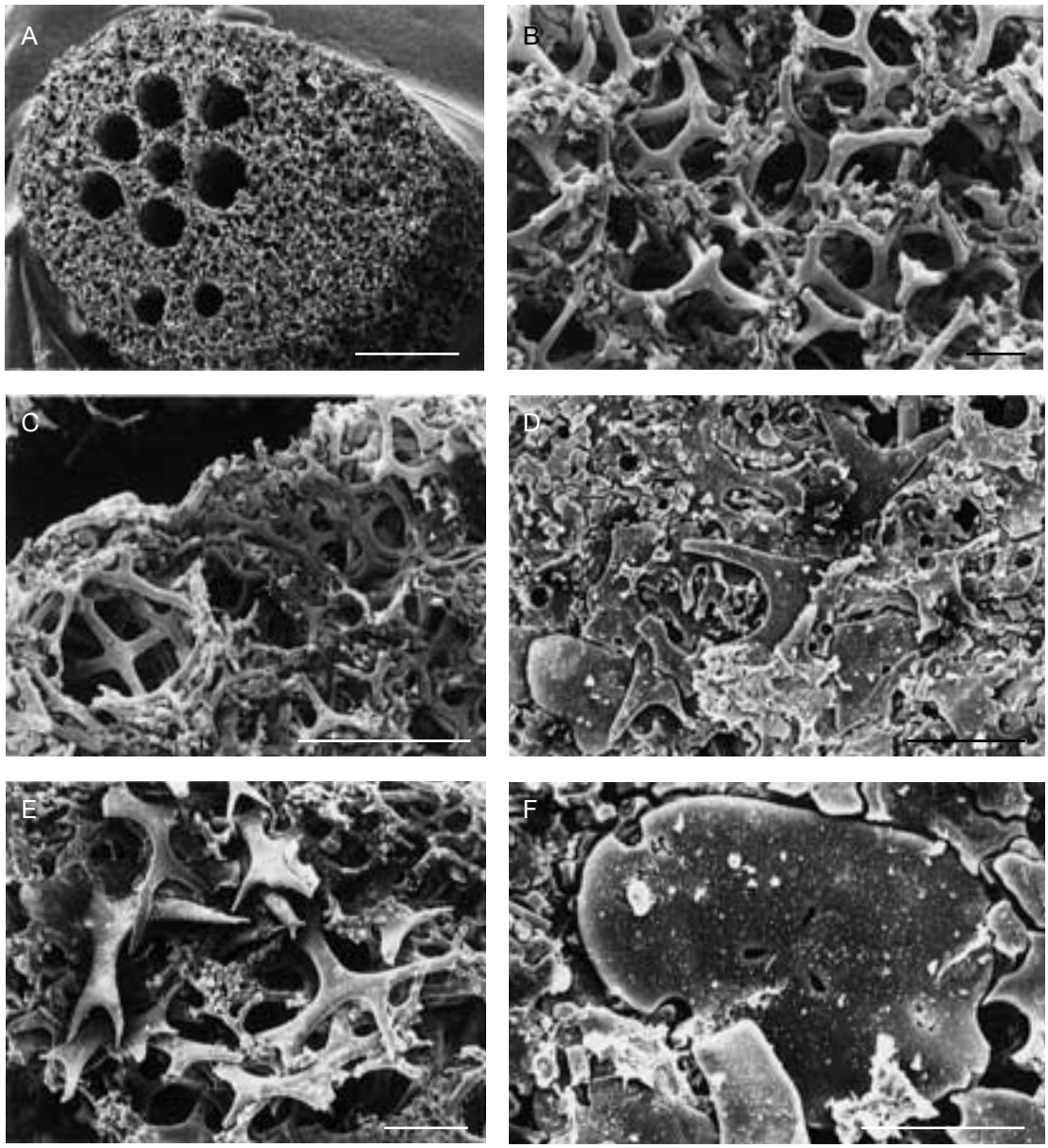

FIG. 3. — *Theonella ukrainica* n. sp.; **A**, cross-section of a branch showing vertical canals, NHM ZN5D; **B**, choanosomal skeleton showing regular tetraclone desma with smooth rays and terminal articulation, NHM ZN5D; **C**, choanosomal skeleton composed of tightly packed and deformed tetraclones from subdermal region (surface to the top), NHM ZN5D; **D**, dermal surface showing dermalia developed as phyllotriaenes and discotriaenes; between them modified and tightly locked (infilling entirely the space between dermalia) outermost choanosomal tetraclone desma, NHM ZN10C; **E**, typical dermal phyllotriaenes as seen above choanosomal skeleton, NHM ZN10C; **F**, Dermal discotriaene with axial canals (eroded) visible, NHM ZN10C. Scale bars: A, 2 mm; B, D, E, 200 µm; C, 500 µm; F, 100 µm. All SEM photographs.

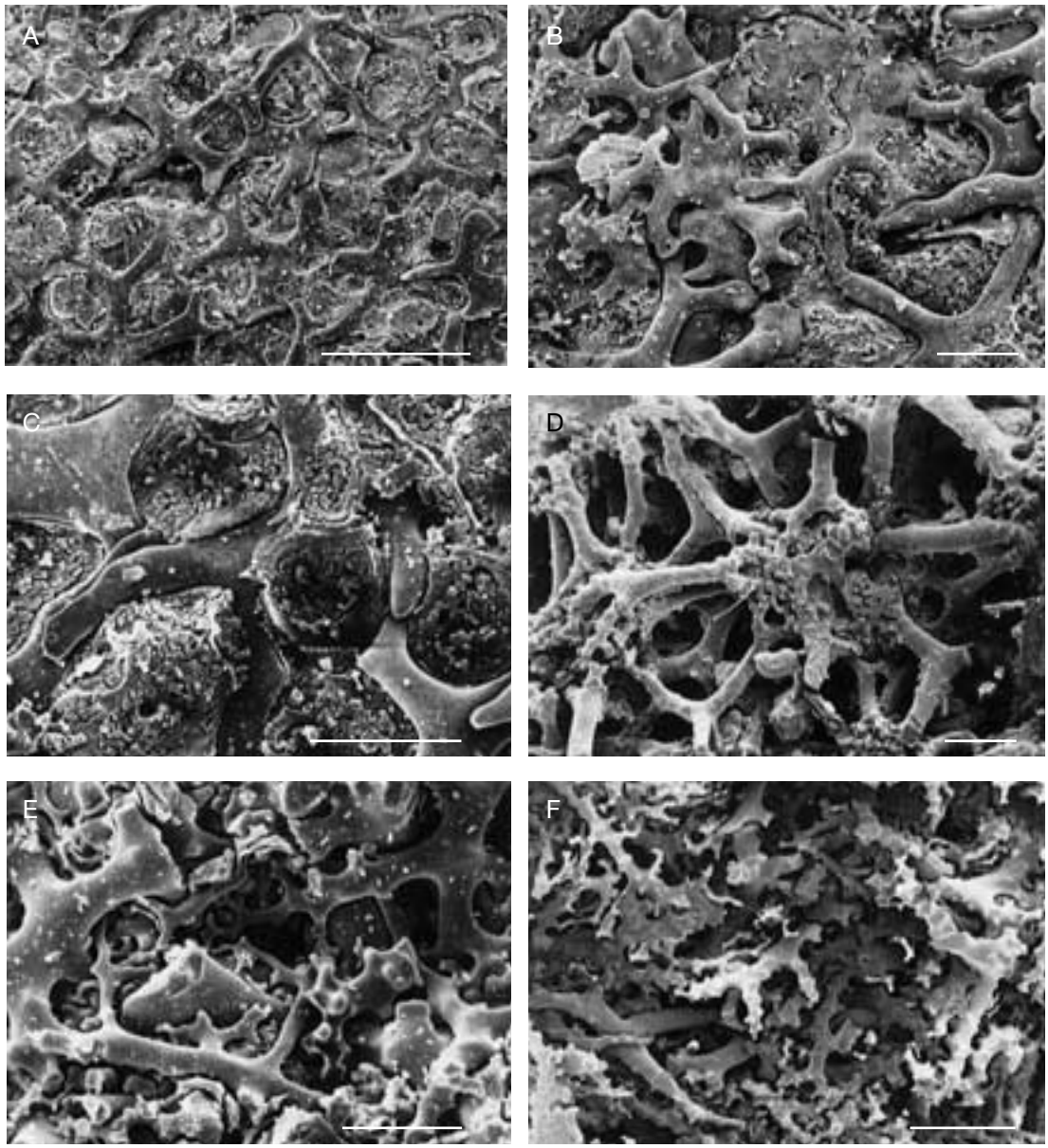

FIG. 4. — *Lerouxia digitata* n. sp.; **A**, dermal surface with phyllotriaenes *in situ*, NHM ZN4; **B**, details of dermal surface showing various phyllotriaenes, NHM ZN4; **C**, details of the dermal surface showing spaces between dermalia completely infilled with tightly locked modified outer choanosomal desmas, NHM ZN4; **D**, choanosomal skeleton composed of regular tetraclone desmas with terminal articulation as developed in younger parts of a sponge, holotype NHM ZN7; **E**, dense skeleton composed of modified irregular tetraclones from subdermal part of the older part of a sponge, holotype NHM ZN7; **F**, dense choanosomal skeleton composed of strongly modified tetraclone desmas, resembling rhizoclones, form the base of the sponge, paratype NHM ZN8. Scale bars: A, 500 µm; B-D, F, 200 µm; E, 100 µm. All SEM photographs.

Genus *Lerouxia* Moret, 1926

REMARKS

The new genus *Lerouxia* Moret has been included by this author into the newly established family Lerouxidae Moret, 1926. There is, however, no difference either in choanosomal skeleton or in dermalia between Lerouxidae Moret and Theonellidae Lendenfeld, thus Lerouxidae are considered by me as a younger synonym of Theonellidae. The genus *Lerouxia* differs from *Theonella* in dermal phyllotriaenes which have rounded clads, in having large spherical articulation centres, as well as in irregular tetraclone desmas which have tuberculated apices.

Lerouxia digitata n. sp.
(Figs 2I-K; 4)

MATERIAL. — Six variously preserved specimens. Holotype NHM ZN7; paratype NHM ZN8.

ETYMOLOGY. — The name of the species refers to its digitate shape.

DIAGNOSIS. — Large digitate sponge pierced by numerous sinuous or irregular longitudinal canals, which may approach the lateral surface and then may be partly open. Choanosomal desmas are irregular tetraclones with smooth clads and tuberculated apices. Articulation of several desmas form large spherical centres. Dermalia are phyllotriaenes with rounded clad tips. Between dermalia is a dense layer of interlocking flat spicules resembling rhizoclones.

DESCRIPTION

Large up to 15 cm high digitate sponge, sometimes with knobby protuberances, up to 4 cm thick at the base. No spongocoel or osculum. Entire sponge pierced by numerous loosely spaced, more or less vertical but sinuously or irregularly longitudinal canals, which at the base may reach 2 mm in diameter, but on average are only 0.7-1.0 mm large. They also may be close to the surface, so when dermal skeleton removed, in many cases they are visible as sinuous furrows of the same diameter. In the centre of a branch (in 50% of cases) there is a loose bunch of smaller, 0.1 to 0.5 mm diameter, vertical canals. Branches have rounded tips. The whole sponge is covered by the dense dermal skeleton of phyllotriaenes (470-650 μm in size) or, more rarely, small (230 µm in size) irregular discotriaenes. Between dermal phyllotriaenes occurs a dense layer of tightly interlocking irregular flat spicules resembling rhizoclones. Choanosomal skeleton composed of irregular (except at a pole of a branch and in the centre) tetraclones 400-530 μm in size with smooth clads and strongly branched tuberculated apices. Articulation of several desmas forms large spherical articulation centres. Generally, the skeleton, except at the tips, gives the impression of oversilicification by being very dense. In the lower portion of the sponge, skeleton becomes extremely dense and tetraclones interwoven and strongly modified (irregular) to the point when they resemble rhizoclones.

REMARKS

The specimens included by me in *L. digitata* were most probably included into *Discodermia* by Oakley (1942). This is the first report of this Cretaceous genus (see Moret 1926) from the Tertiary. The holotype of this species, here on the Fig. 2J, was also illustrated earlier by Piaskovsky (1929: 138, fig. 1 left-larger specimen). This new species differs from the Cretaceous species of *Lerouxia* in the shape of dermal phyllotriaenes and choanosomal desmas.

Family CHENENDOPORIDAE Schrammen, 1924

Genus *Chenendopora* Lamouroux, 1821

REMARKS

So far no dermalia have been reported in the genus *Chenendopora* Lamouroux. My own, unpublished studies of the Upper Cretaceous *Chenendopora* from Schrammen's (1910) collection, revealed that small phyllotriaene dermalia occur in this genus; very similar dermalia are present in the described new species. Because of their small size, dermalia were earlier most probably overlooked. Relationship between the families Chenendoporidae Schrammen and Theonellidae Lendenfeld must be clarified, as so far the main difference between those two families was the absence of dermalia in *Chenendopora*, which is now known not to be the case. This needs, however, more detailed studies of the Mesozoic *Chenendopora* species.

Chenendopora piaskovskii n. sp.
(Figs 2E-H; 5)

MATERIAL. — Holotype, fragmentary specimen NHM ZN1; paratype, fragmentary specimens NHM ZN11.

ETYMOLOGY. — To honour the discoverer of this sponge fauna, geologist B. V. Piaskovsky.

DIAGNOSIS. — Plate-like or flabellate tetracladine sponge with small tuberculated tetraclones in the choanosomal skeleton and dermalia as small phyllotriaenes with pointed clad tips. Upper surface with numerous large canal openings running obliquely into the wall. Lower surface smooth with much smaller evenly distributed canal openings.

DESCRIPTION

These are fragments of plate-like or leaf-shaped sponge up to 10 × 6 cm large and with wall about 1 cm thick that thins toward the edge. Lower side more or less smooth with traces of concentric growth and irregular narrow elevations. It displays irregularly distributed rounded openings about 0.24-0.30 mm in diameter, which are loosely spaced. The upper side, which is slightly eroded in all specimens, displays large canal openings 0.6-0.8 mm in diameter, and canals which run close to the surface to enter after some distance obliquely the wall. These canals and their openings are arranged in irregular vertical (radial) series giving an appearance of irregular radial striation. Skeleton very dense, composed of stout and strongly tuberculated tetraclones 400-700 µm in size (average 600 µm). These tubercles in most cases are oval or elongated. Dermal skeleton preserved only in few places, composed of very small and poorly branched phyllotriaenes with pointed tips of clads, and cladomes 270-360 µm in diametre. Rhabd short, conical.

REMARKS

These are, most probably, the specimens which were erroneously considered by Oakley (1942) as representatives of the genus *Corallistes*. This is the first report of the Cretaceous genus *Chenendopora* from the Tertiary. The new species differs from other species of this genus in more regular and differently sculptured desmas, in the presence of dermalia (unknown in the Cretaceous forms) and in being rather leaf or plate-shaped than conical or cylindrical as other forms.

Suborder *INCERTAE SEDIS*

Family PLINTHOSELLIDAE Schrammen, 1910

REMARKS

Plinthosellidae Schrammen, 1910, in which dermalia occur in the form of siliceous discs, are usually regarded by paleontologists as Tetracladina and often compared with the Recent genus *Neopelta* Schmidt. The genus *Neopelta* has also dermal siliceous discs, but smooth monocrepid desmas. It had been included in the Neopeltidae Sollas, 1888 and defined as "Rhabdosa in which ectosomal spicules are monocrepid discs" (Sollas 1888). Based on their monocrepid desmas, Neopeltidae are regarded by Lévi & Lévi (1988) and Lévi (1991) as Dicranocladina Zittel. Lévi (1991) expressed some doubts concerning tetracladine nature of desmas in *Plinthosella*. The adult strongly tuberculated desmas in my material may pose doubts about their real nature (tetracrepid versus monocrepid) as no axial canal can be observed. Young desmas from my specimen display tetractine geometry. Despite this they are still very different from typical young tetraclones (tetracrepid desma). For these reasons I prefer to leave the question of subordinal attribution of *Plinthosella* open, until detailed re-evaluation of this problem can be based on more material. Plinthosellid sponges were first described from the Upper Cretaceous of Germany (Schrammen 1910) and then from France (Moret 1926) and Poland (Hurcewicz 1966). More recently, their abundant presence in the Eocene of the USA was reported, without description, by Finks (1986).

Genus *Plinthosella* Zittel, 1878

Plinthosella magna n. sp.
(Figs 2L; 6)

MATERIAL. — Holotype, the only specimen in the collection NHM ZN3.

ETYMOLOGY. — The species name *magna*, in Latin "great", refers to relatively large size of this species.

DIAGNOSIS. — Club-shaped sponge with shallow depression at the upper pole in which a cluster of rounded openings of short canals occurs. Desmas are

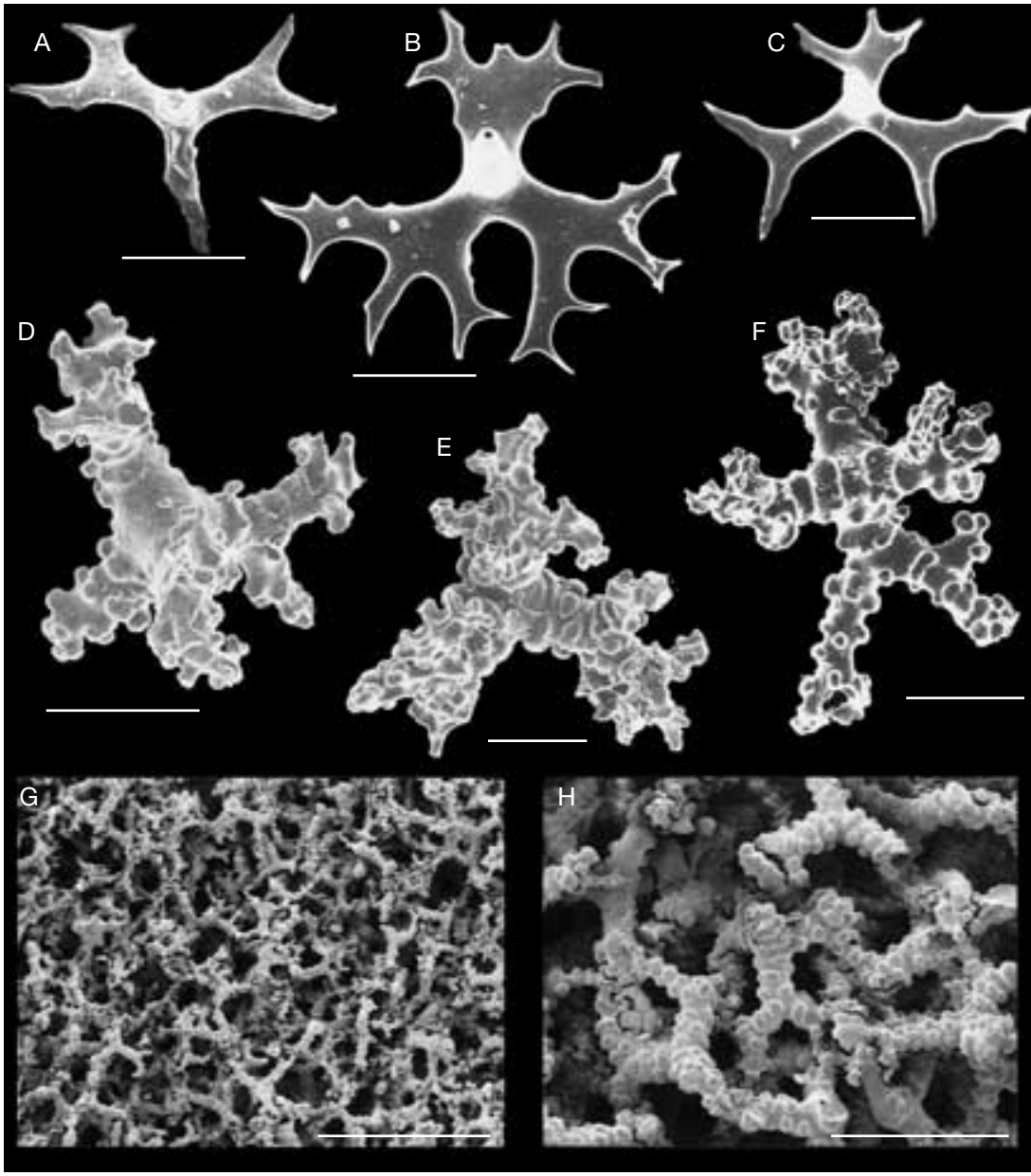

FIG. 5. — *Chenendopora piaskovskii* n. sp., holotype, NHM ZN11; **A**-**C**, Loose dermal phyllotriaenes of different shapes; **D**-**F**, choanosomal tetraclone desmas in various orientation; **G**, surface view of choanosomal skeleton composed of desmas; **H**, details of choanosomal skeleton composed of tuberculated tetraclones showing terminal articulation. Scale bars: A, D-F, 200 µm; B, C, 100 µm; G, 1 mm; H, 500 µm. All SEM photographs.

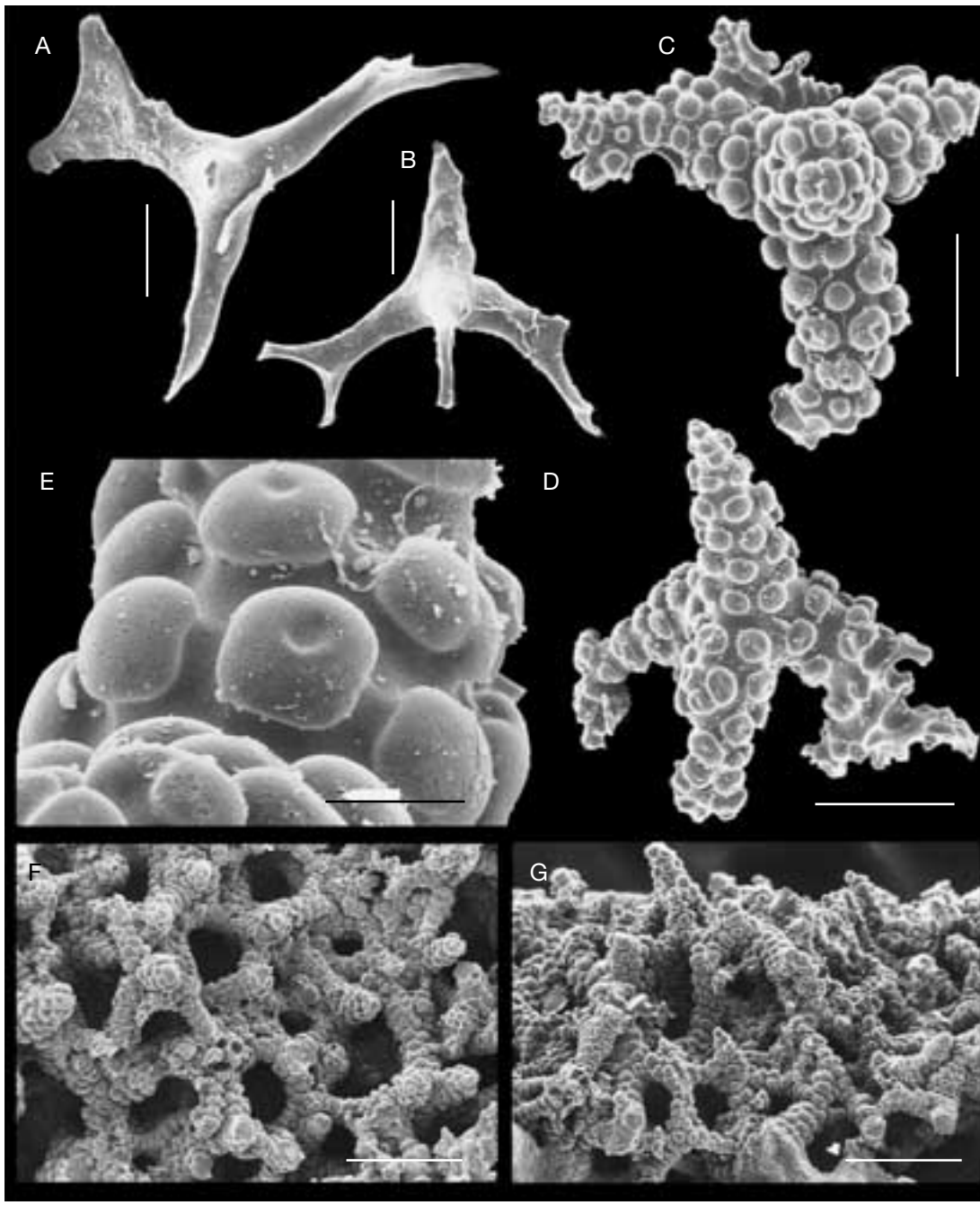

FIG. 6. — *Plinthosella magna* n. sp., holotype NHM ZN3; **A**, **B**, loose young, still smooth tripodial desmas in top and side views; **C**, **D**, typical tripodial strongly tuberculated desmas in top (C) and lateral (D) views; **E**, details of adult desmas to show character of tuberculation; **F**, **G**, choanosomal skeleton in top (F) and lateral (G) views to show its very dense character and nonterminal articulation of desmas. Scale bars: A, B, 100 µm; C, D, 200 µm; E, 50 µm; F-G, 500 µm. All SEM photographs.

tripodial strongly tuberculated with the upper conical ray bearing no articulation. Desmas articulation non-terminal. No dermalia have been observed.

DESCRIPTION

Club-like specimens about 7.5 cm high and 4 cm thick maximum bearing slightly depressed and excentrically located shallow depression about 1.5 cm in diameter at the upper pole. Numerous very densely spaced and 0.5 mm in diameter round canal openings occur on the bottom. These canals continue first vertically, then diverge outward and extend in irregular manner through the sponge. Outer surface smooth, bearing only very loosely spaced canal openings 0.5-0.8 mm in diameter. Skeleton dense and composed of heavy desmas, measuring 600 × 500-600 µm. They are completely covered with numerous large (58 µm across) mushroom-shaped and round tubercles. Young desmas nearly smooth and measure 500 µm in width and 400 µm in height. Desmas have tetractine geometry and are tripodial, i.e. only three inner (directed toward the sponge interior) rays display articulations, while the outer ray (directed toward the sponge surface) has no articulation and is developed in the form of a high narrow cone. Also on the young desmas there is no indication of any articulation on the outer conical ray. No dermal skeleton has been observed. Articulation of desmas is strictly non terminal.

REMARKS

This must be the specimen which was erroneously considered by Oakley (1942) as rhizomorine *Jereica clavaeformis* Pomel.

The Cretaceous lithistids with tripodial tuberculated desmas, having one ray conical and without articulation, are attributed to the family Plinthosellidae Schrammen, 1910, which has siliceous plates as dermalia. No dermalia are preserved in the investigated material, but desmas are very similar to those occurring in the Upper Cretaceous *Plinthosella* Zittel (see Zittel 1878; Schrammen 1910; Moret 1926; Hurcewicz 1966). My specimen differs from the Cretaceous forms in larger size and club shape, in canalization, as well as in details of desma morphology. Similar tripodial desmas occur in some Cretaceous tetracladines, but then they are limited only to the outermost layer of choanosomal skeleton, the rest being composed of typical tetraclones. In the investigated specimen, the whole skeleton is built of the same type of tripodial desmas.

Among Recent demosponges, morphologically close desmas occur in *Desmanthus* Topsent, 1893 (see Lévi & Lévi 1989), which is, however, encrusting in habit and composed of one layer of desmas that are accompanied by styles or tylostyles.

GENERAL REMARKS

Nothing can be said about ecology of the investigated sponges, because we lack precise data on sponge-bearing rocks and geological situation (today most probably they are at the bottom of an artificial lake), but surprising is the fact that they occur in clayey sediments, while most of known lithistid faunas are associated with more or less calcareous rocks. Exceptional too is the excellent preservation of sponges, with dermalia in most cases *in situ*, which excludes any transport. In fact, the most plausible explanation for such preservation is a catastrophic burial by sediment. Clay, on the other hand, protected these sponges from silica dissolution and/or precipitation, thus leaving the original articulated spicules. A curious feature of most sponges described here is their very heavy silification, unknown among Recent lithistids, which is difficult to explain.

The long ranges of lithistid genera have been already noted by Lévi & Lévi (1988) and Lévi (1991), who described Cretaceous genera in the Recent fauna of New Caledonia. The investigated lithistids confirm this feature as they are represented by genera known previously from the Upper Cretaceous only, as well as by one Recent genus. Such wide stratigraphical range of many hexactinellid and lithistid sponges seems a common feature (Pisera 1999).

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