

The oldest birotule-bearing freshwater sponges from the Upper Cretaceous–lower Paleocene Deccan volcanic-associated sediments of India

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A new fossil occurrence of freshwater sponges (Porifera: Demospongiae) is reported from the Deccan volcanic associated Naskal intertrappean locality, deposited in an interval of <100 kyr across the Cretaceous/Paleogene (K/Pg) boundary. This is the oldest record of siliceous fossil birotule spicules (gemmuloscleres) belonging to asexual resting stages typical of the order Spongillida. The analysis supports the ascription of these fossils to the family Palaeospongillidae. The diagnosis and description of *Longibiotula* Pronzato and Manconi gen. nov. and its type species *Longibiotula antiqua* Manconi and Samant sp. nov. from the Naskal intertrappean is based on skeletal and gemmular spicular morphotraits. The findings have provided evidence of the presence of diversified groups of freshwater sponges during the Late Cretaceous on the Indian subcontinent and Gondwanaland. From the biogeographic context, the findings track the evolutionary trends of the oldest continental sponges in the Asian and Australasian/Insular Pacific regions.

Key words: Porifera, Palaeospongillidae, inland water sponges, conservative morphotraits, gemmules, siliceous skeleton, palaeobiodiversity, palaeogeography, Cretaceous, Paleocene, Deccan traps.

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Introduction

The fossil freshwater sponges (Porifera: Demospongiae), known from both Laurasia and Gondwana, belong to the order Spongillida Manconi and Pronzato, 2002, which comprises three families with fossil taxa, i.e., Palaeospongillidae Volkmer-Ribeiro and Reitner, 1991, Potamolepididae Brien, 1967, and Spongillidae Gray, 1867. The oldest Spongillida

fossil records (only spicules) dates back to the Permian–Carboniferous (Schindler et al. 2008), and the Late Jurassic (*Spongilla purbeckensis* Hinde, 1883). Unfortunately, fossil records of inland water sponges are very scarce, due to their fragile skeletal siliceous architecture (Pronzato et al. 2017).

Most fossil Spongillida are hard to identify to the family, genus, or species level because they lack gemmuloscleres, which are one of the most important diagnostic morpho-

traits for systematics and phylogeny. Till date, the oldest known entire gemmule is of *Palaeospongilla chubutensis* Volkmer-Ribeiro and Reitner, 1991 (Palaeospongillidae) from the Lower Cretaceous of Patagonia (Volkmer-Ribeiro and Reitner 1991).

The gemmuloscleres remains of other fossil species of the families Spongillidae and Potamolepidae share similar morphotraits with living genera, e.g., *Anheteromeyenia* Schröder, 1927; *Corvospongilla* Annandale, 1911; *Ephydatia* Lamouroux, 1816; *Eunapius* Gray, 1867; *Radiospongilla* Penney and Racek, 1968; *Spongilla* Linnaeus, 1759; *Trochospongilla* Vejdovsky, 1883; *Oncosclera* Volkmer-Ribeiro, 1970, and *Potamophloios* Brien, 1970 (Pisera 2006; Pisera et al. 2013, 2016; Pronzato et al. 2017).

From the Deccan volcanic province, some unidentified spicules of freshwater sponges have been recorded from the Deccan infra (Lameta Formation) and intertrappean sediments of central India and the intertrappean beds of northwestern India (Samant and Mohabey 2009, 2014; Samant et al. 2014), but definite record of fossil freshwater sponges of Spongillida is scarce. Recently, the new genus *Palaeocorvospongilla* Pronzato and Manconi, 2021, of the family Palaeospongillida was described from the Deccan intertrappean sediments of India (Maastrichtian, Upper Cretaceous) with the new species *Palaeocorvospongilla cretacea* Manconi and Samant, 2021 (Samant et al. 2021).

The present study records the oldest fossil birotule-bearing freshwater sponge (Porifera: Demospongiae) of a new genus and species of Palaeospongillidae from the Naskal intertrappean deposit in the south-eastern part of the Deccan volcanic province.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:7B9F49CE-E5E9-46CD-BC9A-17C204352BC1.

Institutional abbreviations.—PGDG, Museum Postgraduate Department of Geology, Nagpur University, India; PGNU, Postgraduate Department of Geology, Nagpur University, India.

Other abbreviations.—NSKQ, Naskal Quarry section.

Geological setting

The Upper Cretaceous–lower Paleocene Deccan volcanic-associated sediment covers an area of ~500,000 km² in the south, western and central parts of India. The Deccan volcanic flows are associated with infratrappean (deposited below the volcanic flows) and intertrappean sediments (deposited in-between the two volcanic flows). Vertebrates, invertebrates, micro and megafauna have been discovered in both infratrappean and intertrappean sediments (Mohabey 1996; Mohabey and Udhoji 2000; Khosla and Sahni 2003). The Naskal section is located at 17°14'21" N, 77°53'16" E,

in the Ranga Reddy District in the state of Telangana, India (Fig. 1A). This section has a thickness of <3 m and a lateral exposure of <15 m and an aerial distribution of <5 m². It occurs between Flow-3 and Flow-4 at an elevation of 624 m. In the Naskal locality there are three geographically separated sections designated as Naskal-A, Naskal-B, and Naskal GSI Quarry (Wilson Mantilla et al. 2022: fig. 3). Based on Ar⁴⁰/Ar³⁹ plagioclase dating of the flows, it is indicated that the permissible age range of the Naskal intertrappean sediments is between 66.136 and 66.056 Ma at 68% confidence (Wilson Mantilla et al. 2022), thus deposited close to the Cretaceous/Paleogene boundary.

All the three Naskal sections were targeted for the sampling but the sponge spicules were recovered only from the Naskal GSI Quarry section (Fig. 1). The sponge spicule bearing section has a thickness of 120 cm comprises black to grey cherty limestone, hard yellowish shaly mudstone, loose shaly to carbonate mudstone to marlstone, white mudstone, and dark clay with sandy lenses in ascending stratigraphic order (Fig. 1B). Naskal B (Fig. 1C) which is ~7 m west of the Naskal GSI Quarry section yielded only palynomorphs (for details see Wilson Mantilla et al. 2022).

Palaeoecology and age of the Naskal Intertrappean.—The Naskal intertrappean beds have yielded a rich mammal record (summarised in Wilson Mantilla et al. 2022), including the first Indian record of a Cretaceous mammal (Prasad and Sahni 1988). In addition to mammals, it has other vertebrates such as fish, anurans, squamates, sphenodontian, turtles, and crocodylians (Prasad and Sahni 1988; Prasad 2012). Palynoflora of Naskal is represented by marker Maastrichtian taxa, i.e., *Crybelosporites intertrappea*, Maastrichtian–Paleocene taxa, i.e., *Gabonisoris vigourouxii*, *Mulleripollis bolpurensis*, and Paleocene taxa, i.e., *Striacolporites striatus* and *Echistephanocolpites meghalayensis*. Overall, palynoassemblage indicates the presence of transitional flora where Maastrichtian palynomorphs were depleted and Paleocene flora was dominating.

Material and methods

Samples of shale, carbonate mudstone, and marlstone (100 g each) were treated with 5% hydrochloric acid (HCl) until the effervescence subsided. This was followed by thorough washing with distilled water and treatment with 5% hydrofluoric acid (HF) for 5 minutes to remove the thin siliceous secondary coating on the fossils. To remove organic matter, samples were sometimes treated with dilute nitric acid (HNO₃) and 5% potassium hydroxide (KOH). Every chemical treatment was followed by washing the sample with distilled water. After chemical treatments, the sieved samples were divided into two aliquots, one for the preparation of slides for Light Microscopy (LM) using polyvinyl alcohol and Canada balsam, and the other for the preparation of stubs for Scanning Electron Microscopy (SEM).

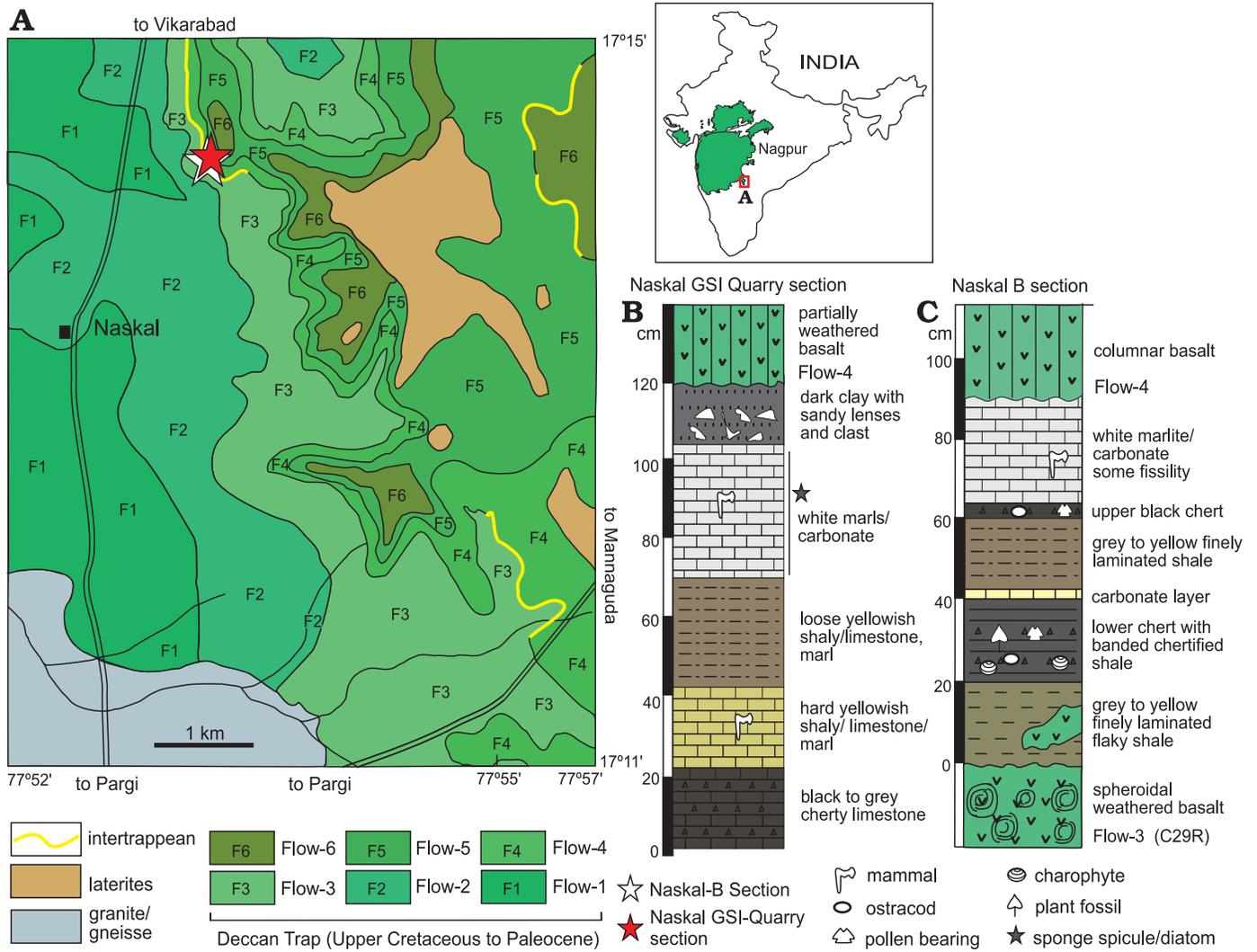


Fig. 1. Map of India showing Deccan volcanic province (green area). A. Location of Naskal intertrappean, Naskal B (white star) and Naskal GSI Quarry sections (red star); map modified after Ahluwalia (1990) and Wilson Mantilla et al. (2022). B. Sponge spicule and diatom bearing horizon in Naskal GSI Quarry section. C. Palynomorph bearing Naskal B section (modified after Wilson Mantilla et al. 2022).

All the slides were studied under a transmitted light Olympus BX51 (Japan) microscope, and the photographs were taken with a DP 20 (Olympus, Japan) camera. A total of 25 spicules from each category were studied and measured under the LM microscope. For SEM studies, the sponge spicules bearing sample was spread over a glass slide and the slide was scanned under a microscope using a 10X objective. The spicules were picked up with the help of hair attached to the dissecting needle and placed over the SEM stub. Later, the stub was coated with gold/palladium, and SEM observations were carried out under the Jeol microscope (Japan) at the Jawaharlal Nehru Aluminium Research Development and Design Centre (JNARDDC), Nagpur, India.

The holotype and paratype material, including the rock samples, studied slides and SEM stubs, are housed in the Museum of the Postgraduate Department of Geology (PGDG), RTM Nagpur University, Nagpur, India. The acronym followed by sample number of the (a) holotype rock

sample is PGDG/NSKQ/2019; (b) slides (SL) followed by numbers are PGNU/NSKQ/SL-1 to 13; (c) SEM stubs (ST) followed by numbers are PGNU/NSKQ/ST-1, 2.

Terminology of morphotraits follows Manconi and Pronzato (2002). The systematic status of taxa was checked in the World Porifera Database (Voogd et al. 2023).

Systematic palaeontology

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Perez, and Boury-Esnault, 2012

Order Spongillida Manconi and Pronzato, 2002

Family Palaeospongillidae Volkmer-Ribeiro and Reitner, 1991

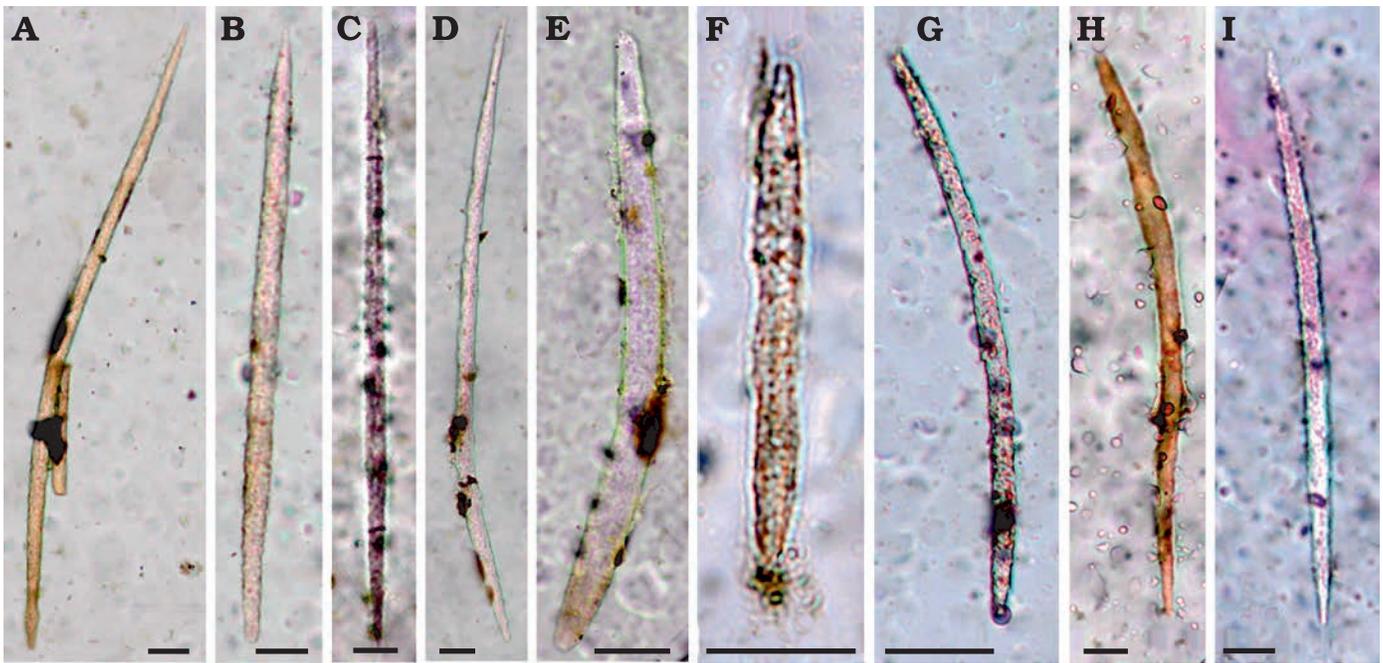


Fig. 2. Megascleres of palaeospongillid sponge *Longibiotula antiqua* gen. et sp. nov. from Upper Cretaceous–lower Paleocene of Naskal GSI Quarry (India). A–I. Oxeas (slides PGNU/NSKQ/SL-1–13) slim to stout with variably pointed tips. Diagenetic processes affect all spicules to various degree. Scale bars 20 μ m. {fig. will be greyscale in printed version}

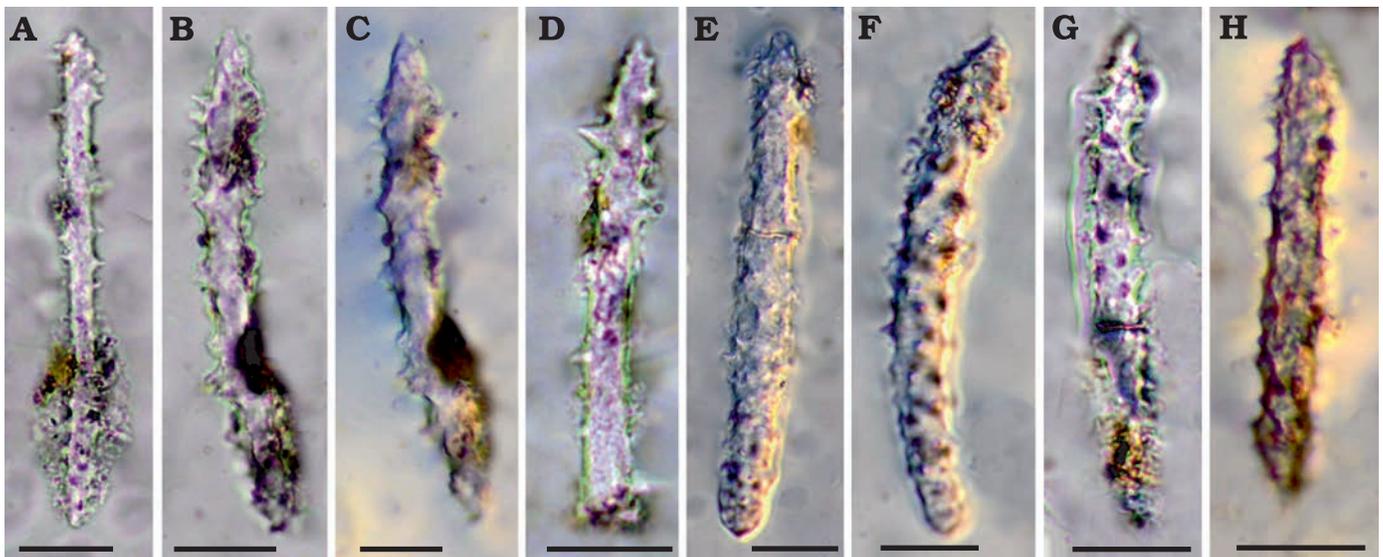


Fig. 3. Megascleres of palaeospongillid sponge *Longibiotula antiqua* gen. et sp. nov. from Upper Cretaceous–lower of Paleocene of Naskal GSI Quarry (India). A–H. Acanthoxeas (slides PGNU/NSKQ/SL-1–13) with large spines. Diagenetic processes affect all spicules to various degree. Scale bars 20 μ m.

Genus *Longibiotula* Pronzato and Manconi nov.

Zoobank LSID: urn:lsid:zoobank.org:act:9A389B3D-118E-42AA-AD9E-1AF484CE7681

Type species: *Longibiotula antiqua* Manconi and Samant, by monotypy.

Etymology: In reference to the long shaft of birotules gemmuloscleres, gender feminine.

Diagnosis.—*Longibiotula* is characterised by gemmuloscleres slender birotules with very long spiny shaft, and two types of skeletal megascleres, i.e., long slim oxeas and short acanthoxeas.

Longibiotula antiqua Manconi and Samant sp. nov.

Figs. 1–5.

Zoobank LSID: urn:lsid:zoobank.org:act:A55B4EB4-F32C-41D0-B20C-C1609F643060

Etymology: From Latin *antiqua*, old.

Type material: Holotype, rock sample PGDG/NSKQ/2019, slides PGNU/NSKQ/SL-1–13, stubs PGNU/NSK/ST-1, 2.

Type locality: Naskal GSI Quarry, 17°14'21" N, 77°53'16" E, Ranga Reddy District, Telangana State, India.

Type horizon: White marl/carbonate layers of Naskal GSI Quarry, Naskal intertrappean beds (Upper Cretaceous–lower Paleocene).

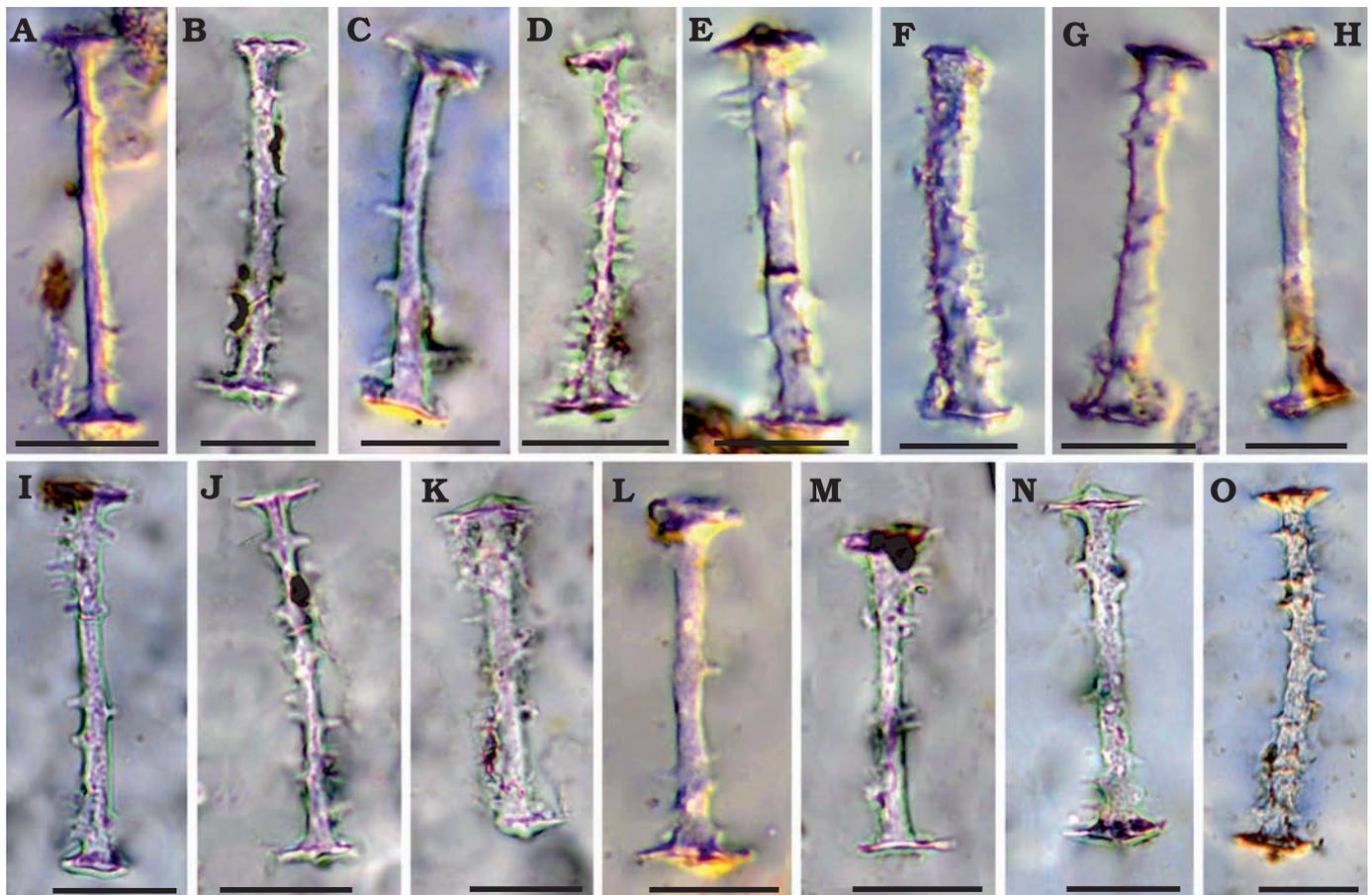


Fig. 4. Gemmuloscleres of palaeospongillid sponge *Longibirotulula antiqua* gen. et sp. non. from Upper Cretaceous–lower Paleocene of Naskal GSI Quarry (India). A–O. Birotules (slides PGNU/NSKQ/SL-1–13) slender, spiny, with long shaft. Diagenetic processes affect all spicules to various degree. Scale bars 20 μ m.

Diagnosis.—*Longibirotulula antiqua* sp. nov. is characterized by slender gemmuloscleres birotules with long spiny shaft, straight to slightly curved, with large scattered spines variably dense and numerous. Rotules flat with indented margins. Skeletal megascleres of two types, slim oxeads microspiny to smooth and short, stout acanthoxeads.

Description.—Skeletal megascleres monaxial with two morphotypes. Slim, long, microspiny to smooth oxeads ($142\text{--}425 \times 6\text{--}13 \mu\text{m}$) rarely sinuous. Shorter, stouter acanthoxeads ($71\text{--}104 \times 6\text{--}9 \mu\text{m}$) straight to slightly curve with dense, large spines. Microscleres absent. Entire gemmules are not found because organic matter associated with gemmular theca is not preserved. Fossil remains are only represented by siliceous spicules. Gemmuloscleres birotules with very long, straight to slightly curved, spiny shaft ($47\text{--}76 \mu\text{m}$ in length, $3\text{--}6 \mu\text{m}$ in thickness), with spines large, numerous, variably dense, and rotules flat with indented margins ($12\text{--}19 \mu\text{m}$ in diameter).

Remarks.—Spicule deposits suggest that the Naskal intertrappean palaeolake was inhabited by a population of sponges with resting stages at the time of deposition. In addition, centric diatoms (*Aulacoseira* spp.) and aquatic to semiaquatic flora were also part of the biotic community.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

The association of centric diatoms *Aulacoseira* sp. with sponge spicules in the uppermost part of the intertrappean indicates the development of eutrophic conditions in the lake, likely due to volcanogenic input in the palaeolake. The presence of resting stages in the sponge remains (gemmuloscleres) suggests possible seasonal variations of water level.

Gemmulation processes, synchronised with the local long-term seasonal rhythm, represent the most successful evolutionary strategy in the life cycle of sponges to colonize inland water; gemmules are asexual propagules able to survive in unfavourable climatic/environmental critical phases and to perform dispersal and defensive roles to persist in situ; architecture of gemmules and their morphotraits show a wide adaptive radiation worldwide (Manconi and Pronzato 2002, 2008, 2009, 2015, 2016a, b; Manconi 2008).

Although entire gemmules have not been found in the Naskal fossil remains, *Longibirotulula antiqua* Manconi and Samant sp. nov. is well distinguished from the rest of the

known fossil taxa by a unique spicular complement lacking skeletal microscleres, and composed of skeletal monaxons (long slim oxeas, shorter acanthoxeas) and long gemmuloscleres birotules. The combination of these three spicular morphs of *Longibiotula antiqua* Manconi and Samant sp. nov. partially resembles with that of some fossil and living taxa of the order Spongillida.

Gemmuloscleres morphologies and morphometries of *Longibiotula antiqua* Manconi and Samant sp. nov. indicate divergence from fossils birotule-bearing species of the worldwide reported genus *Ephydatia* Lamouroux, 1816 (Pronzato et al. 2017), i.e., (i) *Ephydatia fossilis* Traxler, 1894 (Miocene in age, western Palaearctic, Romania) with stout, spiny birotules (41–69 μm in length) and rotules with indented margins (Traxler 1894); (ii) *Ephydatia kaiserii* Rauff, 1926 (pre-middle Eocene in age, south-western Afrotropical, Namibia) with entire gemmules bearing smooth birotules (44–65 μm in length) and non-incised margins of flat rotules (Rauff 1926); (iii) *Ephydatia chiliana* Pisera and Sáez, 2003 (Late Miocene in age, south-western Neotropical, Atacama Region, Chile) with birotules (39–45 μm in length) bearing spiny shaft and rotules with irregular margins, often deeply incised (Pisera and Saez 2003), and (iv) *Ephydatia cf. facunda* Weltner, 1895 (middle Eocene in age, Northern Nearctic, Canada) with stout birotules (26–57 μm in length) with spiny shaft and strongly incised margins of both rotules (Pisera et al. 2016).

As for extant birotules-bearing Spongillida, *Longibiotula antiqua* Manconi and Samant sp. nov. slightly resembles some taxa, but gemmulosclere outline and/or rotules morphs differ from species of e.g., *Anheteromeyenia* Schröder, 1927; *Corvoheteromeyenia* Ezcurra de Drago, 1979; *Corvomeyenia* Weltner, 1913; *Dosilia* Gray, 1867; *Heteromeyenia* Potts, 1881; *Racekiela* Bass and Volkmer-Ribeiro, 1998, and *Umborotula* Penney and Racek, 1968 (Penney and Racek 1968; Manconi and Pronzato 2002, 2015, 2016b; Pronzato and Manconi 2019a).

The fossil *Longibiotula antiqua* Manconi and Samant sp. nov. partly shares gemmuloscleres outline and length (47–76 μm) with extant species of *Ephydatia* (e.g., 45–50 μm , *Ephydatia robusta* Potts, 1887), and *Heteromeyenia* (e.g., 75–88 μm , *Heteromeyenia stepanowi* Dybowski, 1884). The *Longibiotula antiqua* Manconi and Samant sp. nov. birotules morphs and length particularly resembles the slender birotules known from the species of the genus *Heterorotula* Penney and Racek, 1968 e.g., *Heterorotula kakahuensis* (Traxler, 1896) (38–44 μm from New Zealand), *Heterorotula multidentata* (Weltner, 1895) (64–84 μm from Australia, Penney and Racek 1968; 32–48 μm from New Caledonia, Rützler 1968) and *Heterorotula caledonensis* (Rützler, 1968) (30–100 μm from New Caledonia) (Penney and Racek 1968; Rützler 1968; Racek 1969; Pronzato and Manconi 2019b).

As for megascleres, smooth to microspiny long oxeas of *Longibiotula antiqua* Manconi and Samant sp. nov. (142–425 \times 6–13 μm) partly show similarity with the megascleres morphometric values in the species of *Heterorotula* (Penney

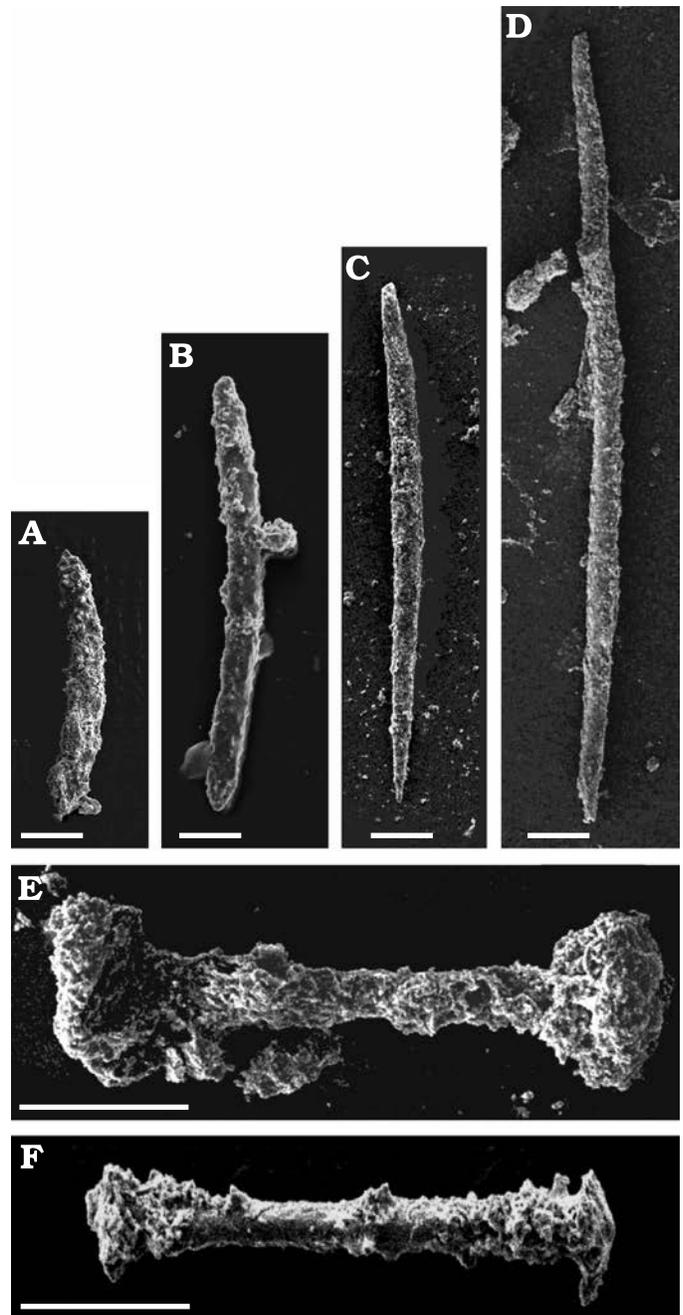


Fig. 5. Spicular complement of skeleton and gemmules of palaeospongillid sponge *Longibiotula antiqua* gen. et sp. nov. from Upper Cretaceous–lower Paleocene of Naskal GSI Quarry (India) (slides PGNU/NSKQ/ST-1, 2). A, B. Acanthoxeas short with dense spines. C, D. Oxeas fusiform, long and with acute tips. E, F. Birotules with long shaft. Diagenetic processes affect all spicules to various degree. Scale bars 20 μm .

and Racek 1968; Racek 1969; Volkmer-Ribeiro and Motta 1995; Rützler 1968; Pronzato and Manconi 2002, 2019b), namely (i) the Australian endemic lineage, e.g., *Heterorotula capewelli* (Bowerbank, 1863) (195–330 \times 13–18 μm , type species), *Heterorotula nigra* (Lendenfeld, 1887) (224–360 \times 7–13 μm), *Heterorotula multidentata* (284–320 \times 10–18 μm), *Heterorotula multiformis* (Weltner, 1910) (330–420 \times 13–20 μm), (ii) the New Zealand–New Caledonia endemic lin-

eage with *Heterorotula kakahuensis* (170–288 × 8–22 μm) and *Heterorotula caledonensis* (100–150 × 8–19 μm) and, in addition, with (iii) the Neotropical endemic lineage *Heterorotula fistula* Volkmer-Ribeiro and Motta, 1995 (196–361 × 16–31 μm).

Furthermore, short acanthoxeas of *Longibiotula antiqua* (71–104 × 6–9 μm, here interpreted as gemmular cage components) partly show similarity with those of *Heterorotula*, which were reported as a short skeletal megascleres and/or belonging to the gemmular cage, particularly evident in *H. kakahuensis* endemic to New Zealand (Pronzato and Manconi 2019b: fig. 7C, D) and *H. caledonensis* endemic to New Caledonia (Pronzato and Manconi 2019b: fig. 4A, B).

In conclusion, the gemmuloscleres and megascleres morphotraits of *Longibiotula antiqua* gen. et sp. nov. are similar to that of some species of *Heterorotula* known from living populations in Australia, New Zealand, and New Caledonia and from subequatorial Brazil fossils remains, suggesting a Gondwanan track which is not seen in the Afrotropical Region (Manconi and Pronzato 2009).

The old evolutionary history and radiation of Spongillida seem to be written in the gemmular architecture of coeval fossil remains. The *Longibiotula antiqua* Manconi and Samant sp. nov. from the Deccan intertrappean sediments close to the Cretaceous/Paleogene boundary, presumably displays a radial arrangement of birotule spicules in the gemmular theca. In contrast, the Deccan Upper Cretaceous (Maastrichtian, Chron 30N) intertrappean sediments of Malwa Group were inhabited by *Palaeocorvospongilla cretacea* characterized by a totally different spicular complement of spiny stout oxeas/strongyles/strongyloxeas as gemmuloscleres and pseudobiotules as skeletal microscleres (Samant et al. 2021). The gemmules of the Early Cretaceous *Palaeospongilla chubutensis* Ott and Volkmer, 1972, from Patagonia (Volkmer-Ribeiro and Reitner 1991) has oxeas gemmuloscleres which are almost radially, irregularly arranged in the gemmular theca. On the basis of these record, the family Palaeospongillidae is enlarged and now comprises five monotypic genera: *Eospongilla* (*Eospongilla morrisonensis* Dunagan, 1999), *Longibiotula* Pronzato and Manconi gen. nov., *Lutetiospongilla* (*Lutetiospongilla heili* Richter and Wuttke, 1999), *Palaeocorvospongilla* Pronzato and Manconi, 2021, and *Palaeospongilla* Ott and Volkmer, 1972.

The discovery of the new species *Longibiotula antiqua* confirm that the Deccan volcanic province in India is a favourable area to study the natural history of freshwater sponges adaptive processes. The data give us more information about how the anatomy of Spongillida have changed or persisted over time and how they have always been able to drive a morphological diversification by a successful evolution of resistant bodies, i.e., gemmules (Manconi and Pronzato 2002, 2015, 2016a). Importantly, the long lasting structural conservative trend of freshwater sponges (Pisera 2006; Pronzato et al. 2017; Samant et al. 2021) seems to be confirmed by Deccan spicule morphologies that remained almost unchanged through tens of millions of years.

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