Renewed Study of the Type Material of *Palaeospongilla chubutensis* Ott and Volkheimer (1972)

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Introduction

The first fossilized gemmule-bearing freshwater sponge was described by Ott and Volkheimer (1972) from the Patagonian Lower Cretaceous (Aptian) at the Chubut River valley, in Argentina. However, an accurate reading of the original description shows that the photograph of the gemmules presented in Fig. 3 does not show the thick gemmular wall and the particular arrangement of gemmoscleres shown in Fig. 5. Also the drawings of the gemmoscleres shown in Fig. 6 do not resemble the gemmoscleres photographed in Fig. 5. In a second paper (Volkheimer and Ott 1973), the authors presented a study of the fauna and flora found associated with *P. chubutensis* and concluded that the paleohabitat was a lacustrine one subjected to strong seasonal droughts. This second paper proposed a phyletic relationship of *P. chubutensis* with the extant genus *Spongilla* and, more particularly, with *Spongilla alba* (Carter 1849). Soon after, Racek and Harrison (1975) proposed a strong relationship of *Palaeospongilla* with the extant genus *Radiospongilla*. Only drawings were presented and reference was made to a deposition of the preparations in the Australian Museum (Sydney) and the Smithsonian Institute (Washington). Based on these discrepancies between the illustrations and the phylogenetic ideas given by the original authors and by Racek and Harrison, the present authors decided to undertake a renewed study of these very important fossil materials, which represent the only entirely preserved freshwater sponges.

Material and Methods

The holotype material of *P. chubutensis* and two paratypes are deposited at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina). Three pieces of a further paratype are housed with the collection of the Bayerische Staatssammlung für historische Geologie und Paläontologie (Munich, West Germany). One thin section of a paratype (no. Z 4748) is deposited at the Australian Museum (Sydney, Australia). The thin sections, which were made from a topotype (Racek and Harrison 1975) could not be found at the Smithsonian Institute or at the Australian Museum. New thin sections and SEM preparations were made from the paratype deposited in Munich. The

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Fossil and Recent Sponges

thin section loaned from the Australian Museum was throughly restudied and photographed.

The SEM studies were carried out by the junior author with a Cambridge 360. New preparation methods were used to figure out the spicular skeleton and preserved soft parts as well as preserved gemmules. The probes were etched for 3 h with 5% Titriplex-III-solution ($C_{10}H_{14}N_2O_{18}$*$2H_2O$) (Reitner and Engeser 1987). This method permits etching very fine and sensitive structures, e.g., small gemmoscleres and acanthose microscleres, which are preserved in mono- or paucicrystalline calcite. Under the SEM, backscatter technique (secondary electrons) was used. This method makes it possible to distinguish irregularities on the surface structures caused by special contrast and therefore gives a much better view of spiny structures.

Description of the Species

1. Palaespongilla chubutensis Ott and Volkheimer

The renewed study of these fossil specimens revealed that the original description of Ott and Volkheimer and also the redescription presented by Racek and Harrison (1975) apply to an association of two genera. The occurrence of such associations is a common fact among extant freshwater sponges (Volkmer-Ribeiro and de Rosa-Barbosa 1972; Racek 1969).

Part of the material described as *Palaeospongilla chubutensis* is now synonymized under *Spongilla patagonica* n.sp. The main part of the sponge material is *Palaeospongilla chubutensis* sensu strictu.

Palaeospongillidae new family
Type genus: *Palaeospongilla* Ott and Volkheimer 1972, as presently redefined.

Diagnosis: Fossil freshwater sponges with gemmules devoid of gemmoscleres but with a thin inner coat and a thin pneumatic coat.

Gemmules in groups or isolated and protected by an outer armature of tangentially arranged megascleres.

Palaeospongilla Ott and Volkheimer 1972, redefined
Palaeospongilla Ott and Volkheimer 1972, p. 53 (partim)
Type species: *Palaeospongilla chubutensis* Ott and Volkheimer 1972, as presently redescribed.

Diagnosis: Sponge forming thick crusts. Gemmules without gemmoscleres, with a conspicuous inner coat and thin pneumatic coat. Foramen devoid of a porous tube. Gemmules single but more usually packed in groups of two or several, each package or each single gemmule protected by an outer envelope of tangentially arranged megascleres. Megascleres sparsely spined and curved oxea. Microscleres not detected.

Palaeospongilla chubutensis Ott and Volkheimer 1972 (Figs. 1; 2a,b; 3a,b)

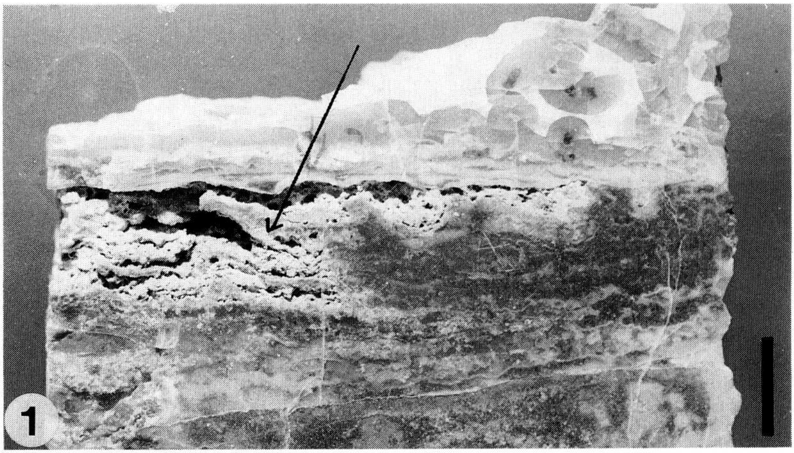


Fig. 1. Paratype of *Palaeospongilla chubutensis* deposited at Museo Bernardino Rivadavia, Buenos Aires. *Arrow* points to the sponge fossilized crust. Scale = 1 cm

Palaeospongilla chubutensis (Ott and Volkheimer 1972; p. 53 partim and Figs. 2,3,4)
Holotype: As originally designated (Ott and Volkheimer 1972, Fig. 2)
Paratypes: As originally designated (Ott and Volkheimer 1972, p. 53)

Redescription

Sponge forming overlaying crusts around the stems of aquatic plants and plant remains (Fig. 1) (Ott and Volkheimer 1972, Fig. 2). Skeleton consists of main ascending skeletal fibers and of secondary thick fibers placed at right angles to main fibers thus composing a reticulum of square meshes (Ott and Volkheimer 1972, Fig. 3).
Megascleres: Stout, straight to feebly curved, sparsely, abruptly pointed oxea (length, 230–260 μm; width, 15–18 μm).
Microscleres: not detected; Gemmoscleres: absent
Gemmules: As described in the generic definition. Diameters: 483–644 μm
Distribution: Hitherto known only from type locality (valley of the Chubut River, 16 km from locality of Cerro Condor, Chubut Province, Argentina)
Age: Patagonian lower Cretaceous (Aptian), Chubut Group (Ott and Volkheimer 1972, p. 53)

Preserved Reproductive Characters

This exceptionally well-preserved fossil allows study first of the reproductive process of a Cretaceous freshwater sponge. The preserved oocytes, oocyte for-

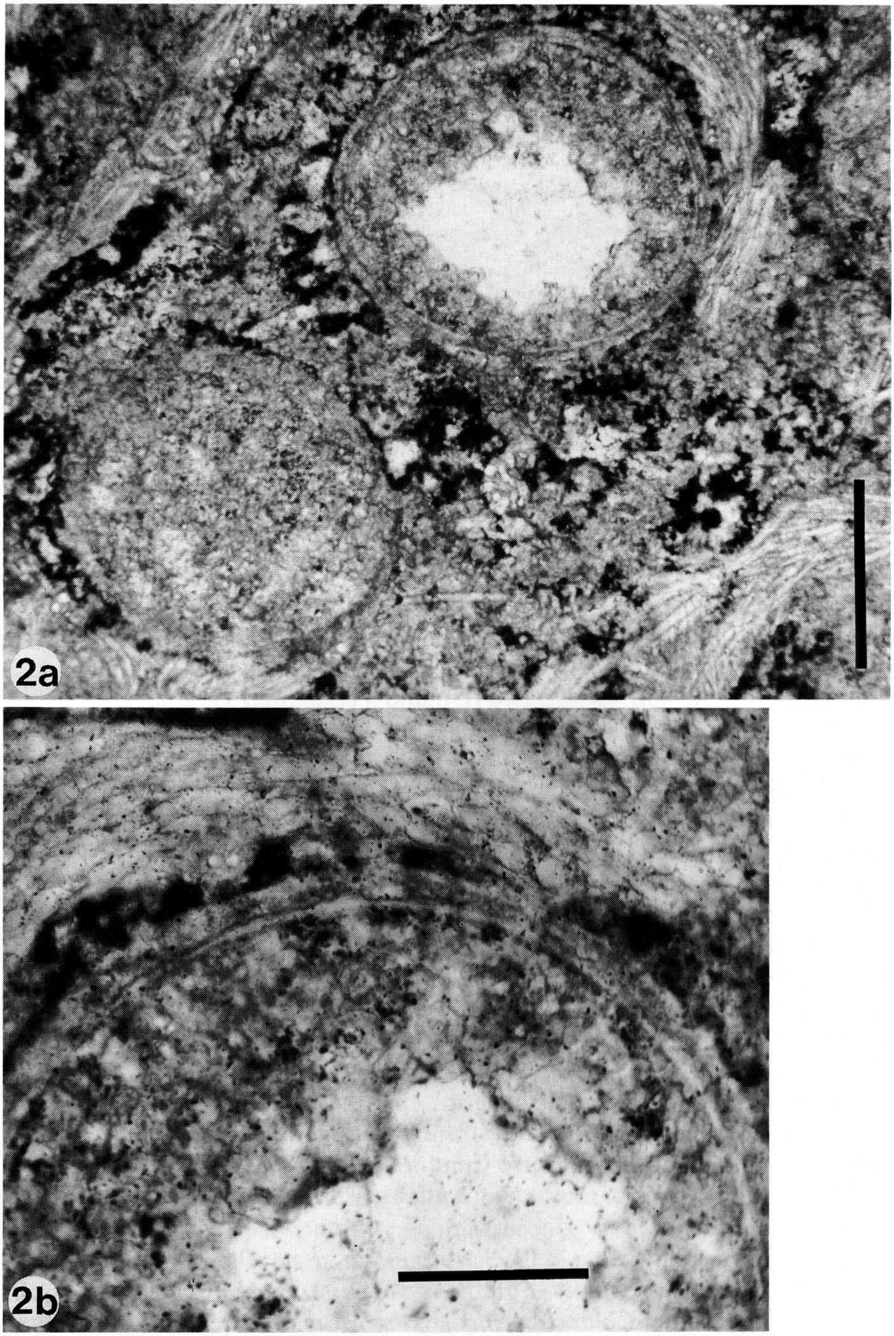


Fig. 2. a Gemmule formation in *P. chubutensis* photographed from the thin section deposited at the Australian Museum. To the right coats already formed, to the left inner coat in the forming, area of the foraminal tube last to be formed. Notice spongocytes groupped around the coats. Scale = 250 μm. **b** Detail of right gemmule of **a**. Notice inner gemular coat, pneumatic coat and the tangentially arranged megascleres of the common envelope. Scale = 125 μm

mation, and gemmule formation are comparable with extant freshwater sponges. The study of the thin section of *Palaeospongilla chubutensis* deposited in the Australian Museum (Sydney) revealed that the sponge was forming gemmules after a period of oocyte production (Fig. 2a,b). One mature oocyte (Fig. 3a,b) can be seen side by side with several empty follicles. The cytological characteristics of this oocyte and of the gemmules of *Palaeospongilla chubutensis* are listed in the legends for the figures (Fig. 2a,b; 3a,b) and generally conform with the literature on this subject (Simpson 1984).

The oocytes of *Palaeospongilla chubutensis* share a large number of identities with the oocytes of Tetractinomorpha according to the descriptions and illustrations of Liaci et al. (1971).

The oocyte was fossilized at the moment when phagocytosis was finished and a follicle epithelium was already isolated from the mesohyle cells (synvivodiagenetic). At this moment nuclear extrusion were taking place and a second nutritional phase to the oocyte was starting with forming of a crown of nurse cells. The nuclei of such nurse cell are conspicuously placed close to the follicle wall and the cell processes are already orientated towards the oocyte surface (Fig.3b).

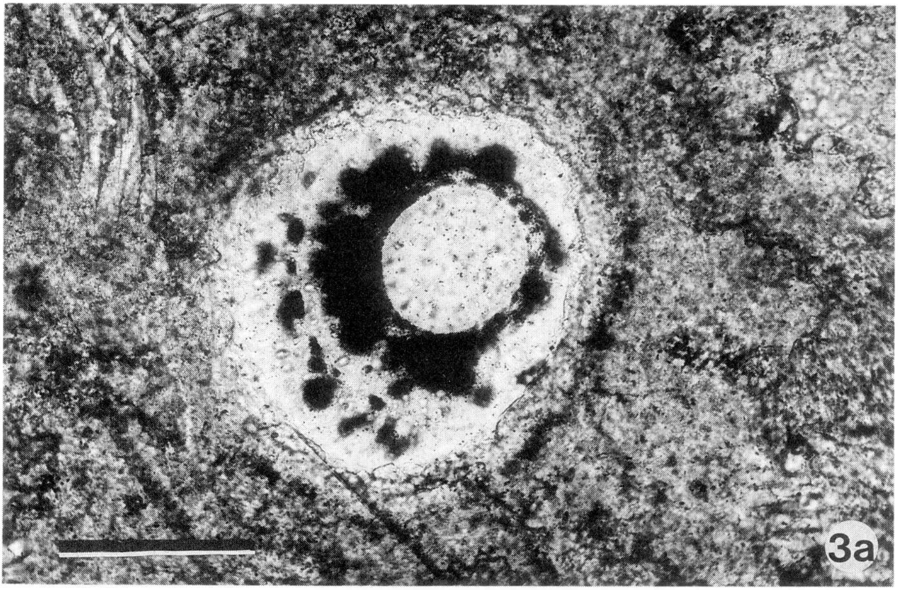
Diameter of the oocyte plus follicle: 330 μm; diameter of the nucleus: 133 μm.

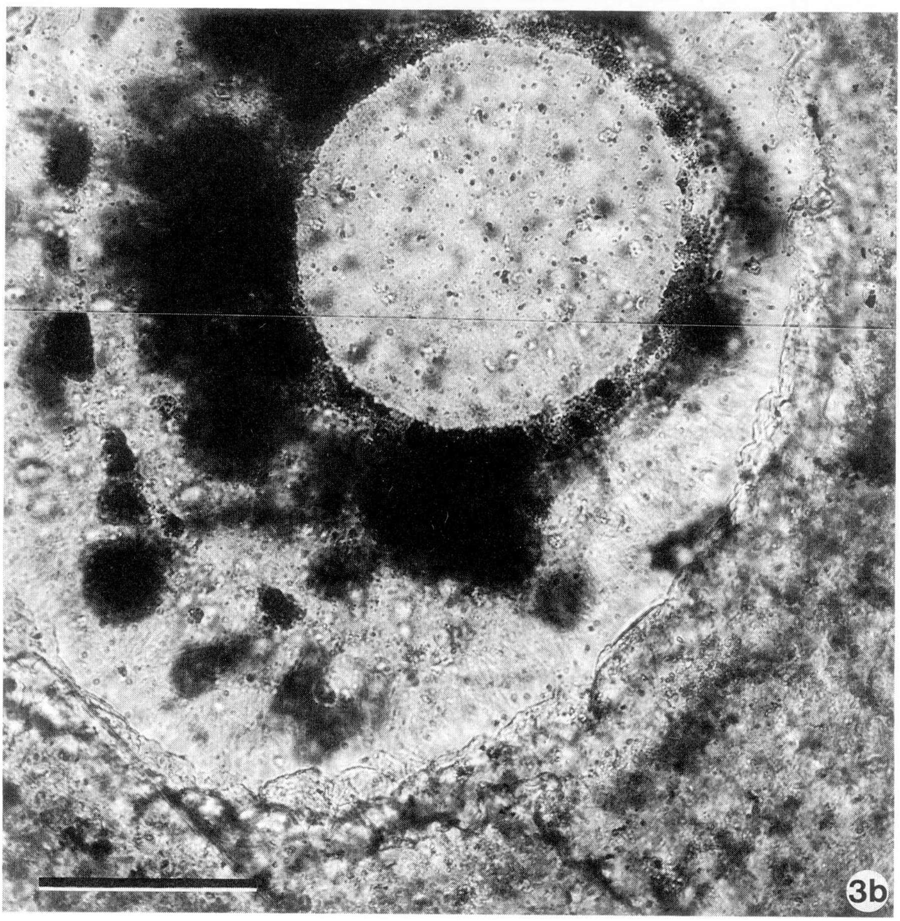
The great number of empty follicles and young gemmules, suggest an alternation of reproductive processes with drastic reduction of the time interval which elapses between sexual reproduction and gemmulation in extant freshwater sponges of temperate regions (Frost et al. 1982). Three hypotheses can tentatively explain this fact:

1. The sponge was living in a temperate region but in a habitat seasonally submerged for short periods.
2. A sudden drought occurred which induced precocious gemmulation.
3. The sponge was living in a tropical habitat subjected to seasonally long periods of drought.

Discussion

Palaeospongilla chubutensis displays characteristics not seen in any other presently known extant freshwater sponges. For this reason, a new family is proposed to contain this monotypic fossil genus. Among the extant freshwater sponges only the *Spongilla aspinosa*/*Spongilla inarmata*-*Spongilla spoliata* group of species (Volkmer-Ribeiro and Maciel 1983) have the same common character as seen in *Palaeospongilla chubutensis*, that gemmules have no gemmoscleres and are protected by a capsule of normal megascleres. However, in the three extant species each gemmule has its own capsule, which is in extreme close contact with the inner gemmule wall, so that some megascleres could be embedded in the gemmule wall. These capsules also exhibit no distinctive particular arrangement of megascleres which are woven in disorderly fashion around the gemmule (cf. Fig. 2 in Volkmer-Ribeiro and Traveset 1987). The inner gemmular coat of these extant species is quite thin and distinguishing three layers, including a pneumatic


3a


3b

coat is difficult. A very conspicuous foraminal collar is also present in the gemmules of the three extant species. The fossil freshwater sponge has no microscleres, which are present in *Spongilla*. The only microscleres within the described sponges are related to a new species, *Spongilla patagonica* n.sp. (Fig. 5a,b). Also remarkable is the localization of the gemmules of *Palaeospongilla chubutensis* from base to the top layer of the sponge, whilst in the extant *Spongilla* species the gemmules are usually located close to the sponge surface. The three *Spongilla* species form thin skeletal fibers which support waving branches and pierce the sponge surface as hispid projections. *Palaeospongilla chubutensis*, on the contrary, seems to have flat, thick, foliated crusts with lobose contour and a smooth surface (Fig. 2 in Ott and Volkheimer 1972)

2. Spongilla patagonica n.sp.
Family Spongillidae Gray (1867), sensu Volkmer-Ribeiro (in press)

Spongilla Lamarck (1816) sensu Penney and Racek (1968)

Palaeospongilla Ott and Volkheimer 1972, p. 53 (partim)

Spongilla patagonica n.sp. (Figs. 4a,b; 5a,b)

Palaeospongilla chubutensis Ott and Volkheimer 1972; p. 53 (partim, Fig. 5)
Palaeospongilla chubutensis Racek and Harrison 1975; p. 158 (partim)

Derivatio nominis: After Patagonia, a landscape in Argentina
Holotype: The holotype is located on the paratype specimen of *Palaeospongilla chubutensis* which is deposited within the Bayerische Staatssammlung für Historische Geologie und Paläontologie, Munich.
SEM preparation deposited in the Institut für Paläontologie der Freien Universität Berlin IPFUB/JR/89; (Figs. 4a,b; 5a,b).

Description

Megascleres slim, gradually sharp pointed, slightly curved, smooth oxea (length 210–260 μm, width 7–10 μm).
Microscleres: usually straight, spined oxea; some slightly curved oxea occur also (length 100–110 μm, width 9–10 μm).
Gemmoscleres: short, slightly curved to strongly bent, rarely straight, strongly

Fig. 3. **a** Maturing oocyte of *P. chubutensis* (thin section deposited at the Australian Museum). Notice surrounding folicle ephitelium and the collagen matrix starting to form outside the epithelium. Nucleolus displaced from the sectioning plane. Scale = 250 μm. **b** Detailed magnification of **a**. Notice dense material being extruded from the nucleus and the lastly phagocytized microgranular cells aligned midway between the follicle epithelium and the nuclear extrusions. The collar of nurse (spherulous) cells starting to differentiate, their nuclei are seen bounding the epithelium cells and their processes are already oriented towards the egg surface. Scale = 125 μm

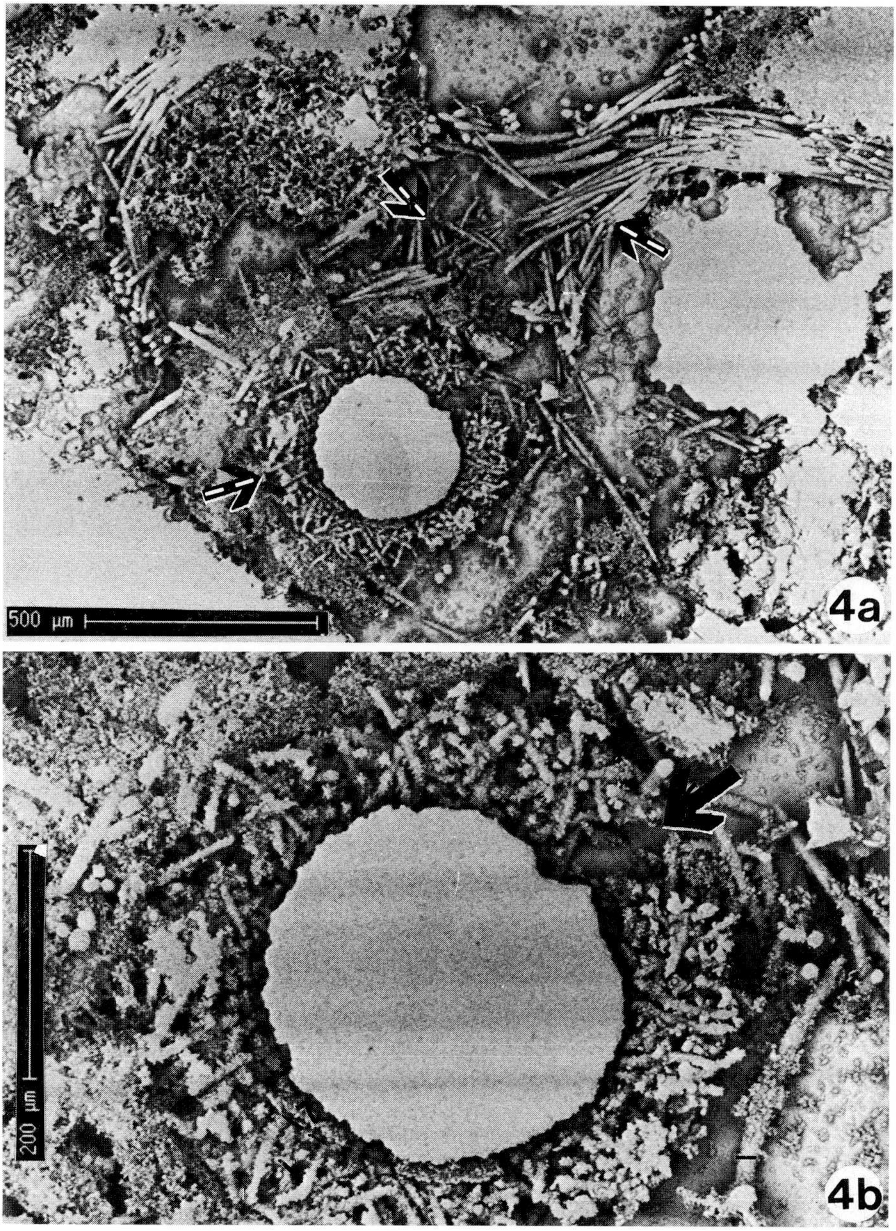


Fig. 4. SEM micrographs of *Spongilla patagonica* n.sp. **a** *Bottom arrow* points to one gemmule with gemmoscleres in situ: *left arrow* points to microscleres: *right arrow* indicates the thinner magascleres of *S. patagonica* placed in close contact with the stout megascleres of *P. chubutensis.* **b** Same gemmule as **a** at larger magnification: the *arrow* indicates the place occupied by the long foraminal nipple; the gemmule is seen to have had a conspicuous inner coat and a large pneumatic coat where gemmoscleres were randomly embedded

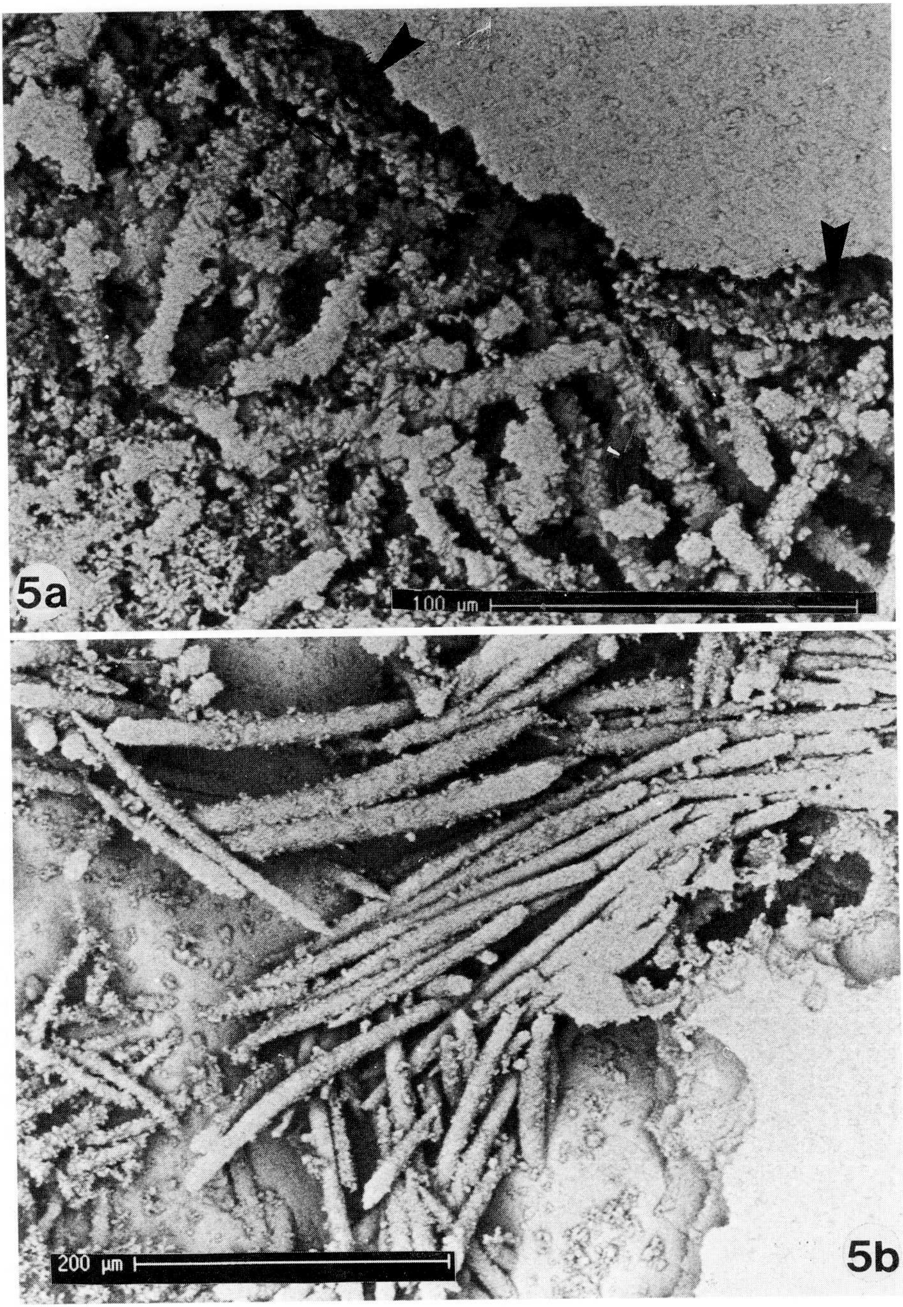


Fig. 5. a Same gemmule as Fig. 4a and b, showing details of the gemmular coats and of the gemmoscleres' shape; the *two arrows* indicate the place occupied by the inner gemmular coat. **b** *Spongilla patagonica* n.sp.; Detailed magnification of the area indicated by the left arrow in Fig. 4a shows the megascleres of *P. chubutensis* in the *upper part* and those of *S. patagonica* n.sp. in the *middle* and *bottom parts* of the photograph; *at left* grouping of microscleres of *S. patagonica* n.sp.

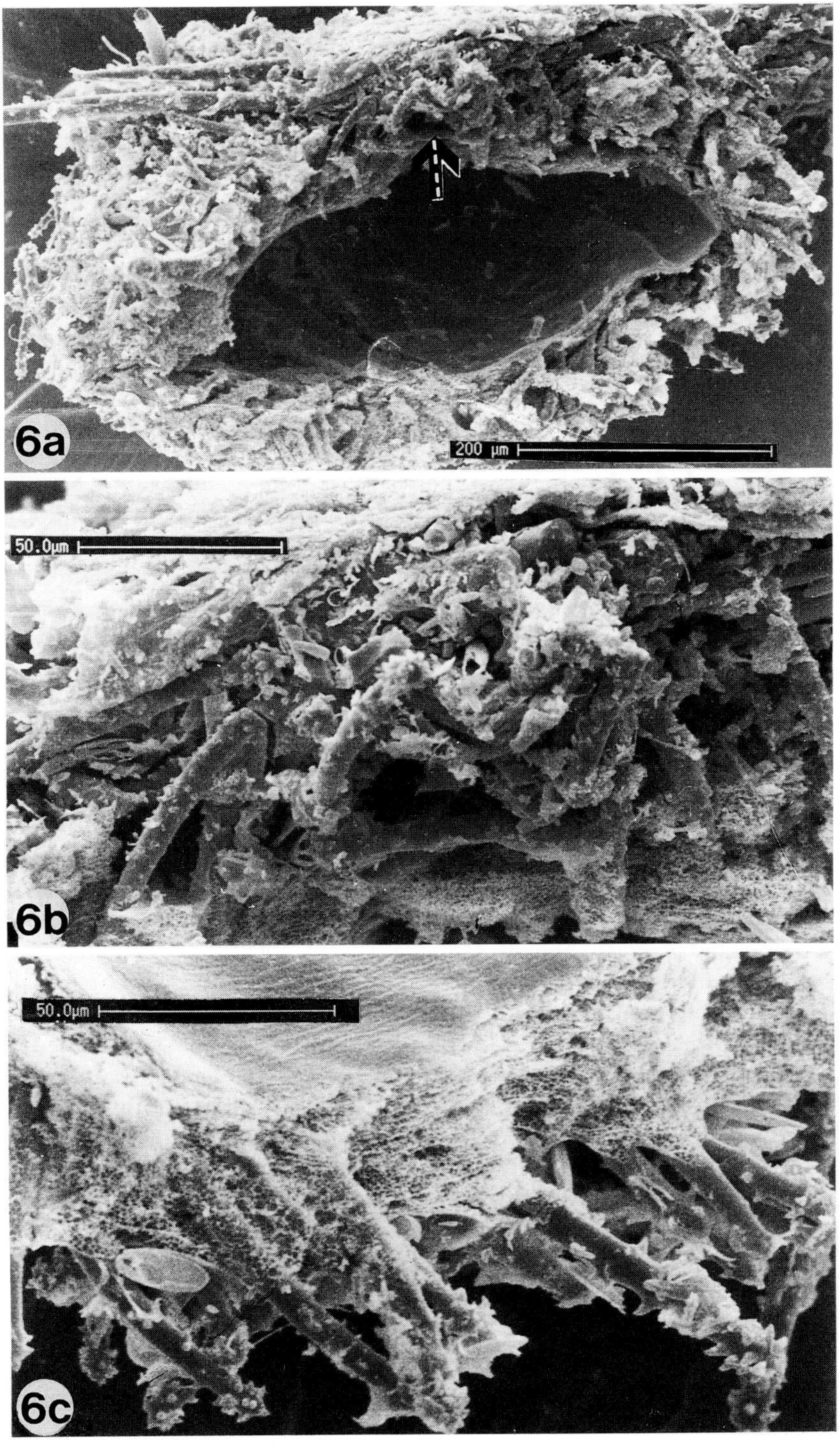
spined, cylindrical amphistrongyla, some spines larger and recurved, extremities of the scleres with a starlike profile (length 70–80 μm, width 8 μm).
Gemmules: spherical, with a thick inner- and a large pneumatic coat. The gemmoscleres are within the pneumatic layer randomly orientated and loosely packed, the tips of the spicules sometimes protruding beyond the outer surface of the gemmule coat. Foramen is single, nipple-like, extending to the surface of the pneumatic coat. The gemmule of Fig. 4b has a diameter of 469 μm. The inner coat is 20 μm and the pneumatic coat is 100 μm thick.

Distribution and geological age: Same as for *Palaeospongilla chubutensis*.

Discussion

On exhaustive microscopic scrutiny and SEM preparation of material isolated from one paratype (Munich specimen) of *Palaeospongilla chubutensis*, two gemmules could be detected which are completely different from those of *Palaeospongilla chubutensis*. The gemmule coatings and gemmoscleres (Figs. 4a,b; 5a,b) are almost identical to those of the extant *Spongilla alba* Carter 1849. The gemmoscleres are identical with the ones illustrated by Ott and Volkheimer (1972, p. 58, Fig. 5), and by Racek and Harrison (1975, p. 160, Fig. 6). SEM preparations were made of gemmules of the extant species *Spongilla alba* (Fig. 6a-c) from material collected by E.H. Cordero from Jacarepagua, coastal lagoonal area of Rio de Janeiro, Brazil, in June 31, 1940. [The specimen is deposited in the Porifera collection of Museu de Ciencias Naturais of Fundacao Zoobotanica do Rio Grande do Sul (MCN), no. 1271]. The gemmules of the fossil and the extant species exhibit close affinities of the inner coat, the pneumatic coat, the foraminal area, the gemmoscleres, and the gemmosclere embedding within the pneumatic coat. A further characteristic feature of the two species is the possession of microscleres which are longer and thinner than the gemmoscleres (cf. *Spongilla alba* in Volkmer-Ribeiro and Traveset 1987, p. 227, Fig. 3). The description of a new species is justified by the fact that the fossil material does not allow for a precise perception of the spines covering the microscleres. The fossil species shows dimensions which are smaller than those shown by Penney and Racek (1968) for *Spongilla alba*. The observed dimensions agree with those presented by the same authors for *Spongilla wagneri*, a species placed by Poirrier 1976 into synonymy with *Spongilla alba*. *Spongilla alba* is thus phylogenetically closely related to *Spongilla patagonica* n.sp.

Fig. 6. SEM micrograph of a gemmule of the extant *Spongilla alba* Carter 1849 (from specimen MCN no. 1271). **a** Cross-section of gemmule; notice inner coat and thick pneumatic coat; gemmoscleres randomly embedded in the pneumatic coat. **b** Magnification of the area indicated by the *arrow* in **a** shows scanty spongin gluing the gemmoscleres together and the thin outer coat. **c** Detail of the gemmular walls of *S. alba*; notice gemmoscleres protruding from the pneumatic coat and the extremely variable shape of the gemmoscleres' extremities


6a
200 µm
50.0µm
6b
50.0µm
6c

General Remarks

Racek and Harrison (1975) rejected the possibility of a spicular mixture of two distinct species. Both fossil species were silicified synvivodiagenetically and exhibit no overlapping growth. Only one kind of gemmule type was recognized. Epizoism is a common feature among extant marine (Ruetzler 1970) and freshwater sponges Racek 1969; Volkmer-Ribeiro and de Rosa-Barbosa 1972). The degree of skeletal development in the associated species depends strongly on which species is the dominant one. In the present case *Palaeospongilla chubutensis* was the dominant species and the skeletal fibers described by Ott and Volkheimer belong to this species. *Spongilla patagonica* must have formed tiny patches of isolated gemmules covered by skeletal fibers soon overgrown by *Palaeospongilla chubutensis*.

The taxonomic review of *Palaeospongilla chubutensis* proposed by Volkheimer and Ott (1973) was caused by Racek's advice (p. 459) to the authors as to the close relationship between their species and *Spongilla alba* Carter 1849. However, Racek and Harrison (1975) proposed a close relationship of *Palaeospongilla chubutensis* with the extant genus *Radiospongilla* Penny and Racek (1968). They considered *Palaeospongilla chubutensis* a stem group from which the genera *Radiospongilla* and *Spongilla* evolved, each of them inheriting part of the double spicular set of *Palaeospongilla*. The fossil sponge supported Penny and Racek's (1968 p. 63) proposal of a monophyletic origin of all gemmule-producing freshwater sponges, grouped by the authors (op.cit) in the Spongillidae. *Radiospongilla* would lead the rodlike structures up to the birotulated gemmoscleres on account of the incipient rotules found in the gemmoscleres of some species of *Radiospongilla*.

After Marshall's (1883) and Brien's (1967) ideas of a polyphyletic origin for freshwater sponges, Volkmer-Ribeiro (1986, in press) restricted the family Spongillidae sensu Penney and Racek (1968). A large number of genera considered as spongillids by these authors have been transferred into the families Potamolepidae Brien and Metaniidae Volkmer-Ribeiro (1986). However, the restricted family Spongillidae is still considered by Volkmer-Ribeiro as an artificial grouping of genera deserving further studies. The close morphological similarity betwen *Spongilla alba* and *Spongilla patagonica* n.sp. is linked with the distribution and ecology of the taxon *Spongilla alba*, and *Spongilla cenota* (Harrison 1974). According to Harrison (1974), *Spongilla alba* has a circumlitoral distribution in tropical and subtropical areas with a strong tolerance to brackish waters. This ecological preference if extended to *Spongilla patagonica* fits well into the paleohabitats inferred by Ott and Volkheimer (1972) and Volkheimer and Ott (1973) for the fossil fauna and flora associated with *Palaeospongilla chubutensis*, i.e., a lacustrine habitat in a Mediterranean climate. Also the fact that both sponge species were forming gemmules at the moment of fossilization agrees with the proposition of a habitat subjected to periodical droughts.

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