ON THE STATUS OF THE RADIOLARIAN GENERA LONCHOSPHAERA POPOFSKY, 1908 AND ARACHNOSTYLOUS HOLLANDE AND ENJUMET, 1960

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Abstract The article discusses the structural and taxonomic problems of the radiolarian genera Lonchospaera Popofsky, 1908 and Arachnostylos Holland and Enjumet, 1960. To solve them the author studied their initial skeletons that represent the main basis of radiolarian taxonomy at genus and suprageneric levels. He concluded that Arachnostylos is a younger synonym of Lonchospaera and that this genus is a member of the family Excentroconchidae Holland and Enjumet, 1960. The type species is re-described and two new species of Lonchospaera (L. mariae n. sp. and L. cauleti n. sp.) are described herein.

Keywords: Radiolaria, Entactinaria, Quaternary, Taxonomy.

INTRODUCTION

This article is a small part of my long lasting study undertaken for the knowledge of Mesozoic and Cenozoic entactinarian Radiolaria. I shall discuss in it the status of two very rarely cited and little known Quaternary radiolarian genera, Lonchospaera Popofsky, 1908 and Arachnostylos Holland and Enjumet, 1960, on the basis of the structural study of their initial skeleton that represents the most important criterion for genera and suprageneric taxonomic units (De Wever et al., 2001). The knowledge of this skeleton will allow us to situate the two genera in the phylogenetic tree of radiolarians and to suggest their relationship with other radiolarian genera.

The genus Lonchospaera was described by Popofsky (1908) on the basis of four specimens, of whom three illustrated, found in the material collected from the Antarctic waters by the Deutsche Südpolar Expedition (1901-1903) and assigned to a single species, Lonchospaera spicata Popofsky, 1908. According to the initial description, its skeleton consists of a medullary shell and a cortical one, both separated from one another by an empty space and interconnected through six to ten or more radial bars that are prolonged outside into conical spines. As Popofsky mentioned, the number of radial spines is smaller in the younger specimens and greater in the older ones. According to the original description and illustrations, the medullary shell is irregular and consists of curved bars that form meshes of irregular shape and size. The radial spines give rise to some lateral branches inside the cortical shell, in the proximity of its wall. These branches ramify and represent additional inner connections between the radial spines and the cortical shell. This shell is spherical and formed of thin bars framing irregular polygonal meshes. Unlike the main spines that have their origin in the medullary shell, the cortical shell has also a variable number of shorter and thinner external spines originating on its surface. According to Popofsky this genus is doubtlessly close to the genera Spongopila Haecelk, 1881, Rhizoplegma Haecelk, 1881, and Lychnospaera Haecelk, 1881, and would be especially intermediary between the first two genera. Consequently, Popofsky assigned this new genus to the family Astrosphaeridae Haecelk.

Campbell (1954), in his controversial taxonomic synthesis of Radiolaria that continues to give us so many nomenclatural problems due to the mechanical application of the ICZN, considered the genus Lonchospaera a synonym of the genus Rhizoplegma Haecelk, 1881, although Popofsky had mentioned the differences between them. We know now that these differences are much greater, even at the level of order or suborder.

Finally, Petrushevskaya (1975) illustrated other 13 specimens of Lonchospaera from samples of the Antarctic Leg 29 of the Deep Sea Drilling Project and, as usually, being much interested in the inner structures of Radiolaria, she approximately illustrated the medullary skeleton of most of these specimens. Of course, it is very difficult to understand these inner structures, especially when they are very complicated, when the specimens are not in lateral, diagnostic positions, when the medullary shell is screened by the cortical shell, and when one does not know exactly what to look for. What Petrushevskaya wrote about these structures is that they resemble irregular polyhedra with a variable construction and that the inner structure of the type species appears like a silicoflagellate skeleton of about 18-20 μm in diameter. In spite of her erroneous remarks and her drawings of the internal skeletons, at least one specimen she illustrated (Petrushevskaya, 1975, pl. 17, fig. 8), and which I re-illustrate herein (Fig. 1f, 2c) indicating at the same time the nomenclature of its skeletal elements, shows that she was very close to the understanding of the true internal structure of this genus. As concerns the position of this genus in the taxonomic system of Radiolaria, Petrushevskaya included it in the family Hexastylyidae Haecelk that, in her opinion, was synonym of the families Centrolonchidae Campbell (1954), Stigmosphaeridae Hollande and Enjumet (1960), and Heliasteridae Hollande and Enjumet (1960). The genus Arachnostylos Hollande and Enjumet, 1960, represented also by only its type species, A. tregouboffi Hollande and Enjumet, 1960, has been very well illustrated by Mrs. O. Ferru who illustrated their monograph, both as concerns its initial skeleton and
cortical shell (Fig. 1d), but the structure of its initial skeleton and the relationships with other genera were not well understood by the authors because they included it in the family Heliasteridae Hollande and Enjumet. The type genus of this family is Heliaster Hollande and Enjumet (a homonym name substituted later by Hollandosphaera Deflandre, 1973) whose skeleton has a bar-centred initial spicule derived from the tetrapetaloid spicule of the genus Tetrapetalon Hollande and Enjumet, 1960. At its turn, this tetrapetaloid structure is the characteristic structure of the family Hexalonchidae Haeckel, 1881 (Dumitrică, 1985, p. 186, fig. 4; De Wever et al., 2001, p. 210-212, fig. 133). What is important in the monograph of Hollande and Enjumet (1960) relative to the two genera discussed in the present paper is that the genus Arachnostylus and the family Heliasteridae have been assigned to the same nucleo-axopodial superfamily group, the Periaxoplastidians, as the genus

Fig. 1 Specimens of Lonchosphaera illustrated by Popofsky (1908) (a-e), Hollande and Enjumet (1960) (d), and Petrushevskaya (1975) (e-o). a-c Lonchosphaera spinata Popofsky; a, lectotype; b, c, younger specimens; the scale bar above Fig. b is for Figs. a-c. d Arachnostylus tregouboffi Hollande and Enjumet, 1960, holotype, living specimen with central capsule. e-o Specimens of Lonchosphaera illustrated by Petrushevskaya (1975) with her own determinations: L. spicata Popofsky (e-i), Lonchosphaera sp. B (j-o); Figs. i, k, m, o represent the inner (medular) skeleton as seen by Petrushevskaya in the specimens g, j, l and in a here not illustrated specimens. Scale bar of 50 μm (copied from Petrushevskaya, 1975) is for Figs. e-o.
Excentroconcha Mast and the family Excentroconchidae. This group comprises radiolarians with a heteropolar nucleo-axopodial structure and an enormous axoplast, which is either independent of the nucleus or juxta-nuclear. This position is rather similar to that of the axoplast of the nassellarian Radiolaria. Moreover, for the discussion regarding the taxonomic position of the genus Arachnostylus and its relationships with other radiolarians it is very important that Hollande and Enjumet (1960: fig. 1.6) found that it has the same nucleo-axopodial structure as Excentroconcha, with the axoplast independent of the nucleus and without an axoflagellar cytoplasm (Fig. 2h).

From the above discussions one can very well notice the incertitude concerning the internal structure of the genera Lonchospaera and Arachnostylus and their family status. In the present article, based on the study of several specimens found in one Quaternary sample, (NP1-7-3), collected during the NAUTIPERC dives off Peru (5°-6°S) (De Wever et al., 1995) and the interpretation of the internal structure of the initial (medullary) skeletons of the two genera illustrated in the papers by Popofsky (1908), Hollande and Enjumet (1960) and Petrushevskaya (1975), and re-illustrated herein, I shall describe the initial and internal structure of the skeleton of these genera and discuss their taxonomic status. As usually, to better see this structure I used individual slides and slicing technique of the specimens mounted in Canada balsam according to the method I described in De Wever et al. (2001: 436-439).

SAMPLES STUDIED

This article could not have been written without the study of the samples collected during the deep-sea dive campaign conducted with the submersible Nautile during the NAUTIPERC cruise (March-April 1991) along the northern Peruvian continental margin off Paita. Of all the sediment samples studied (De Wever et al., 1995) only a single one, NP1-7-3, collected from a depth of 5246 m and located at 5°36'S/81°54'W, contained relatively frequent specimens of the genus Lonchospaera. According to its micropaleontological contents the age of this sample is late Quaternary.

Other samples collected from the cores recovered from SW Pacific during the Leg 21 of the Deep Sea Drilling Project (Dumitrică, 1973) allowed finding other entactinarian species (work in progress) in the Paleocene and Eocene with which the genus Lonchospaera could be compared.

STRUCTURE OF THE INITIAL SKELETON

The building of the skeleton of Lonchospaera, as well as that of all entactinarian Radiolaria, starts from an initial spicule that consists of a median bar (MB) with three rays or spines at each end of the bar. Two rays (A), one at each end of MB, are coplanar and apically directed. They are always free, not interconnected by arches. The other four rays, two at each end of MB, diverge in lateral downward directions and represent the so-called basal rays (B). Unlike the apical rays, they are interconnected in pair by two arches, which we can call basal arches (ba) and which are situated on both sides of MB. At their turn, these arches are interconnected by an antapical arch (aa) lying in an axial plane perpendicular to MB. This arch gives rise to an antapical ray or spine (AA), so that this genus has seven rays, of which six are primary, originated in MB, and the seventh is secondary, originated in the antapical arch.

This type of structure is the most simple in this genus. It was found in a small specimen illustrated by Petrushevskaya (1975: pl. 17, figs 7, 8) and re-illustrated herein (Fig. 2c), and in some specimens, from whom two are herein illustrated (Figs. 2b, 3a-c), from the NAUTIPERC dive (De Wever et al., 1995). Beside this simple medullary shell there are also more complicated structures (Figs. 2d-f, 3d-h). These complex medullary shells have a primary layer represented by the structure described above surrounded by a second layer represented by an equatorial ring (er) formed of opposite and slightly distal branches originated in the basal rays and lying in the equatorial plane (Figs. 2d, f, 3e, h), or even more complicated (Figs. 1d; 2e, f, 3g), with an additional distal antapical arch in the plane of MB that connects the antapical ray with the equatorial ring. All these additional arches that form the second medullary layer are originating in pairs of opposite branches of the radial spines lying in planes perpendicular on the planes of the primary arches. The same complex structure can very well be seen, in antapical view, in the species Arachnostylus tregouboffi Hollande and Enjumet, the type species of the genus Arachnostylus (Figs. 1d). To better understand it, I re-illustrated the original drawing at a greater magnification and named the skeletal elements (Fig. 2f).

TAXONOMY

Class Radiolaria Müller, 1858
Subclass Polycystina Ehrenberg, 1838, emend. Riedel, 1967
Order Entactinaria Kozur and Mostler, 1982
Type genus: Excentroconcha Mast, 1910.
Diagnosis. Entactinarian Radiolaria having as primary skeleton a six-rayed and bar-centred initial spicule with basal rays interconnected two by two by one basal arch on both sides of MB; basal arches interconnected antapically by an antapical arch perpendicular on MB and bearing one to three antapical rays. Shell usually present, spongy or latticed.
Remarks. Until present, the family comprised only the genera Gonosphaera Jørgensen, 1905, represented by a spicular skeleton without an external shell, and Excentroconcha Mast 1910, with the spicule of the genus Gonosphaera excentrically placed in a spongy or latticed spherical shell. Both genera are characterised by having two antapical rays originated in an antapical arch perpendicular on MB (Dumitrică, 2001). The genus Lonchospaera with its synonym genus Arachnostylus
oblige us to enlarge the diagnosis of this family to include in it also the genus *Lonchosphaera* that has the same system of arches between the basal rays of the initial spicule but only one antapical ray. The assignation of *Lonchosphaera* to the family Excentroconchidae is also supported, as I mentioned above, by the perfect resemblance of the nucleo-axopodial complex of *Excentroconcha* and *Arachnostylus* (Hollande and Enjumet, 1960, p. 27, fig. 1). This system of initial skeleton is one of the most simple systems of the superfamily Centrocuboidea Hollande and Enjumet, 1960. The oldest genus with the same type of medullary shell as that of *Lonchosphaera* is the genus *Solicubulus* Dumitrică, 1983 from the Oxfordian of Eastern Carpathians and early Tithonian of Solnhofen area (southern Germany). Other unpublished species with the same spicule are known in the Paleocene and Eocene of southwest Pacific (Dumitrică, work in progress). The Paleocene sediments from the same area contain also a new genus with the same spicule but with two additional antapical rays situated on both sides of the axial antapical ray (Fig. 2g) (work in progress).

**Range:** Late Jurassic (Oxfordian or older) to Recent.

**Genus** *Lonchosphaera* Popofsky 1908, emended herein

**Type species:** *Lonchosphaera spicata* Popofsky, 1908.

1908 *Lonchosphaera* Popofsky, p. 217, non Campbell, 1954, p. 68.

1960 *Arachnostylus* Hollande & Enjumet, p. 93.
1975 Lonchosphaera Popofsky. – Petrushevskaya, p. 567. Emended diagnosis. Test consisting of two concentric shells, a spherical, latticed, rarely spongy-like cortical shell, and a centrally placed medullary shell consisting especially of a bar-centred six-rayed initial spicule and three arches. Spicule consisting normally of a median bar, two apical rays, four basal rays and an antapical ray, all rays prolonged outside the shell wall into spines. Basal rays connected by two arches in the plane of MB; these arches are interconnected, at their turn, by an antapical arch transversal on MB from which one antapical spine is originating. Basal spines may be also interconnected proximally in the equatorial plane by four arches that form an equatorial ring. Other additional arches may also develop around the main ones. Among these arches, most common is an antapical arch developed in the plane of MB from the antapical ray that connects this ray with the equatorial ring (Fig. 2e, f). Cortical shell connected with the medullary one usually through seven rays, rarely more, that extend outside the shell into spines with circular cross section. When the number of these rays is greater than seven, the additional ones are tertiary since they arise from the equatorial ring or from some medullar arches. Many other spines may arise from the surface of the cortical wall.

Remarks: As discussed above, neither Popofsky (1908), nor Petrushevskaya (1975) understood the initial structure of this genus, although Petrushevskaya illustrated a specimen with the initial structure very well drawn (pl. 17, figs. 7, 8), which I re-illustrated in the present article (Fig. 1e, f) and to which I only attached the name of rays and arches (Fig. 2c). Popofsky, especially, made such a mess of the skeletal elements of the medullary shell in his drawings so that it is impossible to see a certain regularity or symmetry in this shell. Of course, Entactinaria as a structural skeletal construction and taxonomic unit at the level of order were not known at that time, but a detailed morpho-structural analysis could have pointed out a heteropolarity of the first shell. The genus Arachnostylus is undoubtedly a junior synonym of Lonchosphaera. The initial spicule and arches of the holotype of the type species, A. tregouboffi, which is positioned in a slightly eccentric medullary shell, is illustrated by Hollande and Enjumet (1960: pl. 43, fig. 3).

To better recognize its structure, in Fig. 2f of the present article the initial shell of the holotype is re-illustrated and much magnified. One can very well see that its spicule and initial skeleton are quite similar to those of the specimen from Fig. 2e that belongs to the genus Lonchosphaera.

Lonchosphaera resembles also Excentroconcha by having the same nucleo-axopodial system (Fig. 2h) and the same system of initial arches, but differs by having a single antapical ray instead of two, a concentric instead of eccentric medullary shell, and a latticed cortical shell. What one can also easily see is that the cortical shell of the type species, L. spicata Popofsky, 1908, formed of thin bars, having wide irregular polygonal meshes, and bearing long radial spines, resembles the cortical shell of the holotype of the species Arachnostylus tregouboffi Hollande and Enjumet so that one can doubtlessly say that these two genera and their type species are synonymous. Unlike both type species, all the specimens illustrated by Petrushevskaya (1975), as well as those I found in the NAUTIPERC dive sample, have cortical shells with numerous small, rounded or oval pores, generally broad intervening bars and a thicker shell-wall. Although Petrushevskaya determined as L. spicata some specimens with this type of rather massive cortical shell I consider that we should restrain the diagnosis of this species to the specimens with cortical shell similar to that of the type species of both genera. In fact we could ask which morphological characters should be taken into account to discriminate between the species of the genus Lonchosphaera. A primary criterion should probably be the construction of the medullary shell, simple or complex, and the morphology of the cortical shell. The simple medullary shell seems to characterize the smaller specimens and the complex medullary shell the larger specimens. These differences do not seem to depend on the biological age of the specimens because the diameter of the cortical shell, when single, does not increase with its age. It can increase only by the increase of the thickness of the shell wall or by adding another layer of cortical shell.

Range: Quaternary to probably late Pliocene so far as known. Maybe? also Late Miocene to ?Pliocene in DSDP Leg 90-594-16-2 and 26-2 (Chatham Rise, South of New Zealand) (Caulset, 1985, p. 853, Tab. 3).

Lonchosphaera spicata Popofsky, 1908

Figs. 1a-d, 2f

1908 Lonchosphaera spicata Popofsky n. sp., p. 218, pl. 24, fig. 2; pl. 25, figs. 2, 7; non Petrushevskaya, 1975, pl. 17, figs. 4-8.

1960 Arachnostylus tregouboffi Hollande and Enjumet n. sp., p. 93, pl. 43, fig. 3.

1985 Lonchosphaera spicata Popofsky. - Caulset, p. 853, tab. 3.

Description. Initial skeleton as the genus, but also with an equatorial ring and sometimes an additional antapical arch larger than the primary one and situated in axial plane perpendicular on the primary one. Cortical shell spherical made of thin bars that form relatively wide polygonal meshes of irregular shape, size and arrangement. Both shells interconnected by 7 or more radial bars that extend outside into relatively long radial spines circular in cross section and of various diameter and length. Six of these spines originate in the median bar of the initial spicule and one in the antapical arch. A few additional spines originate in the distal arches of the inner skeleton. Many other thinner spines originate in the wall of the cortical shell. Inside cortical shell all radial bars bear a distal verticil of three ramified branches that represent additional connections between the radial bars with the cortical shell.

Lectotype. Since Popofsky did not designated a holotype I consider as lectotype the specimen illustrated by him on his Pl. 24, fig. 2 (Fig. 1a in the present article). It has not only plate priority but it is also the most complete specimen illustrated, with complete cortical shell permitting a better comparison with A. tregouboffi.

Remarks. In the absence of an illustration it is difficult to include undoubtedly under the above synonymy the
specimens determined by Caulet (1985) as *Lonchosphaera spicata* Popofsky because it is possible that they belong to one of the following species or to both as it is the case of the specimens illustrated by Petrushevskaya (1975).

**Range and occurrence.** Antarctic waters and Mediterranean Sea, Recent. In the Antarctic waters it was found at 0-300 m depth, at the boundary with the Antarctic ice cap (Popofsky, 1908), and in the Mediterranean Sea a single specimen was recorded in the bay of Alger at 200 m depth, and abundant specimens have been recorded off Villefranche-sur-Mer at 1000-1500 m water depth (Hollande and Enjumet, 1960).

**Lonchosphaera mariae** n. sp.

Figs. 1e-k, 2b, c, 3a-c

1975 *Lonchosphaera spicata* Popofsky. – Petrushevskaya, p. 567, pl. 17, figs.7-8.

**Description.** Medullary skeleton simple consisting only of the initial spicule, the two basal arches and the antapical arch and connected to the cortical shell by only seven radial bars. Cortical shell spherical, relatively thick walled, with numerous circular or oval pores of relatively equal size. Surface bearing usually short conical spines of whom the seven spines originating in the medullary shell are longer. Inside the cortical shell the radial bars bear rarely verticils of subcortical branches. Since the nodes of the verticils are very close to the cortical shell due to the smaller diameter of the latter, they appear sometimes just as costae on its inner surface.

**Material.** Three specimens in sample NP1-7-3 plus the specimen illustrated by Petrushevskaya (1975: pl. 17, fig. 7, 8).

**Holotype.** Fig. 3c, sample NP1-7-3, coll. Musée Cantonal de Géologie Lausanne, nr. MGL 96911, individual slide.

**Dimensions.** Diameter of medullary shell 17-20 μm, of cortical shell 70-98 μm.

**Remarks.** Externally this species differs from the type species by having a well-developed cortical shell with broad intervening bars, circular or oval pores and, especially, a simple medullary shell.

**Etymology.** The species is dedicated to Maria Petrushevskaya for her great contribution to the
knowledge of Cenozoic radiolarians and for having illustrated many species of Lonchosaephaera. Range and occurrence. Pliocene to Recent in southern Pacific and, especially, in the Antarctic sector. Since the species seems to be a cold-water dweller, its presence in the Quaternary subequatorial sediments collected by NAUTIPERC dive could be explained by the cold Peru Current.

Lonchosaephaera cauleti n. sp.
Figs. 11-n, 2d, e, 3d-h
1975 Lonchosaephaera sp. C. Petrusherksyana, p. 630, pl. 17, figs. 11-15.
Description. Shell generally moderately large, spherical, bearing numerous short conical spines and small circular or oval pores of irregular arrangement and slightly variable sizes. Medullary shell complex, with equatorial ring and sometimes additional arches around the primary system of arches. Radial spines usually in a number of seven to probably ten, all with a verticil of three branches inside the cortical shell. These branches are dichotomically divided and may cover the entire inner surface of this shell.
Material. 16 specimens in sample NP1-7-3, NAUTIPERC dive off Peru.
Holotype. Figs. 2e; 3f, g, coll. Musée Cantonal de Géologie Lausanne, nr. MGL 96912, individual slide.
Dimensions. Diameter of medullary shell 27-30 μm, of cortical shell 85-118 μm, most of them more than 100 μm.
Remarks. Lonchosaephaera cauleti n. sp. resembles externally L. mariae n. sp. from which it differs in having the cortical shell slightly larger and, especially, in having a more complex medullary shell. In the material I studied this species is about four times more frequent than L. mariae n. sp.
Etymology. The species is dedicated to my colleague Pierre Caulet, Charavine, France, for his contribution to the knowledge of Cenozoic radiolarians and his continuous effort to update the radiolarian data bank (RADGEN). Range and occurrence. Pliocene to Recent in southern Pacific and especially in the Antarctic sector. Its presence in the subequatorial Pacific off Peru can have the same explanation as for the species L. mariae n. sp.

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REFERENCES


