CENOZOIC SPUMELLARIAN RADIOLARIA WITH ECCENTRIC MICROSPHERE

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Abstract The article presents 3 Cenozoic spumellarian Radiolaria families (*Suttoniidae*, *Patulibracchiidae* and *Heliodiscidae*) that have genera with eccentric microsphere. Ten such genera are discussed, of which four are new (*Homunculodiscus*, *Parasuttonium*, *Cryptomanicula* and *Helioferrusa*), and 19 species of which eleven are new. These genera evolved independently and in different directions, proving that there are no phylogenetic relationships between these families, and that if some structures are common they are the result of the eccentric position of the microsphere and of its migration during evolution. All species discussed are illustrated in eleven figures with photos at optical or scanning electron microscope.

Keywords: Cenozoic, spumellarian Radiolaria, eccentric microsphere, initial structures, evolution.

INTRODUCTION

Cenozoic radiolarian taxa discussed and described in this article are part of a study of internal structures of Mesozoic and Cenozoic spumellarian and entactinarian Radiolaria started about 40 years ago as basis of a more natural taxonomy. Although they are all spumellarians that start their skeletal building with a microsphere, they belong to at least 3 families: Suttoniidae Schaaf emend. Dumitrică, Patulibracchiidae Pessagno, and Heliodiscidae Haeckel emend Dumitrică, united here by having an eccentric microsphere. The family Pyloniidae Haeckel that has also an eccentric microsphere is not discussed here because it has been discussed with other occasions by Dumitrică (1988, 1989), De Wever et al. (2001), and others. The article intends to prove the taxonomic value of this eccentric microsphere, the skeletal diversity of such taxa, their evolution, if possible, and relationships with other radiolarians. A few of the taxa discussed in this article have already been published (Dumitrică, 1978, 1983; Dumitrică in De Wever et al., 2001). For a better understanding of them I add here a few other new species and genera found in the meantime.

STUDIED SAMPLES

With a few exceptions, the radiolarian specimens on whom this short article is based come from a few samples from cores extracted during Leg 21 of the Deep Sea Drilling Project (DSDP) located in southwest Pacific, as follows:

1. DSDP 21-205-7-1, 70-72 cm, South Fiji Basin, 25°30.99'S/177°53.95'E, water depth 4320 m, cored interval 56-65 m, late Miocene, NN9 zone, glass rich foram nanno ooze (Burns, Andrews et al., 1973).
2. DSDP 21-206-24-5, 70-72 cm, New Caledonia Basin, 32°00.75'S/165°27.15'E, water depth 3196 m, cored interval 210-219 m, foram bearing nanno ooze, Late Miocene, NN11 (Burns, Andrews et al., 1973).

3. DSDP 21-207A, 14CC, south Lord Howe Rise, 36°57.75'S, 165°26.06'E, water depth 1389 m, cored interval 169-178 m, upper part of the *Chiphragmalithus cristatus* nannoplankton Zone, Middle Eocene, Porangan stage (Burns, Andrews et al., 1973).

4. DSDP 21-207A, 15CC, same location and age as above, cored interval 178-187 m.

5. DSDP 21-208-30CC, southwestern Pacific, north Lord Howe Rise, 26°06.61'S, 161°13.27'E, water depth 1545 m, cored interval 548-557 m, early Paleocene, *Prinsius martini* nannoplankton Zone (Burns, Andrews et al., 1973).

6. DSDP 21-208-31CC, same hole, cored interval 558-567 m, early Paleocene, *Chiasmolithus danicus* nannoplankton Zone (Burns, Andrews et al., 1973).

7. DSDP 21-208-32CC, same hole, cored interval: 567-576 m, same age, but the base of the *Chiasmolithus danicus* zone (Burns, Andrews et al., 1973).

8. 83-481, sect. II, 73-75 cm, Quaternary, sample from core taken by R/V Ocean Researcher 1 from the Pacific area around Taiwan, exact location not given. Sample provided by Dr. Kuei-Yu Yeh in 1998 (for detail see Cheng & Yeh, 1989; Yeh & Cheng, 1990).

9. PROA 96P, 241-243 cm: 5°12'N/177°43'E; water depth 5,828 m. The age, according to Sanfilippo & Riedel (1970, p. 448) is late Middle Miocene, bottom of *Diartus pettersoni* Zone. The sample was provided by W.R. Riedel about 40 years ago.

10. DODO 123D, 10°25'S/63°15'E, depth 3,115 m, Eocene, siliceous calcareous ooze. Central Indian Ocean Basin (sample provided by W.R. Riedel about 40 years ago, see Riedel, 1971).

11. Sample 1315. Radiolarian Shale Formation, late Badenian, Middle Miocene, Păușești Otăsău village,

Tilvici valley, Getic Depression, Romania (see Dumitrică, 2016 for location). The sample, collected in 1966 is from the upper half of the formation and consists of a bed about 5 cm thick of indurated yellow marl full of large and very well preserved specimens of *Centrocubus cladostylus* Haeckel, *Lychnosphaera regina* Haeckel, and *Diplospongos dendrophorus* Mast (Dumitrică, 1983) and with a phaeodarian fauna (Dumitrică, 1965, 2016). This bed was later found also in the locality Ocnele Mari (sample OM 54), in the same Getic Depression. As mentioned in a recent paper (Dumitrică, 2016) both exposures are unrecognizable at present; the former has been in 1967 covered by a landslide and the latter was unrecognizable about 15 years ago, when I revisited it, being completely covered by soil.

TAXONOMY

The holotypes of all the new species described in this article will be stored in the Musée Cantonal de Géologie Lausanne (MGL).

Class Radiolaria Müller, 1858

Subclass Polycystina Ehrenberg, 1838, emend. Riedel, 1967

Order Spumellaria Ehrenberg, 1875

Family Suttoniidae Schaaf, emend. Dumitrică 1983, re-emended herein

Type genus. *Suttonium* Schaaf, 1976, emend. Dumitrică, 1983

Emended diagnosis. Bilaterally symmetrical spumellarians with initial skeleton consisting of an eccentric microsphere with or without primary rays and a crescent-shaped *deuteroconcha*. Skeleton thin made usually of 2 parallel cortical lattice plates interconnected by short bars. Rays, when present, surrounded by a cortical shell forming three arms in the most evolved members.

Discussion. Before discussing the taxonomy of this family it is necessary a short history of the evolution of its meaning and its skeletal peculiarity.

The family Suttoniidae was erected by Schaaf (1976) on the basis of a peculiar specimen assigned to a new species and genus (*Suttonium praedicator* Schaaf) found in the Quaternary sediments from southwestern Pacific. He mentioned that this species has some similitudes with the spumellarian species *Rhopalastrum ? anumalum* described by Sutton (1896) from the Eocene of Barbados, but he specified that the very good preservation of the specimen of his new species “does not permit any doubt (sic!): *Suttonium praedicator* must be assigned to the order Nassellaria”. According to him, the microsphere represents the cephalis, the second shell the thorax, and the three arms the abdomen. According also to him, the two lateral arms are developed around the primary lateral rays (Lr and Ll) of the initial nassellarian spicule and the antapical arm around the dorsal (D) ray. What followed has proven how imprudent is to be completely certain in the science of life, especially when knowledge is incomplete and the study is superficial.

Dumitrică (1983) in a special study of the skeleton of the 3 species known in this genus showed that *Suttonium* is not at all a nassellarian genus, but a special spumellarian,

as Sutton (1896) had suggested for the species he had described. It is a spumellarian that has the arms similar in structure to the arms of some Hagiastriidae, from which it differs by the fact that in the course of its evolution the microsphere underwent a trend toward migration from the second chamber and the latter from the cortical three-rayed chamber suggesting a nassellarian skeleton.

The two new genera – *Homunculodiscus* and *Parasuttonium* – described below and that belong also to the family Suttoniidae allowed a better understanding of the history of this family and of its structural morphology. At present, when we know that the hagiastriids have a special type of microsphere, which is never spherical, and a pyloniacean mode of growth in their early ontogenetical stages (Dumitrică in De Wever et al., 2001), whereas the microsphere of *Suttonium* and of all Suttoniidae is a simple sphere, and shell growth is simple, it is difficult to sustain such a filiation. Consequently, despite the structural similarity of arms any relationship between *Suttonium* and the higumastriids is excluded.

Based on what we already know on the skeletal structure of the species of the genus *Suttonium* and on the structures of the new species and genera herein described we have now a general image of the initial and general structures of the members of this family.

The skeleton of the Suttoniidae consists of 2 parts: a disk-shaped skeleton and a special initial structure. This initial structure consists, at its turn, of an eccentric spherical microsphere and a crescent-shaped attached chamber. By comparison with the initial stages of some foraminifers, I name this crescent-shaped second chamber *deuteroconcha* from the Greek *deuter-*, *deuteron-* second, secondary, and *concha* – shell. The side to which the deuteroconcha is attached to the microsphere is not casual. It is always attached to the side directed to the distalmost margin from the microsphere. To have an orientation of the shell of the genera with eccentric microsphere discussed in the present article, by comparison with the skeleton of Nassellaria I considered *apical* the part with the microsphere and *antapical* the part with the deuteroconcha. And because the two chambers (microsphere and deuteroconcha) are always together I prefer to name this structure *diploconchal structure*, from the Greek *diplo* – double and *concha* – shell. Microsphere is very small (about 13 µm) in the oldest species (*Homunculodiscus nascens* nov. sp.) but can arrive to about 40 µm in the Quaternary species *Suttonium praedicator* Schaaf, when it is free from the constraints of a surrounding skeleton. The skeleton outside the diploconchal structure is usually a very flat disc formed, on both faces, by a porous cortical plate. The two faces of the disc are interconnected by short bars disposed irregularly or radially. These bars may be free or interconnected in the equatorial plane by bars parallel to the two faces. In optical view the perpendicular bars connecting the two faces appear as dark points and the horizontal bars interconnecting the perpendicular bars appear as less dark short lines. All this inner structure gives the shell a special ornamentation generally characteristic of species when looked in transmitted light.

The two new genera – *Homunculodiscus* Dumitrică and *Parasuttonium* Dumitrică obliged us to emend for the second time the diagnosis of this family to include in it not only species with 3 arms like the type genus but also

genera with disc-shaped shell with or without arms because they have also an eccentric microsphere and a deuterconcha

Range. Lower Paleocene to Recent and, generally, sparse.

Genus *Homunculodiscus* nov. gen.

Type species. *Stylodictya tainemplekta* Caulet, 1991.

Diagnosis. Test circular disc-shaped and very thin consisting of two parallel porous plates interconnected by short bars perpendicular to plates, most of them interconnected also in the equatorial plane of the disc by bars forming characteristic curved structures well visible in transmitted light. Pores circular, disposed commonly in radial rows and increasing slightly in diameter from the centre to periphery. Microsphere without primary radial spines. Deuterconcha tending to reduce the lobes from three to one.

Remarks. This new genus differs from *Stylodictya* Ehrenberg, to which the type species was originally assigned (Caulet, 1991), by having an eccentric microsphere, a diploconchal initial structure, no primary radial spines, and a different shell structure.

The diploconchal structure, and especially the deuterconcha of this genus, shows a rapid and interesting evolution. In the earliest species (*Homunculodiscus nascens* nov. sp., Fig. 1, very early Paleocene) this chamber is very small and divided into 3 very small globular chambers. At younger levels of the early Paleocene (Figs. 2 and 3) this chamber is better individualized and the number of chambers starts reducing. At last, in the middle Eocene species *Homunculodiscus tainemplekta* (Caulet) (Fig. 3g and Fig. 4) this chamber is very well individualized, is larger than the microsphere and together with it makes a well characteristic body that suggests a homunculus, and that is well separated from the rest of the shell by a more or less disturbed oval circle.

Etymology. From the Latin *homunculus* – small man and *discus* – disc, due to the shape of the central shell of the type species. Masculine gender.

Range and occurrence. Lowermost Paleocene to lowermost Oligocene.

Homunculodiscus nascens nov. sp.

Figures 1a-g

Description. Shell disc-shaped, circular or subcircular, very thin and with irregular margins. Margins with very small and thin spines. Shell consists of two perforate cortical plates interconnected by irregularly or radially arranged transversal bars that look like black points in transmitted light giving the shell a punctiform ornamentation. Transversal bars free or interconnected by equatorial bars arranged in short arches of different directions. Pores circular, most of them radially distributed. Diploconchal structure consisting of a very small eccentric microsphere and a small crescent shaped deuterconcha divided into two or three chambers much smaller than the microsphere. Microsphere with circular pores smaller than

those of the disc.

Material. Eight photographed specimens of which only 3 mounted on fig. 1.

Holotype. Figure 1a, 1b., coll. MGL 103554.

Dimensions. Diameter of microsphere 13 μm , of shell 173-249 μm .

Etymology. From the Latin word *nascens* – that is giving birth, because it is the first species that started the lineage of this genus.

Remarks. This is the oldest and most frequent species of this genus in the studied samples. It differs from the younger species of the genus in having the deuterconcha rather disorderly formed and rather small.

Range and occurrence. Lowermost Paleocene, DSDP 21-208-32 CC and 31 CC, north Lord Howe Rise, southwestern Pacific.

Homunculodiscus cauleti nov. sp.

Figure 2a-h

Description. Shell disc-shaped, very thin, consisting of two parallel porous plates interconnected by short transversal bars that, in transmitted light look like black spots. They are either irregularly arranged or, most of them are aligned to form arches or incomplete ellipses around the diploconchal structure. Microsphere small, spherical. Deuterconcha antapically disposed, usually crescent-shaped. Usually there is another crescent-shaped chamber beyond it. The latter is usually part of an elliptical circle surrounding the diploconchal structure. Pores circular, densely arranged in circular or radial rows, the latter especially toward periphery. These rows may be separated by radial beams prolonged into thin short peripheral spines. Periphery irregular, frayed as if not finished.

Material. Eight specimens, of which four illustrated, in the upper lower Paleocene.

Holotype. Figures 2b, 2f, coll. MGL 103555.

Dimensions. Diameter of microsphere 14 μm , of shell 185-224 μm .

Etymology. The species is named for Dr. Jean-Pierre Caulet who described for the first time the species that will become the type species of the genus.

Remarks. This species seems to be intermediate between *Homunculodiscus nascens* and *H. tainemplekta* (Caulet). It has better marked crescent-shaped deuterconcha and elliptical circles around it than *Homunculodiscus nascens* nov. sp.

Range and occurrence. Recorded only in the upper lower Paleocene sample DSDP 21-208-30 CC, north Lord Hove Rise, southwestern Pacific.

Homunculodiscus tribullatus nov. sp.

Figure 3a-d

Description. Shell disc-shaped and very thin consisting of two parallel porous plates interconnected by numerous transversal bars, some of them interconnected by equatorial bars forming inside short arches of different orientations. Microsphere eccentric, small with circular pores separated by thin intervening bars. Deuterconcha consisting of two spherical unequal chambers sensibly smaller than the microsphere and attached at the antapical part of the latter. Pores of disc circular, densely distributed quincuncially and radially. Connections between the two

Fig. 1 a-g. *Homunculodiscus nascens* nov. gen., nov. sp. **a-b** – holotype; **b**, detail, double magnification of central part of fig. **a**; **c-e** – paratype 1, **d-e** detail of central part, double magnification of fig. **c**, focused at two levels. **f-g** – paratype 2; **g** – double magnification of central part of fig. **f**. **a, c**, DSDP 21-208-32CC, early Paleocene. **f**, DSDP-21-208-31CC, early Paleocene. Scale bars for **a, b, c, f** = 50 μ m.

porous plates by transversal bars distributed irregularly and, in places, in short arches. Periphery irregular, frayed, with short thin spines representing prolongations of the inner radial structures.

Material. Two specimens in upper lower Paleocene, DSDP 21-208-30 CC.

Holotype. Fig. 3a, c, coll. MGL 103556.

Dimensions. Diameter of shell 133-190 μ m, of microsphere 17-18 μ m.

Etymology. In Latin from having 3 balls (*bulla*) (microsphere and two of the deuterioconcha).

Remarks. Presence of the two practically similar specimens in the type sample suggests that they are not varia-

tion of the other two Paleocene species but an independent species resulted from the evolution of the *Homunculodiscus nascens* n. sp. This species differs from *H. nascens* nov. sp and *H. cauleti* nov. sp. by the two spherical and well-defined chambers of deuterioconcha.

Range and occurrence. Upper lower Paleocene, DSDP 21-208-30 CC, north Lord Howe Rise, southwestern Pacific.

Homunculodiscus tainemplecta (Caulet, 1991)

Figure 3e, 3g; Figure 4a-d.

1991 *Stylodictya tainemplekta* n. sp. – Caulet, p. 533, pl. 1, figs. 8, 9.

Fig. 2 a-h. *Homunculodiscus cauleti* nov. gen., nov. sp., DSDP 21-208-30CC; scale bars of figs. **a-d** = 50 μ m, of figs. **e-h** same bars = 25 μ m. **e** represents the central part of **a**; **f** represents the central part of **b**; **g** represents the central part of **c**; **h** represents the central part of **d**.

2005 *Stylodictya tainemplecta* Caulet. – Funakawa & Nishi, p. 218.

2015 *Stylodictya tainemplekta* Caulet. – Kamikuri, p. 148, pl. 18, fig. 6.

Description. Shell flat, very thin and circular, consisting of two perforated parallel cortical plates interconnected by very short bars perpendicular to the disc which, at

their turn, are interconnected inside shell by bars in equatorial plane parallel to the disc forming a special inner ornamentation in optical view. Microsphere eccentric with very small and equal circular pores. Deuteroconcha larger than the microsphere, crescent-shaped and with pores sensibly larger than those of the microsphere. This diploconchal shell forms a characteristic homunculoid

Fig. 3 a-d. *Homunculodiscus tribulatus* nov. gen., nov. sp., DSDP 21-208-30 CC; **a, c** – holotype; **c** – detail of central part of **a**, double magnified. **b, d** – paratype, **d** – central part of **b** double magnified. **e, g** – *Homunculodiscus teinemplecta* (Caulet), DSDP 21-207A-15CC; **e** – detail of central part of fig. **g**, double magnified. Fig. **f, h** – *Cryptomanicula absconsa* nov. gen., nov. sp. paratype; **f** – detail of surface of central part of fig. **h**, focused on surface, **h** focused on middle part, DSDP 21-208-30 CC. Scale bar for entire specimens = 50 μm .

Fig. 4 a-d - *Homunculodiscus tainempecta* (Caulet), DSDP 21-207A-CC. Scale bar for all figures = 50 μm .

structure and is surrounded by a hallow-shaped circular or oval ring. This ring may be usually surrounded, at its turn, by a second, imperfect ring. The rest of the disc has an inner structure formed either by short curved ribbons or by punctiform connections between the two plates. Pores on all shell circular, dense, increasing in size distally and radially disposed especially outside the central part.

Dimensions. Diameter of shell 165-233 μm , of microsphere 13-14 μm , of deuteroconcha 21-37 μm , of first ring around the diploconchal structure 42-46/48-56 μm .

Remarks. The middle Eocene specimens from Lord Howe Rise are perfectly comparable with those from Kerguelen Plateau. The stratigraphic level of the FAD of this species is unknown because in both the samples from the Kergue-

len Plateau and in those from the Lord Howe Rise, there are barren intervals or sedimentation gaps between the radiolarian bearing early Paleocene and middle Eocene sediments cored in the Lord Howe Rise holes 207A and 208 of the Deep Sea Drilling Project, Leg 21. For the same reason it is impossible to know the species from whom *H. tainempecta* originated although *H. cauletti* nov. sp. seems to be a possible candidate as mentioned under *H. cauletti* nov. sp.

Range and occurrence: Middle Eocene or earlier to early Oligocene, Kerguelen Plateau (Caulet, 1991); middle Eocene, SW Pacific, south Lord Howe Rise, DSDP21-207A-14CC and 15CC; middle-late Eocene transition from western North Atlantic and Antarctic oceanic area (Maud Rise). According to Funakawa & Nishi (2005) the

last occurrence of this species is at 33.8-34 Ma, at the boundary between the late Eocene *Eucyrtidium spinosum* Zone and early Oligocene *Eucyrtidium antiquum* Zone in Southern Ocean (Maud Rise).

Genus *Suttonium* Schaaf, 1976, emend. Dumitrica, 1983a

Type species. *Suttonium praedicator* Schaaf, 1976

Remarks. In my article on the genus *Suttonium* (Dumitrica, 1983a) I had mentioned that the structure of the arms of this genus resembles perfectly the arm structure of some Cretaceous and Jurassic Hagiastridae, as for example *Higumastra* Baumgartner. On the basis of this similitude I had supposed that the origin of this genus should be in one of the late Cretaceous higumastrins. At present, when we know that the hagiastrid have a special type of microsphere, which is never spherical, and a pyloniacean mode of growth in their early ontogenetical stages (Dumitrica in De Wever et al., 2001), whereas the microsphere of *Suttonium* and of all Suttoniidae is a simple sphere, and shell growth is simple, it is difficult to sustain such a filiation. Consequently, despite the structural similarity of arms any relationship between *Suttonium* and the higumastrins is excluded. Until present its origin remains somehow questionable. The spherical microsphere with dense circular pores of similar size and rather regular disposition, and the crescent shape deuterococoncha attached to it on the antapical side suggest a close relationship with the genus *Homunculodiscus* n. gen., and especially with *Homunculodiscus tainemplecta* (Caulet). The presence of the three primary rays and of the arms around them seem to make this idea questionable although quite possible. If so, the three spines of this genus that constitute the centre around which the arms are built, plus the apical spine present usually on the microsphere of *Suttonium* and especially on the older species could have derived from 4 of the many rays lying in the equatorial plane and forming the radial structure of skeleton of *Homunculodiscus*. In this situation, the short bars connecting the central rays of the arms of *Suttonium* with the cortical shell in planes perpendicular to the disc, and that form a structure resembling that of the arm of some hagiastrids, are similar to the bars perpendicular to the disc connecting the multiple rays with the two cortical plates. A good candidate for this origination is until present the specimen illustrated by Nishimura (2001, pl. 2, fig. 17) as *Suttonium riedeli* Dumitrică from the late Paleocene *Bekoma bidartensis* Zone. Certainly, this specimen does not belong to *S. riedeli*, which is a species with slender arms. Nishimura's specimen has short and very broad arms and belongs to a new, undescribed species. With this morphology Nishimura's specimen suggests that the arms of *Suttonium* appeared by the reduction of the two cortical plates of the disc of the genus *Homunculodiscus* in the interradial portions after the appearance of the three rays. This change seems to have been rather fast at geological scale, somewhere in the middle Paleocene, since the specimen illustrated by Nishimura comes from the late Paleocene and the three primitive species of *Homunculodiscus* herein described are early Paleocene in age.

Once appeared, the evolution of the genus *Suttonium* followed a migration trend of the microsphere from the deuterococoncha and of the latter from the three-rayed cortical

shell (Dumitrică, 1983a, p. 39-40, fig. 2). The consequence of this trend is the appearance of a nassellarian morphology having the microsphere as a cephalis, deuterococoncha as thorax and cortical shell as abdomen, and the magnification of the angle between the lateral arms from around 120° in *Suttonium riedeli* Dumitrică to 120° or greater in *S. anomalum* (Sutton) and finally to 180° in *S. praedicator* Schaaf.

Range. Late or middle Paleocene to Holocene.

Suttonium riedeli Dumitrică, 1983a

1983a *Suttonium riedeli* Dumitrică, p. 44, pl. 3, figs. 1, 2. non *Suttonium riedeli* Dumitrică in Nishimura, 2001, p. 298, pl. 2, fig. 17.

Remarks. This is the oldest described species of the genus *Suttonium*, based on two photos provided by Dr. W. R. Riedel. This species differs from *S. anomalum* (Sutton) in the relation between the microsphere and the cortical shell, the former being almost completely included in the cortical shell. It differs also in having the antapical arm inflated on the proximal part, this inflated part being separated from the central part of shell by a constriction resulted from the presence of two opposite branches of the primary antapical ray in equatorial plane.

As discussed above, the late Paleocene specimen illustrated by Nishimura (2001, p. 298, pl. 2, fig. 17) as *Suttonium riedeli* does not belong to this species but represents an older new species, the oldest in fact, that makes the transition between *Homunculodiscus* and *Suttonium*.

Range and occurrence. Upper Paleocene to lower Eocene; DSDP 40-11-4, 70-73 cm and DSDP 96-3-5, 42-44 cm.

Suttonium anomalum (Sutton), 1896

Figure 6c

1896 *Rhopalastrum* (?) *anomalum* Sutton, p. 59, fig. 1.

1983a *Suttonium anomalum* (Sutton). – Dumitrică, p. 42, pl. 2, figs. 1-4; pl. 3, figs. 3, 4, 6-8, 11.

2015 *Suttonium anomalum* (Sutton). – Kamikuri, p. 148, pl. 18, fig. 9.

Remarks. It seems that Schaaf (1976) was not convinced that Sutton's species is congeneric with *Suttonium praedicator* Schaaf because in his very short note he (Schaaf, 1976, p. 792) wrote that Sutton's species is the only species "presenting some similitudes" with his new species and genus. That is why he did not include Sutton's species in the genus *Suttonium*.

Range and occurrence. Upper Eocene to Pleistocene, subtropical to equatorial Pacific, and Caribbean area (Barbados).

Suttonium praedicator Schaaf, 1976

Figure 6d

1976 *Suttonium praedicator* Schaaf, p. 789-792, pl. 1, figs. 1-5.

1983 *Suttonium praedicator* Schaaf. – Dumitrică, p. 42, pl. 1, figs. 1-6; pl. 2, figs. 5-8; pl. 3, figs. 9, 10, 12-15.

Remarks. *S. praedicator* is the last evolutionary species of the genus and it is interesting by having the two lateral arms perfectly opposed, and the microsphere and the apical portion of deuterococoncha out of the cortical shell.

Range and occurrence. Upper Pleistocene? to Holocene, surface sediments, southern tropical Pacific.

Genus *Parasuttonium* nov. gen.

Type species. *Parasuttonium taiwanense* nov. sp.

Diagnosis. Test flat, three-armed, consisting of two parallel latticed plates with circular pores of rather regular size and radial or irregular disposition. Central structure consisting of a spherical and slightly eccentric latticed microsphere with 3 primary rays. Rays prolonged outside to form three latticed arms around them. Distal part of primary rays simple, not forked. Microsphere rather large, surrounded on the antapical side by a bilobate deutoconcha.

Remarks. By its type species from the Quaternary of western Pacific around Taiwan, this genus is very close to *Suttonium* Schaaf by having a large latticed microsphere, a bilobed deutoconcha on the antapical side of the microsphere and 3 radial bars originated in the microsphere: one axial and two lateral. It differs from *Suttonium* in not having the arms free but included in the skeletal disc, and in having the primary rays prolonged as spines outside the arms. In the three species of *Suttonium* the arms terminate into two curved opposite spines in planes perpendicular to the shell, one on each face, whereas this new genus has no such terminations. Moreover, in *Suttonium* the arms are hollow and the inner rays are connected with the wall of the arms only in perpendicular planes to the plain of the shell, whereas in *P. taiwanense* the spines are connected to the disc by branches in all directions.

It is strange the occurrence of *Parasuttonium* only in the Quaternary because its morphology is intermediate between that of *Homunculodiscus* (the disc-shaped skeleton) and *Suttonium* (three-rayed shell and a beginning of arms). With such a mixed characters, its FAD should have been somewhere in the middle or late Paleocene, before the FAD of *Suttonium riedeli*. Probably this enigma will be solved in future by another interpretation of its morphology or by finding much older species of this genus.

Etymology. From the Latin and Greek *para* – alongside, aside, closely related, and *Suttonium*.

Range and occurrence. Very rare in the Quaternary.

Parasuttonium taiwanense nov. sp.

Figures 6a-b

Description. Shell flat, large and thin with microsphere bearing 3 primary equidistant rays surrounded, toward the periphery of disc, by a tube and equally 3 short and wide intercallary arms without tubes or with partly formed ones. Microsphere slightly eccentric, with a bigger portion between the lateral primary rays and smaller and equal portions between lateral rays and the antapical ray. It has many densely and irregularly arranged circular pores. Deutoconcha bilobed. Pores of shell circular, visibly larger than those of the microsphere and arranged either irregularly or in radial rows. The three primary rays thin, conical, needle-shaped, and more or less prolonged beyond the tubes into needle-shape spines. They are connected to the tube by irregularly arranged short branches. The apically prolonged tube of the holotype has also a central ray similar to the other three tubes.

Material. Two specimens, both from sample 83-481, section II, 73-75 cm of R/V Ocean Researcher 1 of National Science Council, Taiwan.

Holotype. Figure 6a, coll. MGL 103557.

Dimensions. Diameter of microsphere 20-21 μm , of shell with arms 205 μm , of axial spine 128 μm , angle between the three rays about 120°.

Etymology. The species is named from Taiwan since it comes from sediments cored in the Pacific area around Taiwan.

Occurrence: Western Pacific around Taiwan, superficial sediments, Quaternary.

Family Patulibrachiidae Pessagno, 1971, emend Dumitrica, 2001 in De Wever et al.

Type genus. *Patulibracchium* Pessagno, 1971.

Remarks. In an emendation of the family Patulibrachiidae Pessagno (Dumitrica in De Wever et al. 2001, p. 142-143) based on the study of the initial skeleton, I included in this family 5 genera, of which 4 are known from early Jurassic to latest Cretaceous. The only Cenozoic genus was *Trimanacula* Dumitrică. According to the definition, all members of this family have 3 arms developed along the three primary rays (two lateral and one antapical) and a very small heptagonal microsphere. In this article I describe, from the early Paleocene, a new genus, *Cryptomanacula* n. gen., with a circular spongodiscid shaped discoidal or slightly lenticular shell, and an initial skeleton similar to that of *Trimanacula*, but without arms. This is the only case of armless Patulibrachiidae, which proves the priority of initial skeleton over external morphology in taxonomy. This proves also that for most Cenozoic radiolarians, which have the skeleton preserved in opal, their study in transmitted light is the best method for the knowledge of internal structure.

Genus *Trimanacula* Dumitrică, 1991

Type species. *Trimanacula centropina* Dumitrică, 1991

Range. Early Paleocene to early Pliocene.

Trimanacula penultima Dumitrică, 1991

Figure 7b

1991 *Trimanacula penultima* Dumitrică, 1991, p. 54, pl. 3, fig. 5; pl. 4, fig. 2; pl. 8, figs. 7, 8; pl. 9, figs. 11-13.

Remarks. The species is very rare, represented until present by only the holotype. It evolved probably from the genus *Patulibracchium* Pessagno, its probable forerunner, by the reduction of the arms probably during the Cretaceous-Tertiary boundary crisis. Judging from the morphology of the holotype, it seems that it is a young specimen with the arms incompletely developed. This holotype differs from *T. centropina* Dumitrică especially by the angle between the lateral primary rays that reaches 160°, rather close to that of some Campanian species of the genus *Patulibracchium* illustrated by Pessagno (1971).

Range and occurrence. Earliest Paleocene, DSDP 21-208-31 CC, Lord Howe Rise, SW Pacific.

Trimanacula centropina Dumitrică, 1991

Figures 7a, f

1972 *Trigonactinium* sp. – Petrushevskaya & Kozlova, pl. 17, fig. 2.

1987 *Suttonium* sp. – Petrushevskaya, p. 1451, fig. 4 (9-10).

Fig. 5 a-e - *Cryptomanicula absconsa* nov. gen., nov. sp.; **a** – holotype, **b** – same, central part magnified. **c-e** – paratype with one cortical layer struck off with a razor blade: **c** – general view from the surface, **d** – same, viewed from the struck off face, focussed on primary rays; **e** – same, focussed on the 7-sided initial ring. All scale bars = 50 µm

1991 *Trimanicula centrospina* Dumitrică, p. 52, pl. 3, fig. 4; pl. 4, figs. 1, 3, 4; pl. 7, figs. 8-10; pl. 8, figs. 1-6, 9-11; pl. 9, figs. 1-10.

2001 *Trimanicula centrospina* Dumitrică – De Wever et al., p. 142-143, fig. 82. 1-2.

Remarks. Due to its range and regular three-rayed shell, this species evolved, directly or through a yet unknown intermediary species, from the early Paleocene species *Trimanicula penultima* Dumitrică by a slight migration of the microsphere towards the centre and, as a consequence, regularization of the skeleton that from bilateral-

ly symmetrical and cross-shaped became regularly three radial with angles of about 120° between arms.

Range and occurrence. Early Oligocene to early Pliocene so far as known.

Genus *Cryptomanicula* nov. gen.

Type species. *Cryptomanicula absconsa* nov. sp.

Diagnosis. Shell thin, lens-shaped, circular and spongy, without arms. Initial skeleton of *Trimanicula* type included in the centre of shell, and the three primary rays not prolonged beyond periphery of shell. Inner shell with

Fig. 6 a-b. *Parasuttonium taiwanense* nov. gen., nov. sp., Quaternary; **a** – holotype, **b** – paratype, incomplete specimen. **c** – *Suttonium anomalum* (Sutton). **d** – *Suttonium praedicator* Schaaf (from Dumitrică, 1983, pl. 1, fig. 1; pl. 3, fig. 14). Scale bars for **6a-c** = 50 μ m.

Fig. 7 a, f. *Trimanicula centrospina* Dumitrică, holotype rephotographed, AMPH 6P, 21-23 cm., **f** – same, central part of **a**, double magnified. **b.** *Trimanicula penultima* Dumitrică, holotype rephotographed, DSDP 21-208-31 CC. **c-e** – *Cryptomanicula absconsa* Dumitrică nov. gen., nov. sp., same, paratype as that illustrated on fig. 3h, focused at another level; **d, e** – detail of centre focused on surface and on microsphere, respectively, DSDP 21-208-30 CC. Scale bar of **a-c** = 50 μ m.

many secondary and tertiary rays, none of them extended outside periphery of shell.

Etymology. From the Latin *crypta* – hidden and *manicula* – small hand. Feminine gender.

Remarks. By its external shape and the spongy shell, this genus resembles a spongodiscid from which it differs in having an initial skeleton of *Trimanicula* type as described and illustrated by Dumitrică (1991, pl. 3, figs. 4, 5; pl. 8, figs. 2, 3, 9-11). This structure is very well visible in the holotype and sectioned paratype of the type species of *Cryptomanicula* (Fig. 5). Its origin was probably in the species *Trimanicula penultima* Dumitrică, although no transitional species was until present discovered. Absence of such species is not surprising given the extreme scarcity of the genus *Trimanicula* in the Paleocene.

5; pl. 8, figs. 2, 3, 9-11). This structure is very well visible in the holotype and sectioned paratype of the type species of *Cryptomanicula* (Fig. 5). Its origin was probably in the species *Trimanicula penultima* Dumitrică, although no transitional species was until present discovered. Absence of such species is not surprising given the extreme scarcity of the genus *Trimanicula* in the Paleocene.

Range and occurrence. DSDP21-208-30CC, early Paleocene, *Prinsius martini* nannoplankton Zone, so far as known.

Cryptomaniacula absconsa nov. sp.

Figures 3h; 5a-e; 7c

Description. Shell thin, lens-shaped with circular outline. Microsphere eccentric with 3 primary rays, of which one axial (antapical) and two lateral. Angle between lateral rays much greater than between lateral rays and the axial one. Rays not prolonged outside periphery of the disc and not visible on the surface. Besides primary rays shell contains a greater number of secondary and tertiary rays originated in the first and second extramicrospheric ring, respectively (Fig. 5c).

Material. Three specimens in the late early Paleocene sample DSDP 21-208-30 CC, Lord Howe Rise, SW Pacific. Two specimens are entire (figs. 3h; 4a, 4b) and one has one surface sectioned off (figs. 5c-e) to know the internal structure of shell.

Holotype. Specimen from Figs. 5a, 5b, coll. MGL 103558.

Dimensions. Diameter of holotype 239 μm , of paratype 260 μm , diameter of microsphere 12.5 μm , angle between lateral rays 150-155°, between lateral primary rays and axial primary ray 100-110°, distance between microsphere and apical border 100 μm , distance between microsphere and antapical border 128 μm .

Remarks. Perfection of the circular outline of this species suggests the possibility of the presence of other Paleocene species that could make the transition between it and *Trimaniacula penultima* Dumitrică. The close relationship with this species is also suggested by the wide opening of the angle between the two lateral primary rays.

Etymology. From the Latin *absconsus* – hidden, because the initial skeleton of this species is hidden inside the lenticular disc and difficult to see.

Range and occurrence. DSDP21-208-30CC, early Paleocene, *Prinsius martini* nannoplankton Zone.

Family Heliodiscidae Haeckel, 1881, emend. Dumitrică, 1984

Type genus. *Heliodiscus* Haeckel, 1862.

Diagnosis. Test consisting of a double medullary shell with eccentric microsphere and a cortical shell that can be lenticular, spherical, discoid and simple or multiple, and connected to medullary shell by numerous beams directed to the two faces.

Remarks. Hollande & Enjumeat (1960) seem to be the first researchers who remarked the eccentric position of the microsphere in the outer medullary shell. In the Addendum of their monograph they described two new taxa: *Excentrodiscus echinatus*, a new genus and species with a spherical cortical shell and a double medullary shell with an eccentric microsphere, and *Astrophacus viminalis*, a new species with external characters of *Astrophacus* Haeckel, but with eccentric instead of concentric microsphere. Due to this similarity they questioned the accuracy of Haeckel's observation concerning the position of the microsphere in this genus.

Regarding *Heliodiscus phacodiscus* Haeckel, the type species of the type genus of the family, we have no information concerning the position of its microsphere

within the outer medullary shell because the central part of the type specimen illustrated by Haeckel (1862, pl. 17, figs. 5-7) is obscured, probably due to the thickness of the cortical shell. In the specimen of the same species illustrated by Tan & Chen (1999, fig. 5-118), as well as in other Quaternary species of this genus illustrated with drawings by them, the microsphere is also invisible. However, given its Quaternary age and the eccentric position of the microsphere in other Quaternary species of the genus *Heliodiscus*, we can rather confidently ascertain that it is also eccentric in the type species because the Phacodiscidae and Coccodiscidae were already extinct before the Quaternary and even the Pliocene. My assertion could be considered groundless because Haeckel (1862, pl. 28, figs. 11, 12), in his monograph on the living Radiolaria from Messina, illustrated the first coccodiscid (*Coccodiscus darwinii* Haeckel) and even described in detail the structure of its soft body. He wrote (Haeckel, 1862, p. 485-486) that he found the only specimen in the water from Messina and he preserved it in liqueur to study its soft body later. Knowing generally from my practice the occurrence of the Coccodiscidae and Phacodiscidae I was always intrigued by the presence of this genus and species in the living plankton and I was feeling that something is not in order with it. In my opinion, it had no place among the living plankton from Messina. I thought that Haeckel either cheated or made a mistake when he included this species in his monograph. But how could he describe in detail the soft body of this species? Imagination? I raised this problem last year during the last meeting of our group of co-authors of the Project of Catalogue of Neozoic Radiolaria, which included Jean-Pierre Caulet, Luis O'Dogherty, Noritoshi Suzuki and myself. I expressed my strong doubt about the presence of the species *Coccodiscus darwinii* in the living plankton illustrated in Haeckel monograph. I expressed my feeling that Haeckel knew the Eocene fauna from Barbados at the time when he wrote this monograph and he included this species to have one more genus in it. Noritoshi Suzuki who had worked in the "Joint Haeckel and Ehrenberg Project (2009) didn't agree with me arguing that at that time Haeckel did not had samples from Barbados. However, looking in the collection of photos he had made from Haeckel's house and collection in Jena, he fortunately found and showed us a photo of an individual slide with Haeckel's hand writing on which it was written: "*Coccodiscus Darwinii* Haeckel, 1862, Barbados". It was the holotype of this species. This was exactly the proof I had looked for long time, the proof that *Coccodiscus darwinii* was not a living species but an Eocene one as most of the coccodiscids.

A somehow similar problem could raise *Heliodiscus asteriscus* Haeckel. Tan & Chen (1999, p. 208, fig. 5-121) illustrated with a drawing a specimen of this species in whose centre of the outer medullary shell they drew a darker spot suggesting probably that the microsphere is centrally disposed. If so, this drawing is certainly wrong. A photo of the same species published in Dumitrică (1978, pl. 2, fig. 4) shows clearly an eccentric microsphere represented by an eccentric dark spot. To be completely sure of the position of the microsphere I sectioned a specimen of this species according to the method I described in De Wever et al. (2001, p. 436-439). The spec-

imen had been found in the late middle Miocene sample PROA 96P in which the microsphere was very difficult to see due to the thick cortical shell, but it became rather well visible in eccentric position after scratching out a part of this shell. Nigrini (1967, pl. 3, figs. 1a, 1b) and Kawakami (2001, pl. 1, fig. 13) illustrated also specimens of this species with well visible eccentric microsphere. This suggests that the two species (*H. phacodiscus* and *H. asteriscus*) are congeneric and that both belong to the genus *Heliodiscus*.

According to the emended definition (Dumitrică, 1984; De Wever et al., 2001) the main characteristic of this family is the presence of a double medullary shell with eccentric microsphere and of a latticed cortical shell that has various geometrical shapes: (lens, disc or sphere) and consists of a variable number of layers.

The fossil record proves that the spherical heliodiscids are the oldest members of the family. They are known from the late Santonian-early Campanian from western Kamchatka (Vishnevskaya & Dumitrică, 2003; Vishnevskaya, 2006). The lenticular and disc-shaped heliodiscids (*Heliodiscus* and *Excentrococcus*) are known since the Miocene and they have probably their origin in horizontal gene transfers between *Excentrodiscus* and a phacodiscid species probably during the late Paleogene or early Miocene when the lens-shaped phacodiscids were still frequent.

Range and occurrence. The oldest representatives of the family are known in late Santonian - early Campanian from western Kamchatka Peninsula (Vishnevskaya & Dumitrică, 2003; Vishnevskaya & Bernard, 2004; Vishnevskaya, 2006). At this stratigraphic level the family is represented by spherical species with 3 or 4 shells belonging to the genera *Excentrodiscus* and probably *Excentrosphaerella*. *Excentrosphaerella* seems also to occur in the early Paleocene, represented probably by *Haliomma teuria* Hollis (1997). Until present no other species of this genus is known in the Cenozoic except the type species occurring in the late middle Miocene of Romania. In exchange, the genus *Excentrodiscus* is rather well represented by several species in the Eocene and Oligocene.

Genus *Heliodiscus* Haeckel, 1862

Type species. *Heliodiscus phacodiscus* Haeckel, 1862.

Diagnosis. Cortical test lenticular and single with a double medullary shell with eccentric microsphere.

Remarks. Morphologically *Heliodiscus* resembles very well the Paleogene Phacodiscidae, as for example *Astrophacus* Haeckel, 1881, *Periphaena* Ehrenberg, 1873, etc., from which it differs in having the double medullary shell with eccentric microsphere. This resemblance is probably the result of a horizontal gene transfer between a phacodiscid species and a species of *Excentrodiscus*, genus frequent in the Paleogene and later. It could be also the result of a convergence but I do not see how, all radiolarians being planktonic organisms.

Range. Miocene to Recent. It seems that this genus is not present in the Paleogene because no lenticular morphospecies with eccentric microsphere have been illustrated in any Paleogene species (Sanfilippo & Riedel, 1973; Funakawa et al., 2006; Kamikuri, 2015, and others).

Heliodiscus riedeli nov. sp.

Figures 8b, e, f; 9a

Description. Shell large, disc-shaped with a small double medullary shell and a wide cortical shell. Microsphere very small, eccentric in the outer medullary shell and connected to it through a few cylindrical beams of different length. Outer medullary shell spherical or slightly prunoid with wide circular or polygonal pores separated by thin intervening bars and included in the cavity of the cortical shell to which it is connected with the two faces of this shell by a bunch of very short rays. Cortical shell flat, very thin and perforated by numerous very small polygonal pores arranged either disorderly or, partly, radially. Periphery of disc armed with numerous three-bladed, short, and pyramidal spines disposed in several planes.

Material. Eight specimens in sample PROA 96P, 241-243 cm, late middle Miocene.

Holotype. Figure 8b, coll. MGL 103559.

Dimensions. Diameter of microsphere 17-19 µm, of outer medullary shell 47-54 µm, of cortical shell 241-295 µm.

Etymology. The species is named for William R. Riedel for his great contribution to the study of Cenozoic radiolarians. It is also in the sample provided by him that this species was found.

Remarks. This species differs from all the other species of this genus in having a large, completely flat disc-shaped cortical shell and many short pyramidal spines on periphery.

Range and occurrences. Late middle Miocene, central Pacific.

Heliodiscus bipolaris n. sp

Figures 8d, e, h

Description. Medullary test double, prunoid with an eccentric microsphere. Cortical shell ovoid in face view and lenticular in side view, the broader part at the end where the microsphere is closer to the outer medullary shell. The two ends of cortical shell with a bunch of numerous irregular and short spines. No opening visible at these ends.

Material. A single specimen in DSDP 21-206-29CC.

Holotype. The illustrated specimen, coll. MGL 103560.

Dimensions. Diameter of microsphere 14 µm, of outer medullary shell 40-50 µm, length of cortical shell 135 µm, breadth of cortical shell 102 µm.

Etymology. Having two poles.

Remarks. This species differs from the other species of the genus by not having a circular outline but an elliptical one in face view and peripheral spines only at the two ends of the cortical shell.

Range and occurrence. Late Miocene, New Caledonia Basin, DSDP 21-206-29CC.

Genus *Helioferrusa* nov. gen.

Type species. *Helioferrusa hollandei* nov. gen., nov. sp.

Diagnosis. Skeleton of *Heliodiscus* type but bearing a peripheral porous ring instead of spines. Microsphere eccentric in the outer medullary shell.

Etymology. The generic name comes from the Greek *helios* – Sun and *Odette Ferru* who illustrated the radiola-

rian species from the monograph by Hollande & Enjume (1960) with wonderful drawings similar in quality to those made by Adolf Giltch for Haeckel's 1887 monograph. Feminine gender.

Remarks. This genus resembles a *Coccodiscus* Haeckel from which it differs in having a double medullary shell with eccentric microsphere and originated very probably in *Heliodiscus riedeli* nov. sp. with which its cortical shell resembles very well and with which it co-occurs in the late middle Miocene assemblage from sample PROA 96P.

Range and occurrence. Late middle Miocene so far as known.

Helioferrusa hollandei nov. sp.

Figures 9b, c, h, i

Description. Shell thin disc-shaped consisting of 4 shells: a double medullary shell with an eccentric microsphere, a large main cortical shell, and a peripheral equatorial ring. Microsphere very small, eccentric in the outer medullary shell. Outer medullary shell prunoid or subspherical, with large circular or polygonal pores and included in the cavity of the cortical shell with whom it is connected to the two faces of the latter by a bunch of oblique radial beams. These beams do not cross this shell. Cortical shell large, disc-shaped or lenticular and a little thicker than the diameter of the outer medullary shell. It has numerous very small circular to oval pores of various sizes and irregularly or, partly, radially disposed. This shell is surrounded by a peripheral ring with similar pores but usually smaller. Inside this ring there are radial costae that divide its circumference in unequal segments. Periphery of ring with tiny thorns.

Material. Four specimens, from the late middle Miocene sample PROA 96P.

Holotype. The illustrated specimen, coll. MGL 103561.

Dimensions. Diameter of microsphere 17-19 μm , of outer medullary shell 49-54 μm , of cortical shell 173-232 μm , of peripheral ring 232-330 μm .

Etymology. The species is dedicated to André Hollande, co-author of the valuable monograph on living Radiolaria from the Gulf of Alger.

Remarks. In this species I included two morphotypes: one found in sample PROA 96P (Fig. 9b), represented by 7 specimens, the other one in sample DSDP 21-205-7-1, 70-72 cm from South Fiji Basin, which is late Miocene (NN10 Zone) in age (Fig. 9c). These two morphotypes are practically contemporaneous but morphologically rather different. The morphotype from the sample PROA 96P has the cortical shell flat, very thin similar to that of *Heliodiscus riedeli* nov. sp., and the peripheral ring has thin intervening bars between pores. The morphotype from the sample DSDP 21-205-7-1, 70-72 has the lenticular cortical shell, with rather convex faces and larger pores, and the peripheral ring has much smaller pores, separated by larger intervals, approximately as large as diameter of pores. These differences seem to be rather important, at least at subspecies level, but because I found a single specimen with such characters in that sample I do not know what signification they could have.

Range and occurrence. Late middle Miocene from tropical and subtropical Pacific.

Genus *Excentrodiscus* Hollande & Enjume, 1960

Type species. *Excentrodiscus echinatus* Hollande & Enjume, 1960.

Remarks. This genus is the longest-ranged taxon of the family. I included in this article two new species from the Eocene and one from the middle Miocene.

Range and occurrence. Late Santonian or early Campanian to Recent.

Excentrodiscus dodo nov. sp.

Figures 9d, e

?2015 *Excentrodiscus* aff. *oculatus* (Ehrenberg). – Kamikuri, p. 148, pl. 15, figs. 3, 4, 6, 8.

Description. Cortical shell small, spherical with numerous circular pores. Pores equal, hexagonally framed, rarely pentagonally framed. Intervening bars triangular in transverse section forming crests. At vertices of frames test develops very small pointed thorns that make the surface of test rough. Inside cortical shell there is a spherical double medullary shell with an eccentric microsphere. Microsphere with a few polygonal pores and connected to outer medullary shell through very thin radial beams of different length depending of their position. They stop in the wall of outer medullary shell. Outer medullary shell spherical, thin-walled with polygonally framed circular pores. This shell gives rise to many thin radial bars that connect it to cortical shell.

Material. One specimen in sample DODO 123D.

Holotype. The illustrated specimen, individual slide, stored in the MGL 103562.

Dimensions. Diameter of microsphere 18 μm , of outer medullary shell 55 μm , of cortical shell 122 μm .

Etymology. The species is named after the sample DODO of the Scripps Institution of Oceanography, California, in which the species was found.

Remarks. The shell of *Excentrodiscus dodo* resembles that of *E. kamikurii* nov. sp. in size and thickness of shell, but differs from it in not having spines, and in the fact that the beams connecting the microsphere with the outer medullary shell are not aligned with those connecting the latter with the cortical shell. It resembles also the middle/late Eocene specimens determined by Kamikuri (2015) as *Excentrodiscus* aff. *oculatus* (Ehrenberg) by not having long spines and by the type of cortical pores.

Range and occurrence. Middle? Eocene, DODO 123 D, Central Indian Ocean Basin.

Excentrodiscus kamikurii nov. sp

Figures 9f, g

cf. 2015 *Excentrodiscus* aff. *oculatus* (Ehrenberg). – Kamikuri, p. 148, pl. 15, figs. 3, 4, 6, 8.

Description. Microsphere very small, eccentric, with 8-10 wide polygonal pores interconnected to outer medullary shell through 8-10 very thin beams of various length depending of their position in shell. Outer medullary shell spherical, rather thin and latticed with polygonally framed circular pores. Intervening bars thin, triangular in transverse section. Cortical shell spherical, rather thin-walled with numerous circular pores. Intervening bars thin with sharp crests and short and thin by-spines at vertices. Cortical shell bears 8-10 needle shaped spines about as long as skeleton ray. These spines are originated either

in the microsphere or in the wall of the outer medullary shell, no one in the cortical shell.

Material. One specimen in sample DODO 123D.

Holotype. The illustrated specimen, individual slide, coll. MGL 103563...

Dimensions. Diameter of microsphere 16-17 µm, of outer medullary shell 57 µm, of cortical shell 125 µm.

Etymology. The species is named for Dr. Shin-ichi Kamikuri, Ibaraki University, Japan, for his contribution to the knowledge of Cenozoic radiolarians and for having illustrated some specimens of Eocene *Excentrodiscus*.

Remarks. Shell of this species resembles the shell of the co-occurring species in sample DODO 123D from which it differs in having radial spines. It resembles very much the Recent species *Excentrodiscus echinatus* Hollande & Enjume from the Gulf of Alger in shape and size of shells from which it only differs in having a smaller number and shorter spines. The specimens illustrated by Kamikuri (2015) as *Excentrodiscus* aff. *oculatus* (Ehrenberg) are rather similar to this new species from whom they differ especially in having shorter spines.

Range and occurrence. Middle? Eocene of Indian Ocean.

Excentrodiscus grigorei nov. sp.

Figures 10a-d

?1978 *Excentrodiscus* sp. – Dumitrică, pl. 4, figs. 5-6.

2001 *Excentrodiscus* sp. – Dumitrică in De Wever et al., p. 124, Fig. 69.2, 69.5.

2010 *Excentrodiscus japonicus* (Nakaseko & Nishimura). – Kamikuri, pl. 2, figs. 13a-b, 14a-b.

Description. Cortical test spherical to slightly ovoid, thick-walled in mature stage. Pores circular or oval on the inner side of cortical shell polygonally (pentagonally or hexagonally) framed externally, with sharp crests and thin spines at vertices. Medullary shell double, with a very small eccentric and polyhedral microsphere and a slightly oval outer medullary shell. Outer medullary shell interconnected with microsphere through about 7-8 unequal beams and with the cortical shell by about double number of equal radial bars. All beams cylindrical and not continued among shells.

Material. Numerous specimens in the Middle Miocene (late Badenian) Radiolarian Shale Formation from Subcarpathians and Getic Depression of Romania.

Holotype. Figure 10a, coll. MGL 103564.

Dimensions. Diameter of microsphere 23 µm, of external medullary shell 70 µm, of cortical shell 150-190 µm.

Etymology. The species is dedicated to the geologist Grigore Popescu who defined for the first time the Radiolarian Shale Formation in the Miocene of Subcarpathian area.

Remarks. This species differs from the specimen illustrated as *Excentrodiscus* sp. in Dumitrică 1978 (pl. 4, figs. 5-6) in having a smaller number of pores and thicker cortical shell in mature stage, but resembles the one illustrated in De Wever et al (2001) although both are from the same formation. Specimens assignable to this new species have been illustrated by Kamikuri (2010) from late Neogene of middle to high latitude of North Pacific and assigned to *Excentrodiscus japonicus* (Nakaseko & Nishimura, 1974). However, Nakaseko and Nishimura's species, originally determined as *Prunulum japonicum*, differs from *Excentrodiscus grigorei* nov. sp. by having many

more and much smaller pores. So, the two species are not synonym.

Range and occurrence. Middle Miocene (late Badenian), Radiolarian Shale Formation, Subcarpathians and Getic Depression, Romania.

Genus *Excentrococcus* Dumitrică, 1978

Type species. *Excentrococcus annulatus* Dumitrică, 1978.

Diagnosis. Test flat, disc-shaped with an eccentric microsphere in an outer medullary shell. Medullary shell surrounded by 2-6 circular or oval latticed rings.

Remarks. This genus resembles the genus *Flustrella* Ehrenberg from which it differs in having the microsphere eccentric in the second shell.

Range. Middle Miocene to Recent so far known.

Excentrococcus annulatus Dumitrică, 1978.

Figures 8a, 8c

1972 Phacodiscidae? gen. indet. Petrushevskaya & Kozlova, pl. 19, fig. 15.

1973 *Xiphospira* sp. cf. *X. circularis* Kling, p. 635, pl. 7, fig. 16, non 11-15, 17.

1978 *Excentrococcus annulatus* Dumitrică, p. 238, pl. 2, fig. 12; pl. 5, figs. 19, 23.

1992 *Excentrococcus annulatus* Dumitrică – Sugiyama & Furutani, p. 202, pl. 12, fig. 4; ?pl. 16, fig. 4.

1992 *Excentrosphaerella sphaeroconcha* Dumitrică – Sugiyama & Furutani, p. 202, pl. 12, figs. 1, 2; ?pl. 16, fig. 3.

1999 *Perichlamidium* sp. cf. *Ommatodiscus perichlamyidium* Dreyer – Tan & Chen, p. 209, fig. 5 – 122.

2004 *Excentrococcus annulatus* Dumitrică. – Kamikuri et al., pl. 8, fig. 10.

Description. Test flat consisting of a double medullary shell with a very small eccentric microsphere; this structure surrounded by two to maximum six latticed circular or oval rings. When number of rings is maximum, shell is oval with an end open and external outermost rings are thinner, irregular and with smaller pores.

Dimensions. Maximum length of shell around 150-160 µm.

Remarks. The species is very variable in shape and number of rings, probably depending on the biological age of specimens and environment. The common number of shells is six and maximum eight, as the specimen illustrated in Fig. 8a of the present paper or in Tan & Chen (1999) and Kamikuri et al. (2004). Up to the level of four shells the rings have large pores. The fifth and sixth rings are less regular and their pores are smaller, and the outermost seems to become slightly spongy. As the species is disc-shaped and the outer medullary shell is partly outside (fig. 8c), the maximum thickness of the disc is as great as the diameter of this shell. As a rule, the largest or the most complete specimens are oval and have a pylome marked by an indentation at one end (Fig. 8a in the present paper and in Kamikuri et al., 2004) or by an open ring (Tan & Chen, 1999). This pylome or indentation is situated on the direction in which the microsphere is most close to outer medullary shell. This signifies that there is a correlation between the position of the microsphere and the pylome.

Range and occurrence. Middle Miocene to Recent, cosmopolitan.

Fig. 8 **a, c** - *Excetrococcus annulatus* Dumitrică; **a** – mature specimen, face view, DSDP 21-205-7-1, 70-72 cm, scale bar 100 μ m; **c** – other specimen, transversal section along the longitudinal axis showing the eccentric microsphere, DSDP 21-206-29CC, scale bar = 100 μ m. **b, f, g** - *Heliodiscus riedeli* nov. sp., PROA 96P. **d, e, h** - *Heliodiscus bipolaris* nov. sp. focused at centre, on surface, and in lateral view, respectively, scale bar = 50 μ m, DSDP 21-206-29CC.

Genus *Excentrosphaerella* Dumitrică, 1978

Type species. Excentrosphaerella sphaeroconcha Dumitrică, 1978

Range and occurrence. Santonian-Campanian of Kamchatka? (Vishnevskaya, 2006) to middle Miocene (late Badenian), Radiolarian Shale Formation of Romanian Subcarpathians and Getic Depression).

Excentrosphaerella sphaeroconcha Dumitrică, 1978

Figures 10e-h; 11a-b

?1887 *Actinomma* (*Actinommura*) *capillaceum* Haeckel, p. 255, p., 29, fig. 6.

1978 *Excentrosphaerella sphaeroconcha* Dumitrică, p. 238, pl. 5, figs. 17, 18, 22.

non 1992 *Excentrosphaerella sphaeroconcha* Dumitrică - Sugiyama & Furutani, p. 202, pl. 12, figs. 1, 2; ?pl. 16, fig. 3.

Fig. 9 **a** – *Heliodiscus riedeli* nov. sp, specimen broken and repaired during life, PROA 96P. **b** - *Helioferrusa hollandei* nov. gen., nov. sp., holotype, scale bar = 100 µm; **h** – portion of shell more magnified, PROA 96P; **c** – *Helioferrusa hollandei* nov. sp., paratype, scale bar = 100 µm ; **i** – portion of shell more magnified, DSDP 21-205-7-1, 70-72 cm. **d, e** – *Excentrodiscus dodo* nov. sp., holotype, focused on surface of cortical shell and half sectioned showing the outer medullary shell and the eccentric microsphere, DODO 123 D, scale bar = 50 µm. **f, g** – *Excentrodiscus kamikurii* nov. sp., partly sectioned showing the outer medullary shell, the eccentric microsphere, and the cortical shell, respectively; **g** – same, overturned showing the cortical shell, a spine is blocked in the pore of a nassellarian *Sethochytris* sp., DODO 123D, scale bar = 50 µm.

Fig. 10 a-d. *Excentrodiscus grigorei* nov. sp.: **a** – holotype; **b** – young specimen with incompletely built cortical shell; **c** – mature specimen with cortical and outer medullary shells partly broken off showing inside the eccentric microsphere in oblique antapical position. **e-h.** *Excentrosphaerella sphaeroconcha* Dumitrică: **e** – mature specimen with cortical shell partly broken off showing details of its wall, of the third shell and of the numerous rays connecting the two shells; **f, h** – young specimens with tuberculate and normal cortical shell, respectively. Scale bar of all specimens = 100 μm , all specimens from sample 1315, Radiolarian Shale Formation, Păușești Otăsău, Romania.

Description. Microsphere very small and eccentric in a spherical or slightly prunoid outer medullary shell. Outer medullary shell with large circular or oval pores. Third shell spherical, rather thin-walled with polygonal to circular or subcircular pores and thin intervening bars. Cortical shell spherical, rather thin-walled and with numerous irregular polygonal pores and thin intervening bars. All shells interconnected by numerous filamentous beams, their number increasing with each shell so that between the third and the fourth shell their number is about one hundred or more. These beams are prolonged outside cortical shell into short and thin conical spines.

Dimensions. Diameter of microsphere 13–14 μm , of outer medullary shell 55–65 μm , of third shell 117–123 μm , of cortical shell 217–280 μm .

Remarks. The species illustrated by Sugiyama & Furutani (1992) as *Excentrosphaerella sphaeroconcha* does not belong to this species but to *Excentrococcus annulatus* Dumitrică. *E. sphaeroconcha* has all shells sphaerical whereas the specimen illustrated by them is flat as *Excentrococcus* and the shells outside outer medullary shell are ring-shaped. The best argument for this assignment is that the second, the third and the fourth shells are all focussed on their surface, whereas if they were spherical only the second shell could show its pores, the other two would have shown an optical section of their wall (see Dumitrică 1978, pl. 5, figs. 17, 18, 22, and Fig. 11 of the

present paper). The number of shells is not an argument to assign this specimen to *Excentrosphaerella*, important is that they be spherical.

Excentrosphaerella sphaeroconcha Dumitrică, as illustrated by SEM (Fig. 10f, g), resembles very much the type species of the subgenus *Actinommura* (*Actinommura*) *capillaceum* Haeckel (1887, p. 255, pl. 29, fig. 6): the same morphology of the last two shells with polygonal pores, thin intervening bars, the same type of connection between them by numerous (around 100) filamentous beams that extend outside cortical shell into thin spines, and also rather similar diameters. The only difference is inside the middle shell. Haeckel illustrated a single microsphere, whereas the middle Miocene species from Romania has clearly a double medullary shell with an eccentric microsphere (Fig. 11b). The problem is: are the two species synonyms? If we agree that they are, we should consider that the specimen illustrated by Haeckel had also an eccentric microsphere inside the shell he considered as being microsphere but he could not see it. However, in the entire specimen illustrated by Dumitrică (1978, pl. 5, fig. 17) the eccentric microsphere seems to be rather well visible as a black area. There is also another argument in favour of the synonymy of the two species: the size of the microsphere. Haeckel considered the diameter of his so-called microsphere as being of 0.4 mm.

Fig. 11 a, b. *Excentrosphaerella sphaeroconcha* Dumitrică, partly sectioned specimen showing the inner shells, focused on the third and second shell, respectively, sample 1315, Radiolarian Shale Formation, Păușești Otăsău, Romania, scale bar = 100 μm .

The microspheric diameter of the Heliodiscidae is usually 13–20 μm but usually closer to the smallest value than to the greatest one. In this case, the diameter of the “microsphere” of *A. capillaceum* (0.4 mm) is more than double the measured diameter of the microsphere of the Heliodiscidae and closer to the diameter of the outer medullary shell of the members of this family. The conclusion would be that the two species could be synonym and that the genus *Excentrosphaerella* could be a junior synonym of *Actinommura* Haeckel 1887. However, since a certain

doubt of this synonymy exists, especially also because in the same subgenus Haeckel included *Actinommura arcadophorum* Haeckel 1887, which is an entactinarian of the genus *Rhizosphaera* Haeckel (Dumitrică, 2017) I prefer to consider the two genera valid and belonging to 2 independent families.

Range and occurrence. Rather frequent at some levels of the Radiolarian Shale Formation in both Subcarpathians and Getic Depressions, late middle Miocene (late Badenian), Romania.

CONCLUSION

During the Cenozoic, eccentric microsphere occurred in at least 3 not closely related spumellarian Radiolaria families: Suttoniidae, Patulibracchiidae and Heliodiscidae, and are rather sparse in radiolarian assemblages. The members of the first family have in common not only an eccentric microsphere but also a diploconchal initial structure consisting of the eccentric microsphere to which is attached a crescent shape deuterococoncha on its antapical part.

During evolution, the deuterococoncha of *Homunculodiscus* nov. gen. showed a trend towards unification of the initially 3-4 very small chambers, characteristic of the earliest Paleocene species *H. nascens* nov. sp., into two spherical larger chambers (*H. trilobatus* nov. sp.) or a small single crescent shaped chamber (*H. cauleti* nov. sp.), in the youngest levels of the early Paleocene, to finally a chamber larger than the microsphere (*H. tainemplecta* (Caulet)) in the Eocene. At the same time the inner structure tended to form arches and finally circles or ellipses around the diploconchal structure.

In the genus *Suttonium* Schaaf, that probably originated in the genus *Homunculodiscus* by developing 3 primary beams, during evolution the microsphere tended to get out of deuterococoncha and the latter from the regularly triradial cortical shell, the final shape of shell resembling the letter T.

The genus *Parasuttonium* nov. gen. has a morphology intermediate between that of *Homunculodiscus* and that of *Suttonium*, and it should also contain several older species proving this interpretation.

The genus *Trimanicula* Dumitrică, among the Patulibracchiidae, tended, on the contrary, to have all rays under 120° from the initially T-shaped position between the earliest Paleocene *T. penultima* Dumitrică and the early Oligocene to early Pliocene *T. centrospina* Dumitrică.

The genus *Cryptomanicula* nov. gen., is very strange for the Patulibracchiidae because it has no outer arms but a perfect disc-shaped skeleton, which is an exception in this family.

The Neogene genus *Heliodiscus* Haeckel arose probably by a horizontal gene transfer between *Excentrodiscus* Hollande & Enjumeat and *Phacodiscus* Haeckel or other phacodiscids during the early Miocene, from the latter inheriting the lenticular shape of the cortical shell.

The genus *Helioferrusa* nov. gen., originated in *Heliodiscus*, quite probably *H. riedeli* nov. sp., by appearance of a peripheral ring instead of peripheral spines.

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