The generic revision of the Reussellids (Foraminifera)

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ABSTRACT - The study of the apertural complex in the type species of the reussellid genera leads to a reassessment of the classification of these taxa. The genus Reussella has so many characteristics in common with Bulimina that it is reclassified in the Buliminidae. The family Trimosinidae is retained and redescribed to contain the genera Trimosina, Mimosina and Fijella only. Pyramidina is retained in the Turrilinidae on account of the praebulimine toothplate.

The absence of an internal toothplate and the very un-bulimine apertural face in Reussella, was created by Schwager (1877) under the preoccupied name Reussia, for high trochospiral Foraminifera easily distinguished from other forms by a remarkable triangular, almost pyramidal form, with Verneulina spinulosa Reuss, 1850 as the type species. Although some years passed before the genus became generally accepted, it was finally incorporated in the systematic schemes, always more or less closely allied to Bulimina.

Cushman (1927) created a separate subfamily for Reussia, changing its name to Reussellinae when the synonymy of Reussia was shown (Cushman, 1933). Throughout his publications he maintained the Reussellinae as a distinct subfamily in the Buliminidae (Cushman, 1948). In 1929, Cushman discussed the position of some of the reussellid genera, including Chrysalidinella Schubert, 1907, Trimosina Cushman, 1927 and Mimosina Millett, 1900. Reussella was described as a development of Bulimina, differing by being triangular but with the same kind of aperture.

Galloway (1933) proposed the name Reussella to replace the preoccupied Reussia and classified it in the Turrilinidae, Buliminidae. It was kept separate from the Buliminidae, partly on account of the absence of 'an internal ribbon or pillar' as present in Bulimina (Galloway, 1933, p.357).

The restudy of all known reussellid taxa by Cushman (1945) resulted in redescriptions and a systematic arrangement which set the scene for all subsequent classifications. He classified Reussella, Trimosina, Mimosina, Pavonina and Chrysalidinella in the Reussellinae, Buliminidae.

Despite the thorough study of the Bulimina, Uvigerina and Bolivina-like taxa, Hofker (1951) devoted little attention to Reussella. He described and briefly discussed two new species and classified Reussella in the Buliminidae, discussed the status of Chrysalidina, and erected Valvopavonina and Valvobifarina. Later, he discussed in great detail the relation between the different, for the Cretaceous important, buliminid genera (Hofker, 1957). He concluded that Reussella showed distinct affinities to Praebulimina and Bulimina, but regarded Pyramidina Broten, 1948 as nothing but an ontogenetic development of Reussella.

Loeblich & Tappan (1964) classified Reussella in the Pavonininae, reducing the Reussellinae to synonymy. They figured two specimens from the Vienna Basin and reproduced Hofker's drawing (Hofker, 1951, p.143) of the toothplate of Reussella spinulosa. Besides Reussella, they included Pavonina, Acostina, Chrysalidinella, the synonymised Chrysalidinoides, Fijella, Mimosina, Trimosina, Tubulogenerina and Valvobifarina in the Pavonininae. It was mentioned in passing that the more primitive, true toothplate-bearing forms might be separately classified in the Reussellinae, while the more advanced forms would be kept in the Pavonininae (Loeblich & Tappan, 1964, p.562).

Haynes (1981) incorporated the proposals by Loeblich & Tappan, 1964 concerning the reussellids without discussion.

In their latest classification, Loeblich & Tappan (1987) presented a considerable number of changes. For the Buliminacea, they propose the recognition of the Reussellidae alongside the Siphogenerinoididae, Buliminidae, Bulimellidae, Uvigerinidae, Trimosinidae, Pavoninidae and Millettiidae. They reduced the Reussellidae to include Reussella, Acostinarya, Chrysalidinella, Compressigerina, Fijella and Valvobifarina only. Mimosina and
Trimosina are the sole genera in the Trimosinidae, while Pavonina, Bifarinella and Finlayina make up the Pavoninidae.

The instability in the classification of the Reussellidae sensu lato indicates the need for a detailed study of the taxa in question, in order to obtain all the necessary comparative data afresh.

SYSTEMATIC DESCRIPTIONS
Order Foraminiferida Eichwald, 1835
Suborder Rotalinata Lankester, 1885
Superfamily Buliminacea Jones, 1875
Family Buliminidae Jones, 1875
1875 Buliminida Jones, in Griffith & Henfrey: 320
1927 Reussinacea Cushman: 68, nom. rej.
1933 Reusellinae Cushman: 223, nom. nov.
Type species. Bulimina d’Orbigny, 1826
Type species. Bulimina marginata d’Orbigny, 1826
Genus Reussella Galloway, 1933
1877 Reussia Schwager, non McCoy, 1854: 26, fig.66, nom. rej.
1933 Reussella Galloway: 360, nom. nov.
Type species. Verneuilina spinulosa Reuss, 1850, original designation.

Reussella spinulosa (Reuss, 1850) (Pl.1, figs 1-4)
1850 Verneuilina spinulosa Reuss: 374, pl.47, fig.12
1933 Reussella spinulosa (Reuss); Galloway: 360, pl.33, fig.4
1964 Reussella spinulosa (Reuss); Loeblich & Tappan: 563, fig.3 only
Types. Syntypes are probably present in the Naturhistorisches Museum Wien.
Type locality. Near Grinzing, Vienna, Austria: Badener Tegl, Badenian.
Material examined. Topotypes, courtesy H.J. Hansen.
Description. Test free, pyramidal, sharply triangular in cross-section, regularly increasing in size, 4 whorls, triserial; chambers low tetrahedral, wider than high, edges rather sharp, may slightly overhang the previous whorl, marked by a short spine at the very edge, in regular series, almost flush with the surface; intercameral sutures arched, spiral suture almost straight, distinct; aperture central at the apex of the test, apertural face almost terminal, formed by the top of the two previous chambers and for 1/3 by the ultimate chamber, apertures a large elliptical opening lying along the basal suture, bordered by a low lip which descends into the lumen to form the top of the toothplate; toothplate an elegant thin plate with a free, curved border, fuses with the foraminal lip at its topmost, peripheral side; wall calcareous, optically distinctly radial, distinctly perforate, with larger pores tending to seam the sutures.

Remarks. Reussella differs from Bulimina in the pronounced angularity of the test; the chambers are tetrahedral rather than spherical and the aperture is more ovate and oriented in a Turrilina-like fashion. Although the preservational state of the available tootypes hinders critical observation of the relation between toothplate and foramen, the attachment seems to be intermediary between the very simple turrelline and more extensive bulimine one. Observations of modern Reussella species show that most have a toothplate more akin to Bulimina, rather than Turrilina.

The study of material from the Vienna Basin shows that more than one species of Reussella is present in the Badenian. A revision of the genus is clearly needed to clarify the taxonomic status of most of its species.

According to F. Rogl, the Reuss collection is present in the Naturhistorisches Museum Wien. It is composed of an impressive number of numbered bottles and assemblage slides for which the catalogue is unfortunately missing (Rogl, 1986, and letter of 28 September 1989).

Family Uvigerinidae Haeckel, 1894
1894 Uvigerina Haeckel: 185
1927 Uvigerinidae Haeckel; Galloway & Wissler: 74
1933 Anguloerininae Galloway: 377
1966 Trifarininae Srinivasan: 242
Type genus. Uvigerina d’Orbigny, 1826
Type species. Uvigerina pygmaea d’Orbigny, 1826
Genus Compressigerina Bermúdez, 1949
1949 Compressigerina Bermúdez: 219
Type species. Uvigerina coartata Palmer, 1941, original designation.

Compressigerina coartata (Palmer, 1941) (Pl.1, figs 5-7)
1941a Uvigerina compressa Palmer, non Cushman: 182, pl.15, figs 10-11, nom. rej.
1941b Uvigerina coartata Palmer: 304, nom. nov.
1949 Compressigerina coartata (Palmer); Bermúdez: 219
Holotype. 18-64, Paleontological Research Institute, New York.
Type locality. Tejar, San José, Calzada de Marianao, Havana Province, Cuba; Cojimar Formation, Upper Oligocene.

Explanation of Plate 1

Figs 1-4. Reussella spinulosa (Reuss), topotypes from Nußdorff, Vienna Basin; Fig.1, Habitus, showing the distinct angular outline of the test (100µm); Fig.2, Endview of the test, with the rounded aperture and the low apertural lip surrounding the aperture in a Bulimina-like fashion (25µm); Fig.3, Overview of an opened specimen, showing the regular disposition of the chambers and the succession of the toothplates (100µm); Fig.4, Close-up of a toothplate, demonstrating its bulimine nature (10µm).

Figs 5-7. Compressigerina coartata (Palmer), holotype; Habitus, note the compressed and twisted nature of the test (100µm); Fig.6, Close-up of the aperture, produced on a Trifarina-like, laterally compressed neck (20µm); Fig.7, Internal view of a tootype, showing a foraminal neck and remnants of the toothplate (25µm).

Figs 8-12. Trimosina milletti Cushman, lectotype; Habitus, note the Reussella-like outline, and the differentiating peripherally produced spine-like extensions of the chambers (100µm); Fig.9, Endview, showing the partially broken last chamber with the semi-elliptical upper and slit-like lower aperture (100µm); Fig.10, Paralectotype, habitus (100 µm); Fig.11, Apertural view, clearly showing the double aperture (25µm); Fig.12, Kerteh specimen. Internal view with the toothplate sitting over the foramen and attached in different places to the chamber wall (100µm).
Material examined. The holotype, and topotypes, courtesy P.R. Hoover.

Description. Test free, at first rounded in section but quickly reduced to a compressed, twisted outlook, periphery apparently carinate, initial stage triserial, later reduced to twisted biserial; chambers at first rounded and inflated, then laterally compressed; sutures indistinct, depressed; aperture produced on a short, compressed neck, apparently harbouring the cristate top of a lip continuous with the toothplate; wall calcareous, opaque, perforate, earlier parts may be ornamented with fine, low costae.

Remarks. The presence of an aperture produced on a phialine neck with a small everted lip and the angularity of the chambers shows clearly that this genus is allied to Trifarinida and Angulogerina. The preservational state of the investigated specimens precludes a complete and detailed description. However, sufficient evidence is available to retain it as a genus in its own right and to prove its alliance to the Uvigerinidae instead of the Reussellidae.

Family Trimosinidae Saidova, 1975
1975 Trimosinidae Saidova: 56
1981 Mimosininae Saidova: 56

Type genus. Trimosina Cushman, 1927

Type species. Mimosina spinulosa var. Millett, 1900, original designation.

Genus Trimosina Cushman, 1927
1927 Trimosina Cushman: 64

Type species. Trimosina milletti Cushman, 1927 (= Mimosina spinulosa var. Millett, 1900).

Trimosina milletti Cushman, 1927 (Pl.1, figs 8-12)
1900 Mimosina spinulosa var. Millett: 548, pl.4, fig.13
1927 Trimosina milletti Cushman: 64, pl.13, fig.20

Lectotype. 1955:1:1:3543, British Museum (Natural History), London, herein designated.

Type locality. Malay Archipelago, St.13; Recent.

Material examined. 1955:11:1:3543-3642, syntypic series; 1956:6:27:143-148, and 1956:6:27:149-197, Malay Archipelago ex coll. Millett; Andaman Isles, Suez, Coast of Anam, ex coll. Sidebottom; Kerimba Archipelago, also Tibuti, Somaliland, ex coll. Heron-Allen & Earland; British Museum (Natural History).

Specimens from 'Galathea' St.376, 4°30'N 103°28'E, off Kerteh, Trengganu, -10m.

Description. Test free, elongate, triangular in section, gradually tapering, chambers arranged in regular triserial series throughout ontogeny, 3 to 4 whorls; chambers subtetrahedral to subspherical, distinctly inflated, drawn-out peripherally into a pointed projection bearing one strong spine; sutures distinct, narrow, depressed, gently arched; aperture double, apertural face not delimited, superior aperture subtriangular, staying below the apex of the chamber, separated from the lower aperture by a fairly narrow thickened band of usually imperfect apertural chamber wall, lower aperture an elongate slit with a denticulate upper edge, parallel to the basal suture, apertures not bordered by an everted lip, toothplate in one part, multiple attachments to the inside of the chamber at the upper aperture; wall calcareous, hyaline, finely and densely perforate, optically distinctly radial, earlier part of the test appears to be ornamented by numerous fine, low ridges running between the pores.

Genus Fijiella Loeblich & Tappan 1962
1962 Fijiella Loeblich & Tappan: 109

Type species. Trimosina simplex Cushman, 1929, original designation.

Fijiella simplex (Cushman, 1929) (Pl.2, figs 1-4)
1929 Trimosina simplex Cushman: 158, fig.2
1962 Fijiella simplex (Cushman); Loeblich & Tappan: 109

Holotype. CC10365, Smithsonian Institution, Washington DC.

Type locality. 40, 50 fms off Fiji; Recent.

Material examined. Holotype and CC 10366, 12 paratypes; also 'Galathea' St. 485, 8°48'S 115°16'E, South of Bali, -62m.

Description. Test free, pyramidal to sub-pyramidal, triangular in section, early part regularly increasing in size, later part constant width, 6 whorls, triserial; chambers low tetrahedral, in regular series, flush with the test surface, the outer edge may be slightly spinose; sutures distinct, intercameral ones curved, spiral suture gently undulate; apertural face terminal, apical, triangular and slightly convex, commonly bordered by thickened imperfect apertural rims, ornamented with numerous small upright spines, aperture slit-like, partially covered by a low-lying extensively curved lip, lip divided into two pieces, a larger sigmoidally wrapped denticulate plate and a smaller less denticulate one curved into the hollow left by the larger one; toothplate large, perforated by a few large holes, fuses partly with the foraminal spines, partly with the foraminal lips; wall calcareous, optically distinctly radial, perforate, pores tending to sear the edges of the individual chambers, often slightly produced on low mounds.

Remarks. Although superficially similar to Reussella, the peculiar apertural face and especially the toothplate show it to be

Explanation of Plate 2

Figs 1-4. Fijiella simplex (Cushman), paratype; Fig.1, Habitus, showing the very triangular outline of the test (200μm); Fig.2, Close-up of the apertural face, with the highly convoluted, double lip (50μm); Fig.3, South off Bali. Overview of opened specimen, showing the reticellid organisation of the test (100μm); Fig.4, Close-up of two successive toothplates, with the peculiar attachment mode visible in the lower part (50μm).

Figs 5-11. Mimosina hystrix Millett, lectotype; Fig.5, Habitus, (Microspheric) showing the mixed seriality and the characteristic outwardly projecting spines (100μm); Fig.6, Endview, with the large double aperture. Note the imperforate area surrounding the apertures (25μm); Fig.7, Paralectotype. (Megalospheric), biserial throughout. Note also the much reduced nature of the projecting spines (200μm); Fig.8, Apertural view, with the very wide bordered by not entirely closed apertural lips (50μm); Fig.9, Stereopair, demonstrating the highly complicated nature of the toothplate and its relation to the aperture and foramen (100μm); Fig.10, Close-up of a juvenile chamber. Note the one single aperture (25μm); Fig.11, Stereopair, showing the toothplate morphology and its relation to the foramen (100μm).
The generic revision of the Reussellids (Foraminiferida)
a distinct genus. The apertural face is covered with spines and tubercles which may deceive one into believing that a supplementary cribrate aperture is present. If extra openings are at all present then it is due to subsequent damage or perhaps reproduction.

**Genus Mimosina Millett, 1900**

1900 *Mimosina* Millett: 547

**Type species.** *Mimosina histrix* Millett, 1900, subsequent designation by Cushman, 1927.

*Mimosina histrix* Millett, 1900

(Pl.2, figs 5-11)

1900 *Mimosina hisptrix* Millett: 549, pl.4, figs 14, 15

1927 *Mimosina hisptrix* Millett; Cushman: 64

**Lectotype.** ZF4903, British Museum (Natural History), London, herein designated.

**Type locality.** Malay Archipelago, St. 10; Recent.

**Material examined.** 1955:11:1:3382-3394, and slide Malay St. 10 & 27 ex coll. Millett, syntypic series; British Museum (Natural History).

**Description.** Test free, elongate, tapering, slowly but regularly increasing in width, triserial in juvenile stage, later chambers arranged in biserial series; chambers very inflated, spherical, with an outwards projecting spine arising in the middle of the chamber; sutures distinct, depressed, gently arcuate; aperture double, no delineated apertural face, aperture turned towards the coiling axis, upper aperture almost terminal, rounded, bordered by a thickened lip, separated from the lower aperture by a small ridge of perforated chamber wall, lower aperture more ovate, also bordered by a low, thickened lip; toothplate starts from the upper end of the topmost aperture and curves towards the toothplate bending downwards from the ridge between the two apertures, the lower toothplate continues towards the foraminal apertures and fuses with the foraminal opening, wall calcareous, hyaline, distinctly and densely perforate, the wall may be ornamented with thin, short ridges running parallel to each other.

**Remarks.** The description covers the majority of species, apparently belonging to the microspheric generation. A few specimens were found which appear to be megalospheric. These differ from the microspheric ones in being biserial throughout, having more spherical chambers with much reduced projecting spines, and in having more prominent and larger apertural openings. It seems that the aperture becomes double only later in ontogeny as observation of some of the earliest chambers shows only a single aperture.

**Family Turrilinidae Cushman, 1927**

1927 *Turrilinidae* Cushman: 65

1961 *Turrilinidae* Cushman: Loeblich & Tappan: 300

1982 *Praebuliminidae* Loeblich & Tappan: 33, not available

1984 *Praebuliminidae* Loeblich & Tappan: 43

**Type genus.** *Turrilina* Andreae, 1884

**Type species.** *Turrilina aisaica* Andreae, 1884

Genus *Pyramindina* Broten, 1948

1948 *Pyramidina* Broten: 62

**Type species.** *Bulimina curvisuturata* Broten, 1940, original designation.

*Pyramidina curvisuturata* (Broten, 1940)

(Pl.3, figs 1-3)

1940 *Bulimina curvisuturata* Broten: 29, fig.4

1948 *Pyramidina curvisuturata* (Broten); Broten: 62

**Holotype.** Riksmuseet, Stockholm.

**Type locality.** Klagsham, South Sweden; Upper Danian.

**Material examined.** Topotypes, courtesy H.J. Hansen.

**Description.** Test free, elongate, broadly ellipsoidal in outline, periphery slightly lobulate, bluntly triangular in endview, triserial, 2 to 3 whorls; chambers moderately inflated, regularly increasing in size, somewhat angular but broadly rounded; sutures indistinct, slightly depressed, gently curved; aperture subterminal, elliptical, bordered by a low, thickened lip, clearly separated from the basal suture; a straight, narrow toothplate runs from aperture towards the foraminal opening where it is apparently attached adjacent to the top of the foraminal opening, running over a short distance as the plate narrows during its descent; wall calcareous, perforate, opaque.

**Remarks.** All available specimens have been subject to various degrees of diagenesis, thus hindering critical observations.

**Superfamily Pavoninacea Eimer & Fickert, 1899**

Nom. transl. ex fam. Pavoninidae Eimer & Fickert, 1899

1962 *Loxostomidae* Loeblich & Tappan: 110

1981 *Loxostomidae* Loeblich & Tappan: Saidova: 60

1987 *Loxostomataecae* Loeblich & Tappan; Loeblich & Tappan: 50

**Description.** Test free, multilocular, chambers in high trochospiral coils, pluriserial to rectilinar, no internal structures between aperture and foraminal opening, wall calcareous, bilamellar, perforate.

**Member taxa:** Pavoninidae, Buliminellidae, Buliminoididae and Loxostomatidae.

**Family Pavoninidae Eimer & Fickert, 1899**

1899 *Pavoninidae* Eimer & Fickert: 606

1927 *Pavoninidae* Eimer & Fickert; Cushman: 59

**Type genus.** *Pavonia* d'Orbigny, 1826

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**Explanation of Plate 3**

Figs 1-3. *Pyramidina curvisuturata* (Broten), topotypes; Fig.1, Habitus (100µm); Fig.2, Apertural view (25µm); Fig.3, Internal view, with a clearly defined but diagenetised toothplate (25µm).

Figs. 4-9. *Pavonia flabellicornis* d'Orbigny, topotype; Habitus (200µm); Fig.5, Raine Island. Habitus of a juvenile specimen. Note especially the costate ornamentation and the clearly biserial nature of the test (100µm); Fig.6, Habitus of a very large adult (200µm); Fig.7, South of Bali. An opened specimen, showing the simple nature of the test (200µm); Fig.8, Close-up of the upper edge of the test. Note the many tubercles and the apparent absence of apertural openings (25µm); Fig.9, Close-up of the wall, showing the tubulopore-like openings.

Figs 10-12. *Bifarinella ryukyuensis* Cushman & Hanzawa. Macassar Strait; Fig.10, Habitus. Note the very prominent tubulopore-like openings and the initial pluriseriality (200µm); Fig.11, Endview. The aperture appears to consist in a large slit, subdivided by smaller partitions (200µm); Fig.12, South of Bali. Opened specimen, showing the simple nature of the internal organisation (200µm).
The generic revision of the Reussellids (Foraminiferida)
Genus *Pavonina* d’Orbigny, 1826

1826 *Pavonina* d’Orbigny: 260

1951 *Valtavonina* Holker: 35, objective synonym

Type species, *Pavonina flabelliformis* d’Orbigny, 1826, type by monotypy.

*Pavonina flabelliformis* d’Orbigny, 1826

(Pl.3, figs.4-9)

1826 *Pavonina flabelliformis* d’Orbigny: 260, pl.10, figs 10-12

1846 *Pavonina flabelliformis* d’Orbigny: 72, pl.21, figs 9-10

Holotype. FO100. Muséum National d’Histoire Naturelle, Paris, holotype by monotypy.

Type locality. Madagascar; Recent.

Material examined. The holotype, and topotypes from d’Orbigny’s original sample, Muséum National d’Histoire Naturelle, Paris. 1955:10:21:341-347. Bano, and 1955:11:3:788, Kerimba Archipelago, ex coll. Heron-Allen & Earland; P50121. Topogi River, Topogi Formation, Borneo, Pliocene, ex coll. Whittaker: 1959:5:5:900-906, Shore Sands of Madagascar; ZF 2070, Honolulu, ‘Challenger’ Station 260A; ZF 2072, Off Calpentina, Ceylon; 1956:1:7:241-243 and 244-250, Samoa; 1956:1:6:578-595, Taviuimi, Fiji; 1955:5:5:1448, Seychelles, ex coll. Brady; off Bermuda, ex coll. Peary; Gulf of Manara, Ceylon; Andaman Isles, ex coll. Sidebottom; South of Tenerife, ‘Challenger’ Station 1; Torres Strait; Java, ex coll. Millett; Kerimba Archipelago, balsam embedded, ex coll. Heron-Allen & Earland; Ibo, East Africa; Raine Island, ‘Challenger’ Station 185; Barbados; Vavau Anchorage, Fiji; Mauritius, outer Harbour, all ex coll. Heron-Allen & Earland; British Museum (Natural History).

Specimens from ‘Galathea’ St. 485, 8°04’S 115°16’E, South of Bali, - 62m.

Description. Test free, fan-shaped, compressed, initial stage biserial, after about 8 chambers apparently becoming uniserial, due to the embracing of the successive chambers; chambers initially rounded, then laterally compressed and quickly becoming semi-lunar and more and more embracing; sutures distinct, arched; primary aperture appears to be absent but larger pores occur between the tubercles on the side rim of the chamber, chamber interior simple; wall calcareous, hyaline, optically distinctly radial, a septal flap is present, perforate, pores very large, on low raised mounds, arranged in a single row bordering the chamber edges, sometimes with a supplementary row.

Remarks. The presence of a septal flap in this species adds weight to the calls for relinquishing this characteristic for taxonomic purposes above the species level. The absence of a well defined primary aperture makes this an unusual taxon. The ridges present in some specimens indicate that the earliest part may be twisted biserial, but it is never truly triserial.

Genus *Finlayina* Hayward & Morgans, 1981

1981 *Finlayina* Hayward & Morgans: 439

Type species, *Finlayina hornibrooki* Hayward & Morgans, 1981, original designation.

*Finlayina hornibrooki* Hayward & Morgans, 1981

(Pl.4, figs 1-3)

1981 *Finlayina hornibrooki* Hayward & Morgans: 439, figs 1-11

Holotype. TF 1596/1, New Zealand Geological Survey.

Type locality. J41/8609, Taylor’s Quarry, Oamaru, N. Otago, New Zealand; McDonald Limestone, Lower Oligocene.

Material examined. TF 1596/10, 11 paratypes, courtesy B. Hayward.

Description. Test free, irregularly fan-shaped, laterally very compressed, first 14 chambers biserial, then uniserial, producing a central zigzag pattern in the lower part of the test; chambers numerous, semi-lunar, very much drawn-out and very low, almost lint-like, regularly increasing in length, except when changing from biserial to uniserial coiling, not embracing; sutures indistinct, flush with the surface; aperture at the outer upper edge of the chamber, composed of multiple irregular openings, internal structures absent; wall calcareous, perforate, opaque.

Remarks. Differs from *Pavonina* in lacking the characteristic ‘tubulopores’ and the low tubercles sown all over the outer chamber edge, in being distinctly biserial for some 14 chambers, and in lacking the discrete costulation in the earlier part of the test. All available specimens show the effects of heavy diagenesis, thus making critical observations impossible.

This species appears to be related to *Quasibolivinella taylori* Quilty, 1981. Although the latter is reported to be biserial throughout, it shows the same disposition of the earliest chambers, and both the surface and outline are remarkably similar.

Genus *Bifarinella* Cushman & Hanzawa, 1936

1936 *Bifarinella* Cushman & Hanzawa: 45

Type species, *Bifarinella ryukyuensis* Cushman & Hanzawa, 1936, original designation.

*Bifarinella ryukyuensis* Cushman & Hanzawa, 1936

(Pl.3, figs 10-12)

1936 *Bifarinella ryukyuensis* Cushman & Hanzawa: 46, pl.8, figs 7, 8.

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**Explanation of Plate 4**

Figs 1-3. *Finlayina hornibrooki* Hayward & Morgans, paratypes; Fig.1, Habitus (500μm); Fig.2, Partially opened specimen, showing the simple nature of its organisation (250μm); Fig.3, Endview of the test. Note the apparent absence of apertural openings (100μm).

Figs 4-6. *Chrysaidinella donorma* (Brady), holotype; Fig.4, Habitus. Note the slightly ornamented nature of the initial part of the test (150μm); Fig.5, Endview, showing the larger openings making up the aperture (50μm); Fig.6, Ketehe. Opened specimen, demonstrating the simple nature of the internal organisation (100μm).

Figs 7, 8. *Chrysaidinella pacifica* (Uchio); Fig.7, Habitus. Note the initial triangular nature of the test (200μm); Fig.8, Endview of a foramen. Despite the fragmentation or resorption, foraminiferal openings surrounded by mounds are still present (50μm).

Figs 9-12. *Cifella costata* (Heron-Allen & Earland), lectotype; Fig.9, Habitus. The initial coiling appears to be triserial. Note the relation of the costae to the apertural face (100μm); Fig.10, Apertural view, with the large openings forming the aperture (100μm); Fig.11, Paralectotype. Habitus (150μm); Fig.12, Endview of the foramen, demonstrating the simple nature of the organisation of the test (100μm).
The generic revision of the Reussellids (Foraminiferida)
1964 Pavonina ryukyuensis (Cushman & Hanzawa); Loeblich & Tappan: 563, figs.444-4

**Holotype.** CC 23141, Smithsonian Institution, Washington DC.

**Type locality.** 500m North of Kamikatetsu, Kikar-Jima, Rykyu, Japan; Ryuku Limestone, Pleistocene.

**Material examined.** Holotype and CC 23142, 2 paratypes; also Macassar Strait, - 45½°S; Timor Sea, - 30½°S, ex coll. Heron-Allen & Earland; Cebu, ex coll. Sidebottom; all labelled "Bifrina mackinnoni"; British Museum (Natural History).

Tamatam, Madagascar; 1955: 11: 7:45-7:48, Malay Archipelago Museum (Natural History). 'Galathea' St. 379, 4°38" 103°39'E, Bali Sea, - 570m.

**Description.** Test free, triangular flaring, compressed, initially biserial, but after about 4 to 5 chambers becoming rectilinear; chambers at first semi-lunar, but quickly becoming crescentic, regularly increasing in size; sutures distinct, arcuate; aperture not recognised, interior of the chambers simple; wall calcareous, optically distinctly radial, perforate, pores large, on top of low mounds, concentrated along the sutural edges, but also on the free chamber wall.

**Remarks.** The genus differs from Pavonina by lacking embracing chambers and having a much reduced biserial part. The pores are much more prominent close to the sutural junctions and later chambers are crescentic, rather than reniform as in Pavonina.

**Type species.** Chrysalidina dimorpha Brady, 1881, original designation.

Chrysalidina dimorpha (Brady, 1881) (Pl.4, figs 4-6)

1881 Chrysalidina dimorpha Brady: 54
1884 Chrysalidina dimorpha Brady; Brady: 388, pl.46, figs 21,22
1908 Chrysalidina dimorpha (Brady); Schubert: 243
1951 Chrysalidina dimorpha (Brady); Hofker: 175, figs 110-112

**Holotype.** ZF 1273, British Museum (Natural History), London. Holotype by monotypy.

**Type locality.** Hong Kong Harbour, - 7½ms, 'Challenger' Station 2050A; Recent.

**Material examined.** The holotype; also 1955:5:5:55-59, Tamavaté, Madagascar; 1955:11:1:745-748, Malay Archipelago Stations 14 & 22, ex coll. Millett; ZF 340, Gulf of Aden; - 37½m, 'John Murray' Station 27; P50124 Topogi River, Topogi Formation, N. Borneo, Pliocene, ex coll. Whittaker; British Museum (Natural History), 'Galathea' St. 379, 4°38'N 103°39'E, off Kerte, Trengganu, - 40m.

**Description.** Test free, triangular, earlier part may be pluriserial, most of the test rectilinear; chambers triangular, low, well delineated by distinct imperforate band, the outer edge may be reinforced by a slightly carinate edge; sutures distinct, gently curved; true aperture absent, but the apex of each chamber is pierced by an irregular group of larger rounded openings, no internal structures; wall calcareous, hyaline, heavily perforate, coarse pores in regular rows, somewhat smaller than the terminal pores.

**Remarks.** It seems that dimorphism is present in this species, to the extent that microspheric individuals have a pluriserial initial test, while megalospheric ones are rectilinear throughout.

Chrysalidinella pacifica (Uchio, 1952) (Pl.4, figs 7-8)

1952 Chrysalidinoides pacifica Uchio: 154, pl.7, fig.6
1964 Chrysalidinella pacifica (Uchio); Loeblich & Tappan: 563, fig.444/10

**Holotype.** CF 3036, Geological Institute, University of Tokyo.

**Type locality.** Yaene Beach, Ogago-mura, Hachijo Island, Japan; Recent.

**Material examined.** Specimen from ‘Challenger’ Type Slide TS C16, square 3, labelled Chrysalidina dimorpha by Sidebottom, British Museum (Natural History), London.

**Description.** Test free, elongate, at first triangular in section, but quickly becoming quadrangular, triangular part multiserial, then reduced to uniserial; chambers flush with the surface, tetrahedral to sub-cubic, not clearly delimited; primary aperture not observed, foramen pierced by relatively large rounded openings bordered by a low rim, scattered over the septal face; wall calcareous, distinctly perforate.

**Remarks.** Chrysalidinoides was synonymised by Loeblich & Tappan (1964) with Chrysalidinella on the grounds that quadrangularity is known to be adventitious in many dominantly triangular forms. Specimens of the ‘Challenger’ material seen by me reinforce this conclusion, since some of them are quadrangular later in ontogeny. The species pacifica is maintained as it can be differentiated from C. dimorpha by the pores being barely produced and the openings on the apertural face being bordered by low rims (plate 4, fig.9).

Genus Cifellia Gibson, 1989

1989 Cifellia Gibson: 141

**Type species.** Chrysalidina costata Heron-Allen & Earland, 1924, original designation.

Cifellia costata (Heron-Allen & Earland, 1924) (Pl.4, figs 9-12)

1924 Chrysalidina costata Heron-Allen & Earland: 139, pl.8, figs 12-14
1937a Chrysalidinella costata (Heron-Allen & Earland); Cushman: 55

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**Explanation of Plate 5.**

Figs 1-9, Orthocerina quadrilatera d’Orbigny, topotypes; Figs 1-3, Habitus. Note the irregularity in the later stages of ontogeny (1:200μm, 3, 4: 100μm); Fig.4, Endview, showing the peculiar tubular network covering the apertural face (50μm); Fig.5, Opened specimen, showing the organisation of the test (200μm); Fig.6, Endview of a younger specimen, with a more sparse network and showing the large irregular apertural openings (50μm); Figs 7-9, Close-ups of the tubular networks. Note especially the absence of contact between successive networks and the large, irregular holes in the test wall underlying the networks (50μm).

Figs 10-12, Valvobifarina mackinnoni (Millett), lectotype; Fig.10, Habitus (200μm); Fig.11, Andaman Sea. Internal view, showing the simple organisation of the test (100μm); Fig.12, Close-up of an earlier foramen, showing the lip protruding in the lumen and demonstrating the absence of a toothplate (25μm).
The generic revision of the Reussellids (Foraminiferida)
1989 Cifellia costata (Heron-Allen & Earland); Gibson: 141, pl.7, figs 1-8

**Lectotype.** P 35532, British Museum (Natural History), London, herein designated.

**Type locality.** Filter Quarry, Moorabool River, Victoria, Australia; Polyzoa Limestone, Batesfordian, Miocene.

**Material examined.** The syntypic series P 35530, P 35531 and P 35532; British Museum (Natural History), London.

**Description.** Test free, elongate, rounded in section, regularly increasing in diameter, periphery lobulate, juvenile triserial, quickly reduced to a rectilinear series; chambers subspherical, very inflated, up to 6 uniserial chambers; sutures indistinct, depressed, annular; apertural face apical, rounded, somewhat flattened, bordered by an imperforate peripheral band, pierced by a large number of circular openings; no internal structures; wall calcareous, finely and densely perforate, ornamented by numerous thin costae, undercut at the sutural joints.

**Type species.** Orthocerina quadrilatera d'Orbigny, 1839

**Type locality.** Cuba; Recent.

**Material examined.** The holotype, and topotypes from Cuba and Jamaica recovered from the original d'Orbigny samples, MusCum uniserial; chambers subtetrahedral, angular, lower than wide, at section, quadrangularity adventitious, early part triserial, then uniserial; chambers subtetrahedral, angular, lower than wide, at first flush with the test, later in ontogeny overlapping and irregularly arranged over the test; sutures distinct, flush with the surface, may be slightly raised, distinctly curved upwardly; apertural face apical, triangular, aperture multiple, composed of fairly large irregular openings, apertural face covered by a low-lying network of massive cylindroid structures apparently delimiting the apertural openings, no internal structures; wall calcareous, hyaline, distinctly perforate, pores usually arranged in rows parallel to the sutures, raised on low mounds, giving a ‘tubulopore’-like impression.

**Remarks.** The tubular network on top of the apertural face very often has foreign material trapped in the gaps, obscuring the apertures. This may to some extent explain why the original description by d'Orbigny mentions only a single opening. Le Calvez (1977) states that the only available specimen, contrary to d'Orbigny's description, actually possesses a multiple aperture: "...alors qu'il s'agit de pores disséminés sur toute la face orale". Due to curatorial policy, it is impossible to investigate the holotype of Orthocerina in full detail. However, specimens recovered from d'Orbigny's original samples seem to fit the original description, bearing in mind the different degrees of resolving power of our respective instruments. I feel confident that the true nature of Orthocerina is here adequately presented.

The type specimen of Orthocerina is quadrangular in section, but all specimens recovered from the Cuba and Jamaica samples originally used by d'Orbigny are triangular. I maintain that triangular and quadrangular specimens are conspecific, as is indeed the case for Chrysalidina (q.v.).

**Genus Valvohifarinu Hofker, 1951**

1951 Valvohifarinu Hofker: 39

**Type species.** Bifarina mackinnonii Millett, 1900, original designation.

**Valvohifarinu mackinnonii** (Millett, 1900)

**(PL5, figs 10-12)**

1900 Bifarina mackinnonii Millett: 281, pl.2, fig.15

1937b Bifarina mackinnonii Millett: Cushman: 200, pl.23, fig.6 only, err. cit.

1951 Valvohifarinu mackinnonii (Millett); Hofker, 1951: 40, err. cit.

**Lectotype.** 1955:11:1:121, British Museum (Natural History), London, herein designated.

**Type locality.** Macassar Strait. -45fms, Malay Archipelago; Recent.

**Material examined.** Lectotype and 1955:11:1:121, paratypes: 1962.9.7.1-5, from Macassar Strait, ex Millett coll.; Macassar Strait, ex coll. Sidebottom; Sulu, ex coll. Sidebottom; Timor Sea, -30fms, ex coll. Heron-Allen & Earland; Java, ex coll. Millett; specimens from the Kerimba Archipelago, ex Heron-Allen & Earland coll.; British Museum (Natural History). Specimens from ‘Galathea’ Station 379, 4°38’ N 103°39’ E, -40m, off Kerteh, Trengganu; ‘Galathea’ Station 490, 5°09’N 106°47’ E, -63m, South China Sea; ‘Galathea’ Station 490, 5°25’S 117°03’ E, -570m, Bali Sea. Geological Museum, Copenhagen.

**Description.** Test free, elongate, initially triserial, but later reduced to biserial; chambers at first rounded to tetrahedral, but quickly becoming angular, cuneate and laterally compressed with a spine at the lowermost point, individual chambers well marked; sutures distinct; aperture an elongate slit at the apex, slightly everted, interior of the chambers simple; wall calcareous, optically distinctly radiate, perforate, pores coarse, at the top of low mounds, concentrated at the edges of the cuneate chambers.

**Remarks.** The specimens of V. mackinnonii figured by Millett, supposedly from the Malay Archipelago, should be considered lost. Courtesy of Mr Hodgkinson (BMNH), the following details relevant to the Millett collection have come to light. The Millett collection was salvaged through effective action taken by Heron-Allen after Millett's death. Apparently, Heron-Allen found the collection in Millett's house in a very derelict state, with many of the slides open, quite damp, attacked by mould and buried under great piles of dust and rubbish. Heron-Allen tried to rescue as
much as possible, but obviously losses were unavoidable. This also explains the precarious and fragile state of many of the specimens in the Millett collection.

Genera attributed to the Reussellidae

Genus Acostina Bermúdez, 1949
1949 Acostina Bermúdez: 152
Type species. Chrysalogonium pyramidale Acosta, 1940, original designation.

Acostina pyramidale (Acosta, 1940)
1940 Chrysalogonium pyramidale Acosta: 4, pl.1, figs 4-5
1949 Acostina pyramidale (Acosta); Bermúdez: 152
1964 Acostina pyramidale (Acosta); Loeblich & Tappan: 563, fig.444-6

Holotype. Apparently lost, Smithsonian Institution, Washington DC (Buzas, written comm.). Cotypes should be present in the Museo Poey, Havana University, Cuba.

Type locality. North Coast of Cuba, 20°34′N 74°24′W, -1300m, ‘Atlantis’ St. 2971.

Remarks. No specimens have come to hand for investigation. However, based on the drawings provided by Acosta, I wish to make the following suggestions. The triangular shape of the test and the form of the chambers seems to indicate some affinity to Tristix MacFadyen, 1941 or some other Nodosariid taxon. Until specimens become available for further investigation, I propose to remove Acostina from the reussellid taxa and to consider it as incertae sedis.

DISCUSSION

The general habitus of the species studied falls in the category of the high trochospiral forms. The test is elongated along the coiling axis, and the seriality is reduced. Most of the species investigated exhibit a mixed seriality: the juvenile test is often tri- or biserial, but soon becomes reduced (Fijiella, Mimosina, Orthocerina). Chrysalidinella, Cifellia, Finlayina, Orthocerina, Pavonina, Valvohifarina). The remaining genera possess a toothplate with varying degrees of complexity. The simplest toothplate is encountered in Reussella, in which a typically bulimine toothplate connects aperture with foramen, its relation to the apertural lip included. Complexity increases with Fijella (with rather disturbing reminiscences to the apertural complex in Sagrina pulchella, type species of Sagrina d’Orbigny, 1839 [study in progress]), and finally a very convoluted morphology, quite different from the bulimine toothplates, is found in Trimosina and especially in Mimosina.

From early on in the endeavours towards classification, Reussella has been more or less allied to Bulimina. The perceived similarities between representatives of these two genera were based exclusively on the gross outer morphology. Before the work by Hofker (1951), all students seem to have been unaware of the presence of an internal toothplate in Reussella (e.g. Galloway, 1933, p.357-358; Cushman, 1927, until the last re-edition in 1948). Surprisingly, Galloway (1933) uses implicitly the presence of an internal plate in Bulimina to separate Reussella from Bulimina in the subfamily Turrilincae.

Hofker (1951) depicted two new species of Reussella, besides giving a drawing of the toothplate of what he identified as R. spinulosa. From the text, it appears that he studied Recent specimens only. The toothplate figured for Reussella spinulosa seems to be that of specimens from the seas around Borneo and Celebes rather than from Miocene Reussella specimens of the Vienna Basin: apparently he identified some of the Recent forms as R. spinulosa (Hofker, 1951, p.143).

Loeblich & Tappan (1964, also 1987) reproduced Hofker’s drawing of the toothplate of Reussella spinulosa sensu Hofker, and figured two specimens from the Miocene of the Vienna area. One of the specimens drawn agrees very well with the figures provided by Reuss, but the other specimen fits Reussella pulchra Cushman, 1945, also from the Vienna Basin. The toothplate is similar to the one in Bulimina marginata (Revets, 1989, plates 1.
Trimosinidae are maintained and redefined to include the chief difference between the two genera is the form of the chambers, which is tetrahedral in Reussella and rounded in Bulimina, and the orientation of the aperture, lying in a Turritilina-like fashion in Reussella rather than running up the apertural face.

Since the organisational principle of Reussella is shown to be matching that of Bulimina, Reussella is here reclassified in the Buliminidae. A difference in chamber form is useful to characterise genera, but does not constitute in itself a sufficient criterion to separate families. Recent specimens of Reussella only confirm this observation: although many of the species seem have a much larger aperture than R. spinulosa, it is still clearly of the bulimine type, albeit oriented more in a Turritilina-like fashion. However, the strict triseriarity and the low, barely ornamented apertural lip shows the affinity to be bulimine, rather than turritine.

The genus Fijella, originally separated from Trimosina, is very different from Reussella, anatomically speaking. The apertural face is much larger and flatter, ornamented by upwards projecting short spines, and the aperture itself is partially hidden by a heavily modified lip which has fragmented into a double, flap-like protrusion. The original description of the genus mentions the presence of supplementary openings in the central part of the apertural face (Loeblich & Tappan, 1962; also Cushman, 1929). These openings are found in some specimens but are lacking in the large majority of them, including the type specimens. These openings may be due either to taphonomical effects, or may be linked to reproduction. I do not consider them to be primary and therefore disregard them as being of any use for descriptive and taxonomic purposes. The toothplate is an intricate piece of calcite, rather large and perforated by a number of holes, which contacts the septum not only at the foraminal lips, but also at the foraminal spines. The construction of the toothplate differs from the Bulimina-like toothplate in Reussella, but is rather similar to the one in Trimosina. The similarity of the toothplate morphology to the one in Sagrina raises disturbing questions as to which grounds to use for taxonomic decisions. It has become increasingly difficult to argue the relative merits of characteristics used to define supraspecific (and especially suprageneric) taxa.

The analogy in toothplate anatomy and the resemblance of the apertural face between Trimosina, Mimosina and Fijella demonstrates affinities between these three genera extending beyond the more superficial resemblances of coiling and test shape. Fijella can be regarded as the more primitive genus in this group: the aperture is not yet double, but the beginnings for it are present (witness the doubling of the apertural lip). Development is taken one step further with Trimosina, in which the aperture has become double, but with the lower one still very narrow; the toothplate is still a single plate, but the multiple attachment sites clearly show the increasing complexity. The pinnacle is reached with Mimosina, with two very prominent primary apertures and (especially) the convoluted toothplate. Therefore, the Trimosinidae are maintained and redefined to include Trimosina, Mimosina and Fijella.

The status of Compressigerina remains still somewhat uncertain because of the state of preservation of the specimens. However, the apertural neck is a very strong indication for uvigerine affinities, and, together with the habitus of the test being reminiscent of Angulogerina, sufficient arguments are available to reclassify it in the Uvigerinidae.

The majority of genera studied deviate substantially from the reussellid or even bulinimid concept, i.e. they lack a toothplate, possess a very uncharacteristic apertural face and have a mixed seriality. I therefore propose to recognise these fundamental differences by introducing the superfamily Pavoninacea.

The genera herein revised in the Pavoninacea fall into two groups. On the one hand there is the group centred round Pavonina, including Finlayina, Bifarinella and to a lesser extent Valvobifarina. They are characterised by the distinctly compressed nature of the test with a marked tendency towards flabelliformity, and an apertural face which is very elongate. On the other hand there is the group centred round Cifellia and Orthocerina. This second group is characterised by uniseriarity in the adult stage, the non-compressed chambers and the apical, multiple aperture.

Other genera to be included in the superfamily are already known to lack internal structures, such as Loxostoma, Aragonia and Bolivinella.

Earlier revisions removed some genera from the Buliminacea, i.e. Bulimina and Buliminoides (Revets, 1990a, b) and Tosaia (Nomura, 1985). The large number of genera herein removed favours the cause for a separate superfamily even more. It is intriguing to note that all forms in the Pavoninacea are eminently shallow water forms. Perhaps this may be a first indication towards solving the mystery of the function of the toothplate.

A rethinking of the classification of the Buliminacea sensu lato, based on generic revisions has become urgent in order to restore stability and increase the understanding of this group.

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