

A revision of the Recent species of *Exilia*, formerly *Benthovoluta* (Gastropoda: Turbinellidae)

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ABSTRACT. The range of shell characters (overall shape, sculpture, columellar plaits, protoconchs) exhibited by fossil and Recent species placed in *Exilia* Conrad, 1860, *Mitraefusus* Bellardi, 1873, *Mesorhytis* Meek, 1876, *Surculina* Dall, 1908, *Phenacoptygma* Dall, 1918, *Palaeorhaphis* Stewart, 1927, *Zexilia* Finlay, 1926, *Graphidula* Stephenson, 1941, *Benthovoluta* Kuroda et Habe, 1950, and *Chathamidia* Dell, 1956 and the anatomy of the Recent species precludes separation of more than one genus. Consequently all of these nominal genera are synonymised with *Exilia*, with a stratigraphical range from Late Cretaceous to Recent. Anatomically, *Exilia* is similar to other ptychatractine genera, but is characterized by a stomach with a long, narrow caecum, a penis with terminal fold surrounding the seminal papilla, and a radula with rachidian teeth with broad lateral flaps. Recent species of *Exilia* are restricted to deep water at middle to low latitudes in the Indian and Pacific oceans. *Exilia hilgendorfi* (Martens, 1897) is treated as a species highly variable within its broad Indo-Pacific distribution, with *Benthovoluta gracilior* Rehder, 1967, *B. claydoni* Harasewych, 1987, and *B. prelleii* Bozzetti, 2001 considered local variants. Three new species are described: *Exilia graphiduloides* sp. nov. (New Caledonia, 520 m), *E. vagrans* sp. nov. (West and SW Pacific, 865-1280 m), and *E. kiwi* sp. nov. (New Zealand, 1386-1676 m).

established among some of these nominal taxa. Schematically, *Exilia* Conrad, 1860, *Palaeorhaphis* Stewart, 1927, and *Graphidula* Stephenson, 1941 are currently used as valid genera for Late Cretaceous to Neogene fossils; and *Surculina* Dall, 1908 and *Benthovoluta* Kuroda et Habe, 1950 are currently used as valid genera for Recent deep-water species from middle to low latitudes. Each of these nominal taxa has had a complex history of family allocation, which has not facilitated comparisons on a broader scale. *Exilia* and *Benthovoluta* are the genera best known in the fossil and Recent literature, respectively.

With the exception of *Benthovoluta claydoni* Harasewych, 1987, which was taken in moderate quantity in the 1980s as a by-product of shrimp trawling off Western Australia, material of *Benthovoluta* and *Surculina* is rare in museum collections and this, in turn, has not facilitated an analysis of the systematics of the group, which can be summarized as follows:

(1) **At family level.** At the time of its establishment by Kuroda and Habe [1950], *Benthovoluta* was then classified in the family Volutidae. Based on Habe's [1952] very schematic illustrations of the radula, it was transferred to Turbinellidae by Kuroda [1965]. Harasewych [1987] described the anatomy of *B. claydoni* and placed *Benthovoluta* in the subfamily Ptychatractinae of the Turbinellidae. *Surculina* was transferred from the Turridae to the Turbinellidae by Rehder [1967].

(2) **At genus level.** Rehder [1967] discussed the relationships of *Benthovoluta* with *Surculina* and kept the two genera as valid, and this has been the accepted genus-level taxonomy to this day.

(3) **At species level.** Thirteen Recent nominal species have, at one time or another, been attributed to *Benthovoluta*. Eight of these were transferred to *Cyomesus* Quinn, 1981 [Harasewych, 1987], now a synonym of *Latiromitra* Locard, 1897 [Bouchet and Warén, 1985], or to other genera [Bouchet and Kantor, 2000], and five species are currently recognized as valid. In addition, four species are

Introduction

The species- and genus-level taxa discussed in this paper have, at one time or another, been classified in half a dozen different neogastropod families, from Fasciolaridae to Volutidae, through Turridae and Turbinellidae, depending on the relative importance given to such shell characters as columellar plaits and subsutural concave sulcus, or to anatomical characters when these became known. No less than 10 nominal genera were established to accommodate the fossil and Recent species considered. Synonymies had already been

regarded as valid in *Surculina* [Rehder, 1967; Cernohorsky, 1973].

The present paper was prompted by the collecting of new deep-water material attributable to the "*Benthovoluta-Surculina*" complex, which demonstrates a more diverse range of shell shapes than earlier described and provide new anatomical material that permit a re-evaluation of genus-level relationships. This has necessitated a review of several Recent and fossil nominal genera with slender fusiform shells and columellar folds. As a result, we have found that Recent *Benthovoluta* is not generically separable from Late Cretaceous to Neogene fossils and that the oldest generic name available for this group is *Exilia*. In this paper, we discuss the generic synonymy and justify the use of *Exilia* and we describe the anatomy and revise the species-level systematics of the Recent taxa. A revision of the species-level systematics of the fossil taxa was outside the scope of our work.

Abbreviations and text conventions: aoe — anterior oesophagus; asg — accessory salivary gland; cae — caecum of stomach; cme — cut mantle edge; col.m — columellar muscle; ct — ctenidium; dd — dead collected specimen; ddg — duct of digestive gland; dg — digestive gland; dgL — duct of gland of Leiblein; gL — gland of Leiblein; hg — hypobranchial gland; lv — live collected specimen; moe — mid-oesophagus; ne — nephridium; ng — nephridial gland; nr — nerve ring; od — odontophore; op — operculum; os — osphradium; p — penis; poe — posterior oesophagus; pr — proboscis; prs — rhynchodaeum (= proboscis sheath); r — rectum; s — siphon; sd — salivary duct; sem.gr — open seminal groove; semp — seminal papilla; sg — salivary gland; st — stomach; t — head tentacle; tes — testis; vL — valve of Leiblein; vodr — ventral odontophore retractor; vpr — ventral proboscis retractor.

Repositories: AMNH — American Museum of Natural History, New York, USA; AMS — Australian Museum, Sydney; DMNH — Delaware Museum of Natural History, Greenville, USA; EASPU — Department of Earth and Atmospheric Sciences, Purdue University, Florida, USA; MNHN — Muséum national d'Histoire naturelle, Paris; NM — Natal Museum, Pietermaritzburg, South Africa; NMNZ — Museum of New Zealand, Te Papa Tangarewa, Wellington, NZOI — New Zealand Oceanographic Institute, Wellington (now NIWA); PRI — Paleontological Research Institution, Ithaca, USA; UCBMP — Museum of Paleontology, University of California, Berkeley, USA; USGS — United States Geological Survey, USNM — National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UWBM — The Burke Museum, University of Washington, USA; WAM — Western Australian Museum, Perth

The fossil and Recent nominal genera

Genus *Exilia* Conrad, 1860

Exilia Conrad, 1860: 291.

Type species (by monotypy): *Exilia pergracilis* Conrad, 1860, Midway Group, Eocene, Alabama, USA (Fig. 1A-D).

Diagnosis: Shell narrowly fusiform, slender; aperture narrowly elongated; anterior canal long, straight, and narrow; columella may be smooth or bear one to four plaits of variable strength; surface with well developed axial and spiral sculpture; protoconch smooth, paucispiral or multispiral, depending on the type of larval development.

Operculum from medium-sized with terminal nucleus to very small with subcentral nucleus, or absent. Proboscis very short, with basal buccal mass; ventral odontophore retractor passing through the nerve ring; single accessory salivary gland; large and bulky gland of Leiblein; stomach with narrow and long caecum; penis with seminal papilla surrounded by a nearly circular fold. Rachidian radular teeth with broad lateral flaps.

Remarks: *Exilia* is rather distinct from the other known Recent genera of Ptychactractinae in its generally narrow fusiform shell with long and straight siphonal canal. Specimens of *E. expeditionis* may superficially resemble *Metzgeria alba* (Jeffreys, 1873), the type species of *Metzgeria* Norman, 1879; the rachidian tooth of the radula of the latter, illustrated by Bouchet & Warén [1985: fig. 393], differs by having no lateral flaps. Species of *Exilia* also superficially resemble species of *Exilioidea* Grant & Gale, 1931, transferred from Buccinidae to Turbinellidae by Bouchet & Warén [1988]. The anatomy of *Exilioidea* is not known but, judging from its radula, it also belongs to Ptychactractinae. The very minute size of the ribbon (less than 140 µm in length) and the narrowly arched, almost wishbone-shaped, central tooth, with socketed central cusps interlocking on successive rows, are unique to this genus.

Anatomically Recent species of *Exilia* are rather uniform, while they differ from other Ptychactractinae in having a large bulky gland of Leiblein, a radula with rachidian teeth with broad lateral flaps, a stomach with narrow and well pronounced caecum, and a penis with seminal papilla surrounded by a nearly circular fold.

The family allocation of *Exilia* has fluctuated considerably until quite recently. Conrad originally

РИС. 1 *Exilia*: меловые и эоценовые виды из Северной Америки. А-Д. *Exilia pergracilis* Conrad, 1860 Нижний эоцен, группа Midway, вблизи Oak Hill, Алабама. А-В. По Benson, 1940: pl. 1, figs 12-13 (UCBMP 11806), 27,9 мм. С-Д. По Benson, 1940: pl. 1, figs 9-10 (UCBMP 11623), 14,8 мм. Е. *Exilia gracilentia* (Meek, 1876). Маастрихт, группа Fort Pierre и формация Fox Hills, Yellowstone River, Монтана. Голотип, по Meek [1876: 364, fig. 45], 22,5 мм. F-G. *Exilia cancellata* (Wade, 1926). Маастрихт, формация Ripley, Dave Weeks place на Coon Creek, McNairy County, Теннесси. Голотип (USNM 32891), 38,7 мм. H-I. *Exilia pergracilis* (Wade, 1926) Маастрихт, формация Ripley, Dave Weeks place на Coon Creek, McNairy County, Теннесси. Голотип (USNM 32888), 48,1 мм. J-M. *Exilia dickersoni* (Weaver, 1912). Middle Eocene, Cowlitz Formation, Cowlitz River, Lower Cowlitz Valley, Washington J-K. USGS 185101, 43,1 мм. L-M. USGS 185102, 49,1 мм. N-O. *Exilia melanopsis* (Conrad, 1860), Маастрихт, Ripley Formation, Tennessee (USNM 32890), 78,1 мм.

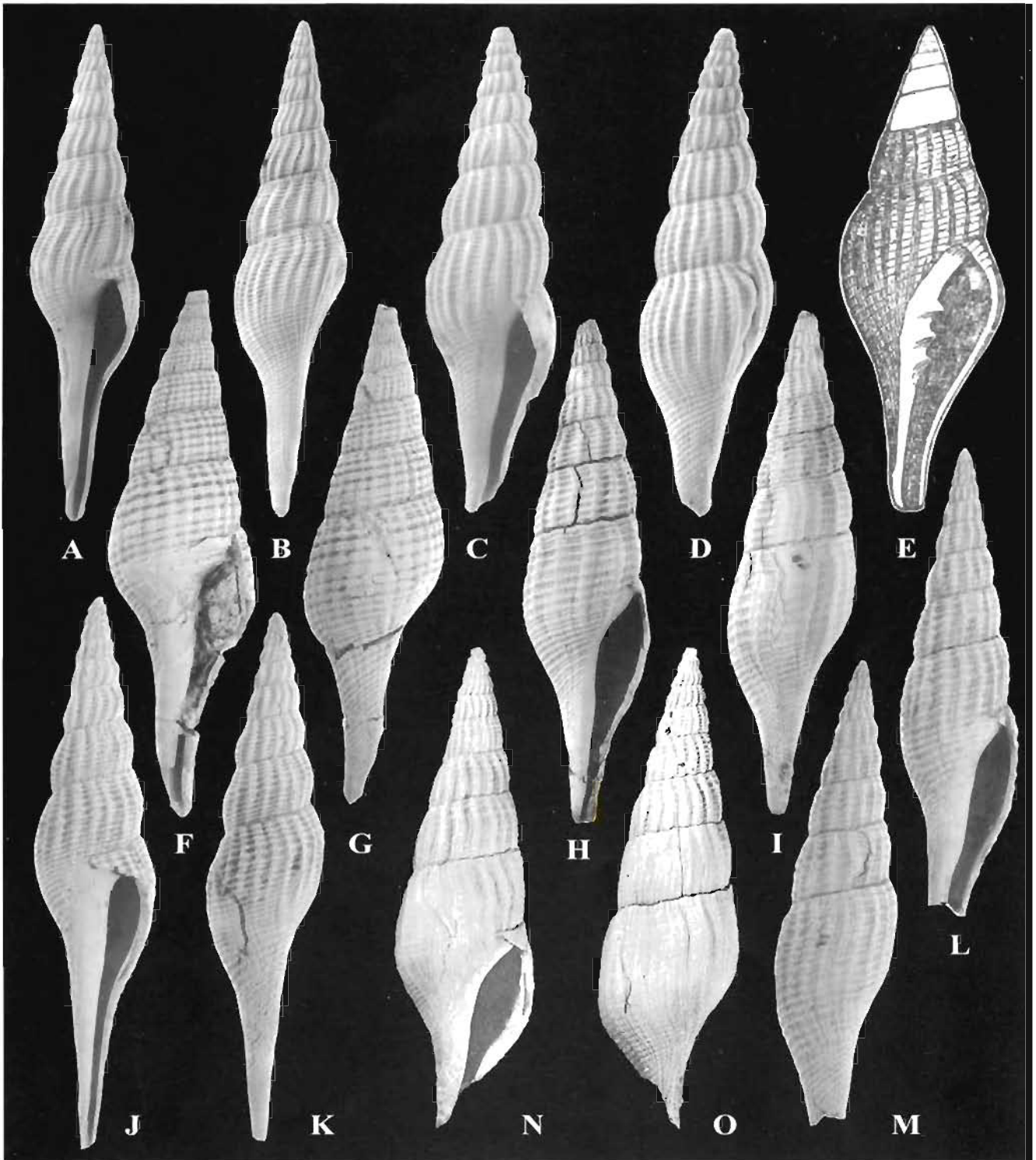


FIG. 1 *Exilia* Cretaceous and Eocene species from North America. A-D *Exilia pergracilis* Conrad, 1860. Lower Eocene, Midway Group, near Oak Hill, Alabama. A-B. Specimen illustrated by Bentson, 1940: pl. 1, figs 12-13 (UCBMP 11806), 27.9 mm. C-D. Specimen illustrated by Bentson, 1940: pl. 1, figs 9-10 (UCBMP 11623), 14.8 mm. E *Exilia gracilentu* (Meek, 1876). Maastrichtian, Fort Pierre Group and Fox Hills Formation, Yellowstone River, Montana. Holotype, figure copied from Meek [1876: 364, fig. 45], 22.5 mm. F-G. *Exilia cancellata* (Wade, 1926). Maastrichtian, Ripley Formation, Dave Weeks place on Coon Creek, McNairy County, Tennessee. Holotype (USNM 32891), 38.7 mm. H-I. *Exilia pergracilis* (Wade, 1926). Maastrichtian, Ripley Formation, Dave Weeks place on Coon Creek, McNairy County, Tennessee. Holotype (USNM 32888), 48.1 mm. J-M. *Exilia dickersoni* (Weaver, 1912). Middle Eocene, Cowlitz Formation, Cowlitz River, Lower Cowlitz Valley, Washington. J-K. USGS 185101, 43.1 mm. L-M. USGS 185102, 49.1 mm. N-O. *Exilia melanopsis* (Conrad, 1860). Maastrichtian, Ripley Formation, Tennessee (USNM 32890), 78.1 mm.

did not assign *Exilia* to any family, but later placed it in the Pleurotomidae [= Turridae] [Conrad 1865]. This view was followed, e.g. by Stewart [1927], Gardner [1933], Wenz [1943], and with doubts also by Powell [1966]. Alternatively, the genus has been classified in various buccinoid families: Fascioliariidae [by, e.g., Hickman 1980], Fusinidae [by, e.g., Bentson 1940], Buccinidae [by, e.g., Thiele 1929] (however Thiele [1934] later reassigned to *Exilioidea* the species that he had included in *Exilia*), or Chrysodomidae [by, e.g., Gardner 1916]. Deviating from these views, Maxwell [1988] correctly placed *Exilia*, together with *Graphidula*, in the subfamily Ptychatractinae of the Turbinellidae.

Conrad [1860] did not give a diagnosis of *Exilia*. The short original description of the type species, *E. pergracilis*, does not even mention characters we would currently regard as diagnostic: "Narrow-fusiform; volutions twelve, convex, with slightly curved, numerous, narrow ribs, and fine closely arranged revolving lines; spire rather longer than aperture, first two whorls smooth; beak perfectly straight, minutely striated to the extremity" [Conrad, 1860]. The protoconch is broken on Conrad's type specimen. Undamaged specimens of *Exilia pergracilis*, *E. perkinsiana* (Cooper, 1894), *E. waihaensis* Suter, 1917, and *E. crassistria* (Koenen, 1885) have a multispiral protoconch of three smooth whorls [Wade, 1926; Gardner, 1933; Bentson, 1940; Beu, Maxwell, 1990; Maxwell, 1992]. *Exilia dalli* Suter, 1907 and *E. wellmani* Maxwell, 1988 from the Miocene of New Zealand have a paucispiral protoconch of about 1.25 whorls with a large bulbous initial whorl and weak axial costellae on the remainder 0.25 whorl or less [Maxwell, 1988]. Similar differences in shape and number of whorls of the protoconch in many other groups of marine gastropods are correlated with planctotrophic and lecithotrophic development respectively. Mode of larval development alone is not to be regarded as a character of supraspecific importance [Bouchet, 1990].

The development of columellar plaits in *Exilia* has been discussed by Vokes [1939], Stewart [1927], Bentson [1940], and Maxwell [1988]. Examination of a large number of specimens show that different specimens of the same species, even from the same locality, may have or lack columellar plaits; the strength and number of columellar plaits may also vary within species. On most species of Paleogene *Exilia* from North America [*E. pergracilis*, *E. perkinsiana*, *E. dickersoni* (Weaver, 1912) (Fig. 1 J-M), *E. microptygma* (Gabb, 1864), and *E. fausta* Anderson and Hanna, 1925], there are one or two columellar plaits, if at all, represented by thin faint threads hidden inside the aperture, or restricted to the columella of juveniles. The high degree of variability in number and strength of columellar plaits is confirmed in the Recent *E. hilgendorfi* (Table 1). The adults lacking columellar plaits do not have them in ontogenesis (see Fig. 4L). Therefore, the columellar folds cannot be regarded as

a reliable diagnostic character of *Exilia* at genus, or even species, level.

The sculpture of *E. pergracilis* consists of narrow, elevated, curved axial ribs and spiral cords, with axials wider and more prominent than spirals, and this sculpture is also characteristic of several other Cretaceous and Paleogene species of *Exilia* [*E. cretacea* Gardner, 1916, *E. lincolnensis* Weaver, 1916 (Fig. 2 H-K), *E. melanopsis* (Conrad, 1860) (Fig. 1 N-O), and *E. clarki* Bentson, 1940]. Axial ribs may also be nearly straight and widely spaced, as in *E. wellmani*. In other species, such as *E. llajasensis* Bentson, 1940, *E. dickersoni*, *E. plana* (Kaunhoven, 1898), *E. crassistria*, and *E. perkinsiana*, almost straight axial ribs intersect spirals cords of equal or nearly equal strength, producing a cancellate pattern. Finally, in species such as *E. dalli*, *E. contigua* (Beyrich, 1856), *E. ottnangensis* (Hoernes, 1875) and *E. attenuata* Philippi, 1851, axial ribs are dominating only on the early whorls, and gradually become obsolete on adult whorls. In fact, sculptural elements can also vary considerably in shape and strength even within species. One of the more remarkable examples of such polymorphism is *E. bentsonae* Hickman, 1980, from the Upper Eocene Keasey Formation in Oregon, where the variation in number and strength of axial ribs and spiral cords sculpture result in two extremes, one with only low arcuate axial ribs, as in "typical" *Exilia*, and another with a row of heavy rounded or elongated nodes along the periphery of the whorl, with intermediate specimens connecting the two [Hickman, 1980, plate 8, figures 5-11 (Fig. 2A-F), specimens from Middle Eocene of western Kamchatka].

To summarize, the morphology of the protoconch, number and strength of columellar plaits and sculptural details are extremely variable and have little diagnostic value at generic level when a range of fossil species traditionally assigned to *Exilia* are considered. The only constant feature of *Exilia* is the slender shape with straight, long, and narrow siphonal canal and high spire. Spire angle among Cretaceous and Paleogene *Exilia* from North America range from 22.5° (*E. lincolnensis*, Fig. 2 H-K) to 28° (*E. cancellata*) with much individual variation within species. Height to width (H/W) ratio ranges between species from 4.3 (*E. terebriformis*) to 5.4 (*E. ordita* and *E. pergracilis*), and within species from 4.9 to 5.4 (*E. pergracilis*). Shell shape and sculpture in fossil *Exilia* are very similar to that of a number of Recent and fossil genera, which we treat as synonyms.

Synonyms (in chronological order).

Mitraefusus Bellardi, 1873: 204.

Type species (by monotypy): *Fusus orditus* Bellardi and Michelotti, 1841, Miocene, Italy (Fig. 3 F-H).

Remarks: When he established *Mitraefusus*, Bel-

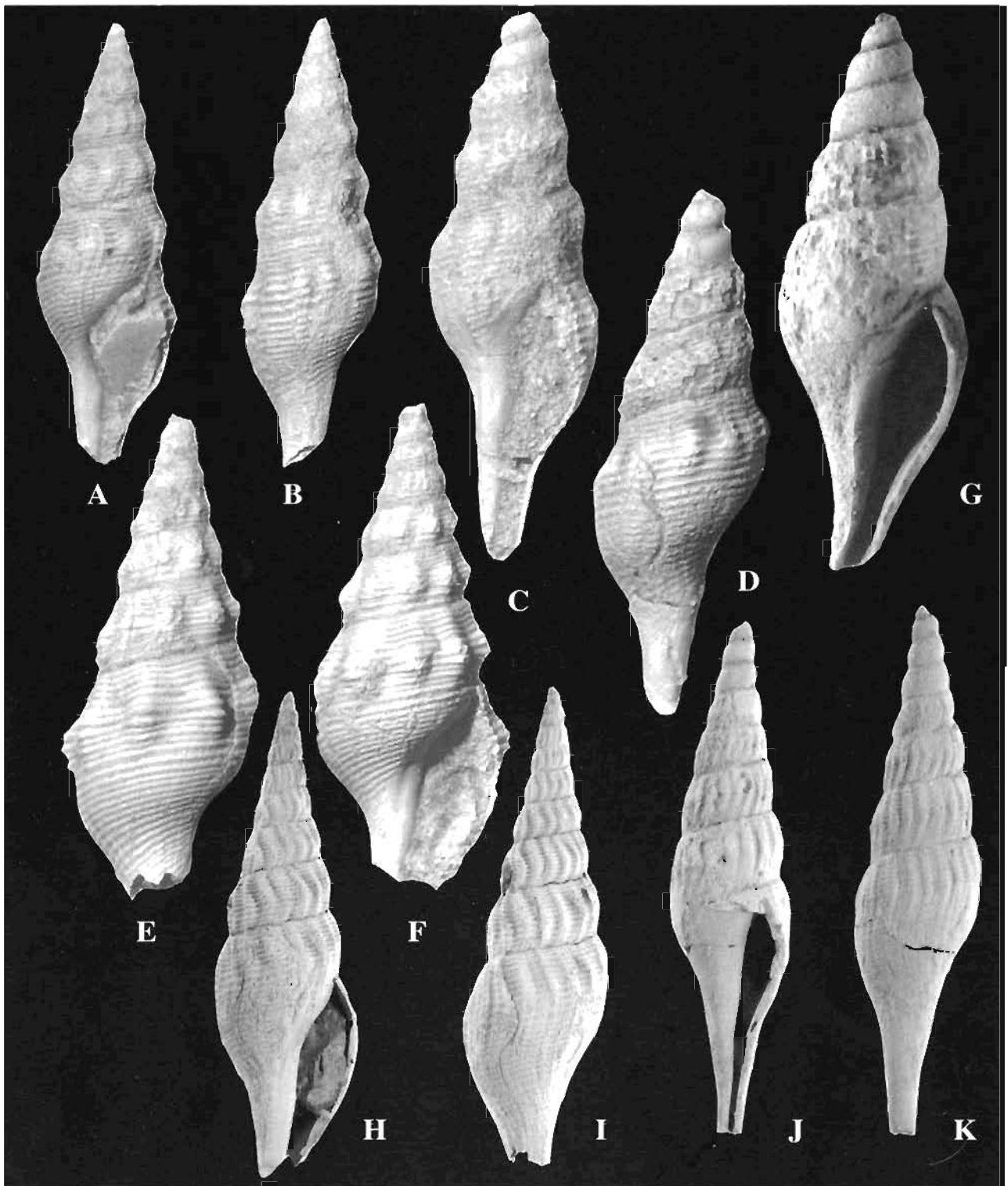


FIG. 2 *Exilia*: Cretaceous and Tertiary species from the northern hemisphere and Antarctica. A-F. *Exilia bentsonae* Hickman, 1980. Middle Eocene, Snatolskaya Formation, Tigil Region, Western Kamchatka. A-B PRI 49417, 27.7 mm. C-D. PRI 49418, 29.1 mm. E-F PRI 49419, 17.8 mm. G. *Exilia* sp. Upper Maastrichtian, Lopez de Bertodano Formation, Seymour Island, Antarctica. EASPU 1109, 18.8 mm. H-K. *Exilia lincolnensis* Weaver, 1916 Upper Eocene, Lincoln Creek Formation, Porter Bluff, Washington. H-I. USGS 1729, 48.2 mm. J-K. UWBM 19936, 30.5 mm.

РИС 2 *Exilia*. Меловые и третичные вид из северного полушария и Антарктики. А-Ф. *Exilia bentsonae* Hickman, 1980. Средний эоцен, Снатольская формация, район Тигиля, западная Камчатка А-В. PRI 49417, 27,7 мм С-Д. PRI 49418, 29,1 мм. Е-Ф. PRI 49419, 17,8 мм. G. *Exilia* sp. Верхний маастрихт. формация Lopez de Bertodano, Сеймур Исланд, Антарктика. EASPU 1109, 18,8 мм. H-K. *Exilia lincolnensis* Weaver, 1916 Верхний эоцен, формация Lincoln Creek Formation, Porter Bluff, Washington H-I. USGS 1729, 48,2 мм. J-K. UWBM 19936, 30,5 мм

lardi placed it "provisionally" in the subfamily Fusinae of the Muricidae. Fischer [1884: 672] and Sacco [1893: 20] thought that *M. orditus* resembled species of *Rostellaria* [= *Tibia*] and classified *Mitraefusus* in Strombidae. However Bellardi's illustration [1873: pl. 11 fig. 1, this paper Fig. 3 F] is idealized, as stated by Sacco [1904: 27 "un po' troppo manierata", i.e. too much retouched]. Sacco [1904, pl. 8, figs. 1-3] gave new illustrations of all the syntypes, of which one is reproduced herein (Fig. 3 G-H). Only one other species *M. ottnangensis* Hoernes, 1875, was ever referred to *Mitraefusus*. The outline of the slender fusiform shell (H/W = 5.4) of *M. orditus* is similar to that of *E. pergracilis*. The sculpture consists of narrow, oblique axial ribs and fine spiral striae and is similar to that of *E. graphiduloides* sp. nov. and *Exilia dickersoni* (Weaver, 1912) (Fig. 1 L-M). Columella without plaits.

Mitraefusus was already synonymised with *Exilia* by Cossmann [1901: 26], and this has been followed by subsequent authors [Sacco, 1904: 27, Bentson 1940, Wenz, 1943]. Although we have not been able to examine material of the type species, judging from the illustrations of syntypes [Sacco, 1904: pl. 8, figs. 1-3; Ferrero Mortara *et al.*, 1982: pl. 7 fig. 7] we accept this synonymy.

Mesorhytis Meek, 1876: 356 (new synonym).

Type species (by original designation): *Fasciolaria?* (*Mesorhytis*) *gracilentata* Meek, 1876, Maastrichtian [Late Cretaceous], Montana, USA (Fig. 1E).

Remarks: *Mesorhytis* was originally established as a subgenus of *Fasciolaria*, although Meek [1876] already in the original description expressed doubts as to the correct family position. The holotype seems to be the only known specimen and the original illustration depicts a reconstructed specimen. Subsequently, Dall described the Recent *Fasciolaria* (*Mesorhytis*) *meeikiana* Dall, 1889 [currently *Latiromitra meekiana*, see Bouchet and Kantor (2000)] and *Fasciolaria* (*Mesorhytis*) *costatus* Dall, 1890, both from deep water in the Caribbean, and Wade [1926] described from the Ripley Formation of Tennessee *Mesorhytis obscura* (Fig. 4E-F) [later transferred to *Graphidula* by Sohl [1964]; see discussion below under *Graphidula*]. *Mesorhytis* was treated as a subgenus of *Vexillum* (family Costellariidae) by Wenz [1943], and Cernohorsky treated it successively as a genus of Vexillinae [= Costellariidae] [Cernohorsky 1970: 52] and a member of the Fasciolariidae [Cernohorsky 1972: 218].

The slender, fusiform shell (H/W = 3.3) of the type species and its sculpture consisting of narrow, straight axial ribs and fine spiral striae are very similar to those of Recent *Exilia*. The columella of the holotype of the type species has three moderately strong plaits, but there is insufficient material to evaluate the variation of this character.

The spire angle of *Fasciolaria?* (*Mesorhytis*) *gracilentata* reaches 32° (according to the original description), which exceeds only slightly the angle of species already attributed to *Exilia*, but does not affect the overall shell proportions.

Based on similarity of shell characters we synonymize *Mesorhytis* with *Exilia*.

Surculina Dall, 1908: 260 (new synonym).

Type species (by original designation): *Daphnella* (*Surculina*) *blanda* Dall, 1908; Recent, Gulf of Panama (Fig. 27 J-K).

Remarks: *Surculina* was originally established as a subgenus of *Daphnella* and classified in the family Turridae. Beside the type species, Dall initially also included in it *Daphnella* (*Surculina*) *cortezii* Dall, 1908, for which he later [Dall 1918] erected the genus *Phenacoptygma*. Grant and Gale [1931] considered *Surculina* a subgenus of *Leucosyrinx*. Powell [1942] followed this allocation, placing the group in the subfamily Cochlespirinae (Turridae), but later [Powell, 1966] transferred *Surculina* to Daphnellinae. Rehder [1967] considered *S. cortezii* to be congeneric with *S. blanda*, thus synonymizing the two nominal genera of which they are type species and, based on the radula of *S. cortezii*, transferred *Surculina* to Turbinellidae. Rehder compared *Surculina* with *Benthovoluta*, but kept them separate.

Surculina has remained little known. The type species is conchologically very similar to two species, described herein, *E. vagrans* sp. nov. and *E. kiwi* sp. nov., the anatomy of which undoubtedly proves their placement within *Exilia*. Both *Surculina blanda* and *E. kiwi* lack an operculum, but the presence of an operculum is variable even within the species. For instance, in *E. vagrans* sp. nov., some specimens have a very small operculum, while most specimens do not have an operculum at all. The small operculum (Fig. 7G) occupies 15% of aperture height and the nucleus is subcentral, while in the other species of *Exilia* in which an operculum is present, it occupies 30% (a significant part of the operculum is usually corroded) to 60% of aperture height and the nucleus is terminal. Thus, absence of operculum in the type species of *Surculina* cannot be regarded as a generic character. The absence of columellar folds in *Surculina* is not of great importance either, as in some species of *Exilia* they are absent, or their presence may be infraspecifically variable. Therefore we consider *Surculina* a synonym of *Exilia*.

Phenacoptygma Dall, 1918: 138 (new synonym).

Type species (by original designation): *Daphnella* (*Surculina*) *cortezii* Dall, 1908; Cortez Bank, Recent (Fig. 27 D-E).

Remarks: This monotypic genus, proposed by Dall without diagnosis or description, was classified

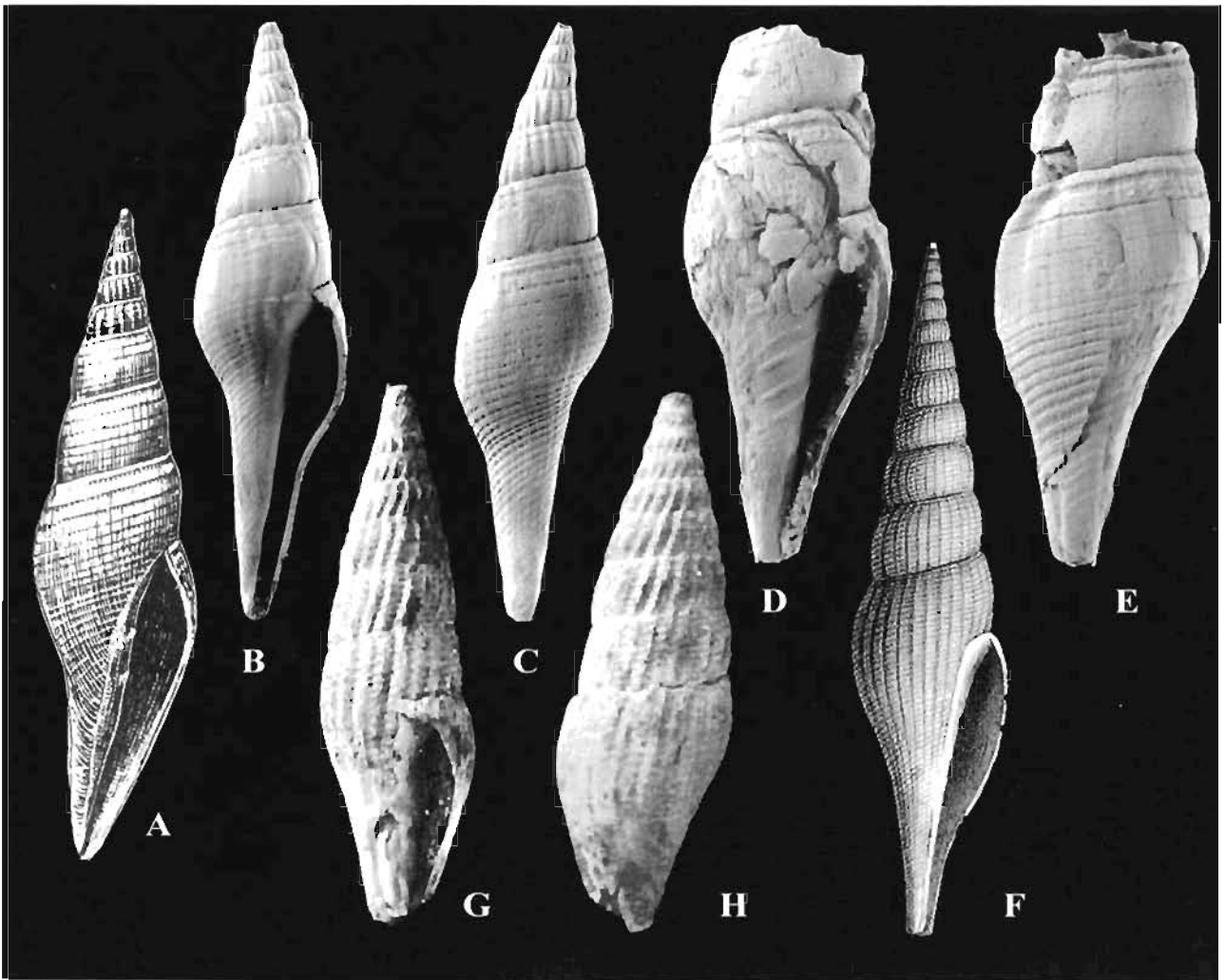


FIG. 3 *Exilia*: A-E. Cretaceous and Eocene species from North America; F-H. Miocene species from Europe. A-E. *Exilia pergracilis* (Aldrich, 1886), type-species of *Palaeorhaphis*. Lower Eocene, Wilcox Group, Gregg's Landing, Alabama. A. Figure copied from Harris (1899: pl. 4, fig. 10), 39.2 mm B-C UCBMP 32447, 39.7 mm D-E. UCBMP 32448, 36.0 mm. F-H. *Exilia ordita* (Bellardi and Michelotti, 1841), type species of *Mitraefusus*. Miocene, Colli Torinesi, Italy. F. Copied from Bellardi (1873 pl. 11 fig. 1), 66.7 mm G-H Syntype BS.009.15.01, Museo Regionale di Scienze Naturali, Torino, 44.5 mm [copied from Ferrero Mortara *et al.*, 1982, pl. 7, fig. 7].

РИС 3 *Exilia*: A-E. Меловые и эоценовые виды из Северной Америки; F-H. миоценовый вид из Европы. A-E. *Exilia pergracilis* (Aldrich, 1886), типовой вид *Palaeorhaphis*. Нижний эоцен, группа Wilcox, Gregg's Landing, Алабама. А. По Harris (1899: pl. 4, fig. 10), 39,2 мм. B-C. UCBMP 32447, 39,7 мм D-E. UCBMP 32448, 36,0 мм. F-H. *Exilia ordita* (Bellardi and Michelotti, 1841), типовой вид *Mitraefusus*. Миоцен, Colli Torinesi, Италия. F. По Bellardi (1873: pl. 11 fig. 1), 66,7 мм. G-H. Синтип BS.009.15.01, Museo Regionale di Scienze Naturali, Турин, 44,5 мм [по Ferrero Mortara *et al.*, 1982, pl. 7, fig. 7].

in the Volutidae, a position followed by Oldroyd [1927].

In the original description of the type species, Dall mentioned that the animal has no tentacles, eyes or snout, nor operculum. This statement is very confusing, since the only neogastropod known that lacks head tentacles is *Olivella* (Olivellidae) [Marcus, Marcus, 1959; Kantor, 1991] and Dall's statement needs confirmation. The radula of *Surculina cortezi* [Rehder, 1967] is typical for *Exilia*. Rehder [1967] considered *S. cortezi* congeneric with

S. blanda, thus synonymizing *Phenacotypgma* with *Surculina*, and placed *Surculina* in the family Turbinellidae.

The name *Phenacotypgma* has been rarely used, but Kuroda [1931] described *Phenacotypgma? kiiense* [= *Voluta hilgendorfi* Martens, 1897].

Zexilia Finlay, 1926: 506.

Type species (by original designation): *Exilia waihaeensis* Suter, 1917, Eocene, New Zealand

Remarks: Finlay established *Zexilia* for *Exilia dalli* Suter, 1907, *E. crassicostata* Suter, 1917, and *E. waihaoensis* Suter, 1917, all from the Tertiary of New Zealand, and placed it in the family Fusinidae. He did not discuss in any detail the differences between *Zexilia* and *Exilia*, and apparently introduced *Zexilia* on his assumption of a different evolutionary history for the New Zealand fauna. The resemblance of species of *Zexilia* to American and European species referred to *Exilia* was already noticed by Finlay and Marwick [1937], but they retained the name *Zexilia* until additional information would become available. Maxwell [1988] pointed out that shell shape, sculpture and protoconch characters of New Zealand species fall within the range of American and European species of *Exilia* and concluded that the differences are "deemed insufficient to warrant even subgeneric separation" and synonymized *Zexilia* with *Exilia*. We follow Maxwell's conclusion.

Palaeorhaphis Stewart, 1927: 419 (new synonym).

Type species (by original designation): *Fasciolaria pergracilis* Aldrich, 1886, Eocene, Alabama, USA (Fig. 3 A-E).

Remarks: In the original description of *Palaeorhaphis*, Stewart [1927] expressed his difficulty "to choose between the Mitridae and the Fasciolaridae", but tentatively allocated the genus to the former. *Palaeorhaphis* has subsequently been considered a member of the Turridae by Thiele [1929] and Wenz [1943], but Powell [1966] had excluded it from this family and suggested instead a position in the Volutidae or the Mitridae. Bentson [1940] discussed the relationships of *Palaeorhaphis* and concluded that it is distinct from *Exilia*, by her classified in the Fusinidae. She admitted, however, that the general shell outlines of these two nominal genera, characterized by a slender, fusiform shape and straight, narrow anterior canal, are nearly identical, as are their protoconchs consisting of 3 smooth whorls. (Indeed, the similarity extends to the specific epithets, and the names of the type species of *Palaeorhaphis* and *Exilia* have occasionally been confused [De Gregorio, 1890].) Bentson [1940] further noted that the shell of *Palaeorhaphis* is "proportionally heavier and stouter" than in *Exilia*.

The height to width ratio of specimens of *P.*

pergracilis Aldrich examined by us ranges from 4.3 to 4.6 and their spire angle is 25° to 26°, which is well within the range of species attributed to *Exilia*. The siphonal canal is wider at its base and narrows more gradually than in most species of *Exilia*, but similar variations in width of siphonal canal are observed in *E. dickersoni* and *E. bentsonae*, where specimens with abruptly and gradually narrowing siphonal canals were found within the same population. Shells of larger specimens of *Palaeorhaphis pergracilis* appear somewhat thicker than the shells of species of comparable size attributed to *Exilia*, but this can hardly be viewed as a diagnostic character. The sculpture of *Palaeorhaphis* consists of straight axial ribs, well developed on the early spire whorls and becoming completely or almost completely obsolete on the last whorl, where the sculpture is dominated by wide, flat cords separated by narrow grooves. This sculpture is not typical of American species of *Exilia*, but is similar to that of European fossil species and is common among Recent species formerly referred to *Benthovoluta*.

Synonymizing the monotypic genus *Palaeorhaphis* with *Exilia* makes *Palaeorhaphis pergracilis* (Aldrich) a secondary homonym of *Exilia pergracilis* Conrad. As there may well be a junior synonym the name of which can be used as a substitute, we do not propose a new name.

Graphidula Stephenson, 1941: 345 (new synonym).

Type species (by original designation): *Graphidula terebriformis* Stephenson, 1941, Maastrichtian [Late Cretaceous], Texas, USA (Fig. 4 A-D).

Remarks: When he established the genus *Graphidula*, Stephenson [1941] also made it the type of a new family Graphidulidae, which he placed between the Buccinidae and the Volutidae, and which was later placed in synonymy of Fasciolarinae by Sohl [1964]. The shell proportions of *Graphidula* (H/W ratio 4.1-4.9, spire angle 20°-26°) fall well within the range of variation of *Exilia*. The protoconch of the type species consists of 2 to 2.5 smooth whorls [Stephenson, 1941]. Columnar plait, when present, are very narrow and widely spaced, and usually concealed inside the aperture. The sculpture of the type species consists of narrow, almost straight, and closely spaced axial ribs, intersected by weaker, broad, flat spiral cords.

РИС. 4. *Exilia*: Меловые (A-D; E-F) виды из Северной Америки в сравнении с современным (G-I) A-D. *Exilia terebriformis* Stephenson, 1941, типовой вид *Graphidula*. A-B. Мaaстрихт. Nacatoch Sand, около Chatfield, Navarro County, Texas. Голотип (USNM 77085), 46.0 мм. C-D. Мaaстрихт. формация Ripley, Coon Creek Tongue, к северу от плотины Union County Lake, Union County, Миссиссиппи, по Sohl, 1964: pl. 28, fig. 24, 25 (USNM 130341), 18.6 мм. E-F. *Exilia obscura* (Wade, 1926). Голотип of *Mesorhytis obscura* Wade. Мaaстрихт, формация Ripley, McNairy County, Теннесси, по Wade [1926: Plate XLVI, figs. 2, 6]. G-I *Exilia graphiduloides* sp. nov. (G, H — экземпляры насыплены двуокисью магния). G. Новая Каледония (BATHUS 4, ст. DW920), 610-620 м, 35.0 мм. H. Новая Каледония (BATHUS 4, ст. DW921), 610-613 м, 28.5 мм. J. Паратип, Новая Каледония, 550 м (MUSORSTOM 4 sta DW197), 35.2 мм. Все раковины в одном масштабе. J-M. Раковины различных форм *E. hilgendorfi* в рентгеновских лучах. J-K — популяции из с.-з. части Индийского океана; L, M — глубоководные популяции из Новой Каледонии, Фиджи и Тонга (раковина на Рис. M — см. Рис. 190).

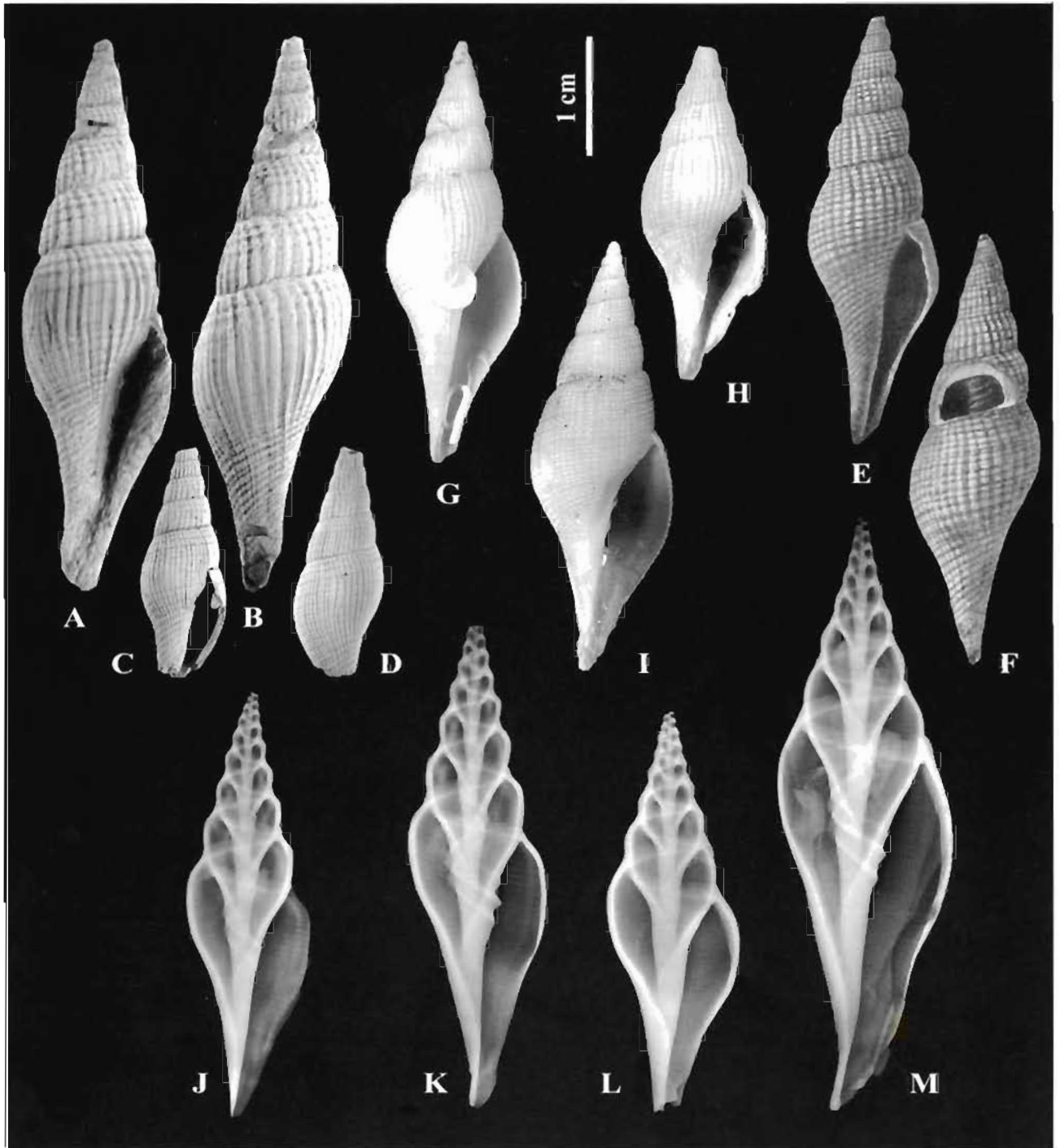


FIG. 4. *Exilia*: Cretaceous (A-D; E-F) species from North America in comparison with the recent one (G-I). A-D *Exilia terebriformis* Stephenson, 1941, type-species of *Graphidula*. A-B. Maastrichtian, Nacatoch Sand, near Chatfield, Navarro County, Texas. Holotype (USNM 77085), 46.0 mm. C-D. Maastrichtian, Ripley Formation, Coon Creek Tongue, north of dam of Union County Lake, 1.1 miles northeast of Pleasant Ridge, Union County, Mississippi. Specimen figured by Sohl, 1964: pl. 28, figs. 24, 25 (USNM 130341), 18.6 mm. E-F. *Exilia obscura* (Wade, 1926) Holotype of *Mesorhytis obscura* Wade. Maastrichtian, Ripley Formation, McNairy County, Tennessee. Copied from Wade [1926: Plate XLVI], figs. 2, 6]. G-I. *Exilia graphiduloides* sp. nov. (G, H — specimens coated with magnesium oxide). G. New Caledonia (BATHUS 4, sta DW920), 610-620 m, 35.0 mm. H. New Caledonia (BATHUS 4, sta DW921), 610-613 m, 28.5 mm. I. Paratype, New Caledonia, 550 m (MUSORSTOM 4 sta DW197), 35.2 mm. All shells at the same scale. J-M. Shells of different forms of *E. hilgendorfi* in X-rays. J-K — populations from the South-West Indian Ocean; L, M — deep-water populations from New Caledonia, Fiji and Tonga (shell on Fig. — see Fig. 190).

In *G. melanopsis* (Conrad, 1860) (Fig. 1 N-O) and *G. pergracilis* (Wade, 1926) [original binomen *Piestochilus pergracilis*, Fig. 1 H-I], there is a sculpture of strong, curved axial ribs and fine spiral cords, which is most similar to the sculpture of fossil species traditionally attributed to *Exilia*. Finally, in species such as *G. cancellata* (Wade, 1926) [original binomen *Piestochilus cancellata*] (Fig. 1 F-G) and *G. obscura* (Wade, 1926) [original binomen *Mesorhytis obscura*] (Fig. 4 E-F), axial ribs and spiral cords of equal strength form a cancellate pattern. This range of sculpture types parallels that observed in *Exilia*. The resemblance between *Graphidula* and *Exilia* was already noticed by Maxwell [1988] and, based on our comparison of a broad range of nominal species traditionally allocated in the two genera, we consider *Graphidula* a synonym of *Exilia*. The Recent *E. graphiduloides* sp. nov. (Fig. 4 G-I) combines a shell sculpture typical of *Graphidula* (compare with Fig. 4 A-D, E-F) and an anatomy that unequivocally places it in the same genus as the other Recent species of *Exilia*.

The synonymization of *Graphidula*, *Palaeorhaphis* and *Exilia* makes *Graphidula pergracilis* (Wade, 1926) [original binomen *Piestochilus pergracilis*], from the Maastrichtian of Tennessee, a secondary homonym of *Exilia pergracilis* Conrad, 1860 and *Fasciolaria pergracilis* Aldrich, 1886. The consequence of the generic synonymy is also that the family Graphidulidae Stephenson, 1941 becomes a subjective synonym of Ptychatractinae Stimpson, 1865.

Sohl [1964] reassigned to *Graphidula* some species formerly classified in *Piestochilus* Meek, 1876 and even discussed *Piestochilus* as a possibly senior synonym of *Graphidula*. However, the general shape (H/W ratio 2.3 to 2.6, spire angle 43°), smooth shell, and short and moderately wide siphonal canal of *P. scarboroughi* (Meek and Hayden, 1857), the type species of *Piestochilus*, clearly separate it from species currently allocated to *Graphidula* or *Exilia*.

Benthovoluta Kuroda et Habe, 1950: 37 (new synonym).

Type species (by original designation): *Phenacoptygma kiiensis* Kuroda, 1931 [= *Voluta hilgendorfi* Martens, 1897], Recent, Japan (Fig. 14).

Remarks: *Benthovoluta* was originally described as a genus of the family Volutidae. Based on Habe's [1952] very schematic illustrations of the radula, it was transferred to Turbinellidae by Kuroda [1965]. Harasewych [1987] described the anatomy of *B. claydoni* Harasewych, 1987 and placed *Benthovoluta* in the subfamily Ptychatractinae of the Turbinellidae. Strangely, however, *Benthovoluta* has still recently been considered a volutid by Noda [1988].

As currently understood, *Benthovoluta* contains four Recent nominal species, of variable shell shape and sculpture, ranging from broad forms with H/W ratio of 2.9-3.1, spire angle of 37°-40°, gently

narrowing siphonal canal, to narrow, slender forms with H/W ratio of 4.0-4.2, spire angle of 24°-27°, and narrow rapidly tapering siphonal canal. Axial sculpture consists of straight, rounded, or roundly angular ribs, which may be well developed to obsolete on the last whorl. Spiral sculpture consists of broad flat cords, separated by incised lines, similar to what is found in *Palaeorhaphis*, or of narrow, rounded cords separated by grooves of similar width. In some specimens the axial sculpture is distinctly stronger, but in others the spiral sculpture dominates, especially on the last whorl. The protoconch is paucispiral and consists of 0.75 to 1.5 smooth whorls. The number of columellar plaits ranges from none to 4 in different specimens of the same species. Despite considerable variation in shell shape and sculpture, all specimens of Recent species attributed before this study to *Benthovoluta* fall within the range of shell shape and sculpture of fossil taxa currently allocated to *Exilia*. The anatomy and radula of, e.g., *E. hilgendorfi* and *E. graphiduloides* sp. nov., confirm that they are congeneric despite rather different shell types.

Kuroda and Habe designated *Phenacoptygma kiiensis* as the type species of *Benthovoluta*, but mentioned *V. hilgendorfi* as its senior synonym, thereby suggesting that they perhaps considered this synonymy doubtful.

Chathamidia Dell, 1956: 118 (new synonym).

Type species (by original designation): *Chathamidia expeditionis* Dell, 1956, Recent, Chatham Rise, New Zealand (Fig. 26).

Remarks: The shell of the type species of this nominal genus is least similar to that of species attributed to *Exilia*. It is rather broad, H/W ratio ranging from 2.4 to 3.0 and spire angle from 45° to 56.5°, thus with shell proportions closer to those of *Piestochilus*. The siphonal canal is long, but broad, and tapering rather gradually, and the spire is shorter than in all the nominal genera discussed above. The axial sculpture consists of broad, straight rounded ribs which can be reduced to axially elongated shoulder knobs, similar to those in *E. bentsonae*; these axial elements are crossed by narrow, rounded spiral cords, separated by thin incised lines, as in some species allocated to *Benthovoluta*, *Exilia*, and *Palaeorhaphis*. *Chathamidia* was originally described in the family Muricidae, but was synonymised with *Surculina* and placed in the subfamily Ptychatractinae of the Turbinellidae by Cernohorsky [1973]. The anatomy of *Chathamidia expeditionis* is very similar to that of Recent species traditionally allocated to *Benthovoluta* and confirms that *Chathamidia* should be synonymised with *Exilia*.

Distribution of *Exilia*

Maastrichtian — eastern, southeastern and central United States (Maryland, New Jersey, Ten-

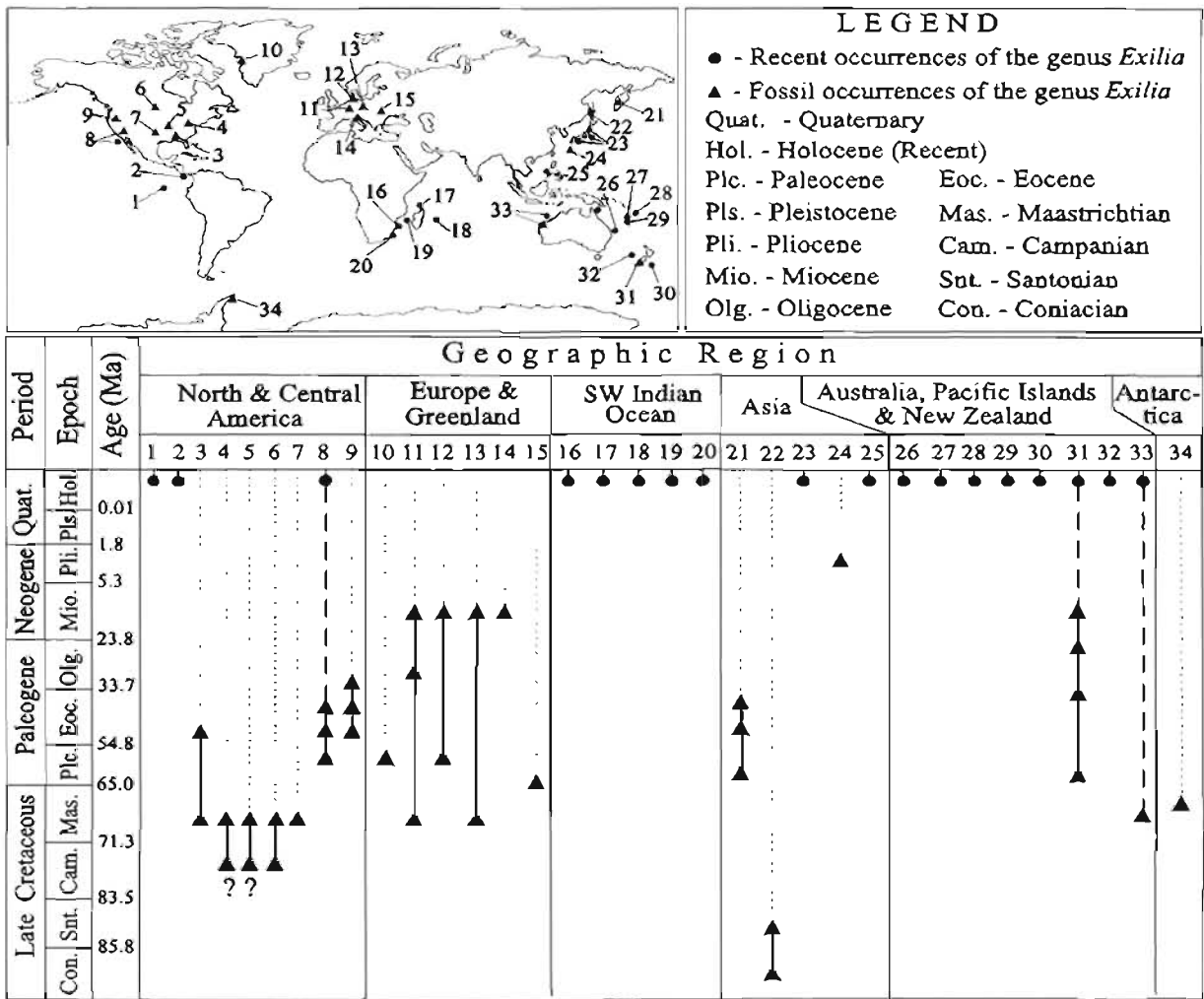


FIG. 5. Stratigraphical and geographical distribution of fossil and Recent representatives of the genus *Exilia*.
 North and Central America: 1. Galápagos Islands. — 2. Gulf of Panama — 3. Alabama and Mississippi. — 4. Maryland and New Jersey — 5. Tennessee. — 6. North Dakota — 7. Texas — 8. California — 9. Oregon and Washington.
 Europe and Greenland: 10. western Greenland — 11. Germany. — 12. Denmark, Belgium, and the Netherlands — 13. Poland and Austria. — 14. Italy — 15. northern Ukraine
 Southwestern Indian Ocean: 16. southern Mozambique — 17. northwestern Madagascar — 18. Réunion Island. — 19. southwestern Madagascar. — 20. Natal, South Africa.
 Asia: 21. Kamchatka. — 22. Sakhalin Island — 23. eastern Japan — 24. Ryukyu Islands — 25. Philippine Islands.
 Australia, Pacific Islands, and New Zealand: 26. Queensland — 27. Vanuatu. — 28. Fiji Islands. — 29. New Caledonia and Loyalty Ridge. — 30. Chatham Rise and Bounty Plateau. — 31. South Island, New Zealand — 32. Tasman Basin — 33. Western Australia — 34. Antarctic Peninsula.

РИС. 5. Стратиграфическое и географическое распространение ископаемых и современных представителей рода *Exilia*.

nessee, Mississippi, Texas, North Dakota), Germany, Poland, eastern Russia (Sakhalin), western Australia, and western Antarctica [the latter record is included with doubt; the species involved (Fig. 2G), still unnamed, only slightly resembles typical *Exilia*].

Paleocene — western United States (California), western Greenland, Denmark, northern Ukraine, eastern Russia (Kamchatka), and New Zealand.

Eocene — eastern and western United States (Alabama, California, Oregon, Washington), eastern Russia (Kamchatka), New Zealand

Oligocene, Miocene and Pliocene [nearly identical distribution during these epochs] — western United States (Washington), Germany, Belgium, Netherlands, Italy, southern Japan, and New Zealand.

Recent — Indo-Pacific: South-West Indian

Ocean, western Australia, southern Japan, Philippines, eastern Australia (Queensland), Vanuatu, New Caledonia, Fiji; Tasman Sea, New Zealand (Chatham Rise and Bounty Trough); Panamanian: off southern California, Gulf of Panama, and Galápagos Islands.

Paleoecology and biogeography (Fig. 5): Fossil occurrences of the genus *Exilia* indicate a cosmopolitan distribution during the Late Cretaceous and Cenozoic. *Exilia* is known from Upper Cretaceous through Neogene deposits from various parts of the world except South America and Africa, which is probably a reflection of insufficient studies of Cretaceous and Tertiary mollusks in these regions. The majority of Cretaceous records are from the European and American provinces [Gardner, 1916; Wade, 1926; Sohl, 1964, 1967; Erickson, 1974; Abdel-Gawad, 1986], which were near the southern border of the North Temperate realm during the Late Cretaceous [Kauffman, 1973; Sohl, 1987]. Single occurrences are known in Sakhalin, western Australia and western Antarctica [Hayami, Kase, 1977, Darragh, Kendrick, 1994], which suggests that *Exilia* was widely distributed in both North and South-Temperate realms at the end of the Cretaceous. Cretaceous (mostly Maastrichtian) species occur in shallow environments (upper and middle shelf depths) both in carbonate and siliciclastic rocks, containing abundant and diverse mollusc assemblages indicative of a warm-temperate environment during deposition. Scattered Paleocene localities are from North- and South-Temperate realms [Bentson, 1940; Kollmann, Peel, 1983; Beu, Maxwell, 1990] and, based on the co-occurrence with other groups of macro- and micro-fossils, the deposits where *Exilia* occurs are interpreted as warm-temperate. The first relatively deep-water (lower shelf to bathyal) occurrences of *Exilia* are from the Late Eocene [Hickman, 1980; Beu & Maxwell, 1990; Maxwell, 1992] both in North- and South-Temperate realms. Miocene *Exilia* are known from shallow to deep shelf environments of northern to southern Europe [Janssen, 1984; Ferrero Morrata *et al.*, 1981] and from the bathyal deposits of New Zealand [Fleming, 1966; Beu, Maxwell, 1990]. Today the genus is confined to bathyal depths at tropical latitudes and in the New Zealand region.

It is noteworthy that Eocene representatives of the genus had multispiral protoconchs, indicating planktotrophic larval development, while Neogene to Recent taxa have paucispiral protoconchs, indicating non-planktotrophic larval development.

The anatomy of *Exilia*

Beside sketches of the radula of a couple of species now attributed to *Exilia* [Habe, 1952, Rehder 1967], the only data on the anatomy of *Exilia* are those published by Harasewych [1987] for *Benthovoluta claydoni* [here treated as a synonym

of *Exilia hilgendorfi*]. In this study, we describe the anatomy of five species of *Exilia* and present illustrations of the radula of a sixth species.

Exilia hilgendorfi

Five specimens were dissected, two from populations from off Madagascar (*Mascareignes II* sta. 63, sta. 80), two from off New Caledonia (deep-water form from BIOGEOCAL sta. CP297 and shallow-water form from BATHUS 3 sta. DW776), and one from Tonga (BORDAU 2 sta. DW1558). In addition, the radula of a paratype of *Benthovoluta gracilior* (USNM 238408; Fig. 16 C-D), from the Philippines, was prepared from the dried soft parts retracted deep into the shell. The description of the anatomy is based on the specimen from *Mascareignes II* sta. 80, which has a shell height of 81.6 mm; last teleoconch whorl height 52.0 mm; aperture height 24.6 mm; siphonal canal length 19.0 mm; shell diameter 20.4 mm.

External anatomy (Fig. 6 A-B): The posterior coils of the body above the stomach were torn off during extraction from the shell. The remaining part consists of 2.5 whorls, the mantle spans one whorl, and the nephridium 0.75 whorl. The pale yellowish body lacks pigmentation. The small, oval operculum (Fig. 6F), occupying 36% of aperture height (but part of it is missing), is semitransparent yellowish-brown, with the columellar muscle attachment extending along 2/3 of its length. The foot is moderately long ($L/W \approx 2.0$). The siphon is rather long. The thin columellar muscle has two deep grooves corresponding to the columellar plaits. The mantle is thin and covers partly the head and completely the penis; the mantle organs are clearly visible through it. The head is narrow and long. The tentacles are rather long, with medium-sized eyes at the base. The axial lamellae of the nephridium are clearly visible through its wall.

Mantle: The ctenidium, with high hanging leaflets, is very long and narrow ($L/W \approx 7.5$), and occupies 80% of mantle length. The osphradium is very large, 0.75× as long and 1.5× as wide as the ctenidium; it is asymmetrical with the right side 1.5× as broad as the left. The hypobranchial gland is covered with a thick mucus layer and is transversely plated. The anal gland was not found.

Digestive system: The organs of the body haemocoel are compactly packed. The contracted proboscis is very short, about 2 mm long (8% of aperture height), smooth and tapering towards the tip; it occupies about 1/3 of the rhynchodaeum (Fig. 6C). The thick-walled rhynchodaeum (= proboscis sheath) is lined with a tall epithelium. The medium-sized, unpaired, branching, ventral proboscis retractor is attached dorsally to the anteriormost part of the rhynchodaeum (Fig. 6C, vpr). However, in the specimen from deepwater off New Caledonia, the retractors were paired; in the specimen from shallow water off New Caledonia there were also smaller, paired retractors at-

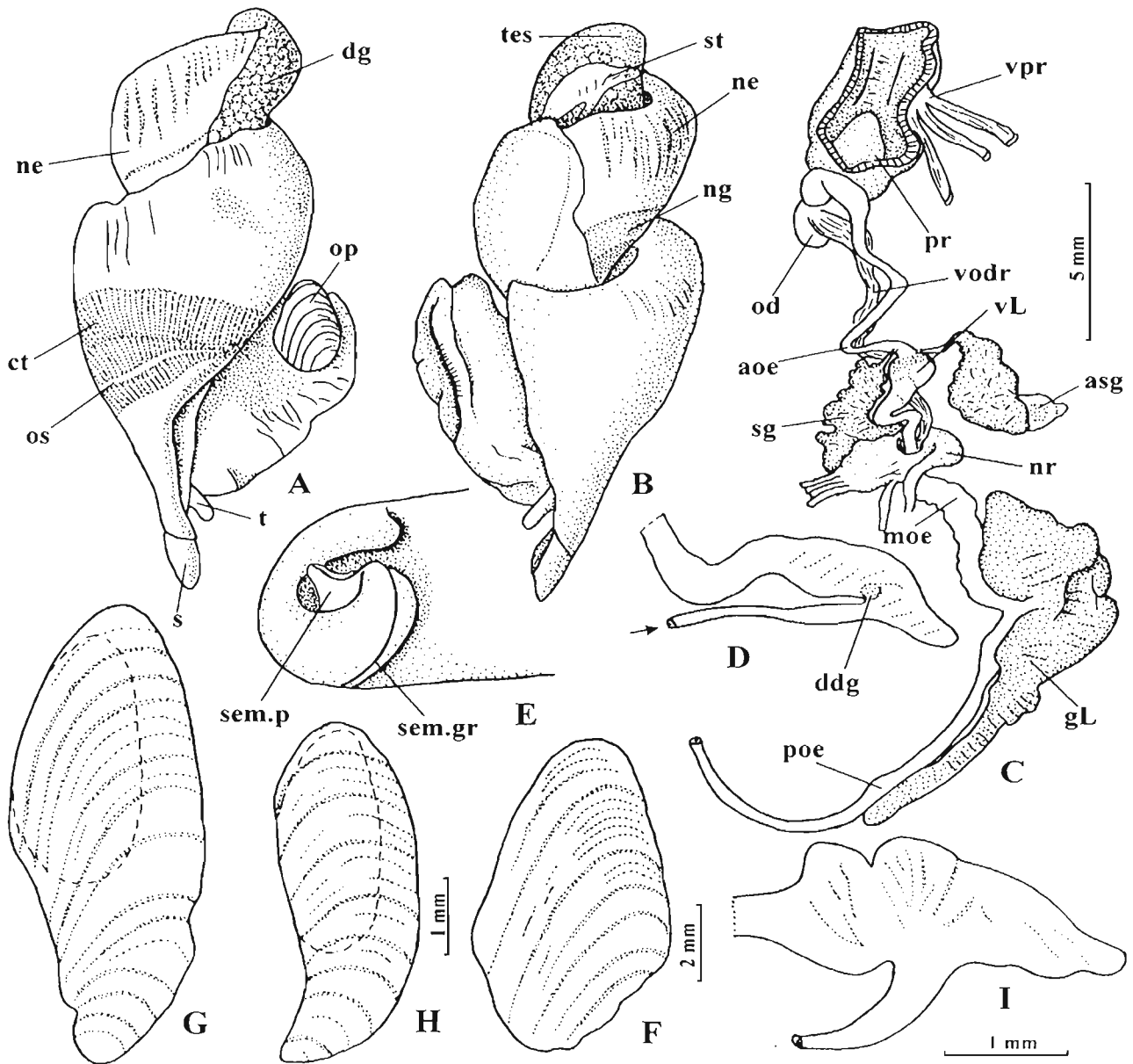


FIG. 6. Anatomy of *Exilia hilgendorfi*. A-F. Male specimen from South West Indian Ocean, *Mascareignes* II, sta. 80, shell height 81.6 mm. A-B. Body, removed from the shell. C. Organs of the body haemocoel, expanded (rhynchodaeum opened to show the proboscis; the gland of Leiblein rotated, to show the duct). D. Outer view of the stomach. E. Tip of the penis. F. Operculum. G. Operculum, specimen from SW Indian Ocean, *Mascareignes* II, sta. 75, shell height 81.8 mm; scale as in Fig. F, the dashed line indicates the place of attachment of the columellar muscle. H-I. Specimen of the "shallow-water" form from New Caledonia, BATHUS 3, sta. DW776, shell height 25.6 mm. H. Operculum. I. Outer view of the stomach. Abbreviations: see p. 2.

РИС. 6. Анатомия *Exilia hilgendorfi*. A-F. Самец из ю.-з. части Индийского океана, *Mascareignes* II, ст. 80, высота раковины 81,6 мм. A-B. Тело, извлеченное из раковины. C. Расправленные органы туловищного гемоцеля (ринходаеум вскрыт, чтобы показать хобот; железа Лейблеина повернута, чтобы показать проток). D. Желудок снаружи. E. Пенис. F. Крышечка. G. Крышечка экземпляра из ю.-з. части Индийского океана, *Mascareignes* II, ст. 75, высота раковины 81,8 мм; масштаб как на рис. F, пунктирной линией обозначено место прикрепления колумеллярного мускула. H-I. Экземпляр "мелководной" формы из Новой Каледонии, BATHUS 3, ст. DW776, высота раковины 25,6 мм. H. Крышечка. I. Желудок снаружи. Обозначения см. стр. 2.

tached laterally, in addition to the single branching retractor; while in the specimen from Tonga the left retractor was more developed than the right one. The attachment of the muscles to the anterior rhynchodaeum indicates that the whole rhyncho-

daeum takes part in proboscis evertion, and when the proboscis is completely everted these retractors are attached to the inner wall of proboscis. The large, muscular buccal mass equals the proboscis in length and projects beyond the rear of the

retracted proboscis (Fig. 6C, od). The radular diverticulum opens in the buccal cavity at the base of the proboscis. The thin buccal tube runs along nearly the whole length of the proboscis. The short and globular odontophoral subradular cartilages are paired, not fused anteriorly. The thin ventral odontophoral retractor passes through the nerve ring (Fig. 6C, vodr), follows the bottom of the cephalic haemocoel and joins the columellar muscle.

The radula (Fig. 12C) is about 2.1 mm long (2.5% of shell height and 8.5% of aperture height) and about 250 μm broad (0.3% of shell height and 1.0% of aperture height), and consists of about 70 transverse rows. The rachidian teeth have a slightly arched basal part with broad lateral flaps and bear 3 sharp cusps, with somewhat attenuated tips, that emanate from the anterior edge of the basal part. The central cusp is slightly shorter and narrower than the lateral ones. The lateral teeth are unicuspid, with a short base measuring in length about 42% of the rachidian width.

After leaving the proboscis the oesophagus forms a rather long loop before opening into the valve of Leiblein. This part of the oesophagus, representing the anterior oesophagus (Fig. 6C, aoe), is thick anteriorly, but later very thin and semitransparent. Between the valve and the opening of the gland of Leiblein, the oesophagus is rather widened and apparently glandular. This part, representing the mid-oesophagus (Fig. 6C, moe), is medium short, measuring about 2 \times proboscis length. The valve of Leiblein is large, much broader than the oesophagus, and pyriform. The posterior oesophagus is very narrow (Fig. 6C, poe), runs along the left side of the gland of Leiblein, and opens into the stomach. The gland of Leiblein is very large, uniformly light-yellowish in preserved specimen. It is massive anteriorly, and posteriorly tubular and tapering. The gland opens into the oesophagus by a very short duct.

The paired, rather compact, acinous, salivary glands are approximately equal-sized, and situated on both sides of the valve of Leiblein, partially covering it. The right gland is thinner than the left one. Immediately after leaving the glands the salivary ducts enter the walls of the oesophagus in front of the valve of Leiblein. There is a small oval-shaped accessory salivary gland, partially embedded in the right salivary gland (Fig. 6C, asg).

The stomach is medium-sized in comparison with the anterior foregut, and is furnished with a well-developed, long and narrow caecum (Fig. 6D). The fixation of the specimen did not permit an examination of the inner anatomy of the stomach. Judging from the outside, the stomach opens near the oesophagus opening to the digestive gland through a single large duct.

Male reproductive system: The seminal vesicle is short, forming very few loops. The pallial part of the genital system consists of a straight duct running on the floor of the mantle cavity, forming a muscular open seminal groove at its mid-length.

The groove runs anteriorly to the base of the long, dorso-laterally compressed penis and then along its inner lateral edge to the distal end; there it passes along the ventral surface of the penis, and along the edge of a nearly closed fold surrounding the seminal papilla, then to the base of the papilla and finally to its tip (Fig. 6E).

Remarks: The external anatomy and foregut were very similar in all studied specimens. The differences concern mainly the proportions of the radula and operculum, which, in fact, largely depend on the age of the animals as the operculum tends to be corroded in large specimens.

The second specimen from Madagascar (*Mascareignes II*, sta. 63) has a shell height of 74.5 mm; last teleoconch whorl height 49.0 mm; aperture height 21.4 mm; siphonal canal length 19.0 mm; shell diameter 17.5 mm. The small operculum occupies 30% of aperture height, but its lower part is missing. The radula (Fig. 11 A-B) is about 2 mm long (2.7% of shell height and 9.3% of aperture height) and 280 μm broad (0.57% of shell height and 1.30% of aperture height), and consists of about 85 rows of teeth. The rachidian teeth bear 3 thick cusps, distinctly tapering at their tips. The base of lateral teeth measures in length about 52% of the width of the rachidian.

The specimen from deep-water off New Caledonia (BIOGEOCAL, sta. CP297) has a shell height of 65.4 mm; last teleoconch whorl height 43.6 mm; aperture height 21.4 mm; siphonal canal length 15.0 mm; shell diameter 19.2 mm. The operculum occupies 40% of aperture height. The radular ribbon (Fig. 11 C-D) is about 2.2 mm long (3.4 % of shell height and 10.3% of aperture height) and 320 μm broad (0.48% of shell height and 1.49% of aperture height), and consists of about 65 transverse rows. The rachidian teeth bear 3 narrow sharp cusps, the central one nearly twice as long as the lateral ones. It is slightly recurved and occasionally has a small serration at its mid-length. [A very similar rachidian tooth was illustrated by Harasewych 1987: fig. 17 for *B. claydoni*]. The lateral teeth have a long base, measuring in length about 65% of the width of the rachidian.

The specimen from more shallow water off New Caledonia (BATHUS 3, sta. DW776) has a shell height of 25.6 mm; last teleoconch whorl height 17.5 mm; aperture height 7.0 mm; siphonal canal length 6.0 mm; shell diameter 8.4 mm. Its operculum (Fig. 6H) is large, narrow-oval, and occupies 60% of the aperture height. The radula (Fig. 11 E-F) is about 1 mm long (3.9 % of shell height and 14% of aperture height) and 210 μm broad (0.82% of shell height and 3% of aperture height), and consists of about 50 transverse rows. The rachidian teeth bear 3 sharp cusps of equal length. The length of the lateral tooth base is 54% of the rachidian width.

The paratype of *Benthovoluta gracilior* has a shell height of 54.0 mm; last teleoconch whorl height 33.5 mm; aperture height 15.5 mm; siphonal

canal length 13.0 mm; shell diameter 12.6 mm. After rehydrating in sodium carbonate, the body was removed and dissected. Although the preservation did not permit a detailed anatomical study, the gross morphology looks similar to that of specimens from the south-west Indian Ocean. The animal has a long siphon, large mantle organs, and long tentacles with rather large eyes. The very thin, transparent, yellow operculum is narrow-elongate oval, its nucleus turned adaxially, and occupies about 37% of aperture height. The radula (Fig. 12 A-B) is about 1.37 mm long (2.5 % of shell height and 8.0% of aperture height) and 230 μ m broad (0.43% of shell height and 1.48% of aperture height), and consists of about 65 transverse rows. The rachidian teeth bear 3 rather obtuse cusps, subequal in length, emanating from the anterior edge of the tooth. The length of the lateral tooth base equals 44% of the rachidian width.

Exilia vagrans sp. nov.

One male specimen (MUSORSTOM 8, sta. CP1129) was dissected. It had a shell height of 32.7 mm; last teleoconch whorl height 21.6 mm; aperture height 10.4 mm; siphonal canal length 6.7 mm; shell diameter 8.6 mm.

External anatomy (Fig. 7 A-B): The body consists of 4 whorls, the mantle spans one whorl, the nephridium 0.5 whorl and the digestive gland 2.25 whorl. The pale yellowish body lacks pigmentation. There is no operculum. The foot is long ($L/W \approx 2.5$). The siphon is medium long. The columellar muscle is thin. The mantle is thin, short, does not cover the head nor the main part of the penis, and the mantle organs are clearly visible through it. The head is narrow and long, partially covered by the siphon. The tentacles are long, with medium-sized eyes at the base. The axial lamellae of the nephridium are clearly visible through its wall.

Although a majority of specimens studied had no operculum, two of them had a small, very thin, transparent and yellow operculum (Fig. 7G), occupying only 15% of aperture height, rounded, with subcentral nucleus in abaxial position.

Mantle: The very long and narrow ($L/W > 8$) ctenidium, with high hanging leaflets, occupies $0.9 \times$ mantle length. The very large osphradium, $0.75 \times$ as long and $3 \times$ as wide as the ctenidium, is asymmetrical with the right side $1.5 \times$ as broad as the left. The hypobranchial gland is covered by a thick mucus layer and is not transversely plated. The anal gland is present but not visible through the mantle.

Digestive system: The organs of the body haemocoel are compactly packed. The contracted proboscis is short, about 2 mm long (19% of aperture height), smooth and tapering towards the tip. The thick-walled rhynchodaeum is lined with a tall epithelium. The powerful, paired, ventral proboscis retractors are attached latero-ventrally to

the anteriormost part of the rhynchodaeum and to the bottom of the body haemocoel. This indicates that the whole rhynchodaeum takes part in proboscis eversion, and when the proboscis is completely everted these retractors are attached to the inner wall of proboscis. The rather short muscular buccal mass lies completely outside the proboscis (Fig. 7E, od) and the radular diverticulum opens in the buccal cavity at the base of the proboscis. The odontophoral subradular cartilages are paired, not fused anteriorly. The large ventral odontophoral retractor passes through the nerve ring, probably follows the bottom of the cephalic haemocoel, and joins the columellar muscle (Fig. 7E, vodr).

The radula (Fig. 12 E-F), which projects slightly beyond the rear of the buccal mass, is about 1.1 mm long (3.4% of shell height and 11% of aperture height) and 150 μ m broad (0.46% of shell height and 1.44% of aperture height), and consists of about 60 transverse rows. The rachidian teeth bear 3 sharp cusps, emanating from the middle part of the basal part of the tooth. The central cusp is slightly longer and narrower than the lateral ones. The basal part is rather narrow, recurved, with broad lateral flaps. The unicuspid lateral teeth have a long base measuring in length 71% of the rachidian width.

After leaving the proboscis the oesophagus forms a short loop before opening into the valve of Leiblein (Fig. 7E, vL). Between the valve and the opening of the gland of Leiblein, the oesophagus is rather widened and apparently glandular. This part, representing the mid-oesophagus, is very short. The valve of Leiblein is large, much broader than the oesophagus, and pyriform. The posterior oesophagus is very narrow, runs along the left side of the gland of Leiblein, and opens into the stomach (Fig. 7E, poe). The stomach is rather large in comparison with the anterior foregut, and furnished with a well developed, long, and narrow caecum. The fixation of the specimen did not permit an examination of the inner anatomy of the stomach. Seen from outside (Fig. 7F), a single large duct, situated near the oesophagus opening, connects the stomach to the digestive gland. The gland of Leiblein is very large, massive and tapering posteriorly, its anteriormost part light yellowish, the rest greenish-gray in fixed condition. It opens into the oesophagus very close to the nerve ring by a very short duct (on Fig. 7E the gland is partially rotated to show the duct — dgL). The paired, rather compact, and acinous salivary glands are approximately equal-sized, situated on both sides of the valve of Leiblein and partially covering it. *In situ* the glands, together with the valve, lie at the right side of the proboscis sheath. Immediately after leaving the glands the rather thick salivary ducts enter the walls of the oesophagus in front of the valve of Leiblein. There is a small oval-shaped accessory salivary gland, situated near the circumoesophageal nerve ring. The rectum contains the remains of food, but without identifiable particles.

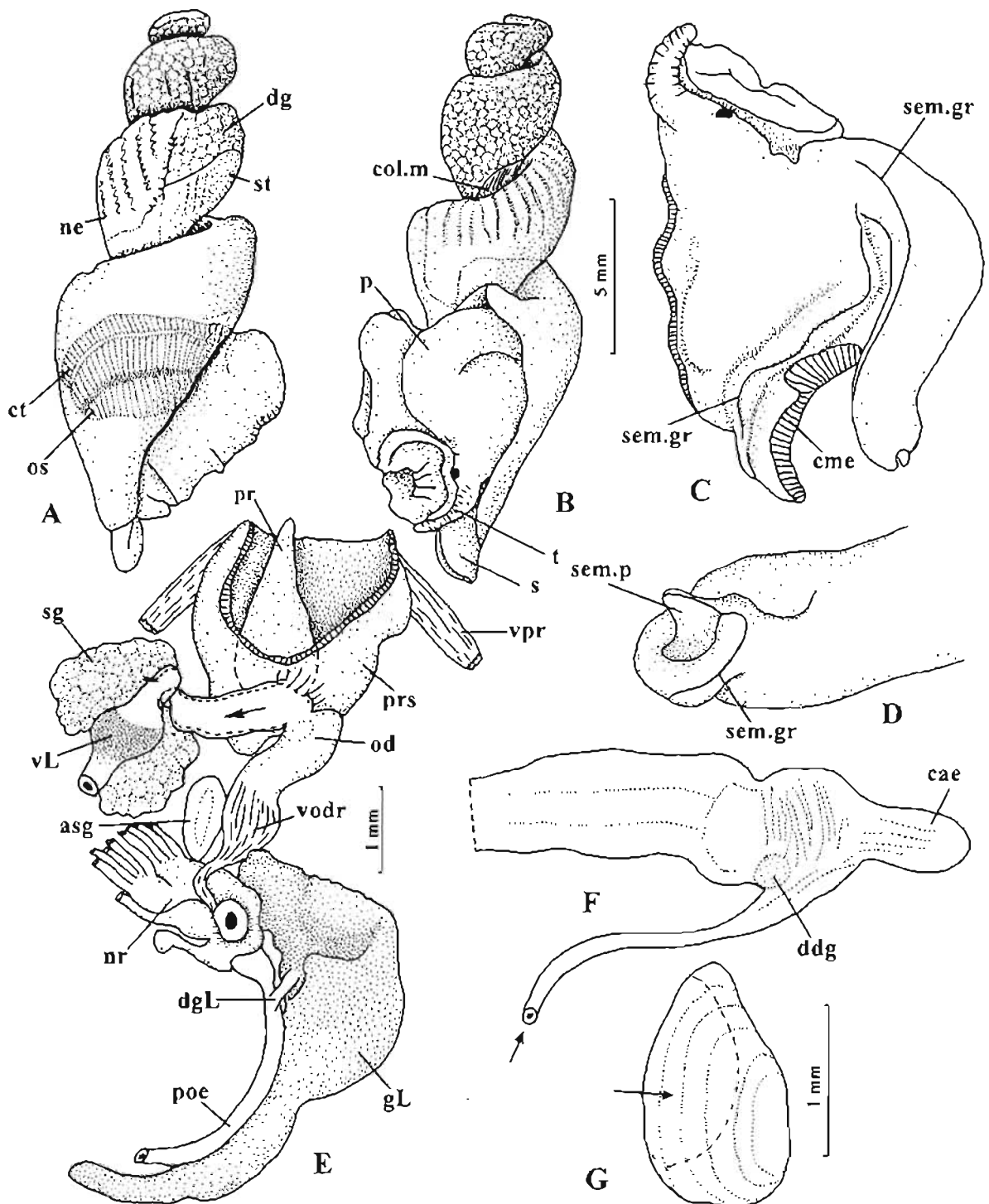


FIG 7. Anatomy of *Exilia vagrans* sp. nov. (A-F. Male specimen from MUSORSTOM 8, sta. CP1129, shell height 32.7 mm. and G. Specimen from MUSORSTOM 8, sta. CP1127). A-B. Body removed from the shell. C. Anterior part of the body with the mantle removed to show the penis and seminal groove. D. Tip of the penis. E. Organs of the body haemocoel, expanded (rhynchodaeum opened to show the proboscis, oesophagus cut posterior to the valve of Leiblein; gland of Leiblein rotated to show the duct, the dashed lines indicate the passing of the salivary ducts inside the wall of the oesophagus). F. Outer view of the stomach (same scale as Fig. E). G. Operculum (the arrow indicates the place of attachment of the columellar muscle). Abbreviations see p. 2.

РИС 7. Анатомия *Exilia vagrans* sp. nov. (A-F. Самец, MUSORSTOM 8, ст. CP1129, высота раковины 32,7 мм и G. MUSORSTOM 8, ста. CP1127). A-B. Тело, извлеченное из раковины. C. Передняя часть тела, мантия удалена, чтобы показать пенис и семенную борозду. D. Пенис. E. Расправленные органы туловищного гемоцеля (ринходаеум вскрыт, чтобы показать хобот; пищевод перерезан позади клапана Лейбейна; железа Лейбейна повернута, чтобы показать проток; пунктирная линия показывает прохождение протоков слюнных желез в стенках пищевода). F. Желудок снаружи (масштаб тот же, что на рис. E). G. Крышечка, пунктирной линией обозначено место прикрепления колумеллярного мускула. Обозначения см. стр. 2.

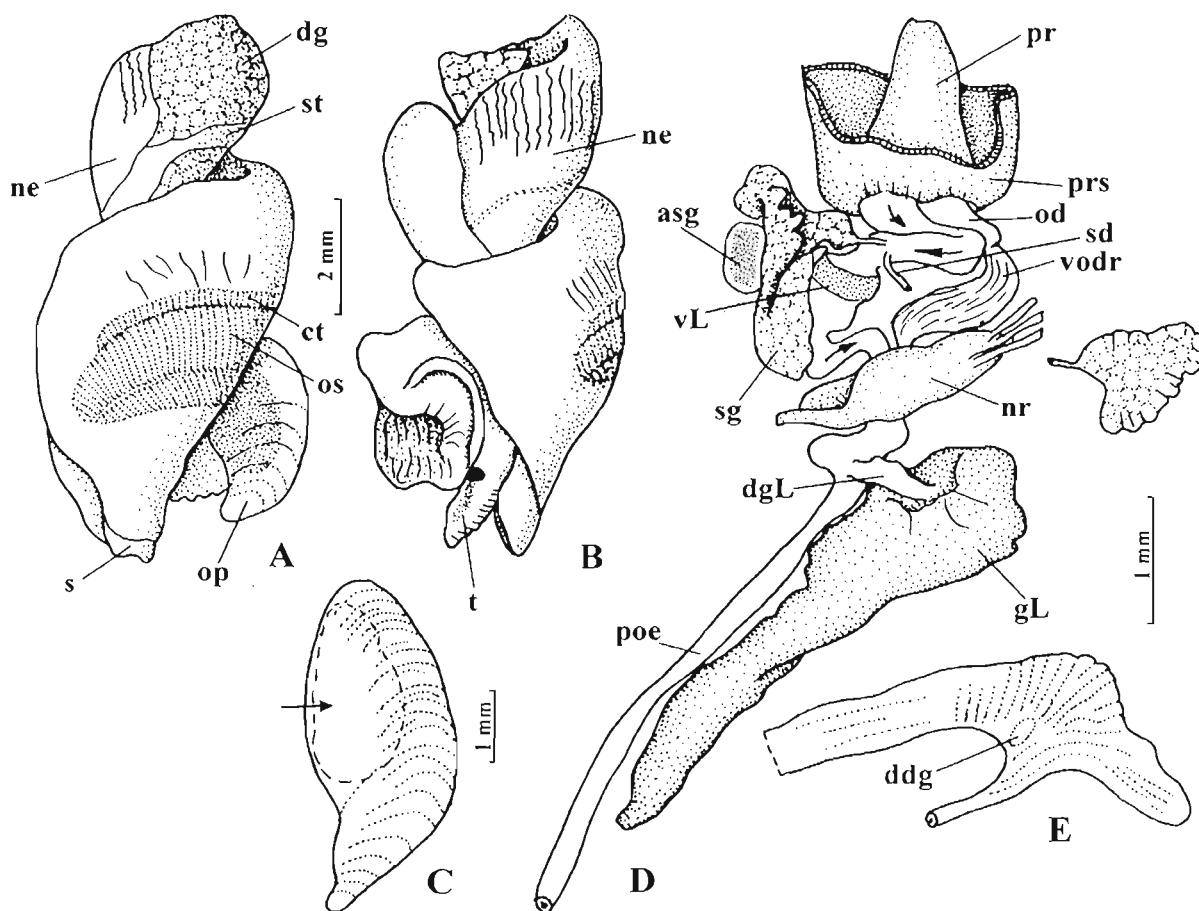


FIG. 8. Anatomy of *Exilia graphiduloides* sp. nov., immature female specimen (MUSORSTOM 4, sta. DW178, shell height 26.8 mm). A-B. Body removed from the shell. C. Operculum (the arrow indicates the place of attachment of the columellar muscle, indicated by dashed line). D. Organs of the body haemocoel, expanded (rhynchodaeum opened to show the proboscis; gland of Leiblein rotated to show the duct). E. Outer view of the stomach (same scale as Fig. D). Abbreviations: see p. 2.

РИС. 8. Анатомия *Exilia graphiduloides* sp. nov., неполовозрелая самка (MUSORSTOM 4, ст. DW178, высота раковины 26,8 мм). A-B. Тело, извлеченное из раковины. C. Крышечка (стрелка и пунктирная линия обозначают место прикрепления колумеллярного мускула). D. Расправленные органы туловищного гемоцеля (ринходеум вскрыт, чтобы показать хобот; железа Лейблейна повернута, чтобы показать проток). E. Желудок снаружи (масштаб тот же, что на рис. D). Обозначения: см. стр. 2.

Male reproductive system: The seminal vesicle is long, highly convoluted and occupies about 1.5 whorl. The pallial part of the genital system consists of a straight duct running on the floor of the mantle cavity and at its mid-length forming an open muscular seminal groove. The groove runs anteriorly to the base of the long, dorso-laterally compressed penis and then along its inner lateral edge to the distal end. There it passes along the ventral surface of the penis, and along the fold surrounding the seminal papilla to its tip (Fig. 7D).

Exilia graphiduloides sp. nov.

One immature female specimen (MUSORSTOM 4, sta. DW178; Fig. 20L) was dissected. It had a shell height of 26.8 mm; last teleoconch

whorl 17.4 mm; aperture height 9.0 mm; siphonal canal height 4.8 mm; diameter 6.7 mm.

External anatomy (Fig. 8 A-B): The upper coils were torn off during removal from the shell, and the remaining part consists of 2.5 whorls; the mantle spans one whorl, the nephridium 0.3 whorl. The body lacks pigmentation except head tentacles grayish in color. The thin, yellow, and transparent operculum is medium-sized, and occupies 50% of aperture height; it is elongate-oval with its nucleus turned adaxially (Fig. 8C). The foot is long ($L/W \approx 2.3$). The siphon is short. The columellar muscle is thin, with two grooves corresponding to the columellar plaits. The mantle is thin, and covers the base of the head; the mantle organs are clearly visible through it. The head is narrow, long, and in the fixed animal partly covered by the siphon. The tentacles are rather long, with medium-sized eyes at the base. The border between the mantle

cavity and the nephridium is represented by a wide deep cleft. The axial lamellae of the nephridium are clearly visible through its wall.

Mantle: The very long and narrow ($L/W \approx 10$) ctenidium, with high hanging leaflets, occupies $0.9 \times$ mantle length. The very large asymmetrical osphradium is $0.75 \times$ as long and $3 \times$ as wide as the ctenidium. The hypobranchial gland, which is covered by a thick mucus layer, is transversely plated as seen through the mantle. The anal gland was not found during the dissection.

Digestive system (Fig. 8D): The organs of the body haemocoel are compactly packed. The contracted proboscis is short, about 1.3 mm long (14% of aperture height), smooth and tapering towards the tip. The thick-walled rhynchodaeum (= proboscis sheath) is lined with a tall epithelium (Fig. 8D, prs). A pair of medium-sized muscles, probably functioning as ventral proboscis retractors, are attached latero-ventrally to the anteriormost part of the rhynchodaeum and to the bottom of the body haemocoel (not shown on the illustration). The rather short muscular buccal mass lies outside the proboscis (Fig. 8D, od) and the radular diverticulum opens in the buccal cavity at the base of the proboscis. The ventral odontophoral retractor passes through the nerve ring, follows the bottom of the cephalic haemocoel, and joins the columellar muscle.

The radula (Fig. 12D) is about 1.3 mm long (4.8% of shell height and 14% of aperture height) and $145 \mu\text{m}$ broad (0.54% of shell height and 1.61% of aperture height), and consists of about 75 transverse rows of teeth. The rachidian teeth bear 3 sharp but stout cusps of equal length, emanating from the anterior edge of the basal part of the tooth. The basal part is rather narrow, recurved, with broad lateral flaps. The unicuspid lateral teeth have a short base measuring in length 37% of the rachidian width.

After leaving the proboscis the oesophagus forms a moderately long loop (slightly longer than the proboscis) before opening into the valve of Leiblein (Fig. 8D, vL). Between the valve and the opening of the gland of Leiblein, the oesophagus is rather widened and glandular. This part, representing the mid-oesophagus, is short, about $1.5 \times$ proboscis length. The valve of Leiblein is moderately large, much broader than the oesophagus, and pyriform. The posterior oesophagus is very narrow (Fig. 8D, poe), runs along the left side of the gland of Leiblein, and opens into the stomach. The stomach is moderately large in comparison with the anterior foregut, and furnished with a well developed, long, and narrow caecum. The fixation of the specimen did not permit an examination of the inner anatomy of the stomach. Seen from the outside (Fig. 8E), a single large duct, situated near the oesophagus opening, connects the stomach to the digestive gland. The uniformly light-yellowish gland of Leiblein is very large, massive anteriorly, tubular and tapering posteriorly. It opens into the oesophagus

very close to the nerve ring by a short duct (on Fig. 8D the gland is partially rotated to show the duct). The paired, rather compact, and acinous salivary glands are approximately equal-sized, situated on both sides of the valve of Leiblein and partially covering it. Immediately after leaving the glands the rather thick salivary ducts enter the walls of the oesophagus in front of the valve of Leiblein. There is a small oval-shaped accessory salivary gland, situated near the circumoesophageal nerve ring.

Exilia kiwi sp. nov.

One male specimen (NMNZ M.59743; Fig. 28 A-B) was dissected. It had a shell height of 37.3 mm; last teleoconch whorl height 29.0 mm; aperture height 16.9 mm; siphonal canal length 6.4 mm; shell diameter 13.0 mm.

External anatomy (Fig. 9 A-B): The upper coils of the body were torn off during extraction from the shell. The remaining part consists of 2 whorls, the mantle spans 0.5 whorl, the nephridium 0.2 whorl. The whitish body lacks pigmentation. There is no operculum. The foot is long ($L/W \approx 2.7$). The siphon is short, slightly protruding beyond the mantle edge. The columellar muscle is thick, and extends for about 1.5 whorls. The mantle is moderately thin, does not cover the head, and the mantle organs are clearly visible through it. The head is broad, with rather long conical tentacles, and there are no eyes.

Mantle (Fig. 9C): The mantle edge is evenly thickened. The very long, curved, and narrow ($L/W \approx 9$) ctenidium, with high-triangular hanging leaflets, occupies nearly the whole mantle length. The large osphradium, $0.75 \times$ as long and $2.5 \times$ as wide as the ctenidium, is symmetrical, with a very narrow axis. The hypobranchial gland is covered by a thick mucus layer and is transversely plated. The rectum opens close to the mantle edge. The anal gland is not visible.

Digestive system: The digestive system is similar to that in other species of *Exilia* (Fig. 9D). The contracted proboscis, nearly cylindrical with slightly folded walls, is very short, about 1.5 mm long (9% of aperture height), and occupies about $2/3$ of the rhynchodaeum.

The radula (Fig. 13 A-B) is about 2.3 mm long (6.2% of shell height and 13.6% of aperture height) and $200 \mu\text{m}$ broad (0.54% of shell height and 1.18% of aperture height), and consists of about 75 transverse rows. At the bending plane, the teeth bear significant damages (Fig. 13A). The rachidian teeth bear 3 long, sharp cusps, emanating from the anterior edge of the basal part of the tooth. The central cusp is narrower and slightly longer than the lateral ones. The basal part is rather narrow, recurved, with moderately broad lateral flaps. The sickle-shaped, unicuspid lateral teeth have a short base measuring in length 27% of the rachidian width.

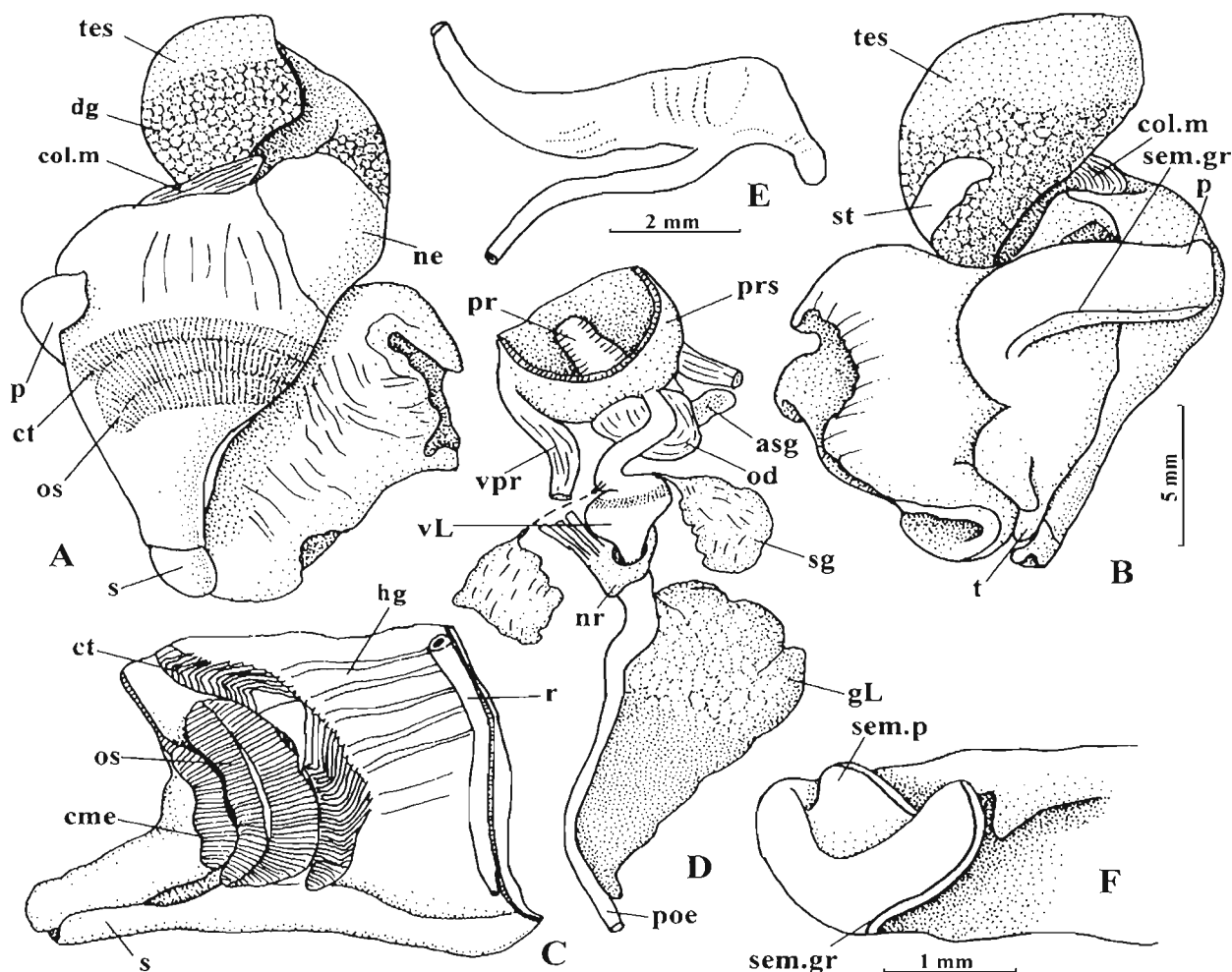


FIG. 9. Anatomy of *Exilia kiwi* sp. nov., male specimen (NMNZ M.59743, shell height 37.3 mm). A-B. Body, removed from the shell. C. Mantle organs (same scale as Fig. A-B). D. Organs of the body haemocoel, expanded (rhynchodaeum opened to show the proboscis). E. Outer view of the stomach (same scale as Fig. D). F. Tip of the penis. Abbreviations: see p. 3.

РИС. 9. Анатомия *Exilia kiwi* sp. nov., самец (NMNZ M.59743, высота раковины 37,3 мм). A-B. Тело, извлеченное из раковины. C. Мантийный комплекс органов (масштаб тот же, что на рис. A-B). D. Расправленные органы туловищного гемоцеля (ринходеум вскрыт, чтобы показать хобот). E. Желудок снаружи (масштаб тот же, что на рис. D). F. Пенис. Обозначения: см. стр. 3.

The small accessory salivary gland is situated at the base of the proboscis, close to the odontophore. The stomach is furnished with a long and narrow caecum (Fig. 9E). The condition of preservation did not allow an examination of its internal structure.

Male reproductive system: The very large testis nearly equals the size of the digestive gland (Fig. 9 A-B, tes). The short seminal vesicle forms few loops. The pallial part of the genital system consists of a slightly sinuous seminal groove with thickened edges, running on the floor of the mantle cavity, anteriorly to the base of the long, dorso-laterally compressed penis, and then along its inner lateral edge to the distal end. There it passes along the

ventral surface of the penis, along the fold surrounding the seminal papilla, and then along the dorsal side of the papilla to its tip (Fig. 9F).

Exilia expeditionis

One male specimen (NMNZ M.60422, specimen illustrated Fig. 26 A-B) was dissected. It had a shell height of 42.1 mm, last whorl height 32.2 mm, aperture height 19.5 mm, siphonal canal length 7.6 mm, diameter 15.4 mm.

External anatomy (Fig. 10 A-B): The upper coils of the body were torn off during extraction from the shell. The remaining part consists of 1.5

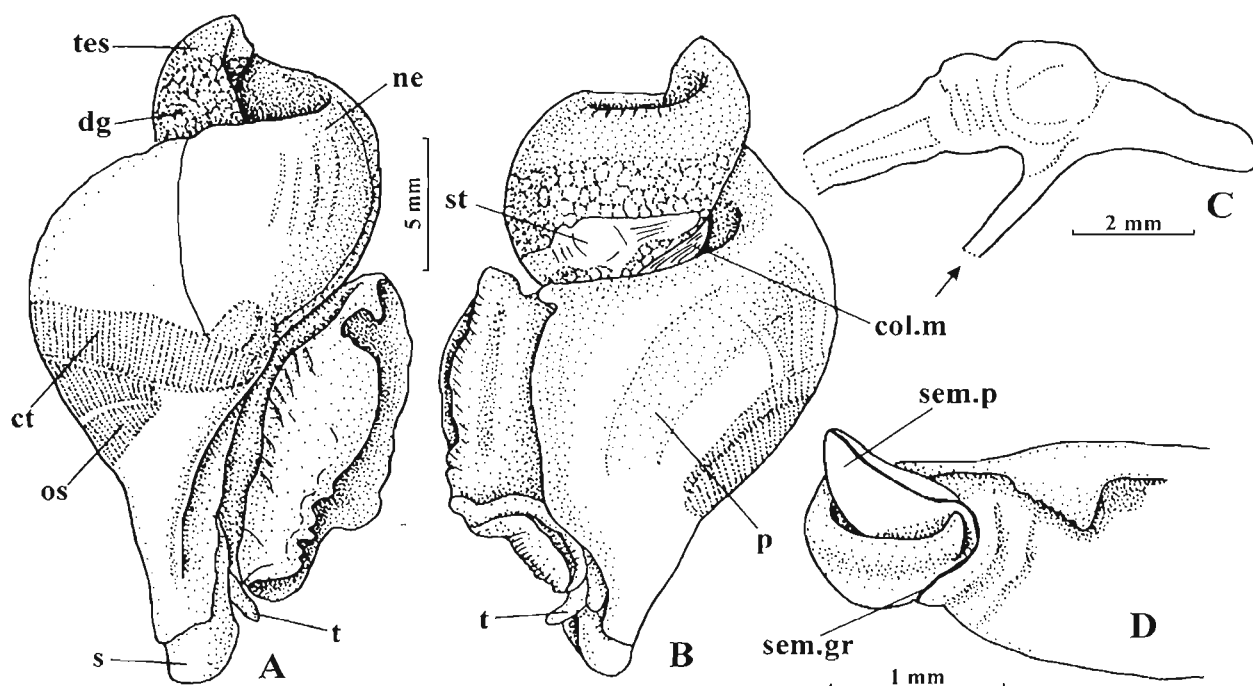


FIG. 10. Anatomy of *Exilia expeditionis* (NMNZ M.60422, shell height 42.0 mm). A-B. Body removed from the shell. C. Outer view of the stomach. D. Tip of the penis. Abbreviations: see p. 2.

РИС. 10. Анатомия *Exilia expeditionis* (NMNZ M.60422, shell height 42.0 mm). A-B. Тело, извлеченное из раковины. C. Желудок снаружи. D. Пенис. Обозначения см. на рис. 2.

whorls, the mantle spans 0.5 whorl, the nephridium 0.25 whorl. The whitish body lacks pigmentation. There is no operculum. The foot is short ($L/W > 1.6$). The siphon is short, slightly protruding beyond the mantle edge. The columellar muscle is thick, and extends for about 1.5 whorls. The mantle is moderately thin, covering the head, and the mantle organs are clearly visible through it. The head is broad, with long conical tentacles and large eyes.

Mantle: The very long, curved, and narrow ($L/W > 11$) ctenidium, with high hanging triangular leaflets, occupies nearly the whole mantle length. The large osphradium, $0.9\times$ as long and $3\times$ as wide as the ctenidium, is asymmetrical, with the right side twice as broad as the left. The hypobranchial gland is covered by a thick mucus layer and is transversely plated. The rectum opens close to the mantle edge. The anal gland is not visible.

Digestive system: The organs of the body haemocoel are compactly packed. The digestive system is in all details similar to that of *Exilia vagrans* sp. nov. The contracted proboscis, smooth and tapering towards the tip, is very short, about 2.5 mm (12% of the aperture height), and occupies about 2/3 of the rhynchodaeum. The branching ventral proboscis retractor is unpaired.

The radula (Fig. 13 C-D) is about 1.9 mm long (4.5% of shell height and 9.3% of aperture height) and 260 μm broad (0.62% of shell height and 1.27% of aperture height), and consists of about 80 transverse rows. The rachidian teeth bear 3 short, stout cusps, emanating from the anterior edge of the

basal part of the tooth. The central cusp is slightly longer than the lateral ones; the base of the left cusp bears indistinct thickened knobs. The basal part is narrow, recurved, with moderately broad lateral flaps. The unicuspid lateral teeth have a short base measuring in length 47% of the rachidian width.

The proboscis and oesophagus are enclosed from all sides by the salivary glands, tightly attached to the rhynchodaeum and oesophagus by numerous connective tissue fibers, and by the gland of Leiblein.

Male reproductive system: The seminal vesicle is long, forms numerous loops and occupies most part of the inner surface of the visceral mass. The pallial part of the genital system consists of a sinuous seminal groove with thickened edges, running on the floor of the mantle cavity. The morphology of the penis is similar to that in other species of *Exilia*, but the fold surrounding the seminal papilla is shorter and not embracing along much of the papilla dorsal side (Fig. 10D).

Exilia sp. A

A specimen from Madagascar was rehydrated from dried soft parts. It had a shell height of 43.0 mm, last whorl height 30.3 mm, aperture height 14.2 mm, siphonal canal length 10.5 mm, diameter 12.7 mm (Fig. 27A). Despite the depth of the catch (1715-1750 m), the animal has large, well develo-

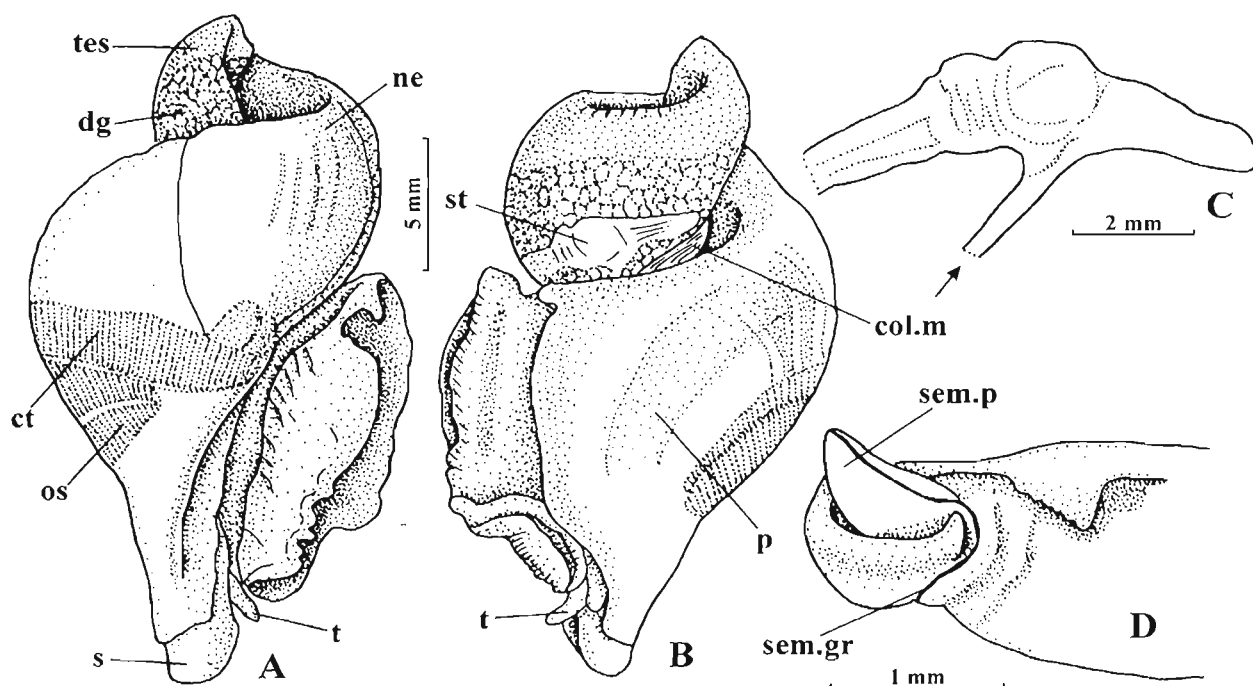


FIG. 10. Anatomy of *Exilia expeditionis* (NMNZ M.60422, shell height 42.0 mm). A-B. Body removed from the shell. C. Outer view of the stomach. D. Tip of the penis. Abbreviations: see p. 2.

РИС. 10. Анатомия *Exilia expeditionis* (NMNZ M.60422, shell height 42.0 mm). A-B. Тело, извлеченное из раковины. C. Желудок снаружи. D. Пенис. Обозначения см. на рис. 2.

whorls, the mantle spans 0.5 whorl, the nephridium 0.25 whorl. The whitish body lacks pigmentation. There is no operculum. The foot is short ($L/W > 1.6$). The siphon is short, slightly protruding beyond the mantle edge. The columellar muscle is thick, and extends for about 1.5 whorls. The mantle is moderately thin, covering the head, and the mantle organs are clearly visible through it. The head is broad, with long conical tentacles and large eyes.

Mantle: The very long, curved, and narrow ($L/W > 11$) ctenidium, with high hanging triangular leaflets, occupies nearly the whole mantle length. The large osphradium, $0.9\times$ as long and $3\times$ as wide as the ctenidium, is asymmetrical, with the right side twice as broad as the left. The hypobranchial gland is covered by a thick mucus layer and is transversely plated. The rectum opens close to the mantle edge. The anal gland is not visible.

Digestive system: The organs of the body haemocoel are compactly packed. The digestive system is in all details similar to that of *Exilia vagrans* sp. nov. The contracted proboscis, smooth and tapering towards the tip, is very short, about 2.5 mm (12% of the aperture height), and occupies about 2/3 of the rhynchodaeum. The branching ventral proboscis retractor is unpaired.

The radula (Fig. 13 C-D) is about 1.9 mm long (4.5% of shell height and 9.3% of aperture height) and 260 μ m broad (0.62% of shell height and 1.27% of aperture height), and consists of about 80 transverse rows. The rachidian teeth bear 3 short, stout cusps, emanating from the anterior edge of the

basal part of the tooth. The central cusp is slightly longer than the lateral ones; the base of the left cusp bears indistinct thickened knobs. The basal part is narrow, recurved, with moderately broad lateral flaps. The unicuspid lateral teeth have a short base measuring in length 47% of the rachidian width.

The proboscis and oesophagus are enclosed from all sides by the salivary glands, tightly attached to the rhynchodaeum and oesophagus by numerous connective tissue fibers, and by the gland of Leiblein.

Male reproductive system: The seminal vesicle is long, forms numerous loops and occupies most part of the inner surface of the visceral mass. The pallial part of the genital system consists of a sinuous seminal groove with thickened edges, running on the floor of the mantle cavity. The morphology of the penis is similar to that in other species of *Exilia*, but the fold surrounding the seminal papilla is shorter and not embracing along much of the papilla dorsal side (Fig. 10D).

Exilia sp. A

A specimen from Madagascar was rehydrated from dried soft parts. It had a shell height of 43.0 mm, last whorl height 30.3 mm, aperture height 14.2 mm, siphonal canal length 10.5 mm, diameter 12.7 mm (Fig. 27A). Despite the depth of the catch (1715-1750 m), the animal has large, well develo-

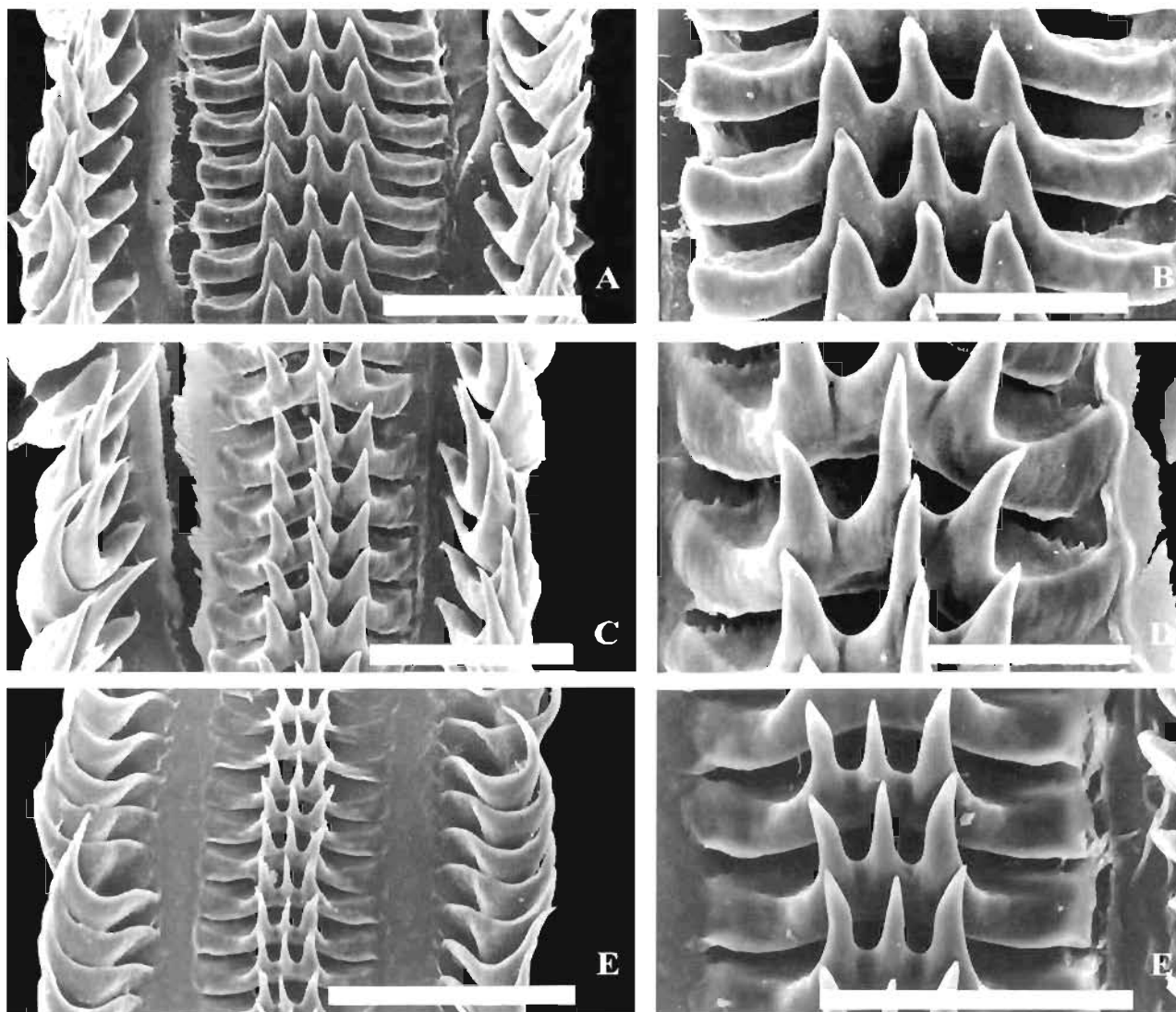


FIG. 11. Radulae of *Exilia hilgendorfi*. A-B. Populations from SW Indian Ocean (*Muscorennes* II, sta 63). A. Dorsal view of the radular ribbon B. Enlarged rachidian teeth. C-D. Deep-water form from New Caledonia (BIOGEOCAL, sta. CP297). C. Dorsal view of the radular ribbon D. Enlarged rachidian teeth. E-F. Shallow-water form from New Caledonia (BATHUS 3, sta DW776). E. Dorsal view of the radular ribbon F. Enlarged rachidian teeth. Scale bars: A, C, E, 100 μ m; B, D, F, 50 μ m.

РИС 11. Радулы *Exilia hilgendorfi*. А-В. Популяции из ю-з. части Индийского океана. А. Дорсальный вид радулярной мембраны В. Увеличенные центральные зубы. С-Д. Глубоководная форма из Новой Каледонии (BIOGEOCAL, ст. CP297). С. Дорсальный вид радулярной мембраны Д. Увеличенные центральные зубы. Е-Ф. Мелководная форма из Новой Каледонии (BATHUS 3, ст DW776) Е. Дорсальный вид радулярной мембраны. Ф. Увеличенные центральные зубы Масштаб: А, С, Е, 100 мкм, В, Д, Ф, 50 мкм.

ped eyes. The long anal gland is clearly seen through the mantle, and extends for 1/4 of a whorl. The long operculum, with nucleus turned adaxially, is 8.2 mm long (58% of aperture height). The nephridium spans 0.25 of a whorl, the mantle 0.66.

The radula (Fig. 13 G-H) is 1.5 mm long (3.4% shell height and 10.6% aperture height) and about 230 μ m broad (0.53% of shell height and 1.62%

of aperture height), and consists of about 55 rows of teeth. The rachidian teeth bear 3 obtuse cusps, emanating from the middle part of the basal part of the tooth, so that the anterior face of the tooth is distinctly concave. The central cusp is slightly longer than the lateral ones. The basal part is rather narrow, recurved, with medium broad lateral flaps.

The second specimen (Fig. 27 B-C) from

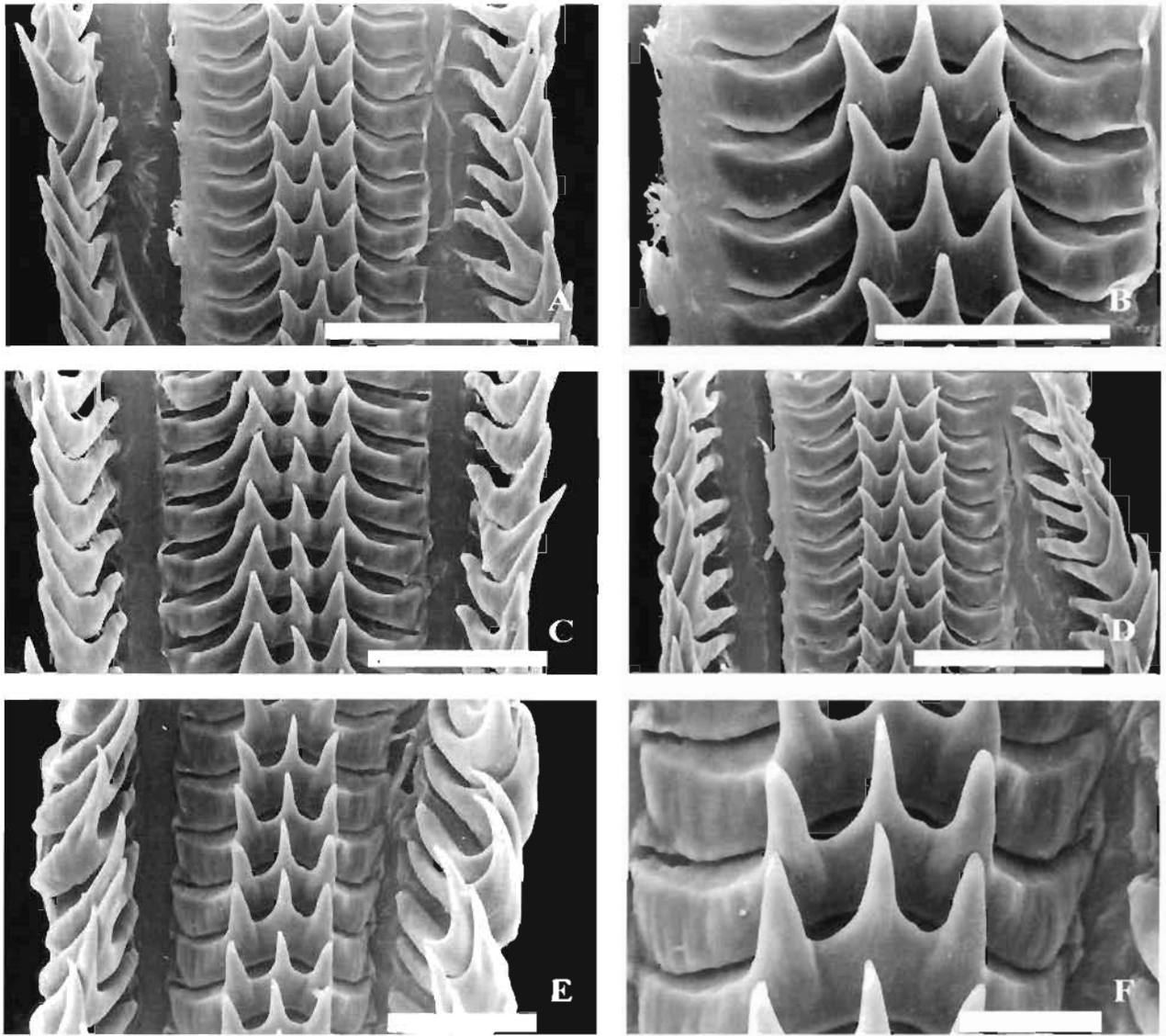


FIG. 12. Radulae of *Exilia* spp. A-B. *E. hilgendorfi*, populations from the Philippines (paratype of *E. gracilior*, USNM 238408). A. Dorsal view of the radular ribbon B. Enlarged rachidian teeth. C. *E. hilgendorfi*, populations from south-west Indian Ocean (*Mascareignes* II, sta. 80). D. *E. graphiduloides* sp. nov., dorsal view of the radular ribbon. E-F. *E. vagrans* sp. nov. E. Dorsal view of the radular ribbon. F. Enlarged rachidian teeth. Scale bars: A, D, 100 μ m; B, C, E, 50 μ m; F, 20 μ m

РИС 12. Радулы *Exilia* spp. А-В *E. hilgendorfi*, популяции с Филиппин (паратип *E. gracilior*, USNM 238408). А. Дорсальный вид радулярной мембраны. В. Увеличенные центральные зубы. С. *E. hilgendorfi*, популяции из ю.-з. части Индийского океана. (*Mascareignes* II, ст. 80). D. *E. graphiduloides* sp. nov., дорсальный вид радулярной мембраны. Е-F. *E. vagrans* sp. nov. Е. Дорсальный вид радулярной мембраны. F. Увеличенные центральные зубы. Масштаб: А, D, 100 мкм, В, С, Е, 50 мкм; F, 20 мкм.

РИС 13. Радулы *Exilia* spp. А-В. *E. kiwi* sp. nov. (NMNZ M.59743). А. Дорсальный вид радулярной мембраны. В. Увеличенные центральные зубы. С-Д. *E. expeditionis* (NMNZ M.60422). С. Дорсальный вид радулярной мембраны. D. Увеличенные центральные зубы. Е-Н. *Exilia* sp. А. Е-Н. Реюньон (MD 32, ст. CP140). Е. Дорсальный вид радулярной мембраны. F. Увеличенные центральные зубы. G-H. Мадагаскар (*Vauban*, ст. CH127). G. Дорсальный вид радулярной мембраны. H. Увеличенные центральные зубы. Масштаб: А, С, Е, G, 100 мкм; В, D, F, H, 50 мкм.

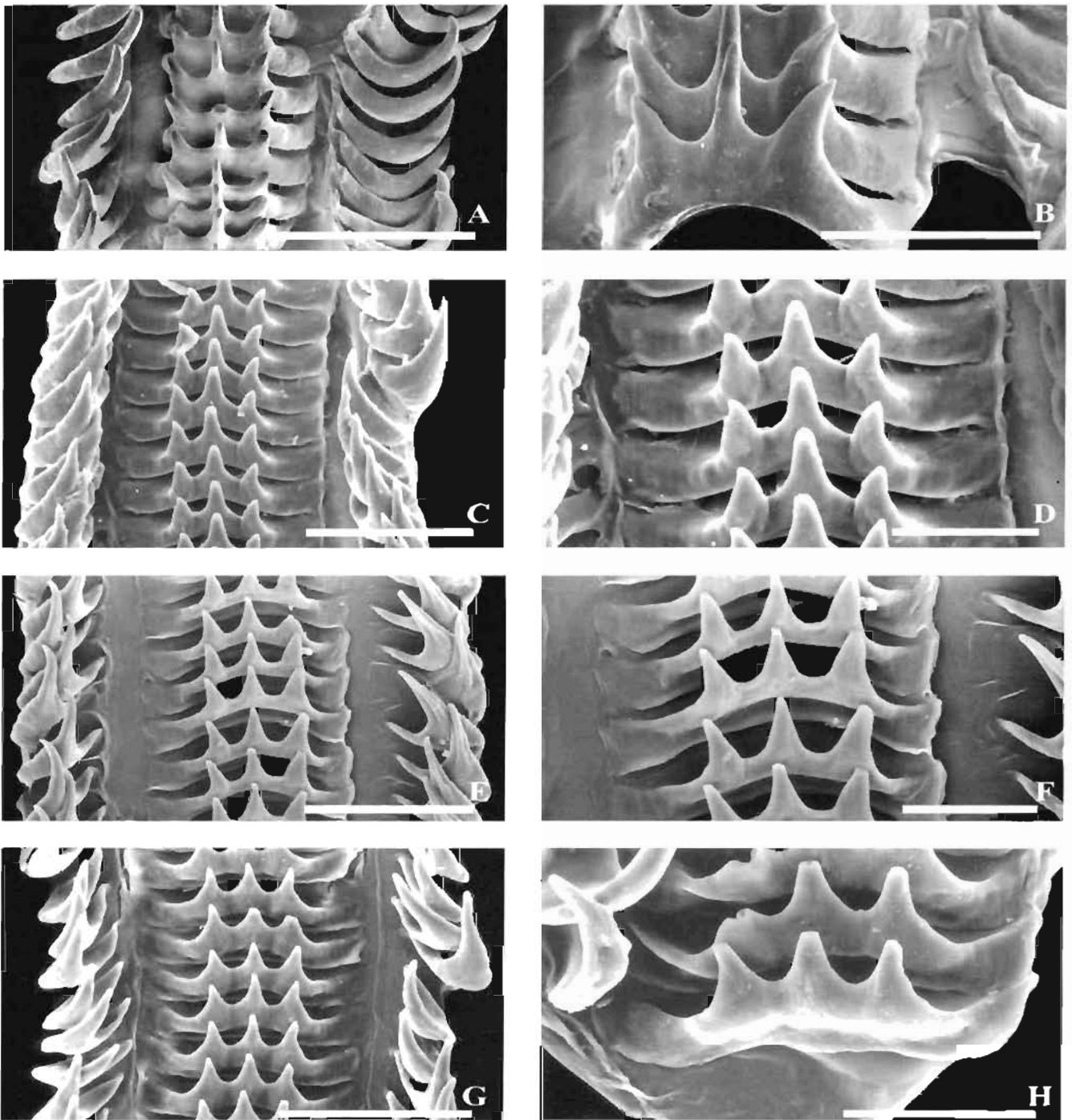


FIG. 13. Radulae of *Exilia* spp. A-B. *E. kiwi* sp. nov. (NMNZ M.59743). A. Dorsal view of the radular ribbon. B. Enlarged rachidian teeth. C-D. *E. expeditionis* (NMNZ M.60422). C. Dorsal view of the radular ribbon. D. Enlarged rachidian teeth. E-H. *Exilia* sp. A. E-F. Réunion (MD 32, sta. CP140). E. Dorsal view of the radular ribbon. F. Enlarged rachidian teeth. G-H. Madagascar (*Vauban*, sta. CH127). G. Dorsal view of the radular ribbon. H. Enlarged rachidian teeth. Scale bars: A, C, E, G, 100 μ m; B, D, F, H, 50 μ m.

Réunion (MD 32, sta. CP140) had a shell height of 59.0 mm, last whorl height 41.3 mm, aperture height 20.8 mm, siphonal canal length 11.3 mm, diameter 17.7 mm. Its radula (Fig. 13 E-F) is about 1.5 mm long (2.5% of shell height and 7.2% of aperture height) and 280 μm broad (0.47% of shell height and 1.35% of aperture height), and consists of about transverse 60 rows. The unicuspid lateral teeth have a short base measuring in length 41% of the rachidian width.

Species level systematics of Recent taxa

Class Gastropoda Cuvier, 1797

Unranked group Caenogastropoda Cox, 1959
Order Neogastropoda Wenz, 1941
Superfamily Muricoidea Rafinesque, 1815
Family Turbinellidae Swainson, 1835
Subfamily Ptychtractinae Stimpson, 1865

Genus *Exilia* Conrad, 1860

Exilia hilgendorfi (Martens, 1897), new combination

(Fig. 6; 11; 12 A-C; 14; 15; 16; 17; 18;
19; 20 A-H; 21)

Voluta hilgendorfi Martens, 1897: 176, pl. 17, fig. 2.

Synonyms:

Mitra plicifera Yokoyama, 1920: 48-49, pl. 2, figs. 16a-b.
Phenacopygma kiiense Kuroda, 1931: 48, fig. 1.
Benthovoluta gracilior Rehder, 1967: 185, figs 5,6 26,
fig. 1, 7, 8-10 (new synonym).
Benthovoluta claydoni Harasewych, 1987: 173-176, figs
10-12, 13-18 (new synonym).
Benthovoluta prelleii Bozzetti, 2001: 19 (new synonym).

Other references:

Benthovoluta hilgendorfi: Kuroda, Habe, 1950: 37, textfig.
4 (operculum), pl. 5, fig. 2, pl. 7, fig. 1 (holotype).
— Habe, 1952: 132, fig. 5 (radula). — Kira, 1962:
92, pl. 33, fig. 3. — Shikama, Horikoshi, 1963: 97,
pl. 79, fig. 7. — Okutani, 1964: 416-417 [as *B.*
hilgendorfi (sic!)]. — Kuroda, 1965: 50. — Kuroda,
Habe, Oyama, 1971: 199, pl. 51, fig. 3. — Cerno-
horsky, 1973: 126-127 (partim). — Habe, 1976: 97,
pl. 1, fig. 4. — Noda, 1980: 32-33, pl. 8, figs
14a-14b. — Harasewych, 1987: 168-169, figs 1-3. —
Noda, 1988: 48, pl. 11, figs 16a-16b, 20a-20b. —
Matsukuma, Okutani, Habe, 1991: 178, pl. 59, fig
14. — Higo *et al.*, 1999: 222. — Okutani, 2000:
423, pl. 210, fig. 3.
Mitra plicifera: Taki, Oyama, 1954: pl. 3, fig. 16 ["ho-
lotype" illustrated, as synonym of *B. hilgendorfi*]. —
Oyama, 1973: 48, pl. 13, fig. 13 (lectotype illustrated).
— Ichikawa 1983: 252, 264.
Benthovoluta gracilior: Cernohorsky 1973: 129. — Hara-
sewych, 1987: 169, figs 4-6.
Benthovoluta claydoni: Matsukuma, Okutani, Habe, 1991:
178, pl. 59, figs 10-11. — Wilson, 1994: 59, pl. 8,
figs. 1A, 1B.

Type material: *V. hilgendorfi*: holotype, Zoologis-
ches Museum Berlin 30277 [not seen]. — *M. plicifera*:
2 syntypes, University Museum, University of Tokyo,
CM 20103 (figured syntype) and CM 20104 [Ichi-
kawa 1983: 252, 264]; Taki and Oyama [1954] figured
the illustrated syntype (CM 20103) as "holotype",
but this does not constitute a valid lectotype desig-
nation under Art. 74.5 of the Code. — *P. kiiense*:
not traced. — *Benthovoluta gracilior*: holotype USNM
637252, 5 paratypes USNM 238408. — *Benthovoluta*
claydoni: holotype WAM 3252-83. — *Benthovoluta*
prelleii: holotype MNHN.

Type locality: *V. hilgendorfi*: "Japan, probably
from Hakodate" [probably in error fide Okutani
1964 and Kuroda *et al.* 1971]. — *M. plicifera*:
Koshiha, L. Musashino, Miura Peninsula, Lower
Pliocene of Japan. — *P. kiiense*: off Kii (exact
location and depth unknown). — *B. gracilior*: Phi-
lippines, Off Cagayan Islands, north Sulu Sea,
9°38'30"N, 121°11'E, 929 m [*Albatross* sta. 5423].
— *B. claydoni*: Western Australia, SW of Imperieuse
Reef, Rowley Shoals, 18°05'S, 118°10'E, 400-401
m. — *Benthovoluta prelleii*: Madagascar, off Tuléar.

Remarks: *Exilia hilgendorfi* has for a long time
been known from a small number of specimens
and was considered endemic to Japan. Two more
nominal species were later described from the
Philippines (*Benthovoluta gracilior*) and western
Australia (*B. claydoni*). The three allopatric nominal
species superficially look rather different (see, e.g.,
Fig. 14A, 16A, 16J). However, a subadult paratype
of *B. claydoni* (Fig. 16G) strongly resembles *B.*
gracilior (Fig. 16 A-E) and differs from it only by
the axial ribs being absent on the last adult whorl;
conversely, one of the paratypes of *B. gracilior* (Fig.
16E) itself also lacks ribs on the last whorl.

Based on our examination of newly obtained
material from different parts of the Indo-Pacific,
we conclude here that there is one species of *Exilia*
that ranges from Madagascar to Tonga, and from
Japan to New Zealand, with a variation that in-
cludes the three nominal species. Over this range,
Exilia hilgendorfi exhibits a three-dimensional ge-
ographical variation that is difficult to apprehend
because of the small size of the samples. Populations
living on soft bottoms (e.g., populations from the
NW Shelf of Australia or off Madagascar) appear
to be less variable, whereas populations from hard
or mixed bottoms on the slopes of New Caledonia,
Vanuatu and Fiji exhibit considerable variation
between stations separated by only tens of kilome-
ters and/or a couple of hundred meters in depth.
The amount of local variation thus appears to reflect
the heterogeneity of the environment.

Exilia hilgendorfi has a paucispiral protoconch
indicating non-planktotrophic larval development.
The discrete geographical and/or bathymetrical
forms that are recognizable at different geographical
scales (Table 1) are probably a reflection of limited
gene flow between populations. It may one day be
possible to sort intrapopulation polymorphism from
geographical polytypy, and formally recognize geo-

Table 1 Summary of conchological and anatomical characters in different populations of *Exilia hilgendorfi*.

Characters	Japan	Vanuatu	SW Indian Ocean	New Caledonia and Fiji, deep-water	New Caledonia and Fiji, shallow-water	Philippines	western Australia	Tasman Sea
Maximum adult size (mm)	84	63	84	89	53	55 (80)	101	63
Color	chestnut brown	dark to light chestnut brown	light straw, usually with slightly darker subsutural band	dirty-white or pinkish with brownish spots	diny-white to pinkish and light brown with darker subsutural band	light straw	white	white to straw
Number of protoconch whorls	1.5	n.a.	1.5	1.5	1.5	0.75?	n.a.	1.5
Maximum diameter of protoconch (μm)	1170	n.a.	1000	?	1000	n.a.	n.a.	800
Sculpture of last adult whorl	spiral grooves + weak or fading axial ribs	narrow spiral cords + weak or fading axial ribs	narrow spiral cords + weak or fading axial ribs	uneven spiral cords	narrow spiral cords + axial ribs	spiral cords	axial ribs usually present	spiral cords
Number of columellar plaits in adults	0, 3, 4	2, 3	2, 3, 4	0, 2, 3	2	2	2, 3	2, 3
Operculum length / aperture height	0.5	n.a.	0.30-0.36	0.40	0.6	0.37	ca 0.4	n.a.
Ctenidium length / width	n.a.	n.a.	7.5	9.5	6.5	n.a.	8	n.a.
Osphradium length / ctenidium length	n.a.	n.a.	0.75	0.58	0.69	n.a.	0.5	n.a.
Osphradium width / ctenidium width	n.a.	n.a.	1.5	2.3	1.6	n.a.	1.0	n.a.
Ventral proboscis retractors	n.a.	n.a.	single, branching	paired	single, branching	n.a.	single	n.a.
Radula width / aperture height (%)	n.a.	n.a.	1.0-1.30	1.49	3.0	1.48	n.a.	n.a.
Radula length / aperture height (%)	n.a.	n.a.	8.5-9.3	10.3	14	8.0	n.a.	n.a.
Lateral tooth base length / rachidian width	n.a.	n.a.	0.42-0.52	0.65	0.54	0.44	n.a.	n.a.
Number of rows of teeth	n.a.	n.a.	70-85	65	50	65	88-97	n.a.
Accessory salivary gland embedded in salivary gland	n.a.	n.a.	embedded	embedded	not	n.a.	n.a.	n.a.

graphical subspecies. However, the material at hand is insufficient to do so now, as it mainly reflects the intensity of sampling efforts in different regions of the Indo-Pacific. For this reason, we describe the different geographical forms separately, but do not formally regard them as subspecies. Because the name-bearing type is from Japan, we give a full description of specimens from Japan and then mainly comparative remarks to characterize specimens from other populations.

Exilia hilgendorfi differs from *E. krigei*, its most similar Recent congener, in usually having columellar folds and in its sculpture of broad, flat spiral cords that do not override the axial ribs. In New Caledonia, juveniles of the deep-water morph strongly resemble juveniles of *E. vagrans* sp. nov., from which they differ by their coarser spiral scul-

pture, lighter shell color, and the presence of a much larger operculum with terminal nucleus.

Distribution: Japan, the Philippines, Madagascar and Réunion, western Australia and Queensland, New Caledonia, Vanuatu, Fiji, the Tasman Sea and New Zealand, alive from 50 m [in Japan] to 1710 m. Recorded from the Pliocene of southern Japan. The material from the Pleistocene of Taiwan illustrated as *Benthovoluta hilgendorfi* by Hu and Tao [1991: 351, pl. 62 figs 23-25] represents a species of Turridae (material examined by us in the National Museum of Natural Science, Taichung).

Populations from Japan

(Fig. 14 A-E; 15)

Material examined: JAPAN. Off Choshi, Honshu, 1

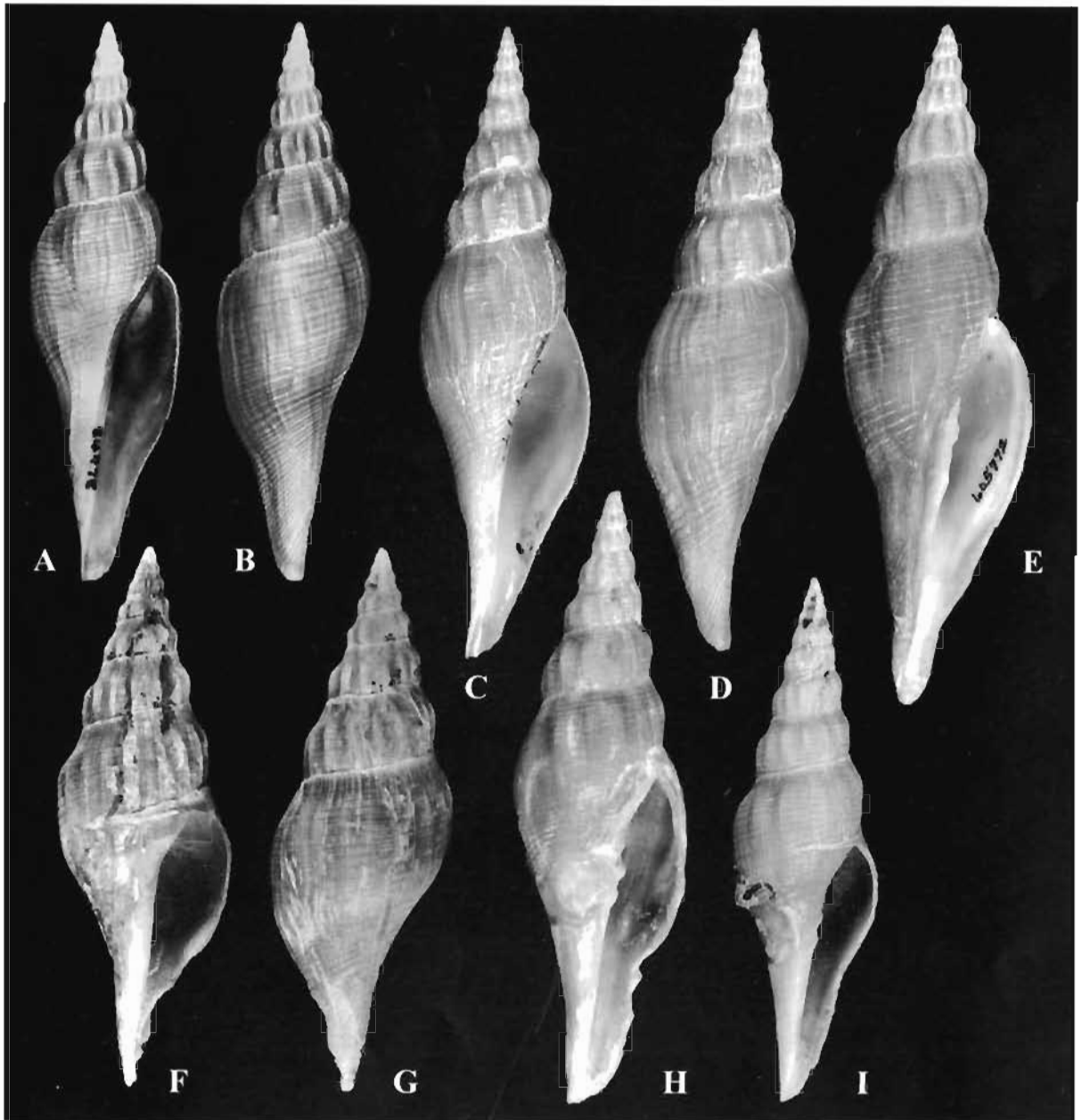


FIG 14 *Exilia hilgendorfi* (Martens, 1897). A-E. Specimens from populations from Japan A-B Kii, Honshu, 180 m (AMNH 84778), 68 mm. C-D. Off Choshu (USNM 824942), 72.5 mm. E Tosa, 280 m (USNM 605772), 83.2 mm. F-I. Specimens from populations from Vanuatu. F-G. Vanuatu (MUSORSTOM 8 sta. CP1080), 58.9 mm. H. Vanuatu, 495-498 m (MUSORSTOM 8 sta. CP1014), 63.0 mm. I. Vanuatu, 547-585 m (MUSORSTOM 8 sta. DW1011), 44.5 mm.

РИС. 14. *Exilia hilgendorfi* (Martens, 1897) A-E. Экземпляры из популяций из Японии. A-B. Кии, Хонсю, 180 м (AMNH 84778), 68 мм. C-D. У Чошю (USNM 824942), 72,5 мм. E. Тоса, 280 м (USNM 605772), 83,2 мм. F-I. Экземпляры из популяций из Вануату. F-G. Вануату (MUSORSTOM 8 ст. CP1080), 58,9 мм. H. Вануату, 495-498 м (MUSORSTOM 8 ст. CP1014), 63,0 мм. I. Вануату, 547-585 м (MUSORSTOM 8 ст. DW1011), 44,5 мм.

lv (USNM 824942, Fig 14 C-D). — Kii, Honshu, 180 m (AMNH 84778, Fig 14 A-B). — Izu-Shoto Island, east Central Honshu, 1 lv (AMNH 268419). — Off Tosa, Shikoku, 280 m, 1 dd (USNM 605772, Fig 14E), 180 m, 1 lv (AMNH 84777).

Distribution: East coast of Japan, from the Boso peninsula and Hachijo I southwards, in 50-480 m

[Higo *et al.*, 1999] (Fig. 15). Also known from the Pliocene.

Description: Shell fusiform, solid, consisting of 1.5 protoconch and up to 8 teleoconch whorls, which are regularly convex except a slightly concave subsutural sulcus; shallow adpressed suture. Protoconch paucispiral, smooth, diameter 1 17 mm, with

large nucleus. Upper teleoconch whorls with rounded shoulder. The axial sculpture consists of strong, slightly prosocline ribs, increasing in number from 12-15 on the first to 14-16 on the penultimate teleoconch whorl, where they become less defined before they disappear on the last adult whorl. The spiral sculpture, which is well and equally defined on all teleoconch whorls, consists of very low, broad, flat cords of uneven width, separated by narrow interspaces always less than half of cord width, and of a very thin, inconspicuous striation that covers the cords. The number of cords on the exposed part of spire whorls increases from 6-7 on the first to 10-11 on the penultimate whorl. The spiral cords are less well defined in the sub-sutural sulcus, and they number up to 60 on the last adult whorl, of which about 30 are on the siphonal canal, where they become much narrower and more rounded. Aperture narrow-elongate, comprising about 37-38% of total shell height. Outer lip thin. Siphonal canal narrow, long, crossing coiling axis. Inner lip with thin glossy callus. Columella with 3 variously developed plaits, the central one stronger; occasionally a fourth, very low plait is present or, conversely, all plaits are obsolete and the columella is nearly smooth.

Color of the shell: protoconch light chestnut brown; upper teleoconch whorls usually lighter than the last one, gradually darkening to chestnut brown.

Dimensions of largest adult: height 83.2 mm, last whorl height 56.6 mm, aperture height 36.2 mm, siphonal canal length 10.3 mm, diameter 22.6 mm.

Operculum [based on Kuroda, Habe, 1950] elongate-oval, with the apical nucleus turned adaxially, occupying about 50% of aperture height.

A mediocre illustration of the radula was published by Habe [1952: 132, fig. 5]. The rachidian has large lateral flaps and bears 3 cusps, the central slightly longer. Lateral teeth unicuspid, with short base.

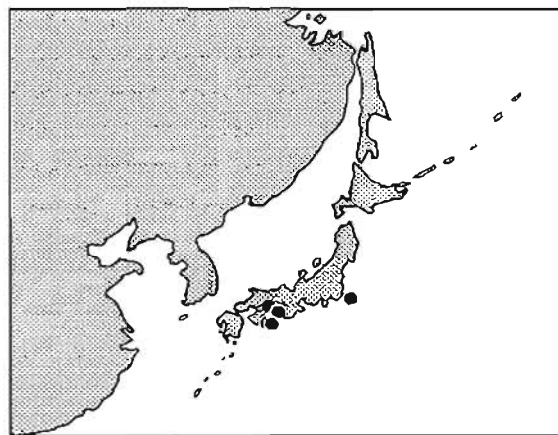
Remarks: The names *Voluta hilgendorfi* Martens, 1897, *Mitra plicifera* Yokoyama, 1920, and *Phenacopygma kiiense* Kuroda, 1931 are all based on specimens from Japanese populations.

Populations from the Philippines

(Fig. 16 A-F)

Material examined: PHILIPPINES. Sulu Sea, off Cagayan Islands, 9°38'30"N, 121°11'E, 929 m [*Albatross*, sta. 5423], 3 lv (holotype of *B. gracilior*, USNM 637252, Fig. 16 A-B; and 2 paratypes, USNM 238408, Fig. 16 C-E) — MUSORSTOM 3 R/V *Coriolis*, sta. DR94, 13°47'S, 120°03'E, 842 m, 1 dd (MNHN, Fig. 16F).

Remarks: Based on the original material of *Benthovoluta gracilior*, this population is characterized by a narrow-fusiform shell with angulated, shouldered whorls, and distinct subsutural sulcus, better pronounced on upper spire whorls. Sculpture consists of strong, slightly prosocline ribs, numbering 9-10 on first teleoconch whorl to 13-15 on penultimate, present or obsolete on last whorl, and



Exilia hilgendorfi, populations from Japan
● examined material and published records

FIG. 15. Distribution of the Japan populations of *Exilia hilgendorfi* (Martens, 1897).

РИС 15. Распространение японских популяций *Exilia hilgendorfi* (Мартенс, 1897)

narrow, rounded, low spiral cords separated by broad grooves, interspaces as broad or slightly narrower than cords. Spiral cords on the exposed part of whorls from 4-6 on the first to 14-16 on the penultimate whorl, 55-70 cords on last teleoconch whorl, about 30 of which are on the siphonal canal. Aperture elongate. Columella with 2 very weak plaits deep inside aperture. Color of the shell: light-straw in live collected specimens. Dimensions of largest adult (holotype of *B. gracilior*): height 54.6 mm, last whorl height 35.7 mm, aperture height 15.6 mm, siphonal canal length 15.1 mm, diameter 12.8 mm. This specimen is subadult, as evidenced by the very thin and simple outer lip. A worn and incomplete specimen (MUSORSTOM 3 sta. DR94, Fig. 16F) suggests that specimens reach at least 80 mm.

Protoconch missing in all specimens studied by us. Harasewych [1987] stated that the protoconch of one of the paratypes (not seen by us) consists of 0.75 whorl. All the protoconchs of *E. hilgendorfi* seen by us consist of 1.5 whorl and the discrepancy between these two values most likely reflect different ways of counting the initial coiling of the protoconch.

The name *Benthovoluta gracilior* is applicable to these populations.

Populations from Vanuatu

(Fig. 14 F-I)

Material examined (all MNHN): VANUATU. MUSORSTOM 8 R/V *Alis*, sta. DW986, 19°21'S, 169°31'E, 602-648 m, 1 dd. — Sta. DW1011, 17°50'S, 168°12'E, 547-585 m, 1 dd (Fig. 14I). — Sta. CP1014, 17°55'S, 168°19'E, 495-498 m, 3 dd (Fig. 14H). — Sta. CP1080,

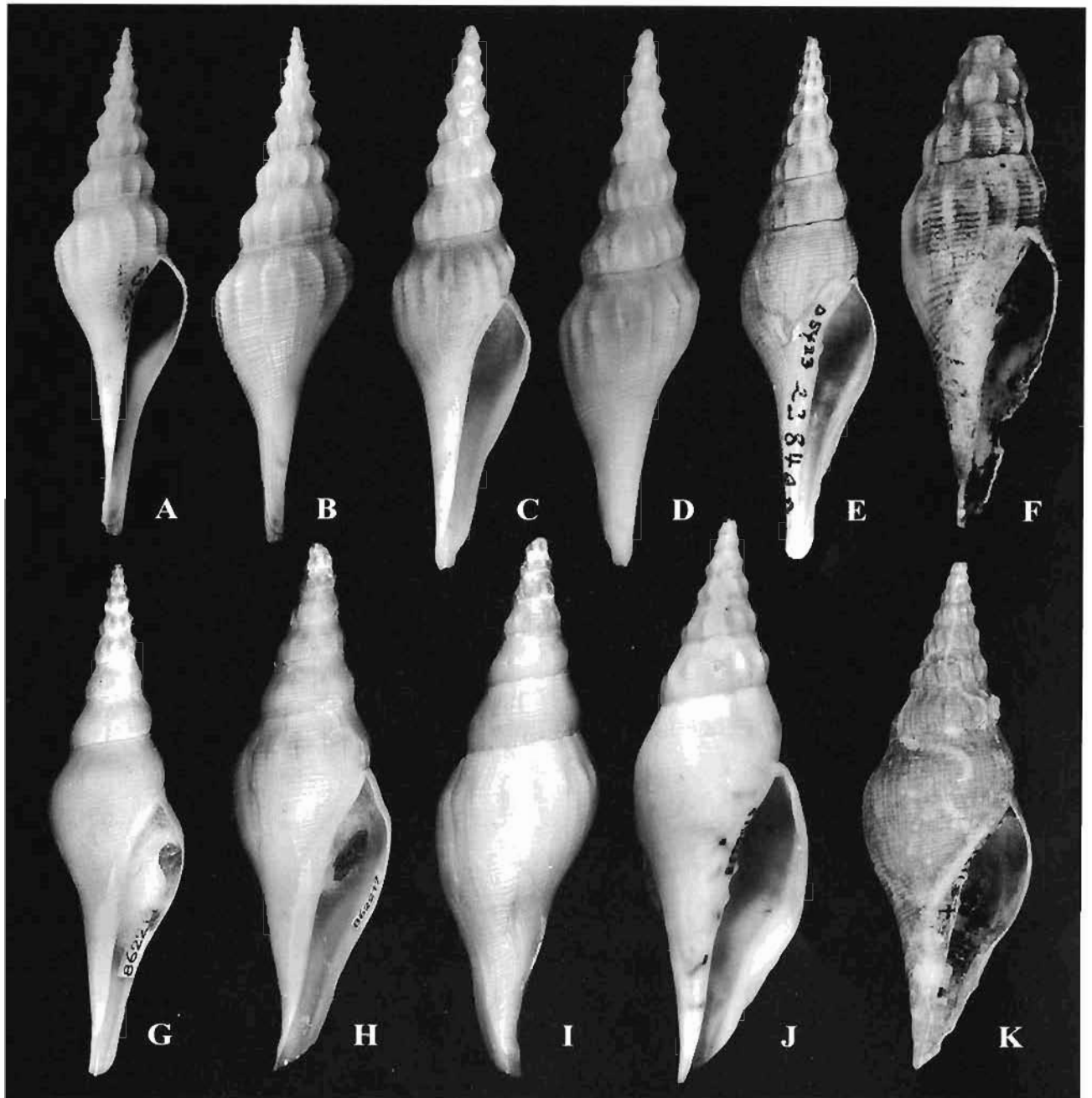


FIG 16. *Exilia hilgendorfi* (Martens, 1897). A-F. Specimens from populations from the Philippines. A-B. Philippines, 929 m, holotype of *Benthovoluta gracilior* Rehder (USNM 637252), 54.6 mm. C-D. Paratype of *B. gracilior* (USNM 238408), 54.0 mm (radula see Fig. 11 A-B). E. Paratype of *B. gracilior* (USNM 238408), 53.6 mm. F. Philippines, 842 m (MUSORSTOM 3 sta DR94), 58 mm. G-K. Specimens from populations from Western Australia and Queensland. G. Western Australia, 400 m, paratype of *Benthovoluta claydoni* Harasewych, 1987 (USNM 862217), 62.0 mm. H-I. Western Australia, 400 m, paratype of *Benthovoluta claydoni* (USNM 862217), 83.8 mm. J. Queensland, 1000 m (AMS C121187), 73.2 mm. K. Western Australia, 370-480 m (AMS 156238), 88.0 mm.

РИС. 16. *Exilia hilgendorfi* (Martens, 1897). A-F. Экземпляры из популяций с Филиппин. A-B. Филиппины, 929 м, голотип *Benthovoluta gracilior* Rehder (USNM 637252), 54,6 мм. C-D. Паратип *B. gracilior* (USNM 238408), 54,0 мм (радула на рис. 11 A-B). E. Паратип *B. gracilior* (USNM 238408), 53,6 мм. F. Филиппины, 842 м (MUSORSTOM 3 ст DR94), 58 мм. G-K. Экземпляры из популяций из западной Австралии и Квинсленда. G. Западная Австралия, 400 м, паратип *Benthovoluta claydoni* Harasewych, 1987 (USNM 862217), 62,0 мм. H-I. Западная Австралия, 400 м, паратип *Benthovoluta claydoni* (USNM 862217), 83,8 мм. J. Квинсленд, 1000 м (AMS C121187), 73,2 мм. K. Западная Австралия, 370-480 м (AMS 156238), 88,0 мм.

NE of Malekula I. 15°57'S, 167°28'E, 799-850 m, 1 dd (Fig. 14 F-G)

LOYALTY RIDGE. BATHUS 3 R/V *Alis* sta DW790, 23°49'S, 169°48'E, 685-715 m, 1 dd. — Sta. DW800, 23°35'S, 169°37'E, 655 m, 1 dd

Distribution: Vanuatu and Loyalty Ridge, shells in 500-800 m (Fig. 21).

Remarks: This population, conchologically very close to the population from Japan, is characterized by a thick, heavy, and slender shell, smaller than that of Japanese specimens, with a shallow, poorly marked subsutural sulcus. The spiral cords are closely set with interspaces narrower than half of cords width. Color of the shell light to dark chestnut-brown. Dimensions of largest adult (MUSORSTOM 8, sta. DW1014): height of 63.0 mm, last whorl height 43.0 mm, aperture height 20.0 mm, siphonal canal length 13.5 mm, diameter 17.7 mm.

Specimens from deeper water in Vanuatu (MUSORSTOM 8 sta CP956, 1175-1210 m, and sta. CP1037, 1058-1086 m) resemble the specimens from deep water off New Caledonia, Fiji and Tonga (Fig. 19 A-H) and are listed with them.

Populations from Australia

(Fig. 16 G-K; 20)

Material examined: WESTERN AUSTRALIA. SW of Imperieuse Reef, Rowley Shoals, 18°05'S, 118°10'E, 400-401 m, 2 lv (paratypes 1-2 of *Benthovoluta claydoni*, USNM 862217, Fig. 16 G-I). — R/V *Soela*, 18°53'S, 116°10'E, 450 m, 2 dd (AMS C142877). — R/V *Soela*, 14°39'S, 121°29'E, 500 m, 4 dd (AMS C143126) — 60-90 miles NW of Port Hedland, 370-480 m, 2 lv (AMS 156238, Fig. 16K).

QUEENSLAND R/V *Lady Basten*, NE of Raine Island, Great Barrier Reef, 11°32'S, 144°10'E, 1000 m, 1 dd (AMS C121187, Fig. 16 J).

Distribution: Western Australia and northern Queensland, alive in 350-596 m [Harasewych, 1987], shells to 1000 m (Fig. 21)

Remarks: This is the form named *Benthovoluta claydoni*. In this population, specimens are rather uniform in shell shape and coloration. They are characterized by a broad-fusiform shell with angulated shoulder on upper teleoconch whorls, which become more rounded with increasing size. Sub-sutural sulcus better pronounced on adapical teleoconch whorls. Sculpture of orthocone axial ribs, stronger on upper whorls, and narrow, rounded, low spiral cords separated by broad grooves, interspaces equal to cords width or broader. Number of axial ribs from 9-10 on first to 11-13 on 4th teleoconch whorl. Number of cords on exposed part of whorls from 5-6 on first to 11-15 on penultimate whorl; up to 55-60 cords on the last whorl, about 25-28 of which are on the siphonal canal. Aperture elongate, comprising (without canal) 32-39% of shell height. Columella usually with 3 plaits, rarely 2. Color of the shell: uniformly white in live collected specimens. Dimensions of largest adult examined: height 87.2 mm, last whorl height 60.0 mm, aperture height 34.0 mm, siphonal

canal height 23.0 mm, diameter 25.5 mm. Specimens of these populations reach a height of 100.9 mm [Harasewych, 1987].

A specimen from off the north of Queensland falls within the range of variation of specimens from Western Australia. This is remarkable in view of the bathymetric discontinuity between the NW Shelf and the Coral Sea.

Populations from the south-west Indian Ocean

(Fig. 17; 21)

Material examined (all in MNHN): MADAGASCAR. Collected by A. Crosnier on R.V. *Vauban*: Chalutage 1, 12°52'S, 48°10.3'E, 420-428 m, 3 dd (Fig. 17E). — Chalutage 38, 12°50'S, 48°09'E, 580-585 m, 1 dd (Fig. 17F). — Chalutage 88, 18°54'S, 43°55'E, 280-310 m, 4 lv. — Chalutage 91, 21°25.5'S, 43°14.5'E, 425-550 m, 2 lv. — Chalutage 98, 22°17.3'S, 43°02.7'E, 600-605 m, 1 lv. — Chalutage 112, 22°18'S, 43°02.2'E, 640-660 m, 2 lv (Fig. 17G). — Chalutage 115, 22°14.8'S, 43°04.3'E, 450 m, 1 lv (Fig. 17C).

Collected by R. von Cosel on trawler *Mascareignes II*: sta. 24, 22°31'S, 43°07'E, 430-460 m, 1 dd. — Sta. 35, 22°25'S, 43°05'E, 450 m, 1 lv. — Sta. 57, 22°26'S, 43°06'E, 460 m, 2 lv. — Sta. 63, 22°27'S, 43°05'E, 530 m, 1 lv. — Sta. 65, 22°26'S, 43°05'E, 520 m, 4 lv. — Sta. 70, 22°25'S, 43°05'E, 530 m, 5 lv, 1 dd. — Sta. 72, 22°11'S, 43°03'E, 540 m, 5 lv. — Sta. 74, 22°26'S, 43°03'E, 540 m, 10 lv. — Sta. 75, 22°13'S, 43°03'E, 560 m, 2 lv (Fig. 6G; 17 D). — Sta. 76, 22°22'S, 43°03'E, 530 m, 12 lv. — Sta. 78, 22°21'S, 43°03'E, 530 m, 1 lv. — Sta. 79, 22°10'S, 43°05'E, 525 m, 1 lv. — Sta. 80, 22°17'S, 43°04'E, 530 m, 1 lv. — Sta. 81, 22°23'S, 43°03'E, 525 m, 22 lv. — Sta. 82, 22°11'S, 43°03'E, 520 m, 1 lv. — Sta. 84, 22°21'S, 43°04'E, 535 m, 13 lv. — Sta. 86, 22°21'S, 43°06'E, 415 m, 1 lv. — Sta. 93, 22°25'S, 43°04'E, 590 m, 1 lv. — Sta. 122, 22°17'S, 43°03'E, 600 m, 2 lv. — Sta. 126, 22°18'S, 43°03'E, 590 m, 2 lv. — Sta. 127, 22°21'S, 43°02'E, 610 m, 1 lv.

Off Tuléar, depth unknown, holotype of *Benthovoluta prelei* Bozzetti, 2001 (Fig. 17 A-B).

RÉUNION. Baie de la Possession, shrimp traps, 600 m, 2 dd (Fig. 17 H-J). — R/V *Marion-Dufresne*, cruise MD 32: sta. DC112, 20°53'S, 55°09'E, 740-780 m, 1 dd. — Off St. Gilles, 700 m, 8 dd (MNHN ex J.C. Martin).

Distribution: Madagascar and Réunion, alive in 310-640 m, shells to 740 m (Fig. 21).

Remarks: Specimens from these populations are characterized by a slender and thin shell, light straw in color, usually with a slightly darker subsutural band. Axial ribs are well defined and present onto the penultimate and last adult whorls (i.e. 11th-12th teleoconch whorls). The spiral cords are closely set, and their interspaces are only about 1/2-1/3 of cords width. Columellar plaits from 2 to 4. The analysis of plait number in nearly 80 specimens from off SW Madagascar shows that this character is size-related (Fig. 18): specimens smaller than 50 mm never have more than 2 plaits, while specimens larger than 70 mm always have three plaits. Similar multiplication of plaits was observed on X-ray photograph of shell from Tonga (Fig. 4M). Specimens with 4 columellar plaits were also found off NW Madagascar (Fig. 17E). Protoconch (Figure

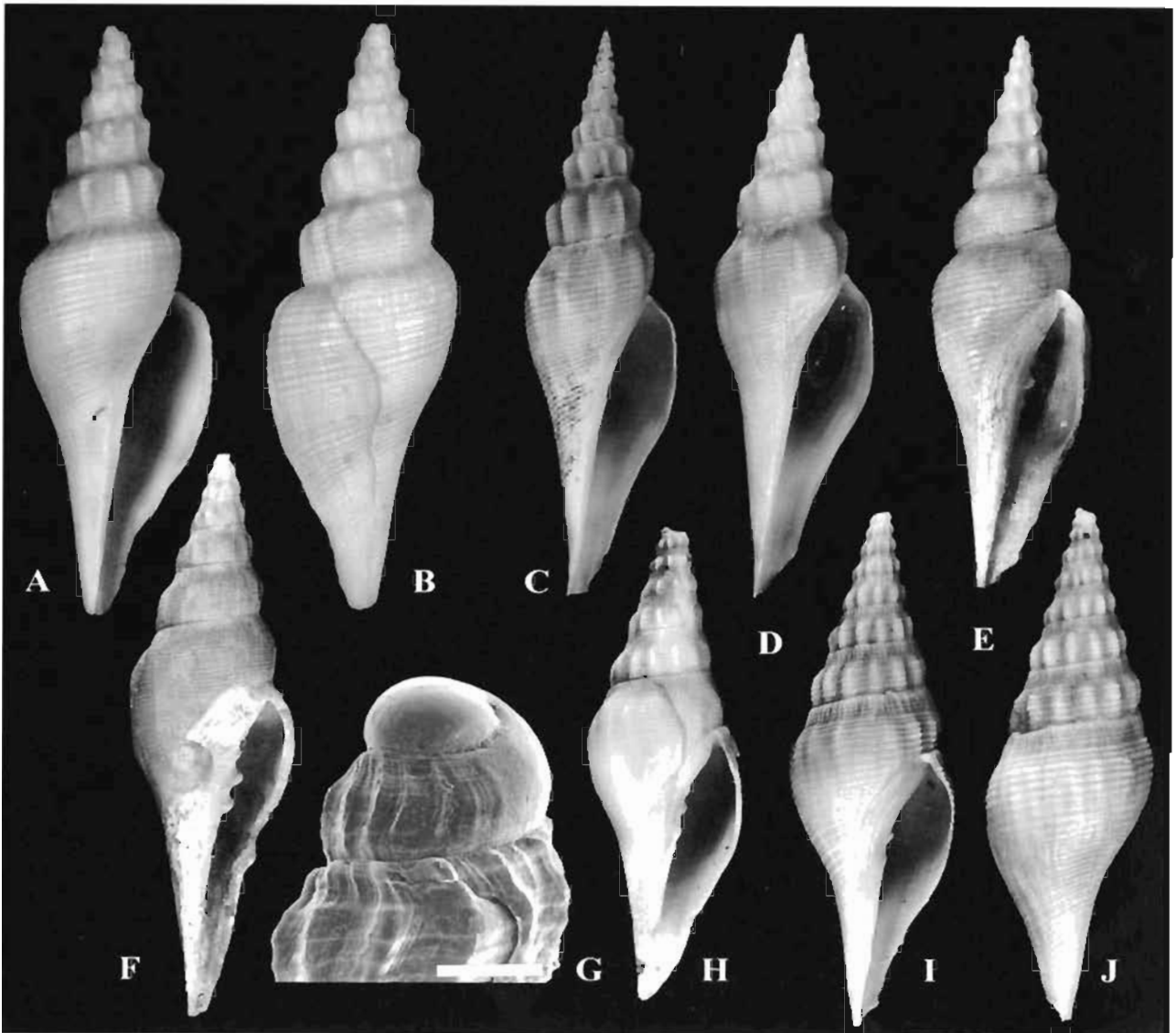


FIG. 17 *Exilia hilgendorfi* (Martens, 1897). Specimens from populations from the south-west Indian Ocean A-B. Holotype of *Benthovoluta prelei* Bozzetti, 2001, Tuléar, 91.0 mm. C. SW Madagascar, 450 m (*Vauban*, sta 115), 82.2 mm. D. SW Madagascar, 560 m (*Mascareignes* II, sta. 75), 81.3 mm. E. NW Madagascar, 420-428 m ($12^{\circ}52'S$, $48^{\circ}10'3'' E$), 83.2 mm (transitional to form *claydoni*). F. NW Madagascar, 580-585 m (*Vauban*, sta 38), 76.6 mm. G. Protoconch, SW Madagascar, 640-660 m (*Vauban*, sta. 112), scale bar 500 μm . H. Réunion, Baie de la Possession, 600 m, 52.3 mm. I-J. Réunion, Baie de la Possession, 600 m, 55.3 mm.

РИС. 17 *Exilia hilgendorfi* (Martens, 1897). Экземпляры из популяций из ю.-з. части Индийского океана А-В. Голотип *Benthovoluta prelei* Bozzetti, 2001, Тулеар, 91,0 мм. С. ю.-з. Мадагаскар, 450 м (*Vauban*, ст. 115), 82,2 мм. D. ю.-з. Мадагаскар, 560 м (*Mascareignes* II, ст. 75), 81,3 мм. E с.-з. Мадагаскар, 420-428 м ($12^{\circ}52'S$, $48^{\circ}10'3'' E$), 83,2 мм (переходный экземпляр к форме *claydoni*) F с.-з. Мадагаскар, 580-585 м (*Vauban*, ст. 38), 76,6 мм. G Протоконх, ю.-з Мадагаскар, 640-660 м (*Vauban*, ст 112), масштаб 500 мкм. H. Реюньон, Baie de la Possession, 600 м, 52,3 мм. I-J. Реюньон, Baie de la Possession, 600 м, 55,3 мм.

16G) paucispiral, consisting of ca 1 smooth convex whorls, diameter 1.0 mm, sculptured by very thin spiral striae continuous with those of the first teleoconch whorl, numbering about 25 at the protoconch/teleoconch boundary, which is marked by a weak opisthocyrt rib. Dimensions of the largest adult ($12^{\circ}52'S$, $48^{\circ}10'3''E$, 420-428 m; Fig. 17E):

height 83.2 mm, last whorl height 53.3 mm, aperture height 26.6 mm, siphonal canal length 19.2 mm, diameter 22.0 mm.

Shells from off NW Madagascar (Fig 17 E-F) are thicker, their axial folds are less pronounced and do not extend on the adult whorls. Off Réunion, at greater depths, the shells are even thicker and

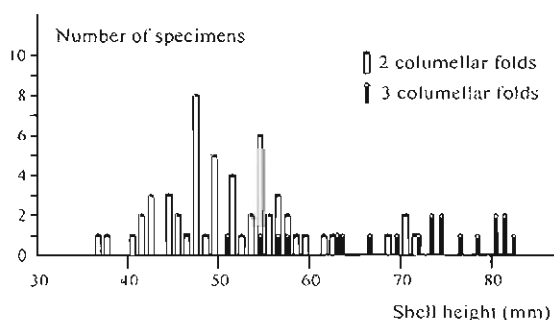


FIG. 18. Correlation between number of columellar folds and shell height in specimens of *Exilia hilgendorfi* (Martens, 1897) from populations from south-west Indian Ocean.

РИС. 18. Корреляция между количеством колумеллярных складок и высотой раковины у *Exilia hilgendorfi* (Martens, 1897) из популяций из ю.-з. части Индийского океана.

shorter (Fig. 16 H-J). The axial ribs are hardly visible in the subsutural zone, but instead there are numerous closely spaced incremental lines, producing a coarsely granulose appearance. These shells are strikingly similar to those of *Exilia* sp. A (Fig. 27 A-C) and the two could easily be considered bathymetrical variants of a single species. However, the radulae suggest that they should be treated as different species.

The shells of specimens from the SW Indian Ocean populations of *Exilia hilgendorfi*, especially the specimens from SW Madagascar, have a strong resemblance to *E. krigei* and differ from it by having (a) a deeper, more concave subsutural sulcus; (b) fewer and more widely spaced axial ribs; (c) broadly spaced spiral cords of more even width; and (d) columellar plaits always present in adult specimens.

Remarks: The name *Benthovoluta prelleii* Bozzetti, 2001 is applicable to this form.

Populations from New Caledonia, Fiji and Tonga (Fig. 19; 21)

The populations from New Caledonia, Fiji and Tonga are more heterogeneous than populations from any other geographical region, but this may reflect the fact that a more diverse range of depths and bottom types has been sampled there. Our material, however, is rather scattered and does not permit a fine analysis of these populations other than in terms of gross bathymetric variation. To facilitate a description of the variation, we have segregated two discrete morphs, which appear to be essentially correlated with bathymetry, although with much overlap.

“Shallow-water” populations from New Caledonia and Fiji (Fig. 19 I-O)

Material examined (all in MNHN): NEW CALEDONIA BIOCAL R/V *Jean-Charcot*: sta. DW33, 23°10'S, 167°10'E, 675-680 m, 6 dd (Fig. 19 L-N). — Sta. DW51, 23°05'S, 167°45'E, 680-700 m, 2 dd.

CHALCAL 2 R/V *Coriolis*: sta. CC2, 24°55'S, 168°21'E, 500 m, 1 dd. — Sta. DW73, 24°40'S, 168°38'E, 573 m, 1 dd.

BATHUS 3 R/V *Alis*: sta. DW809, 23°39'S, 167°59'E, 650-730 m, 1 dd.

BATHUS 4 R/V *Alis*: sta. CP921, 18°47'S, 163°17'E, 610-613 m, 1 dd (Fig. 19K). — Sta. CP950, 20°32'S, 164°56'E, 705-750 m, 1 dd.

LOYALTY RIDGE. MUSORSTOM 6 R/V *Alis*: sta. DW483, 21°20'S, 167°48'E, 600 m, 1 dd, 1 lv.

BATHUS 3 R/V *Alis*: sta. DW776, 24°44'S, 170°08'E, 770-830 m, 1 dd, 1 lv (protoconch Fig. 19J). — Sta. DW778, 24°43'S, 170°07'E, 750-760 m, 2 dd, 1 lv (Fig. 19I). — Sta. CP788, 23°54'S, 169°50'E, 652-750 m, 1 dd. — Sta. DW794, 23°48'S, 169°49'E, 751-755 m, 2 dd.

FIJI. BORDAU 1 R/V *Alis*: sta. DW 1410, 16°06'S, 179°28'E, 400-410 m, 1 dd. — Sta. CP 1452, 16°44'S, 179°59.7'E, 420-508 m, 2 dd.

WALLIS & FUTUNA. MUSORSTOM 7 R/V *Alis*: sta. DW590, Field Bank, 12°31'S, 174°19'W, 400 m, 1 dd.

Distribution: New Caledonia, Loyalty Ridge, Fiji and Wallis & Futuna, live 600-770 m, shells from 410 m.

Remarks: This form is characterized by a small adult size, usually with short spire and long, narrow attenuated siphonal canal. Axial ribs are usually present onto the last teleoconch whorl. The spiral cords are usually closely spaced, interspaces narrower than or rarely equal to cords width. Two columellar plaits are always present, but poorly developed. Shell color ranges from dirty-white to pinkish and light brown, always with a darker subsutural band. The protoconch (Fig. 19J) consists of 1.2 smooth convex whorls, diameter 1.0 mm. Its entire surface, including the nucleus, is covered by very thin spiral striae, numbering 30 at the protoconch/teleoconch discontinuity, which is marked by an opisthocyrt rib. Dimensions of the largest adult (BATHUS 3, sta. DW800): height 52.5 mm, last whorl height 36.4 mm, aperture height 18.0 mm, siphonal canal length 12.3 mm, diameter 15.8 mm. Specimens from these populations have an overall resemblance to shells from the Philippines and differ from them by (1) a generally lower spire, (2) a position of the shoulder in the upper third of the spire whorls.

A rather distinct form, which has been collected at two stations on the Norfolk Ridge (BIOCAL sta. DW33 and sta. DW51), differs by its very broad last whorl (Fig. 19 L-O). It superficially appears very distinct and could represent a separate species. However, from our experience of local variation, on the banks of the Norfolk Ridge, of species with non-planktotrophic development [see, e.g., Vermeij, Bouchet, 1998: fig. 6], we believe that it more likely represents just an extreme local variant of *Exilia hilgendorfi*.

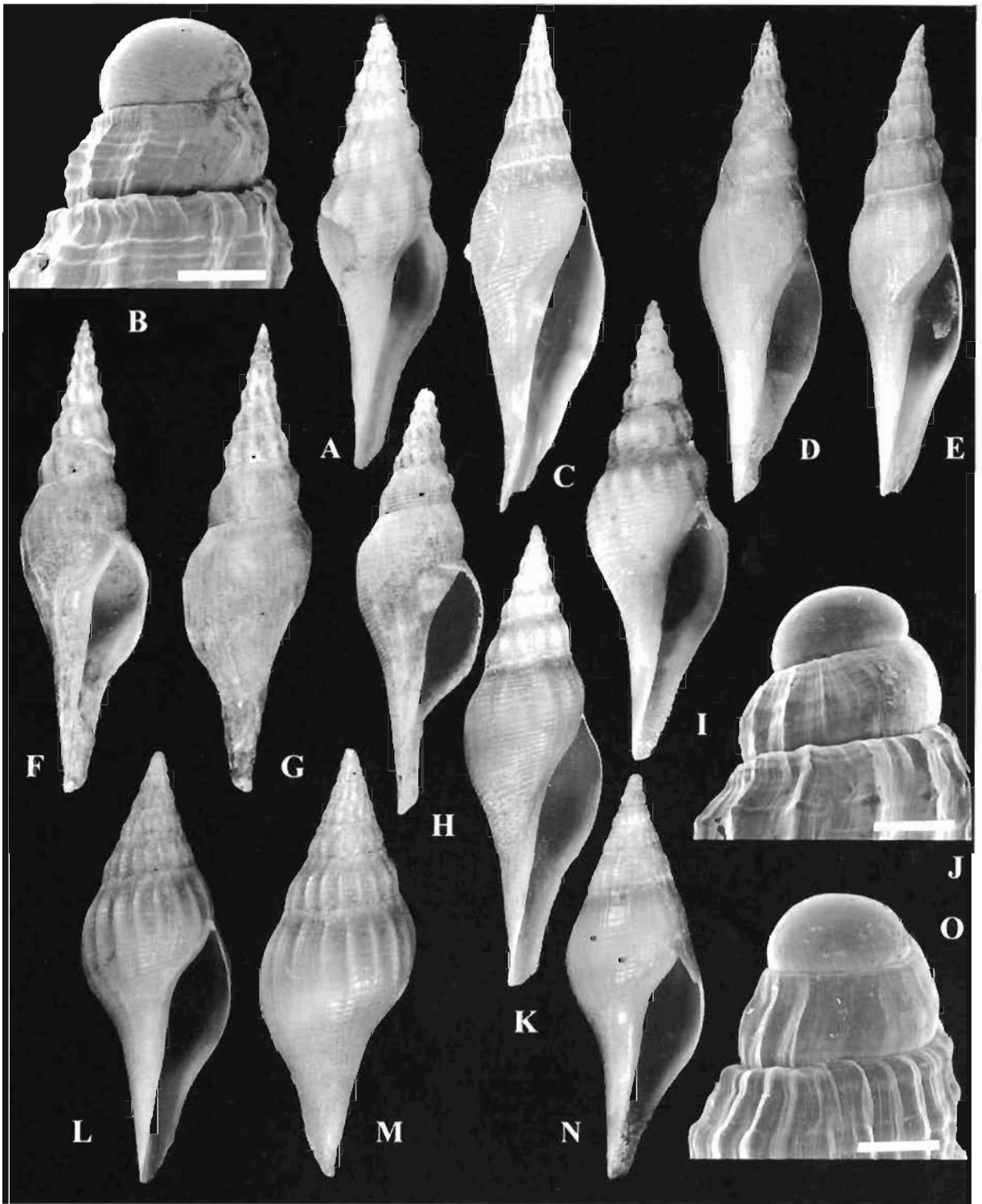


FIG 19 *Exilia hilgendorfi* (Martens, 1897), specimens from populations from New Caledonia, Loyalty Ridge and Tonga. A. New Caledonia, 1140 m (BIOCAL sta CP30), 28.6 mm. B. Protoconch of the same specimen, scale bar 500 μ m. C. Tonga, 630-710 m (BORDAU 2 Sta CP1640), 92.5 mm. D. New Caledonia, 650-800 m (BATHUS 1 sta CP709), 72.2 mm. E. New Caledonia, 908 m (BATHUS 3 sta. CP844), 84.3 mm. F-G. New Caledonia, 960-1100 m (BATHUS 1 sta. CP661), 65.2 mm. H. Loyalty Ridge, 1615-1710 m (BIOGEOCAL sta CP272), 45.2 mm. I. Loyalty Ridge, 750-760 m (BATHUS 3 sta DW778), 31.9 mm. J. Protoconch, Loyalty Ridge, 770-830 m (BATHUS 3 sta. DW776), scale bar 500 μ m. K. New Caledonia, 610-613 m (BATHUS 4 sta. CP921), 43.8 mm. L-M. New Caledonia, 675-680 m (BIOCAL sta. DW33), 30.2 mm. N. New Caledonia, 675-680 m (BIOCAL sta. DW33), 20.6 mm. O. Protoconch, New Caledonia, 680-700 m (BIOCAL sta. DW51), scale bar 500 μ m.

“Deep-water” populations from
New Caledonia, Fiji and Tonga
(Fig. 19 A-H)

Material examined (all in MNHN): CORAL SEA. CORAIL2: R/V *Coriolis*: sta. DE15, 20°51'S, 160°56'E, 580-590 m, 1 dd.

MUSORSTOM 5 R/V *Coriolis*: sta. 321, 21°20'S, 158°02'E, 1000 m, 1 dd.

NEW CALEDONIA. BIOCAL R/V *Jean-Charcot*: sta. CP30, 23°09'S, 166°41'E, 1140 m, 1 dd (Fig. 19 A-B). — Sta. CP60, 24°01'S, 167°08'E, 1480-1530 m, 1 dd. — Sta. CP69, 23°52'S, 167°58'E, 1220-1225 m, 1 dd.

BATHUS 1 R/V *Alis*: sta. CP661, 21°05'S, 165°50'E, 960-1100 m, 1 dd (Fig. 19 F-G). — Sta. CP709, 21°42'S, 166°38'E, 650-800 m, 1 lv (Fig. 19D).

BATHUS 3 R/V *Alis*: sta. CP825, 23°22'S, 168°00'E, 597-605 m, 1 lv. — Sta. CP842, 23°05'S, 166°48'E, 830 m, 1 dd. — Sta. CP844, 23°06'S, 166°46'E, 908 m, 1 dd (Fig. 19E).

HALIPRO 1 R/V *Alis*: sta. C858, 21°42'S, 166°41'E, 1000-1120 m, 1 lv.

LOYALTY RIDGE. BIOGEOCAL R/V *Coriolis*: sta. CP238, 21°28'S, 166°23'E, 1260-1300 m, 2 dd. — Sta. CP272, 21°00'S, 166°57'E, 1615-1710 m, 1 dd (Fig. 19H). — Sta. CP297, 20°39'S, 167°11'E, 1230-1240 m, 1 lv.

VANUATU. MUSORSTOM 8 R/V *Alis*: sta. CP956, 20°33'S, 169°36'E, 1175-1210 m, 1 lv. — Sta. CP1037, 18°04'S, 168°54'E, 1058-1086 m, 1 dd.

FIJI. MUSORSTOM 10 R/V *Alis*: sta. CP1316, 17°14,8'S, 178°22,0'E, 478-491 m, 1 dd. — Sta. CP1330, 17°09'S, 177°56,3'E, 567-699 m, 1 dd. — Sta. CP1331, 17°02'S, 178°01,8'E, 694-703 m, 4 dd. — Sta. CP1342, 16°46,0'S, 177°39,7'E, 650-701 m, 4 dd, 1 lv. — Sta. CP1361, 18°00,0'S, 178°53,7'E, 1058-1091 m, 1 dd.

BORDAU 1 R/V *Alis*: sta. DW 1491, 18°50'S, 178°27'E, 777-787 m, 1 dd.

TONGA. BORDAU 2 R/V *Alis*: sta. DW1558, 18°40'S, 173°52'W, 630-710 m, 1 lv, 1 dd. — Sta. CP1640, 21°09'S, 175°24'W, 564-569 m, 1 dd (Fig. 19 C).

Distribution: New Caledonia, Fiji and Tonga, alive in 600-1240 m, shells in 580-1530 m.

Remarks: There are at least two rather distinct shell types in this group of populations. One type occurs in the Coral Sea, on the Norfolk Ridge, off the east coast of New Caledonia, and off the southernmost island of Vanuatu (BATHUS 1, sta. CP709; BATHUS 3, sta. DW825, sta. CP842, sta. CP844; BIOCAL sta. CP30, sta. CP60; CORAIL 2 sta. DE15; MUSORSTOM 8, sta. CP956), at depths of 597-1140 m. It is characterized by a fusiform shell with very slightly concave subsutural sulcus on the penultimate and last teleoconch whorls and generally poorly developed spiral cords (Fig. 19 A-B, D-E). The protoconch (Fig. 19B)

is very similar to that of other forms, but it is dark-brown and the spiral striae are somewhat more widely spaced. Columellar folds are present, from 2 weak to 3 well pronounced. Coloration is light pinkish with darker brownish areas. Shell height up to 84.3 mm.

The second type was found off the Loyalty Islands, off the east coast of New Caledonia and on the Norfolk Ridge (BATHUS 1 sta. CP661; HALIPRO 1 sta. C858; BIOCAL sta. CP69; BIOGEOCAL sta. CP 272, sta. CP297), at depths of 1000-1710 m. It is characterized by a slightly smaller shell (shell height up to 72 mm), with concave subsutural sulcus on the last whorl, well developed spiral sculpture, and total absence of columellar plaits (Fig. 19 F-G). Coloration is dirty-white, sometimes with brownish spots.

In Fiji, in 491-1058 m (empty shells only), there are specimens with shells that are transitional to the forms from the Tasman Sea. They have two columellar plaits, which vary in development from strong to completely obsolete. Dimensions of largest adult (MUSORSTOM 10, sta. CP1316): height of 89.0 mm, last whorl height 57.3 mm, aperture height 25.5 mm, siphonal canal length 19.5 mm, diameter 21.2 mm.

Off Tonga, in 570-630 m (two empty shells and 1 lv), the specimens are somewhat transitional between this deep-water morph and the Vanuatu form (Fig. 19C). They have 2 or 3 columellar plaits (seen when the shell is slightly turned counterclockwise and not seen in direct apertural view) and darker shells, nearly as dark as in the specimens from Vanuatu. Dimensions of largest adult (BORDAU 2 sta. CP1640): height 92.5 mm, last whorl height 65.0 mm, aperture height 35.0 mm, siphonal canal length 26.0 mm, diameter 25.0 mm.

Juveniles of these deep-water forms may resemble *Exilia vagrans* sp. nov. in the outline and sculpture of the first teleoconch whorls. The two are easily recognized as adults, *E. vagrans* having much finer spiral sculpture and darker shell. For a discussion on sympatry and syntopy of the two species, see Remarks under *E. vagrans*.

Populations from the Tasman Sea
(Fig. 20 A-H; 21)

Material examined: QUEENSLAND. R/V *Kapala*: SE of Brisbane, 27°55'S, 154°03'E, 556-539 m, 1 lv

РИС. 19. *Exilia hilgendorfi* (Martens, 1897), экземпляры из популяций из Новой Каледонии, о-вов Лоялти и Тонга. А. Новая Каледония, 1140 м (BIOCAL ст. CP30), 28,6 мм. В. Протоконх того же экземпляра, масштаб 500 мкм. С. Тонга, 630-710 м (BORDAU 2 ст. CP1640), 92,5 мм. Д. Новая Каледония, 650-800 м (BATHUS 1 ст. CP709), 72,2 мм. Е. Новая Каледония, 908 м (BATHUS 3 ст. CP844), 84,3 мм. F-G. Новая Каледония, 960-1100 м (BATHUS 1 ст. CP661), 65,2 мм. H. О-ва Лоялти, 1615-1710 м (BIOGEOCAL ст. CP272), 45,2 мм. I. О-ва Лоялти, 750-760 м (BATHUS 3 ст. DW778), 31,9 мм. J. Протоконх, о-ва Лоялти, 770-830 м (BATHUS 3 ст. DW776), масштаб 500 мкм. K. Новая Каледония, 610-613 м (BATHUS 4 ст. CP921), 43,8 мм. L-M. Новая Каледония, 675-680 м (BIOCAL ст. DW33), 30,2 мм. N. Новая Каледония, 675-680 м (BIOCAL ст. DW33), 20,6 мм. O. Протоконх, Новая Каледония, 680-700 м (BIOCAL ст. DW51), масштаб 500 мкм.

(AMS C116345, Fig. 20A) — E of Gold Coast, 28°02'S, 153°59'E, 550 m, 2 dd (AMS C116111, Fig. 20B-C).

TASMAN BASIN. R/V *Tangaroa*: sta. P926, 40°33.1'S, 170°57.3'E, 570-572 m, 2 dd juv. (NMNZ). — Sta. P927, 40°50.1'S, 168°14.8'E, 1009-1005 m, 2 dd, 1 lv (NMNZ, Fig. 20F). — Sta. P929, 40°42.8'S, 167°56.0'E, 1029 m, 3 lv (NMNZ, Fig. 20G). — Sta. P940, 41°22.7'S, 166°44.4'E, 2092-2154 m, 1 dd juv. (NMNZ). — Sta. P942, 41°00.6'S, 169°06.0'E, 914 m, 3 dd, 3 lv (NMNZ, Fig. 20 D-E, H).

NEW ZEALAND. R/V *Tangaroa*: sta. Q699(1), off Westport, 41°08.1'S, 170°21.0'E, 695 m, 2 dd juv. (NMNZ). — Sta. Q719, off Greymouth, 42°04.3'S, 170°12.5'E, 750 m, 1 lv juv. (NMNZ). — Sta. 0.564, off Manukau Harbor, 37°06.6'S, 173°54.1'E, 925 m, 1 dd (NMNZ M74829).

Distribution: Eastern Australia, Tasman Basin, New Zealand, alive in 556-1029 m, shells to 2092 m (Fig. 21).

Remarks: These populations are characterized by a rather small, narrow-fusiform shell with concave subsutural sulcus and angulated shoulder, especially on upper teleoconch whorls. Protoconch paucispiral, consisting of 1.2 smooth convex whorls, diameter 0.8 mm. Axial ribs usually well developed, closely spaced, from 13-17 on the first to 12-17 on the last teleoconch whorl. Ribs are more numerous in specimens from deeper water from the Tasman Basin and New Zealand, which also have more lightly built and thinner shells. The spiral sculpture is well developed, with rather broad cords, slightly rounded above, separated by interspaces about of cord width. The number of cords on the exposed part of upper spire whorls increases from 4-5 on the first, to 14-17 on the penultimate, and 47-50 on the last whorl, of which about 25 are on the siphonal canal. Columellar plaits none in juveniles, 2 or 3 in adults. Shell color varies from white in young specimens to straw in adults. Dimensions of largest adult (AMS C116111): height 62.5 mm, last whorl height 39.2 mm, aperture height 20.0 mm, siphonal canal length 13.0 mm, diameter 15.2 mm.

In general appearance this form resembles the populations from the SW of the Indian Ocean.

Exilia graphiduloides

Kantor and Bouchet, sp. nov.

(Fig. 4 G-I; 20 I-N; 24)

Type material: Holotype and 1 paratype in MNHN.

Type locality: North of New Caledonia,

18°51'S, 163°21'E, 550 m [MUSORSTOM 4, sta. DW197].

Material examined: NEW CALEDONIA. MUSORSTOM 4 R/V *Vauban*: sta. DW156, 18°54'S, 163°19'E, 525 m, 1 dd. — Sta. DW178, 18°56'S, 163°19'E, 520 m, 1 lv (protoconch, Fig. 20L). — Sta. DW181, 18°57'S, 163°22'E, 350 m, 3 juv. dd. — Sta. DW197, 18°51'S, 163°21'E, 550 m, 2 dd (holotype, Fig. 20 I-J, and paratype, Fig. 20 M-N).

BATHUS 4 R/V *Alis*: sta. DW918, 18°49'S, 163°16'E, 613-647 m, 1 dd (Fig. 20K). — Sta. DW920, 18°45'S, 163°17'E, 610-620 m, 1 dd. — Sta. DW921, 18°47'S, 163°17'E, 610-613 m, 1 dd.

Distribution: Only known from north of New Caledonia, alive at 520 m, shells in 350-610 m (Fig. 24).

Description: [Holotype, description of protoconch based on the specimen from MUSORSTOM 4, sta. DW178]. Shell narrow-fusiform, solid, consisting of 1+ [nucleus of protoconch of holotype missing] protoconch and 7.75 teleoconch whorls. Protoconch paucispiral, with large nucleus, diameter 1.0 mm, smooth, with 0.8 whorls. Transition between protoconch and teleoconch marked by strong orthocline rib. Teleoconch whorls moderately convex, lacking pronounced shoulder, with shallow impressed suture. Sculpture consisting of weak, orthocline ribs crossed by distinct spiral grooves, producing a coarsely muricated appearance (Fig. 20M). Number of axial ribs increasing from 20 on first teleoconch whorl to 52 on penultimate whorl. On last adult whorl, ribs low, indistinct and irregularly spaced. Spiral sculpture well and equally defined on all teleoconch whorls, consisting of narrow, subequal, closely spaced cords, rounded above, interspaces less than of cord width. Number of cords increasing from 5 on exposed part of the first teleoconch whorl to 18 cords on penultimate whorl; about 70 cords on last teleoconch whorl, of which 40 are on the siphonal canal, where they are 1.5-2 times narrower than on whorl periphery. Aperture narrowly-elongate, comprising 34% (without canal) of total shell height. Outer lip [damaged in holotype] thin, simple. Siphonal canal narrow, long, crossing coiling axis. Inner lip with thin glossy callus. Columella with 3 plaits, the central one stronger and the adapical one weakest.

Color of the shell: protoconch light yellowish tan; first 3 teleoconch whorls whitish, gradually darkening to light chestnut brown on penultimate and last whorl, with the exception of two whitish,

РИС 20. А-Н. *Exilia hilgendorfi* (Martens, 1897), экземпляры из популяций из Тасманова моря. А ю-в. от Брисбена, 556-539 м (AMS C116345), 61,7 мм. В-С. Е. От Gold Coast, 550 м (AMS C116111), 63,0 мм. D-E. Тасманова котловина, 914 м (R/V *Tangaroa* sta. NZOI ст. P942), 31,5 мм. F. Тасманова котловина, 1009-1005 м (R/V *Tangaroa* NZOI ст. P927), 39,2 мм. G. Тасманова котловина, 1029 м (R/V *Tangaroa* NZOI ст. P929), 20,0 мм. H. Тасманова котловина, 914 м (R/V *Tangaroa* NZOI ст. P942), 15,5 мм. I-N. *Exilia graphiduloides* sp. nov. I-J. Голотип, Новая Каледония, 550 м (MUSORSTOM 4 ст. DW197), 53,8 мм. K. Новая Каледония, 613-647 м (BATHUS 4, ст. DW918), раковина, поврежденная крабом, 24 мм. L. Новая Каледония, 520 м (MUSORSTOM 4, ст. DW178), 26,8 мм, протоконх, масштаб 500 мкм. M. Увеличенный участок скульптуры паратипа, масштаб 2 мм. N. Паратип, Новая Каледония, 550 м (MUSORSTOM 4 ст. DW197), 35,2 мм.

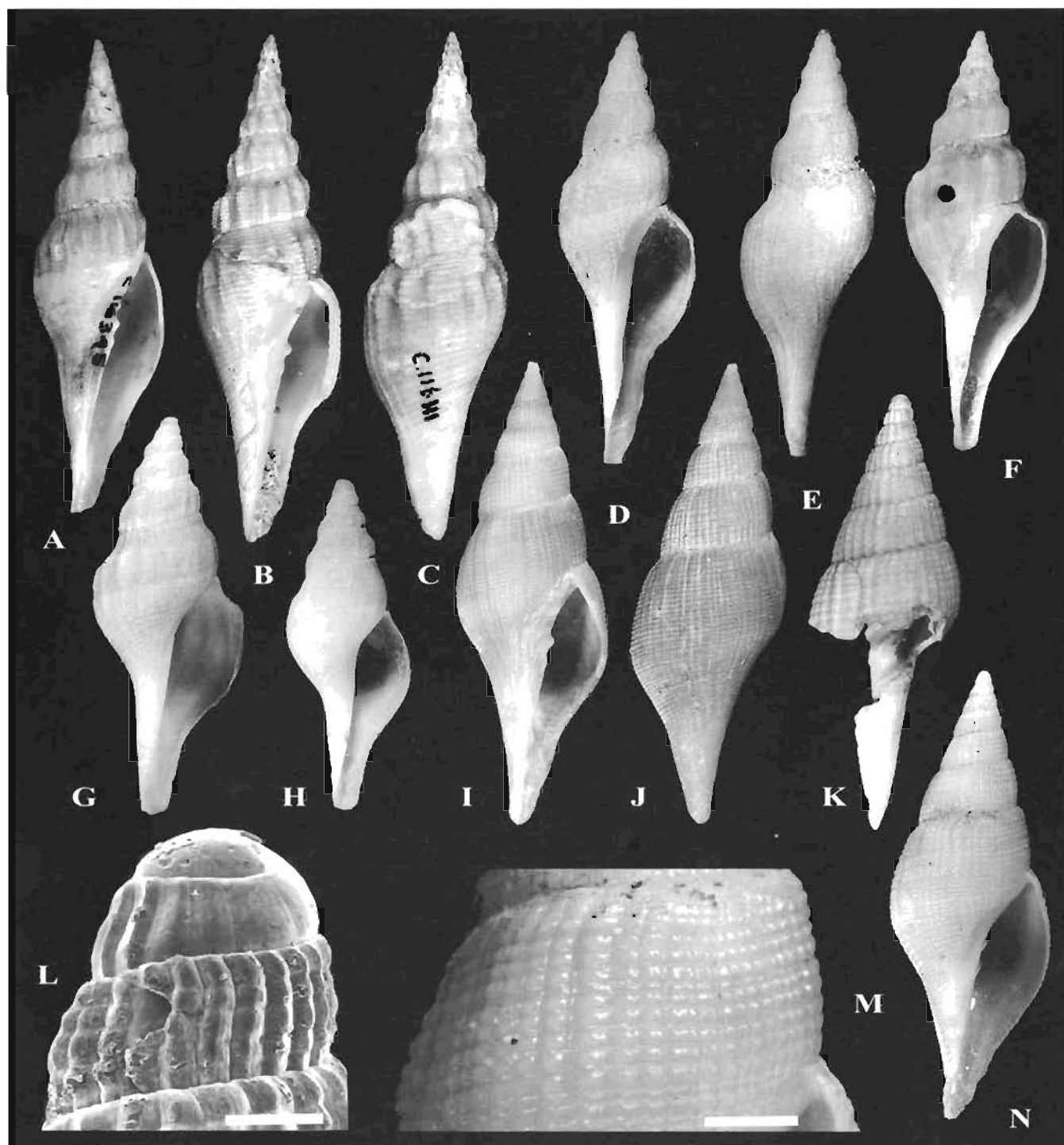


FIG 20. A-H *Exilia hilgendorfi* (Martens, 1897), specimens from populations from the Tasman Sea. A. SE of Brisbane, 556-539 m (AMS C116345), 61.7 mm. B-C E. of Gold Coast, 550 m (AMS C116111), 63.0 mm. D-E. Tasman Basin, 914 m (R/V *Tangaroo*, NZOI, sta. P942), 31.5 mm F Tasman Basin, 1009-1005 m (R/V *Tangaroo*, NZOI sta. P927), 39.2 mm. G. Tasman Basin, 1029 m (R/V *Tangaroo* NZOI sta. P929), 20.0 mm. H Tasman Basin, 914 m (R/V *Tangaroo* NZOI sta. P942), 15.5 mm I-N *Exilia graphiduloides* sp. nov. I-J. Holotype, New Caledonia, 550 m (MUSORSTOM 4 sta. DW197), 53.8 mm K. New Caledonia, 613-647 m (BATHUS 4, sta. DW918), shell peeled by crab, 24 mm. L New Caledonia, 520 m (MUSORSTOM 4, sta. DW178), 26.8 mm, protoconch, scale bar 500 μ m. M. Enlarged sculpture of paratype, scale bar 2 mm. N. Paratype, New Caledonia, 550 m (MUSORSTOM 4 sta. DW197), 35.2 mm.

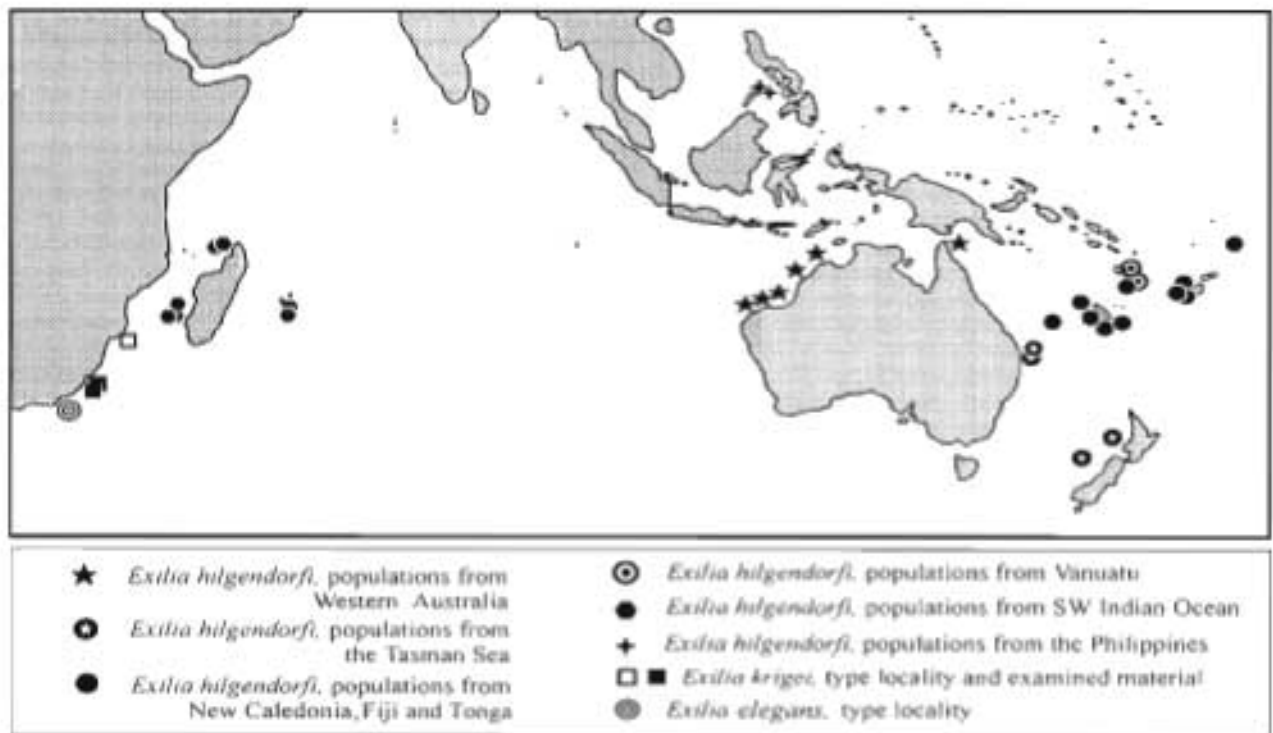


FIG. 21. Distribution of different forms of *Exilia hilgendorfi* (Martens, 1897), *Exilia krigei* (Kilburn, 1971) and *Exilia elegans* (Barnard, 1959)

Рис. 21 Распространение различных форм *Exilia hilgendorfi* (Martens, 1897), *Exilia krigei* (Kilburn, 1971) и *Exilia elegans* (Barnard, 1959)

poorly defined bands, a narrow subsutural one and a broader one on periphery.

Dimensions: height 53.8 mm, last whorl height 37.0 mm, aperture height 18.2 mm, siphonal canal length 10.5 mm, diameter 14.6 mm [the holotype is the largest specimen].

The 35.2 mm high subadult paratype is very similar to the holotype and differs in its slightly lighter color; it has retained its protoconch but it is eroded. The other specimens are very similar to the holotype in shell outline and sculpture pattern and differ in having lighter, whitish shell color.

Описание (голотип, описание протоконха основано на экземпляре со ст. DW178, MUSORSTOM 4). Раковина стройная, удлинненно-веретеновидная, прочная, образована 1+ оборотами протоконха (верхняя часть протоконха у голотипа утеряна) и 7.75 оборотами телеконха. Протоконх малооборотный, с крупным ядром, гладкий, образован 0.8 оборотами, диаметром 1,0 мм. Граница между протоконхом и телеконхом отмечена выраженным ортоклинным осевым ребром. Обороты телеконха умеренно выгнутые, без выраженного плеча, разделены неглубоким вдавленным швом. Скульптура состоит из слабых ортоклинных осевых складок, пересеченных отчетливыми спиральными желобками, образующими грубую решетчатую поверхность (Рис. 20M). Количество осевых

складок возрастает от 20 на первом обороте телеконха до 52 на предпоследнем обороте. На последнем обороте осевые ребра складки неотчетливы и нерегулярно расположены. Спиральная скульптура хорошо развита на всех оборотах телеконха и образована узкими, тесно расположенными, закругленными сверху ребрами с промежутками менее ширины ребра. Количество ребер возрастает от 5 на видимой части первого оборота телеконха до 18 на предпоследнем обороте; на последнем обороте около 70 ребер, из которых 40 расположены на сифональном канале, где они в 1,5-2 раза уже, чем на периферии оборота. Устье узкое, удлиненное, без сифонального канала составляет 34% общей высоты раковины. Наружная губа устья (повреждена у голотипа) тонкая, простая. Сифональный канал узкий, длинный, пересекает ось раковины. Внутренняя губа с тонким блестящим каллусом Колумелла с 3 складками, из которых верхняя самая низкая, а центральная самая высокая.

Окраска раковины: протоконх бледно-желтоватый, верхние три оборота телеконха беловатые, к предпоследнему и последнему оборотам постепенно становятся светло-каштановыми, за исключением двух беловатых плохо выраженных спиральных полос узкой, расположенной ниже шва и более широкой на периферии оборота.

Размеры: высота раковины 53,8 мм, высота последнего оборота 37,0 мм, высота устья 18,2 мм, длина сифонального канала 10,5 мм, диаметр раковины 14,6 мм (голотип является самым крупным экземпляром).

Remarks: *Exilia graphiduloides* sp. nov. is most similar to *E. krigei*. It differs by having (a) much weaker axial ribs, (b) more closely spaced spiral cords, (c) no shoulder concavity, and (d) better developed columellar folds. From all other Recent congeners, *Exilia graphiduloides* sp. nov. differs in the muricated appearance of the shell surface, which resembles that in the extinct species of *Graphidula* and justify synonymizing *Graphidula* with *Exilia* (see Fig. 4).

One 24 mm high specimen (BATHUS 4, sta. DW918) did not survive a predator attack, most likely by a crab (Fig. 20K). The shell bears an incision extending to nearly the whole last whorl. The form of the breakage is very similar to that reported for shallow water *Calappa* [Vermeij, 1993]. Another 26.8 mm high specimen (MUSORSTOM 4, sta. DW178) bears on the 4th and 5th teleoconch whorls traces of repaired breakages from at least two unsuccessful attacks; the form of these breakages is similar to that on the preceding specimen.

Exilia graphiduloides is known only from a small area in the north of New Caledonia where it is sympatric with *E. hilgendorfi*. The two species appear to occupy a similar bathymetric range and they have been taken together in one dredge haul (BATHUS 4, sta. DW921, 610-613 m, empty shells only).

Etymology: The name *graphiduloides* reflects the similarity of the new species with the representatives of the nominal genus *Graphidula*.

Exilia krigei (Kilburn, 1971),
new combination
(Fig. 21; 22)

Benthovoluta krigei Kilburn, 1971: 127-130, figs 2d, 3a, b.

Other references:

Benthovoluta krigei: Kensley, 1973: 180, fig. 686. — Harszewych, 1987: 169-173, figs. 7-9. — Matsukuma, Okutani, Habe, 1991: 178, pl. 59, fig. 8.

Type material: Holotype in Natal Museum 6077: T1561.

Type locality: Mozambique, 50 km eastward of Inhaca Island, depth about 520 m.

Material examined: MOZAMBIQUE. 50 km eastward of Inhaca Island, ca. 520 m, 1 lv (holotype, Fig. 22 A-B). — Inhaca Island, 475 m, 2 lv (USNM 824943, Fig. 22 F-G).

NATAL. Off Scottburgh, 1 lv (NM B1526, Fig. 22 C-D). — Off Umkoma, 2 lv (NM B1525, Fig. 22 E).

Distribution: From southern Mozambique to Natal, South Africa, alive in 475-520 m.

Description: [Based on holotype and material from Natal]. Shell narrow-fusiform, solid, consisting of 1.3 protoconch and up to 9.6 teleoconch whorls with shallow impressed suture, concave above shoulder, convex below it. Protoconch paucispiral with convex whorls, diameter 1.0 mm. Adapical teleoconch whorls usually with gently angular shoulder, although sometimes very poorly

pronounced. Sculpture consisting of strong orthoconic ribs crossed by distinct spiral grooves separating narrow cords. Number of axial ribs rather constant on teleoconch whorls, increasing only slightly from 12-17 (holotype: 12) on the first teleoconch whorl to 14-18 (holotype: 16) on the penultimate whorl. The ribs are usually well pronounced until the 8th teleoconch whorl, but sometimes they become obsolete already on the 4th whorl, and they are usually absent on the last adult whorl. Spiral sculpture well and equally defined on all teleoconch whorls, consisting of low, rather narrow, subequal cords, slightly rounded above, with narrow interspaces usually about 1/3 of cords width, rarely up to 2/3 of cords width in the transition zone to the siphonal canal. The number of cords on the exposed part of upper spire whorls increases from 4-5 (holotype: 5) on the first teleoconch whorl to 19-21 (holotype: 20) on the penultimate whorl. The last adult whorl has 55-62 cords (holotype: 58), of which about 30-38 (holotype: 30) are on the siphonal canal. Aperture narrow-elongate, comprising 29% (holotype) to 32% (average 30%) of total shell height (without the canal). Outer lip thin. Siphonal canal narrow, long, crossing coiling axis. Inner lip with thin glossy callus. Columella without plaits.

Color of the shell: protoconch whitish; teleoconch yellowish to light brownish, upper whorls lighter, last whorl usually with 3 very indistinct brown purplish spiral bands.

Dimensions of largest adult (holotype): height 71.0 mm, last whorl height 46.2 mm, aperture height 22.4 mm, siphonal canal length 14.0 mm, diameter 17.5 mm.

Remarks: The species is variable in the prominence of the axial ribs and degree of shoulder angle, which may be lacking altogether in some specimens (Fig. 22 F-G).

E. krigei is most similar to specimens of *E. hilgendorfi* from the Mozambique Channel off Madagascar, and differs from them by (a) a less concave subsutural zone; (b) more numerous and more closely set axial ribs; (c) more even and more closely set spiral cords; and (d) absence of columellar plaits in adult specimens. It is also superficially similar to *E. graphiduloides* and differs by its larger size and absence of columellar folds. There is strong similarity between *E. krigei* and *E. elegans* (see discussion under *E. elegans*).

The anatomy of *Exilia krigei* is unknown. Kilburn [1971: fig. 2d] illustrated the radula, which is short and consists of 69 rows. The oval, yellowish and transparent operculum occupies 45% of the aperture height, its nucleus turned adaxially; it is very similar to that of *E. hilgendorfi*.

Exilia elegans (Barnard, 1958),
new combination
(Fig. 21; 22 H-M)

Fusivoluta elegans Barnard, 1959: 32, fig. 8a.

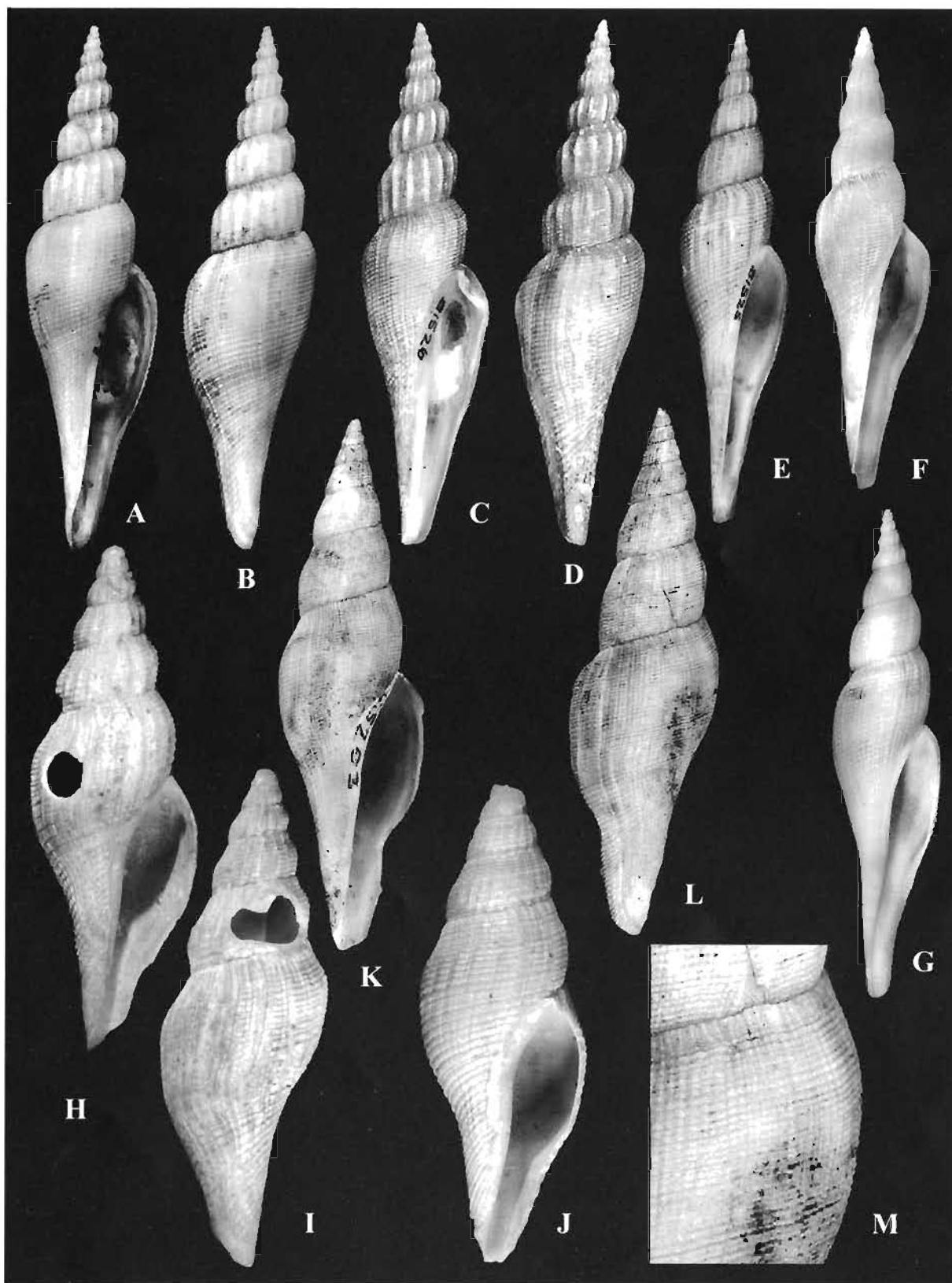


FIG. 22. A-G. *Exilia krigei* (Kilburn, 1971). A-B. Holotype, Moçambique (NM 6077: T1561), 70.8 mm. C-D. Natal (NM B1526), 69.9 mm. E. Natal (NM B1525), 68.7 mm. F. Moçambique, Inhaca Island, 475 m (USNM 824943), 65.6 mm. G. Moçambique, Inhaca Island, 475 m (USNM 824943), 55.6 mm. H-M. *Exilia elegans* (Barnard, 1959). H-I. Holotype, South African Museum. J. Off Qora River, 450-460 m (NM C 6629), 18.1 mm. K-M. Off River Kei, 390 m (NM C 5203), 43.4 mm. M. Enlarged spiral sculpture.

Type material: Holotype in South African Museum, A8803.

Type locality: Off East London, depth about 740 m.

Material examined: Holotype;

TRANSKEI. Off River Kei, 32°49.5'S, 28°33.3'E, 390 m, coarse sand, 1 dd (NM C5203, Fig. 22 H-J). — Off River Qora, 32°53.4'S, 28°49.2'E, 450 m, sandy mud, 1 dd (NM C6629).

Distribution: Eastern Cape Province and southern Transkei, South Africa, shells in 390-740 m.

Description: [Based on holotype and material from Transkei]. Shell narrow-fusiform, solid, consisting of 1.3 protoconch and up to 7.2 teleoconch whorls with shallow impressed suture, concave above shoulder, convex below it. Protoconch paucispiral with convex whorls, diameter 1.0-1.1 mm. Shoulder of adapical teleoconch whorls gently angular in holotype, very poorly pronounced in other specimens. Sculpture consisting of medium prosocline ribs crossed by distinct spiral grooves separating narrow cords. Number of axial ribs on teleoconch whorls ranges from 17 to 19 on the first whorl (holotype: 18), from 17 to 21 on second whorl (holotype: 17), from 16 (holotype) to 25 on third teleoconch whorl. to 14-18 (holotype: 16) on the penultimate whorl. The ribs are more distinct of the first 4 teleoconch whorls, and obsolete on subsequent whorls. The strong, raised incremental lines add to give the shell a coarsely muricated appearance. Spiral sculpture well and equally defined on all teleoconch whorls, consisting of low, narrow, subequal cords, slightly rounded above, with narrow interspaces usually about 1/3 of cords width, up to 2/3 of cords width in the transition zone to the siphonal canal. The number of cords on the exposed part of upper spire whorls increases from 5-6 (holotype: 5) on the first teleoconch whorl to 30 on the penultimate whorl of largest specimen available. The last adult whorl of the holotype has 45 cords, of which about 16 are on the siphonal canal. The largest specimen has about 90 cords on the last whorl, of which 25 are on the siphonal canal. Aperture narrow-elongate, comprising 35% to 37% (holotype) of total shell height (without the canal). Outer lip thin, simple. Siphonal canal narrow, long, crossing coiling axis. Inner lip with thin glossy callus. Columella without plaits. Color of the shell uniformly yellowish.

Dimensions of largest adult: height 43.4 mm, last whorl height 29.3 mm, aperture height 15.0 mm, siphonal canal length 7.5 mm, diameter 11.8 mm.

Dimensions of holotype: height 19.0 mm, last whorl height 13.2 mm, aperture height 7.0 mm, siphonal canal length 2.8 mm, diameter 6.5 mm.

Remarks: The species is slightly variable in the prominence of the axial ribs and degree of shoulder angle.

E. elegans is most similar to specimens of *E. krigiei* and differs from them in having (a) a much finer spiral sculpture (30 instead of 19-21 cords on the penultimate whorl and 90 instead of 55-62 on the last whorl) and (b) more poorly developed axial ribs, which become obsolete after the 4th teleoconch whorl. Despite these differences, it should be noted that there is a 300 km gap between the nearest known occurrences of *E. elegans* and *E. krigiei* and it will be critical to see material from that region to confirm whether they are two valid species or whether some sort of clinal variation may occur.

The species was described and known until now from the dead collected holotype. Although Barnard [1959] placed the species in *Fusivoluta* Martens, 1902 (Volutidae), he mentioned its much smaller protoconch and noted its resemblance with *Benthovoluta hilgendorfi*. Rehder [1969, p. 205], without much discussion, excluded the species from the Volutidae based on the small protoconch size and placed it in the Fasciolaridae (subfamily Fusininae). Kilburn (personal communication) drew our attention to this nominal species and its resemblance to *Benthovoluta*. Although neither radula nor anatomy is known the conchological characters of *E. elegans* are well within the limits of other Recent species of *Exilia*. The holotype is illustrated photographically for the first time. Judging from the size of the specimens in the Natal Museum, the holotype is immature.

Exilia vagrans Kantor and Bouchet,
sp. nov.

(Fig. 23; 24)

Type material: Holotype in MNHN.

Type locality: Vanuatu, off NE Malekula I., 15°54'S, 167°30'E, 1100-1191 m [MUSORSTOM 8, sta. CP1076].

Material examined (all in MNHN): PHILIPPINES. MUSORSTOM 2 R/V *Coriolis*: sta. CP55, 13°54'N, 119°58'E, 865 m, 3 lv. — Sta. CP56, 13°54'N, 119°57'E, 970 m, 3 lv (Fig. 23E).

VANUATU. MUSORSTOM 8 R/V *Alis*: sta. CP956, 20°33'S, 169°36'E, 1175-1210 m, 2 lv. — Sta. CP990, 18°52'S, 168°51'E, 980-990 m, 3 dd. — Sta. CP991, 18°51'S, 168°52'E, 910-936 m, 1 dd. — Sta. CP1008, 18°53'S, 168°53'E, 919-1000 m, 1 dd. — Sta. CP1036, 18°01'S, 168°48'E, 920-950 m, 1 dd, 2 lv (Fig. 23 C-D, F). — Sta. CP1037, 18°04'S, 168°54'E, 1058-1086 m, 1 lv. — Sta. CP1076, 15°54'S, 167°30'E, 1100-1191

РИС. 22. А-Г. *Exilia krigiei* (Kilburn, 1971). А-В. Голотип, Мозамбик (NM 6077: T1561), 70,8 мм. С-Д. Наталья (NM B1526), 69,9 мм. Е. Наталья (NM B1525), 68,7 мм. F. Мозамбик, Inhaca Island, 475 м (USNM 824943), 65,6 мм. G. Мозамбик, Inhaca Island, 475 м (USNM 824943), 55,6 мм. *Exilia elegans* (Barnard, 1959). H-I. Голотип, South African Museum. J. В районе реки Qora, 450-460 м (NM C 6629), 18,1 мм. K-M. В районе реки Kei, 390 м (NM C 5203), 43,4 мм. M. Увеличенная спиральная скульптура.

m, 1 lv (holotype, Fig. 23 A-B, G). — Sta. CP1110, 14°49'S, 167°15'E, 1360 m, 1 dd. — Sta. CP1111, 14°51'S, 167°14'E, 1210-1250 m, 1 lv (Fig. 23 H-I). — Sta. CP1125, 15°58'S, 166°38'E, 1160-1220 m, 1 dd. — Sta. CP1126, 15°58'S, 166°40'E, 1210-1260 m, 4 lv. — Sta. CP1127, 15°59'S, 166°38'E, 1052-1058 m, 1 lv. — Sta. CP1129, 16°01'S, 166°40'E, 1014-1050 m, 5 lv (Fig. 23 J-K).

WALLIS & FUTUNA, MUSORSTOM 7 R/V *Alis*: sta. CP621, 12°35'S, 178°11'W, 1280-1300 m, 4 lv. — Sta. CP622, 12°34'S, 178°11'W, 1280-1300 m, 4 lv. — Sta. CP623, 12°34'S, 178°15'W, 1280-1300 m, 5 lv.

FIJI BORDAU 1 R/V *Alis*: sta. CP 1458, 17°22'S, 179°28'W, 1216-1226 m, 1 lv, 2 dd. — MUSORSTOM 10 R/V *Alis*: sta. CP1361, 18°00'S, 178°53.7'E, 1058-1091 m, 5 lv.

LOYALTY BASIN, BIOGEOCAL R/V *Coriolis*: sta. CP260, 21°00'S, 166°58'E, 1820-1980 m, 1 dd. — Sta. CP260, 21°28'S, 166°23'E, 1260-1300 m, 1 dd.

Distribution: The Philippines and the SW Pacific (Vanuatu, Wallis and Futuna, Fiji, and the Loyalty Basin), alive in 865-1280 m, shells in 508-1820 m.

Description: [Holotype; description of protoconch based on specimen from MUSORSTOM 8 sta. CP1036, Fig. 23C]. Shell narrow-fusiform, solid, consisting of about 1 protoconch and 7.5 teleoconch whorls, with shallow impressed suture, concave above shoulder, convex below it. Protoconch (Fig. 23F) paucispiral, smooth, diameter 0.88 mm, with large bulbous nucleus, protoconch/teleoconch discontinuity marked by strong opisthocyrt ribs. Teleoconch sculpture consisting of strong orthocline ribs extending abapically of shoulder, and crossed by numerous, much narrower spiral cords. In addition, there is a strong microsculpture of incremental riblets, which are particularly thickened and raised in the subsutural sulcus, and give the shell a finely beaded appearance when they cross the spiral cords. The number of primary ribs increases from 10 on the first whorl to 13 on the penultimate whorl, where they are less defined; they are indistinct on the last adult whorl. Spiral sculpture well and equally defined on all teleoconch whorls, consisting of low, narrow, somewhat wavy cords, rounded above, more closely set on adult whorls, interspaces gradually diminishing from more than 1.5 of cords width on the adapical 4 teleoconch whorls to equal to cords width or narrower on the penultimate and last whorls. The number of cords on the exposed part of upper spire whorls increases from 5 on the first teleoconch whorl to 21 on the penultimate whorl. There are no cords in the subsutural sulcus. The last adult whorl has about 80 cords, of which about 30 are on the siphonal canal, where they are about 1.5 times wider than that on the whorl periphery. Aperture moderately broad-elongate, comprising (without the canal) 34% of total shell height. Outer lip thin. Siphonal canal rather wide, long, not crossing coiling axis. Inner lip with thin glossy callus. Columella with 2 very weak, equally developed plaits.

Color of the shell: protoconch dark chestnut

brown; 5 first teleoconch whorls whitish, gradually darkening to chestnut brown on subadult and adult whorls. An ill-defined broad whitish band on the shell base and canal appears to be caused by surface corrosion.

Dimensions: height 53.5 mm, last whorl height 38.0 mm, aperture height 20.0 mm, siphonal canal height 11.7 mm, diameter 15.3 mm.

[Описание: (голотип, описание протоконха основано на экземпляре со ст. CP1036 MUSORSTOM 8, Рис. 23С). Раковина узко-веретеновидная, прочная, состоит приблизительно из одного оборота протоконха и 7,5 оборотов телеоконха. Обороты телеоконха разделены неглубоким вдавленным швом, вогнуты около плеча и выпуклы ниже его. Протоконх (Рис. 23F) малооборотный, гладкий, с крупным вздутым ядром, диаметром 0,88 мм. Граница между протоконхом и телеоконхом отмечена сильным опистоциртным ребром. Скульптура телеоконха образована сильными ортоклинными осевыми складками, простирающимися от шва до плеча и пересеченными многочисленными на много более мелкими спиральными ребрами. Кроме того, имеется четко выраженная микроскульптура, образованная отчетливыми линиями нарастания, которые утолщены и приподняты на пришовной площадке, делая поверхность раковины морщинистой. Количество осевых складок увеличивается от 10 на первом обороте до 13 на предпоследнем. На предпоследнем обороте складки менее выражены, а на последнем обороте — неотчетливы. Спиральная скульптура равномерно хорошо выражена на всех оборотах телеоконха и образована тонкими низкими, слегка волнистыми закругленными сверху ребрышками, более тесно расположенными на последних оборотах. Расстояние между ребрышками постепенно уменьшается от 1,5 ширины ребрышка на верхних 4 оборотах до ширины ребрышка или менее на предпоследнем и последнем оборотах. Количество ребрышек на видимой части оборотов увеличивается от 5 на первом обороте телеоконха до 21 на предпоследнем обороте. На пришовной площадке ребрышки отсутствуют. На последнем обороте располагается около 80 ребрышек, из которых около 30 — на сифональном выросте, где они в 1,5 раза шире, чем на периферии оборота. Устье умеренно широкое, удлиненное, составляет (без канала) 34% общей высоты раковины. Наружная губа тонкая. Сифональный канал довольно широкий, длинный, не перескакивает оси раковины. Внутренняя губа с тонким блестящим каллусом. Колумелла с двумя очень слабыми одинаково развитыми складками.

Окраска раковины: протоконх темно-каштановый; 5 первых оборотов телеоконха беловатые, к предпоследнему и последнему оборотам постепенно темнеют до каштановых. Неотчетливая широкая беловатая спиральная полоса на основании раковины и сифональном выросте вызвана коррозией поверхности раковины.

Размеры: высота раковины 53,5 мм, высота последнего оборота 38,0 мм, высота устья 20,0 мм, длина сифонального канала 11,7 мм, диаметр раковины 15,3 мм].

Remarks: The material examined is very similar to the holotype in shell outline and sculpture pattern, and differs in shell color, from light chestnut brown to dark brown, and degree of angulation of the shoulder, which may be nearly evenly rounded. The columellar plaits are always poorly developed, but a

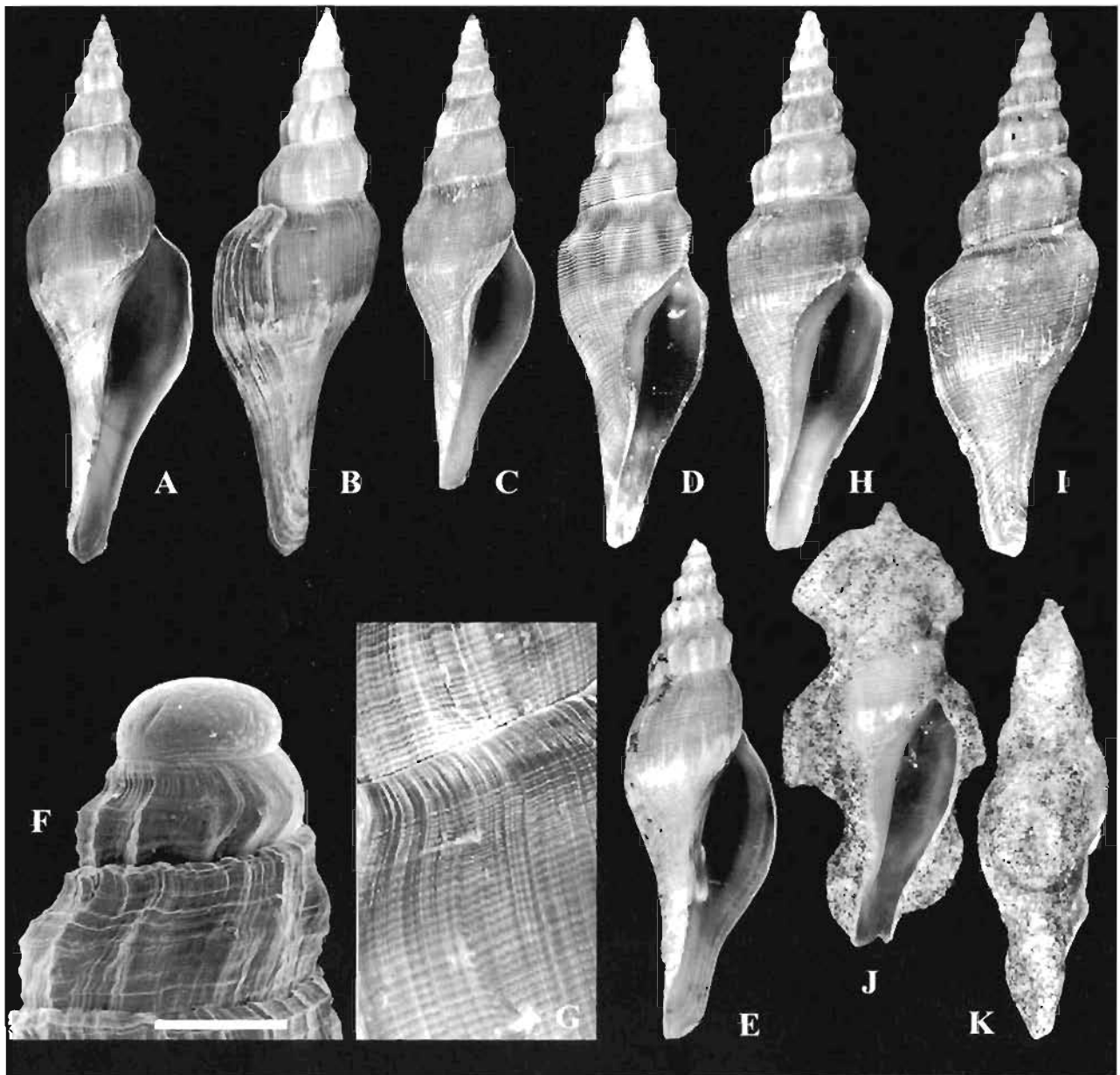


FIG. 23. *Exilia vagrans*, sp. nov. A-B Holotype, Vanuatu, 1100-1191 m (MUSORSTOM 8 sta. CP1076), 53.5 mm. C Vanuatu, 920-950 m (MUSORSTOM 8 sta. CP1036), 41.7 mm. D Vanuatu, 920-950 m (MUSORSTOM 8 sta. CP1036), 40.0 mm. E Philippines, 970 m (MUSORSTOM 2 sta. CP56), 43.0 mm. F. Protoconch of specimen in Fig 23C. scale bar 500 μ m. G Enlarged sculpture of holotype. H-I. Vanuatu, 1210-1250 m (MUSORSTOM 8 sta. CP1111), 47.6 mm. J-K Specimen with attached zoantharians, Vanuatu, 1014-1050 m (MUSORSTOM 8 sta. CP1129), 22.9 mm.

РИС. 23. *Exilia vagrans*, sp. nov. A-B Голотип, Вануату, 1100-1191 м (MUSORSTOM 8 ст. CP1076), 53,5 мм. C. Вануату, 920-950 м (MUSORSTOM 8 ст. CP1036), 41,7 мм. D. Вануату, 920-950 м (MUSORSTOM 8 ст. CP1036), 40,0 мм. E Филиппины, 970 м (MUSORSTOM 2 ст. CP56), 43,0 мм. F Протоконх экземпляра на рис. 22С. масштаб 500 мкм. G. Увеличенная скульптура голо типа. H-I. Вануату, 1210-1250 м (MUSORSTOM 8 ст. CP1111), 47,6 мм. J-K Экземпляр, покрытый зоантариями, Вануату, 1014-1050 м (MUSORSTOM 8 ст. CP1129), 22,9 мм.

third plait is occasionally present. The largest specimen (MUSORSTOM 10, sta. CP1361, from Fiji) has a shell height of 60.7 mm, last whorl height 42.0 mm, aperture height 21.2 mm, siphonal canal height 14.0 mm, diameter 18.0 mm.

Exilia vagrans is most similar to *E. blanda* and

differs from it and other congeners by its salmon to chestnut colour and dark chestnut protoconch, very thin but distinct spiral cords, and strong microsculpture of incremental riblets, particularly strong and raised in the subsutural sulcus. Juveniles of the deep-water form of *Exilia hilgendorfi* from

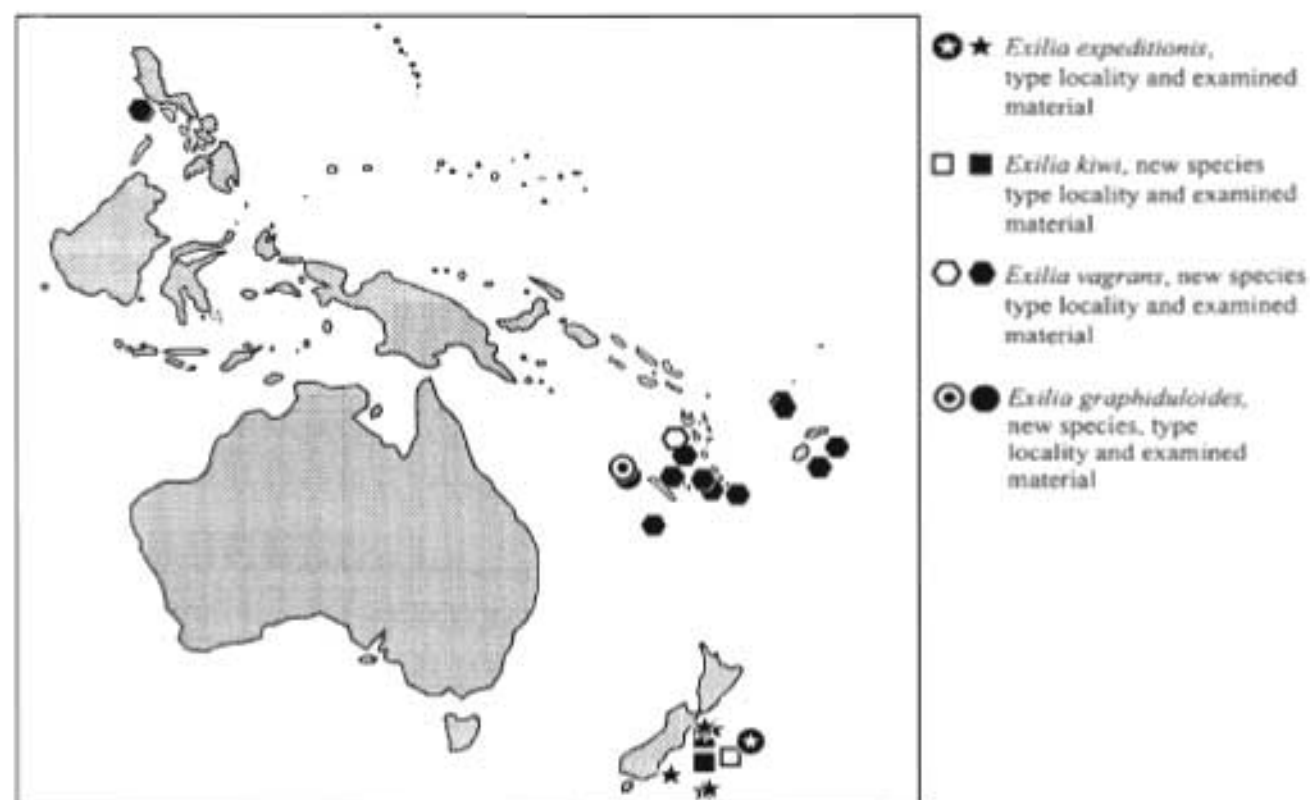


FIG. 24. Distribution of *Exilia expeditionis* (Dell, 1956), *E. kiwi*, sp. nov., *E. vagrans*, sp. nov., and *E. graphiduloides* sp. nov.

РИС. 24. Распространение *Exilia expeditionis* (Dell, 1956), *E. kiwi*, sp. nov., *E. vagrans*, sp. nov. и *E. graphiduloides* sp. nov.

New Caledonia and Fiji may strongly resemble *E. vagrans* in outline and sculpture of the upper whorls. However, the adults can be segregated unambiguously by the much finer spiral sculpture and darker shell of *E. vagrans*. *Exilia vagrans* and *E. hilgendorfi* are sympatric over the whole range of the former, which tends to occupy a deeper bathymetric zone on soft bottoms. However, the two species were collected together at several stations in Vanuatu (MUSORSTOM 8, sta. CP956), Fiji (MUSORSTOM 10, sta. CP1361) and the Loyalty Basin (BIOGEOCAL, sta. CP238). The co-occurrence of living specimens at the Vanuatu and Fiji stations cited indicates occasional actual syntopy (Fig. 25).

Exilia vagrans has been trawled on muddy bottoms, where it probably lives on top of the sediment, as evidenced by the many instances of shells of living snails that carry zoantharians (Fig. 23 J-K). The dark brown protoconch, with sharp protoconch/teleoconch discontinuity, suggests that there is a short free-swimming larval dispersal.

Etymology: From the Latin *vagrans* (adj.), wanderer, by reference to the inferred demersal dispersal of the larvae of this species.

Exilia sp. A

(Fig. 27 A-C)

Material examined: RÉUNION. R/V *Marion-Dufresne*

Cruise MD32: sta. CP140, 20°41'S, 55°38'E, 1612-1690 m, 1 lv (MNHN, Fig. 27 B-C).

MADAGASCAR. R/V *Vauban*: sta. CH127, 18°00'S, 43°00'E, 1715-1750 m, 1 lv (MNHN, Fig. 27A)

Description: [Based on the specimen from MD32, sta. CP140]. Shell fusiform, solid, consisting of 1+ [nucleus of protoconch missing] protoconch and 6.3 convex teleoconch whorls, with adpressed suture. Protoconch and early teleoconch whorls etched. Teleoconch whorls shouldered, angulated at mid-whorl height on adapical whorls, in the upper third on the last three whorls, delimiting a concave subsutural sulcus. Teleoconch sculpture consisting of strong slightly prosocline ribs crossed by low spiral cords. The number of axial ribs increases from 9 on the first intact whorl to 14 on the penultimate whorl, where they are not so strong as on the spire; they are indistinct on the last half of the last whorl. Spiral sculpture consisting of low, rather narrow cords, slightly rounded above, covering the entire shell surface, interspaces equal to or wider than cords width on the adapical 4 teleoconch whorls, slightly narrower than cords on subsequent whorls. The number of cords on the exposed part of upper spire whorls increases from 5 on the first intact teleoconch whorl to 19 on the penultimate whorl. The last whorl has 11 cords, of even width, in the subsutural sulcus, 17, broader, on shoulder and periphery, 11, low,

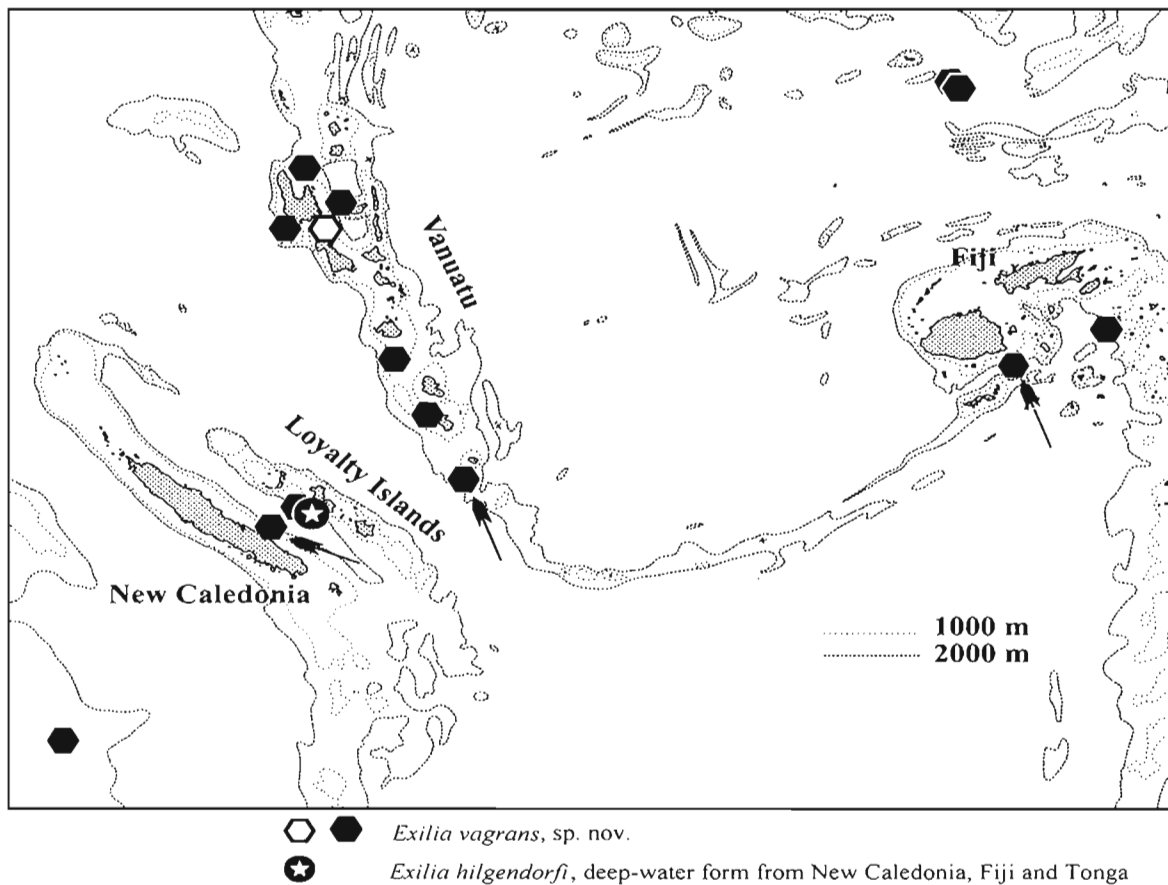


FIG. 25. Distribution of *Exilia vagrans*, sp. nov. of New Caledonia, Loyalty Islands, Vanuatu, and Fiji. The arrows indicate the stations where it was found co-occurring with *E. hilgendorfi*.

РИС. 25. Распространение *Exilia vagrans*, sp. nov. у Новой Каледонии, о-вов Лоялти, Вануату и Фиджи. Стрелки обозначают станции, где вид был найден совместно с *E. hilgendorfi*.

on the transition to the siphonal canal, and about 30, finer and poorly pronounced, on the canal. Aperture oval, comprising (without canal) 35% of total shell height. Outer lip thin. Siphonal canal rather broad, long. Inner lip with thin glossy callus. Columella with 2 very weak equally developed plaits, visible when the shell is turned clockwise 1/3 of a whorl.

Color of the shell: yellowish tan with an inconspicuous subsutural darker band, upper part of spire slightly lighter, on the last whorl there is an inconspicuous lighter band below periphery.

Dimensions: height 59.0 mm, last whorl height 41.3 mm, aperture height 20.8 mm, siphonal canal length 11.3 mm, diameter 17.7 mm.

Distribution: Réunion and Madagascar, alive in 1600-1750 m.

Remarks: The 44.0 mm high specimen from Madagascar (Fig. 27A) is essentially similar to the specimen from Réunion described above, and differs from it in having narrower and more even spiral cords separated by broader interspaces.

Exilia sp. A is superficially very similar to specimens of *E. hilgendorfi* from the south-west Indian Ocean (Fig. 17), that live sympatrically with it but occupies a more shallow bathymetrical range: there, *E. hilgendorfi* is recorded alive in 310-640 m, vs 1690-1715 m for *Exilia* sp. A. *Exilia* sp. A differs from it, and from *E. vagrans*, by having narrower and more numerous axial ribs and subtle differences of sculpture, combining the coarse spiral sculpture of *hilgendorfi* and the fine beading of the incremental riblets of *vagrans*. Despite those differences, *Exilia* sp. A could easily be interpreted as a deep-water form of *E. hilgendorfi* or a form of *E. vagrans*, if it were not for the unique characteristics of its radula: the cusps of the rachidian teeth emanate not from the anterior edge, as in *E. hilgendorfi* and *E. vagrans* and all the other species of *Exilia* that we have studied, but from the middle part of the basal part of the tooth, so that anterior face of the tooth is distinctly concave (Fig. 13 E-H). We hypothesize that these radular differences indicate that *Exilia* sp. A is specifically distinct from *E.*

hilgendorfi and *E. vagrans*, but we remain uncertain of its identity. *Exilia* sp. A also resembles *E. cortezi*, but this is a species from another biogeographical province and its radula is unknown. The material at hand is too scattered and further research on these tropical deep water populations of *Exilia* is needed.

Exilia blanda (Dall, 1908),
new combination
(Fig. 27 J-K)

Daphnella (*Surculina*) *blanda* Dall, 1908: 291, pl. 3, fig. 1.

Other references:

Daphnella (*Surculina*) *blanda*: Kabat, 1996: 7.
Surculina blanda: Powell, 1966: 137, pl. 22, fig. 7 (holotype). — Rehder, 1967: 184, fig. 7 (holotype). — Keen, 1971: 622, fig. 1358.

Type material: Holotype USNM 123119.

Type locality: Costa Rica, SW of Cabo Blanco, 05°30'N, 86°45'W, 1952 m [*Albatross*, sta. 3366].

Distribution: Known only from the type locality.

Material examined: The holotype.

Description: Shell fusiform, thin and fragile, consisting of 7+ [protoconch and upper teleoconch whorl missing] convex teleoconch whorls with shallow, slightly adpressed suture. Upper teleoconch whorls shouldered, slightly angulated at mid-height, with concave subsutural sulcus. Sculpture consisting of weak, opisthocline ribs crossed by low spiral cords separated by distinct grooves. In addition, there is a microsculpture of sigmoid incremental riblets, which are particularly thickened and raised in the subsutural sulcus of the last and penultimate whorls, and give the shell a finely beaded appearance when they cross the spiral cords. The number of primary ribs is 14 on the first preserved teleoconch whorl, 16 on the second whorl, and 12 on the third whorl, where they become obsolete.

Spiral sculpture consisting of low, rather narrow cords, slightly rounded above, covering the entire shell surface except subsutural sulcus of last whorl, interspaces equal to cords width on first 4 teleoconch whorls, slightly narrower than cords on subsequent whorls. The number of cords on the exposed part of upper spire whorls increases from 5 on the first preserved whorl to 12 on the penultimate whorl. The last adult whorl has 43 cords, of which 2 only are in the subsutural sulcus and 20 on the canal. Aperture narrow oval, comprising (without the canal) 38% of total shell height. Outer lip thin. Siphonal canal rather broad, long, crossing coiling axis. Inner lip with thin glossy callus. Columella without plaits, although traces can be seen as two very low swellings at higher magnification.

Color of the shell: yellowish tan, aperture inside more bright.

Dimensions: height 26.5 mm, last whorl height

19.0 mm, aperture height 10.3 mm, siphonal canal length 5.5 mm, diameter 8.0 mm.

Remarks: The small holotype with thin outer lip may be immature. It resembles *Exilia kiwi* sp. nov., which also lacks an operculum (as was stressed for *D. blanda* when the genus *Surculina* was established), but differs from it by its slightly lower spire and much more pronounced spiral cords (these are indistinguishable on the last whorl of *E. kiwi*). Both occur at comparable depth ranges (1952 m for *E. blanda* and 1386-1723 m for *E. kiwi*).

Exilia cortezi (Dall, 1908),
new combination
(Fig. 27 D-I)

Daphnella (*Surculina*) *cortezi* Dall, 1908: 292.

Synonym:

?*Leucosyrinx galapagana* Dall, 1919: 5, pl. 3, fig. 2. (new synonym)

Other references:

Daphnella (*Surculina*) *cortezi*: Kabat, 1996: 9.
Phenacopygma cortezi: Dall, 1925: 23, pl. 1 fig. 7 (USNM 204050). — Oldroyd, 1927: 168, pl. 13 fig. 7 ("type").
Surculina cortezi: Rehder, 1967: 184, fig. 8 ("holotype"), 10 (radula).
Surculina galapagana: Rehder, 1967: 184, fig. 9 ("holotype"). — Keen, 1971: 622, fig. 1359 (copied from Rehder).

Type material: *D. cortezi*: Dall described *Daphnella cortezi* based on two specimens, one (USNM 110613) from *Albatross* sta. 2919, which Dall considered to be "the typical species", and one (USNM 204050) from *Albatross* sta. 4353; the former specimen was illustrated by Oldroyd [1927: pl. 13 fig. 7] as "type", and the latter by Rehder [1967: 185, fig. 8] as "holotype". Although by illustrating the specimen USNM 204050, Dall [1925] implicitly suggested that he was treating that specimen as the name-bearing type, Oldroyd's restriction of the "type" to USNM 110613 was accepted as a valid lectotype designation by Kabat [1996: 9-10] and we follow this interpretation. — *Leucosyrinx galapagana*: two syntypes USNM 96494; one of them is illustrated as "holotype" by Rehder [1967] but this does not constitute a valid lectotype designation under Art. 74.6 of the Code; to stabilize the name in the sense of Rehder, this specimen (Fig. 27 F-H) is here formally designated as lectotype, the second, drilled, syntype (Fig. 27I) becomes paralectotype.

Type locality: *D. cortezi*: Off Cortez Bank, NW of San Clemente Island, California, 32°17'N, 119°17'W, 1800 m [*Albatross* sta. 2919], and off San Diego, 1170 m [*Albatross* sta. 4353]. — *L. galapagana*: off San Cristobal, Galápagos Islands, 00°36.3'S, 89°19'W, 1160 m [*Albatross* sta. 2808].

Distribution: Off California and Galápagos Islands, 1160-1800 m.

Material examined: Syntype of *D. cortezi* from

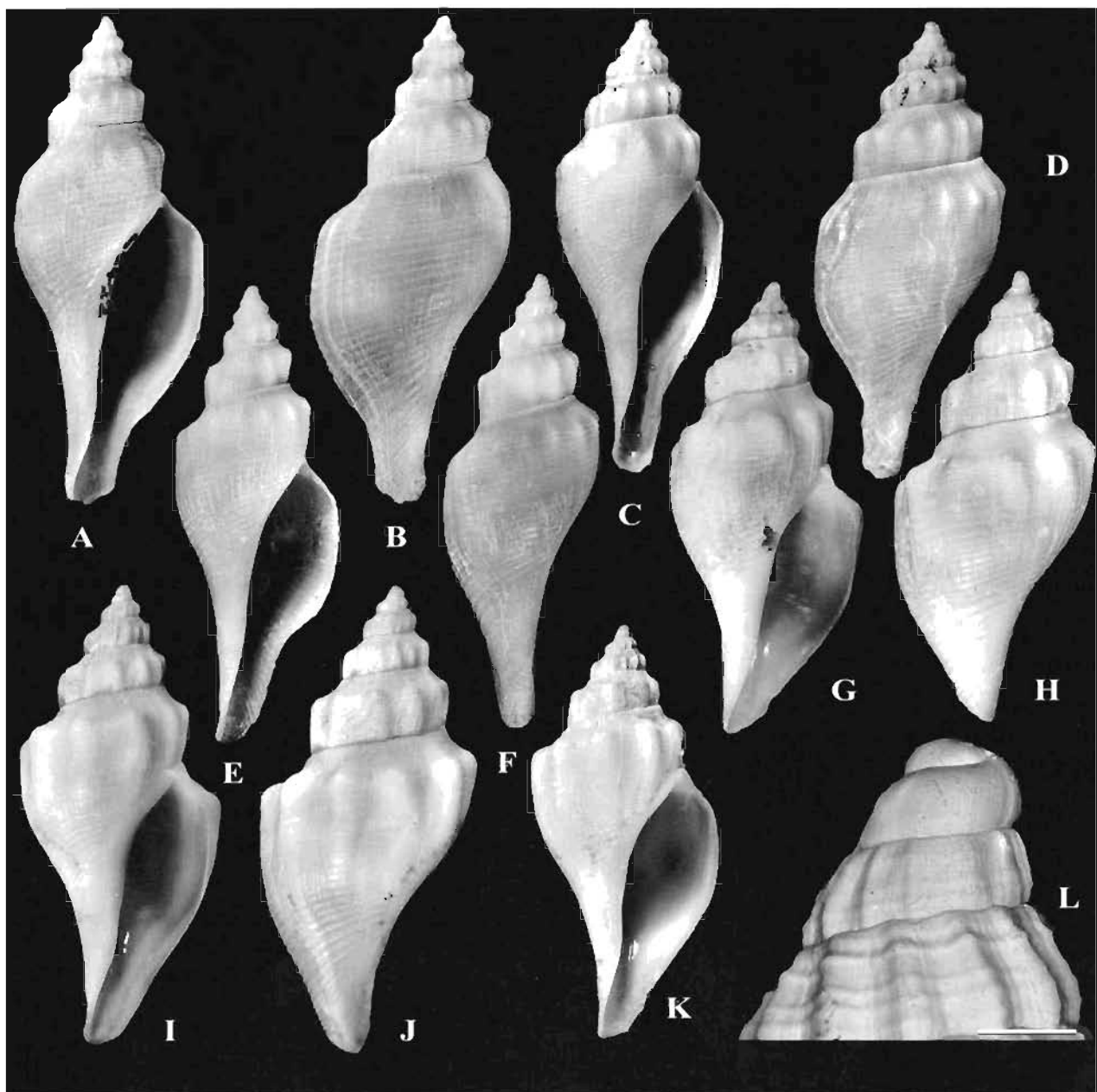


FIG 26 *Exilia expeditionis* (Dell, 1956) A-B. New Zealand, South Island, 939-1019 m (NMNZ M 60422), 42.1 mm C-D. Paratype, Chatham Rise, 476 m (NMNZ M.10584), 27.3 mm. E-F. Mernoo Bank, 999-984 m (NMNZ M.59717), 32.2 mm. G-H Bounty Platform, 726 m (NZOI sta 1698), 26.0 mm I-J. Bounty Platform, 917 m (NZOI sta 1697), 28.8 mm K. Bounty Platform, 808 m (NZOI sta 1689), 30.0 mm L. Same specimen as Fig. E-F. protoconch. Scale bar: 500 μ m.

РИС. 26. *Exilia expeditionis* (Dell, 1956). А-В Новая Зеландия, South Island, 939-1019 м (NMNZ M.60422), 42,1 мм С-Д. Паратип. Chatham Rise, 476 м (NMNZ M.10584), 27,3 мм Е-Ф. Mernoo Bank, 999-984 м (NMNZ M.59717), 32,2 мм. G-H Bounty Platform, 726 м (NZOI ст 1698), 26,0 мм. I-J Bounty Platform, 917 м (NZOI ст. 1697), 28,8 мм К. Bounty Platform, 808 м (NZOI ст 1689). 30,0 мм Л. Протоконх экземпляра на рис. 25 Е-Ф. Масштаб: 500 мкм

Albatross sta. 4353 (USNM 204050; Fig. 27 D-E) and type material of *L. galapagana* (Fig. 27 F-H).

Description [based on lectotype of *D. corzezi*]: Shell fusiform, solid, consisting of 6.5 [protoconch

and upper teleoconch whorls corroded] whorls, with shallow adpressed suture, deeply concave above shoulder, angulated in upper third of whorl height Sculpture consisting of strong orthocline

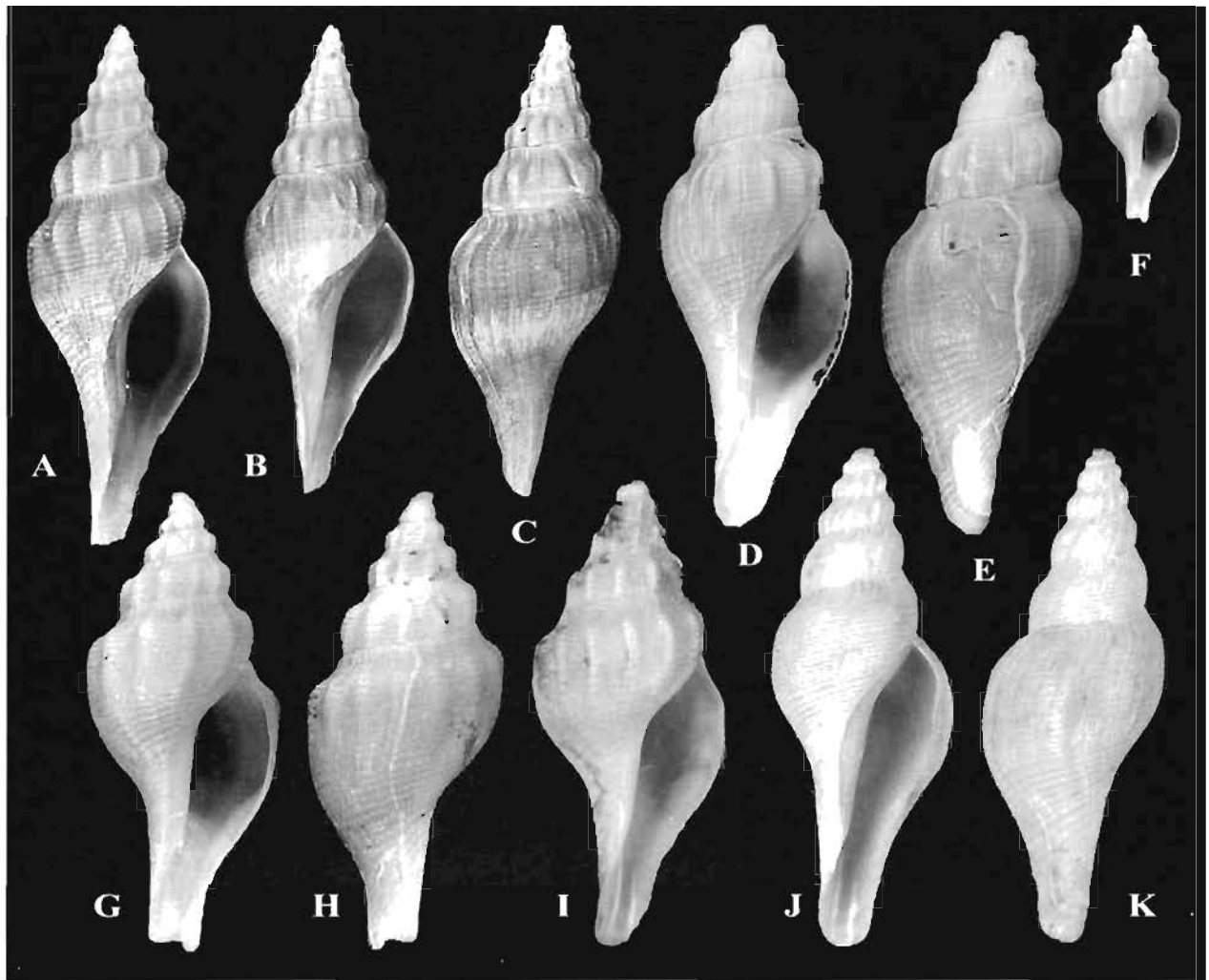


FIG 27 *Exilia* spp. A-C. *Exilia* sp. A. A Madagascar, 1715-1750 m (*Vauban*, sta CH127), 44.0 mm. B-C. Reunion, 1612-1690 m (MD 32, sta CP140), 59.0 mm D-I. *Exilia cortezi* (Dall, 1908) D-E. Off San Diego, California, 1170 m, paralectotype of *D. cortezi* (USNM 204050), 43.5 mm. F-H. Off the Galápagos Islands, 1160 m, lectotype of *Leucosyrinx galapagana* Dall, 1919 (USNM 96494), 16.9 mm. (Fig F is at the same scale as Fig. D-E) I. Paralectotype of *Leucosyrinx galapagana* (USNM 96494), 18.7 mm. J-K. *Exilia blanda* (Dall, 1908) Holotype (USNM 123119), 26.5 mm.

РИС 27. *Exilia* spp. A-C. *Exilia* sp. A. А. Мадагаскар, 1715-1750 м (*Vauban*, ст. CH127), 44,0 мм B-C. Реюньон, 1612-1690 м (MD 32, ст. CP140), 59,0 мм D-I. *Exilia cortezi* (Dall, 1908). D-E У Сан-Диего, Калифорния, 1170 м, паралектотип *D. cortezi* (USNM 204050), 43,5 мм F-H. Около Галапагосских о-вов, 1160 м, лектотип *Leucosyrinx galapagana* Dall, 1919 (USNM 96494), 16,9 мм (Рис. 26F приведен в том же масштабе, что и рис. D-E) I. Паралектотип *Leucosyrinx galapagana* (USNM 96494), 18,7 мм J-K. *Exilia blanda* (Dall, 1908). Голотип (USNM 123119), 26,5 мм.

ribs crossed by low spiral cords separated by distinct grooves. In addition, there is a microsculpture of fine spiral striae that cover both the cords and their interspaces, and of strong incremental riblets, which are particularly thickened and slightly raised in the subsutural sulcus of the penultimate and last whorls, and give the shell a finely beaded appearance when they cross the spiral cords. The number of primary

ribs increases from 12 on the first preserved teleoconch whorl to 15 on penultimate whorl; on the last whorl the ribs are a little depressed at periphery and become obsolete in the last half of the whorl. Spiral sculpture consisting of low cords of uneven width, slightly rounded above, covering the entire shell surface, interspaces equal to or slightly narrower than cords width on upper 2.5 teleoconch

whorls, less than half of cords width on subsequent whorls. The number of cords on the exposed part of upper spire whorls increases from 11 on the first preserved teleoconch whorl to 17 on the penultimate whorl. The last adult whorl has 9 even, narrow cords with equal interspaces in the subsutural sulcus, 19 broader cords on shoulder, periphery, and base, and about 16, gradually narrower but still distinct, on the canal. Aperture oval, comprising (without the canal) 38% of total shell height. Outer lip thin. Siphonal canal rather broad, long, not crossing coiling axis. Inner lip with thin glossy callus. Columella with 2 very weak, equally developed plaits, or rather mere thickenings, visible when the shell is turned clockwise 1/3 of a whorl.

Color of the shell: uniformly yellowish tan, with aperture slightly darker inside.

Dimensions: height 43.5 mm, last whorl height 33.7 mm, aperture height 16.5 mm, siphonal canal length 11.8 mm, diameter 14.3 mm.

Remarks: The lectotype of *Daphnella cortezi* is a large specimen with a shell height of 43.5 mm (upper whorls corroded), while the lectotype of *Leucosyrinx galapagana* is only 16.9 mm high. Their examination reveals an extremely similar sculpture at comparable sizes and suggests their conspecificity (see Fig. 27D and 27F, where both specimens are illustrated at the same scale). The paralectotype was cut open on the dorsal side of the shell, probably by Dall. It can be seen, that on the columella there is a very thin and low spiral ridge, which corresponds to the columellar plait.

We have discussed above the resemblance of *Exilia* sp. A, from deep water in the SW of the Indian Ocean, and *Exilia cortezi*.

Exilia expeditionis (Dell, 1956),
new combination
(Fig. 24; 26)

Chathamidia expeditionis Dell, 1956: 118-119, figs. 159-160.
Sarculina expeditionis. Cernohorsky, 1973: 130 — Powell, 1979: 217, figs. 45.8, 45.9.

Type material: Holotype (M.9260) and paratypes in NMNZ, paratypes in Canterbury Museum.

Type locality: New Zealand, Chatham Rise, M/V *Alert*, 44°04'S, 178°04'W, 476 m.

Material examined (all in NMNZ): Chatham Rise, M/V *Alert*, 44°04'S, 178°04'W, 476 m, 1 lv, paratype (NMNZ M.10584; Fig. 26 C-D). Mernoo bank, Northern Mernoo slope, R/V *Tangaroa*, 42°38.2'S, 176°10.5'E, 999-984 m, 4 lv (NMNZ M.59717; Fig. 26 E-F)

SOUTH ISLAND Papanui Canyon, R/V *Munida* 45°46'S, 171°03'E, 660 m, 1 lv, 2 dd (NMNZ M 58519) — Off Cape Campbell, R/V *Tangaroa*, 42°00'8"S, 174°41'0"E, 939-1019 m, 2 lv (NMNZ M.60422, Fig. 26 A-B)

BOUNTY PLATFORM, 48°50.6'S, 178°41.5'E, 808 m, 1 lv (NZOI sta. 1 689; R/V *Tangaroa*, Fig. 26 K) — 48°29.1'S, 178°16.6'E, 917 m, 1 lv, 1 dd (NZOI sta. 1 697; Fig. 26 I-J). — 48°20'S, 178°30'E, 726 m, 2 lv, 4 dd (NZOI sta. 1 698, Fig. 26 G-H). — 48°10'9"S, 178°15.9'E, 875 m, 1 lv (NZOI sta. 1 703)

Distribution: New Zealand, off the east coast

of South Island to the Chatham Islands, alive in 476-984 m.

Description: Shell fusiform, with comparatively short spire, thin but solid, consisting of 1.3 protoconch and up to 6 very shouldered teleoconch whorls, with shallow impressed suture, concave above shoulder, convex below it. Protoconch (Fig. 26 L, from specimen NMNZ M.59717 illustrated Fig. 26 E-F) paucispiral, diameter 1.1 mm, nucleus not bulbous, with convex, smooth whorls. Teleoconch sculpture consisting of strong orthocone axial ribs crossed by narrow spiral cords separated by distinct grooves. In addition, there is a microsculpture of fine spiral striae that cover both the cords and their interspaces. On the upper whorls the ribs extend also adapically of shoulder, but on later whorls gradually fade in the subsutural sulcus and below periphery, and on the last whorl tend to be restricted to short, broad nodes at the shoulder, with individual specimens ranging from nearly smooth to normally ribbed on the shoulder and periphery. The number of ribs is individually variable, 13-15 on the first teleoconch whorl, 11-16 on the penultimate whorl, 9-17 on the last adult whorl. Spiral sculpture well and equally defined on all teleoconch whorls, consisting of low cords, slightly rounded above, rather narrow but of uneven width, separated by interspaces ranging from about half to more than cords width. The number of cords on the exposed part of upper spire whorls increases from 6-7 on the first to 18-23 on the penultimate whorl. The last adult whorl has 54-71 cords, but these may be rather indistinct in some specimens; the cords are thin and narrow on the subsutural sulcus and shoulder, considerably broader, flattened and closely set on periphery, and narrower again on the canal which has 23-25 cords. Aperture from wide to elongate-oval, high, comprising (without the canal) 45-51% of total shell height. Outer lip thin, simple. Siphonal canal narrow, long, crossing coiling axis. Inner lip with thin and narrow glossy callus. Columella without plaits.

Color of the shell: protoconch whitish; rest of the shell from uniformly white to uniformly yellowish.

Dimensions of the largest specimen (off Cape Campbell, NMNZ M.60422) (Fig. 26 A-B): height 42.1 mm, last whorl height 32.2 mm, aperture height 19.5 mm, siphonal canal length 7.6 mm, diameter 15.4 mm.

Remarks: Specimens from the Bounty Platform (Fig. 26 G-K) are recognizable by their broader (diameter/height 0.38-0.41 instead of 0.31-0.36) and white shells. For comparison with *Exilia kiwi*, see that species.

Exilia kiwi Kantor and Bouchet,
sp. nov.
(Fig. 24; 28)

Type material: Holotype and 3 paratypes in NZOI.

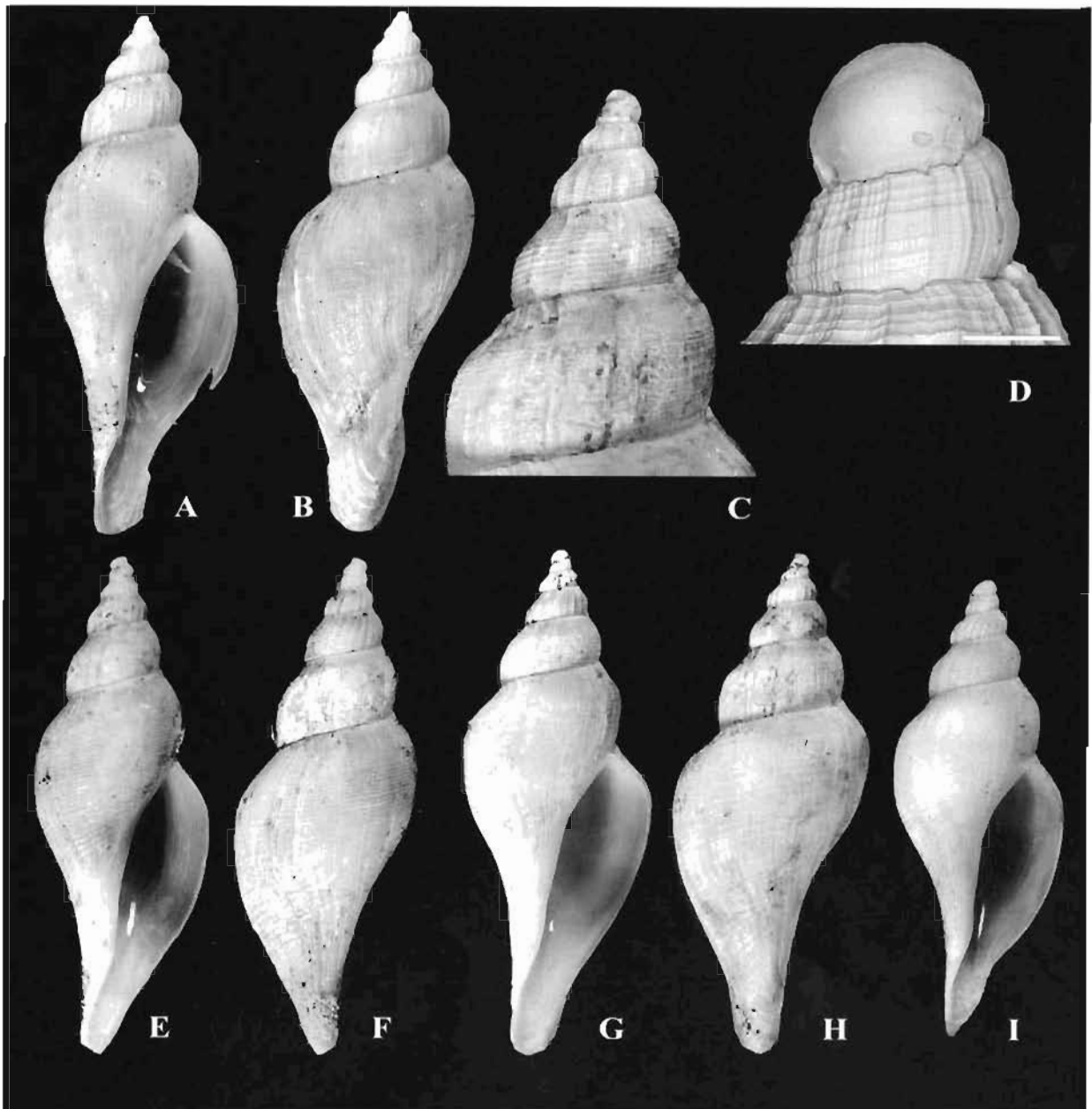


FIG. 28. *Exilia kiwi*, sp. nov. A-B. Mernoo Bank, 1723-1549 m (NMNZ M 59743), 37.3 mm. C-F. Holotype, Bounty Trough, 1386 m (NZOI sta 1068), 31.8 mm. C. Enlarged spire whorls of holotype. D. Protoconch. Scale bar 500 μ m. G-H. Paratype, 26.5 mm. I. Paratype, 21.2 mm.

РИС 28. *Exilia kiwi*, sp. nov. A-B. Мерноо Банк, 1723-1549 м (NMNZ M.59743), 37,3 мм. C-F. Голотип, Bounty Trough, 1386 м (NZOI ст. 1068), 31,8 мм. C. Увеличенные верхние обороты завитка голотипа. D. Протоконх. Масштаб 500 мкм. G-H. Паратип, 26,5 мм. I. Паратип, 21,2 мм.

Type locality: south-east of New Zealand, Bounty Trough, 45°21.2'S, 178°35.8'E, 1386 m [R/V *Tangaroa*, NZOI sta S153].

Material examined: Bounty Trough, 45°21.2'S, 178°35.8'E, 1386 m, 4 iv (R/V *Tangaroa*, NZOI sta. S153; holotype and 3 paratypes, NZOI sta. 1068; Fig. 28). — 45°51.3'S, 174°04.9'E, 1676 m, 1 iv.

MERNOO BANK, R/V *Tangaroa*, 42°41.7'S, 174°28.0'E, 1723-1549 m, 1 iv (NMNZ M.59743; Fig. 28 A-B, anatomy Fig. 9)

Distribution: New Zealand, off the east coast of South Island, alive in 1386-1676 m.

Description: [Holotype] Shell fusiform, with comparatively short spire (last whorl occupying

76% of shell height), thin, fragile, consisting of a little more than 1 protoconch and 5 teleoconch whorls, with slightly concave subsutural sulcus adapically of poorly marked shoulder, regularly convex below, and shallow adpressed suture. Protoconch (Fig. 28D) paucispiral, diameter 1.2 mm, consisting of a large bulbous nucleus and 1 smooth convex whorl. Teleoconch sculpture consisting of numerous, narrow orthocone axial ribs crossed by narrow spiral cords separated by distinct grooves. In addition, there is a microsculpture of incremental lines, that are especially thickened and raised in the subsutural sulcus and produce minute beads at their intersection with spiral cords, and of fine spiral striae that cover all the shell surface. Axial ribs 18 on first 2 teleoconch whorls, becoming indistinct on third whorl, which has only 9 ribs, and obsolete on adult whorls. Spiral sculpture well defined on all teleoconch whorls, consisting of low, narrow cords of even importance, interspaces much broader than cords width, cords slightly rounded above, but flattened in the subsutural sulcus. The number of cords on the exposed part of the first three spire whorls is 7, 10 and 14, respectively. On the penultimate whorl the closely spaced spiral striae become stronger and in the subsutural rim are equal to the primary cords in width and prominence. On the last teleoconch whorl the cords and striae are indistinguishable from each other.

Aperture elongate-oval, high, comprising (without the canal) 43% of total shell height. Outer lip thin, simple. Siphonal canal narrow, moderately long, crossing coiling axis. Inner lip with thin and narrow glossy callus. Columella without plaits.

Color of the shell: uniformly chalky white.

Dimensions of the holotype: height 31.8 mm, last whorl height 24.2 mm, aperture height 13.7 mm, siphonal canal length 6.1 mm, diameter 11.2 mm.

Dimensions of largest adult (NMNZ M.59743): height 37.2 mm, last whorl height 28.7 mm, aperture height 16.8 mm, siphonal canal length 7.5 mm, diameter 13.0 mm.

[Описание: (голотип). Раковина веретеновидная, со сравнительно коротким завитком (последний оборот составляет 76% высоты раковины), тонкая, хрупкая, образована чуть более одного оборотами протоконха и 5 оборотами телеоконха. Обороты телеоконха со слабо вогнутой пришовной площадкой над плохо выраженным плечом, равномерно закруглены и выпуклы ниже плеча и разделены мелким прижатым швом. Протоконх (Рис. 28D) малооборотный, диаметром 1,2 мм, состоит из крупного вздутого ядра и одного гладкого выпуклого оборота. Скульптура телеоконха образована многочисленными узкими ортоклинными осевыми складками, пересеченными узкими спиральными ребрами, разделенными узкими промежутками. Кроме того, имеется микроскульптура из линий нарастания, которые более приподняты и утолщены на пришовной площадке и образуют маленькие узелки в месте пересечения с осевыми складками, и очень токих спиральных ребрышек, покрывающих всю поверхность раковины. На двух верхних оборотах телеоконха расположено 18 осевых складок, которые становятся неотчетливыми на третьем обороте

(на котором всего 9 складок) и исчезают на последующих оборотах. Спиральная скульптура хорошо развита на всех оборотах телеоконха и состоит из низких узких ребер, разделенных промежутками, намного превышающими ширину ребра. Ребра слегка закруглены сверху, но уплощены на пришовной площадке. Количество ребер на видимой части первых трех оборотов телеоконха 7, 10 и 14 соответственно. На предпоследнем обороте тесно расположенные ребрышки становятся более выраженными, а на пришовной площадке становятся равными по размеру ребрам. На последнем обороте ребра и ребрышки не различимы по ширине и степени выпуклости.

Устье удлинено-овальное, высокое, составляет (без канала) 43% общей высоты раковины. Наружная губа тонкая, простая. Сифональный канал узкий, умеренно длинный, пересекает ось раковины. Внутренняя губа с тонким и узким блестящим каллусом. Колумелла без складок.

Окраска раковина равномерно мелово-белая.

Размеры: высота раковины 31,8 мм, высота последнего оборота 24,2 мм, высота устья 13,7 мм, длина сифонального канала 6,1 мм, диаметр раковины 11,2 мм].

Remarks: The paratypes are similar to the holotype in general outline and axial sculpture; their spiral cords are better defined and on the last whorl are more easily distinguished from the spiral striae. A 26.5 mm high paratype (Fig. 28 G-H) has 21 cords on the penultimate and 77 cords on the last whorl, of which 32 are on the canal; a 21.3 mm high paratype (Fig. 28I) there are 23, 64 and 23 cords respectively. In the largest specimen (Fig. 28 A-B), from Mernoo Bank, the spiral sculpture is similar to that of the holotype, the axial ribs are present on the entire third teleoconch whorl and disappear on the 4th.

Exilia kiwi is globally macrosympatric with *E. expeditionis* but occupies a deeper bathymetric zone (1386-1676 m vs 476-984 m for *expeditionis*). It differs from it in having a thinner and more fragile shell, with more regularly convex whorls with less distinct shoulder angulation and weakly concave subsutural sulcus, much narrower axial folds that do not form nodes on the shoulder, much narrower and poorly defined spiral cords. Anatomically *E. kiwi* also differs in not having eyes.

Etymology: *kiwi* is the familiar self-apellation of the inhabitants of New Zealand. It is used as a noun in apposition.

Discussion

Composition of the genus

Fifteen Recent and fossil nominal species have, at one time or another, been attributed to *Benthovoluta*. Six of these were subsequently transferred to *Cyomesus* Quinn, 1981 [Harasewych, 1987], or to *Latiromitra* Locard, 1897, when *Cyomesus* was synonymized with the latter [Bouchet, Warén, 1985, Bouchet, Kantor, 2000]; one has been tentatively placed in the genus *Metzgeria*, and one

belongs in the family Conidae [Bouchet, Kantor, 2000].

Excluded species

Fasciolaria (Mesorhytis) meekiana Dall, 1889 [placed in *Benthovoluta* by Cernohorsky, 1973: 127]: now *Latiromitra meekiana* (Dall, 1889).

Fasciolaria (Mesorhytis) costata Dall, 1890 [placed in *Benthovoluta* by Cernohorsky, 1973: 129]: now tentatively placed in *Metzgeria*.

Prodallia barthelowi Bartsch, 1942 [placed in *Benthovoluta* by Rehder, 1972: 7, and Cernohorsky 1973: 127]: now *Latiromitra barthelowi* (Bartsch, 1942).

Benthovoluta okinavensis MacNeil, 1961: now *Latiromitra okinavensis* (MacNeil, 1961)

Benthovoluta delicatula Shikama, 1971: now *Latiromitra delicatula* (Shikama, 1971).

Teramachia chaunax Bayer, 1971 [placed in *Benthovoluta* by Cernohorsky 1973: 127]: now in the synonymy of *Latiromitra cryptodon* (P. Fischer, 1882).

Benthovoluta sakashitai Habe, 1976: now in the synonymy of *Latiromitra okinavensis* (MacNeil, 1961).

Benthovoluta nakayasui Habe, 1976: probably a synonym of *Borsonia symbiotes* (Wood-Mason et Alcock, 1891) [family Conidae].

Benthovoluta pauciplicata (Yokoyama, 1928). *Mitra pauciplicata* Yokoyama, 1928 [p. 344, pl. 67 fig. 2], described based on two specimens from the Pliocene of Hyuga, Japan, was transferred without comment to *Phenacoptygma*, as *P. pauciplicatum*, by Hatai, Nisiyama [1952: 216]. Makiyama [1959: pl. 65 and unnumbered page facing it] reproduced Yokoyama's original plate and used the combination *Benthovoluta pauciplicata*. The name does not appear to have subsequently been used in the Japanese literature, but *Benthovoluta pauciplicata* has been recorded from the Pliocene [Hu, Lee 1991: 97, pl. 19 figs 8-9] and late Miocene [Hu, Tao 1998: 216, pl. 1 fig. 6] of Taiwan. We have not seen the type material; it appears conspecific with Hu & Lee's Pliocene material from Taiwan which we have examined in the National Museum of Natural Science, Taichung, and belongs to *Latiromitra*. Their Miocene material is very poorly preserved and, in our opinion, not identifiable, even at family level.

Benthovoluta avalatita Hu, Lee, 1991: 96, pl. 19 figs 10, 18. We have examined in the National Museum of Natural Science, Taichung, the holotype (NMNS 000221) of this species from the Pliocene of South Taiwan, and conclude that it is a species of Costellariidae.

Included species (Table 2)

Exilia hilgendorfi (Martens, 1897) [= *Benthovoluta gracilior* Rehder, 1967 = *B. claydoni* Harase-

wych, 1987 = *B. prelleii* Bozzetti, 2001], Indo-West Pacific, [50 m in Japan] 200-1240 m

Exilia blanda (Dall, 1908), Costa Rica, 1952 m

Exilia cortezi (Dall, 1908), California and Galapagos Islands, 1160-1800 m

Exilia expeditionis (Dell, 1956), New Zealand, 476-984 m

Exilia krigei (Kilburn, 1971), southern Mozambique to Natal, 475-520 m

Exilia elegans (Barnard, 1959), Transkei, South Africa, 390-740 m

Exilia kiwi sp. nov., New Zealand, 1386-1676 m

Exilia graphiduloides sp. nov., New Caledonia, 520 m

Exilia vagrans sp. nov., West and SW Pacific, 865-1280 m

Exilia sp. A, SW Indian Ocean, 1600-1750 m.

Comparison with other Ptychatractinae

Only the anatomy of *Benthovoluta claydoni* [= *Exilia hilgendorfi*] had earlier been studied [Harasewych, 1987]. Our observations agree with this earlier study with one important difference: we found an accessory salivary gland, whereas Harasewych did not. In fact the gland can be embedded into the right salivary gland and it was probably overlooked by Harasewych.

The anatomy of *Exilia* is similar to that of the other genera of Ptychatractinae studied so far: *Ceratoxancus* [Kantor, Bouchet, 1997a] and *Latiromitra* [Bouchet, Kantor, 2000]. The anatomy of the type genus, *Ptychatractus* Stimpson, 1865, remain unknown, except the radula [illustrated by Harasewych 1987: fig. 19], as do the anatomy of *Metzgeria* and *Exilioidea*. The characters of the digestive system that unite *Exilia*, *Ceratoxancus* and *Latiromitra* are those enumerated by Bouchet and Kantor [2000]: (1) short or very short proboscis, (2) position of the buccal mass and opening of the radular diverticulum into the buccal cavity at the proboscis base in its contracted position, (3) ventral odontophore retractor passing through the nerve ring, (4) presence of a single accessory salivary gland, (5) large gland of Leiblein, (6) mid-oesophagus with well-developed dorsal glandular folds, and (7) small stomach. It should be noted that most of these character states (except the paired proboscis retractors, a character poorly studied in the Neogastropoda) appear to be plesiomorphic for the Neogastropoda in general [see, e.g. Kantor, 1996]. The relationships of the Ptychatractinae with other families therefore remain obscure. What is known of the anatomy and radula of its included genera appears rather distinctive from other subfamilies of Turbinellidae (which are themselves still poorly known), and there may be grounds for elevating Ptychatractinae to full family rank, as suggested by Kantor and Bouchet [1997b] and done recently by Riedel [2000].

Table 2 Conchological and anatomical characters discriminating the Recent species of *Exilia*.

	<i>hilgendorfi</i>	<i>krigel</i>	<i>elegans</i>	<i>expeditionis</i>	<i>graphiduloides</i> , new species	<i>vagrans</i> , new species	<i>kiwi</i> , new species
Maximum adult size (mm)	101	71	44	42	54	61	47.5
Coloration	white to chestnut brown, sometimes with darker subsutural band	yellowish to light brownish with 3 indistinct purplish spiral bands on the last whorl	yellowish	uniformly white or yellowish	from white to light chestnut brown	chestnut brown	chalky
Number of protoconch whorls	1.5	1.5	1.3	1.0	0.8	0.9	1.3
Maximum diameter of protoconch (μm)	800-1170	1000	1000	1100	1000	880	1000
Sculpture of last adult whorl	spiral cords	axial ribs weak or absent	strong spiral cords	low and narrow spiral cords	spiral cords + nodes on the shoulder or broad ribs	muricated spiral cords	thin spiral cords
Columellar plaits in adults	0, 2, 3, 4	0	0	0	3	2	0
Operculum length / aperture height	0.30-0.50	0.45	n.a.	absent	0.5	absent, or 0.15	absent
Ctenidium length / width	6.5-9.5	n.a.	n.a.	11	10	8	9
Osphradium length / ctenidium length	0.5-0.75	n.a.	n.a.	0.9	0.75	0.75	0.75
Osphradium width / ctenidium width	1.0-2.3	n.a.	n.a.	3	3	3	2.5
Ventral proboscis retractors	single or paired	n.a.	n.a.	single branching	paired	paired	paired
Radular width / aperture height (%)	1.0-3.0	n.a.	n.a.	1.33	1.61	1.44	1.18
Radular length / aperture height (%)	8-14	n.a.	n.a.	9.7	14.0	11.0	13.6
Lateral tooth base length / rachidian width	0.44-0.65	0.56	n.a.	0.47	0.37	0.71	0.63
Number of rows of teeth	50-97	70	n.a.	80	75	60	75
Accessory salivary gland embedded in salivary gland	embedded or not	n.a.	n.a.	not	not	not	not

Anatomically, *Exilia* is readily distinguished from *Ceratoxancus* and *Latiromitra* in having not fused and relatively small salivary glands, a much larger and bulky gland of Leiblein and in the shape of the stomach with a narrow and relatively very long caecum, or posterior mixing area. The penis tip has a large or medium-sized seminal papilla surrounded by a nearly circular fold, and the seminal groove runs along the inner lateral edge of the penis to its distal end, then passes along the ventral surface of the fold to the tip of papilla. This morphology is also very characteristic and uniform in all the species examined, and can be taken as an autapomorphy of *Exilia*.

The radula of *Exilia*, characterized by a broad and narrow central tooth with lateral flaps and laterals with narrow base, is also rather distinctive. Within *Exilia*, the radulae differ between species in terms of size (radular width from 1.0 to 3.0% of aperture height, radular length from 8.0 to 13.6% of aperture height; number of radular rows from 50 to 97), and also in terms of relative size of the laterals (length of lateral tooth base/rachidian base from 37 to 71%) (Table 2). However, the radula of *Exilia* sp. A deviates from the rest of the species in having the cusps emanating from the middle part of the base, rather than from its anterior edge.

Another anatomical character that shows diffe-

rences at species level is the relative width of the osphradium, which can extend from 1× to 3× ctenidium width. The generally very large osphradium of the Ptychactractinae suggests a well-developed distant chemoreception. However, we know close to nothing about the feeding and diet of *Exilia*. The only published indication is by Harasewych [1987], who found fragments of amphipod carapace in the stomach of a specimen of *Benthovoluta claydoni* [= *Exilia hilgendorfi*].

Finally, the number of proboscis retractors varies between, but also within, species of *Exilia*, on the contrary to the situation in *Ceratoxancus* and *Latiromitra*, where the retractors are always paired. In species of *Exilia*, it is paired in *E. graphiduloides*, *E. vagrans*, *E. kiwi*, and at least one population of *E. hilgendorfi* (from deep water off New Caledonia), but unpaired in *E. expeditionis* and other populations of *E. hilgendorfi* (from Madagascar and from

more shallow water off New Caledonia). The taxonomic and phylogenetic significance of this variation is unclear.

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Ревизия современных видов *Exilia*, ранее известной как *Benthovoluta* (Gastropoda: Turbinellidae)

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РЕЗЮМЕ. Изменчивость конхологических признаков (общая форма раковины, скульптура, наличие и степень развитости колумеллярных складок, морфология протоконха) у ископаемых и современных видов, относимых к родам *Exilia* Conrad, 1860, *Mitraefusus* Bellardi, 1873, *Mesorhytis* Meek, 1876, *Surculina* Dall, 1908, *Phenacoptygma* Dall, 1918, *Palaeorhaphis* Stewart, 1927, *Zexilia* Finlay, 1926, *Graphidula* Stephenson, 1941, *Benthovoluta* Kuroda et Habe, 1950 и *Chathamidia* Dell, 1956, а также особенности анатомии современных видов не позволяют выделить более одного рода. Соответственно, все указанные роды синонимизированы с *Exilia*, встречающим-

ся с верхнего мела до настоящего времени. Анатомически виды *Exilia* сходны с видами других родов Ptychtraactinae, но отличаются наличием длинного узкого цекума (задней смешивающей области) желудка, penisом с папиллой, окруженной складкой, и строением центральных зубов радулы, имеющих широкие боковые выросты. Современные виды *Exilia* приурочены к значительным глубинам тропических зон Индийского и Тихого океанов. *Exilia hilgendorfi* (Martens, 1897) рассматривается как

высоко изменчивый вид, имеющий широкое индо-тихоокеанское распространение. *Benthovoluta gracilior* Rehder, 1967, *B. claydoni* Harasewych, 1987 и *B. prellei* Bozetti, 2001 признаются локальными формами *Exilia hilgendorfi*. Описаны три новых вида: *Exilia graphiduloides* sp. nov. (Новая Каледония, 520 м), *E. vagrans* sp. nov. (западная и юго-западная части Тихого океана, 865-1280 м), and *E. kiwi* sp. nov. (Новая Зеландия, 1386-1676 м).

