

New Pacific Species Of *Morum*
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***Morum clatratum* Bouchet, 2002**



***Morum roseum* Bouchet, 2002**

PROTOCONCHS, DISPERSAL, AND TECTONIC PLATES
BIOGEOGRAPHY: NEW PACIFIC SPECIES OF MORUM
(GASTROPODA: HARPIDAE)

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Abstract *Morum clatratum* n. sp. and *Morum roseum* n. sp. are described from depths of 100–200 m in the Marquesas Islands. Mode of development inferred from protoconch morphology and comparison with the protoconchs of *Harpa* with teleplanic larvae suggests that the new species have planktotrophic larval development, and that they are expected to range widely outside the Marquesas. In addition, *Morum kurzi*, *M. macdonaldi*, and *M. teramachii*, with inferred planktotrophic development, and *M. watanabei*, with inferred non-planktotrophic development, are newly recorded from South Pacific localities. The distribution of individual species of *Morum* appears to reflect dispersal during the planktonic phase, rather than movement of the lithospheric plates on the geological scale. The Caribbean *Morum oniscus* and *M. lamarckii*, respectively with inferred non-planktotrophic and planktotrophic development, are treated as separate valid species.

Key words Pacific plate, larval development, protoconch, island endemism, dispersal, vicariance, new species.

INTRODUCTION

The eastern Polynesian fringes of the Indo-West Pacific Province are known for the low species richness of their marine faunas combined with a significant level of local or regional endemism (see, e.g., Rehder 1980). Colonization of isolated islands and maintenance of genetic exchange between islands is generally thought to take place through the dispersal, and drifting of planktonic larvae (Scheltema 1971, 1987, Scheltema & Williams 1983), and narrow distribution ranges are positively correlated with the reduced dispersal capacities associated with the loss of planktotrophy (Leal & Bouchet 1991), resulting in speciation and the appearance of endemic species (for examples see Gofas, 1990, Bouchet & Bail, 1991).

The extreme isolation of the Marquesas in the Pacific has been stressed several times, and it suffices to mention that the nearest land mass is ca. 1500 km away (Society Is.) and the nearest continental mass is 5500 km away (Central America). Within the Marquesas, most individual islands are separated from each other by depths in excess of 2500 m and the sea floor around the archipelago is everywhere deeper than 4000 m. The islands have a volcanic origin, with Eiao in the northwest being the oldest (6.3 MY: Brousse & Bellon, 1974) and Fatu Hiva in the southeast being the youngest (1.3 MY: Duncan & McDougall, 1974). Endemism in the terrestrial biota of the Marquesas has been thoroughly documented to be very high, whereas endemism in the marine biota is rather inconspicuous (Trondle & Cosel, in press). The archipelago presents an impoverished Indo-Pacific fauna with a few local endemics. Among documented gastropod endemics, *Cyrtulus serotinus* (family Fasciolariidae) has a protoconch indicating non-planktotrophic larval development (own observations) and thus conforms with the model of island endemism. The discovery in the Marquesas of new taxa with protoconchs indicating long-lived planktotrophic larval development is therefore paradoxical as it runs contrary to these assumptions. In the present paper I describe two new species of *Morum* from the Marquesas, I record additional species from the South Pacific, and I discuss the significance of the *Morum* protoconch in the context of distribution patterns and tectonic events in the South Pacific.

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SYSTEMATIC DESCRIPTIONS

MURICOIDEA Rafinesque, 1815
 HARPIDAE Bronn, 1849
 MORUMINAE Hughes & Emerson, 1987
 Genus *Morum* Röding, 1798

Type species *Morum purpureum* Röding, 1798 [= *M. oniscus* (Linnaeus, 1767)], by monotypy. Recent, western Atlantic.

Morum clatratum n. sp.
 Figure 1

Morum sp. – Frydman 1991: 13.

Type material Holotype and 2 paratypes, all dd, in MNHN.

Type locality Off Nuku Hiva, Marquesas Is., 08°45.1' S, 140°14.1' W, 108–112 m [MUSORSTOM 9: sta. CP1177].

Material examined Off Nuku Hiva, Marquesas Is., 08°45.1' S, 140°14.1' W, 108–112 m [MUSORSTOM 9 Expedition: sta. CP1177], 3 dd (incl. holotype), collected by P. Bouchet, B. Dayrat, B. Richer de Forges and A. Warén, 25 August 1997.— Off Fatu Hiva, Marquesas Is., 10°31.4' S, 138°39.2' W, 210 m [N.O. 'Marara', sta. 303], 3 dd (incl. 2 paratypes), collected by J. Poupin, 3 Sept. 1990. All material in MNHN.

Measurements Holotype (largest adult), height 60.5 mm, width 34.3 mm. Smallest adult, height 49.5 mm.

Description (holotype) Shell large, solid, pyriform, consisting of 6.1 teleoconch whorls. Whorls regularly convex, spire conical, apical angle 85°, last whorl occupying 85% of total shell height. Protoconch damaged, worn, remaining two whorls smooth, initial part missing. Protoconch / teleoconch transition sharp. Teleoconch whorls convex, rather indistinctly shouldered, sculptured with intersecting axial ribs and spiral cords. Axial ribs orthocline except for short adapical portion that is prosoclinely appressed to preceding whorl; ribs sharp and stronger than spirals on spire whorls, broader and about equal to spirals on last whorl, number increasing from about 14 on first teleoconch whorl to 29 on penultimate, and 42 on last whorl. In addition to the main axial ribs, there is a finer sculpture of thin, sharp, fragile lamellae, which are crowded on the ribs and more widely spaced between them; 5–7 lamellae between consecutive axial rib crests. Thick raised spiral cords form small nodules where they intersect axial ribs; one well defined cord above shoulder, 4 (spire whorls) to 5 (penultimate whorl) below shoulder, 17 on last whorl, 2 on canal. Aperture high, narrow; siphonal canal open, very slightly recurved; outer lip thick, recurved, with 17 subequal denticles; parietal shield broad, thin everywhere except in columellar region where it is thicker, raised, and covered with wart-like pustules in abapical half, and small elongated ridges in adapical half. Ground colour light brownish beige with irregular brownish speckles; 4 brown spiral bands on last whorl, breadth of each band extending over 3–4 spiral cords, dark brown at base of outer lip; parietal shield and aperture white.

Derivation of name From the Latin *clatratus*, -a, -um, latticed, with reference to the shell sculpture.

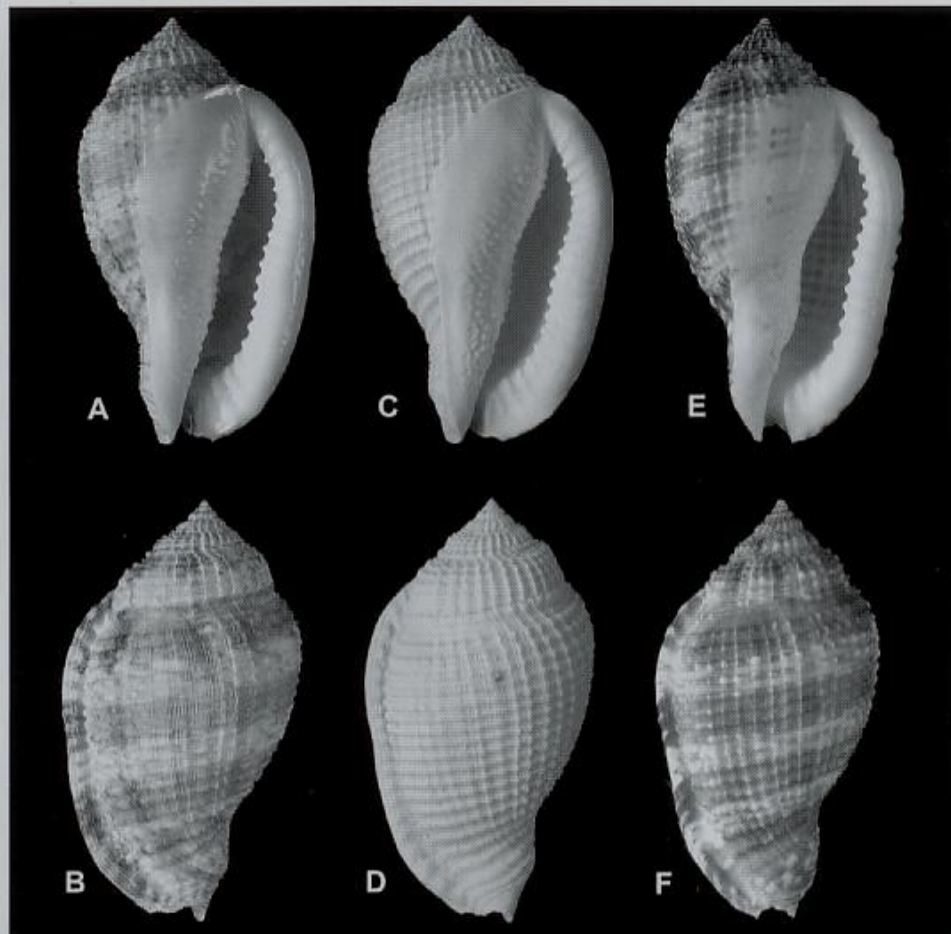


Figure 1 *Morum clatratum* n. sp. A–D holotype, height 60.5 mm; off Nuku Hiva, Marquesas Is., 108–112 m; A–B natural, C–D coated with magnesium chloride. E–F paratype, height 57.0 mm; off Fatu Hiva, Marquesas Is., 210 m.

Geographic range Known only from the Marquesas, dead in 112–210 m.

Comparisons *Morum clatratum* belongs to the species group sometimes recognized as the subgenus *Oniscidia* Mörch, 1852, and it has a general resemblance to *Morum grande* (A. Adams, 1855), *M. teramachii* Kuroda & Habe, 1961, and *M. uchiyamai* Kuroda & Habe, 1961, on the one hand, and *M. amabile* Shikama, 1973, on the other hand. *Morum clatratum*, *M. grande*, *M. teramachii*, and *M. uchiyamai* have in common a high-spired teleoconch, a sculpture of strong spiral cords and frilled axial ribs, and a colour pattern with four dark bands on a lighter ground on the last adult whorl. *Morum grande* differs by its much coarser sculpture (the last whorl of a 51 mm adult has 20 axial ribs and 15 spiral cords). The axial ribs form a spiny projection, strongest at shoulder, where it intersects the spiral cords, whereas they form only a low spineless knob in *M. clatratum*. In *M.*

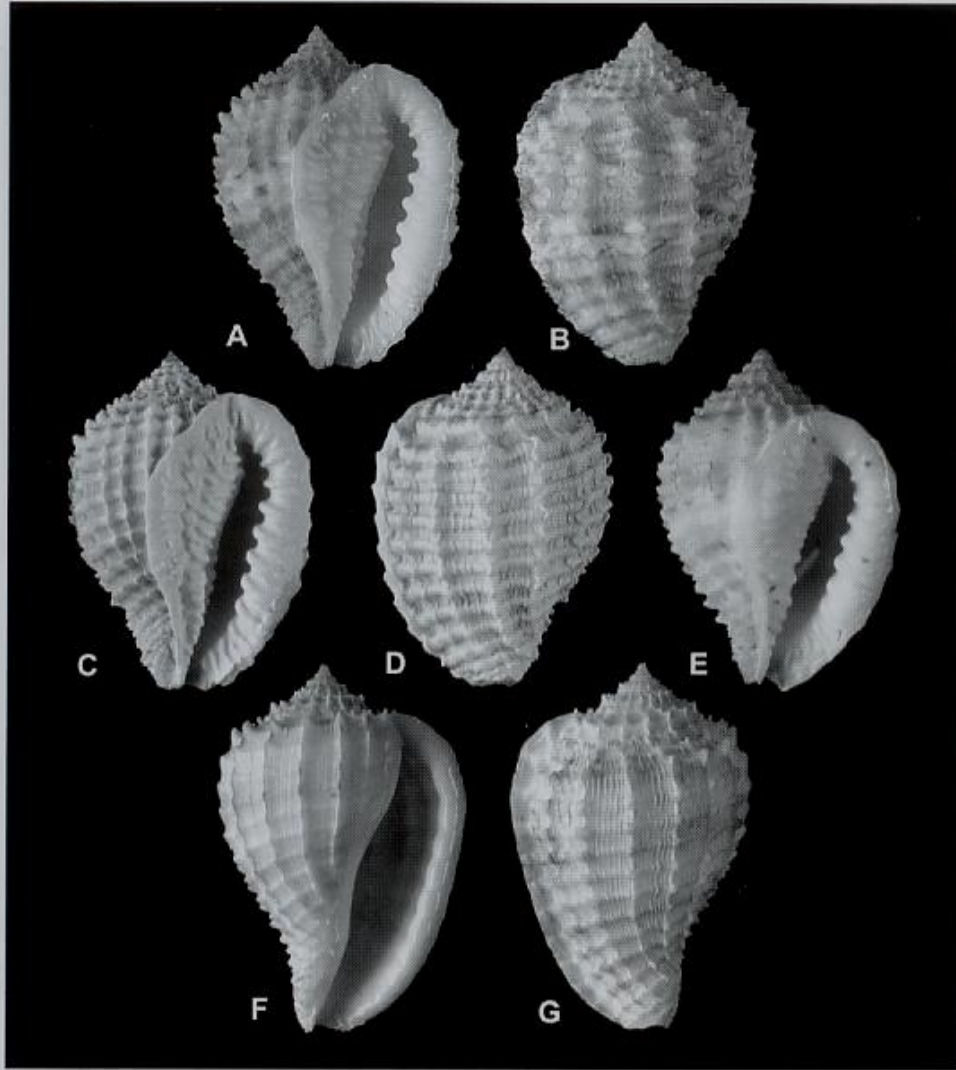


Figure 2 *Morum roseum* n. sp. (A–E) and *M. watanabei* (F–G). A–D holotype, height 21.5 mm; off Fatu Hiva, Marquesas Is, 115–120 m; A–B natural, C–D coated with magnesium chloride. E paratype, height 21.0 mm; off Hiva Oa, Marquesas Is, 105–285 m [MUSORSTOM 9 sta. DW1235]. F–G height 34.0 mm; south of Viti Levu, Fiji, 18°11.8' S, 178°28.1' E, 213 m.

grande, the outer margin of the parietal shield is elevated, and not adherent to the last adult whorl as in *M. clatratum*. *Morum uchiyamai* (which may be only an ecological form of *grande* - see below) also differs by its much coarser sculpture, strongly projecting spines at the intersection between the shoulder cord and the axial ribs, and very strong, widely spaced, secondary lamellae between ribs. *Morum teramachii* differs by its coarser sculpture (the last whorl of a 57 mm adult has 19 axial ribs and 14 spiral cords): except on the shoulder, the spiral cords are low and rather indistinct; the intersection of ribs and cords forms spines on the shoulder, and spineless nodules elsewhere. The parietal

shield is weakly developed and appressed to the last whorl. *Morum amabile* bears a general resemblance to *M. clatratum*, but reaches a smaller adult size (31–36 mm), lacks well defined colour bands on the last whorl, and has coarser sculpture at comparable size. The other species of *Oniscidia* are more strongly dissimilar.

Remarks Two of the shells carry respectively two and three small (diameter 0.5–1 mm) borings on the spire, which appear to be octopus drill holes.

Morum roseum n. sp.
Figure 2 A–D

Type material Holotype (live taken?) and two paratypes in MNHN.

Type locality Off Fatu Hiva, Marquesas Is, 09°44.6' S, 138°51.1' W, 115–120 m.

Material examined (all in MNHN) Marquesas Island (collected by P. Bouchet, B. Dayrat, B. Richer de Forges and A. Warén, MUSORSTOM 9 Expedition, N.O. 'Alis', August–September 1997): Off Nuku Hiva, 08°45.5' S, 140°03.8' S, 86–120 m [MUSORSTOM 9 sta. DW1183], 26 August 1997, 1 dd.— Off Hiva Oa, 09°48.9' S, 139°09.5' W, 117 m [MUSORSTOM 9 sta. DW1208], 28 August 1997, 5 fragments and juv.— Off Fatu Hiva, 09°44.6' S, 138°51.1' W, 115–120 m [MUSORSTOM 9 sta. DW1208], 30 August 1997, 1 lv(?) (holotype), 1 fragment.— Off Hiva Oa, 09°41.8' S, 139°03.5' W, 105–285 m [MUSORSTOM 9 sta. DW1235], 31 August 1997, 1 dd (paratype).— Off Fatu Hiva, 10°28.1' S, 138°41.1' W, 119–122 m [MUSORSTOM 9 sta. DW1242], 1 September 1997, 1 dd (paratype).— Off Motu One, 07°48' S, 140°21' W, 450–455 m [MUSORSTOM 9 sta. DW1281], 7 September 1997, 1 dd.— Off Eiao, 07°52' S, 140°31' W, 416–460 m [MUSORSTOM 9 sta. DW1282], 7 September 1997, 2 dd.

Wallis & Futuna Islands NE of Wallis Island (collected by P. Bouchet, B. Métivier and B. Richer de Forges, MUSORSTOM 7 Expedition, N.O. 'Alis', May 1992): Field Bank, 12°31' S, 174°19' W, 469–475 m [MUSORSTOM 7 sta. DW597], 24 May 1992, 1 fragment.

Measurements Holotype height 21.5 mm, width 15.5 mm; paratypes height 21.0 mm, width 15.5 mm; height 21.0 mm, width 14.5 mm.

Description (holotype) Shell small, solid, pyriform, consisting of 4.5 teleoconch whorls, spire low, broadly conical, apical angle 80°, last whorl occupying 85% of total shell height. Protoconch multispiral, protoconch I diameter ca. 400 µm, protoconch II smooth, consisting of 2.5 whorls, diameter 1500 µm, protoconch / teleoconch transition sharp, marked with raised, prosocline lamellar varix. Teleoconch whorls moderately convex, first 2 whorls shouldered, last whorl with concave subsutural ramp. Sculpture of axial ribs, almost entirely orthocline except for short adapical portion, which is prosoclinely appressed to preceding whorl, sharp on spire whorls, broader but asymmetrical on last adult whorl, abapertural side higher, slightly raised over adapertural side, intersecting thick raised spiral cords, each intersection forming a projecting scale, scales stronger on shoulder cord, interspaces between ribs and cords forming spirally elongate cells. One spiral cord exposed below shoulder cord on spire whorls, 11 below shoulder cord of last whorl, subsutural cord developed on last 2 whorls only, 18 axial ribs on last whorl, 18 on penultimate and 14 on antepenultimate whorls. In addition to the main axial ribs, there is a finer sculpture of thin, sharp, fragile lamellae, 4–8 crowded on the descending, adapertural side of the axial ribs, 3–7 less evenly spaced between ribs. Aperture high, narrow; siphonal canal open, very slightly recurved; outer lip thick, recurved, with 12 bulging denticles corresponding to interspaces between spiral cords, much stronger in

median part of lip, with 1–2 smaller, elongated pustules between them; parietal shield broad but thin, except in columellar region where it is thicker and raised, bearing numerous wart-like, spirally elongated pustules, disposed in parallel on lower part of shield, more irregularly arranged adapically. Ground colour light pinkish brown with irregular, deep violet brown speckles on cords, tip of siphonal canal pink; 4 darker spiral bands, 1 poorly defined subsuturally, 1 on whorl periphery about two cords broad, 1 below about one cord broad, 1 poorly defined covering shell base, outer lip marked with deep violet brown dots where these bands reach aperture; parietal shield and aperture white.

Derivation of name From the Latin *roseus*, -a, -um, pinkish, with reference to the colour of the tip of the siphonal canal.

Geographic range The Marquesas and NE of Fiji, alive (?) in 115–120 m, shells to 470 m.

Comparisons *Morum roseum* is easily distinguished from the other Recent species of *Morum* by the combination of its small adult size, broadly inflated last whorl, and narrow aperture, but it resembles *M. macdonaldi* Emerson, 1981, and *M. kurzi* Petuch, 1979, more than any other species. *Morum macdonaldi* differs by its much smaller adult size (less than 17 mm: it is the smallest *Morum* species), narrower shell with higher spire, and narrow parietal callus. *Morum kurzi* reaches 27 mm, and has a thicker and broader parietal callus, and has a characteristically orange aperture. *Morum roseum* also resembles a miniature *M. praeclarum* Melvill, 1919, but is distinguished by the more complex pustulation of the parietal shield and outer lip, the shorter, almost truncated siphonal canal, the finer sculpture, and the lack of a projecting spine on the shoulder of each axial rib.

NEW RECORDS

Morum bruuni (Powell, 1958)

New records Norfolk Ridge. SMIB 4: sta. DW48, 24°46' S, 168°09' E, 240–245 m, 1 dd.— Sta. DW53, 23°40' S, 168°00' E, 250–270 m, 1 lv.— SMIB 8: sta. DW157, 24°46' S, 168°08' E, 251–255 m, 1 dd.— Sta. DW158, 24°47' S, 168°08' E, 262–290 m, 2 dd.— Sta. DW159, 24°46' S, 168°08' E, 241–245 m, 2 dd.— SMIB 10: sta. DW208, 24°49' S, 168°09' E, 270 m, 1 dd.— LITHIST: sta. DW12, 24°45.7' S, 168°08.1' E, 235–280 m, 2 dd.— NORFOLK 1: sta. DW1653, 23°28' S, 167°51' E, 328–340 m, 1 fragm.— Sta. CP1657, 23°28' S, 167°52' E, 305–332 m, 1 dd.— Sta. CP1676, 24°43' S, 168°09' E, 227–232 m, 1 dd.— Sta. CP1677, 24°44' S, 168°09' E, 233–259 m, 1 dd. (all MNHN).— R.V. *Tangaroa*, sta. BS882, 32°31.8' S, 167°29.5' E, 113–118 m, Wanganella Bank, 1 lv (NMNZ).

Kermadec Ridge. R.V. *Acheron*, sta. BS437, 29°11.9' S, 177°56.2' W, 154 m, off Raoul I., 1 lv.— Sta. BS571, 29°18.8' S, 177°54.2' W, 219–274 m, 1 dd. (both NMNZ).

North Island of New Zealand. R.V. *Tangaroa*, sta. BS719, 37°33.2' S, 176°58.7' E, 134–174 m, 1 fragment (NMNZ).

Distribution (Figure 6) South-West Pacific: Kermadec Ridge, northern North Island of New Zealand, Norfolk Ridge, Lord Howe Rise (Emerson, 1990), Tasman seamounts and New South Wales; alive in 120–270 m, shells to 360 m.

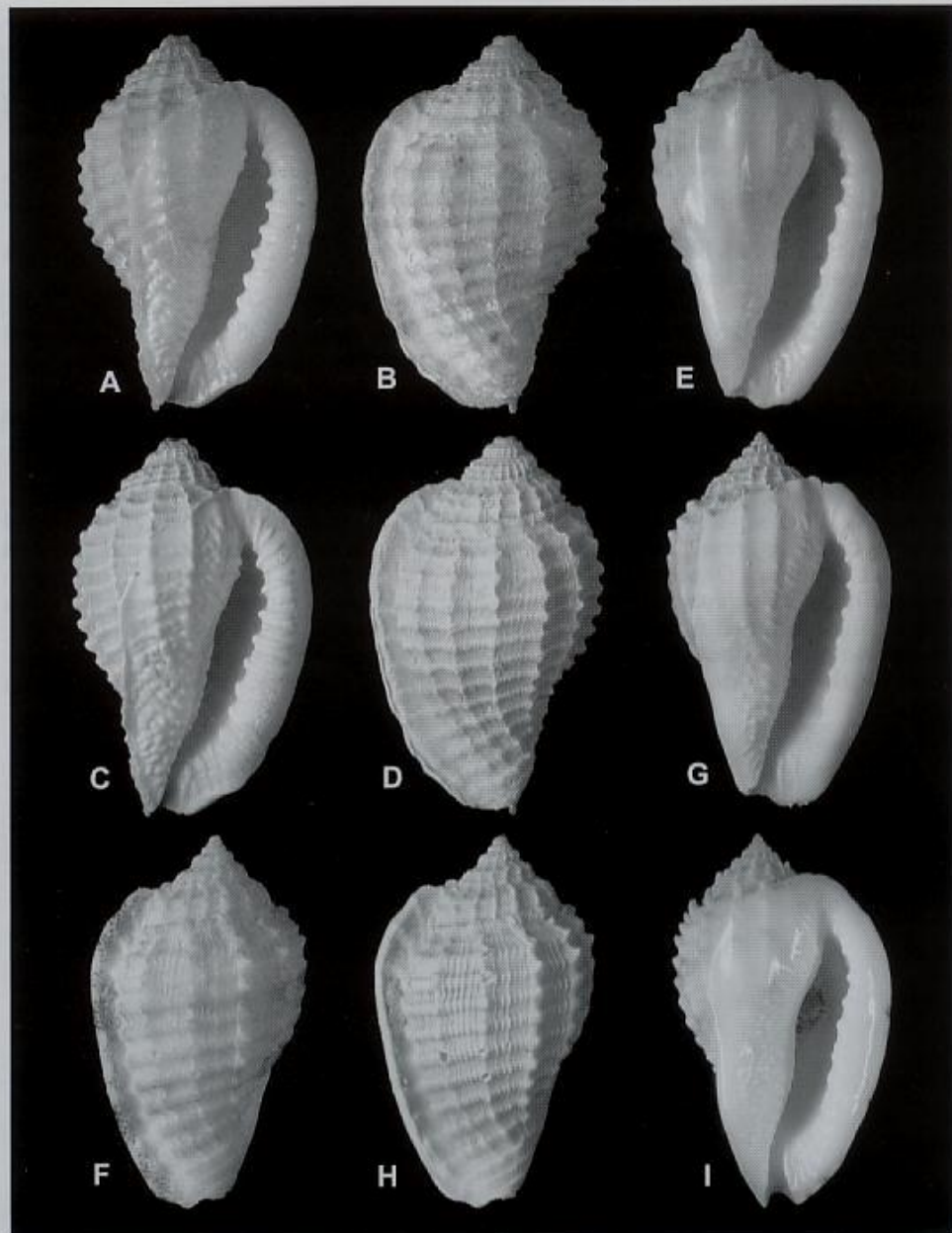


Figure 3 *Morum grande* / *Morum uchiyamai*. A–D *grande* form, height 41.6 mm; North of New Caledonia, 205–215 m [SMIB 6 sta. DW128]; A–B natural, C–D coated with magnesium chloride. E–H *uchiyamai* form, height 40.8 mm; Tonga, 216–237 m [BORDAU 2 sta. DW1610]; E–F natural, G–H coated with magnesium chloride. I *uchiyamai* form, height 52.0 mm; New Caledonia, Loyalty Ridge, 21°00' S, 167°27' E, 250 m [MUSORSTOM 6 sta. DW453].

Morum grande (A. Adams, 1855) / *Morum uchiyamai* Kuroda & Habe, 1961

Figure 3

New records (all MNHN) (*grande* type). New Caledonia. SMIB6: sta. DW128, 19° 06' S, 163°22' E, 205–215 m (North of New Caledonia), 1 dd.— BATHUS 4: sta. DW932, 19°08' S, 163°29' E, 170–190 m, 1 juv. dd.

(*uchiyamai* type). New Caledonia. MUSORSTOM 6: sta. DW399, 20°42' S, 167°00' E, 282 m (Loyalty Ridge), 1 juv. dd.— NORFOLK 1: sta. CP1715, 23°22' S, 168°02' E, 270–312 m, 1 dd.

Fiji. MUSORSTOM 10: sta. CP1387, 18°18.5' S, 178°04.7' E, 229–370 m (south of Viti Levu), 1 fragment (identification tentative).

Tonga. BORDAU 2: sta. CP1533, 21°44' S, 175°20' W, 322–329 m, 1 fragment.— Sta. DW1610, 22°59' S, 175°47' W, 216–237 m, 1 dd.— Sta. DW1630, 23°23' S, 176°18' W, 360 m, 1 lv.

Distribution West Pacific: from middle Japan (Izu peninsula) southwards to the China Sea, Philippines, Queensland, New Caledonia, Fiji and Tonga; alive in 100–360 m.

Remarks The distinction between *M. grande* and *M. uchiyamai* is problematical. Frydman (1991) separated specimens with 17–19 axial ribs and a “strongly curved siphonal canal” as *grande*, and specimens with 13–15 ribs and a “weakly curved siphonal canal” as *uchiyamai*. Dance & Poppe (in Poppe *et al.*, 1999: 11) have raised doubts as to the validity of *M. uchiyamai*, but based on their apparent sympatric occurrence in Tosa Bay, Japan, concluded that they are probably distinct. The present records of both *M. grande* and *M. uchiyamai* from New Caledonia would seem to support the latter view. However, the two forms do not occur in New Caledonia together: *M. grande* having been

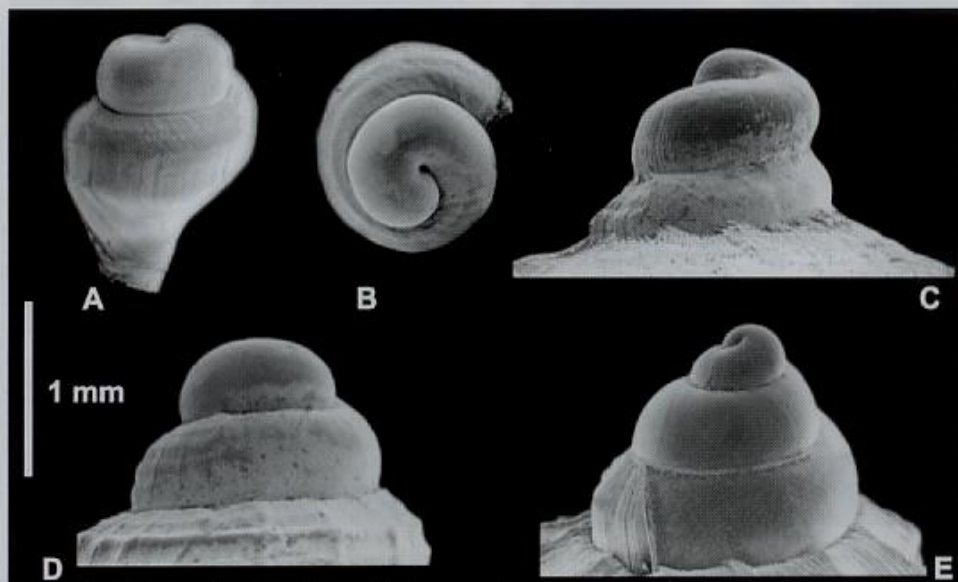


Figure 4 Protoconchs of species of *Morum* contrasting non-planktotrophic (A–D) and planktotrophic (E) modes of development. *Morum oniscus*, Florida. A–B juveniles newly hatched from egg capsule (photos courtesy of R.N. Hughes). C protoconch of subadult specimen. *Morum cancellatum*, China Seas. D protoconch of adult specimen. *Morum kurzi*, Philippines. E protoconch of adult specimen (see also Fig. 5G).

found only in the north and *M. uchiyamai* only in the south. They may prove to be soft-bottom and hard-bottom forms of a single species. A re-evaluation of these nominal species should also include *Morum watsoni* Dance & Emerson, 1967, which is evidently a juvenile of a species in the *grandefuchiyamai* complex (see also Tsuchiya [in Okutani], 2000: 532–535).

Morum kurzi Petuch, 1979

New record Fiji. BORDAU 1: sta. DW1393, 16°45' S, 179°59' E, 426–487 m (Somosomo Strait, between Vanua Levu and Taveuni), 1 broken shell (MNHN).

The damaged and faded specimen is a small adult, 19.5 mm high. The apertural callosity still retains the pale orange hue characteristic of Philippines specimens.

Distribution The Philippines, Solomon Islands (alive in 25–30 m; Emerson, 1990), Fiji.

Morum macdonaldi Emerson, 1981

New record Two shells (MNHN) of *M. macdonaldi* have been collected at Okukina, Takapoto Atoll, Tuamotus Archipelago, by Dr G. Richard. This locality is 5800 km south-east of the previously only known occurrence of *M. macdonaldi*, Kwajalein Atoll, in the Marshall Islands.

Morum ponderosum (Hanley, 1858)

Remarks Two shells of *M. ponderosum* have been collected at Moerai, Rurutu Island, Australes Archipelago by Mr J.P. Lefort, a collector based in Huahine, Society Islands, and are now in his collection. This is presumably the locality "Rurutua" mentioned for one of the specimens illustrated by Poppe & Brulet (in Poppe *et al.*, 1999: pl. 39, fig. 3).

Morum teramachii Kuroda & Habe in Habe, 1961

New records (all MNHN) New Caledonia, Norfolk Ridge. LITHIST: sta. CP16, 23°43.2' S, 168°16.2' E, 379–391 m (Banc Jumeau Ouest), 1 dd, worn.—NORFOLK 1: sta. DW1651, 23°27' S, 167°50' E, 276–350 m, 1 dd.—Sta. DW1704, 23°45' S, 168°16' E, 400–420 m (Banc Jumeau est), 1 dd.—Sta. DW1707, 23°43' S, 168°16' E, 381–493 m, 1 lv(?), 2 dd.—Sta. CP1708, 23°43' S, 168°16' E, 381–384 m, 1 dd, worn.

Distribution Previously known only from the western North Pacific: southern Japan, the Philippines and the Marianas, in 170–448 m (alive in 353 m) (Emerson 1990: 148).

Morum watanabei Kosuge, 1981

Figure 2 F–G

New record Fiji. SUVA2: sta. BS11, 18°11.8' S, 178°28.1' E, 213 m (south of Viti Levu), 1 dd (MNHN).

Remarks The present specimen is a young, uncallused adult, with unthickened lip. I

identify it as *M. watanabei*, rather than *M. cancellatum* Sowerby, 1824, based on the numerous spiral cords, and axial ribs with a spine projecting at the shoulder. The paucispiral protoconchs are essentially similar in *M. cancellatum* and *M. watanabei*. Emerson (1990: 146, figs 6–7) has recorded as *M. cancellatum* an adult, crabbed specimen taken in a trap from a nearby station off Fiji, in 220 m. The two specimens may be conspecific.

THE MORUM PROTOCONCH AND MODES OF LARVAL DEVELOPMENT

The mode of development has been observed in one species of *Morum* only. The Western Atlantic *M. oniscus* (Linnaeus, 1767) has non-planktotrophic development with intracapsular metamorphosis, and hatches as a crawling snail (Work, 1969; Hughes & Emerson, 1987). It has a paucispiral protoconch (Figure 4 A–D). All other species of *Morum* are less common, some of them even quite rare, and their reproduction has remained undocumented, either in the field or in the laboratory. Their mode of development, however, can be inferred from protoconch morphology. The vast body of literature on the correlations between protoconch morphology and mode of development need not be reviewed again in the present paper. I refer to Thorson (1946), Thiriot-Quévieux (1983), Jablonski & Lutz (1980, 1983), Rex & Warén (1982), Scheltema & Williams (1983), and references therein, for a presentation of data and discussion.

Emerson (1990) published SEM photographs of the protoconchs of *M. kurzi*, *M. bruuni* and *M. ponderosum* (Hanley, 1858) and presented the comments of two colleagues on these micrographs. [I have reexamined the MNHN shell of *Morum bruuni* from which he stated he had illustrated the protoconch (Emerson, 1990: figs 18–19). I find that its protoconch does not correspond with the figured specimen, and none of the other *M. bruuni* in MNHN corresponds with it. I suppose a mixing of data has occurred. Emerson's figs 18–19 could possibly represent *M. joelgreeni* Emerson, 1981]. Emerson cited a personal communication from Harasewych who stated that inference of mode of development of *M. kurzi* based on Shuto's criteria (Shuto, 1974) was inconclusive. Conversely, Scheltema (com. pers. to Emerson) concluded that *M. kurzi* and *M. ponderosum* have planktotrophic development, and suggested a planktonic phase of 1 to 2 months duration. Scheltema observed that the protoconch I of "*M. bruuni*" (probably *M. joelgreeni*: see above) has a diameter of 400 μm and from this inferred non-planktotrophic development, even suggesting intracapsular metamorphosis. Based on these comments, Emerson concluded that a planktonic larval stage is present in two species of *Morum* only, and hypothesized non-planktotrophy to be the rule in the other 14 Indo-West Pacific species then known.

Based on my own reexamination of the protoconch morphology in *Morum* and *Harpa* Röding, 1798 (Figures 4–5), I conclude the opposite, i.e. that planktotrophy is the standard condition present in the majority of the Indo-Pacific species, with non-planktotrophy being a derived character state present in a few species only. *Morum* protoconchs belong to the two categories of protoconchs classically recognised in caenogastropods (Table 1).

(a) The paucispiral type of protoconch consists of 1.1–1.2 whorls; it is smooth, has a diameter of 1150–3360 μm , and the protoconch / teleoconch transition is often sharp. Indo-Pacific species with a paucispiral protoconch are *M. cancellatum* (diameter 1200–1380 μm), *M. watanabei* (diameter 1150–1250 μm), and *M. macandrewi* Sowerby, 1889 (diameter 1180 μm). There are proportionally more western Atlantic species with a paucispiral protoconch, and *M. matthwesi* Emerson, 1967, has the largest protoconch in the genus (diameter 3360–3500 μm); although it has 1.8–2.2 whorls, it clearly belongs to

TABLE 1

Protoconch parameters for Indo-Pacific *Morum* species and inferred mode of development (P = planktotrophic; NP = non-planktotrophic). All data original.

Species	protoconch I		protoconch II	n	inferred mode of development
	diameter (μm)	no. whorls	diameter (μm)		
<i>amabile</i> Shikama, 1973	500-625	1.6-1.9	1375-1500	3	P
<i>brunni</i> Powell, 1958	450	2.1-2.2	1525-1650	2	P
<i>cancellatum</i> Sowerby, 1824		1.1-1.2	1200-1380	2	NP
<i>clatratum</i> n. sp.					
<i>exquisitum</i> (A. Adams & Reeve, 1848)	700	1.2	1175	1	P
<i>fatimae</i> Poppe & Brulet, 1999	no data		?		
<i>grande</i> (A. Adams, 1855)	650-700	1.3-1.5	1250-1500	3	P
<i>joelgreeni</i> Emerson, 1981	575-625	1.3-1.6	1200-1350	3	P
<i>kurzi</i> Petuch, 1979	400-460	2.2	1325	2	P
<i>macandrewi</i> Sowerby, 1889		1.2	1180	1	NP
<i>macdonaldi</i> Emerson, 1981	350-375	2.5-2.6	1375	2	P
<i>ninomiyai</i> Emerson, 1986	650	1.45	1325	1	P
<i>ponderosum</i> (Hanley, 1858)	720	2.0	2320	1	P
<i>praeclarum</i> Melvill, 1919	370	2.3	1500	1	P
<i>roseum</i> n. sp.	400	2.5	1500	2	P
<i>teramachii</i> Kuroda & Habe, 1961	550-625	2.0	1425-1475	2	P
<i>uchiyamai</i> Kuroda & Habe, 1961	600-750	1.2-1.6	1275-1500	3	P
<i>vicdani</i> Emerson, 1995	no data		?		
<i>watanabei</i> Kosuge, 1981		1.2	1150-1250	2	NP
<i>watsoni</i> Dance & Emerson, 1967	525	2.0	1500	1	P

the paucispiral type, with no distinction between a protoconch I and protoconch II. Other western Atlantic species with paucispiral protoconchs are *M. lindae* Petuch, 1987 [regarded by Poppe *et al.* (1999) as a synonym of the Neogene fossil *M. dominguense* (Sowerby, 1850)] (diameter 1350–1500 μm , 1.6–1.7 whorls), *M. oniscus* (diameter 1200–1300 μm , 1.7–1.9 whorls) and *M. dennisoni* (Reeve, 1842) (diameter 1880 μm , 1.5 whorls).

(b) The multispiral type of protoconch consists of 1.8–2.8 whorls. Protoconch I is smooth or finely papillose; protoconch II is smooth except for a partly covered spiral keel exposed just above the suture. The transition between protoconchs I and II is rather discrete; that between protoconch II and teleoconch is sharp, with a slightly raised varix. Number of whorls and diameter in different Indo-Pacific species are compiled in Table 1.

For comparison with the *Morum* protoconch, I figure the protoconch of *Harpa major* Röding, 1798 (Fig. 5 A, C, E) (the identification is tentative, as the specimen is very young; it could also be *H. articularis* Lamarck, 1822). It is multispiral. Protoconch I is finely papillar and has a diameter of 500–550 μm ; protoconch II is smooth with one suprasutural spiral cord, has 2.25 whorls and a diameter of 1750 μm . Based on correlations in other families of Caenogastropoda, *Morum* species with a paucispiral type of protoconch are here inferred to have non-planktotrophic larval development. The proto-

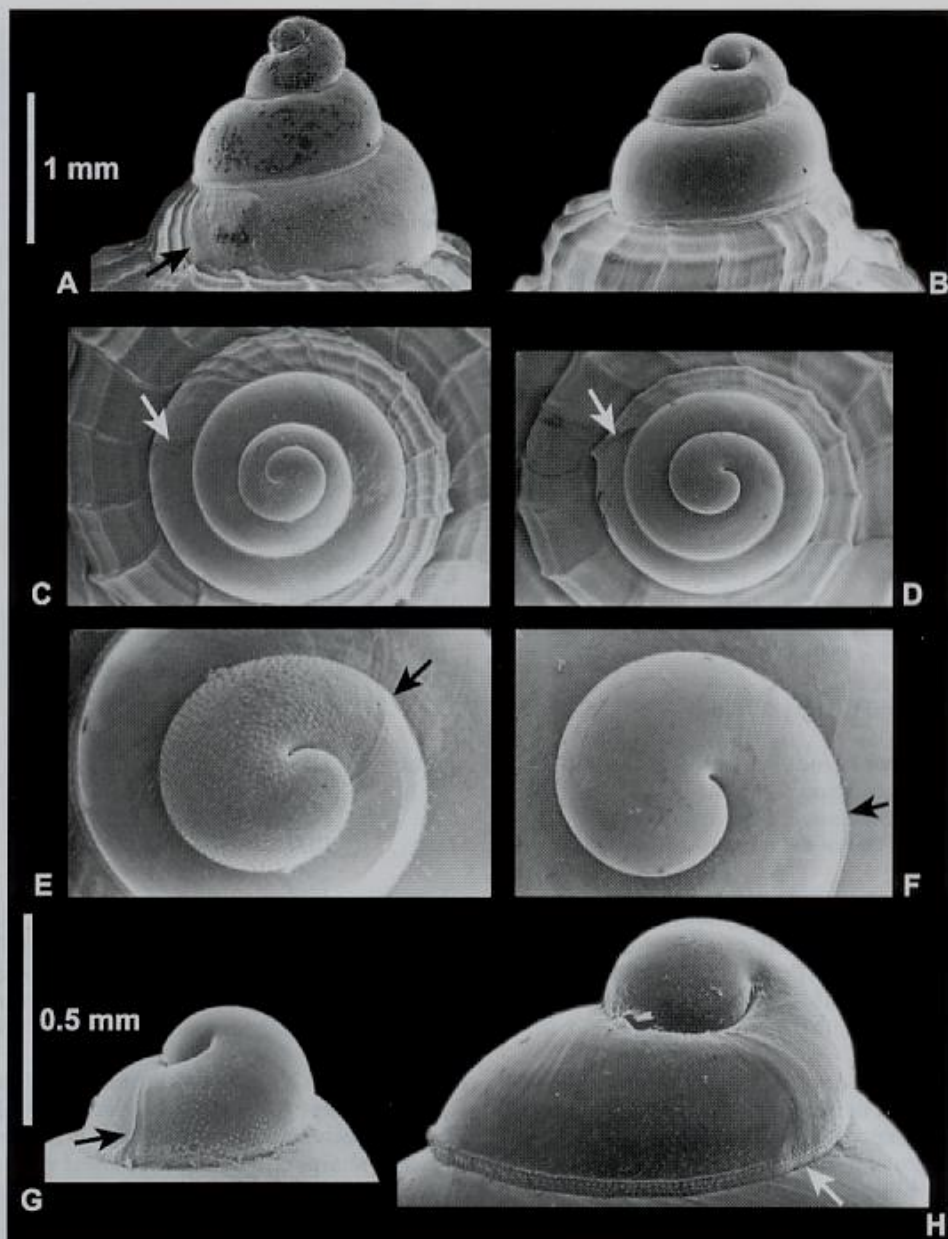


Figure 5 Protoconchs of species of *Harpa* (A, C, E) and *Morum* (B, D, F-H) from which a planktotrophic mode of development can be inferred. The arrows show the protoconch II / teleoconch discontinuity (A, C, D) and the protoconch I / protoconch II discontinuity (E-H), indicating metamorphosis and hatching of the veliger larva, respectively. *Harpa major*, New Caledonia, North lagoon, 42 m. A, C, E protoconch of juvenile specimen. *Morum uchiyamai*, New Caledonia, Loyalty Ridge, 282 m. B, D, F, H protoconch of subadult specimen. *Morum kurzi*. G same specimen as in Fig. 4E. Scale lines 1 mm (A-D) and 0.5 mm (E-H).

conch / teleoconch transition is sharp in certain species (e.g. *M. oniscus*) and gradual in others (e.g. *M. matthewsi*), which probably reflects differences in the respective timings of metamorphosis and hatching. A short, non-feeding, dispersal larval stage may be present in some species, but it is almost certainly absent in *M. matthewsi*.

Conversely, those species of *Morum* with a multispiral type of protoconch are here inferred to have planktotrophic larval development. The diameter of protoconch I (range 350–700 μm) is admittedly larger than protoconch I of many caenogastropods with planktotrophic development, where a diameter of 150–300 μm is typical. However, the protoconch I of *Ranella olearia* (Linnaeus, 1758) has a diameter of 560 μm (Warén & Bouchet, 1990: fig. 88), despite the fact that it has teleplanic larvae, and protoconch I of *Harpa* is also in the same range of diameter. Evidently the diameter of protoconch I alone is not a reliable indicator of developmental mode.

Incidentally, the Caribbean *Morum lamarckii* (Deshayes, 1844), often treated as a synonym of *M. oniscus*, differs from it by multispiral, rather than paucispiral, protoconch. This difference was first noticed by Kaicher (1983: cards 3752, 3760), who treated *M. oniscus* and *M. lamarckii* as distinct species, but regrettably she illustrated the wrong protoconchs with the corresponding adults. Poppe *et al.* (1999) treated *M. lamarckii* as "a good species", while accepting that "it may be merely a subspecies or form of *M. oniscus*". The difference between the protoconchs of *M. oniscus* and *M. lamarckii* reflects non-planktotrophic (Hughes, 1990) vs. inferred planktotrophic larval development, respectively. As poecilogony remains undocumented in marine caenogastropods (Hoagland & Robertson, 1988, Bouchet, 1989), the difference in protoconch type is here interpreted as indicating specific rank.

Within the planktotrophic type, the relative duration of the feeding planktonic stage certainly varies from species to species. Species such as *M. grande* or *M. joelgreeni*, with only 1.3–1.6 protoconch II whorls, presumably have the shortest planktonic life, while *M. macdonaldi* and *M. praeclarum*, with 2.3–2.6 protoconch II whorls, presumably have the longest. While it is impossible to estimate the absolute duration of this planktonic stage from the protoconch morphology, I concur with Scheltema (cited by Emerson, 1990:149) that *Morum* veligers probably spend several weeks to a few months in the plankton.

Harasewych (cited by Emerson, 1990: 149), using Shuto's (1974) criteria, noted that he could not infer the mode of development of *M. kurzi* from its protoconch morphology. In my view, this demonstrates that Shuto's formula does not appropriately describe the correlation between protoconch morphology and mode of development, and not that it is impossible to infer *Morum* mode of development from protoconch morphology. It is appropriate to stress that the number of whorls of the protoconch has, by itself, no meaning: *M. matthewsi*, with 1.8 whorls, is inferred to have non-planktotrophic development, while *M. joelgreeni*, with the same number of whorls, is inferred to have planktotrophic development. In interpreting protoconch morphology, it is important to give attention to other characters such as the size of the initial whorl, the overall size of the protoconch, and the sharpness of the protoconch/teleoconch transition.

Based on the same correlations, mode of larval development can be inferred for fossil species. The following have been examined: *Morum chipolanum* Gardner, 1947 and *M. domingense* Sowerby, 1849 (both Chipola Formation, Lower Miocene, Florida; both non-planktotrophic), *M. harpaeformis* (Grateloup, 1847) (Lower Miocene, SW France; planktotrophic), and *M. minor* (Grateloup, 1847) (Upper Oligocene, SW France; planktotrophic).

In conclusion, planktotrophic and non-planktotrophic developmental modes are both present in Indo-Pacific representatives of *Morum*. Species inferred to have non-planktotrophic larvae are: *cancellatum*, *macandrewi*, and *watanabei*. Species inferred to have planktotrophic larvae are: *amabile*, *clatratum*, *grande*, *joelgreeni*, *kurzi*, *macdonaldi*, *ponderosum*,

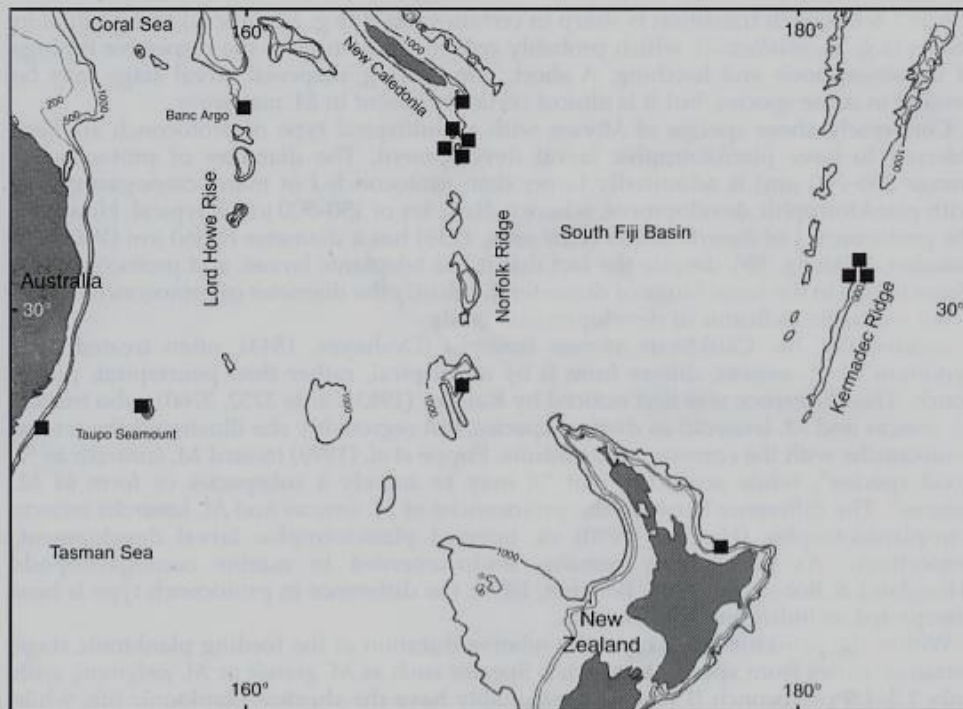


Figure 6 Distribution of *Morum bruuni*. 200, 500 and 1000 m isobaths indicated. Gene flow between the disjunct groups of populations separated by very deep water is probably maintained by planktotrophic larvae, as inferred from protoconch morphology.

praeclearum, *roseum*, *teramachii*, *uchiyamai*, and *watsoni*. No data are available for *M. fatimae* Poppe & Brulet, 1999, and *M. vicdani* Emerson, 1995.

PLATE TECTONICS AND THE DISTRIBUTION OF SPECIES OF *MORUM*

Emerson (1990) discussed the distribution patterns of the West Pacific species of *Morum* and presented "the apparent lack of teleplanic larvae" as the single most important factor to account for what he interpreted as relict distributions. He developed a scenario of distributional patterns based on vicariant events in the tectonic history of the West Pacific region and rejected hypotheses based on dispersal of planktonic larvae. Rather than this scenario based on plate frontiers and movement of the lithospheric plates on the geological scale, I defend the view that instant larval dispersal offers a more parsimonious explanation of modern distribution patterns at the specific level.

Emerson (1990) invoked vicariant events to explain the distribution of *Morum bruuni*, which has a SW Pacific distribution consisting of several disjunct groups of populations (Figure 6): off southeastern Australia, Lord Howe Rise (Argo bank), Taupo seamount, Kaimon Maru, and Wanganella banks on Norfolk Ridge, the north of North Island of New Zealand, and the Kermadec Ridge. Records of empty shells are in the 140–360 m range, and the only live-taken specimen is from 250–270 m. These groups of populations

are separated by distances of 500–2000 km with water depths in excess of 1000 m, that is 500–2000 kilometers of sea bottom where an upper slope species like *M. bruuni* is unable to live. Gondwanian relict distribution is a classic of South-West Pacific terrestrial biogeography (Stevens, 1980), with numerous taxa having vicariant distribution patterns in New Zealand, New Caledonia, and Australia. When evaluating whether the same mechanisms explain the distribution of modern marine biota, it is important to stress the time scale of the tectonic events involved in such vicariant distribution patterns. Australia, New Zealand, and New Caledonia broke up in the Cretaceous (ca. 80 MY ago) and, when the now submerged Norfolk Ridge is taken into consideration, the last vicariant event hypothesized for land vertebrates is dated from the lower Miocene (Balouet, 1990), i.e. ca. 20 MY ago. It should also be stressed that, in the terrestrial faunas and floras of these regions, vicariance following plate tectonic movements best explains disjunct distribution patterns at the generic or family level. With the exception of introduced anthropophile species, the faunas and floras of New Caledonia, New Zealand, and Australia do not have a single species in common, although the generic affinities support the hypotheses of vicariance biogeography.

At the specific level, to explain disjunct distribution between these three land masses by vicariance would require that the taxon in question is at least as old as the tectonic event being considered. In other words, explaining the disjunct SW Pacific distribution of *Morum bruuni* in terms of vicariance would require the species *M. bruuni* to be at least 20 million years old, and (i) to have remained unchanged since, or (ii) to have experienced a parallel morphological evolution in the disjunct populations (orthogenesis). Admittedly, absence of evidence is ambiguous, but, despite the fact that South Australian (Darragh, 1985) and New Zealand (Maxwell & Beu, 1990) Tertiary macro-mollusc faunas are relatively well studied, there are no records of fossil *M. bruuni* in the area. According to Beu (1976), the New Zealand *Morum finlayi* (Laws, 1932), which differs by having more prominent and more rounded spiral cords, may have been ancestral to *M. bruuni*. It is recorded from the lower (19–22 MY) and middle Miocene (12–15 MY) of New Zealand (Beu & Maxwell, 1990: 231). A second species of *Morum* in the lower Miocene of New Zealand is not closely related to the *finlayi-bruuni* lineage. Therefore I reject vicariance as the cause of disjunct distributions of *M. bruuni* in New Zealand and New Caledonia.

Furthermore, vicariance cannot explain the presence of *Morum bruuni* on such guyots as Argo Bank in the Coral Sea. Argo Bank is part of a chain of guyots stretching from the Chesterfield-Bellona Plateau to Lord Howe in the northern part of the Tasman Sea. The age of the volcanic structures supporting the guyots varies from 28 MY (upper Oligocene) in the North (Chesterfield-Bellona) to 6.5 MY in the South (Ball's Pyramid, off Lord Howe) (Missegue & Collot, 1987). An age of 15–20 MY is probable for Argo Bank. During this lapse of time, Argo Bank has always been separated from New Caledonia, Australia and New Zealand by expanses of deep (several thousand meters) water in the order of 500 km or more. The presence of benthic gastropods on the summit areas of these seamounts therefore requires an explanation other than the fragmentation of a former continuous distribution area. Dispersal of and colonization by planktotrophic or demersal non-planktotrophic larvae offers a reasonable hypothesis that rests on the vast corpus of literature on larval biology, population genetics and plankton ecology.

Morum has now been recorded from seven oceanic locales in the Central Pacific: Kwajalein, Marshall Islands (*M. macdonaldi*; type locality), Field Bank, north of Fiji (*M. roseum*; herein), Vanua Levu, Fiji (*M. kurzi*; herein), Takapoto, Tuamotus (*M. macdonaldi*; herein), Rurutu, Australes Islands (*M. ponderosum*; Poppe *et al.*, 1999, and herein), several islands in the Marquesas (*M. clatratum* and *M. roseum*, herein), and Oeno and Henderson, Pitcairn group, SE Polynesia (*M. ponderosum*; Preece, 1995). The mode of

development of these species has been inferred from protoconch morphology to be planktotrophic. Larvae of *Morum* have not been positively identified in plankton catches from Pacific waters (see e.g. Scheltema & Williams, 1983), but this is not surprising in view of the rarity of the adults. With the Pitcairn Is and Fatu Hiva both younger than 2 MY (references cited by Preece, 1995; Duncan & McDougall, 1974), occurrence of species of *Morum* on such oceanic islands is best explained by the settlement of planktonic veligers originating from other insular populations in the Pacific. The patchy records of many species on the Pacific Plate largely reflects the fact that the archipelagoes of the South Pacific are still inadequately sampled. Considering its inferred mode of development, *M. clatratum* should not be expected to be a Marquesas endemic, but to have a more extensive distribution in the West Pacific.

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