# Diversity and distributions of the submarine-cave Neritiliidae in the Indo-Pacific (Gastropoda: Neritimorpha)

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## Abstract

Sediment samples from approximately 100 submarine caves on tropical islands in the Indian, Pacific and Atlantic oceans were examined to elucidate the global diversity and distribution of obligate submarine-cave snails of the family Neritiliidae. Shells accumulated from the Indo-West Pacific samples comprise five genera and nine species of extant neritiliids, whereas there were none from the Atlantic. Four new genera and four new species are herewith described: *Laddia lamellata*, *Micronerita pulchella*, *Teinostomops singularis* and *Siaesella fragilis*; previously known species include *Laddia traceyi* comb. n., *Pisulina adamsiana*, *Pisulina biplicata*, *Pisulina maxima* and *Pisulina tenuis*. Of these nine species, seven have wide, largely overlapping distributions; species richness is highest in and around the Indonesian and Philippine region, as in countless cases of shallow-water fishes, corals, echinoderms, bivalves and other gastropods. Examination of protoconch morphology revealed five species with a fairly long, planktotrophic larval period and four species with non-planktotrophic early development. No clear relationship was found between distribution range and dispersal capability deduced from the developmental mode, whereas the non-planktotrophs had higher levels of geographic differentiation in shell morphology. Fossil assemblages from cryptic environments suggest a Tertiary origin of the submarine-cave Neritiliidae. The oldest extant genus, *Laddia*, appeared in the Miocene, while two other Tertiary genera, *Bourdieria* and *Pisulinella*, have become extinct. The submarine-cave Neritiliidae thus do not seem to have remained in the same cave systems or the same local regions for millions of years, but seem to be relatively young, active colonizers of both continental and oceanic islands, having repeatedly expanded their distributions over the Indo-West Pacific. Despite the fact that they are undoubtedly restricted to caves and similar cryptic habitats, transoceanic dispersal appears to have played as important a role in forming present distributions as did tectonic events, in species with or without a planktotrophic larval period.
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## Introduction

Marine caves are nearly or completely dark, semi-closed ecosystems. Such caves maintain a stable and oligotrophic environment with little turbulence caused by wind and waves, and without photosynthesizers. Although the biomass per unit area is small, their cryptic fauna includes various invertebrate groups such as sponges, polychaetes, bryozoans, brachiopods, crustaceans and molluscs, many of which are obligate cave dwellers or stygobites. Some stygobites in marine caves have been regarded as relicts of archaic lineages with primitive characteristics; others show ecological and phylogenetic affinities with deep-sea species (e.g. Iliffe et al. 1984; Holsinger 1988; Kobluk 1988; Vacelet et al. 1994; Vacelet and Boury-Esnault 1995; Hayami and Kase 1993, 1996; Sket 1996; Harmelin 1997). Marine-cave environments may be classified into anchialine, littoral and submarine (Stock et al. 1986). Of these, special attention has been paid to anchialine caves where the water is brackish, diluted by rain, and supplied with terrestrial nutrients (Sket 1996; Pohlman et al. 1997). Anchialine caves have yielded many interesting invertebrate (mainly crustacean) taxa, including previously undescribed species, genera, families, orders and even a class (Iliffe et al. 1984; Boxshall and Iliffe 1987; Iliffe 2000).

Submarine caves, i.e. submerged cave passages filled with full-strength (euhaline) seawater, have attracted less attention from systematists and are usually regarded as a less restricted habitat where a 'normal' (epigean) marine fauna is able to immigrate and survive (Sket 1996). However, this is not entirely true, and unique taxa do exist in these caves. Submarine caves with a single entrance commonly consist of an outer twilight section supporting a high benthic population and an inner dark section with low benthic biomass and density (Gili et al. 1986; Fichez 1991; Hayami and Kase 1996). The outer section is often dominated by the brachiopod-sclerosponge community which is also found in less sheltered environments such as the undersides of corals and overhangs and the interior of crevices (Kobluk 1988); epigean species also occur accidentally in this section. In contrast, the inner section is inhabited by a special assortment of obligate submarine-cave species (e.g. Kase and Hayami 1992; Vacelet et al. 1994; Tabuki and Hanai 1999).

Since 1989 we have been conducting biological sampling in submarine caves on tropical and subtropical islands in the Indo-Pacific, Caribbean and Atlantic Oceans. During the course of these studies we have found a molluscan community that is distinctive in species composition and reproductive biology (Kase and Hayami 1992; Hayami and Kase 1993, 1996). A number of new and little known species have been discovered, as well as living features of many interesting species previously known only as empty shells (e.g. Hayami and Kase 1993; Kase and Kano 1999; Kano and Kase 2002). The molluscan material from submarine caves of karstic origin has many advantages for biogeographic studies. In this low-energy environment, the sediments on the cave floors are composed almost wholly of calcareous mud and bioclasts, containing molluscan shells and other organic remains. Physical, chemical and biological destruction or erosion is negligible and the shells are preserved in excellent condition for centuries (Hayami and Kase 1993, 1996; Kitamura et al. 2003). Although the density of individuals is extremely low in the oligotrophic cave environments, this good state of preservation allows us to accumulate large quantities of shell specimens that retain characters for species identification (see Bouchet et al. 2002). Moreover, various characteristics of the early developmental stages, i.e. the external features of embryonic and larval shells, are directly observable in the preserved shells (Kase and Hayami 1992; Hayami and Kase 1993; Kano and Kase 2000b). This condition makes the material suitable for the inference of ecology and dispersal ability of their larvae (e.g. Jablonski and Lutz 1983; Buckland-Nicks et al. 2002; Kano 2006). By taking advantage of these features Hayami and Kase (1996) documented and discussed the geographic distributions of diverse cave-dwelling bivalve species around the Philippine Sea, but no global-scale study has ever been carried out for a taxonomic group.

Here we focus on the gastropods of the Neritiliidae, a recently acknowledged monophyletic group in the superorder Neritimorpha or Neritopsina (Kano and Kase 2000b, 2002; Kano et al. 2002). The family includes three extant genera, *Neritilia*, *Platynerita* and *Pisulina*, which occupy an unusual range of habitats. *Neritilia* lives in freshwater streams, brackish estuaries, interstitial and anchialine waters and groundwaters, while *Platynerita* has been found only in streams (Sasaki and Ishikawa 2002; Kano and Kase 2003, 2004; Kano et al. 2003). Curiously, no marine species of the family is known from outside caves. *Pisulina* exclusively inhabits submarine caves (Kano and Kase 2000b, 2002; Kano et al. 2002), and a cryptic habit has been suggested also for the Miocene genus *Pisulinella* and the Oligocene *Bourdieria* (Kano and Kase 2000a; Lozouet 2004). Our recent study revealed that this group is more diverse in submarine caves than previously documented and that several species and genera remain to be described. The purposes of this paper are: (1) to describe new neritiliid taxa based on the extensive accumulated cave samples; (2) to illustrate the geographic distributions of the submarine-cave species, both newly named and previously known; (3) to infer their reproductive biology and dispersal capability from protoconch characteristics; and (4) to document and discuss the global diversity and biogeographic pattern of living and fossil species of the Neritiliidae.

## Material and methods

We collected sediment samples from the floors of approximately 100 submarine caves on tropical and

subtropical islands in the Indo-Pacific, Caribbean and Atlantic Oceans, with the help of skilled SCUBA divers. The surveyed caves vary in size and topography, but mostly are meandering limestone grottoes formed by groundwater during some lower sea-level stages. Because these caves are now hydrologically inactive, the temperature and salinity of the cave waters seem to be almost equal to those of the open sea throughout the year. The cave sediments are generally very fine, except for organic remains, and almost free of terrigenous clastic materials. Tubular sediment cores taken at the innermost parts of some caves indicated that the environment seems to have been maintained under tranquil but never oxygen-depleted conditions (Hayami and Kase 1996). Radiocarbon dating suggested that sedimentation in a cave in Okinawa is as slow as in bathyal trough and trench environments, and that molluscan shells are preserved in excellent condition for centuries (Kitamura et al. 2003).

The collected sediments were sieved with a 0.5-mm mesh and the shells were picked out under binocular microscopes. The characteristic protoconch and teleoconch morphology as well as shell microstructure readily distinguish the neritiliid shells from other micromollusc shells (Kano and Kase 2000a, b, 2001, 2002). Despite our extensive sorting, the sediments from the Caribbean (i.e. Grand Cayman) and Atlantic (Bermuda) caves have not yielded any neritiliids, whereas the latter were abundant in the majority of the Indo-West Pacific samples. Fig. 1 shows the explored islands and island groups in the Indo-West Pacific region, including Cocos and Christmas (Indian Ocean), Phuket (Andaman), Okinawa, Cebu, Sipadan (Sabah), Bali, Ogasawara (or Bonin), Saipan (Marianas), Yap, Palau, Pohnpei (Caroline), Majuro (Marshall), Nauru, Hawai'i, Vanuatu, New Caledonia, Fiji, Tonga, and Tahiti (French Polynesia). We found many semi-closed cave ecosystems with a number of presumably stygobite invertebrates in Christmas, Okinawa, Sipadan, Saipan, Palau, Hawai'i, Vanuatu, New Caledonia, Fiji, Tonga and Tahiti, and our samples from these islands and island groups should be representative of the species diversity of submarine-cave molluscs in those regions. Conversely, limited sampling effort and/or the lack of appropriate collection sites in Cocos, Bali, Ogasawara and Majuro resulted in low numbers of recovered neritiliid species, so that the diversity of the family is likely to be underestimated there.

Most of the accumulated neritiliids belonged to *Pisulina*, a genus revised in an earlier study (Kano and Kase 2000b), but a total of over 500 specimens were found to belong to other members of the family. We prepared approximately 100 such shells for scanning electron microscope (SEM) observation using standard techniques: cleaning with an ultrasonic cleaner, drying, mounting on stages, coating with gold and examination

under a SEM (JEOL T330A) or in a low-vacuum mode without metal coating in another SEM (JEOL 5200LV). The holotype of the Miocene species 'Neritilia' traceyi Ladd, 1965 from the Bikini Atoll was loaned from the US National Museum of Natural History, Washington D.C. (USNM), and examined and photographed under the 5200LV. The remaining material is deposited in the National Science Museum, Tokyo (NSMT), or the Muséum National d'Histoire Naturelle, Paris (MNHN). Terminology follows Kano and Kase (2000b).

Kano and Kase (2000b) discovered living individuals of *Pisulina adamsiana* Nevill & Nevill, 1869 and *P. maxima* Kano & Kase, 2000 from the totally dark, innermost parts of caves, while other species of the submarine-cave Neritiliidae were represented only by empty shells. This is probably because they live in narrow fissures of the caves (see Tabuki and Hanai 1999) and at the same time they are exceedingly rare (see Bouchet et al. 2002). As noted above, conchological characters are very useful in species identification and familial assignment for neritiliids, but phylogenetic relationships within the family are often deducible exclusively from soft-part anatomy or molecular analysis (e.g. Kano and Kase 2002, 2004). Hence, sound generic assignment is difficult for new species represented only by empty shells. The species described herein are all distinct in conchological features (especially in protoconch morphology) from the species of the known five genera and from each other. We therefore establish several new genus-level taxa, rather than allocating the new species to known extant genera, which are defined using a number of anatomical and radular characters (Kano and Kase 2002, 2003).

## Systematic section

Family Neritiliidae Schepman, 1908.

### *Laddia* gen. n.

**Etymology**

Named after the American palaeontologist Harry Stephen Ladd, who thoroughly studied Cenozoic fossil gastropods from Pacific islands. Gender of genus name: feminine.

**Type species**

*Neritilia traceyi* Ladd, 1965.

**Diagnosis**

Shell small, up to 4.7 mm, white, elliptic or hemispherical. Protoconch multispiral, inclined relative to teleoconch; embryonic shell covered with a thin calcareous layer; larval shell with several spiral ridges near
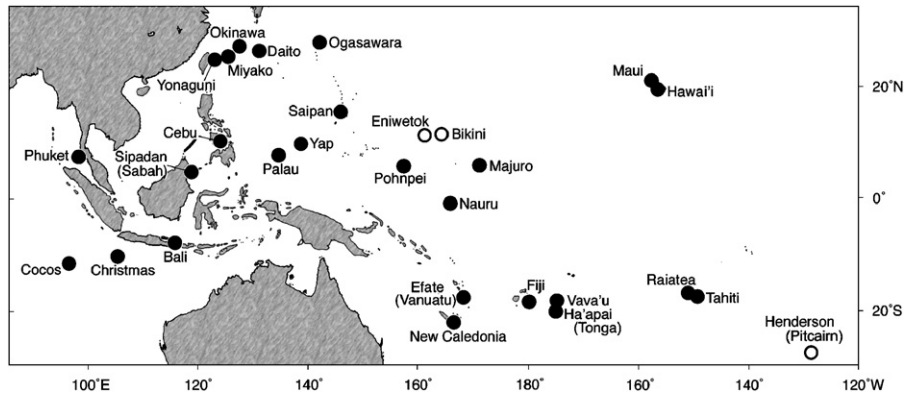
**Fig. 1.** Map showing localities of submarine cave samples in the Indo-West Pacific (solid circles). Open circles denote fossil faunas with submarine-cave neritiliid genera in this region.

aperture. Early teleoconch sculptured with sparse, ca. 3 μm wide spiral ridges. Teleoconch aperture without protuberance inside; adaxial margin of inner lip convex or slightly sinuous.

### Remarks

The type species, *Laddia traceyi*, was described from a single fossil specimen recovered from a drill hole on Bikini Atoll. In his original description Ladd (1965) assigned this Miocene species to the fresh- and brackish-water genus *Neritilia*. He stated that the shell shape of *L. traceyi* is comparable to those of the Recent *Neritilia*, especially in sharing the edentulous inner lip of the aperture, and this led him to conclude that *L. traceyi* was a non-marine species which lived in pools of fresh or brackish water that once existed on Bikini (Ladd 1965, 1966). However, *Laddia* is an exclusively submarine cave inhabitant, and numerous specimens morphologically identical to the holotype have been found in Recent caves in the Indo-West Pacific.

*Laddia* resembles another submarine-cave genus, *Pisulina*, rather than *Neritilia* in shape and colour of the teleoconch (Fig. 2A–D). However, we consider that *Laddia* is phylogenetically closer to *Neritilia* and *Platynerita*, as the three genera share a characteristic, thin calcareous layer covering the embryonic shell (Fig. 2E, F; Kano and Kase 2003, figs. 4, 6). To our knowledge such a layer has never been found in other neritiliids (Table 1) or any other gastropods. On the other hand, a remarkable structure found in *L. traceyi* and *Laddia lamellata* sp. n. seems to warrant creating the new genus: the two species have sparse, fine spiral ridges on the early teleoconch whorls (Figs. 2E, F and 3B, C), whereas no such ridges are present in *Neritilia* or *Platynerita*. The new genus further differs from *Neritilia* and *Platynerita* in lacking a protuberance inside the teleoconch aperture near the base (see Kano and Kase 2001, fig. 3), as in the submarine-cave *Pisulina* and *Pisulinella*. The presence and absence of the protuberance may also suggest concentric and paucispiral

opercula, respectively (see below). *Laddia* thus might represent a transitional evolutionary state between the two submarine-cave genera and the limnic *Neritilia* and *Platynerita*.

### *Laddia traceyi* (Ladd, 1965) comb. n.

*Neritilia traceyi* Ladd, 1965: pp. 191, 192, pl. 1: figs. 3, 4. – Ladd (1966, p. 57, 58, pl. 10: figs. 26, 27).

### Material examined

Holotype (USNM 648336): Drill hole 2B at depth of 2154–2164.5 feet (656.5–659.7 m), Bikini Atoll, Marshall Islands; Lower Miocene [Tertiary *e*].

Additional material: AUSTRALIA – cave near 'Boat Cave' diving site, near McPherson Point, north coast of Christmas Island, Indian Ocean, depth 2.4 m, November 1999, 2 specimens (NSMT-Mo73779); cave at 'Thunder Dome' diving site, north coast of Christmas Island, 10°28.4′S, 105°36.4′E, depth 7.7–10.2 m, December 1999, 4 specimens (NSMT-Mo73780). JAPAN – cave at 'W-arch' diving site, northwest of Irabu Island, Miyako Islands, Okinawa, 24°51.7′N, 125°09.7′E, depth 13–15 m, 1992, 1 specimen (NSMT-Mo73781). NORTHERN MARIANAS – cave near 'Grotto' diving site, north of Saipan Island, 15°15.3′N, 145°49.5′E, depth 12–30 m, November 1997, 103 specimens (30 specimens NSMT-Mo73782); cave near 'Tinian Grotto' diving site, west of Tinian Island, depth 51 m, November 1997, 1 specimen (NSMT-Mo73783). HAWAI'I – 'Worm Cave' diving site, off Ahihi-Kinau, Makena, Maui Island, 20°35.3′N, 156°25.8′W, depth 26 m, October 1997, 1 specimen (NSMT-Mo73784); 'Bubble Cave' diving site, off Ahihi-Kinau, 20°38.9′N, 156°26.3′W, depth 2 m, October 1997, 1 specimen (NSMT-Mo73785); 'Long Lava Tube' diving site, off Pali Kaholo, South Kona, Hawai'i Island, 19°21.8′N, 155°56.8′W, depth 8–11 m, November 1997, 9 specimens (NSMT-Mo73786); 'Gustav Cave', off Ka'û Loa Point,
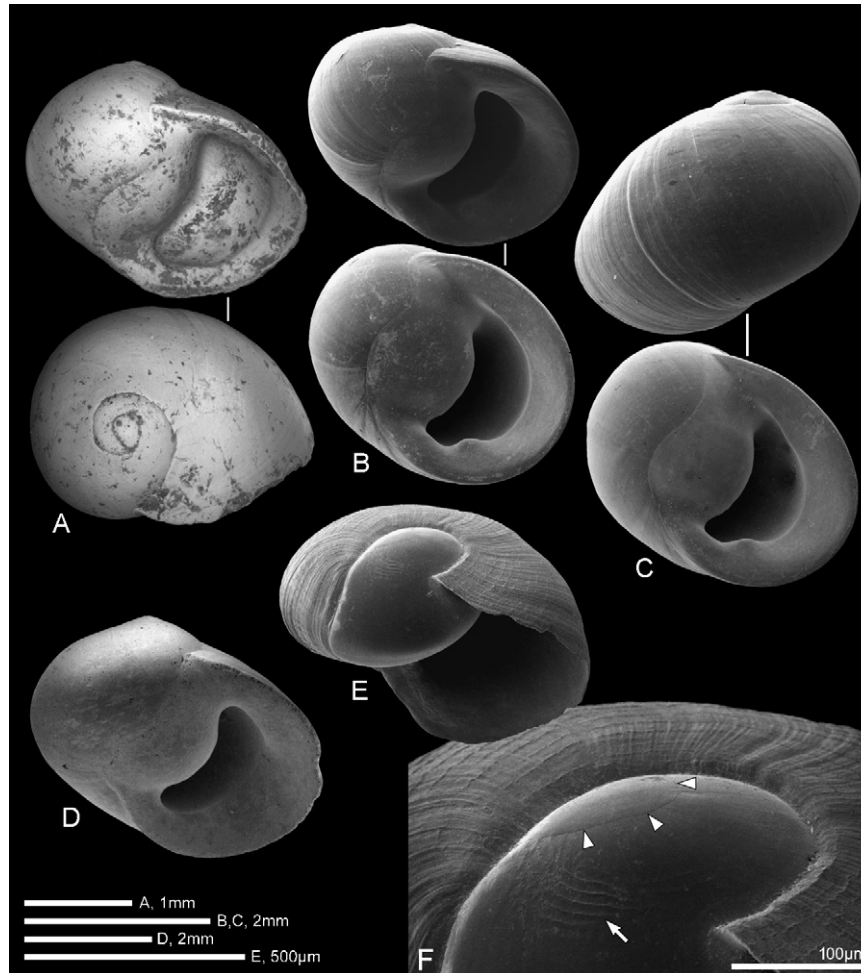
**Fig. 2.** *Laddia traceyi* (Ladd, 1965) comb. n. (A) Frontal and apical views of holotype from Bikini, Marshall Islands (USNM 648336). (B) Frontal and apertural views, Nauru (NSMT-Mo73788). (C) Posterior and apertural views, Nauru (NSMT-Mo73788). (D) Frontal view, Saipan Island, Marianas (NSMT-Mo73782). (E) Oblique apical view of juvenile specimen with 0.7 of a teleoconch whorl, Hawai'i Island (NSMT-Mo73786). (F) Close-up of protoconch in E, showing presence of 5 spiral ridges on shoulder near aperture (arrow) and thin calcareous layer spread over embryonic shell (arrowheads).

South Kona, 19°19.1′N, 155°53.2′W, depth 8 m, November 1997, 1 specimen (NSMT-Mo73787). NAURU – cavern, off Aiwo, 0°32.6′S, 166°54.5′E, depth 15–25.5 m, November 1999, 334 specimens (100 specimens NSMT-Mo73788; 50 specimens MNHN).

**Distribution and age**

Southeast Asia to central Pacific (Fig. 4A). Early Miocene to Recent.

**Description**

Shell small, up to 4.60 mm wide, 3.89 mm high, 4.72 mm in maximum dimension (2.67, 2.16 and 2.75 mm, respectively, in holotype), white (cream in holotype), thick, solid, elliptic- to oval-neritiform with a low spire (Fig. 2A–D). Multispiral larval shell ovate, about 360 μm wide and 250 μm high, largely surrounded by first teleoconch whorl; exposed drop-shaped area 270–350 μm in maximum dimension (Fig. 2E); surface smooth except for faint growth lines and 5 or 6 spiral ridges on shoulder near aperture; a very thin additional calcareous layer spreads over apex, covering embryonic shell (Fig. 2F); apertural lip slightly convex at middle, very discordant with first teleoconch whorl. Teleoconch whorls up to 2.5 in number, inflated with round periphery; suture shallowly impressed; surface sculptured with sparse, ca. 3 μm wide spiral ridges in early whorls (Fig. 2E, F) but smooth in last whorl except for faint growth lines. Aperture narrow, crescent-shaped; outer lip sharp along margin, heavily thickened interiorly into a distinct inner ridge that bears a tubercle near base; inner lip covered with a smooth, thick, widely spread callus; adaxial margin of inner lip convex, with several indistinct teeth.

**Remarks**

*Laddia traceyi* was originally described from an early Miocene specimen recovered from the drill hole 2B on

**Table 1.** Conchological characteristics of neritiliid genera

| Genus | Maximum shell size[a] | Inner lip tooth[b] | Outer lip teeth[c] | Internal protuberance[d] | Protoconch formation[e] | Larval shell layer[f] |
|---|---|---|---|---|---|---|
| *Pisulina* | 4.0–13.7 | 1 | 0 | 0 | 0/1 | 0 |
| *Pisulinella*[†] | 2.9–4.0 | 1 | 1 | 0 | 0 | 0 |
| *Bourdieria*[†] | 4.0 | 1 | 1 | 0 | 0 | 0 |
| *Micronerita* | 2.3 | 1 | 0 | 0 | 1 | – |
| *Siaesella* | 2.3 | 0 | 0 | 0 | 0 | 0 |
| *Teinostomops* | 2.0 | 0 | 0 | 1 | 0 | 0 |
| *Laddia* | 3.2–4.7 | 0/1 | 0 | 0 | 0 | 1 |
| *Platynerita* | 6.3 | 0 | 0 | 1 | 0 | 1 |
| *Neritilia* | 1.4–5.7 | 0 | 0 | 1 | 0 | 1 |

[a]Range of maximum shell sizes (mm) of included species.
[b]Inner lip of teleoconch aperture: 0 = edentulous, 1 = bearing a tooth or teeth.
[c]Outer lip of teleoconch aperture: 0 = edentulous, 1 = bearing several teeth or weak protuberances interiorly.
[d]Protuberance inside teleoconch aperture near base: 0 = absent, 1 = present.
[e]Protoconch formation (and supposed early development of animal): 0 = multispiral (planktotrophic), 1 = paucispiral (lecithotrophic or benthic).
[f]Thin calcareous layer covering embryonic shell: 0 = absent, 1 = present.
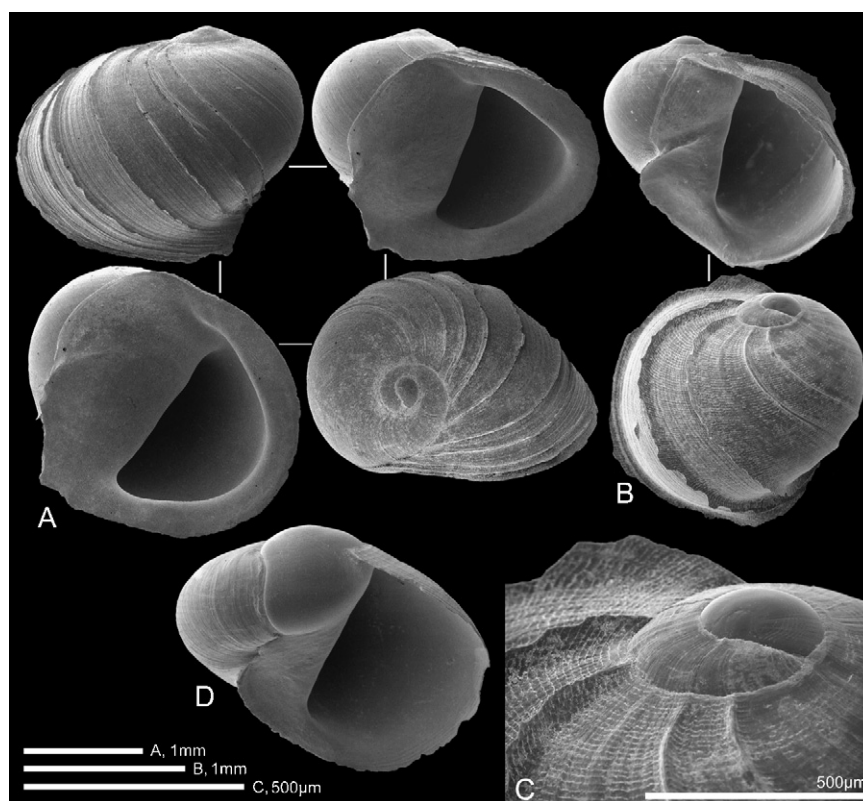[†]Extinct genera.



**Fig. 3.** *Laddia lamellata* sp. n. (A) Posterior, frontal, apertural and apical views of holotype (NSMT-Mo73789). (B) Oblique apertural and posterior views of immature paratype (NSMT-Mo73790). (C) Close-up of apex in B, showing fine spiral ridges on early teleoconch whorls. (D) Frontal view of juvenile paratype with 0.8 of a teleoconch whorl (NSMT-Mo73790). All specimens from Long Lava Tube, Hawai'i Island.

Bikini Island. Based on an apparent resemblance in shell shape, Ladd (1965) allocated this species to the limnic genus *Neritilia* as the oldest freshwater mollusc known from the open Pacific. The same drill hole yielded another freshwater snail, *Gyraulus bikiniensis*, at a depth of 1723–1734 feet (Ladd 1965), as well as a high-island land snail, *Ptychodon subpacificus*, at a depth of 1807–1818 feet (Ladd 1958). Ladd argued that the
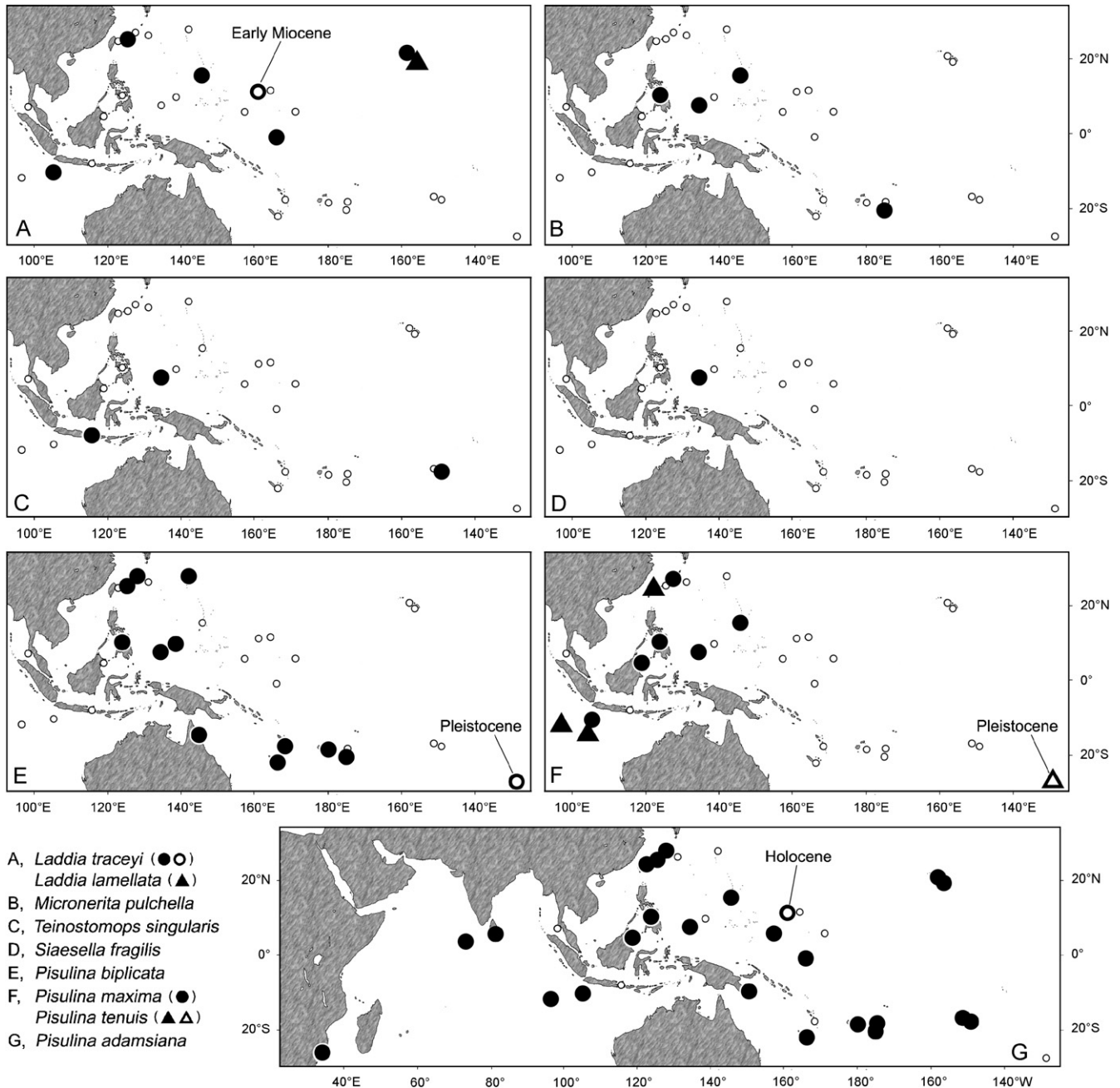
**Fig. 4.** Collection sites of nine submarine-cave neritiliid species (solid circles and triangles). Fossil occurrence of four species is shown as open circles and triangle in A and E–G. Small open circles denote localities of submarine cave samples that did not yield species concerned. Some specimens of *P. biplicata* and *P. adamsiana* were accumulated from beach drifts and dredged samples; most probably they had been transported from cryptic habitats by water movements, gravity or hermit crabs (see Kano and Kase 2000b).

occurrence of these non-marine molluscs further supports the conclusion from a petrographic study of the limestones, that during the Miocene Bikini and nearby Eniwetok stood higher above the sea than they do today (Schlanger 1963). However, the holotype of *L. traceyi* (Fig. 2A) is morphologically identical with the young shells of this species accumulated from the Recent submarine caves, and no such shells have been found in freshwater streams or brackish waters. This suggests

that *L. traceyi* is not a freshwater species but has long lived in the submarine-cave environment. Besides the non-marine *Gyraulus* and *Ptychodon*, the Miocene section of that drill hole yielded a number of marine gastropods (Ladd 1966, 1972, 1977), including the cave neritiliid *Pisulina subpacifica* Ladd, 1966.

It is interesting to note how similar the early Miocene holotype is to the Recent specimens, despite the great time gap of some 20 million years between them.

The submarine cave environment harbours 'living fossil' molluscs that have not altered their morphology over a long geological period (Kase and Hayami 1992; Hayami and Kase 1996). Another neritimorph gastropod, *Neritopsis radula* (Linnaeus, 1758), is such an example: today this species exclusively inhabits submarine caves and similar cryptic voids (Kano et al. 2002), and its fossil record dates back to the Eocene (Batten 1984). Moreover, Ladd (1960) argued that the central Pacific islands including Bikini were the centre of dispersal for various marine organisms and that the species diversity of molluscs there was higher in the Miocene than it is today (see Discussion section below). Thus the similarity between the Miocene and Recent specimens of *L. traceyi* is possibly attributed to the antiquity of the submarine-cave habitat and to the morphological conservatism of that cave species over a long timespan. On the other hand, Ladd also mentioned that during the deep-drilling operation micro-shells may have circulated in the drilling fluid, so there is some doubt as to the exact depth from which the shells were derived and whether they possibly came from a somewhat shallower horizon (Ladd 1965). In the latter case, *L. traceyi* may not have existed in the early Miocene and may actually be a younger species.

This species is a relatively common component of the Neritiliidae in the Recent submarine caves of Christmas in the Indian Ocean, the Marianas, Nauru and Hawai'i, and probably in unexplored caves of other oceanic islands in the western to central Pacific, yet it is much less numerous than the species of *Pisulina* and no living specimen has been discovered.

## *Laddia lamellata* sp. n.

### Etymology
The species epithet refers to the lamellated teleoconch; it is adjectival for the purposes of nomenclature.

### Type material
Holotype (NSMT-Mo73789): empty shell from 'Long Lava Tube' diving site, off Pali Kaholo, South Kona, Hawai'i Island, 19°21.8′N, 155°56.8′W, depth 8–11 m, November 1997. Paratypes: HAWAI'I – type locality, November 1997, 11 specimens (NSMT-Mo73790); 'Gustav Cave', off Ka'û Loa Point, South Kona, Hawai'i Island, 19°19.1′N, 155°53.2′W, depth 8 m, November 1997, 2 specimens (NSMT-Mo73791).

### Distribution and age
Known only from Hawai'i Island, Hawai'i (Fig. 4A). Recent.

## Description
Shell small, up to 3.15 mm wide, 2.39 mm high, 3.18 mm in maximum dimension (2.83, 2.29 and 2.86 mm, respectively, in holotype), white, thin, hemi-spherical-neritiform with a low spire (Fig. 3A, B). Protoconch nearly identical to *L. traceyi*, with exposed drop-shaped area 300–350 μm in maximum dimension (Fig. 3C, D). Teleoconch whorls up to 2.1 in number, inflated with round periphery; suture shallowly impressed; surface ornamented with thin, irregularly spaced axial lamellae and sculptured with sparse, ca. 3 μm wide spiral ridges in early whorls (Fig. 3B, C). Aperture wide, semicircular in outline; outer lip sharp along margin, thickened into a distinct inner ridge along its interior; inner lip covered with a smooth, very widely spread callus; peristome projected at lower columellar side as a thin plate with its tip turned up; adaxial margin of inner lip slightly sinuous.

## Remarks
*Laddia lamellata* is morphologically distinct from the type species, *L. traceyi*, in having a flared apertural lip and thin axial plates on the teleoconch whorls (Fig. 3A, B). Even in juvenile specimens, the apertural lip of the present species projects at the lower columellar side as a thin plate (Fig. 3B, D). The two *Laddia* species are also different in shell thickness (much thinner in *L. lamellata* than in *L. traceyi*), and this probably accounts for the presence or absence of ornamentation at the margin of the apertural inner lip (simple and nearly straight in the former, callous with indistinct teeth in the latter). Otherwise, their shells are very similar; especially their protoconch morphology and surface microsculpture of the teleoconch whorls are identical. One might assume that the lamellated specimens are an ecophenotype of *L. traceyi*, but the absence of intermediate forms and their co-occurrence in the caves of Hawai'i Island seem to justify their separation as two independent species.

## *Micronerita* gen. n.

### Etymology
A combination of *mikros* (Greek), meaning small, and *Nerita*, a genus of gastropods of similar shell shape. Gender of genus name: feminine.

### Type species
*Micronerita pulchella* sp. n.

### Diagnosis
Shell minute, up to 2.3 mm, white, elliptic. Protoconch paucispiral, without inclination with respect to teleoconch, smooth but ornamented by ca. 15 wavy spiral

ridges close to aperture. Teleoconch aperture without protuberance inside; adaxial margin of inner lip convex.

### Remarks

The sole species of the genus, *M. pulchella*, has a paucispiral, smooth protoconch (Fig. 5B, E–G), suggesting a benthic or lecithotrophic early development (see Discussion). The multispiral protoconch in planktotrophic species of Neritiliidae bears a diagnostic conchological feature of the family: the tilted coiling axis of the whorls and the several spiral ridges on the shoulder near the aperture (see Fig. 2F; Kano and Kase 2000b, figs. 4, 10). Despite the absence of these two major characters, the shape of the teleoconch whorls and aperture clearly indicates phylogenetic affinity with the other members of Neritiliidae, especially the submarine cave genus *Pisulina*. Additionally, the squarish projection on the inner apertural margin of the holotype (Fig. 5A) somewhat approaches the conspicuously quadrangular protuberance in *P. adamsiana* and *P. subpacifica* (Kano and Kase 2000b, figs. 1, 15). The present species also resembles some cryptic species of the freshwater and brackish water genus *Neritilia*, i.e. *N. pusilla* (Adams, 1850) and *N. littoralis* Kano, Kase & Kubo, 2003, in the gross shape and size of the teleoconch (Kano and Kase 2001; Kano et al. 2003), but its aperture differs in lacking the protuberance inside and in having the convex adaxial margin of the inner lip.

Paucispiral protoconchs and non-planktotrophic early development have repeatedly evolved from the plesiomorphic multispiral protoconch and planktotrophic development, respectively, in the superorder
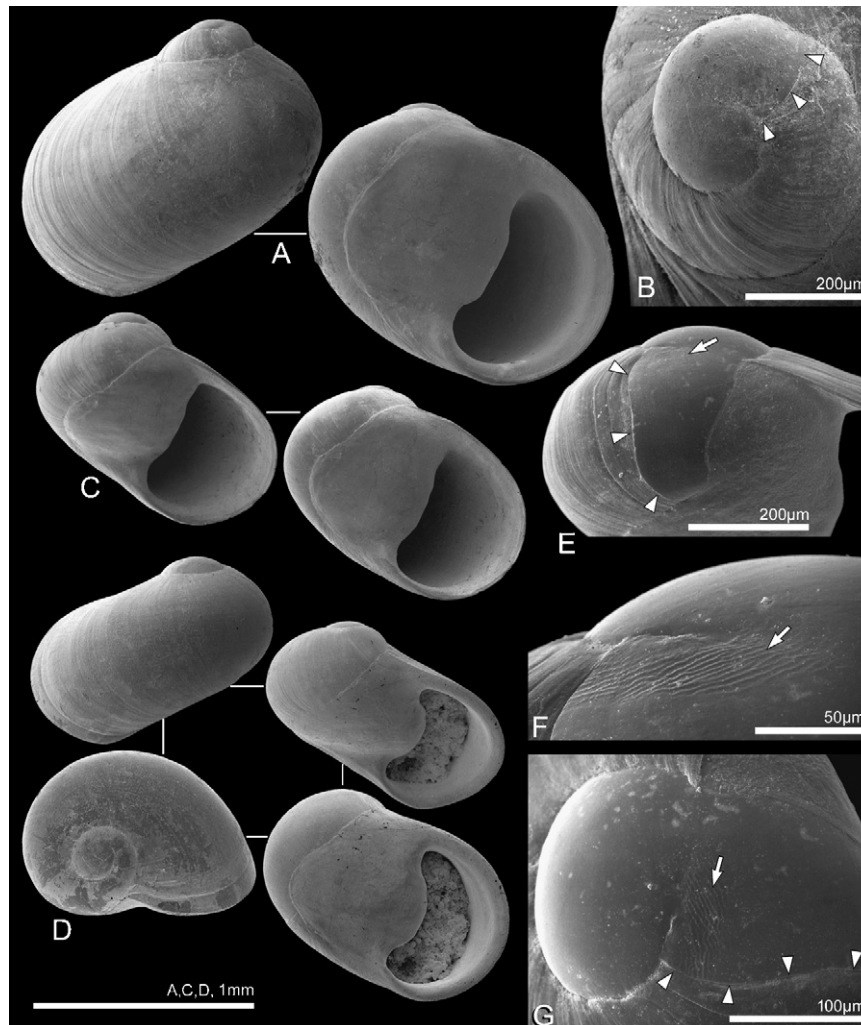


**Fig. 5.** *Micronerita pulchella* sp. n. (A) Posterior and apertural views of holotype from Saipan, Northern Marianas (NSMT-Mo73792). (B) Close-up of apex in A, showing demarcation line of paucispiral protoconch (arrowheads). (C) Frontal and apertural views of paratype from type locality (NSMT-Mo73794). (D) Posterior, frontal, apical and apertural views of paratype from Palau (NSMT-Mo73793). (E) Frontal view of juvenile paratype with 0.8 of a teleoconch whorl, Ha'apai, Tonga (NSMT-Mo73797), showing presence of wavy spiral ridges close to aperture (arrow) and demarcation line of apertural lip (arrowheads). (F) Close-up of spiral ridges in E. (G) Oblique apical view of paucispiral protoconch in E.

**Table 2.**  Characteristics of the protoconch in submarine-cave Neritiliidae

| Species | Diameter and height (µm) | Shape[a] | Presumed early development |
|---|---|---|---|
| *Pisulina adamsiana* | 360 × 250 | m | Planktotrophic |
| *Pisulina subpacifica*[†] | No data | m | Planktotrophic |
| *Pisulina biplicata* | 310 × 250 | p | Non-planktotrophic |
| *Pisulina maxima* | No data | p | Non-planktotrophic |
| *Pisulina tenuis* | 330 × 270 | p | Non-planktotrophic |
| *Pisulinella miocenica*[†] | No data | m | Planktotrophic |
| *Pisulinella aucoini*[†] | No data | m | Planktotrophic |
| *Bourdieria faviai*[†] | No data | m | Planktotrophic |
| *Laddia traceyi* | 360 × 250 | m | Planktotrophic |
| *Laddia lamellata* | 360 × 250 | m | Planktotrophic |
| *Micronerita pulchella* | 360 × 300 | p | Non-planktotrophic |
| *Teinostomops singularis* | No data | m | Planktotrophic |
| *Siaesella fragilis* | 530 × 380 | m | Planktotrophic |
| *Neritilia vulgaris*[b] | 360 × 250 | m | Planktotrophic |

[a]Protoconch shape: m = multispiral, p = paucispiral.
[b]Limnic species for comparison (Kano and Kase 2003).
[†]Extinct species.

Neritimorpha (Holthuis 1995; Kano 2006). Therefore a common presence of simple paucispiral protoconchs in two or more neritimorph taxa does not necessarily indicate close relations. Among the Neritiliidae a paucispiral protoconch has been found in *P. maxima*, *Pisulina biplicata* Thiele, 1925 and *Pisulina tenuis* Kano & Kase, 2000. These three *Pisulina* species are similar in teleoconch morphology and probably constitute a clade in the genus, i.e. they should have a common ancestor with this paucispiral protoconch (Kano and Kase 2000b). In contrast, this protoconch of *Pisulina* differs from that of *Micronerita pulchella* in the surface microsculpture. The former has 15–25 longitudinal folds near the suture with the first teleoconch whorl (Kano and Kase 2000b, fig. 5), while the latter instead has approximately 15 wavy spiral ridges close to the aperture (Fig. 5E–G). Their sizes are also a little different (Table 2). The morphological differences between protoconchs in *Pisulina* and *Micronerita* may thus represent independent evolution of non-planktotrophic development; the relative uniformity of teleoconch shape in all members of *Pisulina* also suggests that the three non-planktotrophic *Pisulina* are more closely related to the planktotrophic *P. adamsiana* than to the non-planktotrophic *M. pulchella*.

## *Micronerita pulchella* sp. n.

### Etymology

From *pulchellus* (Latin), meaning pretty. The species epithet is adjectival for the purposes of nomenclature.

### Type material

Holotype (NSMT-Mo73792): empty shell from cave near 'Grotto' diving site, north of Saipan Island, Northern Marianas, 15°15.3′N, 145°49.5′N, depth 18 m, November 1997. Paratypes: PALAU – 'Virgin Hole' diving site, west of Ngemelis Island, Rock Islands, 7°07.3′N, 134°14.1′E, depth 17 m, April 1995, 14 specimens (NSMT-Mo73793). NORTHERN MARIANAS – type locality, depth 13–21 m, November 1997 and October 1999, 13 specimens (7 specimens NSMT-Mo73794; 6 specimens MNHN); cave near 'Tinian Grotto' diving site, west of Tinian Island, depth 50–51 m, November 1997, 15 specimens (NSMT-Mo73795). PHILIPPINES – cavern off Balicasag Island, Panglao, Bohol, 9°32.7′N, 123°40.7′E, depth 17–40 m, May 1994, 1 specimen (NSMT-Mo73796). TONGA – cave west of Mo'ung'one Island, Ha'apai Group, 19°23.2′S, 174°28.6′W, depth 26 m, November 1996, 4 specimens (NSMT-Mo73797).

### Distribution and age

Southeast Asia to South Pacific (Fig. 4B). Recent.

### Description

Shell small, up to 2.26 mm wide, 1.79 mm high, 2.30 mm in maximum dimension (1.50, 1.35 and 1.54 mm, respectively, in holotype), white, thin but solid, elliptic- to elongate-neritiform with a relatively high spire and a pointed apex (Fig. 5A, C, D). Protoconch paucispiral, about 360 µm wide and 300 µm high, simple dome-shaped in apical view, glossy, smooth, without inclination to teleoconch (Fig. 5B); visible portion surrounded by teleoconch 300–350 µm in maximum dimension, ornamented by ca. 15 wavy spiral ridges close to aperture (Fig. 5E–G); apertural lip slightly sinuous, clearly demarcated from teleoconch. Teleoconch whorls up to 1.6 in number, inflated with round periphery; suture shallowly impressed; surface smooth except for faint growth lines. Aperture wide to

relatively narrow, semicircular to crescent-shaped; outer lip slightly thickened along its interior; inner lip covered with a smooth, thin, widely spread callus; adaxial margin of inner lip roundly convex, with several indistinct teeth (Fig. 5D) or bearing a somewhat squarish protuberance (Fig. 5A).

### Remarks

Although this species has a paucispiral protoconch and consequently lecithotrophic or benthic early development (see Discussion), its geographic distribution is relatively wide, ranging from the Philippines to Tonga (Fig. 4B), and shells from these peripheral islands are identical to those collected from the type locality (Northern Marianas; Fig. 5A, C). However, specimens collected from Palau, near the centre of the distribution area, are different from the holotype in having a more elongate outline of the shell, a smaller aperture and a roundly convex (rather than squarish) margin of the apertural inner lip (Fig. 5D). These morphological differences may represent genetic divergence and reproductive isolation of the Palau population from others, but their teleoconchs are otherwise unremarkable and the size and shape of the protoconch are identical in all specimens. We tentatively treat the Palau specimens as an intraspecific variation of *M. pulchella*.

## *Teinostomops* gen. n.

### Etymology

Referring to *Teinostoma*, a vitrinellid genus of similar shell shape. Gender of genus name: masculine.

### Type species

*Teinostomops singularis* sp. n.

### Diagnosis

Shell minute, up to 2.0 mm, white, ovate. Protoconch multispiral, slightly inclined relative to teleoconch; embryonic shell partly exposed; larval shell sculptured with many pits bearing granules; suture line of larval shell descending near aperture, revealing previous suture. Teleoconch aperture with two protuberances inside at upper and lower columellar sides; adaxial margin of inner lip edentulous, slightly concave.

### Remarks

This new genus is known from only four empty shells of the type species, *T. singularis*. Their shape is reminiscent of certain vitrinellids (Caenogastropoda) in having a somewhat depressed umbilical area, a thin callus and a slightly concave adaxial margin of the apertural inner lip (Fig. 6A, C). However, the inclined, convolute protoconch whorls visible in the four

shells clearly indicate a phylogenetic position in the Neritiliidae.

In contrast, the protoconch of *T. singularis* exhibits unique features that warrant the separation of the new species from other neritiliids at generic level. In this family multispiral protoconchs convolute strongly and their suture line generally abuts the surface more adapical to the previous suture, so that the number of coils cannot be counted from the outside (Kano and Kase 2000b). However, the last protoconch whorl in *T. singularis* descends near the aperture, so that the previous suture and approximately 1.4 whorl of the larval shell can be seen (Fig. 6D). This protoconch is also unique in having less inclination (ca. 10°) of the coiling axis than in other genera of the family (e.g. ca. 30° in *Pisulina* and *Pisulinella*; Kano and Kase 2000a, b).

The apparent absence of spiral ridges in the protoconch is another peculiarity diagnostic of *T. singularis*. The multispiral protoconchs of Neritiliidae have several spiral ridges on the shoulder near the aperture (e.g. Fig. 2F), and the ridges are a major conchological trait of the family (Kano and Kase 2000b). In *T. singularis*, however, the inclination of the protoconch coiling axis is small and the last protoconch whorl descends adapically near the aperture, so that the first teleoconch whorl most probably covers the ridges on the protoconch shoulder. The minute pits and granules within, which are scattered all over the surface of the larval shell without any evident pattern (Fig. 6E), are still another protoconch feature diagnostic of *T. singularis*. Similar pits with granules have been found in *Pisulina adamsiana*, but in that species the pits appear only near the aperture of the larval shell, arranged in a spiral direction, and sometimes give rise to short grooves by being connected with each other (Kano and Kase 2000b, fig. 4C, D). The pits in the protoconchs of *Neritilia rubida* (Pease, 1865), *N. succinea* (Récluz, 1841), and *N. manoeli* (Dohrn, 1866) are randomly scattered all over the surface of the larval shell, but differ from those of *T. singularis* in being tinier and denser and in lacking granules within (Kano and Kase 2000b, fig. 10B; Kano and Kase 2003).

The edentulous aperture of the type species, as well as its inside protuberances on the upper and lower columellar sides (Fig. 6B), suggests certain phylogenetic affinities within the family Neritiliidae. All species of the fresh- and brackish-water *Neritilia* and *Platynerita* possess comparable edentulous apertures with a protuberance inside at the base (Kano and Kase 2001, 2003), whereas the apertures of other submarine-cave genera are usually ornamented with a tooth or teeth on the inner and/or outer lip and always lack the protuberance inside (Kano and Kase 2000a, b; Lozouet 2004). In the former, limnic genera the operculum has a flat outer surface and an outline that conforms to the interior outline of the aperture (see Kano and Kase
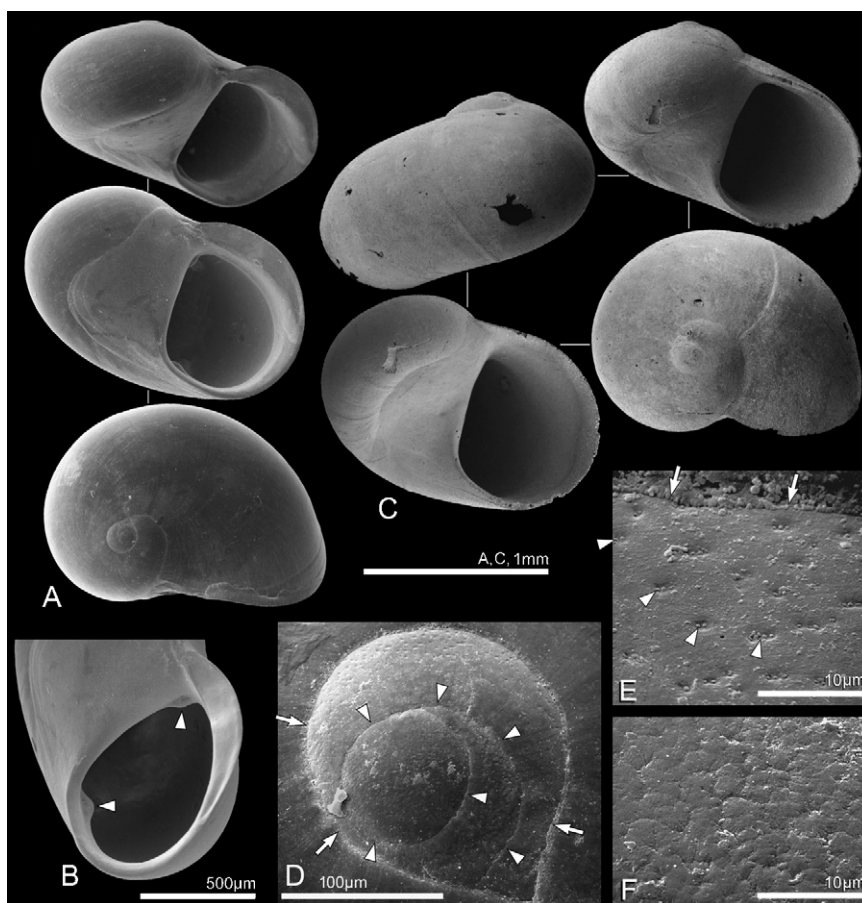
**Fig. 6.** *Teinostomops singularis* sp. n. (A) Anterior, apertural and apical views of holotype from Bali, Indonesia (NSMT-Mo73798). (B) Oblique view of aperture in A, showing protuberances inside at upper and lower columellar sides (arrowheads). (C) Posterior, frontal, apertural and apical views of paratype from Palau (NSMT-Mo73800). (D) Multispiral protoconch of holotype, showing suture lines of larval shell (arrowheads) and first teleoconch whorl (arrows). (E) Close-up of larval shell surface in D, showing pits and granules within (arrowheads) near suture line of teleoconch whorl (arrows). (F) Close-up of reticulate surface of embryonic shell in D.

2003, figs. 1, 3), and when it retracts, the protuberance acts as its innermost stop. In *Pisulina* (the only submarine-cave neritiliid genus collected alive), on the other hand, the operculum has a concave exterior surface (Kano and Kase 2000b, fig. 8) that allows its deep retraction into the narrow aperture. *Teinostomops* may thus have a flat, aperture-fitting operculum and closer relations to *Neritilia* and *Platynerita*.

The protoconch of *T. singularis*, however, lacks the characteristic, undoubtedly homologous layer covering embryonic shells in all species of *Neritilia*, *Platynerita* and *Laddia* (Fig. 2F; Kano and Kase 2003, fig. 4). This conflicting sharing of shell characters obscures the phylogenetic position of *Teinostomops* (Table 1).

### *Teinostomops singularis* sp. n.

#### Etymology

The species epithet refers to the solitary occurrence in the caves; it is adjectival for the purposes of nomenclature.

#### Type material

Holotype (NSMT-Mo73798): empty shell from cavern, Menjagan Island, off the northwest tip of Bali Island, Indonesia. Paratypes: PALAU – cave at 'Siaes Tunnel' diving site, southwest of Siaes drop-off, ca. 6 km northwest of Aulong Island, Rock Islands, 7°18.7′N, 134°13.6′E, depth 25–53.5 m, April 1995, 1 specimen (NSMT-Mo73799); 'Virgin Hole' diving site, west of Ngemelis Island, Rock Islands, 7°07.3′N, 134°14.1′E, depth 17 m, April 1995, 1 specimen (NSMT-Mo73800). SOCIETY ISLANDS – 'Cave Arue' diving site, west of Tahiti Island, 17°30.9′S, 149°32.1′W, depth 22–30 m, December 1996, 1 specimen (MNHN).

#### Distribution and age

Southeast Asia to South Pacific (Fig. 4C). Recent.

#### Description

Shell minute, up to 1.96 mm wide, 1.38 mm high, 2.01 mm in maximum dimension (1.70, 1.11 and 1.75 mm, respectively, in holotype), white, thin but

solid, ovate with a low spire (Fig. 6A, C). Protoconch axis inclined approximately 10° relative to teleoconch axis. Embryonic shell surrounded by larval shell; visible portion 80–90 μm in diameter (Fig. 6D); surface showing indistinct reticulate pattern (Fig. 6F). Larval shell multispiral; exposed drop-shaped area 200–255 μm in maximum dimension; surface sculptured with many pits bearing granules up to 0.5 μm in diameter (Fig. 6E); suture line descended near aperture, revealing previous suture. Teleoconch whorls up to 1.5 in number, inflated with round periphery; suture shallowly impressed; surface smooth except for faint growth lines. Aperture wide, semicircular, with two protuberances inside at upper and lower columellar sides (Fig. 6B); outer lip sharp along margin, slightly thickened along its interior; inner lip covered with a smooth, thin, widely spread callus; umbilical area slightly depressed; adaxial margin of inner lip edentulous, slightly concave.

### Remarks

Despite their widely spread geographic provenience (Fig. 4C), the four collected shells are very similar to each other in protoconch and teleoconch morphology. The holotype specimen from Bali has a somewhat flared outer lip of the aperture, but this is probably due to the irregular, repairing growth of a damaged shell margin (Fig. 6A).

## *Siaesella* gen. n.

### Etymology

Named after Siaes Tunnel, the only known locality of the type species. Gender of genus name: feminine.

### Type species

*Siaesella fragilis* sp. n.

### Diagnosis

Shell minute, up to 2.3 mm, cream in colour, thin, ovate. Protoconch multispiral, very large (ca. 530 μm wide), slightly inclined relative to teleoconch; embryonic shell partly exposed; larval shell sculptured with 5 or 6 spiral ridges near aperture and with many pits arranged in a spiral direction. Teleoconch aperture without protuberance inside; adaxial margin of inner lip edentulous, concave near base.

### Remarks

The type species *S. fragilis* has an inclined protoconch with several spiral ridges on its shoulder (Fig. 7C, D), which clearly indicates its phylogenetic allocation to the Neritiliidae. However, this protoconch is exceptionally large for the family (Table 2). Accordingly, the number of larval shell coils is more numerous than in other species (Fig. 7E shows the number of larval shell coils to

be greater than two). The spirally arranged micro-pits all over the larval shell are comparable to those found in *Neritilia vulgaris* (Kano and Kase 2003, fig. 4), but the protoconch of *S. fragilis* lacks the thin calcareous layer characteristic of *Neritilia*, *Platynerita* and *Laddia* (Table 1; see also above). The teleoconch of *S. fragilis* is even more distinctive. It is very small, thin and fragile; the aperture lacks any teeth or protuberances, and the adaxial margin of its inner lip is concave near the base (Fig. 7A, B). Such features are typically found in the juvenile shells of other neritiliid species, and this is possibly a result of paedomorphic evolution in relation to the food-limited cave environments (see Hayami and Kase 1996). In any case, the phylogenetic position of *S. fragilis* within the family is totally unknown at present.

## *Siaesella fragilis* sp. n.

### Etymology

The species epithet refers to the fragile shell; it is adjectival for the purposes of nomenclature.

### Type material

Holotype (NSMT-Mo73801): empty shell from cave at 'Siaes Tunnel' diving site, southwest of Siaes drop-off, ca. 6 km northwest of Aulong Island, Rock Islands, Palau, 7°18.7′N, 134°13.6′E, depth 25–53.5 m, April 1995. Paratypes: PALAU – type locality, April 1995, 25 specimens (20 specimens NSMT-Mo73802; 5 specimens MNHN).

### Distribution and age

Known only from Siaes Tunnel, Palau (Fig. 4D). Recent.

### Description

Shell minute, up to 2.17 mm wide, 1.87 mm high, 2.27 mm in maximum dimension (1.74, 1.42 and 1.74 mm, respectively, in holotype), cream in colour, thin, fragile, ovate with a low spire (Fig. 7A, B). Protoconch axis inclined approximately 10° relative to teleoconch axis. Embryonic shell largely surrounded by larval shell; visible portion 65–70 μm in diameter; surface showing indistinct reticulate pattern (Fig. 7E). Larval shell multispiral with more than 2 whorls, very large, about 530 μm wide and 380 μm high, with exposed drop-shaped area 250–295 μm in maximum dimension; surface sculptured with many pits arranged in a spiral direction and with 5 or 6 spiral ridges near aperture (Fig. 7D, E); apertural lip biconvex, somewhat opisthocline and very discordant with first teleoconch whorl. Teleoconch whorls up to 1.5 in number, inflated with round (Fig. 7A) or somewhat angular (Fig. 7B) periphery; suture very shallow; surface smooth except
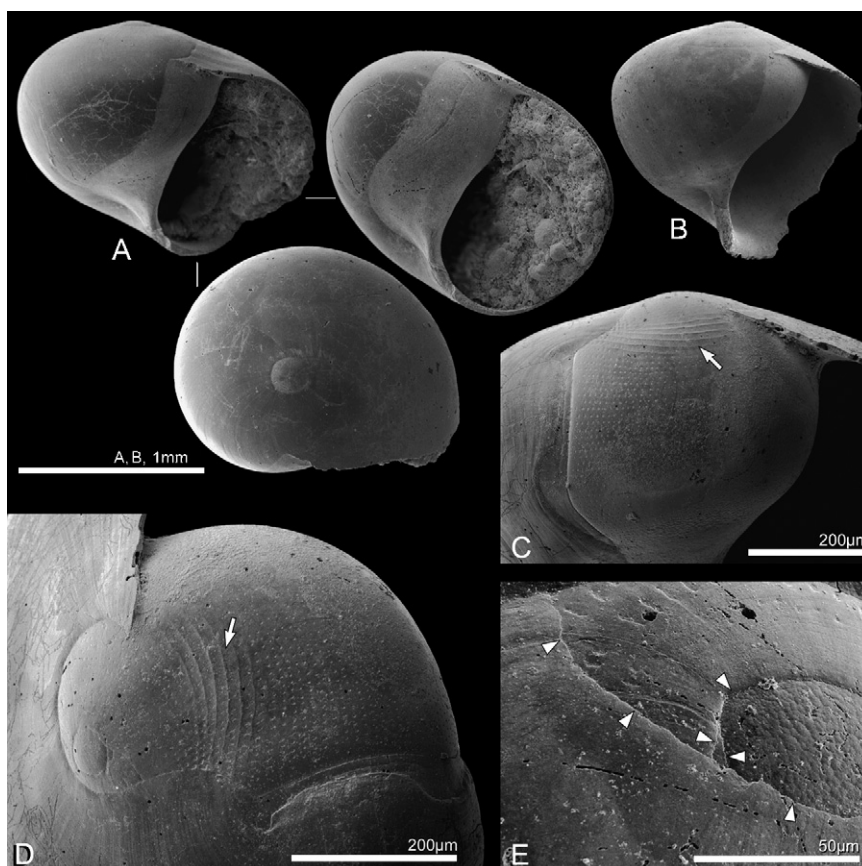
**Fig. 7.** *Siaesella fragilis* sp. n. (A) Anterior, apertural and apical views of holotype (NSMT-Mo73801). (B) Anterior view of paratype (NSMT-Mo73802). (C) Frontal view of juvenile paratype with 0.7 of a teleoconch whorl (NSMT-Mo73802), showing several spiral ridges on shoulder (arrow) and spirally arranged pits. (D) Oblique apical view of C. (E) Close-up of apical area in D, showing suture lines of larval shell (arrowheads) and reticulate surface of embryonic shell; note first whorl of larval shell visible under second and third whorls (small triangular area near centre). All specimens from Siaes Tunnel, Palau.

for faint growth lines. Aperture wide, semicircular; outer lip thin, without thickening along its interior; inner lip covered with a very thin callus; adaxial margin of inner lip edentulous, concave near base; umbilical area shallowly depressed.

**Remarks**

The specimens of *S. fragilis* were collected exclusively from surface sediments in the submarine cave Siaes Tunnel. All the specimens are worn to varying degrees, and void spaces in the whorls are filled with sparry calcite (Fig. 7A). The shells must have been plain white originally but subsequently stained cream, as in the case of the Miocene *Pisulinella* from Eniwetok (Kano and Kase 2000a). From the same sediments, the enigmatic shells of *Pluviostilla palauensis* (class Gastropoda: superorder unknown) have been discovered in similarly worn condition, while a few specimens of the latter species were so fresh that they appear to have been taken while still living in the cave (Kase and Kano 1999). We suppose that *S. fragilis* is also an extant species, regardless of the fossil-like appearance of the type

specimens. As noted above, sediments in submarine caves are finely laminated and disturbances by benthic animals and water currents are much less obvious than on the outside of the caves (Hayami and Kase 1996). This suggests that our sediments (and the shells in them) taken from near the surface in Siaes Tunnel had been deposited recently in geological time.

## *Pisulina* Nevill & Nevill, 1869

**Remarks**

This genus has been revised in an earlier study (Kano and Kase 2000b). Here we present additional records and taxonomic comments based on newly obtained cave samples.

## *Pisulina tenuis* Kano & Kase, 2000

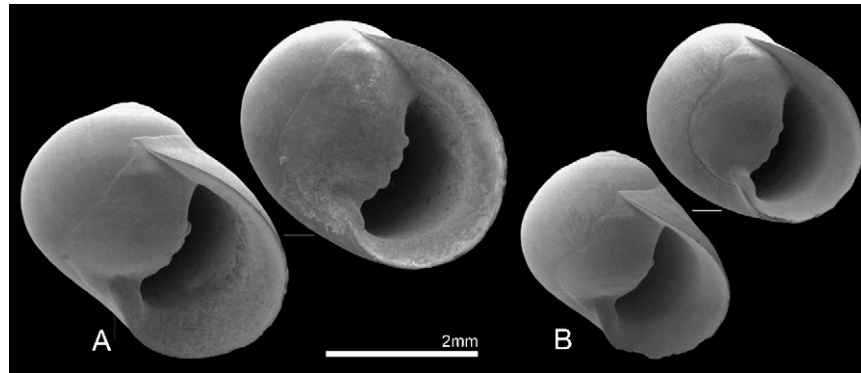*Pisulina tenuis* Kano and Kase, 2000b: p. 125, 126, fig. 20.

**Fig. 8.** *Pisulina tenuis* Kano & Kase, 2000. (A, B) Anterior and apertural views of two specimens from Thunder Dome, Christmas Island (NSMT-Mo73803).

*Pisulina* sp. – Kano and Kase (2000b, p. 126, 127, fig. 21).

**Material examined**

AUSTRALIA – cave at 'Thunder Dome' diving site, north coast of Christmas Island, 10°28.4′S, 105°36.4′E, depth 7.7–10.2 m, December 1999, more than 400 specimens (100 specimens NSMT-Mo73803; 30 specimens MNHN); cavern at 'Aquarium Wall' diving site, north of Cocos Keeling, 12°06.3′S, 96°50.3′E, depth 38–71 m; December 1999, 1 specimen (NSMT-Mo73804).

**Distribution and age**

Known from Yonaguni (Okinawa; type locality), Christmas and Cocos Keeling (Indian Ocean), and Henderson (Pitcairn Group) (Fig. 4F). Middle or late Pleistocene to Recent.

**Remarks**

In our earlier paper we described *P. tenuis* as a species endemic to Yonaguni Island (Kano and Kase 2000b), whereas we also noted two similar shells from the middle or late Pleistocene uplifted cave-sediments on Henderson Island. The latter fossils appeared to be different from *P. tenuis* by their thicker shells and higher spires, but were left unnamed on account of their low number and somewhat poor preservation (Kano and Kase 2000b).

Newly sorted sediments from a Recent submarine cave on Christmas Islands contained many specimens of this *P. tenuis* group. Interestingly, these vary considerably in shell thickness and height of spire; some have a thin shell with a low spire and resemble the holotype of *P. tenuis*, whereas others have a thick shell with a relatively high spire and are nearly identical to the Pleistocene fossils from Henderson (Fig. 8A). Some other specimens even somewhat approach *P. biplicata* in having a high conical spire and in lacking the concavity of the whorls below the sutures (Fig. 8B). However,

these conchological differences are gradual with intermediate forms, and we conclude that the specimens from Yonaguni, Henderson and Christmas all belong to a single taxon, *P. tenuis*, and that their shells are not necessarily thin, regardless of the literal meaning of the species name.

This species seems to be most closely related to *P. maxima*, sharing the same protoconch morphology, shell form, surface microsculpture, and number and shape of the inner lip teeth, but *P. maxima* has a much larger and thicker shell and a wider aperture (Kano and Kase 2000b, Fig. 18). The distribution areas overlap in Christmas, but the two species have never been collected in the same cave.

## Discussion

### Diversity of submarine-cave Neritiliidae

Kano and Kase (2000b) recognised five species in the submarine-cave neritiliid genus *Pisulina*. Four of these are extant (*P. adamsiana*, *P. biplicata*, *P. maxima* and *P. tenuis*), the fifth is extinct (*P. subpacifica*; late Miocene). Three additional fossil species have also been described as presumable dwellers of ancient submarine caves (Kano and Kase 2000a; Lozouet 2004): *Pisulinella miocenica* (middle to late Miocene), *Pisulinella aucoini* Lozouet, 2004 (early Miocene) and *Bourdieria faviai* Lozouet, 2004 (late Oligocene). This study has added five more obligatorily cave-dwelling species: *Laddia traceyi*, *L. lamellata*, *Micronerita pulchella*, *Teinostomops singularis*, and *Siaesella fragilis*. This increases the number of submarine-cave neritiliid species to 13; they are classified in seven genera, four of which are monospecific.

These numbers of species and genera from submarine caves contrast with those of the limnic fauna in the family. Ten species have been described from present-day fresh and brackish (including anchialine) waters

(Kano and Kase 2002, 2003, 2004; Kano et al. 2003), and two fossil species of Neritiliidae are considered as Tertiary freshwater components (Lozouet 2004). Moreover, at least eight Recent species from freshwater streams remain undescribed. A total of 20 limnic species are classified in three genera: *Neritilia* (15 spp.), *Platynerita* (3 spp.) and an unnamed genus (2 spp.) (Kano, unpublished). Thus the Neritiliidae seem less speciose in submarine-cave environments than in fresh- and brackish-water habitats as deduced from morphology-based classification, but phylogenetically more diverse in the former environment. As noted above, the phylogenetic position of a neritimorph species is largely uncertain if it is represented by empty shells only, and in this case its generic assignment may be rather subjective. However, certain shell characters, especially the protoconch morphology, are known to serve very well for generic assignment in Gastropoda (e.g. Warén 1991; Kano and Kase 2000b; Warén and Bouchet 1993, 2001). Comparison of several conchological traits, which we consider as likewise conservative, shows that the limnic *Neritilia* and *Platynerita* are invariable (Table 1), regardless of the obvious differences in their gross shell shape and reproductive anatomy (Kano and Kase 2003, 2004; Kano et al. 2003). This trend of phylogenetic diversity seems to concur with our hypothesis that the limnic species of Neritiliidae have their origin in the cryptic marine environment of the early Cenozoic: all the living neritiliid species show a degenerative open-pit eye without a vitreous body, regardless of the habitats varying from submarine caves to surface freshwater streams (Kano and Kase 2002; Kano et al. 2002).

## Geographic distributions

Fig. 4 shows the known localities of nine submarine-cave neritiliid species, of which seven have been collected from more than one locality, and the remaining two species (*Laddia lamellata* and *Siaesella fragilis*) are endemic to Hawai'i and Palau, respectively. Despite their restricted occupation of caves and similar cryptic habitats, they are distributed widely in the tropical and subtropical Indo-West Pacific. *Pisulina adamsiana*, for example, exhibits the widest distribution, ranging longitudinally across almost half the globe, from eastern Africa to the South Pacific. This fairly common species occurs not only in the vicinity of continents but also on remote oceanic islands of volcanic origin (Fig. 4G).

The range sizes of the other six species are smaller but still unexpectedly large for obligate cave dwellers. *Laddia traceyi* has been found in the caves of disjunct oceanic islands including Christmas of the Indian Ocean, Okinawa, Northern Marianas, Nauru and Hawai'i, as well as in the lower Miocene deposits of Bikini (Fig. 4A). *Micronerita pulchella*, *Teinostomops*

*singularis*, and *Pisulina biplicata* have been found on western and southern Pacific islands. The last species has been recovered also from Pleistocene sediments in an uplifted cave on Henderson Island in the Pitcairn Group (Kano and Kase 2000b); this is the eastern limit of the distribution of submarine-cave Neritiliidae in the Indo-Pacific (Fig. 4E). The distributions of *M. pulchella* and *T. singularis* are apparently discontinuous with a wide gap in Melanesia (Fig. 4B, C), but this is probably because our sampling effort is still insufficient and further cave exploration would lead to the discovery of these species in that region. Unfortunately, we could not survey any submarine caves in the New Guinea and Solomon Islands, where species diversity of marine organisms is the second highest in the world, next to the East Indies or the Indonesian and Philippine region (IPR) (e.g. Paulay 1997; Briggs 1999; Bellwood and Hughes 2001; Mora et al. 2003). In addition, *T. singularis* is exceedingly rare, with so far only four shells available from four caves. Even with our extensive sorting, this rarity may have prevented us from collecting specimens in areas where this species actually occurs.

*Pisulina maxima* is another widespread (but less extensive) species and is relatively common, with a few 100 specimens collected from 10 caves around the Philippine Sea and in Christmas Island (Kano and Kase 2000b). Here it is interesting to note that specimens of its presumed sister species, *P. tenuis*, occur commonly in caves at the western fringe of this distribution. No representative of this latter species has been collected from caves in the vast area of the western and central Pacific, but *P. tenuis* has been recovered from Pleistocene sediments on Henderson Island (along with *P. biplicata;* see above).

In contrast, *Laddia lamellata* seems to be restricted to Hawai'i Island, where the plausible sister species, *L. tracey*, co-inhabits the same caves. The Hawai'i islands are at the eastern periphery of the range of the latter, widespread species (Fig. 4A); the speciation of *L. lamellata* may have taken place in this isolated area, where founder speciation has produced a distinctive marine fauna (Paulay 1997; Paulay and Meyer 2002; McDowall 2003). The origin of *Siaesella fragilis*, another species endemic to a single island (Fig. 4D), is totally unknown as the result of the obscure phylogenetic relations of this monospecific genus (see above; Table 1).

## Reproductive biology

Early development of marine organisms is either planktotrophic or non-planktotrophic. Planktotrophic species spend their early life stages as feeding larvae, while others hatch as crawl-away juveniles or fully-grown, non-feeding lecithotrophic larvae. In addition to

direct observation of the egg and larva, the early ontogeny of molluscs can be deducible from protoconch or prodissoconch size and morphology (Jablonski and Lutz 1983; Buckland-Nicks et al. 2002; Kano 2006). The protoconch or prodissoconch consists of both embryonic and larval shells (or protoconchs I and II in gastropods, prodissoconchs I and II in bivalves) in species with planktotrophic development; the embryonic shell forms during the intracapsular period and the succeeding larval shell gradually develops during the larval period. In non-planktotrophic species, on the other hand, there is no additional growth of the larval shell and the protoconch or prodissoconch consists exclusively of a relatively large embryonic shell formed prior to hatching.

Employing this criterion, Kase and Hayami (1992) and Hayami and Kase (1993, 1996) estimated that approximately 70% of the submarine-cave bivalve species are non-planktotrophic developers. They also found that many of the non-planktotrophs have a hat-shaped prodissoconch-I, which is suggestive of parental incubation of the young. Such high rates of non-planktotrophic development and brooding are unusual for bivalves in low-latitudinal shallow seas and rather comparable with the ratios for deep-sea bivalve faunas (Hayami and Kase 1996). Both submarine-cave and deep-sea environments are characterised by low levels of primary production and durophagus predation, and these conditions may have led to the production of fewer and larger offspring (so-called K-selected reproductive strategy; Kase and Hayami 1992).

Little is known about the developmental mode of submarine cave gastropods, but at least *Neritopsis radula* (Linnaeus, 1758), a well-known 'living fossil' neritimorph that exclusively inhabits submarine caves and similar cryptic voids today, has developed a paucispiral protoconch and non-planktotrophic development (Kano and Kase 2000b; Kano 2006). The same selection pressure in caves may have driven the non-planktotrophy of Neritiliidae. Among the nine neritiliid species so far collected from Recent submarine caves, five have a multispiral protoconch with both embryonic and succeeding larval shells, hence a long planktotrophic period. The remaining four species (*Pisulina biplicata*, *P. maxima*, *P. tenuis*, and *Micronerita pulchella*) have a paucispiral protoconch composed exclusively of a relatively large embryonic shell, hence lecithotrophic or benthic development (Table 2). All four extinct cave-species had multispiral protoconchs (Kano and Kase 2000a; Lozouet 2004), as do all species in the limnic *Neritilia* and *Platynerita* (Kano and Kase 2003, 2004). The planktotrophic phase is thus abbreviated only in extant submarine-cave species among the Neritiliidae. Moreover, it seems likely that the species of *Pisulina* and *Micronerita* acquired their non-planktotrophic development independently, given the

microsculptural difference in their paucispiral protoconchs (see above). Kano (2006) showed that non-planktotrophic early development has evolved at least four times in *Neritopsis* (Neritopsidae), *Pisulina* (Neritiliidae), *Nerita* and *Theodoxus* (Neritidae) in the superorder Neritimorpha. The present finding thus increases that number to five.

The duration of the planktotrophic larval phase is unknown for any neritiliid species, whereas 2–3 months have been suggested for two neritimorphs, *Smaragdia viridis* (Linnaeus, 1758) of Neritidae and *Cinnalepeta pulchella* (Lischke, 1871) of Phenacolepadidae (Scheltema 1971; Kano 2006). Somewhat shorter duration may be expected for the planktotrophs in Neritiliidae, which have smaller sizes of the protoconch and fewer larval shell whorls (Table 2; Kano and Kase 2000b; Kano 2006). The non-planktotrophs should have a much shorter duration of pelagic period if one is present at all. The presence or absence of a lecithotrophic pelagic phase cannot be deduced from protoconch morphology (Hadfield and Strathmann 1990), although a non-feeding pelagic larva has never been confirmed in Neritimorpha and benthic development has been observed in all four non-planktotrophic species studied in culture, namely *Nerita reticulata* Quoy & Gaimard, 1844, *Nerita japonica* Dunker, 1859, *Theodoxus fluviatilis* (Linnaeus, 1758), and *Fluvinerita tenebricosa* (Adams, 1851) (see Kano 2006). Within the superorder Vetigastropoda, *Trochus niloticus* Linnaeus, 1767 has a non-feeding pelagic phase of up to 10 days (Hadfield and Strathmann 1990), and this is possibly the longest duration for non-feeding gastropod larvae.

## Dispersal ability and range size

The duration of the pelagic larval period, which varies from zero in crawl-away juveniles to over a year in certain planktotrophs (e.g. Buckland-Nicks et al. 2002), profoundly affects the dispersal capability of otherwise benthic species and is a primary determinant of their geographic range and genetic structure (e.g. Collin 2001; Meyer 2003; see also Lester and Benjamin 2005). Rather surprisingly, this seems to be true for at least some obligate cave dwellers. Kano and Kase (2004) discovered the stygobitic species *Neritilia cavernicola* in anchialine caves on two islands in the Philippines that are situated 200 km apart and have long been separated by a deep strait. Analyses of mitochondrial DNA sequences indicated that all individuals investigated were part of a panmictic population and their seemingly isolated (dark and brackish) habitats did not limit gene flow. Rearing observations confirmed that a marine planktotrophic phase and consequent migration between islands via ocean currents are the most plausible cause of the gene flow in *N. cavernicola*. This migration

model based on larval dispersal may be widely applicable to anchialine-cave stygobites with insular distributions (Kano and Kase 2004).

On the other hand, it is known that some obligate marine-cave taxa (species and genera) have benthic or lecithotrophic early development and yet extensive and disjunct insular distributions. These taxa include amphipod, copepod, ostracod and remipede crustaceans in anchialine caves (Holsinger 2000; Iliffe 2000; for review see Kano and Kase 2004) and certain bivalve molluscs in submarine caves (Hayami and Kase 1993, 1996). Boxshall and Iliffe (1987) suggested independent colonization of anchialine waters on oceanic islands by invoking ancestral, once widespread, deep-sea species, and Boxshall (1989) developed this further by stating that anchialine habitats on islands and continents are connected via deep-water 'crevicular corridors'. Other authors favour dispersal by ocean currents on floating objects and/or by mobile and migratory animals as vectors (e.g. Maddocks and Iliffe 1991; Danielopol et al. 1994; Hayami and Kase 1996). In any case, more limited dispersal capability and distribution range, and higher levels of population structure, can be expected for these non-planktotrophic developers than for their planktotrophic relatives, but this has not yet been tested in any cave-dwelling organisms.

In the present study we recognised five planktotrophic species and four non-planktotrophic species among the recent submarine-cave Neritiliidae. The most extensive distribution is found in a planktotrophic species (*Pisulina adamsiana*; Fig. 4G), but the two endemics restricted to a single respective locality are also among the planktotrophs (*Laddia lamellata* and *Siaesella fragilis*; Fig. 4A, D). The four non-planktotrophs all have considerably wide distributions centred in the West Pacific (Fig. 4B, E, F). There is therefore no clear relationship between dispersal capability and distribution range in the cave Neritiliidae.

However, a difference exists in the presence or absence of intraspecific variation in shell morphology. Each of the five planktotrophs has a uniform shell shape throughout its distribution range; we detect no geographic variation even among the shells of *Pisulina adamsiana* from the Indian Ocean, Hawai'i and French Polynesia (Kano and Kase 2000b). This provides a clear contrast to the existence of conspicuous variation in the non-planktotrophic species. The number and shape of teeth along the apertural inner lip vary among geographic populations in the non-planktotrophic *Pisulina biplicata*: specimens from Japan and the Philippines generally bear three squarish teeth, while those from Micronesia and the southern Pacific commonly have more than three round teeth (Kano and Kase 2000b, fig. 17A). The shells of *Pisulina tenuis* are always thin with a low spire in Yonaguni Island, but thick with a relatively high spire in many specimens from Christmas

and Henderson islands (Fig. 8; Kano and Kase 2000b, figs. 20, 21). The shells of *Micronerita pulchella* collected from Palau, near the centre of the species' distribution area, are clearly distinguished from specimens from other localities in having a more elongate outline, a smaller aperture and a roundly convex, rather than squarish, margin of the apertural inner lip (Fig. 5). Among the four non-planktotrophs only *Pisulina maxima* lacks evident geographic variation in shell morphology; this is probably because its distribution range is confined to the IPR and is less extensive relative to the three other species. The species with non-planktotrophic development thus have higher levels of geographic differentiation (and probably higher levels of population genetic structure) than do species with planktotrophic development.

The pelagic phase of some weeks (see above) is undoubtedly responsible for the intraspecific uniformity in the planktotrophic species, while the non-planktotrophs should also have certain means of migration, even if the latter is a much less frequent event, to achieve their present widespread distributions. In the absence of known bathyal or abyssal neritiliids, a deep-sea origin for the submarine-cave species seems very unlikely. Hayami and Kase (1996) argued the importance of rafting for byssate bivalves, which sometimes attach themselves to other organic materials, including annelid tubes and soft sponges. Those semi-sessile bivalves apparently are good dispersers, regardless of their benthic development, and not comparable with the free-living gastropods. However, drifting of post-larval juveniles via the use of mucous threads has also been confirmed in culture and field observations for shallow-water gastropods with benthic development (Martel and Chia 1991). The eggs of the Neritiliidae are not pelagic but are laid in capsules and attached to a hard substratum as usual for aquatic neritimorphs (Andrews 1935; Holthuis 1995; Kano and Kase 2003), but this substratum might be a floatable object (wood, algae, sponge, etc.). It is therefore possible that the non-planktotrophic species of the submarine-cave Neritiliidae drift as embryos or post-larval juveniles, or more conceivably, that they disperse during their phase as non-feeding pelagic larvae that may last for several days (see above).

Owing to high dispersal capability, planktotrophic species should not only be widespread geographically but also geologically long-ranging with low extinction rates (e.g. Jablonski and Lutz 1983; Jablonski and Roy 2003). The fossil records of the extant species of submarine-cave Neritiliidae are very scarce, with only five specimens available, including the planktotrophic *Pisulina adamsiana* from the Holocene, the non-planktotrophic *P. biplicata* and *P. tenuis* from the middle or upper Pleistocene, and the planktotrophic *Laddia traceyi* from the lower Miocene (Ladd 1966, 1977;

Kano and Kase 2000b). Of these, *P. adamsiana* very closely resembles the upper Miocene species *P. subpacifica* (Kano and Kase 2000b), while the other Recent submarine-cave Neritiliidae lack apparent relatives among the known extinct taxa. Regarding the longevity of extinct species, all the fossil taxa of Neritiliidae have been recovered exclusively from their single (type) localities and horizons, except for the planktotrophic *Pisulinella miocenica* from upper and middle Miocene sediments (Kano and Kase 2000a, b; Lozouet 2004). These fossil records are rather inconclusive but do not contradict the above-mentioned hypothesis on the relationship between developmental mode and species longevity, with the presence of three planktotrophic, geologically long-ranging lineages and two non-planktotrophic, very young species.

## Biogeographic pattern

The present study of the Neritiliidae provides some of the most comprehensive information to date on the global geographic pattern of a phylogenetic group inhabiting marine caves, not only submarine but anchialine ones, in the Recent and geological past. Many previous marine-cave explorations have been conducted in the Caribbean, Mediterranean or on Atlantic islands (e.g. Iliffe et al. 1984; Vacelet and Boury-Esnault 1995; Jaume and Boxshall 1996; Iliffe 2000). The Indo-West Pacific oceans have largely been neglected in this context, especially the IPR, where species diversity of marine organisms is the highest in the world (Paulay 1997; Briggs 1999, 2000; Mora et al. 2003). Such area-biased sampling may possibly have misled zoologists in the discussion of marine cave biogeography. Occurrences of similar anchialine-cave species on opposite sides of the Atlantic have been explained by plate tectonics and vicariance as primary

mechanisms for the dispersal of 'Mesozoic relicts' (Iliffe et al. 1984; Stock 1993), but the findings of new species in other areas can dramatically change the perception of the species group's biogeography (e.g. Danielopol et al. 2000; Humphreys 2000). Additionally, marine cave organisms studied in previous works were mostly crustacean families and genera for which no cavernicolous species have been recovered from fossil assemblages. When palaeontological information is unavailable, molecular data are the only means for dating evolutionary events, but marine cave taxa have not been studied in this context, except for the population genetics of the anchialine snail *Neritilia cavernicola* in a small area of the Philippines (Kano and Kase 2004). The ancient colonization of marine caves is therefore supposed based on the disjunct known organismic distributions themselves, in association with the apparently limited dispersal of direct-developing offspring across the ocean (e.g. Stock 1993; Jaume and Boxshall 1996; Humphreys 2000), rather than on rigorous palaeontological or molecular evidence.

The Recent submarine-cave Neritiliidae have been found exclusively in the Indo-West Pacific, whereas despite our sampling and sorting no cave sediments from Bermuda and Grand Cayman have yielded any member species. The vast majority of the Indian Ocean area harbours only one species (Fig. 4G). Species richness is highest in and around the IPR (Fig. 9), as in the countless cases of shallow-water animals including corals, fishes, echinoderms, bivalves and gastropods (Ladd 1960; Kay 1990; Paulay 1997; Briggs 1999, 2000, 2005; Bellwood and Hughes 2001; Mora et al. 2003; Carpenter and Springer 2005). The highest number of species (6) was observed in Palau, one of the most extensively investigated localities in our study, but the diversity centre of the Recent submarine-cave neritiliids may actually be in the IPR itself, as in the cases of other snail families and fishes (see Briggs 1999; Carpenter and
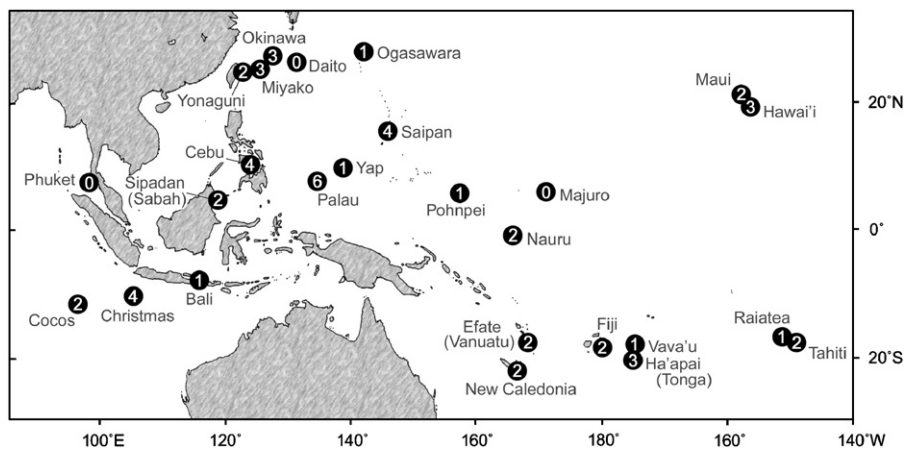


**Fig. 9.** Species richness of Recent submarine-cave Neritiliidae in the Indo-West Pacific; number of species collected from each locality (0–6) is shown in solid circles. East Pacific, Caribbean and Atlantic caves did not yield any neritiliid species.

Springer 2005). Submarine caves in this important region, especially Indonesia, have not yet been sampled sufficiently.

The first occurrence of the fossil submarine-cave Neritiliidae (*Bourdieria faviai*) dates back to the upper Oligocene of the Aquitaine Basin, France. Specimens of *B. faviai* have been found abundantly, in association with Neritopsidae and Pickworthiidae (Lozouet 2004), representative gastropod families in Recent tropical submarine caves (Kase and Hayami 1992; Kase 1998; Kano and Kase 2000b). In addition to the present diversity centre in the IPR, this occurrence of the oldest species in Europe coincides with the general pattern of the tropical, reef-associated fauna. The present IPR centre of shallow-water faunal diversity is considered to owe its origin to the Tethys Sea; in the Palaeogene period the area of greatest diversity appears to have extended from Europe and North Africa to India, but then migrated eastward; by the late Miocene the diversity centre in the IPR was evidently well established (Briggs 1999, 2000). Although further sampling and re-evaluation of neritimorph specimens may reveal older cave-neritiliid species, the presence of *B. faviai* in the Palaeogene centre of marine biodiversity suggests that the distribution history of the submarine-cave Neritiliidae concurs with those of other tropical, reef-associated taxa, and that the same driving force has created the present biogeographic pattern in both epigean and hypogean (cave) organisms.

*Pisulinella*, another fossil-cave genus of Neritiliidae, has been recovered from the Lower Miocene of the same Aquitaine Basin (Lozouet 2004) as well as from middle to upper Miocene of the Eniwetok Atoll in the central Pacific (Ladd 1966; Kano and Kase 2000a). Together with *Laddia traceyi* in the Lower Miocene of Bikini Island, the Tertiary occurrences of submarine-cave Neritiliidae were confined to Europe and the central Pacific. With respect to the central Pacific Ladd (1960) suggested that a former giant archipelago accounted for the rich fauna of molluscs in Tertiary time (Ladd 1958, 1965, 1966, 1972, 1977), and concluded that the original faunistic centre was located there and that prevailing winds and currents had carried species into the IPR. However, re-examination of fossil specimens from the IPR, especially those of micro-molluscs, may reveal greater past species diversity in epigean and hypogean habitats there.

Regardless of the hypothesis, the submarine-cave Neritiliidae have a relatively recent origin on the geological time scale, traced definitely to the late Oligocene but probably earlier in the Tertiary (Lozouet 2004). The oldest living genus (*Laddia*) appeared in the Miocene; two other Tertiary genera (European *Bourdieria* and wide-ranging *Pisulinella*) have become extinct. These stygobitic Neritiliidae thus do not seem to have remained in the same cave systems or the same local regions for millions of years, but seem to be relatively young, active colonizers that have repeatedly expanded their distributions over the Indo-West Pacific. Five of the six living genera (*Pisulina*, *Laddia*, *Micronerita*, *Teinostomops* and *Siaesella*) have wide-ranging geographic distributions centred in the IPR, with known localities on both continental and oceanic islands. Transoceanic dispersal should have played as important a role in forming present distributions as did tectonic events, in species with or without a planktotrophic larval stage.

An interesting question about the biogeography of marine caves concerns the difference between submarine and anchialine habitats: do inhabitants of the former, fully saline habitats experience less difficulty in migration and dispersal than those of the latter in a brackish-water milieu? We consider that the present study of the Neritiliidae is not an exceptional case for marine-cave biogeography, whether submarine or anchialine, although vicariance is often stressed as the principal cause of the 'disjunct distributions of the Mesozoic relics' in the latter habitat (e.g. Stock 1993). When more caves are explored in the Indo-West Pacific and more precise data are available on their distributions, the importance of dispersal via ocean currents may be appreciated in many, if not most, of the marine-cave taxa, including those with benthic early development (see Danielopol et al. 1994; Kano and Kase 2004).

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