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Almost terrestrial: Small supratidal species of *Nerita* (Gastropoda, Neritidae) in the Western Pacific

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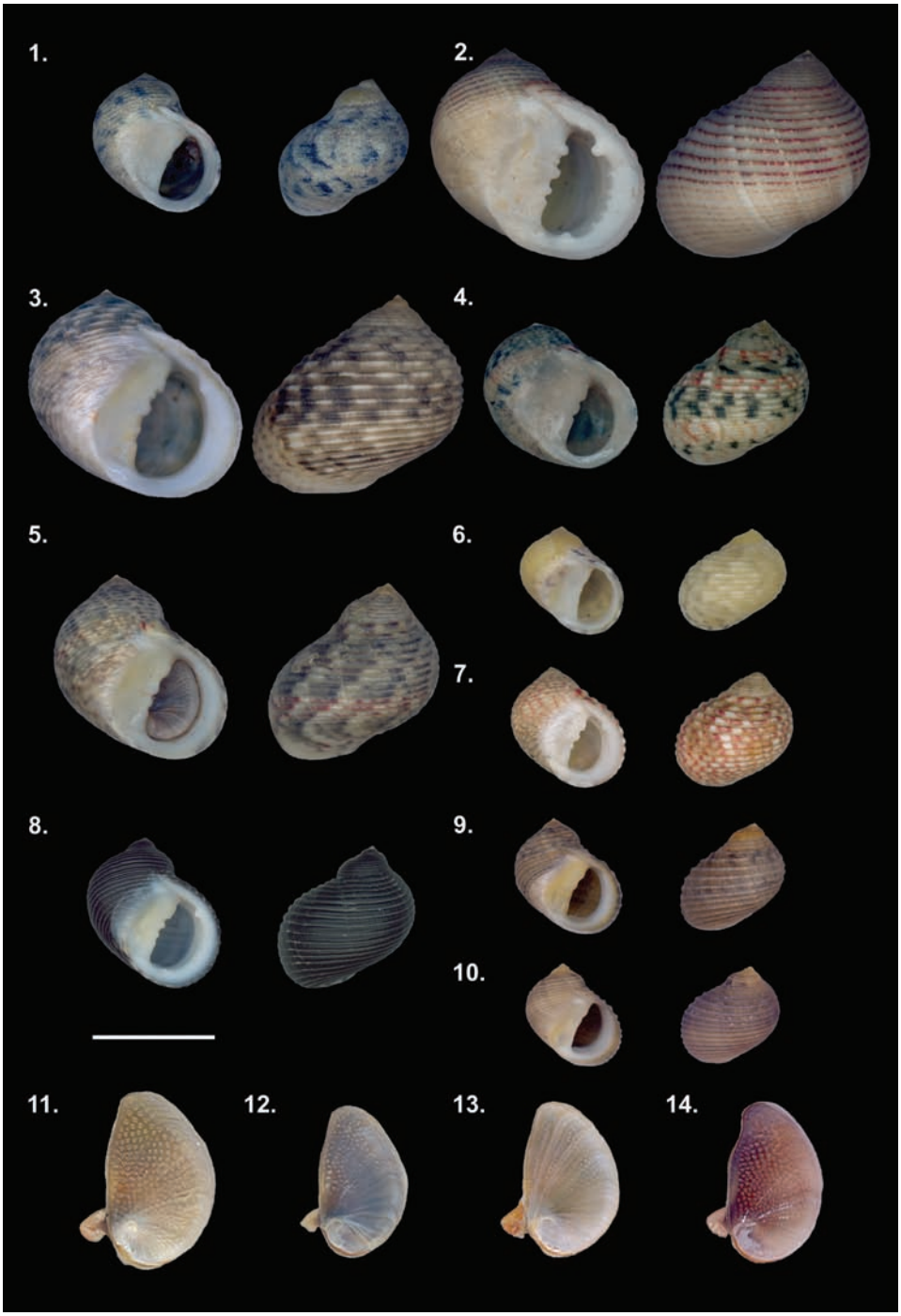
Several small-bodied, taxonomically confusing species of *Nerita* (*Cymostyla*) occupy the highest reaches of the marine intertidal zone on Indo-West Pacific shores. We provide molecular and morphological evidence that *N. filosa* Reeve, 1855, *N. guamensis* Quoy and Gaimard, 1834, *N. helicinoides* Reeve, 1855, and *N. tristis* Pilsbry, 1901, are distinct species. The first three of these species are confined to the highest levels of pitted limestone shores and have narrow geographic ranges. *Nerita tristis* belongs to a different subclade relative to the other species and has a wider geographic range, occurring on both limestone and volcanic shores. The pitted limestone environment has enabled these small nerites and members of the Littorinidae to become nearly terrestrial.

Keywords: Gastropoda, Caenogastropoda, Neritidae, *Nerita*, taxonomy, ecology, intertidal zone, supratidal zone, Western Pacific.

INTRODUCTION

Professor Edi Gittenberger, to whom this paper is dedicated, is a world authority on the systematics and evolution of land snails. He has also, however, delved into marine gastropods from time to time. It therefore seems particularly appropriate to honour him by writing about snails that effectively straddle the ecological divide between land and sea.

Species of *Nerita* are characteristic elements of the high intertidal fauna throughout the tropics and subtropics, but nowhere do species of this genus reach higher shore levels than in the tropical Indo-West Pacific. Familiar examples of such nearly terrestrial species include *Nerita (Ritena) plicata* Linnaeus, 1758, ranging from East Africa to Hawaii and Clipperton Atoll (Kaiser, 2007; Crandall et al., 2008); and the shade-loving *N. (Amphinerita) insculpta* Récluz, 1841, with a more restricted distribution in the eastern Indian and western Pacific Oceans. Less well known, and taxonomically more confusing, is a group of small-bodied species that have been variously referred to as *N. helicinoides* Reeve, 1855, *N. guamensis* Quoy and Gaimard, 1834, *N. filosa* Reeve, 1855, and *N. tristis* Pilsbry, 1901 (Mienis, 1992, 1994; Krijnen et al., 1997, 2005). These taxa have been lumped into one, two, or three valid species, but these judgments are based on cursory observations of shells. Molecular sequences indicate that at least four reciprocally monophyletic units are involved, which belong to two distinct clades within the subgenus *Cymostyla* (Frey & Vermeij, in press). Although these species closely resemble each other in shell characters, careful examination reveals consistent morphological differences among them that accord with the molecular evidence. Based on an examination of type material and our own specimens, we here review the taxonomy of these small nerites and comment on their ecological and geographic distributions.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MATERIALS AND METHODS

This study is based on specimens collected by MAF in the course of sampling for a comprehensive molecular-phylogenetic analysis of *Nerita* (Frey & Vermeij, in press). Voucher specimens are housed in the Vermeij collection. In addition, we examined shells of small upper-shore nerites from various western Pacific sites, collected by GJV and housed in the Vermeij collection. Thanks to the kindness of Kathie Way and Roberto Portela Miguez at the Natural History Museum, London (NHM), and Paul Callomon at the Academy of Natural Sciences of Philadelphia (ANSP), we were able to examine type lots of nearly all the taxa we discuss in this paper.

SYSTEMATICS

Nerita Linnaeus, 1758

Type species: *Nerita peloronta* Linnaeus, 1758, by subsequent designation of de Montfort (1810) (Recent, West Indies).

Subgenus *Cymostyla* von Martens, 1887

Type species: *Nerita undata* Linnaeus, 1758, by original designation (Recent, western Pacific). For stabilization of *N. undata*, see Krijnen et al. (2006).

Remarks.—Species of *Cymostyla* have shells characterized by an elevated spire, rounded or very slightly angulated last whorl, fine spiral ribs, a flat to convex septal surface sculptured with antero-posteriorly oriented irregular ridges, septal margin with one or two variably expressed central denticles, and an internally thickened outer lip whose adaxial side bears a ridge marked by fine denticles, of which the adapical-most and sometimes abapical-most are slightly enlarged. The operculum is usually concave and granulated on its outer surface. As revised by Frey & Vermeij (in press), all living species of *Cymostyla* occur in the Indian and western Pacific Oceans, collectively extending from the Red Sea and East Africa east to Fiji, Tonga, and the Marshall Islands but not Polynesia. Fossil species are known from the Miocene of Europe (Strausz, 1966). Tropical American species that have previously been assigned to *Cymostyla* based on shell and opercular characters belong to a genetically distinctive New World clade that includes *Nerita peloronta*, and which therefore corresponds to *Nerita* s.s. (Frey & Vermeij, in press; Vermeij et al., 2008).

Molecular phylogenetic analyses reveal that most species traditionally assigned to

◀ Figs **1-14**, Shells and opercula. **1**, *Nerita affinis* Reeve, 1855 (NHM 1975591); **2**, *Nerita filosa* Reeve, 1855 (NHM 19750601); **3**, *Nerita guamensis* Quoy and Gaimard, 1834 (GJV pers. coll.); **4**, *Nerita helicinoides* Reeve, 1855 (NHM 19750607); **5**, *Nerita helicinoides laevilabris* Pilsbry, 1901 (ANSP 70857); **6**, *Nerita martensiana* Pilsbry, 1901 (ANSP 80489); **7**, *Nerita pellisserpentis* Reeve, 1855 (NHM 1975611); **8**, *Nerita tristis* Pilsbry, 1901 (ANSP 80406); **9**, *Nerita tristis* (GJV pers. coll., Anatahan, Northern Marianas); **10**, *Nerita tristis* (GJV pers. coll., Saipan); **11**, *Nerita filosa* (MAF pers. coll., Rocher à la Voile, New Caledonia); **12**, *Nerita guamensis* (MAF pers. coll., Anigua, Guam); **13**, *Nerita helicinoides* (MAF pers. coll., Cape Zanpa, Okinawa, Japan); **14**, *Nerita tristis* (MAF pers. coll., Chino River, Kushima, Miyazaki, Kyushu, Japan, collected by Y. Kano). Scale bar: 10 mm for shells, 5 mm for opercula.

Cymostyla belong to a monophyletic clade, which is divided into two subclades (Frey & Vermeij, in press). Three of the small, high-spired species reviewed here (*N. filosa*, *N. guamensis* and *N. helicinoides*) fall within a subclade containing both the large *N. quadricolor* Gmelin, 1791, from the Red Sea and western Indian Ocean, and *N. spengleriana* Récluz, 1844, from the western Pacific (= the *N. quadricolor* subclade). The fourth species, *N. tristis*, is part of a subclade, containing *N. undulata* Gmelin, 1791, *N. maxima* Gmelin, 1791, and, presumably, *N. nigrita* Röding, 1798 (= the *N. undata* subclade). The phylogenetic evidence therefore indicates that the small, high-spired, almost supratidal morphotype of *Cymostyla* in the Indo-West Pacific has independently arisen at least twice from larger, thicker-shelled ancestors living within the upper intertidal zone. According to our previous phylogenetic analyses, *N. helicinoides* appears as the sister species to *N. filosa* and *N. guamensis*; populations of these three species, which are widely scattered from southern Japan to New Caledonia and Fiji, all occur on high, sharp, pitted limestone shores. Both *N. quadricolor* and *N. spengleriana* likewise occur exclusively on limestone (Vermeij, 1971). Members of the *N. undata* subclade often occur on volcanic shores, but may also be found on limestone, and on mangrove roots and trunks (Vermeij, 1971, 1973).

Nerita (*Cymostyla*) *filosa* Reeve, 1855 (figs 2, 11)

Nerita filosa Reeve, 1855, pl. 10, fig. 48a, b.

Description, based on syntypes (NHM 19750601).— Shell moderately large for group, maximum diameter 20.4 mm; shell globose, with a high spire; sutures indistinct, shallow; spiral sculpture consisting of 23 to 24 weak ribs, the abapical 15 or so obsolete; septum smooth or sculptured with ten very weak ridges, its edge with two central denticles and a broad adapical tooth; outer lip thin, with seven to ten denticles on its inner side, the adapical and to a lesser extent the abapical tooth more prominent than the others.

Remarks.—Reeve (1855) named and illustrated *N. filosa* without citing a locality. Mienis (1994) rediscovered the taxon in New Caledonia.

MAF collected specimens here tentatively assigned to *N. filosa* at three sites in New Caledonia and one locality on Viti Levu, Fiji. Our specimens consistently differ in details of sculpture and dentition from Reeve's syntypes. Shells from our sites have 20, not 23 to 24, weak ribs. The septum of our specimens bears three to four (Fiji) or four distinct denticles medially on its edge, not two as in Reeve's specimens. The Fiji specimens have no denticles on the inner side of the outer lip, whereas the New Caledonia shells consistently have 13, the adapical-most and abapical-most tooth being stronger than the others. Reeve's shells have seven to ten denticles. Opercula were not preserved in Reeve's material. In our specimens, the very thin, weakly concave operculum is finely granulated to almost smooth and has a nearly straight adaxial margin, as in *N. quadricolor* and *N. spengleriana*. Interestingly, in our molecular analyses, *N. filosa* formed a paraphyletic clade (Frey & Vermeij, in press), suggesting either incomplete lineage sorting, introgression with putative sister species *N. guamensis* or, alternatively (and perhaps not unlikely), that *N. filosa*, as currently understood, contains multiple cryptic species. A comprehensive phylogeographic investigation would help clarify the above.

Nerita (*Cymostyla*) *guamensis* Quoy & Gaimard, 1834 (figs 3, 12)

Nerita guamensis Quoy & Gaimard, 1834, p. 191.

Description, based on material in the Vermeij collection.—Shell small, maximum

diameter 14.2 mm, globose, with high spire; subsutural area slightly depressed; spiral sculpture consisting of 21 to 22 low ribs; septum smooth, its edge with two (sometimes three) very weak central denticles; outer lip either smooth within or with 11 to 13 very low denticles, sometimes with the adapical-most tooth and rarely with the abapical-most tooth slightly enlarged; operculum flat to very slightly concave, smooth to very finely granulated, its adaxial margin straight.

Remarks.—All specimens of this species we have seen come from Guam, the southernmost of the Mariana Islands. On Guam, the species occurs exclusively on pitted limestone shores, and is absent from volcanic shores on the southern part of the island. Specimens on the leeward (western) coast tend to reach larger sizes than those on the windward (eastern) side. Among three populations from the leeward side (Anigua, Camel Rock and Tipalao Beach), maximum diameter is 14.2 mm, 13.5 mm and 13.3 mm, respectively. East-coast populations from Pago Bay, Togcha Bay and Tagachan reach 10.3 mm, 11.0 mm and 12.1 mm in maximum diameter, respectively. Among these populations, there also exist two distinct colour morphs (red and green). However, based on genetic analyses, individuals do not sort according to colour (MAF, unpublished findings).

Mienis (1992) interpreted *N. guamensis* very broadly to include *N. helicinoides*, *N. mitchelli* Oldroyd, 1933, and *N. tristis*, and gave the distribution of the species as extending from the Ryukyu Islands and southern mainland Japan to northeastern Taiwan, the Bataan Peninsula of Luzon in the Philippines (type locality of *N. mitchelli*), and the Mariana Islands. In their survey of the fauna of the volcanic islands of the northern Marianas, Vermeij et al. (1984) likewise assigned small dark nerites from Anatahan to *N. guamensis*. These are here reassigned to *N. tristis* (see below under that species).

Nerita (*Cymostyla*) *helicinoides* Reeve, 1855 (Figures 1, 4-7, 13)

Nerita helicinoides Reeve, 1855, pl. 18, fig. 80a, b.
Nerita affinis Reeve, 1855, pl. 18, fig. 81a, b.
Nerita pellisserpentis Reeve, 1855, pl. 19, fig. 83a, b.
Nerita helicinoides var. *laevilabris* Pilsbry, 1895, pp. 177-178, pl. 4, fig. 32.
Nerita martensiana Pilsbry, 1901, p. 397.

Description, based on syntypes of N. helicinoides (NHM 19750607).—Shell small, maximum diameter 14.6 mm, globose, with high spire; subsutural area slightly depressed; last whorl sculptured by 22 to 23 very weak ribs, with the abapical 13 to 14 often obsolete; septum smooth to very weakly ribbed, flat to concave, its margin with one or two weak central denticles; outer lip usually smooth on its inner side except for on abapical tooth, but some individuals with 13 to 16 very weak denticles.

Remarks.—Reeve (1855) described and illustrated *N. helicinoides* from an unknown locality. Subsequently, however, specimens very closely resembling the syntypes have been found in Okinawa. Based on examination of the syntypes of *N. helicinoides* (NHM 19750607), *N. affinis* (NHM 1975591), *N. pellisserpentis* (NHM 1975611), *N. helicinoides* var. *laevilabris* (ANSP 70857), and *N. martensiana* (ANSP 80489), we agree with Mienis (1992) that all these taxa are junior synonyms of *N. helicinoides*. Pilsbry's taxa are from the "Loochoo" (= Ryukyu) Islands, of which Okinawa is a part.

In shell morphology, *Nerita helicinoides* is extremely similar to *N. guamensis*. It differs by having even less prominent spiral sculpture, especially abapically, and by having slightly more numerous denticles (13 to 17 as compared to 11 to 13) inside the outer lip. The septum in *N. helicinoides* sometimes bears weak ridges, which are not observed in *N. guamensis*. Differences with *N. filosa* are also slight. *Nerita filosa* has fewer denticles (seven

to ten versus 13 to 17) on the inner side of the outer lip, and has 23 to 24 instead of 22 to 23 spiral ribs. In his account of the gastropods of the Bonin Islands, Fukuda (1993) lists *N. helicinoides laevilabris* from Chichijima. He describes the shells as having bright rose-pink maculations, and the operculum as having the granules absent or indistinct. This description is consistent with assignment of this material to *N. helicinoides*.

Based on molecular analyses, *N. helicinoides* shows clear, fixed genetic differences compared to *N. filosa* and *N. guamensis*, that, in turn, suggest a late Miocene divergence (Frey and Vermeij, in press). Unfortunately, we have not been able to evaluate whether *N. helicinoides* and *N. helicinoides* var. *laevilabris* show evidence of genetic differentiation, and suggest this as an avenue for future study.

Nerita (*Cymostyla*) *tristis* Pilsbry, 1901 (figs 8-10, 14)

Nerita helicinoides var. *tristis* Pilsbry, 1901: 302.

Description, based on syntypes (ANSP 80406).— Shell small, maximum diameter 13.2 mm, globose, with high spire; adapical area of last whorl somewhat concave; last whorl inflated, evenly convex, sculptured with 18 to 19 spiral ribs; septum flat to very slightly concave, smooth or with very faint ridges, its margin with two quite strong central denticles; inner side of outer lip with 12 to 14 denticles, the abapical-most and adapical-most tooth stronger than the others; operculum granulated, its columellar margin with a broad, distinct sinus.

Remarks.—The syntypes of *N. tristis* (ANSP 80406) come from the "Loochoo" (= Ryukyu) Islands. We have seen very similar shells from Oku, Okinawa; Miyazaki, Kyushu Island; Miyake-Jima in the Izu Islands south of Tokyo; Hachijo-Jima in the Ogasawara (= Bonin) Islands; Anatahan in the northern Mariana Islands; and Aguigan and Saipan in the geologically southern (but politically Northern) Mariana Islands. The number of ribs varies somewhat among populations: 13 to 14 in specimens from Oku, Okinawa; 17 to 18 in Miyake-Jima; 13 to 14 in Anatahan; and 16 to 18 in Aguigan and Saipan. Size also varies dramatically, from a maximum of 20.6 mm at Aguigan to 13.0 mm (Hachijo), 12.8 mm (Miyake-Jima), 17.8 mm (Kyushu), 10.0 mm (Oku), 9.3 mm (Agingan Point, Saipan) and 10.5 mm (Anatahan). Specimens from Kyushu, Miyake-Jima and Anatahan occur on volcanic rock, whereas those in Okinawa, Aguigan and Saipan occur on limestone.

As previously noted, *N. tristis* appears more closely related to the *N. undata* complex than the *N. helicinoides* group (Frey & Vermeij, in press). Preliminary results reveal that *N. tristis*, as currently understood, is composed of multiple, genetically unique populations (MAF, unpublished data). To determine the taxonomic status and connectivity among these populations, we recommend further detailed phylogeographic study.

GENERAL DISCUSSION

The species question.—With the advent of molecular techniques to distinguish reciprocally monophyletic evolutionary units, it has become clear that many, if not most, taxa that were once considered to be single, variable species in fact consist of multiple distinct species. This is certainly the case with the small high-shore nerites reviewed here. In most cases, including the taxa considered here, slight morphological differences correspond to distinct molecular units. Taxonomic splitters are thus often vindicated in according significance to seemingly minor differences in features of the shell.

It is highly likely that additional species in this group of small upper-shore nerites

will be discovered through increased sampling and further molecular investigation. Based on protoconch and opercular characters, Kano (2006) has shown that *N. helicinoides* lacks a planktonic larval stage, accounting for its limited distribution in the Ryukyu and perhaps the Ogasawara Islands. Other related species are also highly localized: *N. guamensis* appears to be restricted to Guam, whereas specimens resembling *N. filosa* come from two disjunct populations, one in New Caledonia, the other in Fiji. Pitted limestone shores on high islands elsewhere in the western Pacific may therefore also support endemic species in this clade.

The Indo-West Pacific littorinid genus *Tectarius* resembles the *N. filosa-guamensis-helicinoides* clade in habitat and distribution. All species inhabit pitted limestone shores in the Ryukyu Islands, the Philippines, eastern Indonesia, New Guinea and the Solomon Islands, as well as in Guam, the Cook Islands and Polynesia (Reid and Geller, 1997; Rosewater, 1972, 1982). In Guam, *T. viviparus* Rosewater, 1982, occurs together with *N. guamensis*, and like that species is endemic to Guam and lacks planktonic larval stages (Vermeij, 1971, 1973; Rosewater, 1982).

Nerita tristis, a member of the *N. undata* subclade of *Cymostyla*, appears to have a slightly broader geographic distribution than do members of the *N. filosa-guamensis-helicinoides* clade. It is currently known from the Ryukyu Islands and southern mainland Japan, and the Izu, Ogasawara, and Mariana Islands south to Aguigan and Saipan. Similar to *N. helicinoides*, *N. tristis* (and other members of the *N. undata* subclade) may also possess non-planktotrophic larvae (Y. Kano, pers. comm.). Thus, a more detailed phylogeographic study is expected to reveal strong genetic differentiation within this species.

An approach to terrestriality.— Although neritimorph gastropods have invaded the land on several occasions (Kano et al., 2002), no species of *Nerita* can be said to be truly terrestrial. It is striking, however, that the most nearly terrestrial members of this genus—*N. filosa*, *N. guamensis* and *N. helicinoides*—all live on pitted limestone shores in oceanic conditions. Several littorinids—the West Indian *Cenchritis muricatus* (Linnaeus, 1758) and members of the Indo-West Pacific genus *Tectarius*—likewise extend further landward in this habitat than on other types of rocky shore. High-shore Caribbean nerites—*Nerita peloronta* and *N. versicolor* Gmelin, 1791—and many species of *Echinolittorina* also occupy pitted limestone but do not extend as high on the shore as does *C. muricatus* (Vermeij, 1973). In the Indian Ocean, pitted limestone shores are likewise occupied by species of *Nerita* and *Echinolittorina*, but members of the nearly terrestrial *N. filosa* group and of *Tectarius* are absent there (Reid, 2007). The Hawaiian Islands, where pitted limestone shores also occur, also lack these extreme high-shore specialists. Given that island habitats have produced local, truly terrestrial endemic gastropods from marine ancestors among Truncatellidae both in Polynesia and on Barbados in the West Indies (Rosenberg, 1996), further research on nearly terrestrial nerites and littorines may lead to a better understanding of the environmental conditions that push species to such specialization and that enable some lineages to leave the sea altogether.

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