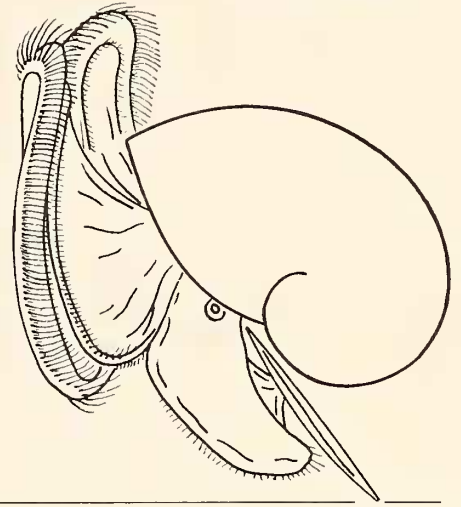


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ISSN 0042-3211

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler (1901–2000), Founding Editor

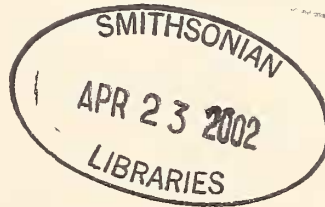
Volume 45

April 1, 2002

Number 2

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The *Veliger* (ISSN 0042-3211) is published quarterly in January, April, July, and October by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Periodicals postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to *The Veliger*, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

Scope of the journal

The Veliger is an international, peer-reviewed scientific quarterly published by the California Malacozoological Society, a non-profit educational organization. *The Veliger* is open to original papers pertaining to any problem connected with mollusks. Manuscripts are considered on the understanding that their contents have not appeared, or will not appear, elsewhere in substantially the same or abbreviated form. Holotypes of new species must be deposited in a recognized public museum, with catalogue numbers provided. Even for non-taxonomic papers, placement of voucher specimens in a museum is strongly encouraged and may be required.

Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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Memberships and subscriptions are by Volume only and follow the calendar year, starting January 1. Payment should be made in advance, in US Dollars, using checks drawn from US banks or by international postal order. No credit cards are accepted. Payment should be made to *The Veliger* or "CMS, Inc." and *not* the Santa Barbara Museum of Natural History. Single copies of an issue are US \$25.00, postage included. A limited number of back issues are available.

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The Genus *Nodilittorina* von Martens, 1897 (Gastropoda: Littorinidae) in the Eastern Pacific Ocean, with a Discussion of Biogeographic Provinces of the Rocky-Shore Fauna

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Abstract. The Recent members of the genus *Nodilittorina* in the eastern Pacific Ocean are revised. Hitherto eight to 10 species have been recognized, but this total is now increased to 18, of which three are named as new. The majority of the taxa fall into three species complexes: six in the *N. porcata* group, two in the *N. modesta* group, and six in the *N. aspera* group. Within each of these complexes, species identification from shells alone is difficult, as a result of remarkable intraspecific variation. Since all species of the genus have pelagic eggs and planktotrophic development, it is suggested that this variation may be partly of ecophenotypic origin. Discrimination is confirmed by species-specific characters of the penis and supported by some features of the spermatozoa and pallial oviducts. Radular characters are more constant throughout the genus. The four additional species are *N. araucana*, *N. peruviana*, *N. galapagensis*, and *N. fernandezensis*. Anatomical features, radulae, and a range of shells are figured for each species. Geographical distributions are mapped in detail (from 777 samples examined) and cases of sympatric occurrence provide strong support for the discrimination of members of the three species complexes.

There is insufficient morphological differentiation among the species to permit formal phylogenetic analysis. Some of them show similarities with congeners in the western Atlantic, but there are no obvious sister-species pairs. A species endemic to the oceanic islands off Chile, *N. fernandezensis*, shows a clear relationship with a largely temperate Southern Hemisphere group, the subgenus *Austrolittorina* (here redefined).

Of particular interest are the distributions of the 15 *Nodilittorina* species within the Tropical Eastern Pacific Region (TEP; hitherto referred to as the "Panamic Province" in the molluscan literature). These strongly support the classification of the region into four provinces, Cortez, Mexican, Panamic (with a southern Ecuadorean element), and Galápagos, as previously suggested for fishes, which (like *Nodilittorina* species) are dependent upon shallow-water rocky substrates. The boundaries between these provinces correspond with habitat gaps, of either open water (Galápagos) or inhospitable coastline of sand, mud, and mangroves (Sinaloan, Central American and Colombian Gaps). The implications for processes of dispersal and speciation, and also for future systematic studies of the rocky-shore fauna, are discussed.

INTRODUCTION

The eastern Pacific Ocean stretches from the shores of Alaska to Tierra del Fuego, and includes tropical islands as far west as the Islas Revillagigedo, Clipperton Atoll, the Galápagos, and the Juan Fernández Archipelago. Within this expanse there occur three principal genera of the littorinid subfamily Littorininae (using the classification of Reid, 1989a). The northern temperate genus *Littorina* includes seven native species in this region, of which two extend as far south as Baja California (Reid, 1996). The genus *Littoraria* is exclusively tropical and includes five species from mangrove habitats and one from rocky shores (Reid, 1999a). The remaining members of the subfamily that are of native occurrence and maintain reproducing populations are all members of the genus *Nodilittorina*; these can be found from Baja California to southern Chile and on all the oceanic islands. In addition to these eastern Pacific natives, there are three introduced *Littorina* species recorded from San Francisco Bay and

Washington (Reid, 1996), and *Cenchritis muricatus* (L.) has been introduced to the Gulf of California (Bishop, 1992; Chaney, 1992). Recently, three tropical species of Indo-West Pacific origin have been recorded from the eastern Pacific for the first time, two of *Littoraria* and one of *Peasiella*, but these appear to be only occasional immigrants (Reid & Kaiser, 2001).

Nodilittorina is the largest genus in the family Littorinidae, with an estimated 60 species worldwide. Most of these are tropical, and in the temperate northern hemisphere they are replaced (with little geographical overlap) by species of *Littorina*. In contrast, in the southern hemisphere, *Nodilittorina* species extend throughout the temperate latitudes. All the species occur typically on intertidal rocks, usually in the littoral fringe and upper eulittoral zone, where they graze on epilithic and endolithic algae. They are usually the dominant large invertebrates at these levels on the shore, and have therefore been the subject of much work on ecology and physiology. Ex-

amples include studies in Australia (Underwood & McFadyen, 1983; Chapman, 1994, 1998), South Africa (McQuaid, 1981a, b, 1992), Hong Kong (Ohgaki, 1985; Mak, 1998; Mak & Williams, 1999), Japan (Ohgaki, 1988, 1989), Hawaii (Struhsaker, 1968), the Mediterranean (Palant & Fishelson, 1968), Brazil (de Magalhães, 1998), and the Caribbean (Borkowski, 1974; Britton, 1992; Lang et al., 1998; see also McQuaid, 1996b, for a review of littorinid ecology). The ecology of these littorinids has, however, received relatively little attention in the eastern Pacific region (Vegas, 1963; Markel, 1971; Vermeij, 1973; Jordan & Ramorino, 1975; Garrity & Levings, 1981; Garrity, 1984), although they have often been mentioned in studies of littoral zonation (Hedgpeth, 1969; Cinelli & Colantoni, 1974; Paredes, 1974; Romo & Alveal, 1977; Santelices et al., 1977; Brattström, 1990).

Despite this ecological importance, the taxonomy of *Nodilittorina* species remains poorly understood. As discussed below, even a satisfactory definition of the genus is not available. There have been no modern studies of the systematics of this group in the eastern Pacific. The first species to reach European collections was the Peruvian *N. peruviana*, named by Lamarck (1822), and on his great South American journey, d'Orbigny (1835–1846) obtained both this and the Chilean *N. araucana*. Further material was brought back by Cuming, from which Philippi (1846a) described three tropical species. There soon followed taxonomic studies on material from Mexico (Menke, 1851; Carpenter, 1857b, 1864a), Central America (C. B. Adams, 1852a, b; Mørch, 1860; Carpenter, 1863; von Martens, 1900), and the Galápagos (Stearns, 1892, 1893a, b). Meanwhile, monographs of worldwide littorinids had appeared in the great nineteenth century conchological iconographies (Philippi, 1846b–1848; Küster, 1853, 1856; Reeve, 1857–1858; Weinkauff, 1878, 1882; Tryon, 1887). With limited material available, the earlier authors distinguished many shell variants as species; for example, Philippi (1847) included eight in this eastern Pacific group. Later, the trend was to synonymize many names; Weinkauff (1883) accepted only six of Philippi's taxa, Tryon (1887) only four, and Dall (1909) likewise had a broad concept of species in this group. Twenty-eight names were introduced in the nineteenth century, and three more in the twentieth (Bartsch & Rehder, 1939; McLean, 1970; Rosewater, 1970). For much of the twentieth century, authors continued to accept a wide degree of intraspecific variation in species that were defined by shell characters alone, so that the influential *Sea Shells of Tropical West America* by Keen (1971, following taxonomy of Rosewater, 1970) included only eight (plus seven additional names listed uncritically as Fossaridae, see discussion of *N. porcata* group). This book has been the basis for several regional faunal lists (Finet, 1985, 1994; Alamo & Valdivieso, 1987, 1997; Kaiser, 1997). The modern taxonomy of the Littorinidae has been transformed by the use of anatomical and radular characters,

correlated with details of shell sculpture and pattern (e.g., Bandel & Kadolsky, 1982; Reid, 1986, 1989a, 1996), and this has led to a proliferation of recognized species and to more rigorous phylogenetic definitions of genera. In a list of worldwide Littorinidae Reid (1989a) gave eight species in this eastern Pacific group (with two additional species doubtfully in synonymy) and, for the first time, all were included together in *Nodilittorina*.

Many workers have commented on the confusing variability and uncertain taxonomy of the littorinids of the eastern Pacific, especially those related to *Nodilittorina porcata* and *N. aspera*. In 1971 Keen remarked of "*Littorina aspera*" that "it is possible that careful work will demonstrate the desirability of recognizing more than one species within this complex." However, despite advances in littorinid taxonomy in other parts of the world, the eastern Pacific *Nodilittorina* species have remained neglected. The present study aims to revise the taxonomy of this group, based on personal field collections and examination of the major museum collections. Particular emphasis is placed on characters of the reproductive system (penis, paraspermatozoa, pallial oviduct, egg capsules) which are known to be important for the discrimination of littorinid species (Reid, 1986, 1996, 1999a). Fossil material has not been included. In general, fossil littorinids are extremely scarce, as expected for a group living primarily on hard intertidal substrates. Furthermore, the shells of *Nodilittorina* species are so variable and also show such close resemblance to some members of *Littoraria* and *Littorina*, that fossil material would be difficult to interpret. The only possible fossil member of the genus *Nodilittorina* that has been recorded from tropical America is *Littorina seminole* Petuch from the Pliocene Caloosahatchee Formation of Florida (Petuch, 1991).

As a result, 18 *Nodilittorina* species are recognized in the eastern Pacific Ocean, where hitherto only eight to 10 were generally accepted. Their geographical distributions are plotted in detail, and congruent patterns among species complexes, as well as cases of sympatry, provide support for the new species definitions. Of particular interest are the distributions of the 15 species within the Tropical Eastern Pacific Region (TEP) which suggest its division into four provinces, Cortez, Mexican, Panamic, and Galápagos. Although this division has previously been recognized in some other animal groups, in the molluscan literature the entire TEP has been regarded as uniform and referred to as the "Panamic Province." The boundaries between these provinces correspond with habitat gaps, of either open water or inhospitable coastline of sand, mud, and mangroves. The recognition of these gaps has important implications for systematic, evolutionary, and genetic studies of the rocky-shore fauna.

MATERIALS AND METHODS

During this study, all material in the collections of the following institutions has been examined: the Natural

History Museum, London (BMNH), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), the Muséum National d'Histoire Naturelle, Paris (MNHN), and the Zoölogisch Museum, Amsterdam (ZMA). Much additional material, of species and from geographical regions that were otherwise poorly represented, has been obtained from the Los Angeles County Museum of Natural History (LACM), the California Academy of Sciences (CAS), the Charles Darwin Research Station, Ecuador (CDRS) and the personal collections of K. L. Kaiser (KLK) and G. J. Vermeij. All available primary type material has been examined (in one case a photograph) from these institutions, and also from the Academy of Natural Sciences of Philadelphia (ANSP), the Museum of Comparative Zoology, Harvard University (MCZ), the Muséum d'Histoire Naturelle, Geneva (MHNG), the Museum für Naturkunde, Berlin (MNB), and the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt (SMF). Paratypes of some species are housed in the American Museum of Natural History (AMNH) and in the Santa Barbara Museum (SBM), but these were not examined. Personal collections were made in Costa Rica (1985), Mexico (1994), Chile and Peru (1998), and Ecuador (1998), and are deposited in BMNH. In total, 777 samples have been examined. Fossil material is extremely scarce and has not been included in this study.

Shell dimensions were measured with vernier calipers or, for the smallest species, with a camera lucida and scale, to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, and the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. Shell shape was quantified as the ratios H/B and H/LA (relative spire height, SH), and the range of these ratios is quoted. Shell sculpture is described by reference to primary and secondary grooves, ribs, the periphery, and microstriae. Primary grooves are incised spiral lines or grooves that are visible on the early teleoconch whorls. On the spire the primary grooves are counted between successive sutures, but on the last whorl they are counted from the suture to the periphery of the whorl (so that one or more extra grooves are visible). Secondary grooves appear by interpolation, usually on the penultimate or final whorl, and sometimes not at all. The spaces between the grooves are referred to as ribs, whether or not they are strongly raised. Microstriae are fine incised spiral lines that cover the entire surface and are visible only under low magnification; they may be present in addition to primary grooves, but in the smallest species (the *N. porcata* group) the distinction between primary grooves and microstriae is sometimes arbitrary. The periphery is the junction between the upper part of the final whorl and the base of the shell; it is usually marked by a strong or slight angulation (e.g., Figure

18R), or by a rib slightly larger than the rest (e.g., Figure 12B), or more rarely by a keel or flange (e.g., Figure 1N). The suture generally runs one or two ribs above the periphery, or is situated at the peripheral rib. Protoconch whorls were counted as recommended by Reid (1996); the protoconch in Figure 22G has 2.7 whorls. To describe the coiling of the operculum, the opercular ratio was defined as the ratio of two parallel measurements, the diameter of the spiral part divided by the maximum length (Reid, 1996). The relative radular length is the total radular length divided by shell height.

Living animals were relaxed in 7.5% (volume of hydrated crystals to volume of fresh water) magnesium chloride solution. Animals were fixed in 10% seawater formalin buffered with borax, and stored in 80% ethanol before dissection. Anatomical drawings were made by camera lucida, and shading and drawing conventions are indicated in the captions of Figures 3, 4, and 13. For general accounts of the anatomy of littorinids, see Reid (1986, 1989a, 1996). Sperm samples were removed from the seminal vesicles of relaxed, living animals, fixed in 0.5% seawater formalin, examined immediately by light microscopy, and drawn by camera lucida. Alternatively, sperm were removed from specimens fixed and stored in seawater formalin, but not from material stored in ethanol (in which shrinkage of paraspermatozoa by about 20% occurs, Reid, 1996). For four species, egg capsules were obtained by confining individual females in beakers of seawater left overnight; these were drawn using a compound microscope and camera lucida. Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 5 min, rinsed in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination in a scanning electron microscope. Unworn portions of radulae were viewed in three orientations: in standard flat view from vertically above the radula (to show shapes of tooth bases), at an angle of 45° from the front end of the radula (to show shapes of tooth cusps), and at an angle of 45° from the side of the radula (to show relief). The shape of the rachidian tooth was quantified as the ratio of the total length (in flat view) to the maximum basal width.

Synonymies are not exhaustive, but attempt to list all new names (including nomina nuda) and new combinations, major taxonomic works and faunistic lists, and significant morphological descriptions. Where valid names are represented by syntypic series of dry shells, lectotypes have been designated. This is considered necessary for stability, since identification from shells alone can be difficult (ICZN, 1999, Art. 74.7.3). Lectotypes are also designated in cases where syntypes are not all conspecific.

Distribution maps were plotted from the material examined, with the addition of literature records (where these extended the known range and were considered reliable). Localities are listed only when they are range lim-

the penis and of egg capsules in his revision of littorinid genera. On this basis he raised *Nodilittorina* to a full genus and showed clearly that it was more closely related to "*Littorina* (*Melarhaphé*) *ziczac* (Gmelin)" (i.e., the *N. ziczac* group of the western Atlantic) than to *Tectarius*. Abbott (1954) also noted that "*L.*" *ziczac* and "*L. mauritiana*" (a misidentification of *N. unifasciata*) might well not belong to *L. (Melarhaphé)*, depending upon the penial shape of its type species, *M. neritoides* (L.). Shortly afterward, Habe (1956) introduced the subgenus *N. (Echinolittorina)* for *N. tuberculata*, because its rachidian tooth was narrower than that of the type of *Nodilittorina* (*N. pyramidalis*). The new genus *Granulilittorina* was subsequently added by Habe & Kosuge (1966) for a species with unusual serrated egg capsules (*N. vidua*).

In two monographs of Indo-Pacific littorinids, Rosewater (1970, 1972) included a worldwide list of species and presented a revised generic classification. Although characters of penis, egg capsule, and radula were considered, this scheme still emphasized similarities of shell sculpture. Thus the smooth-shelled species currently assigned to *Nodilittorina* were distributed among five subgenera of *Littorina*, the nodulose forms placed in *Nodilittorina s.s.* and its subgenus *Echinolittorina*, and granulose species in *N. (Granulilittorina)*. Rosewater (1970) noted that while nodulose sculpture was "the most obvious character of *Nodilittorina*" it showed considerable variability within some species. Nevertheless, smooth-shelled species with penes closely similar to those of *Nodilittorina* species were placed in a new subgenus *Littorina (Austrolittorina)*. This scheme was widely followed (e.g., Keen, 1971; Abbott, 1974). Additional information on penes and radulae resulted in transfer of three more members to *Austrolittorina* from the subgenus *Littoraria* (Ponder & Rosewater, 1979). A further modification (Rosewater, 1981) was the description of another new subgenus, *Fossarilittorina*, for the small, umbilicate species, but this was still assigned to *Littorina*.

It was not until the work of Bandel & Kadolsky (1982) on western Atlantic *Nodilittorina* species that the genera of Littorinidae were revised to take account of all available evidence. Using published accounts of penes, spawn, and development, and new information on radulae, opercula, and shell mineralogy, they redefined *Nodilittorina* to include, for the first time, both smooth-shelled and nodulose species. They showed not only that shell sculpture was a poor indication of relationships, but also that the rachidian tooth and operculum (both emphasized by earlier authors) were widely variable and subject to evolutionary convergence within *Nodilittorina*. They recognized three subgenera: *Nodilittorina s.s.* (the great majority of species), *Tectininus* (for *N. antonii* (Philippi)), and *Liralittorina* (for *N. striata* (King & Broderip), later removed to *Littorina*, see Reid, 1989a). They also raised *Fossarilittorina* to full generic status. This unfamiliar arrangement was not, at first, widely followed. However,

Reid (1986), in a monograph of *Littoraria*, added additional anatomical data on many *Nodilittorina* species, besides new characters of spermatozoa and pallial oviduct, and presented a preliminary cladistic analysis of the family. This almost entirely supported the new scheme (although *antonii* was removed to *Echininus*).

The most recent revision of the classification of Littorinidae was by Reid (1989a), based on a cladistic analysis of a wide range of morphological characters from examples of all known subgeneric groups. In this new scheme 40 species were placed in *Nodilittorina*, but a precise definition of this genus remained elusive since the only synapomorphy discovered was a dubious character of head pigmentation that was not uniquely derived. Subgenera within *Nodilittorina* were also not clearly defined; three were recognized, *Fossarilittorina*, *Echinolittorina*, and *Nodilittorina s.s.*, but lacked strong synapomorphies. In the past decade this generic classification of the Littorinidae has become widely accepted (see reviews by McQuaid, 1996a; Reid, 1996; Reid & Geller, 1997).

Diagnosis: Shell: conical to globular; occasionally with pseudo-umbilicus; often an eroded parietal area; adult sculpture of spiral grooves, with or without spiral microstriae, sometimes with granular or nodular sculpture, or sometimes becoming entirely smooth; mineralogy aragonitic, of crossed-lamellar structure with fine outer layer. Head-foot: tentacles pale with 2–3 longitudinal black stripes, or all black. Male: prostate gland open; anterior vas deferens open; penial vas deferens usually open; usually a single mamilliform gland and a penial glandular disc, borne together on a projection of penial base, but either or both may be absent. Paraspermatozoa: usually with rod-pieces. Female: copulatory bursa in relatively posterior or anterior position; egg groove of pallial oviduct coiled in a single spiral of one whorl through albumen gland, sometimes an additional loop in capsule gland and/or in jelly gland. Spawn and development: pelagic capsules, usually cupola-shaped with concentric rings on upper side, containing single ova; development planktonic. Radula: rachidian tooth longer than wide, sometimes considerably narrowed, 3 cusps, central one elongate; 4 cusps on each of lateral and inner marginal (occasionally reduced), but one major cusp on each is elongate; outer marginal with narrowed neck and projection on outer side of base, 4–10 cusps (modified from Reid, 1989a).

Remarks: The phylogenetic analysis of Reid (1989a) was based on a morphological survey of a large number of littorinid species, including 35 assigned to *Nodilittorina*, but in the cladistic analysis these were represented by a single example from each of the supposed subgeneric groups, together with a few species of uncertain relationships. The genus *Nodilittorina* was represented by *N. (Fossarilittorina) meleagris*, *N. (? Fossarilittorina) modesta*, *N. (Echinolittorina) dilatata* (d'Orbigny), and *N.*

(*Nodilittorina*) *pyramidalis*. In the resulting cladogram, the genus appeared as a monophyletic group, but the only synapomorphy was coloration of the head, considered to be a weak character since it was shared with two unrelated groups. It appeared therefore that most of the character states used in the diagnosis (see above) were pleiomorphic and not indicative of close relationship. Three subgenera were tentatively distinguished, based on absence of penial glands (*Fossarilittorina*) and position of the copulatory bursa (at the posterior end of the straight section of the pallial oviduct in *Echinolittorina*, anterior in *Nodilittorina* s.s.), but again these character states were not unique or even (in the case of the posterior bursa) apomorphic. There was a suggestion of some correlation with biogeography, since *Fossarilittorina* and *Echinolittorina* were restricted to the Atlantic and eastern Pacific regions. There is also some limited support from mitochondrial gene sequence analysis: six *Nodilittorina* species were included as an outgroup in a study of *Littorina* (Reid et al., 1996), and the four members of *Echinolittorina* (all from the Atlantic) formed a clade. An early molecular study of Central American littorinids (Jones, 1972), based on allozymes and myoglobin, failed to unite seven species of *Nodilittorina*, but also did not demonstrate the integrity of five species of the undoubtedly monophyletic *Littoraria* (Reid, 1999a, b) and can therefore be disregarded.

Another question relating to the phylogeny and definition of *Nodilittorina* is the correct classification of the Atlantic species *Littorina* (*Liralittorina*) *striata*. This has been placed in *Nodilittorina* by some authors (Rosewater, 1981; Bandel & Kadolsky, 1982), although it appears as the basal extant species of *Littorina* (sister-group to *Nodilittorina*) in a species-level cladogram of that genus (Reid, 1996). Molecular evidence from both mitochondrial (Reid et al., 1996) and nuclear gene sequences (Winnepenninckx et al., 1998), and also from radular muscle proteins (Medeiros et al., 1998), support placement in *Littorina*.

Nevertheless, many uncertainties remain about the classification and phylogeny of this group. The genus is still not adequately defined by any unique morphological synapomorphy, and it may prove to be a paraphyletic or polyphyletic assemblage consisting of those littorinine species that do not fall into any of the other more well-defined genera (i.e., *Melarhaphe*, *Peasiella*, *Mainwarinia*, *Tectarius*, *Cenchritis*, *Littorina*). A particular concern is that none of the recent morphological or molecular analyses has included members of a group of *Nodilittorina* species from the southern oceans (considered part of subgenus *Nodilittorina* by Bandel & Kadolsky, 1982, and by Reid, 1989a; but here referred to the subgenus *Austrolittorina*, see Remarks on *N. fernandezensis*) that show some resemblances to *Littorina striata* (e.g., shape of pallial oviduct) as well as to typical *Nodilittorina* members (e.g., penis and paraspermatozoa). *Fossarilittorina* too is

a problematic group, with the Atlantic *N. meleagris* as type species (Rosewater, 1981). This is characterized by an unusual penis with closed sperm duct and no large glands, and its possible relationship to the eastern Pacific *N. modesta* and *N. porcata* groups remains unclear. Attempts have been made (Reid, unpublished) to include all recognized *Nodilittorina* species in a morphological phylogenetic analysis, but the results show an almost complete absence of structure, owing to relatively few informative characters and widespread homoplasy. These problems may only be resolved by means of new molecular studies, since the available morphological evidence is inadequate.

Meanwhile, the definition of *Nodilittorina* proposed by Reid (1989a) is followed here, although it is considered premature to assign the eastern Pacific species to any of the three constituent subgenera. The subgenus *Austrolittorina* is, however, used here for *N. fernandezensis*, to emphasize its closer relationship to *N. unifasciata*, the Australian type species of the subgenus (Rosewater, 1970), than to all the other eastern Pacific species. Unfortunately, the continuing uncertainty surrounding the phylogenetic relationships of *Nodilittorina* may, when resolved, have nomenclatural consequences. The type species of *Nodilittorina* was designated by Abbott (1954) as *N. pyramidalis*, an endemic Australian species which is in several respects atypical. Although its shell is nodulose (like such "typical" species as *N. dilatata* and *N. trochoides*), its pallial oviduct is identical to that of *N. (Austrolittorina) unifasciata*, and its penis has a papillose filament unique in the genus. It is possible that *N. pyramidalis* may prove to be a member of the *Austrolittorina* group, so that *Austrolittorina* may fall in the synonymy of *Nodilittorina*. If, in addition, it were to be discovered that the *Austrolittorina* group does not form a clade together with the other *Nodilittorina* species, the genus *Nodilittorina* (with *Austrolittorina* in synonymy) would have to be employed in a more restricted sense than at present.

In the following systematic account, the *Nodilittorina* species of the eastern Pacific are divided into three informal groups: six species in the *N. porcata* group, two in the *N. modesta* group, and six in the *N. aspera* group. This is convenient since the groups are easy to recognize morphologically. Furthermore, in each case, the included species are sufficiently similar that each group may well prove to be monophyletic. The relationships of the remaining four species are unclear and they are dealt with last.

The *Nodilittorina porcata* Group

Considerable confusion has surrounded the identification and nomenclature of a group consisting of the following six species: *N. atrata*, *N. porcata*, *N. santelena*, *N. fuscilineata*, *N. parcipicta*, and *N. albicarinata*. All are small (less than 7.6 mm) and share a number of shell

features that are unusual in the genus *Nodilittorina*. Most striking is their protean plasticity of shell shape, sculpture, and coloration, which in some of these species equals that of any other littorinids. Once the species have been separated by anatomical criteria, it becomes clear that each shows a parallel and analogous range of shell variation. Thus shell shape ranges from globular to rather tall-spined and, while most show a perforated pseudo-umbilicus (or at least a crescentic area adjacent to the columella), this is closed or absent in juveniles and some adults. Shell sculpture consists of spiral microstriae, sometimes sufficiently regular and widely-spaced to be termed primary spiral grooves. Whereas some shells develop no further sculpture and therefore appear macroscopically smooth, others produce strong spiral ribs which, particularly at the periphery, may become flanged keels or carinae. Shell coloration is highly variable in all these species. Most can occur in an unpigmented white form, but more often develop a conspicuous pattern of brown or black axial stripes, spots, and spiral bands. In the Discussion it is argued that this striking variability in shell characters may be largely under ecophenotypic control. Certain anatomical characters are also shared by this group, including the absence of the penial glandular disc, peculiar twist to the end of the penial filament (slight or absent in two species), and flexure between straight and spiral portions of the pallial oviduct. These characters are likely synapomorphies and suggest that the group is a monophyletic one. They also share similar radulae, with pointed cusps; this, however, is characteristic of juvenile and small adult littorinids (see Reid, 1996, in *Littorina*) and may simply be an allometric effect of small size. Within the group, subjective similarities in shell, penes, and paraspermatozoa suggest two sub-groups, *N. atrata*, *N. porcata*, and *N. santelenae*, on one hand, and *N. fuscolineata*, *N. parcipicta*, and *N. albicarinata*, on the other.

Not surprisingly, this extreme intraspecific variation in shell shape has resulted in a confused taxonomy, at not only the specific but also the familial level. The earliest name is *Littorina porcata* Philippi, 1846, and this has continued to be widely applied to members of the group. In his catalogue of shells from Panama, C. B. Adams (1852a, b) described four species, of which only *atrata* was confidently placed in *Littorina* (then applied in a broad sense, including most members of the subfamily Littorininae); two of the remainder were doubtfully included, with the comment that they might be members of *Narica* (= *Vanikoro*, Vanikoroidae), while the fourth was doubtfully assigned to *Adeorbis* (Vitrinellidae). In fact, all are synonyms of *Nodilittorina atrata*, emphasizing its extreme variability. Succeeding authors were also uncertain about the familial assignment of these taxa and, on account of their usual possession of umbilicus and spiral carinae, often listed them as species of *Fossar* (H. & A. Adams, 1854) or *Fossarus* (A. Adams, 1855; Carpenter,

1857a, 1863, 1864a; Tryon, 1887; Turner, 1956; Keen, 1971; Abbott, 1974; Finet, 1985), a genus variously classified as littorinid, as a monotypic cerithioidean family and, most recently, as a member of the Planaxidae (Houbert, 1990). In recognition of this resemblance to *Fossarus*, Rosewater (1981) introduced *Fossarilittorina* as a subgenus of *Littorina* and included five names that have been applied to members of the *N. porcata* group (although the type species was the Atlantic *N. meleagris*). Bartsch & Rehder (1939) described a new taxon as a member of the littorinid genus *Peasiella* (see Reid, 1989b; Reid & Mak, 1998), misled by the trochoidal shell shape. The most widespread of the group, *N. atrata*, has also been misidentified as a species now assigned to *Iselica* (Pyramidellidae) and possibly as another now recognized as a *Tricolia* (Turbinidae) (see synonymy of *N. atrata*). In describing the new species *albicarinata*, McLean (1970) tentatively referred it to *Littorina*, and called for a detailed examination of the relationships of this eastern Pacific group with *Fossarus*. Their classifications as littorinids was finally established beyond doubt when Reid (1989a) described the general anatomy of *N. porcata* s.l. in a review of littorinid phylogeny, and placed it in the genus *Nodilittorina*.

At the specific level, members of the *N. porcata* group have been neglected by systematists. Only the species *porcata* was included in the nineteenth century monographs of *Littorina* (Philippi, 1847; Reeve, 1857; Weinkauff, 1882; Tryon, 1887) and none was mentioned in von Martens' (1900) monograph of *Littorina* in Central America. Carpenter (1863) reviewed the taxa of C. B. Adams (1852a, b) from Panama, but reduced only one to synonymy. New taxa were added by A. Adams (1855), Carpenter (1864), Bartsch & Rehder (1939), and McLean (1970), and two additional species are described here. Keen (1971) figured "*Peasiella*" *roosevelti* and "*Littorina*" *albicarinata*, but other names in the group were simply listed uncritically as species of *Fossarus*. In Rosewater's (1970) list of worldwide Littorinidae, the only name that might apply to this group was *Littorina* (*Melarthaple*) *umbilicata* (this is doubtful; see Taxonomic History of *N. atrata*). In the only other recent attempt to list the species of Littorinidae, Reid (1989a) gave *N. porcata* (which included *N. atrata*) and *N. albicarinata*. Elsewhere in the systematic literature the members of the *N. porcata* group have appeared only in faunistic lists.

No critical revision has previously been attempted for these taxa and is only possible now owing to the availability of anatomical material. It was the diagnostic penial differences that provided the first intimation that six distinct species are involved. These differences in shape are subtle, but the interpretation is supported by their correlations with shell traits. Most importantly, each of the species is not only sympatric but also syntopic (i.e., occurring together in the same microhabitat) with at least one other in the group and, in such cases, the diagnostic

penial and shell traits are maintained. For those pairs not known to occur sympatrically, morphological differences are of the same order and, taken together with widely separated geographical ranges, support their specific status. Characters of the oviduct and radula are not generally useful for discrimination.

Identification of these species still poses a challenge, and the most useful features are summarized in Table 1. Since there is only partial overlap of their geographical ranges, and the number of sympatric taxa is not known to exceed three, information about geographical origin of samples is useful. If this is known, examination of shells is almost always adequate for identification. However, the critical characters are not usually the most obvious features such as shell outline, smooth or carinate sculpture, perforated or closed pseudo-umbilicus, or white as opposed to patterned surface. Instead, the details of color pattern and of microsculptural striation are more significant (Table 1). Penial characters can be used to confirm identification of male specimens, but even here, occasional problems are encountered if penes are strongly contracted or contorted before fixation, or when mamilliform penial glands are missing (a rare abnormality, seen in two of the approximately 100 males examined).

In addition to their morphological similarity, the six members of the *N. porcata* group share some similarity in their ecology. Whereas most species of *Nodilittorina* are typically found among the superficially bare rocks and crevices of the littoral fringe, extending down to the uppermost eulittoral, those of the *N. porcata* group are generally to be found at a lower level, among barnacles, in crevices, and in shallow pools, in the mid to upper eulittoral zone. Whether this is simply a reflection of their small size, or of some physiological or dietary characteristic, is unknown.

Nodilittorina atrata (C. B. Adams, 1852)

(Figures 1A–I, 3A–G, 4A, F, G, H, 5A, 6)

Littorina atrata C. B. Adams, 1852a:395–396, 537 (Panama; lectotype (Turner, 1956) MCZ 186444, seen, Turner, 1956:pl. 9, fig. 5, Figure 1E herein; approx. 200 paralectotypes MCZ 186445, seen; 26 paralectotypes BMNH 1865.11.22.92, seen; 9 paralectotypes BMNH 1865.11.24.181, seen). C. B. Adams, 1852b:171–172, 313. Carpenter, 1857a:273. Carpenter, 1863:352. Vermeij, 1973:324.

Littorina atrata—Carpenter, 1857a:326.

Fossarus atratus—Carpenter, 1863:352. Tryon, 1887:272, pl. 52, fig. 10. Hertlein & Strong, 1939:371. Morrison, 1946:10–11. Turner, 1956:33, pl. 9, fig. 5. Keen, 1971:454, fig. 772.

Fossarina atrata—Carpenter, 1864b:550.

Littorina (Fossarilittorina) atrata—Rosewater, 1981:30. Finet, 1985:13.

Littorina (?) excavata C. B. Adams, 1852a:396, 537 (Panama; holotype MCZ 186422, seen, Turner, 1956:pl. 13,

fig. 2). C. B. Adams, 1852b:172, 313. Carpenter, 1857a:273.

Fossar excavatus—H. & A. Adams, 1854:320.

Fossarus excavatus—Carpenter, 1857a:326. Carpenter, 1863:352. Pilsbry & Lowe, 1932:124. Turner, 1956:47, pl. 13, fig. 2. Keen, 1971:454.

Littorina (Fossarilittorina) excavata—Rosewater, 1981:30. Finet, 1985:13.

Littorina (?) foveata C. B. Adams, 1852a:397, 537 (Panama; lectotype (Turner, 1956) MCZ 186454, seen, Turner, 1956:pl. 9, fig. 6; 1 paralectotype lost). C. B. Adams, 1852b:173, 313. Carpenter, 1857a:273.

Fossar foveatus—H. & A. Adams, 1854:320.

Fossarus foveatus—Carpenter, 1857a:326. Carpenter, 1863:352. Turner, 1956:50–51, pl. 9, fig. 6. Keen, 1971:454.

Adeorbis (?) abjecta C. B. Adams, 1852a:407–408, 539 (Panama; lectotype (Turner, 1956) MCZ 186338, seen, Turner, 1956:pl. 9, fig. 7; 15 paralectotypes MCZ 186339, seen). C. B. Adams, 1852b:183–184, 315. Carpenter, 1857a:273. Turner, 1956:27, pl. 9, fig. 7.

Fossar abjectus—H. & A. Adams, 1854:320.

Fossarus abjectus—Carpenter, 1857a:326. Carpenter, 1863:354. Hertlein & Strong, 1955a:137. Keen, 1971:453. Finet, 1985:17.

Lacuna abjecta—Pilsbry & Lowe, 1932:124.

Fossar variegatus A. Adams, in H. & A. Adams, 1854:319–320; 3:pl. 33, fig. 7a, b (operculum) (*nomen nudum*).

Fossar variegatus A. Adams, 1855:187 (Eastern Seas [in error, here corrected to Panama]; 4 syntypes BMNH 1968821, seen).

Fossarina variegata—Nevill, 1885:171.

Littorina porcata—Nevill, 1885:138 (not Philippi, 1846).

Nodilittorina (Nodilittorina) porcata—Reid, 1989a:100, fig. 5h (in part, includes *N. porcata*). Skoglund, 1992:15, 16, 33, 34 (in part, includes *N. porcata*).

Fossarus angiostratus—Morrison, 1946:10 (not *Littorina angiostratus* C. B. Adams, 1852, which is an *Iselica*, Pyramidellidae; personal observation of lectotype MCZ 186442). Hertlein & Strong, 1955a:137 (not C. B. Adams, 1852). Finet, 1985:17 (as *F. angiostratus*; not C. B. Adams, 1852).

Littorina (Melarhapha) ? angiostratus—Jones, 1972:2 (not C. B. Adams, 1852).

Littorina angiostratus—Rosewater, 1980:7, figs. 7, 8 (radula) (not C. B. Adams, 1852).

Littorina (Fossarilittorina) angiostratus—Rosewater, 1981:30 (not C. B. Adams, 1852).

Nodilittorina (Nodilittorina) angiostratus—Skoglund, 1992:15. Kaiser, 1993:106. Kaiser, 1997:27. (All not *Littorina angiostratus* C. B. Adams, 1852).

Nodilittorina angiostratus—Finet, 1994:18 (not *Littorina angiostratus* C. B. Adams, 1852).

? *Littorina (?) Melarhapha) umbilicata*—Rosewater, 1970:424 (not *Littorina umbilicata* d'Orbigny, 1840, which is a *Tricolia*, see Keen, 1971:358; personal observation of holotype in BMNH).

? *Littorina umbilicata*—Alamo & Valdivieso, 1987:26. Alamo & Valdivieso, 1997:18. Paredes, Huamán, Cardoso, Vivar & Vera, 1999:22. (All not d'Orbigny, 1840).

See also Synonymy and Taxonomic History of *N. porcata*.

Taxonomic history: The history of this species is one of considerable complexity, involving uncertain generic as-

Table 1
 Summary of the most useful characters for the identification of the six species of the *Nodilittorina porcata* group.

Character	<i>N. atrata</i>	<i>N. porcata</i>	<i>N. santelmae</i>	<i>N. fuscolineata</i>	<i>N. parvipicta</i>	<i>N. albicarinata</i>
1. Geographical range	El Salvador to N Peru, Isla del Coco, Galápagos Is	Galápagos Is	S Ecuador, N Peru	El Salvador to S Ecuador	S Baja California, Sinaloa to Michoacán (Mexico)	SW Baja California, Gulf of California
2. Shell						
—pseudo-umbilicus	present	present	absent	present	present	absent
—smooth form	yes	yes	yes	rare	no	yes
—carinate form	yes	peripheral carina only	rare	strong ribs only	yes	yes
—all white form	yes	yes	no	no	rare	yes
—most common pattern	broad black and white stripes from suture to base, with black band above periphery	dark marbling or fine axial stripes, with spots on basal ribs	brown with white band at suture and base	pale with brown lines or long dashes on ribs	small brown spots on all ribs	brown with white carinae
3. Penis						
—filament tip	pointed, twisted	pointed or hooked, twisted	slightly pointed, twisted	pointed, not twisted	blunt, not twisted	pointed, twisted
—mamilliform gland projection of base	moderately large, on projection of base	moderately large, attached directly to base	small, on projection of base	small, attached directly to base	large, attached directly to base	large, on projection of base
—pigment on base	absent	sometimes present	sometimes present	sometimes present	sometimes present	present

signment, synonyms, misidentification, and confusion with other members of a complex of similar species. In the account of the shells of Panama in which C. B. Adams (1852a, b) first described this species, he introduced three additional taxa which prove to be its synonyms, a measure of the great intraspecific variability of this species. *Littorina atrata* included largely black shells with small umbilicus, although he noted its variability in shape and sculpture. *Littorina foveata* was based upon patterned shells with a wide umbilicus, and *L. excavata* referred to the smooth, globular white form (as in Figure 1H), of which Adams had only a single specimen. These latter two were both only doubtfully assigned to *Littorina*, and Adams suggested that *Narica* (= *Vanikoro*) might be more suitable. The last taxon, *Adeorbis abjecta*, was based upon shells with a low, eroded spire; again the generic assignment was tentative; and Adams noted a resemblance to "*Littorina*" *porcata*; Carpenter (1863) placed it in the synonymy of "*Fossarus*" *atratus*. For almost 100 years these names were scarcely mentioned in the literature, except in the reviews of Carpenter (1857a, 1863) and iconography of Tryon (1887), and there as species of *Fossarus*. During the middle part of the twentieth century, studies of West American mollusks increased, and these supposed *Fossarus* species appeared in several faunistic lists (Pilsbry & Lowe, 1932; Hertlein & Strong, 1939; Morrison, 1946). The types of C. B. Adams were figured by Turner (1956), but even Keen (1971) simply listed them, unfigured, as *Fossarus* species. That they were in fact littorinids was eventually recognized by Rosewater (in Jones, 1972; Rosewater, 1980, 1981), and Vermeij (1973), who used the genus *Littorina*, and confirmed by Reid (1989a), who used *Nodilittorina*. Another synonym is *Fossar variegatus*, an almost entirely neglected name. This was based on material in the Cuming Collection, but in his description A. Adams (1855) gave the incorrect locality "Eastern Seas"; the four syntypes are somewhat eroded, but are clearly examples of a form of *N. atrata* that is common in Central America, and could easily have been collected by Cuming during his travels in the region.

Hitherto, no authors have discriminated among all six members of the *N. porcata* complex, and there has therefore been much misidentification, although geographical distribution can sometimes be used to recognize the species intended. Since *porcata* Philippi, 1846 is the oldest name, it has been the most widely used in the past decade (following Reid, 1989a; see Skoglund, 1992; Kaiser, 1993, 1997; Finet, 1994). However, both *N. atrata* and *N. porcata* occur together in the Galápagos Islands, and so the names used in faunistic lists of Galápagos species (Stearns, 1893b; Hertlein & Strong, 1939, 1955a; Vermeij, 1973; Kaiser, 1993, 1997; Finet, 1985, 1994) cannot be confidently assigned in the synonymics. To add to the confusion, the name *angiostoma* also appears frequently in the literature. This is a misidentification; *Littorina an-*

giostoma C. B. Adams, 1852, is an *Iselica*, belonging to the Pyramidellidae (figured by Turner, 1956:pl. 13, fig. 1). This name has been used mainly in works on the Galápagos fauna (Hertlein & Strong, 1955a; Finet, 1985, 1994; Kaiser, 1993, 1997), and these also list at least one other species (usually *porcata* or *abjecta*). It seems likely that *angiostoma* was used for shells of the white ecotype, and *porcata* for patterned shells. However, this distinction does not separate *N. atrata* s.s. and *N. porcata* s.s. in the Galápagos, so that again the synonymy cannot be resolved. For convenience, in these doubtful cases, uses of the name *atrata* and its synonyms (including *angiostoma non* C. B. Adams) for Galápagos shells are listed above, while uses of *porcata* (and its synonym *roosevelti*) are given in the synonymy of *N. porcata*.

Curiously, in his influential work on Indo-Pacific Littorinidae in which all species recognized worldwide were listed, Rosewater (1970) did not give any of the names discussed above. Instead, the older name *Littorina umbilicata* appears, doubtfully assigned to the subgenus *Mel-larhaphé*. This may have been intended to refer to some of the members of the *N. porcata* group, although the distribution given ("Peru and Chili," perhaps following Dall, 1909) is not correct (*N. atrata* and *N. santelenae* only just reach far northern Peru). If so, this is another misidentification, since *Littorina umbilicata* d'Orbigny, 1840, is in fact a species of *Tricolia* (Keen, 1971). The name also appears in several recent lists of Peruvian mollusks (Alamo & Valdivieso, 1987, 1997; Paredes et al., 1999), in which *Tricolia umbilicata* is listed separately, suggesting that "*L. umbilicata*" might indeed be intended for *N. atrata* and/or *N. santelenae*.

Diagnosis: Shell small, globular to tall, smooth to carinate; coarse, irregular microstriae; usually a large, perforated, pseudo-umbilicus; may be white, but common pattern is broad black or brown axial stripes from suture to base and broad band above periphery, on white ground. Penis with pointed and twisted filament tip, moderately large mamilliform gland on long projection of base, no glandular disc.

Material examined: 73 lots (including 26 penes, 11 sperm samples, eight pallial oviducts, one egg capsule, five radulae).

Shell (Figures 1A–I): Mature shell height 2.1–7.5 mm. Shape variable; high turbinate to low-spined, globular or slightly patulous ($H/B = 1.00–1.53$; $SH = 1.24–2.21$); spire whorls rounded, suture distinct; periphery of last whorl usually rounded, but may be marked by a rib or carina; solid. Columella straight, narrow, flared and flattened at base; pseudo-umbilicus usually large, perforated, outlined by sharp keel continuous with outer apertural lip, but sometimes only narrow imperforate crescentic area (pseudo-umbilicus narrow or absent in most juveniles).

Sculpture variable; smoothest shells covered with coarse, rather irregular, spiral microstriae (rarely becoming obsolete above periphery of last whorl); sometimes 5–16 indistinct ribs may develop on last whorl (peripheral rib and 2–3 on base are strongest); strongly sculptured shells with few sharp or carinate ribs, 2–3 on base, strongest rib at periphery, 1–7 above periphery (juveniles 2 on base, 1 at periphery, 1 at shoulder), entire surface with strong microstriae; periostracum occasionally produced into minute bristles (to 100 μm) on basal and peripheral ribs of strongly sculptured shells. Protoconch 0.26–0.29 mm diameter. Color variable, may change abruptly; frequently entirely white externally (especially in smooth, globular shells), sometimes with irregular large blotches of black, fine brown speckles, or continuous dark brown band between shoulder and periphery; most common color is striking black and white pattern, with broad, black or dark brown oblique axial stripes from suture to base, usually fused between shoulder and periphery to form irregular continuous dark band; rarely entirely black but for few white flames on base; columella and aperture usually pink-brown to dark purple-brown (even in white shells), with anterior and often posterior unpigmented band.

Animal: Head and sides of foot grey to black; 2 black lines along tentacle, seldom meeting at tip; usually a narrow white band across snout. Opercular ratio 0.41–0.47. Penis (Figures 3A–G): filament tip pointed and twisted; sperm groove with a kink, distal portion shallower, extending to filament tip; single mamilliform penial gland on long lateral appendage at 0.4–0.6 total penial length (mamilliform gland absent in one specimen); glandular disc absent; base not pigmented. Euspermatozoa 79–107 μm ; paraspermatozoa (Figures 4G, H) oval, 14–26 μm ; rod-pieces single (rarely two), filling cell or projecting at one end (rarely both ends), 14–21 μm , blunt or slightly rounded at ends, parallel-sided or slightly tapering; granules large, spherical, distinct. Pallial oviduct (Figure 4A) with flexure and constriction between spiral and straight sections; copulatory bursa opening at anterior end of straight section, extending back to start of spiral portion. Spawn (Figure 4F) a pelagic cupola-shaped capsule 160 μm diameter, sculptured with four concentric rings, containing single ovum 40 μm diameter; protoconch indicates planktotrophic development.

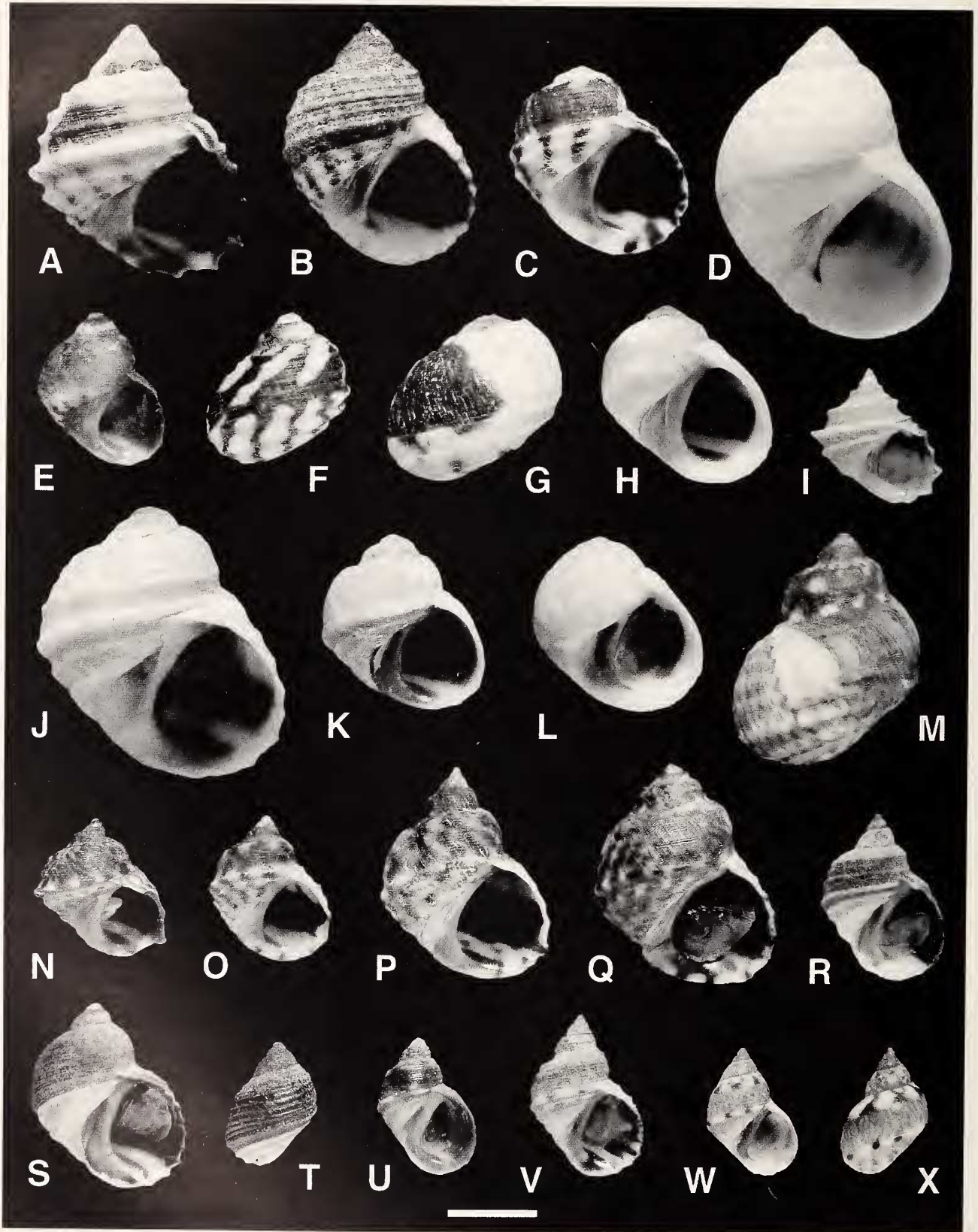
Radula (Figure 5A): Relative radular length 2.1–3.5. Rachidian: length/width 1.11–1.68; major cusp pointed and elongate leaf-shaped. Lateral and inner marginal: major cusps pointed or slightly rounded. Outer marginal: 5–7 cusps.

Habitat: Among uppermost oysters and barnacles; in crevices and shallow pools in mid to upper eulittoral; on sandstone, basalt, concrete; sheltered to exposed coasts, sometimes in silty, mangrove-fringed channels; often abundant.

Range (Figure 6): El Salvador to northern Peru, Isla del Coco, Galápagos Islands. Range limits: Los Cobanos, Sonsonate, El Salvador (LACM 73-56, 3 specimens); Isla Zacatillo, Golfo de Fonseca, El Salvador (LACM 73-57); Coyolita, Honduras (USNM 749644); San Juan del Sur, Nicaragua (USNM 60677); Puerto Utria, Choco, Colombia (LACM 34-106.20, 1 specimen); Same, Esmeraldas, Ecuador (BMNH 2001151); El Rubio and Punta Mero, Tumbes, Peru (LACM 72-85, 1 specimen); Isla del Coco (USNM 130103; KLK); Galápagos Islands (Isla Santiago, USNM 807236; Isla Floreana, personal observation; Isla San Cristobal, BMNH 20001152; Isla Bartolomé, BMNH 20001153; Isla Santa Cruz, BMNH 20001154). The record from Los Cobanos is an isolated patch of hard substrate on a largely sedimentary coast, the Central American Gap (Glynn & Ault, 2000). The species is common in the Golfo de Fonseca, Isla del Coco, the Galápagos Islands and elsewhere, but only single specimens have been seen from Colombia and Peru.

Remarks: The shell of *N. atrata* is among the most variable of all littorinid species, ranging from globular to tall, umbilicate to imperforate, smooth to carinate, white to black-patterned. There is no apparent geographical component to this variation; for example, the distinctive smooth, white, globular shells are recorded from the Galápagos Islands, Ecuador, Panama, and Costa Rica. However, it is notable that of the available museum collections, most individual samples encompass a relatively restricted range of shell variation, and extreme variability in color or sculpture from a single locality is unusual. Personal collections suggest that there may be a correlation with microhabitat, though this requires further investigation. For example, at Punta Chocolatera (Peninsula Santa Elena, Guayas, Ecuador) a sample from crevices among barnacles in the upper eulittoral comprised ribbed shells, mostly with strong black patterning (BMNH 20001155, Figure 1F), whereas a sample from shallow pools on an open rock platform only 20 m distant comprised only white, smooth, globular shells (BMNH 20001156, similar to Figure 1H). A similar, but less perfect, correlation was observed nearby at Anconito (BMNH 20001157, 20001158). In general, samples from lower tidal levels (mid eulittoral) and from pools appear to be more smooth and sometimes white in color, whereas those from among barnacles are more strongly ribbed or carinate. Shell color may change abruptly on a single individual, for example from black patterned to entirely white or vice versa (Figure 1G). Sculpture does not show similarly sudden change, although relatively smooth shells sometimes develop low ribs on the final part of the last whorl. A possible interpretation of these observations is that the species are susceptible to ecophenotypic effects on shell form and coloration (see Discussion).

This is the most widely distributed of the six species in the *N. porcata* group. It is sympatric with *N. fuscoli-*



neata from El Salvador to Ecuador, with *N. porcata* in the Galápagos Islands, and with *N. santelenae* in southern Ecuador and northern Peru. In each case, these can be found in the same microhabitat as *N. atrata*, although some differences in habitat range are likely (see Remarks on all three). These four potentially sympatric species can be distinguished by penial shape but, owing to the great range of variation, identification from shells alone is sometimes difficult (Table 1). In the Galápagos Islands both *N. atrata* and *N. porcata* may be white; the latter usually shows fine, regular microstriae, an angled periphery, and a strong peripheral and two basal ribs; in *N. atrata* the microstriae are coarser and more irregular, the periphery rounded and, if ribs are present at all, they are uniformly developed over the whorl. Patterned shells are more distinctive; in *N. atrata*, the common black and white pattern of broad axial stripes from suture to base and broad dark band above the periphery is diagnostic; dark shells of *N. porcata* are usually marbled or finely striped, with brown spots on the basal ribs and often a pale basal band. In southern Ecuador and northern Peru, shell coloration again usually distinguishes *N. atrata* from sympatric *N. santelenae*; the latter is commonly brown or black with a white band on the base and often a second at the suture, or (in the smooth algal-dwelling form) mottled yellow-brown with strong brown and white spots at shoulder and periphery. The shell of *N. fuscolineata* is smaller, more delicate, with markedly rounded whorls and regular ribs bearing a pattern of dark lines or dashes.

Nodilittorina porcata (Philippi, 1846)

(Figures 1J–Q, 3H–O, 4B, I, 5B, 6, 22E)

Littorina porcata Philippi, 1846a:139 (ad insulas Gallapagos [Galápagos Islands, Ecuador]; lectotype (here designated, 6.1 × 5.0 mm) BMNH 1968218/1, seen, Philippi, 1847:3, *Littorina* pl. 6, fig. 14, Figure 1J herein; 1 paralectotype BMNH 1968218/2, seen; 2 probable paralectotypes BMNH 1998193, seen). Carpenter, 1857a:186. Reeve, 1857:sp. 89, pl. 16, fig. 89. Stearns, 1893b:444. *Littorina porcata*—Philippi, 1847:3:14, *Littorina* pl. 6, fig.

14. Carpenter, 1857a:326, 360. Weinkauff, 1882:78–79, pl. 10, fig. 12. Weinkauff, 1883:215.

Littorina (Littorina) porcata—Tryon, 1887:242, pl. 41, fig. 10.

Fossarus porcatus—Keen, 1971:454, fig. 780.

Littorina (Fossarilittorina) porcata—Rosewater, 1981:30. Finet, 1985:13.

Nodilittorina (Nodilittorina) porcata—Reid, 1989a:100 (in part, includes *N. atrata*). Reid, 1989b:53. Skoglund, 1992:15, 16, 33, 34 (in part, includes *N. atrata*). Kaiser, 1993:106. Kaiser, 1997:27.

Nodilittorina porcata—Finet, 1994:18 (in part, includes *N. atrata*).

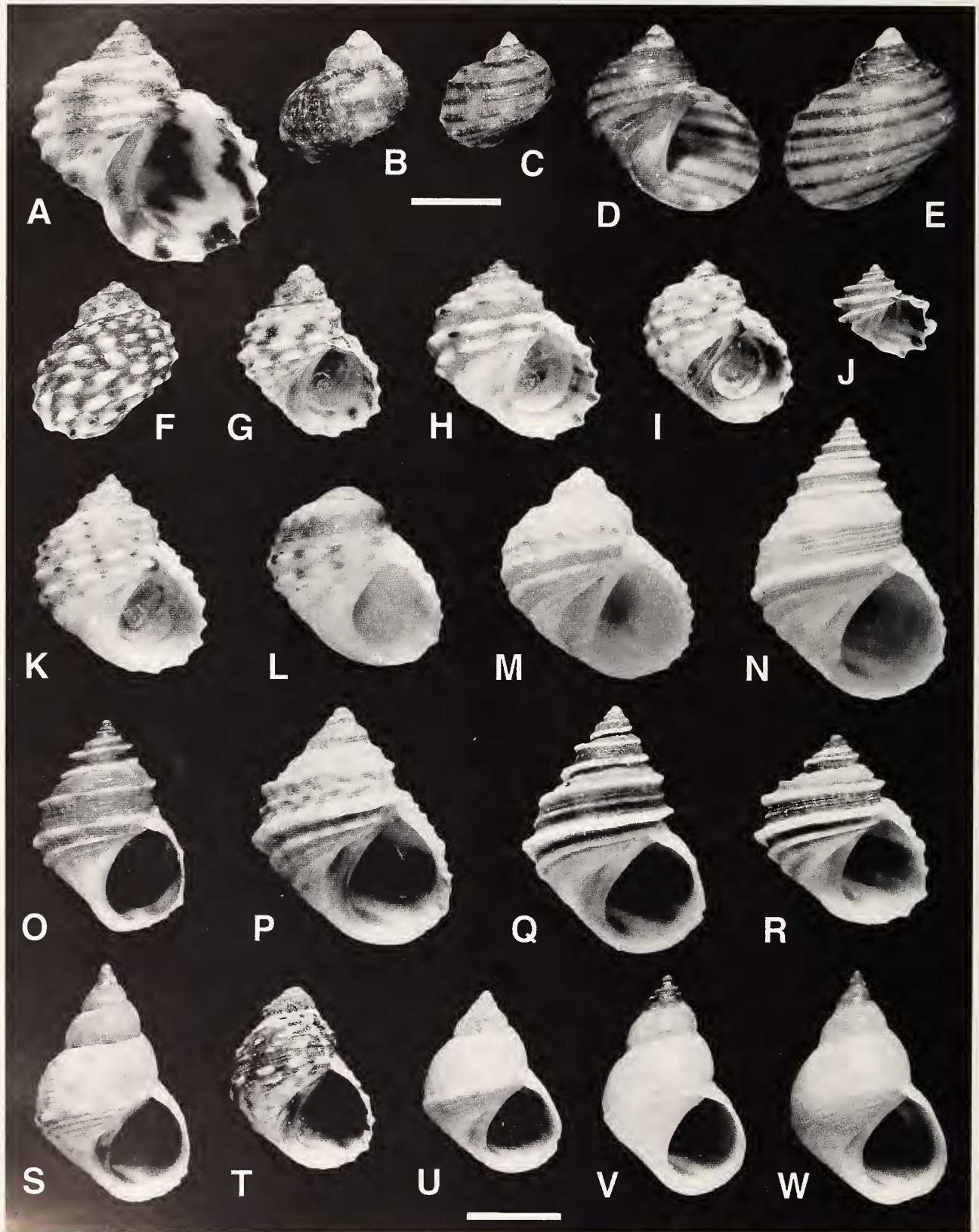
Peasiella roosevelti Bartsch & Rehder, 1939:8–9, pl. 2, figs. 1–3 (Sullivan [Sullivan] Bay, James Island [Isla Santiago], Galápagos; holotype USNM 472575, seen, Figure 1N herein). Keen, 1971:367, fig. 191. Finet, 1985:13.

See also Synonymy and Taxonomic History of *N. atrata*.

Taxonomic history: The types of *Littorina porcata* are large and white, with variably developed ribs on the last whorl. In contrast, *Peasiella roosevelti* was based on a single, small, darkly patterned shell with strong peripheral keel. Surprisingly, in view of the longstanding assignment of other members of the *N. porcata* group to the genus *Fossarus*, Philippi (1846a) immediately classified his species as a member of *Littorina*, and it was subsequently included in several monographs of the genus (Philippi, 1847; Reeve, 1857; Weinkauff, 1882; Tryon, 1887); only Keen (1971) referred it to *Fossarus*. The trochoidal shape and umbilicus of the form described by Bartsch & Rehder (1939) are indeed reminiscent of the littorinid genus *Peasiella*, but that has a multispiral operculum (Reid, 1989b; Reid & Mak, 1998), a feature missing from the type, which was inhabited by a pagurid crab. Since *porcata* is the oldest name in the *N. porcata* group, it has been frequently misapplied to the more widespread *N. atrata*. These two very similar species occur together on the Galápagos Islands, and previous authors working on the fauna have not distinguished them, so that synonymy

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Figure 1. Shells of *Nodilittorina porcata* group: *N. atrata* (A–I), *N. porcata* (J–Q), and *N. santelenae* Reid, sp. nov. (R–X). A. Isla Pedro González, Panama (USNM 587820). B. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001159). C. Punta Pitt, Isla San Cristobal, Galápagos Islands (BMNH 20001152). D. Baltra Channel, Isla Santa Cruz, Galápagos Islands (BMNH 20001160). E. Lectotype of *Littorina atrata* C. B. Adams, 1852; Panama (MCZ 186444). F. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001155). G. Punta Egas, Isla Santiago, Galápagos Islands (USNM 807236). H. Montezuma, Costa Rica (USNM 664373). I. Muisne, Esmeraldas, Ecuador (BMNH 20001161). J. Lectotype of *Littorina porcata* Philippi, 1846; Galápagos Islands (BMNH 1968218/1). K. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (KLK). L, M, O–Q. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (L, BMNH 20001167; M, Q, BMNH 20001164; O, P, BMNH 20001168). N. Holotype of *Peasiella roosevelti* Bartsch & Rehder, 1939; Bahía Sullivan, Isla Santiago, Galápagos Islands (USNM 472575). R. Holotype of *N. santelenae* Reid, sp. nov.; Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20000309). S, T. Paratypes of *N. santelenae* Reid, sp. nov.; Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20000310). U. Salinas, Guayas, Ecuador (USNM 368112). V. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001171). W, X. Anconcito, Guayas, Ecuador (BMNH 20001170). Scale bar = 2 mm.



mies cannot be accurately compiled (see Synonymy and Taxonomic History of *N. atrata*).

Diagnosis: Shell small, globular to turbinate; peripheral rib or carina, smooth or ribbed above; fine, regular microstriae; large, perforated pseudo-umbilicus; often white; if patterned, then dark marbling or fine stripes above periphery, spots on base. Penis with pointed or hooked, twisted filament tip, moderately large mamilliform gland closely attached to base, no glandular disc.

Material examined: 30 lots (including 19 penes, 1 sperm sample, 2 pallial oviducts, 3 radulae).

Shell (Figures 1J–Q, 22E): Mature shell height 1.9–6.1 mm. Shape variable; turbinate to low-spired and globular ($H/B = 1.04–1.26$, $SH = 1.29–1.83$); spire whorls rounded, with distinct suture, often appearing turreted (owing to shoulder angulation and strong peripheral rib just above suture); last whorl usually with angulate periphery marked by strong rib or carina, sometimes rounded but still with peripheral rib; solid. Columella straight, narrow, flared, and flattened at base; pseudo-umbilicus large, perforated (narrow or imperforate in juveniles), outlined by sharp keel continuous with outer apertural lip. Sculpture variable; usually sharp or carinate peripheral rib and 2 basal ribs; smooth above periphery or with 1–6 rounded ribs developing on last whorl; occasionally all but peripheral rib become obsolete; fine, regular spiral microstriae usually present over entire surface (Figure 22E), but globular shells lacking ribs may be microscopically smooth; periostracum occasionally produced into fine bristles (to 200 μm ; Figure 22E) on basal and peripheral ribs. Protoconch not seen. Color variable, may change abruptly; white or grey with brown to black oblique or wavy axial stripes, or fine marbling or irregular marks; base with brown spots on ribs, and often a pale spiral band on rib anterior to periphery; color pattern may become paler or disappear toward end of last whorl; shells may appear entirely white, although spire usually shows dark pattern unless heavily eroded; aperture dark brown or orange-brown, with anterior (sometimes also posterior) unpigmented band, columella brown.

Animal: Head and sides of foot black; two thick black lines along tentacle, usually meeting at tip. Opercular ratio 0.42–0.53. Penis (Figures 3H–O): filament tip pointed and twisted, often giving hooked appearance; sperm groove with a kink, distal portion shallower, extending to filament tip; single mamilliform penial gland closely attached to base at 0.2–0.4 total penial length; glandular disc absent; base often slightly pigmented. Euspermatozoa length unknown; paraspermatozoa (Figure 4I) oval; rod-pieces single (rarely two), projecting at one or both ends, 11–19 μm , blunt, slightly tapering; granules large, spherical, distinct. Pallial oviduct (Figure 4B) with marked flexure and constriction between spiral and straight sections; copulatory bursa opening at anterior end of straight section, extending back to start of spiral portion. Spawn and development not observed.

Radula (Figure 5B): Relative radular length 1.3–1.8. Rachidian: length/width 0.94–1.27; major cusp pointed and elongate leaf-shaped. Lateral and inner marginal: major cusps pointed. Outer marginal: 6–7 cusps.

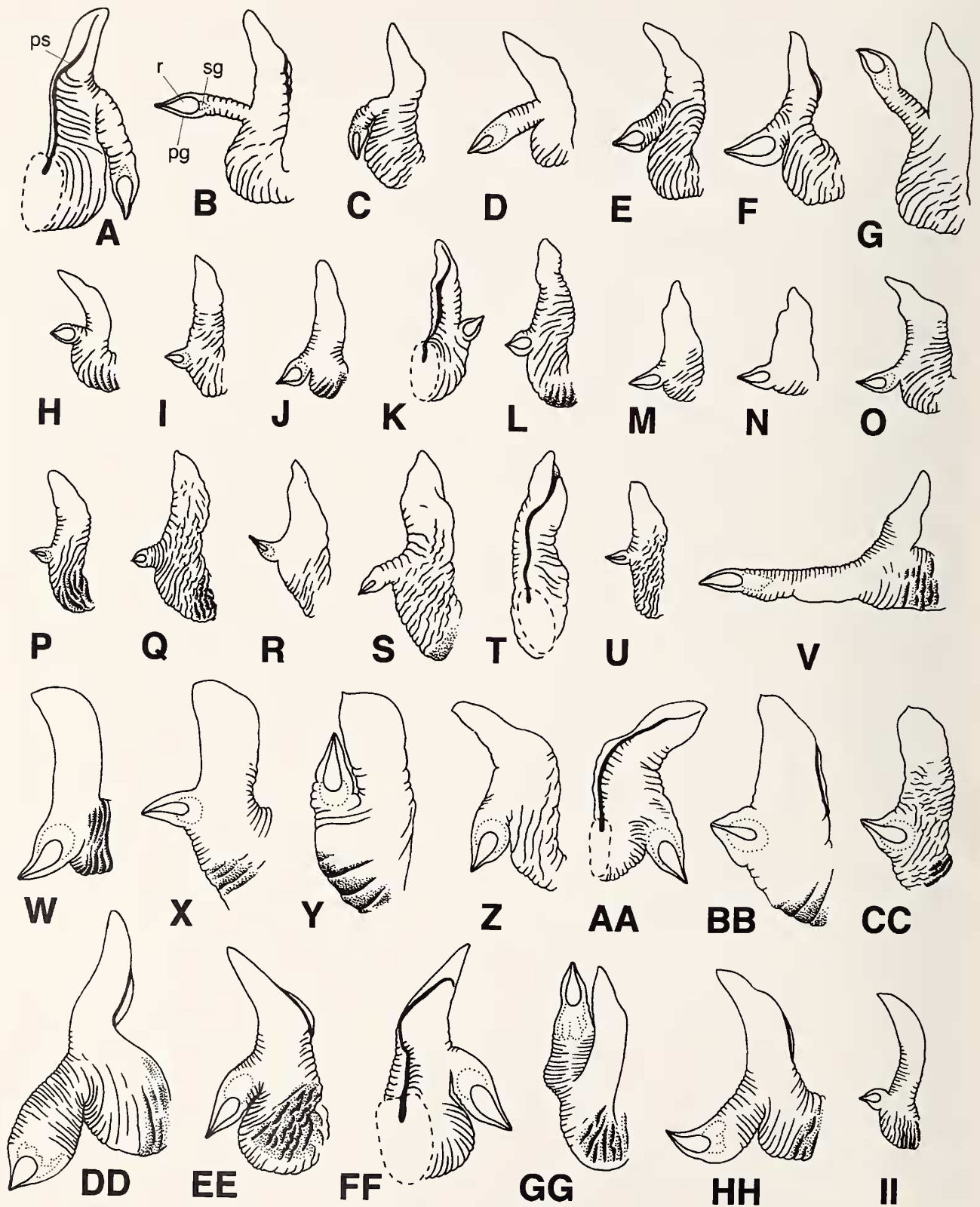
Habitat: In pits and shallow pools on basalt rocks and rock platforms, also concrete; upper eulittoral, sheltered to semi-exposed coasts; often abundant. In the Galápagos, *N. porcata* has also been reported from mangroves (Hedgpeth, 1969; Kay, 1991), but whether this refers to this species, *N. atrata* or both, is unknown.

Range (Figure 6): Galápagos Islands only. Records from islands of Santa Cruz (BMNH 20001164), San Cristobal (BMNH 20001165), Bartolomé (BMNH 20001166), Santiago (USNM 807236), Fernandina (LACM 72-196), Isabela (LACM 33-163, 34-276), Baltra (LACM 66-206), and Genovesa (LACM 33-174).

Remarks: This species is highly variable in shape, sculpture, and coloration. The two named taxa represent extremes of the range of variation; the types of *Littorina porcata* are large, smooth or ribbed, and white, whereas the type of *Peasiella roosevelti* is small, sharply keeled, and darkly patterned. However, there seems no doubt that these are conspecific. Sculpture above the periphery varies from smooth to ribbed within some microsympatric

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Figure 2. Shells of *Nodilittorina porcata* group (continued): *N. fuscolineata* Reid, sp. nov. (A–E), *N. parcipicta* (F–M), and *N. albicarinata* (N–W). A. Holotype of *N. fuscolineata* Reid, sp. nov.; Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 19990422). B. Isla San Pedrito, Costa Rica (LACM 72-22). C. Punta Penca, Guanacaste, Costa Rica (LACM 72-38). D, E. Isla Alcatraz, Costa Rica (LACM 72-46; two views). F. Mazatlán, Sinaloa, Mexico (BMNH 20001177). G. Boca de Tomatlán, Jalisco, Mexico (BMNH 20001178). H, I, K. 7 km NE of San José del Cabo, Baja California Sur, Mexico (BMNH 20001179). J. Playa de los Muertos, Puerto Vallarta, Jalisco, Mexico (BMNH 20001180). L. Lectotype of *Fossarus parcipictus* Carpenter, 1864; Cabo San Lucas, Baja California Sur, Mexico (USNM 4060). M. Topolobampo, Sinaloa, Mexico (BMNH 20001176). N, P–R. Balandra, Baja California Sur, Mexico (BMNH 20001182). O. Holotype of *Littorina albicarinata* McLean, 1970; El Requeson, Bahía Concepción, Baja California Sur, Mexico (LACM 1399). S. Puerto Lobos, Sonora, Mexico (USNM 862206). T. Playa Coromuel, Baja California Sur, Mexico (BMNH 20001186). U–W. Bahía Agua Verde, Baja California Sur, Mexico (USNM 264989). Scale bars A–E = 1 mm; F–W = 2 mm.



collections, and ribbed specimens usually show smooth spires. Spire height too varies substantially within single samples. The variation in shell color is peculiar, since available samples are either white or darkly patterned, and not a mixture of both. Samples collected from the same locality in different years can differ strikingly in coloration; for example, shells from the precise location of basalt rocks beside the dock of the Charles Darwin Research Station in Academy Bay, Santa Cruz Island, were white (and smooth) in collections made in 1988 and 1989, but brown (and ribbed) in 1998 (personal observation; BMNH 20001164, 20001167; CDRS). Close examination of white shells with well preserved spires shows that the early whorls are in fact brown. Furthermore, adults with predominantly brown shells can be found in which the coloration abruptly becomes pale or white on the last whorl (Figure 1M). As in some other members of the *N. porcata* group, these observations suggest that shell color (and perhaps also sculpture) may be influenced by ecophenotypic effects (see Discussion).

In museum collections from the Galápagos Islands, this species is often mixed with the closely similar *N. atrata*, and the two are syntopic in the habitats described above (personal observation). Nevertheless, there is probably some microhabitat or behavioral segregation between them, since in samples from Academy Bay, Santa Cruz Island, brown shells of *N. porcata* were frequently overgrown with a fine filamentous alga, whereas white shells of *N. atrata* from the same shores were not. The discrimination of these two species is discussed in the Remarks on *N. atrata*.

Nodilittorina santelenae Reid, sp. nov.

(Figures 1R–X, 3P–U, 4C, J, K, 5C, 6)

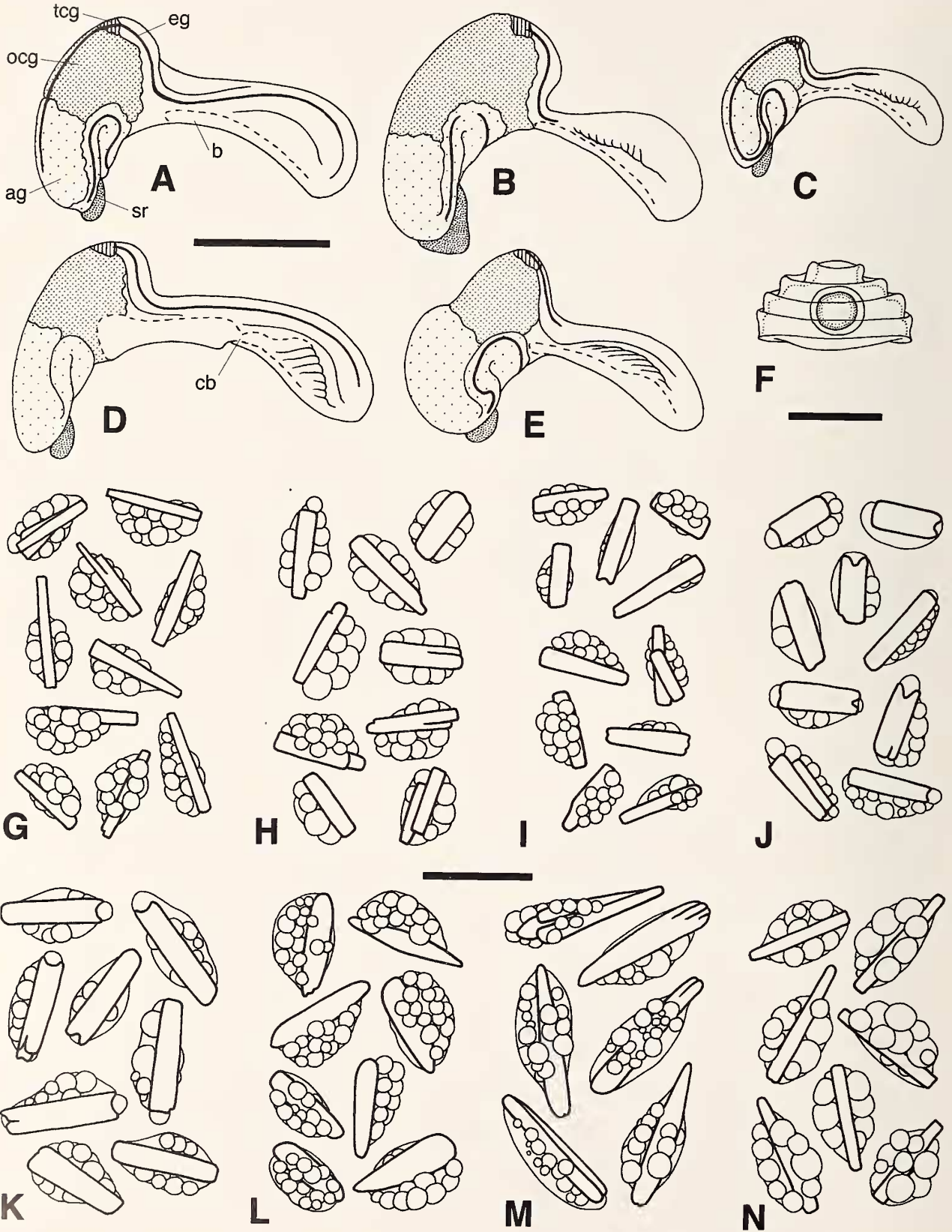
Etymology: Name derived from the type locality on the Peninsula Santa Elena, Ecuador.

Types (Figure 1R): Holotype BMNH 20000309. 19 paratypes BMNH 20000310 (Figures 1S, T); 100 paratypes in alcohol BMNH 20000311, 4 paratypes USNM 894294. Type locality: Punta Carnero, Peninsula Santa Elena, Guayas Province, Ecuador.

Taxonomic history: In ANSP there is a sample of six shells of this species collected by C. E. White in Ecuador, bearing the name *Lacuna guayaquilensis* Bartsch (ANSP 144844); the name was apparently never published by Bartsch. *Fossarus guayaquilensis* Bartsch, 1928, is a different taxon, a true member of the genus *Fossarus* (Bartsch, 1928). In some lists of Peruvian mollusks there appears the name *Littorina umbilicata*, without locality (Dall, 1909; Alamo & Valdivieso, 1987, 1997; Paredes et al., 1999; also world list of Littorinidae in Rosewater, 1970). This is a misidentification (see Taxonomic History of *N. atrata*), but might possibly be intended for the present species (perhaps also including *N. atrata*).

Diagnosis: Shell small, narrowly turbanate; smooth with impressed lines, or with low ribs and microstriae; pseudo-umbilicus small; usually imperforate; commonly brown with basal and sutural white band. Penis with slightly pointed, twisted filament tip, small mamilliform gland on short projection of base, no glandular disc.

Figure 3. Penes of *Nodilittorina porcata* group: *N. atrata* (A–G), *N. porcata* (H–O), *N. santelenae* Reid, sp. nov. (P–U), *N. albicarinata* (V, DD–HH), *N. parcipicta* (W–CC), *N. fuscilineata* Reid, sp. nov. (II). A, B. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001159; shell H = 3.9 mm, 3.7 mm). C. Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001162; shell H = 2.9 mm). D. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001156; shell H = 2.9 mm). E, F. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (BMNH 20001163; shell H = 4.2 mm, 3.5 mm). G. Baltra Channel, Isla Santa Cruz, Galápagos Islands (BMNH 20001160; shell H = 4.5 mm). H–N. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (H, K, BMNH 20001169, shell H = 2.7 mm, 3.1 mm; I, J, BMNH 20001168, shell H = 3.2 mm, 3.3 mm; L, BMNH 20001164, shell H = 3.9 mm; M, N, BMNH 20001167, shell H = 2.8 mm, 3.3 mm). O. Punta Pitt, Isla San Cristobal, Galápagos Islands (BMNH 20001165; shell H = 3.4 mm). P, Q, S, T. Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20000311; shell H = 3.2 mm, 4.0 mm, S, T, 3.9 mm; two views). R. Anconcito, Guayas, Ecuador (BMNH 20001170; shell H = 2.9 mm). U. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001171; shell H = 2.5 mm). V, HH. Playa Coromuel, Baja California Sur, Mexico (V, BNMH 20001186, shell H = 3.4 mm; HH, BMNH 20001185, shell H = 3.6 mm). W. Playa Coromuel, Baja California Sur, Mexico (BNMH 20001174; shell H = 4.0 mm). X, Y. Bahía Santa María, Baja California Sur, Mexico (BMNH 20001173; shell H = 3.8 mm, 4.1 mm). Z, AA, BB. Topolobampo, Sinaloa, Mexico (BMNH 20001176; shell H = 3.7 mm, 3.5 mm; Z, AA, two views). CC. Punta Telmo, Michoacán, Mexico (BMNH 20001181; shell H = 3.6 mm). DD–GG. Balandra, Baja California Sur, Mexico (BMNH 20001182; shell H = 4.7 mm, 5.0 mm; EE, FF, two views, 3.7 mm). II. Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 19990422, holotype of *N. fuscilineata* Reid, sp. nov.; shell H = 2.8 mm). Abbreviations and shading conventions: pg, mamilliform penial gland; ps, penial sperm groove (thick line); r, reservoir of mamilliform penial gland (visible by transparency); sg, subepithelial glandular tissue of penial gland (dotted line; usually visible by transparency); dashed line, cut base of penis; stipple in folds of penial base indicates black pigment. Scale bar = 1 mm.



Material examined: 17 lots (including 9 penes, 4 sperm samples, 3 pallial oviducts, 4 radulae).

Shell (Figures 1R–X): Mature shell height 1.7–5.6 mm. Shape narrowly to elongately turbinate ($H/B = 1.13–1.57$, $SH = 1.36–1.84$); whorls moderately rounded, slightly angled at periphery, suture distinct. Columella narrow, slightly thickened and convex in center; pseudo-umbilicus usually only a narrow imperforate crescentic area, but sometimes small, perforated. Sculpture variable; smoothest shells have 7–17 impressed striae (more closely spaced posteriorly) above slight rib at periphery of last whorl, 6–9 striae or 2–3 indistinct ribs on base, no additional microstriae, but sculpture sometimes becomes indistinct; sculptured shells show total of 4–12 low rounded or narrow ribs (of which peripheral rib and one to two above only rarely become carinate) on last whorl with spiral microstriae between. Protoconch 2.3 whorls, 0.28 mm diameter. Color variable; darkest shells dark brown to black, with narrow white line or broad band on base; usually with additional white band at suture; base sometimes faintly spotted; paler shells cream with broad grey-brown or indistinctly mottled band between periphery and shoulder; smoothest shells pale yellow-brown with faint brown mottling throughout, and prominent alternating brown and white blotches at shoulder and periphery; aperture brown with anterior (and sometimes posterior) pale stripe, or yellow-brown with external pattern showing through in palest shells; columella purple-brown.

Animal: Head black, rarely an unpigmented line across snout, two black lines along tentacle, not meeting at tip; sides of foot speckled black or grey. Opercular ratio 0.38–0.43. Penis (Figures 3P–U): filament tip pointed and twisted, sometimes giving slightly hooked appearance; sperm groove with a kink, distal portion more open, extending to filament tip; single very small mamilliform penial gland on short, narrow projection of base at 0.3–0.5 total penial length; glandular disc absent; base sometimes slightly pigmented. Euspermatozoa 100–107 μm ; paras-

permatozoa (Figures 4J, K) oval; rod-pieces single (rarely two), usually projecting at one or both ends, or at least filling cell, 11–23 μm , oblong, parallel-sided, ends blunt or hollowed; granules large, spherical, distinct. Pallial oviduct (Figure 4C) with flexure and constriction between spiral and straight sections; copulatory bursa opening at anterior end of straight section, extending back to capsule gland. Spawn not observed; protoconch indicates planktotrophic development.

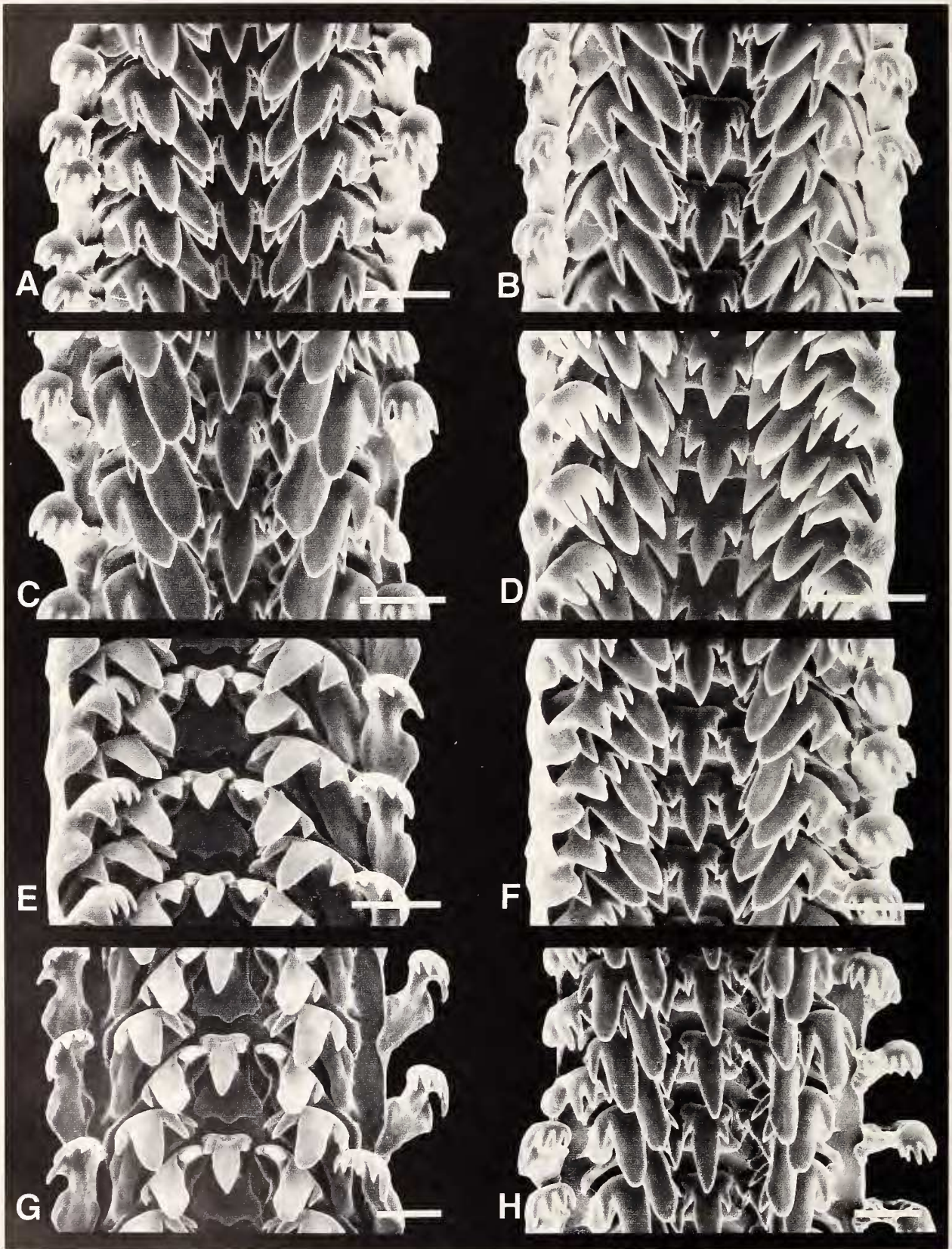
Radula (Figure 5C): Relative radular length 1.0–2.1. Rachidian: length/width 1.13–1.77; major cusp pointed and elongate leaf-shaped. Lateral and inner marginal: major cusps pointed or slightly rounded. Outer marginal: six cusps.

Habitat: Among barnacles in mid to upper eulittoral, often in empty tests; in shallow pools with fine filamentous green algae, on rock platform, upper eulittoral; on sandstone and mudstone; semi-sheltered bays and wave-exposed headlands; usually abundant.

Range (Figure 6): Southern Ecuador and northern Peru. Recorded from Peninsula Santa Elena, Guayas, Ecuador (Punta Carnero, BMNH 20000310; Anconcito, BMNH 20001170; Punta Chocolatera, BMNH 20001171; La Libertad, LACM 66-116; Playas, LACM 70-13); El Rubio and Punta Mero, Tumbes, Peru (LACM 72-85); Talara, Piura, Peru (USNM 368553, 1 specimen); Paita, Piura, Peru (USNM 368579, 368580, 1 specimen each).

Remarks: This species has a narrowly restricted range and is therefore seldom represented in museum collections. In the field, it is microsympatric with *N. atrata* among barnacles, but extends lower on the shore, and is much more common than that species where they occur together (personal observation, Peninsula Santa Elena); juvenile *N. paytensis* can also be found commonly in this microhabitat. The habitat among filamentous algae in shallow pools is unusual for this genus, and here it was found abundantly with only very few *N. atrata* (personal

Figure 4. Pallial oviducts (A–E), egg capsule (F) and paraspermatozoa (G–N) of *Nodilittorina porcata* group: *N. atrata* (A, F, G, H), *N. porcata* (B, D), *N. santelenae* Reid, sp. nov. (C, J, K), *N. parcipicta* (D, L, M), *N. albicarinata* (E, N). A, F. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001159; shell H = 5.2 mm). B, I. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (BMNH 20001169; shell H = 5.0 mm). C, K. Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20000311; shell H = 5.0 mm). D. Bahía Santa María, Baja California Sur, Mexico (BMNH 20001173; shell H = 4.9 mm). E. Balandra, Baja California Sur, Mexico (BMNH 20001182; shell H = 4.8 mm). G. Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20000311). H. Muisne, Esmeraldas, Ecuador (BMNH 20001161). J. Anconcito, Guayas, Ecuador (BMNH 20001170). L, M. Playa Coromuel, Baja California Sur, Mexico (BMNH 20001175). N. Playa Coromuel, Baja California Sur, Mexico (BMNH 20001185). Abbreviations and shading conventions for pallial oviducts: ag, albumen gland (light stipple; opaque and translucent portions not usually distinguishable in gross dissection); b, copulatory bursa (dashed line; visible by dissection; only the part separated as a sac from lumen of straight section of pallial oviduct is indicated); cb, constriction in copulatory bursa; eg, egg groove (thick line; visible externally when darkly pigmented and if not concealed by swollen oviducal glands); ocg, opaque capsule gland (mid stipple); sr, seminal receptacle (heavy stipple); teg, translucent capsule gland (cross-hatching); some internal folding of lumen in straight section is visible by transparency. Scale bars A–E = 1 mm; F = 0.1 mm; G–N = 20 μm .



observation, Anconcito, Peninsula Santa Elena). As in all members of the *N. porcata* group, sculpture and color vary widely; the palest, smoothest, most elongate shells were found among algae in the sheltered microhabitat of a shallow pool, whereas samples from among barnacles on exposed headlands were dark, ribbed, and lower spired. This distinction was maintained over a distance of a few meters on a shore at Anconcito, suggesting that ecophenotypic influences may be important (see Discussion).

Confusion is possible with two species with which it is syntopic, *N. atrata* and *N. paytensis*. The former has a more rounded, globular, slightly patulous shape, with a distinctive black and white pattern (including a prominently striped base) or entirely white shell; the penis of *N. atrata* has a narrower tip and larger mamilliform penial gland, carried on a longer projection of the base. Juvenile *N. paytensis* of similar size are tall-spined, with flat whorls giving a conical outline, and an angled periphery; the surface is glossy, with regular incised primary grooves and no raised ribs; the color pattern of dark brown with pale sutural and basal bands is similar, but brown axial flames are usually prominent, especially at the suture. *Nodilittorina santelenae* was also syntopic with *N. fuscolineata* at Punta Carnero, the type locality of both; the latter species is more low spired and globular, with a lined or dashed pattern on prominent ribs, and penial form is diagnostic of both. The smooth-shelled form of *N. santelenae* shows a remarkable convergence with the shell of the broadly sympatric (but not syntopic) *Littoraria rosewateri* Reid; although the latter is larger (5–12 mm), coloration and sculpture are similar (cf. Reid, 1999a: fig. 9A), but anatomically it is quite different (the penis lacks a mamilliform gland but shows a glandular disc, the penial vas deferens is closed and the oviduct is multispiral) and the usual habitat is among supralittoral marsh grass in mangrove areas, so confusion is unlikely.

Nodilittorina fuscolineata Reid, sp. nov.

(Figures 2A–E, 3II, 5D, 6)

Etymology: Latin: “dark-lined,” in reference to color pattern.

Types: Holotype BMNH 19990422 (Figure 2A). Type

locality: Punta Carnero, Peninsula Santa Elena, Guayas Province, Ecuador.

Taxonomic history: This species has not previously been recognized as distinct. It is rare in museum collections, and generally found in mixed lots with *N. atrata*. Some of the authors writing on *N. atrata* (and its synonyms) in Central America (see Synonymy of *N. atrata*) might have included this species, but owing to its rarity this is unlikely.

Diagnosis: Shell small, globular to turbinate, often translucent; usually with strong spiral ribs and microstriae; large, perforated pseudo-umbilicus; pale, with brown lines or long dashes on ribs. Penis with long, pointed filament, small mamilliform gland closely attached to base, no glandular disc.

Material examined: 15 lots (including 1 penis, 1 radula).

Shell (Figures 2A–E): Shell height to 2.8 mm. Shape turbinate to globular or slightly patulous (H/B = 1.00–1.25, SH = 1.38–1.67); whorls well rounded, suture distinct; usually delicate and translucent. Columella straight, narrow, expanded and flattened at base; pseudo-umbilicus moderate to large, perforated, outlined by sharp keel continuous with outer apertural lip. Sculpture of rather uniform spiral ribs; on spire whorls 1–3 ribs visible; on last whorl 2–3 ribs on base, peripheral rib, and 3–4 ribs above periphery, rarely with 1 or 2 smaller interpolated riblets on last whorl; ribs vary from low and rounded to sharp and raised, but are rarely absent; spiral microstriae present over entire surface. Protoconch 3.0 whorls, 0.34 mm diameter, with fine spiral riblets. Color cream to pale brown, usually with continuous brown lines or long dashes on ribs, and a band or a few large blotches at suture; occasionally pattern is irregularly marbled, but sutural blotches and lines on base remain visible; aperture with external pattern showing through, columella purplish or pale brown.

Animal (description of holotype): Head black, narrow unpigmented stripe across snout, two black lines along tentacle, not meeting at tip; sides of foot black. Penis (Figure 3II): filament long, pointed, not twisted; sperm groove extending to filament tip; single small mamilliform penial gland closely attached to base at 0.25 total

Figure 5. Radulae of *Nodilittorina porcata* group: *N. atrata* (A), *N. porcata* (B), *N. santelenae* Reid, sp. nov. (C), *N. fuscolineata* Reid, sp. nov. (D), *N. parcipicta* (E, F), and *N. albicarinata* (G, H). A. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (BMNH 20001163; at 45°; shell H = 5.0 mm). B. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (BMNH 20001169; at 45°; shell H = 5.0 mm). C. Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20000311; at 45°; shell H = 5.0 mm). D. Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 19990422, holotype of *N. fuscolineata* Reid, sp. nov.; at 45°; shell H = 2.8 mm). E, F. Topolobampo, Sinaloa, Mexico (BMNH 20001176; two views of radula, flat and at 45°; shell H = 4.7 mm). G, H. San Felipe, Baja California Norte, Mexico (BMNH 20001183; two views of radula, flat and at 45°; shell H = 5.2 mm). Scale bars = 20 μm.

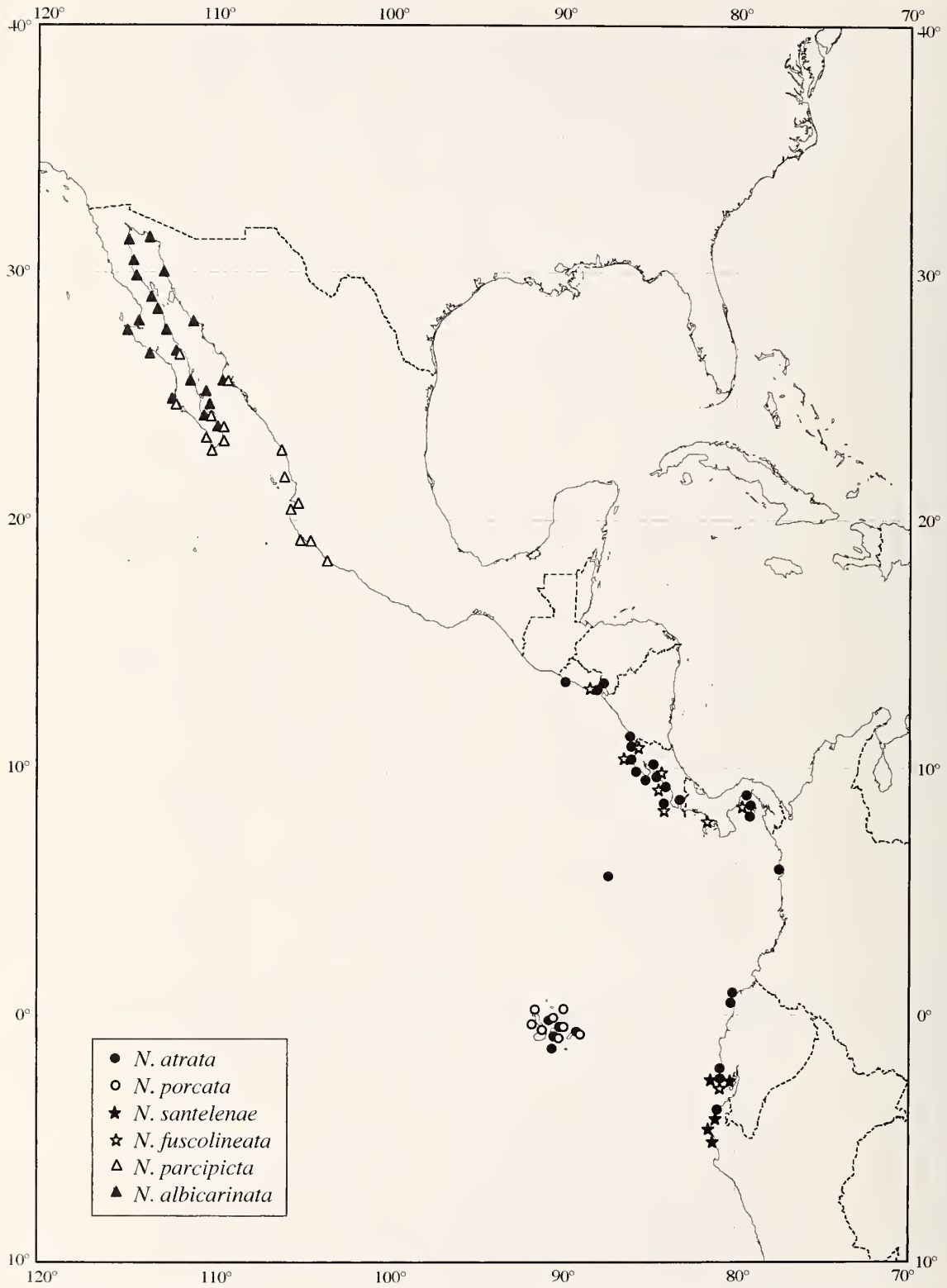


Figure 6. Geographical distribution of *Nodilittorina porcata* group (all records based on material examined).

penial length; glandular disc absent; base slightly pigmented. Sperm not seen. Pallial oviduct not seen. Spawn not observed; protoconch indicates planktotrophic development.

Radula (Figure 5D): Relative radular length unknown. Rachidian: length/width 1.06; major cusp pointed and leaf-shaped. Lateral and inner marginal: major cusps moderately pointed. Outer marginal: 6 cusps.

Habitat: Of the available collections, only the holotype was collected alive, among barnacles in the upper eulittoral, on an exposed siltstone headland on a sandy coast. The typical habitat of this species is uncertain. All other material seen (14 lots in LACM) was collected dead in sediments from depths of 2–100 m, often mixed with *N. atrata*; neither *N. atrata* nor any other member of the genus occurs subtidally, so this must represent material washed from the eulittoral zone. Many live collected samples of the broadly sympatric *N. atrata* are available from within the range of this species, yet only at the type locality has a single *N. fuscolineata* been found among them. A possible explanation is that this species is found in relatively exposed or offshore localities (where sampling is less frequent), unlike *N. atrata* which occupies a range of habitats. This is supported by the fact that many of the localities for dead *N. fuscolineata* (as well as the type locality) are peninsulas or islands; furthermore, it appears to be absent from relatively sheltered mainland sites such as the Panama Canal Zone and the Golfo de Nicoya in Costa Rica (both represented by numerous and large collections of *N. atrata*).

Range (Figure 6): El Salvador to southern Ecuador. Range limits: Isla Zacatillo, Golfo de Fonseca, El Salvador (LACM 73-57, 1 specimen); Bahía Jobo, Costa Rica (LACM 72-17); Isla del Cano, Costa Rica (LACM 72-63); Bahía Honda, Panama (LACM 38-131, 1 specimen); Isla Taboga, Panama (LACM 65-25, 1 specimen); Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 19990422, holotype only).

Remarks: As mentioned above, this species is so far represented by only a single live-collected specimen, as well as 50 dead shells from 14 localities (LACM), and is therefore by far the rarest of the *N. porcata* group in museums. This may reflect a less accessible habitat (see Habitat).

The shell of *N. fuscolineata* is distinctive, with regular ribs marked by brown lines or dashes, well rounded whorls and delicate texture, and these characters make it easily separable from the broadly sympatric *N. atrata* (a larger, more solid shell, very variable in form, but never with such rounded spire whorls nor with a lined pattern). The shell characters are, however, somewhat similar to those of *N. parcipicta*, although that species is larger (to 5.9 mm), more solid, and has a finer spotted (rarely dashed, and never lined) pattern on the ribs, or may even be unpatterned. Fortunately, the sole living specimen ex-

amined was a male and, assuming this to be typical, the penial shape is diagnostically different from those of both *N. atrata* and *N. parcipicta*. The penis is more similar to that of the latter in its lack of a marked twist to the filament tip. Their geographical ranges are not known to overlap, *N. parcipicta* being restricted to Mexico. These shell and penial similarities suggest that *N. fuscolineata* and *N. parcipicta* are sister species. If the inferred habitat of *N. fuscolineata* on exposed shores is correct, this is another similarity between the two.

Nodilittorina parcipicta (Carpenter, 1864)

(Figures 2F–M, 3W–CC, 4D, L, M, 5E, F, 6, 22F)

Fossarus parcipictus Carpenter, 1864a:476 (Cape St Lucas [Cabo San Lucas, Baja California, Mexico]; lectotype (Palmer, 1963) USNM 4060, seen, Palmer, 1963:pl. 65, figs. 4, 5, Figure 2L herein; paralectotype USNM 678706, seen). Palmer, 1963:342, pl. 65, figs. 4, 5. Keen, 1971:454. Abbott, 1974:136 (may include *N. atrata* or *N. fuscolineata*). Skoglund, 1992:34.

Fossarus cf. *atratus*—McLean, 1970:127 (not *Littorina atrata* C. B. Adams, 1852 = *N. atrata*).

Taxonomic history: This species has been largely neglected since its description, and has not hitherto been referred to a littorinid genus. The lectotype was figured by Palmer (1963), and the name was listed by Keen (1971) and Abbott (1974). The latter gave a range “Baja California to Panama,” but the species does not occur so far south, and records of *N. atrata* and/or *N. fuscolineata* may have been included. In describing the new species *N. albicarinata*, McLean (1970) remarked that it often occurred together with “a species of *Fossarus*, cf. *atratus*” by which, from the brief description, he apparently intended *N. parcipicta*; this is supported by the inclusion of one specimen of *N. parcipicta* among the paratypes of *N. albicarinata* (LACM 1400).

Diagnosis: Shell small, globular to turbinata; strong spiral ribs and microstriae; large, perforated pseudo-umbilicus; white or yellow, with small brown spots on ribs. Penis with broad, blunt filament, large mamilliform gland closely attached to base, no glandular disc.

Material examined: 30 lots (including 15 penes, 4 sperm samples, 5 pallial oviducts, 4 radulae).

Shell (Figures 2F–M, 22F): Mature shell height 2.3–5.9 mm. Shape turbinata to globular or slightly patulous (H/B = 0.83–1.25, SH = 1.27–1.74); whorls rounded, suture distinct. Columella straight, narrow, expanded, and flattened at base; pseudo-umbilicus usually large, perforated, outlined by sharp keel continuous with outer apertural lip, but sometimes narrow or imperforate. Sculpture of rather uniform, sharp spiral ribs; on spire whorls only 1–2 ribs visible; on last whorl 2–3 ribs on base, peripheral rib, and 2–4 ribs above periphery, but with smaller interpolated ribs on largest shells total number on

last whorl up to 11; ribs vary from low to strongly carinate; spiral microstriae present over entire surface (Figure 22F). Protoconch 2.7 whorls, 0.34 mm diameter. Color white to pale yellow, sometimes lacking pattern, but usually with small brown spots on ribs; darkest shells have irregular axial stripes, blotches or transverse dashes of dark brown or black; aperture with external pattern showing through, only rarely with peripheral dark band or pale anterior stripe, columella cream to dark brown.

Animal: Head black to grey, unpigmented stripe across snout, two black lines along tentacle, not meeting at tip; sides of foot speckled black to pale grey. Opercular ratio 0.39–0.42. Penis (Figures 3W–CC): filament broad, blunt, or minutely pointed, not (or only slightly) twisted; sperm groove extending to filament tip; single large mamilliform penial gland closely attached to base at 0.2–0.4 total penial length (mamilliform gland absent in one specimen); glandular disc absent; base often slightly pigmented. Euspermatozoa 64–93 μm ; paraspermatozoa (Figures 4L, M) oval; rod-pieces single (rarely 2–3), usually projecting at both ends or at least filling cell, 16–28 μm , slightly tapering or fusiform, ends rounded; granules large, spherical, distinct. Pallial oviduct (Figure 4D) with flexure and constriction between spiral and straight sections; copulatory bursa opening near anterior end of straight section, constricted at about one-third of its length, extending back beneath capsule gland. Spawn not observed; protoconch indicates planktotrophic development.

Radula (Figures 5E, F): Relative radular length 1.2–2.1. Rachidian: length/width 1.06–1.44; major cusp pointed and elongate leaf-shaped. Lateral and inner marginal: major cusps pointed or slightly rounded. Outer marginal: 5–6 cusps.

Habitat: In small, shallow rock pools in upper eulittoral; in crevices among barnacles; on granite, conglomerate and concrete; wave-exposed headlands, and sometimes sheltered bays.

Range (Figure 6): Southern Baja California, mainland coast of Mexico from Sinaloa to Michoacán. Range limits: Bahía Magdalena, Baja California Sur (USNM 218336, 1 specimen); Punta Lobos, Todos Santos, Baja California Sur (BMNH 20001172); Bahía Santa Maria, near Cabo San Lucas, Baja California Sur (BMNH 20001173); Playa Coromuel, 3 km N of La Paz, Baja California Sur (BMNH 20001175); El Requeson and El Coyote, Bahía Concepción, Baja California Sur (LACM 63-37); Topolobampo, Sinaloa (BMNH 20001176); Mazatlán, Sinaloa (BMNH 20001177); Punta Telmo, Michoacán (BMNH 20001181). This species only just penetrates the Gulf of California, but is common at its limits at both Bahía Concepción and Topolobampo. The lack of records south to Oaxaca may simply reflect lack of collecting of this small species with a preference for exposed and inaccessible localities.

Remarks: This species is somewhat less variable in shell characters than others in the *N. porcata* group; most specimens show a spotted pattern, and it is not known to occur in a smooth form. Although sometimes found on sheltered shores, most of the available samples are from wave-exposed shores, which are more strongly exposed than shores on which other members of this group have been found. This, combined with its restriction to the shores of Baja California and southern Mexico, and absence from most of the Gulf of California, emphasizes the oceanic character of its distribution. A similar distribution on the coast of Mexico is shown by the likewise oceanic species *Littoraria pintado pullata* (Carpenter), although that species also occurs on the eastern Pacific islands (Reid, 1999a).

There is limited sympatry between *N. parcipicta* and *N. albicarinata*, but the latter is found only in moderately sheltered habitats, and there are only three recorded instances of syntopy. At Playa Coromuel (personal observation) both species were common among the uppermost barnacles on a sheltered shore, but *N. parcipicta* was found mainly at slightly lower tidal levels than *N. albicarinata*, and the spire whorls of the former were more strongly eroded. At Topolobampo (personal observation) only a single *N. albicarinata* was found together with moderately common *N. parcipicta*, among sparse barnacles on a concrete ramp, in a sheltered, silty bay. In addition, both species are recorded from El Requeson, Bahía Concepción (LACM 1400), and said to occur together by McLean (1970). These two species are easily distinguished by shell characters: *N. albicarinata* is usually imperforate, often somewhat tall-spined, smooth, and grey to white in color, unlike any shell of *N. parcipicta*; sculptured forms of *N. albicarinata* are sharply carinate at the shoulder and periphery, and (at least on the spire whorls) the carinae are white on a brown ground, unlike the more globular, umbilicate shells of *N. parcipicta* with regular spotting on uniform, rounded ribs.

A more similar shell is that of *N. fuscolineata*, but that is distinguished by smaller size, delicate texture, and pattern of brown lines or long dashes on the ribs; the two are allopatric (*N. fuscolineata* occurring to the south of El Salvador) and are possible sister species (see Remarks on *N. fuscolineata*).

Nodilittorina albicarinata (McLean, 1970)

(Figures 2N–W, 3V, DD–HH, 4E, N, 5G, H, 6)

Littorina dubiosa—McLean, 1961:464 (not C. B. Adams, 1852 = *N. dubiosa*).

Littorina albicarinata McLean, 1970:127, fig. 36 (El Requeson, Concepcion Bay, Baja California, 26°38'N, 111°50'W; holotype LACM 1399, seen, Figure 2O; 263 paratypes LACM 1400, seen, one is *N. parcipicta*; 4 paratypes USNM 681630, seen; 4 paratypes each AMNH, ANSP, CAS, MCZ, SBM). Keen, 1971:365, fig. 180.

Littorina (Littorinopsis) albicarinata—Abbott, 1974:69, fig. 566.

Littorina (Fossarilittorina) albicarinata—Rosewater, 1981:30.

Nodilittorina (Nodilittorina) albicarinata—Reid, 1989a:99, Skoglund, 1992:15.

Taxonomic history: McLean (1961) at first identified the smooth form of this species as *Littorina dubiosa*, and suggested that keeled shells might belong to the same species. Later (1970), he described the distinctive form with white carinae under the new name, and again remarked on the variation in sculpture. The species is abundant within its range, and the paucity of literature references is a reflection of the relatively few malacological studies in the Gulf of California. In ANSP and USNM there are several lots of the tall-spined, smooth, white form of this species labelled "*Littorina cognatus* Hemphill, MS"; this name does not appear to have been published and was not included in the list of Hemphill's taxa by Coan & Roth (1987).

Diagnosis: Shell small, turbate to tall; smooth with impressed striae, or carinate with microstriae; narrow, imperforate pseudo-umbilical area; often grey to white; if patterned, then white carinae on brown shell, especially on spire. Penis with pointed, slightly twisted filament tip, opening of sperm groove behind tip, large mamilliform gland on stout or long lateral appendage, no glandular disc.

Material examined: 40 lots (including 19 penes, 4 sperm samples, 6 pallial oviducts, 7 radulae).

Shell (Figures 2N–W): Mature shell height 2.3–7.6 mm. Shape turbate to tall-spined ($H/B = 1.13–1.77$; $SH = 1.46–2.30$); spire whorls rounded, suture distinct; periphery of last whorl only slightly angular, but may be marked by a rib or carina; solid. Columella straight, narrow, slightly pinched at base of pillar; pseudo-umbilicus usually only a narrow, imperforate area or absent, but sometimes narrowly perforated. Sculpture variable; smoothest shells with 6–13 impressed lines above periphery (sometimes increasing to 23 on last whorl) and similar but less distinct fine striae on base, periphery usually marked by a slight rib; almost all shells have a prominent rib at shoulder and another at periphery of early spire whorls (may be lost by erosion), even if they become smooth on last whorl; strongly sculptured shells with shoulder and peripheral ribs persisting as sharp carinae, with additional 2 ribs below suture, 1 between carinae, and 3 on base, giving total of 8 more or less carinate ribs, with coarse microstriae between; periostracum occasionally produced into minute bristles (less than 100 μm) on basal and peripheral ribs of strongly sculptured shells. Protoconch 2.8 whorls, 0.29–0.34 mm diameter. Color variable; spire usually brownish with white dashes or lines marking shoulder and peripheral rib; pattern may persist, with white carinae and ribs on brown ground; shells often

white, fawn, or chalky blue-grey on last whorl; occasionally with fine brown spots, mottling or fine axial zigzags on last whorl, strongest at suture and periphery; color pattern always fades to white toward inner part of base; columella and aperture brown, with anterior unpigmented band, columella sometimes white.

Animal: Head and sides of foot black; two black lines along tentacle, meeting (or almost so) at small black terminal spot. Opercular ratio 0.44–0.51. Penis (Figures 3V, DD–HH): filament tip pointed and slightly pinched; sperm groove with a kink, not extending to filament tip; single large mamilliform penial gland on stout (and in fully relaxed specimens very long) lateral appendage at 0.4–0.5 total penial length; glandular disc absent (but in contracted specimens an extension of glandular material of mamilliform gland may resemble a small glandular disc); base pigmented. Euspermatozoa 71–86 μm ; paraspermatozoa (Figure 4N) oval; rod-pieces single, filling cell or projecting at one or both ends, 16–24 μm , blunt or slightly rounded at ends, parallel-sided or occasionally slightly tapering; granules large, spherical, distinct. Pallial oviduct (Figure 4E) with flexure and constriction between spiral and straight sections; copulatory bursa opening at anterior end of straight section, extending back to start of spiral portion. Spawn not observed; protoconch indicates planktotrophic development.

Radula (Figures 5G, H): Relative radular length 1.9–3.1. Rachidian: length/width 1.13–1.54; major cusp pointed and elongate leaf-shaped. Lateral and inner marginal: major cusps pointed or slightly rounded. Outer marginal: 6–8 cusps.

Habitat: Among uppermost barnacles and in crevices, upper eulittoral; on volcanic conglomerate, basalt, concrete; sheltered coasts; often abundant; habitat notes with one lot (Puerto Lobos, Sonora, Mexico, USNM 862206) "in grasses," presumably supralittoral halophytic salt-marsh grass.

Range (Figure 6): Southwestern Baja California and Gulf of California. Range limits: Laguna Manuel, Baja California Norte (USNM 106528); Punta Abreojos, Baja California Sur (USNM 265774); Bahía Magdalena, Baja California Sur (USNM 332443); Ensenada de los Muertos, Baja California Sur (G. J. Vermeij Collection); Balandra, 30 km N of La Paz, Baja California Sur (BMNH 2001182); San Felipe, Baja California Norte (BMNH 20001183); Puerto Peñasco, Sonora (USNM 665246); Punta San Antonio, Guaymas, Sonora (LACM 73-6); Topolobampo, Sinaloa (BMNH 2001184, 1 specimen). The distribution of this species is apparently disjunct, with no records from the inhospitable exposed coast between La Paz and Bahía Magdalena. It is apparently common farther north in suitable lagoonal and sheltered habitats on the western coast of Baja California. Although common

Table 2

Summary of the most useful characters for the identification of the two species of the *Nodilittorina modesta* group.

Character	<i>N. modesta</i>	<i>N. conspersa</i>
1. Geographical range	Baja California, Mexico, Costa Rica, Clipperton Atoll	Oaxaca (Mexico), El Salvador to Ecuador, Isla del Coco, Galápagos Islands
2. Shell		
—primary grooves on spire whorls	usually 6–7	usually 4–5
—all white form	yes, especially in strongly sculptured shells	no, always patterned
—color pattern	if present, minute grey-brown dots on white shell, often becoming obsolete on last whorl	always with small orange-brown dots on white shell
3. Tentacle pattern	fine transverse black lines	two longitudinal black lines
4. Penis		
—filament length	long, 0.7–0.8 total length	short, 0.25–0.35 total length
—filament tip	tapering to pointed tip	bluntly hooked tip

at Guaymas, only a single specimen was found in a suitable habitat at Topolobampo (personal observation).

Remarks: Confusion is possible with two or three sympatric species. It is only rarely syntopic with *N. parvipicta* among barnacles, in the narrow zone of sympatry in southern Baja California and the southeastern Gulf of California, but the shells of these two species are readily discriminated (see Remarks on *N. parvipicta*). In the Gulf of California *N. albicarinata* occurs on the same shores as *N. penicillata*, a larger species lacking carinate sculpture, of which juveniles show a diagnostic shell pattern of axial brown lines with a spiral brown line on the shoulder and another on the base. Another broadly sympatric species is *Littoraria rosewateri* Reid; although there are no available records of these two occurring syntopically, they may well do so, since the typical habitat of *L. rosewateri* is among supralittoral marsh grasses, from which a sample of *N. albicarinata* has been collected (see Habitat). The shells of these two species can be remarkably similar. *Littoraria rosewateri* closely resembles tall-spined, smooth forms of *N. albicarinata*, but the former reaches larger size (5–12 mm), never shows an enlarged peripheral or shoulder rib on early whorls or on last whorl, the color is polymorphic in large samples, and there is never a pale anterior band within the aperture. Anatomical characters are diagnostic; the tentacles of *L. rosewateri* show transverse bands, the penis has a large glandular disc and no mamilliform penial gland, and the pallial oviduct is multispiral. It is interesting that the algal-dwelling form of *N. santelenae* also shows convergence with *L. rosewateri*.

Recently it has been suggested that the radulae of *Littoraria* species show ecophenotypic plasticity of cusp shape according to the substrate, whether rock or plants (Reid & Mak, 1999). It is unusual to find a member of the genus *Nodilittorina* on a plant substrate, providing an

opportunity to test this hypothesis in the genus. Two radulae were examined from the sample collected on grasses, but did not display any differences from the rest.

The *Nodilittorina modesta* Group

In the older literature, the familiar white littorinids of the eastern Pacific, usually with a pattern of minute brown dots, were generally known by the specific name of *conspersa* Philippi, 1847, but then for the past 30 years by the earlier name of *modesta* Philippi, 1846 (Rosewater, 1970; Keen, 1971; Reid, 1989a). However, close examination of penial shape has revealed two species in this group, with sympatry at two localities in southern Mexico and Costa Rica. The penial differences are small, but entirely consistent even in sympatry, and are correlated with shell differences (Table 2). Philippi (1846a, 1847) named four species in this group, and from his precise descriptions of shell sculpture it is possible to identify the two valid species as *N. modesta* and *N. conspersa*, although their synonymies are complex.

These two species are evidently sister taxa. They share a similar white shell, often with a pattern of brown dots. This pattern is difficult to quantify, since although the dots are laid down along the prosocline growing edge of the shell, their alignment is chiefly in opisthocline series or somewhat irregular, and bears no constant relation to the conspicuous spiral sculpture of the shell. (For comparative purposes, in the descriptions below the dots have been counted along an opisthocline series between periphery and suture on the last whorl). In both species the shell varies from rather smooth to strongly sculptured with spiral grooves, sometimes within a sample, but no correlation with microhabitat or geographical range has been noticed. They share several unusual (probably synapomorphic) anatomical features of the penis, oviduct, and radula. The penis is elongate, lacks a mamilliform

gland, and the glandular base is not clearly differentiated into a glandular disc, in contrast to all other known *Nodilittorina* species except the two Atlantic species *N. meleagris* and *N. mespillum* (Mühlfeld). In the pallial oviduct, a loop of the renal oviduct projects into the center of the spiral loop of the albumen gland, which has not been seen in other *Nodilittorina* species. The radulae share the presence of an additional pair of denticles at the concave anterior edge of the rachidian tooth, which is absent elsewhere in the genus (or only slightly and variably developed in some individuals of the *N. aspera* group). Their habitat is also similar, in the upper eulittoral on wave-exposed shores, whereas other large species of the genus occupy the littoral fringe.

Specimens of both species from localities in Oaxaca and Costa Rica sometimes contained a commensal polyclad plathyhelminth (R. Sluys, personal communication). Single worms up to 5.5 mm long are found in the mantle cavity, which they may fill completely, although the host sustains no apparent damage. A similar commensal has been observed in *N. apicina* and *N. tenuistriata*, but has not apparently been recorded in other littorinids.

Nodilittorina modesta (Philippi, 1846)

(Figures 7A–F, 8A–F, N, P, Q, 9A, B, 10, 22G, H)

Littorina modesta Philippi, 1846a:141 (Sitka, Nova Albion [Alaska]; insulam Mauritiū [Mauritius]; both in error, here restricted to Mazatlán, Mexico; lectotype (here designated, 19.6 × 13.2 mm, 'Sitka') BMNH 1968224, seen, Philippi, 1847:*Littorina* pl. 6, fig. 12, Figure 7E herein; 3 paralectotypes BMNH 1968224, seen; 3 additional specimens probably from same lot, BMNH 19990404, seen). Middendorff, 1849:394. Carpenter, 1857a:216, 224, 286. Reeve, 1858:sp. 107, pl. 18, fig. 107. Keen, 1958:282. Keen, 1971:366, fig. 183 (in part, includes *N. conspersa*). Holguín & González, 1989:115, fig.

Littorina modesta—Philippi, 1847:3:48–49, *Littorina* pl. 6, fig. 12. Menke, 1851:164. Carpenter, 1857a:237, 326. Weinkauff, 1882:52–53, pl. 6, figs. 13, 16.

Littorina sitchana var. *modesta*—Carpenter, 1864b:655.

Littorina (Littorinopsis) modesta—Rosewater, 1970:423. Abbott, 1974:69 (in part, includes *N. conspersa*).

Nodilittorina (? *Fossarilittorina*) *modesta*—Reid, 1989a:98 (in part, includes *N. conspersa*).

Nodilittorina modesta—Emerson, 1995:13 (in part, includes *N. conspersa*).

? *Littorina albida* Philippi, 1848:3:63–64, *Littorina* pl. 7, fig. 9 (Real Llejos [El Realejo, Nicaragua]; types not found). ? Weinkauff, 1882:81, pl. 11, fig. 1.

? *Littorina (Littorinopsis) albida*—von Martens, 1900:576, 582.

Littorina conspersa—Carpenter, 1857a:257 (in part, includes *N. conspersa*). Carpenter, 1864b:541, 598, 623 (in part, includes *N. conspersa*). Weinkauff, 1883:217 (in part, includes *N. conspersa*).

Littorina (Melaraphe) conspersa—Carpenter, 1857b:346–347 (in part, includes *N. conspersa*).

Littorina (Melaraphe) aspera var. *conspersa*—Tryon, 1887:249, pl. 44, figs. 80, 81 (in part, includes *N. conspersa*).

Littorina (Melarhaphe) conspersa—von Martens, 1900:577, 586 (in part, includes *N. conspersa*).

Littorina conspersa—Pilsbry & Lowe, 1932:124 (not Philippi, 1846). Keen, 1958:282, fig. 174 (in part, includes *N. conspersa*). Villamar, 1965:123 (not Philippi, 1846).

Littorina (Melarhaphe) philippii var. *alba* von Martens, 1900:577, 585, pl. 43, fig. 13 (Mazatlan, Mexico; 5 syntypes MNB 102847, seen).

Littorina (Melarhaphe) conspersa var. *puncticulata*—von Martens, 1900:577, 786–587 (in part, includes *N. conspersa*; not Philippi, 1847 = *N. conspersa*).

Littorina aspera—Keen, 1971:365, fig. 181 (part) (in part, includes *N. aspera*, *N. penicillata*, *N. dubiosa*, *N. apicina*, *N. interrupta*).

Taxonomic history: Philippi was meticulous in his descriptions of details of shell shape and sculpture, but he had limited material available, leading him to describe four species in the *N. modesta* group. The identity of the oldest of these, *Littorina modesta* Philippi, 1846, is clear; it was described from material in the Cuming Collection (BMNH), and the specimen figured by Philippi (1847) is here designated lectotype. Philippi (1847) himself described the characteristically numerous and deep grooves of the shell. The listing of *Littorina albida* in the synonymy of *N. modesta* is not certain; the types are lost, and its inclusion is based on the rounded whorls, 5–6 primary spiral grooves, white columella with brown margin, and dark brown posterior aperture, all described by Philippi (1848); this species has not since been recorded from Nicaragua, but it is within the known range. The second species in the *N. modesta* group is here identified as *N. conspersa* (Philippi, 1847), with *Littorina puncticulata* Philippi, 1847, as a synonym. The only other available name was introduced by von Martens (1900) for young specimens of *N. modesta*; these he described as var. *alba* of *Littorina philippii* (itself a synonym of *N. apicina*), apparently misled by the axial lines of brown dots.

Although few subsequent authors have described shells in such detail as Philippi, the largely separate geographical distributions of the two species make it possible to compile the synonymies of each. However, it was an error in the type locality of *Littorina modesta* that led to an initial confusion in the nomenclature of this group. Philippi (1846a, 1847) described *Littorina modesta* from Sitka (Alaska) and Mauritius. Subsequent authors therefore generally used either the names *conspersa* and *puncticulata* (Adams, 1852a, b) or *conspersa* alone (e.g., Carpenter, 1857a, b, 1863, 1864b; Weinkauff, 1883; von Martens, 1900; Keen, 1958) for the two species now recognized in the tropical eastern Pacific. The earlier name *modesta* was correctly used only by Menke (1851); others employed it for a species believed to occur in the northern Pacific (Middendorff, 1849; Carpenter, 1857a, b; Reeve, 1858; Weinkauff, 1882; Keen, 1958). Carpenter (1863, 1864b) even suggested that this enigmatic *modesta* was

a variety of the northern Pacific *Littornia sitkana* Philippi, 1846. This confusion was eventually resolved by examination of the types of *Littorina modesta*, and the name was reinstated for the supposed single species of the tropical eastern Pacific (Rosewater, 1970; Keen, 1971); it has been used in this sense by all subsequent workers.

Some authors have had an even broader concept of these species, combining them in various ways with members of the *N. aspera* group. Tryon (1887) reduced the *N. modesta* group to a subspecies of *Littorina aspera* (followed only by Schwengel, 1938). Von Martens (1900) described heavily marked specimens of *N. modesta* as a variety of *Littorina philippii* (= *N. apicina*), and his figure was reproduced as "*Littorina aspera*" by Keen (1971). It has also been suggested that *N. paytensis* is a southern subspecies of *Littorina modesta* (Keen, 1971; Vermeij, 1973; Rosewater, in Finet, 1985).

Only Philippi (1847), Weinkauff (1882; who followed Philippi's species concepts almost exactly), and C. B. Adams (1852a, b) have previously recognized more than one species in the *N. modesta* group in Central America, basing distinctions on differences in shell outline and degree of sculpture. These features are in fact more variable within the two species of the group than was recognized by these early authors, so that their distinctions do not correspond exactly to that made here on anatomical grounds (see also Taxonomic History of *N. conspersa*).

Diagnosis: Shell moderately large, spire whorls moderately rounded; 6–7 primary spiral grooves; sculpture of incised lines only, or with deep grooves 1–3 times rib width; all white or with minute grey-brown dots. Tentacles with fine transverse black lines. Penis with long, tapering filament, glandular flange at base, no mamilliform gland.

Material examined: 58 lots (including 26 penes, 4 sperm samples, 7 pallial oviducts, 5 radulae).

Shell (Figures 7A–F, 22G, H): Mature shell height 4.5–19.6 mm. Shape high turbinate ($H/B = 1.33–1.79$, $SH = 1.38–1.89$); spire whorls moderately rounded, suture distinct; periphery of last whorl weakly angled. Columella straight, broad, hollowed, and pinched (sometimes with slight protruberance) at base; occasionally a small imperforate pseudo-umbilical area; eroded parietal area in larger shells. Sculpture of 6–7 (rarely 5 or 8) primary spiral grooves on spire whorls; these may remain as incised lines only (1–2 secondary grooves may appear near suture on last whorl), numbering 9–13 above periphery of last whorl (11–17 in total including basal grooves), or become wider and deeper near periphery, but sometimes become obsolete on last whorl; in strongly sculptured shells grooves are wider and deeper throughout, separating rounded ribs on spire whorls, on last whorl, ribs are then raised (occasionally sharp), separated by grooves 1 to 3 times rib width, with narrow interpolated rib ap-

pearing in grooves near suture (rarely in all grooves above periphery), grooves on last whorl then up to 20 above peripheral rib (up to 27 in total); spiral microstriae absent (Figure 22H). Protoconch 2.7 whorls, 0.31 mm diameter, sculptured by spiral ribs (Figure 22G). Color white, with pale brown or lilac-grey apex; often unpatterned (especially when strongly sculptured); otherwise covered with small grey, brown, or black spots aligned in oblique (opisthocline) series (numbering 14–25 spots from peripheral rib to suture on last whorl); spots frequently become obsolete on last whorl; aperture pale orange-brown to dark brown, often darkest posteriorly, with broad pale basal band, usually also a more diffuse shoulder band, external spotting showing through near margin (spotting may be visible even in externally unpatterned shells); columella white to brown, or white pillar with brown margin.

Animal: Head (Figures 8A, E): Black to grey, unpigmented stripe across snout, tentacle with fine transverse lines of black or grey, pale beneath; sides of foot black to pale grey. Opercular ratio 0.30–0.38. Penis (Figures 8A–F): filament long (about 0.7–0.8 total length), tapering to pointed or slightly mucronate tip, subepithelial glandular tissue near tip and surrounding sperm groove along anterior edge, filament differentiated from base by smooth anterior edge and slight constriction below swollen glandular sides of sperm groove (differentiation sometimes indistinct); sperm groove open to tip; base with annular wrinkles except at posterior edge with slight glandular flange (opaque subepithelial glandular tissue sometimes visible, approaching surface at minute papilla, although this is not a true mamilliform gland), base occasionally slightly pigmented. Euspermatozoa 57–61 μm ; paraspermatozoa (Figures 8P, Q) round to oval; rod-pieces single (rarely two), filling cell, 13–21 μm , broad, bluntly rounded, hexagonal in section; granules large, spherical, distinct. Pallial oviduct (Figure 8N) with long straight section; large copulatory bursa opening near posterior end of straight section, extending back to albumen gland; small loop of renal oviduct usually projects into center of spiral of albumen gland. Spawn not observed; protoconch indicates planktotrophic development.

Radula (Figures 9A, B): Relative radular length 2.5–5.9. Rachidian: length/width 1.21–1.47; major cusp elongate, blunt or rounded at tip; 2 extra denticles at concave anterior edge. Lateral and inner marginal: major cusps elongate rectangular, blunt at tip. Outer marginal: 8–10 cusps.

Habitat: Rock faces, shallow rock pools, and among barnacles and mussels; in upper eulittoral; recorded on granite and volcanic conglomerate; usually on wave-exposed open coasts, apparently rare at sheltered sites. A study of zonation and temperature relations by Markel (1971) included both this species and *N. conspersa* (as *Littorina modesta*).

Range (Figure 10): Southern Baja California, southern Gulf of California, Mexico, Costa Rica, Islas Revillagigedo and Clipperton Atoll. Range limits: Bahía Magdalena, Baja California Sur (USNM 264568, 2 specimens); 4 km S of Todos Santos, Baja California Sur (USNM 794301); Bahía Santa María, near Cabo San Lucas, Baja California Sur (BMNH 20001187); Punta Pescadero, Baja California Sur (BMNH 20001188); Playa Coromuel, 3 km N of La Paz, Baja California Sur (BMNH 20001189, 1 specimen); Isla Espiritu Santo, Baja California Sur (USNM 538110, 1 specimen); Isla Carmen, Baja California Sur (USNM 558508, 1 specimen); Guaymas, Sonora (BMNH 20001190, 1 specimen; USNM 701409, 4 specimens); Topolobampo, Sinaloa (BMNH 20001191, 3 specimens); Mazatlán, Sinaloa (BMNH 20001192); Puerto Angel, Oaxaca (BMNH 20001192); Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001194, 40 specimens); Isla Socorro (USNM 60648; KLK); Clipperton Atoll (KLK, 2 specimens). The species is rare in the Gulf of California (a total of only 12 specimens have been seen from north of La Paz and Mazatlán). There is only a single locality record from Central America, although 40 specimens were collected. The species is common on Isla Socorro (and was also listed from Isla Clarion by Emerson, 1995), but only two specimens are known from Clipperton Atoll, where it is probably an occasional immigrant (it was not recorded in a list of the mollusks by Emerson, 1994). As discussed in the Taxonomic History above, *N. modesta* was for long thought to occur in the northern Pacific, following the erroneous locality of Sitka given by Philippi (1846a, 1847).

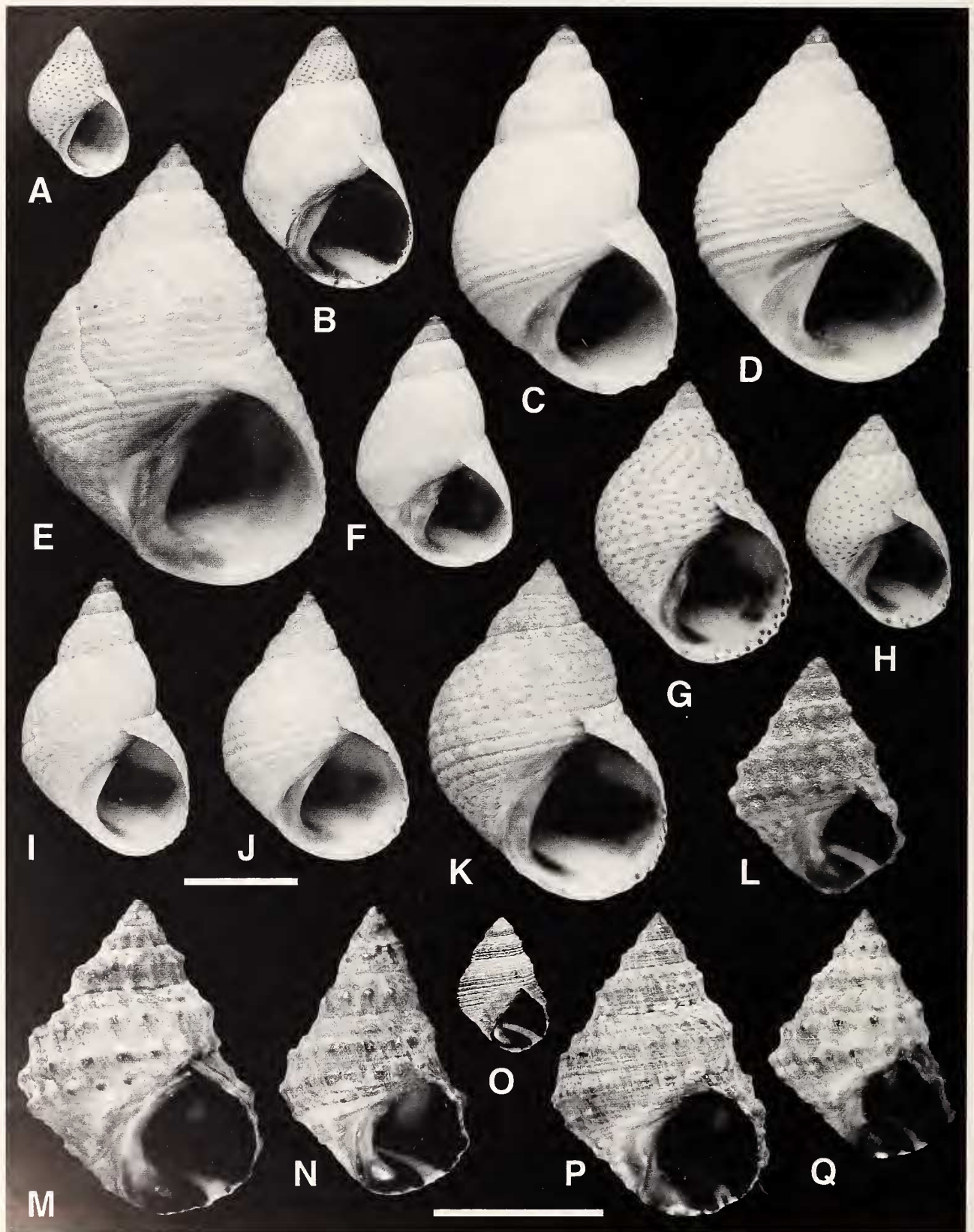
Remarks: This species is closely similar to the other member of the *modesta* group, *N. conspersa*; the characters most useful for discrimination are listed in Table 2. Geographical range is a useful criterion. So far, sympatric collections have been seen from only two localities, Puerto Angel (Oaxaca, Mexico) and near Puerto Quepos (Costa Rica), almost 1500 km apart; evidently both species sometimes disperse across the intervening Central American Gap (see Discussion). (If *Littorina albida* is correctly synonymized with *N. modesta*, El Realejo in Nicaragua is another site of sympatry.) In living or well preserved animals, the shape of the penis is diagnostic, but the differences are subtle and sometimes hard to discern if the filament is not clearly differentiated from the base (e.g., Figures 8C, E). Surprisingly, the coloration of the tentacles provides an equally accurate diagnostic character, with fine black transverse lines in *N. modesta* and a pair of longitudinal black lines in *N. conspersa*. The paraspermatzoa differ slightly, the rod-pieces of *N. modesta* being broader. No significant differences were observed in the pallial oviducts or radulae. Without the benefit of anatomical information, shell variation in this group is initially confusing, since the most obvious features of the variation, strength of sculpture and presence of colored

dots, do not separate the two taxa. Instead, a subtle and not entirely diagnostic character, the number of primary spiral grooves on the spire whorls, is most useful. There are several other minor differences: all-white shells occur only in *N. modesta*; if present, the dots are smaller, more numerous and grey or blackish brown (rather than orange-brown) in *N. modesta*; sculpture may be weak or strong in both, but grooves do not exceed the width of the ribs in *N. conspersa*; the spire whorls are slightly flatter in *N. conspersa*. Individually, these differences seem insignificant but, nevertheless, at the localities of sympatry, all specimens can be separated by shell characters alone, and the majority of unlocalized shells can be confidently assigned.

Nodilittorina conspersa (Philippi, 1847)

(Figures 7G–K, 8G–M, O, R, S, 9C, 10)

- Littorina conspersa* Philippi, 1847:2:200–201. *Littorina* pl. 4, fig. 14 (Oceanus Pacificus Real Llejós in America centrali [El Realejo, Nicaragua]; neotype (here designated, 12.0 × 8.0 mm, El Realejo, Nicaragua) BMNH 199990405/1, seen, Figure 7J). Carpenter, 1857a:208, 230, 326 (in part, includes *N. modesta*). Carpenter, 1864b:538, 623 (in part, includes *N. modesta*). Weinkauff, 1882:64–65, pl. 8, figs. 10, 11 (in part, includes *N. modesta*). Weinkauff, 1883:217 (in part, includes *N. modesta*). Stearns, 1891:327.
- Littorina conspersa*—C. B. Adams, 1852a:396. C. B. Adams, 1852b:172. Carpenter, 1857a:273. Morch, 1860:69. Carpenter, 1863:352–353 (in part, includes *N. modesta*). Biolley, 1907:22. Morrison, 1946:10. Keen, 1958:282 (in part, includes *N. modesta*). Hertlein, 1963:239.
- Littorina (Melaraphe) conspersa*—H. & A. Adams, 1854:314. von Martens, 1900:577, 586 (in part, includes *N. modesta*).
- Littorina (Melaraphe) conspersa*—Carpenter, 1857b:346–347 (in part, includes *N. modesta*).
- Littorina (Melaraphe) aspera* var. *conspersa*—Tryon, 1887:249, pl. 44, figs. 82, 83 (in part, includes *N. modesta*).
- Littorina aspera conspersa*—Schwengel, 1938:2.
- Littorina puncticulata* Philippi, 1847:2:201. *Littorina* pl. 4, fig. 15 (Oceanus Pacificus Real Llejós in America centrali [El Realejo, Nicaragua]; types not found). Weinkauff, 1882:63, pl. 8, fig. 9 (in part, includes *N. modesta*).
- Littorina puncticulata*—C. B. Adams, 1852a:396, 400. C. B. Adams, 1852b:176.
- Littorina (Melaraphe) puncticulata*—H. & A. Adams, 1854:314.
- Littorina (Melaraphe) conspersa* var. *puncticulata*—von Martens, 1900:577, 786–587 (in part, includes *N. modesta*).
- ? *Littorina* (? *Littorinopsis*) *conspersa* var. *fortisulcata* Nevill, 1885:138 (Nicaragua; *nomen nudum*).
- Littorina modesta*—Keen, 1971:366, fig. 183 (in part, includes *N. modesta*). Montoya, 1983:332 (in part, includes *N. modesta*). Finet, 1985:13 (not Philippi, 1846). Alamo & Valdivieso, 1987:26, fig. 39 (not Philippi, 1846). Alamo & Valdivieso, 1997:18, fig. 39 (not Philippi, 1846).



Littorina modesta modesta—Vermeij, 1973:324 (not Philippi, 1846).

Littorina (Littorinopsis) modesta—Abbott, 1974:69 (in part, includes *N. modesta*).

Nodilittorina (? *Fossarilittorina*) *modesta*—Reid, 1989a:98, pl. 2, fig. e (in part, includes *N. modesta*). Skoglund, 1992:16 (not Philippi, 1846). Kaiser, 1997:27 (not Philippi, 1846).

Nodilittorina modesta—Finet, 1994:18 (not Philippi, 1846).

Taxonomic history: No original type material of *Littorina conspersa* is known to exist. Nevertheless, there is no doubt as to its identity, since Philippi's (1847) figure clearly shows the relatively flat whorls and slightly patulous shape, and he accurately described the five grooves on the penultimate whorl and pair of divided ribs near the suture of the last whorl, thus differentiating it from the similar *N. modesta*. To stabilize the concept of this taxon, a neotype is designated. Philippi (1847) noted that the material from El Realejo, Nicaragua, on which his description was based, was obtained from Petit. The neotype is from the same type locality, and was collected by R. B. Hinds on the voyage of the *Sulphur* (1836–1842). It is possible that Philippi's material might have originated from this same source, since both Hinds and Petit were in contact with Cuming in London, but there is no direct evidence for this. The types of *Littorina puncticulata* are lost; it is included in the synonymy of *N. conspersa* (as first noted by Carpenter, 1857a) because of the four ribs on the penultimate whorl and the presence of a dotted pattern despite the strong sculpture (strongly sculptured *N. modesta* tend to be white); Philippi's (1847) description of a riblet in each groove on the last whorl could apply to either of the species in the *N. modesta* group.

The longstanding confusion of the names *conspersa* and *modesta* has been discussed in the Taxonomic History of *N. modesta*. Previously, very few authors have recognized more than one species in the *N. modesta* group in Central America. Philippi (1847; followed by Weinkauff, 1882) recognized three from the single locality El Realejo (Nicaragua) and believed a fourth, *Littorina modesta*, to be from Alaska and Mauritius. His *Littorina conspersa* was based on elongate, relatively weakly sculptured shells, while *Littorina puncticulata* was introduced for globular, ribbed examples now known to be a

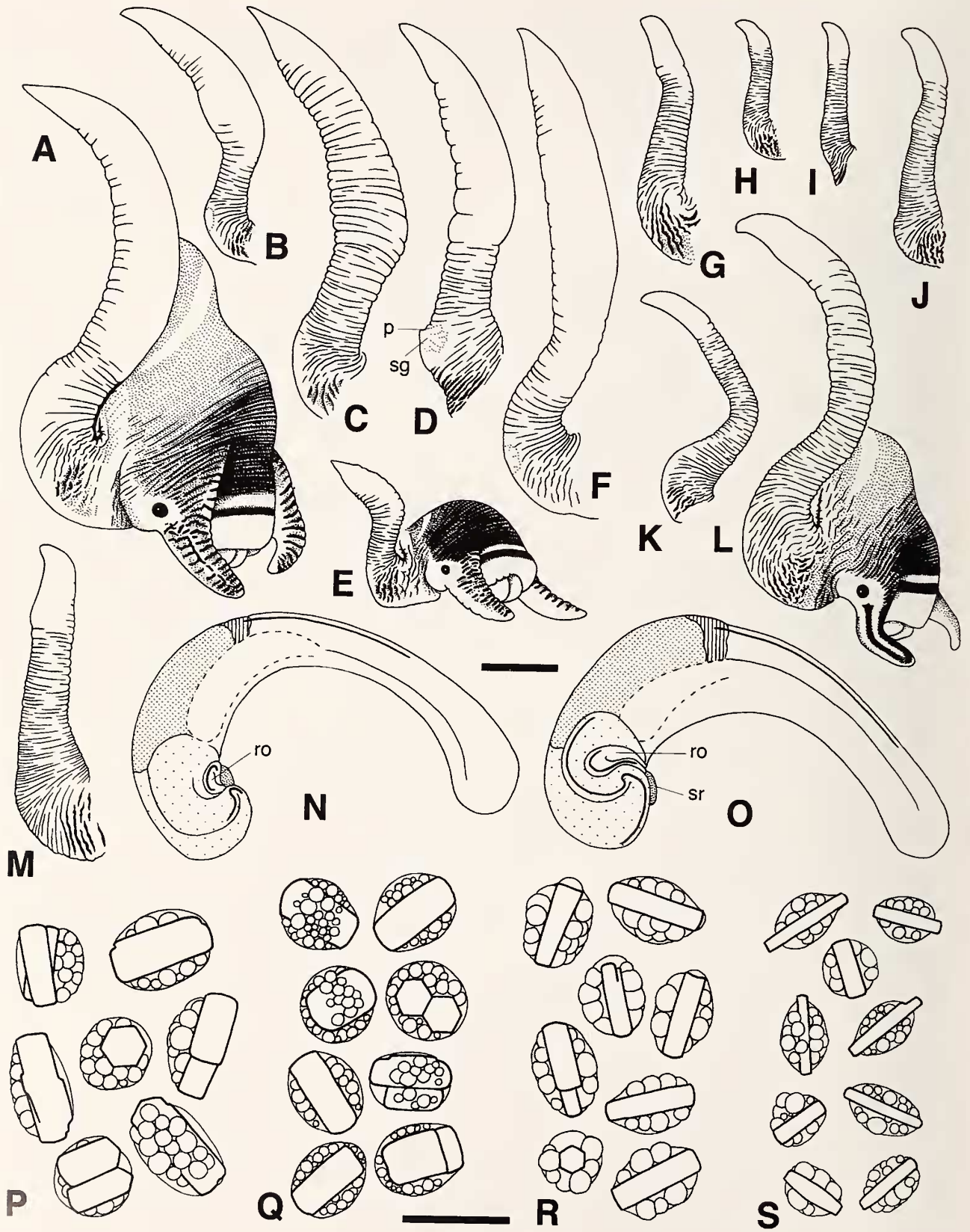
form of the same species (the third, *Littorina albida*, was probably an elongate, weakly sculptured form of *N. modesta*; see Taxonomic History of *N. modesta*). C. B. Adams (1852a, b) likewise separated more and less sculptured forms as *Littorina puncticulata* and *L. conspersa* (although he noted some intergradation); these were synonymized by Carpenter (1863). All subsequent authors recognized only a single species in the region (including Weinkauff, 1883), although von Martens (1900) still used *Littorina conspersa* var. *puncticulata* for strongly ribbed shells.

Diagnosis: Shell moderately large, spire whorls moderately flattened; 4–5 primary spiral grooves; sculpture of incised lines only, or with deep grooves 0.5–1 times rib width; pattern of small orange-brown dots. Tentacles with two longitudinal black lines. Penis with short filament, bluntly hooked at tip, glandular flange at base, no mammilliform gland.

Material examined: 53 lots (including 15 penes, 5 sperm samples, 10 pallial oviducts, 4 radulae).

Shell (Figures 7G–K): Mature shell height 4.4–18.2 mm. Shape high turbate to slightly patulous (H/B = 1.42–1.65, SH = 1.48–2.07); spire whorls moderately flattened, suture distinct; periphery of last whorl weakly angled. Columella straight, broad, slightly hollowed and pinched (sometimes with slight protruberance) at base; rarely a small imperforate, pseudo-umbilical area; eroded parietal area in larger shells. Sculpture of 4–5 (sometimes 6) primary spiral grooves on spire whorls; these may remain as incised lines only, numbering 8–10 above peripheral rib of last whorl (11–14 in total including basal grooves), but usually become slightly wider and deeper toward periphery; grooves rarely become obsolete on shoulder of last whorl; in strongly sculptured shells grooves are deeper throughout, separating rounded ribs on spire whorls, on last whorl ribs are raised (most strongly so near periphery), rounded, separated by grooves 0.5 to 1 times rib width, narrow interpolated rib may appear in 2 posterior grooves near suture (rarely in all grooves above periphery), or occasionally 1–3 posterior ribs become divided by a secondary groove, grooves on last whorl then up to 16 above peripheral rib (up to 23 in total including basal

Figure 7. Shells of *Nodilittorina modesta* (A–F), *N. conspersa* (G–K), and *N. galapagensis* (L–Q). A. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001194). B. Mazatlán, Sinaloa, Mexico (BMNH 20001192). C. 7 km NE of San José del Cabo, Baja California Sur, Mexico (BMNH 20001195). D. Locality unknown (BMNH 20001196). E. Lectotype of *Littorina modesta* Philippi, 1846; locality unknown (BMNH 1968224/1). F. Bahía Santa María, Baja California Sur, Mexico (BMNH 20001187). G. Same, Esmeraldas, Ecuador (BMNH 20001200). H. Tarcoles, Costa Rica (BMNH 20001205). I. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001206). J. Neotype of *Littorina conspersa* Philippi, 1847; El Realejo, Nicaragua (BMNH 19990405/1). K. Bahía Chatham, Isla del Coco, Costa Rica (KLK). L. Holotype of *Littorina (Tectarius) galapagensis* Stearns, 1892; Isla Santiago, Galápagos Islands (USNM 102509). M. O. Q. Punta Estrada, Isla Santa Cruz, Galápagos Islands (M, BMNH 20001274; O, BMNH 20001275; Q, BMNH 20001276). N. P. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (N, BMNH 20001273; P, BMNH 20001277). Scale bars A–K = 5 mm; L–Q = 5 mm.



grooves); spiral microstriae absent. Protoconch 0.31 mm diameter, sculptured by spiral ribs. Color white, with pale brown or lilac-grey apex; patterned with small orange-brown (sometimes grey-brown) spots, aligned in oblique (opisthocline) series (commonly less than 16 spots from peripheral rib to suture on last whorl, but up to 26); aperture orange-brown with 2 broad pale bands, external spotting showing through near margin; columella orange-brown to purple-brown, pillar sometimes white.

Animal (Figure 8L): Head black to pale grey, unpigmented stripe across black snout, tentacle with two longitudinal black lines, usually meeting close to tip, grey beneath; sides of foot black to pale grey. Opercular ratio 0.32–0.37. Penis (Figures 8G–M): narrow, vermiform; filament short (about 0.25–0.35 total length), with subepithelial glandular tissue, bluntly hooked tip, filament differentiated from base by slight constriction and lack of annular wrinkles (distinction sometimes unclear); sperm groove open to tip; base with fine annular wrinkles except at basal posterior edge with slight glandular flange (opaque subepithelial glandular tissue sometimes visible), base usually slightly pigmented. Euspermatozoa 54–71 μm ; paraspermatozoa (Figures 8R, S) round to oval; rod-pieces single (rarely two), filling cell or projecting, 9–22 μm , blunt, hexagonal in section; granules large, spherical, distinct. Pallial oviduct (Figure 8O) with long straight section; large copulatory bursa opening near posterior end of straight section, extending back to albumen gland; small loop of renal oviduct projects into center of spiral of albumen gland. Spawn not observed; protoconch indicates planktotrophic development.

Radula (Figure 9C): Relative radular length 3.6–5.1. Rachidian: length/width 1.40–1.50; major cusp elongate, rounded at tip; 2 extra denticles usually present at concave anterior edge. Lateral and inner marginal: major cusps elongate rectangular, blunt or rounded at tip. Outer marginal: 8 cusps.

Habitat: Rock faces, and among barnacles and mussels;

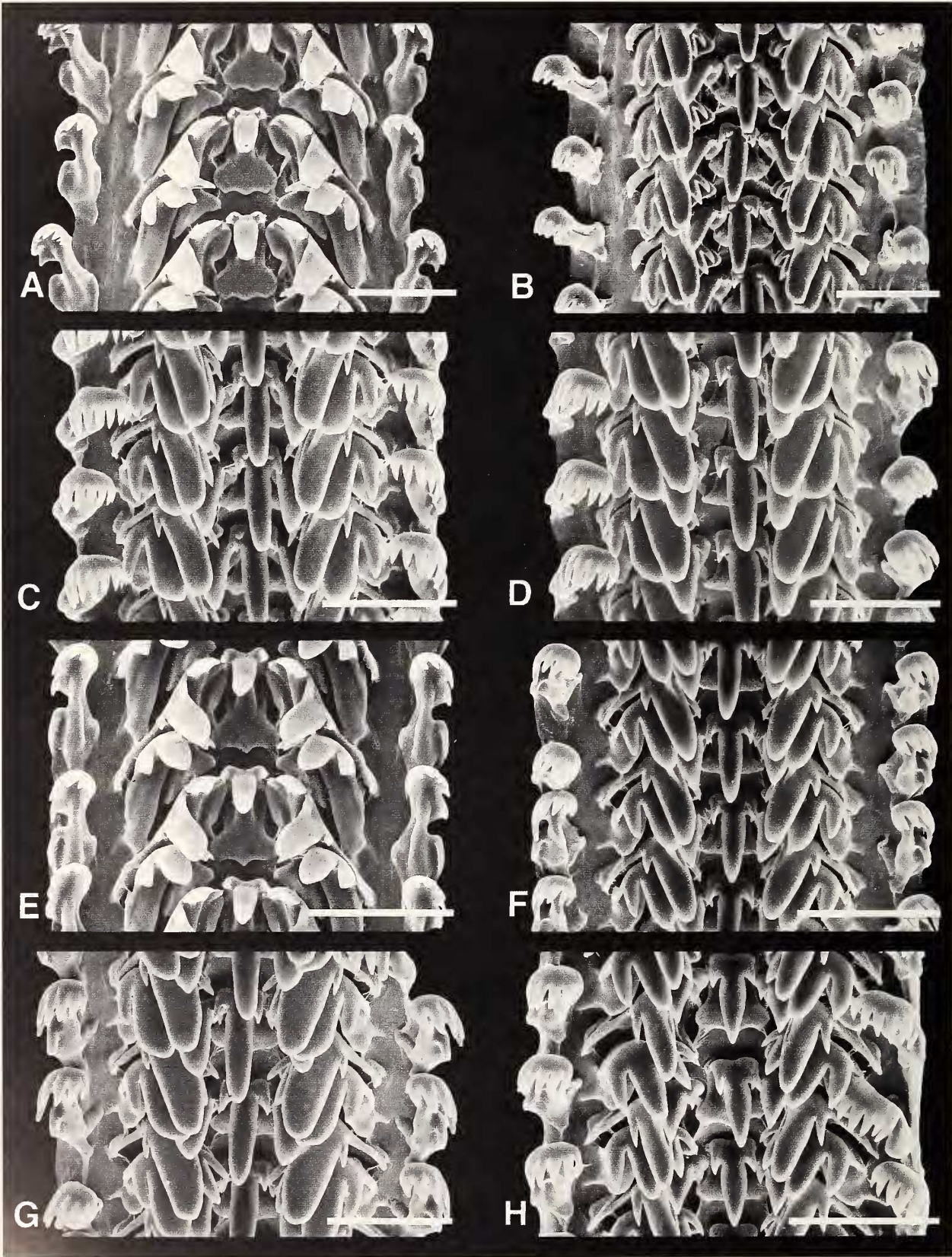
in upper eulittoral and low littoral fringe, below level of sympatric *N. dubiosa* and *N. tenuistriata*; recorded on basalt, volcanic conglomerate, sandstone, mudstone, and concrete; usually on wave-exposed open coasts, scarce at sheltered and turbid sites. Bakus (1975) recorded it only in protected sites at Isla del Coco. For ecological studies and descriptions of zonation see Markel (1971, includes *N. modesta*), Cantera et al. (1979), Garrity & Levings (1981), Garrity (1984) (all as *Littorina modesta*).

Range (Figure 10): Oaxaca (Mexico), El Salvador to northern Peru, Isla del Coco and Galápagos Islands. Range limits: Puerto Angel, Oaxaca (BMNH 20001198, 7 specimens); Playa El Cucu, San Miguel, El Salvador (CAS, 4 specimens); Punta Amapala, El Salvador (USNM 780446); Isla del Coco, Costa Rica (BMNH 20001199; KLK); Isla de Malpelo, Colombia (USNM 122854; KLK); Punta San Francisco, Bahía Solano, Colombia (USNM 819734); Isla Gorgona and Isla Gorgonilla, Colombia (USNM 819735); Same, Esmeraldas, Ecuador (BMNH 20001200); Punta Carnero, Guayas, Ecuador (BMNH 20001201); 46 km from Caleta Mero, Tumbes, Peru (Alamo & Valdivieso, 1987, 1997); Paita, Piura, Peru (Stearns, 1891); Galápagos Islands (Isla Santiago, USNM 807235; Isla Santa Cruz, BMNH 20001202; Isla Española, BMNH 20001203; Isla San Cristobal, BMNH 20001204). At the most northerly site, Puerto Angel, this species is much less common than *N. modesta*. It is relatively frequent in the Galápagos Islands on suitably exposed shores and also at Isla del Coco. The accuracy of the most southerly record (Stearns, 1891) might be doubted, since the reliability of another in the same publication is questionable (see Range of *N. galapagensis*).

Remarks: See Remarks on *N. modesta* and Table 2 for discrimination from *N. conspersa*. Specimens of *N. conspersa* from the Galápagos Islands do not appear to differ anatomically from mainland examples, but their shells are slightly more tall-spired than most of the latter, and their

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Figure 8. Penes (A–M), head pigmentation (A, E, L), pallial oviducts (N, O), and paraspermatozoa (P–S) of *Nodilittorina modesta* group: *N. modesta* (A–F, N, P, Q) and *N. conspersa* (G–M, O, R, S). A, Q. Mazatlán, Sinaloa, Mexico (BMNH 20001192; shell H = 10.0 mm). B. Playa de los Muertos, Puerto Vallarta, Jalisco, Mexico (BMNH 20001197; shell H = 7.8 mm). C, N, P. Bahía Santa María, Baja California Sur, Mexico (BMNH 20001187; shell H = 11.6 mm, 12.0 mm). D. Punta Pescadero, Baja California Sur, Mexico (BMNH 20001188; shell H = 11.1 mm). E. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001194; shell H = 6.2 mm). F. Puerto Angel, Oaxaca, Mexico (BMNH 20001193; shell H = 12.5 mm). G, J, S. Ballenita, Guayas, Ecuador (BMNH 20001207; shell H = 7.4 mm, 7.7 mm). H, I. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001208; shell H = 5.4 mm, 5.9 mm). K. Punta Estrada, Isla Santa Cruz, Galápagos Islands (BMNH 20001202; shell H = 7.2 mm). L. Puerto Angel, Oaxaca, Mexico (BMNH 20001198; shell H = 9.8 mm). M, R. Same, Esmeraldas, Ecuador (BMNH 20001200; shell H = 10.5 mm). O. Tarcoles, Costa Rica (BMNH 20001205; shell H = 11.2 mm). Abbreviations: p, papilla on penial base; ro, loop of renal oviduct projecting into albumen gland; sg, subepithelial glands in penial base (dotted line; sometimes visible by transparency); sr, seminal receptacle. Shading conventions as in Figures 3, 4. Scale bars A–O = 1 mm; P–S = 20 μm .



whorls a little more rounded, which might indicate a degree of genetic differentiation of the island populations.

The *Nodilittorina aspera* Group

Six species are included in this group: *N. aspera*, *N. tenuistriata*, *N. dubiosa*, *N. apicina*, *N. penicillata*, and *N. paytensis*. Superficially, the shells are very similar, and as a result these are perhaps the most confusing and difficult to identify of the *Nodilittorina* species of the region. These are medium to large members of the genus, with white to blue-grey shells, usually with a conspicuous dark pattern of axial stripes and, typically, a spiral black line, band or grey zone above the periphery which is prominent on the spire whorls, but fades on the last whorl. The aperture is brown, with two pale bands. The sculpture is of spiral grooves, which sometimes become wide and separated by prominent ribs.

Not surprisingly, considerable uncertainty has surrounded the taxonomy of these species. All but one (*N. tenuistriata* Reid, sp. nov.) were named before 1864, but this was a fortuitous result of limited availability of material and lack of appreciation of the range of shell variation. The first to be named was *Littorina aspera* Philippi, 1846, followed by *Littorina paytensis* Philippi, 1847. In 1851 Menke provisionally named *Littorina apicina*, but was unwilling to separate it as a distinct species from *L. aspera* in the same collection from Mazatlán. With a larger volume of material from Mazatlán at his disposal, Carpenter (1857b) correctly distinguished two species in this complex, *L. aspera* and *L. philippii* (= *N. apicina*) and later (1864a) described *Littorina penicillata* as a variety of the latter. Meanwhile, C. B. Adams (1852a, b) used the name *Littorina aspera* for large ribbed shells from Panama, whereas smaller smooth shells (now known to be conspecific) were doubtfully identified as *L. parvula* (a *nomen dubium* introduced by Philippi, 1849) and provisionally renamed *L. dubiosa*. Thus several early authors recognized two species in the complex, a ribbed form named *aspera* and a smaller, smoother shell variously named *apicina*, *dubiosa*, *parvula*, or *philippii*. In Mexico (Menke, 1851; Carpenter, 1857b, 1864a) this distinction did indeed correspond to that now made on anatomical grounds between *N. aspera* and *N. apicina*. However, the intraspecific variation in size and sculpture was not appreciated

and therefore farther south in Central America (where *N. apicina* is rare) the names *aspera* and *dubiosalparvulaphilippii* were applied to rough and smooth extremes of the single common species (for which the valid name is *N. dubiosa*) (C. B. Adams, 1852a, b; Carpenter, 1863). This distinction of two species contrasting in sculpture was continued in systematic revisions by Weinkauff (1882), von Martens (1900), and Keen (1958), in which *aspera* was applied to ribbed shells of both *N. aspera* and *N. dubiosa*, whereas *philippii/dubiosa* included a range of smoother forms (*N. apicina*, *N. penicillata*, *N. dubiosa*, and even *N. modesta* and *N. interrupta*). There was, however, an alternative tendency to combine these variable and troublesome shells as a single species, for which the earliest name *aspera* was employed (Weinkauff, 1883; Tryon, 1887; Keen, 1971; Abbott, 1974). Tryon (1887) even included the *N. modesta* group under the specific name *aspera*. In the literature of the past 30 years there has been no attempt to revise the *N. aspera* group, despite the observation by Keen (1971) that careful study might reveal a complex of species. The faunistic lists of areas of Mexico, Central America, and the Galápagos that appeared during the twentieth century have almost all listed only *aspera* (Biolley, 1907; Morrison, 1946; Hertlein, 1963; Montoya, 1983; Finet, 1985, 1994; Holguín & González, 1989; Emerson, 1995; Kaiser, 1997), although an exception was that of Pilsbry & Lowe (1932) in which the names *aspera*, *penicillata*, and *philippii* were listed. Curiously, the predominantly southern species *N. paytensis* has sometimes been recognized as distinct in revisions and worldwide lists (Weinkauff, 1882, 1883; Rosewater, 1970; Keen, 1971), and in the Peruvian literature (Vegas, 1968; Peña, 1971b; Alamo & Valdivieso, 1987, 1997; Paredes et al., 1999), despite its close resemblance to other members of the *N. aspera* group. If synonymized at all, it was combined with another (but not closely related) southern species, *N. araucana* (Tryon, 1887; Dall, 1909; Hertlein & Strong, 1955b; Reid, 1989a; Finet, 1994), or doubtfully reduced to a subspecies of *N. modesta* (Keen, 1971; Vermeij, 1973; Finet, 1985). The other southern species in the *N. aspera* group, *N. tenuistriata* Reid, sp. nov., has hitherto appeared only in Peruvian literature, identified as *Littorina aspera* (Alamo & Valdivieso, 1987, 1997; Paredes et al.,

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Figure 9. Radulae of *Nodilittorina modesta* (A, B), *N. conspersa* (C), *N. dubiosa* (D), *N. aspera* (E, F), *N. tenuistriata* Reid, sp. nov. (G), and *N. penicillata* (H). A, B. Bahía, Santa María, Cabo San Lucas, Baja California Sur, Mexico (BMNH 20001187; two views of radula, flat and at 45°; shell H = 10.9 mm). C. Ballenita, Guayas, Ecuador (BMNH 20001207; at 45°; shell H = 7.9 mm). D. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001229; at 45°; shell H = 11.3 mm). E, F. Puerto Marques, Acapulco, Guerrero, Mexico (BMNH 20001217; two views of radula, flat and at 45°; shell H = 11.3 mm). G. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001223; at 45°; shell H = 11.2 mm). H. San Felipe, Baja California Norte, Mexico (BMNH 20001250; at 45°; shell H = 8.2 mm). Scale bars = 50 µm.

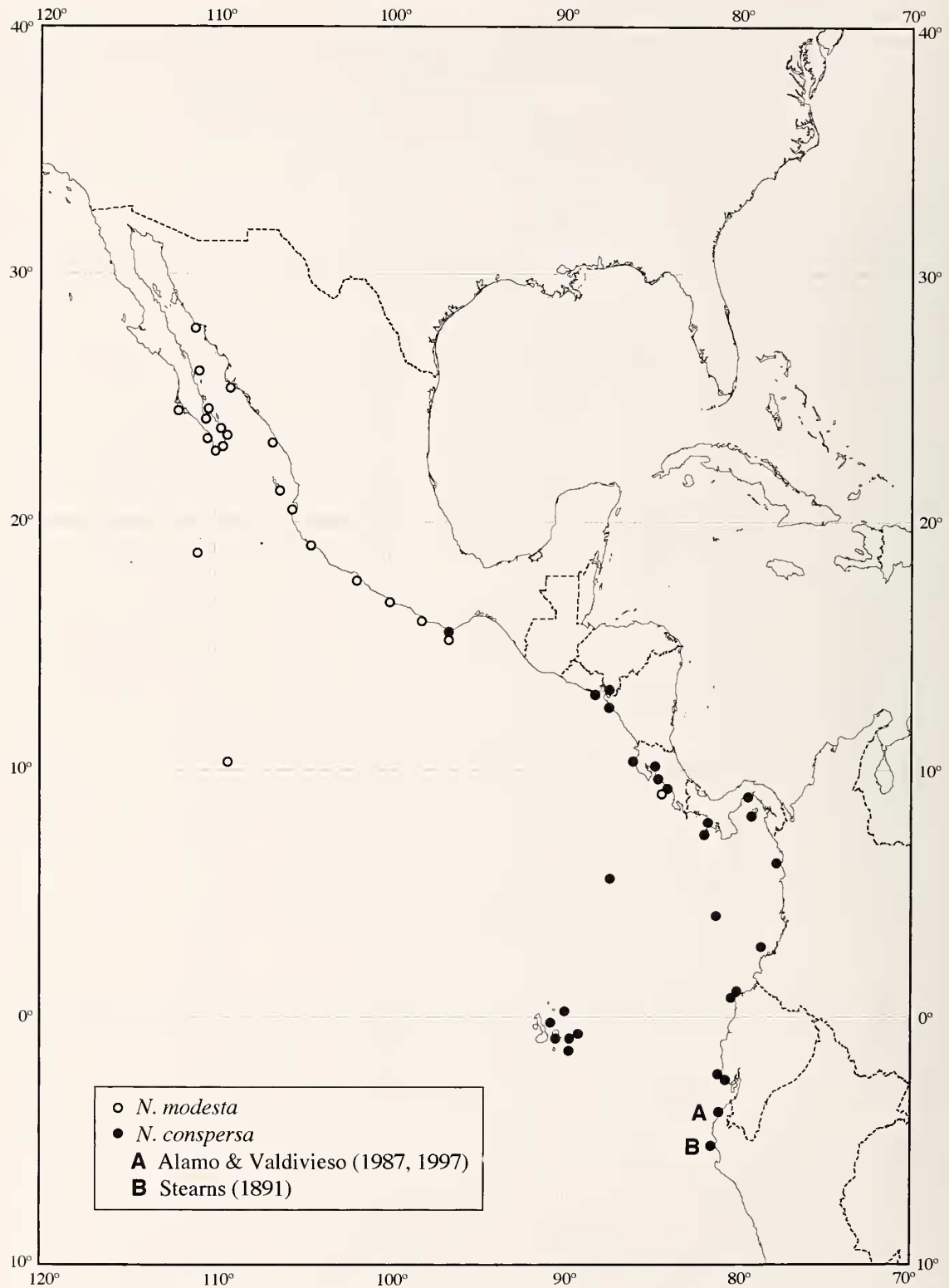


Figure 10. Geographical distribution of *Nodilittorina modesta* group (records based on material examined and quoted literature sources).

1999). In the two most recent worldwide lists of species of Littorinidae, Rosewater (1970) included *Littorina aspera*, *L. penicillata*, and *L. paytensis*, whereas Reid (1989a) gave only *N. aspera*, with *N. penicillata* and *N. paytensis* both of doubtful status.

As in the other species complexes of *Nodilittorina*, the crucial observations leading to discrimination of these difficult taxa have been the discovery of sympatric and syntopic occurrences, localities at which the distinctive shell types co-occur on rocks on the shore (though often at slightly different levels within the uppermost eulittoral and littoral fringe). At the southern tip of Baja California three species co-occur (*N. aspera*, *N. apicina*, *N. penicillata*); in southern Mexico two (*N. aspera*, *N. apicina*); in Nicaragua four (*N. aspera*, *N. tenuistriata*, *N. dubiosa*, *N. apicina*); in Costa Rica four (*N. tenuistriata*, *N. dubiosa*, *N. apicina*, *N. paytensis*); and in Ecuador three (*N. tenuistriata*, *N. apicina*, *N. paytensis*). Correlated with these shell types are differences in the shape of the penis, but these are more subtle than is often the case in littorinids, and are not always diagnostic. Other anatomical features, such as the paraspermatozoa and copulatory bursa, also provide discriminating characters in some cases, but radulae do not. The most useful characters for identification of species in this complex are summarized in Table 3.

Another key to the understanding of the *N. aspera* complex is the recognition that the strength of shell sculpture is variable in most species; that is, the width and depth of the spiral grooves varies, although their number is more constant. Early authors identified those large shells with strong ribs and wide grooves as *aspera*, and separated smaller smoother forms as *apicina*, *philippii*, *parvula*, and *dubiosa*, as discussed above. In fact, most species (except *N. tenuistriata*) can show almost completely smooth shells in dwarf or stunted forms, and strong spiral ribs are seen only on the last whorl of large examples of *N. aspera* and *N. dubiosa*. Surprisingly, in this group, shell color pattern is a more reliable guide for rapid identification in the field (Table 3), although in other members of the genus (e.g., *N. porcata* group) this is variable. The intensity of the dark pattern does nevertheless show variation and is especially dark in dwarf shells, which can be found for example in saline pools high in the eulittoral zone. As in the *N. porcata* group, it is suggested that this may be a case of ecophenotypic variation (see Discussion).

There is a parallel between the *N. aspera* group and the complex of black and white shells (informally known as the *N. ziczac* group) found in the Caribbean and western Atlantic, which consists of at least four (Reid, 1989a) or as many as six (Bandel & Kadolsky, 1982) species. Whether they share common ancestry is not yet known. When the origin of specimens is not known, confusion can arise; for example, von Martens (1900) erroneously described a Caribbean species (*N. interrupta*) as *Littorina*

philippii var. *latistrigata*, believing it to have originated from the Pacific coast of Costa Rica.

Nodilittorina aspera (Philippi, 1846)

(Figures 9E, F, 11A–H, 13A–F, 15A, J, K, 17)

Littorina aspera Philippi, 1846a:139 (Sitka, New Albion [Alaska]; Mexico; Conchagua, San Salvador [El Salvador]; here restricted to Mazatlán, Mexico; lectotype (here designated, 16.6 × 10.9 mm) BMNH 1968217/1, seen, Figure 11A; 3 paralectotypes BMNH 1968217/2, seen). Middendorff, 1849:394. Carpenter, 1857a:162, 216, 224, 286. ? Troschel, 1858:135, pl. 11, fig. 4 (radula). Keen, 1958:282, ? fig. 173 right (in part, includes *N. dubiosa*). Keen, 1971:365, fig. 181 (part) (in part, includes *N. apicina*, *N. penicillata*, *N. dubiosa*, *N. modesta*, *N. interrupta*). Holguín & González, 1989:114, fig.

Littorina aspera—Philippi, 1847:2:200 (in part, fig. is *N. dubiosa*). Menke, 1851:163–164 (in part, includes *N. apicina*). Carpenter, 1857a:235, 237, 257, 326, 348 (in part, includes *N. dubiosa*). Carpenter, 1864b:623 (in part, includes *N. dubiosa*). Weinkauff, 1882:60–61 (in part, figs. are *N. dubiosa*). Weinkauff, 1883:220 (in part, includes *N. apicina*, *N. dubiosa*, *N. penicillata*). Carpenter, in Brann, 1966:pl. 38, fig. 397.

Littorina (Melaraphe) aspera—H. & A. Adams, 1854:314. von Martens, 1900:577, 587, ? pl. 43, fig. 15 (in part, includes *N. dubiosa*, *N. apicina*). Tryon, 1887:249, pl. 45, fig. 87 (in part, includes *N. modesta*, *N. conspersa*, *N. apicina*, *N. penicillata*).

Littorina (Melaraphe) aspera—Carpenter, 1857b:348–349 (includes *N. dubiosa*).

Littorina (Austrolittorina) aspera—Rosewater, 1970:423. Abbott, 1974:69, fig. 561, pl. 3, fig. 561 (in part, includes *N. dubiosa*, *N. apicina*, *N. penicillata*).

Nodilittorina (Nodilittorina) aspera—Reid, 1989a:99 (in part, includes *N. dubiosa*, possibly *N. penicillata*). Skoglund, 1992:15 (in part, includes *N. dubiosa*, possibly *N. penicillata*).

Nodilittorina aspera—Emerson, 1995:13.

Littorina irrorata—Reeve, 1857:sp. 56, pl. 11, fig. 56a, b (not *Turbo irroratus* Say, 1822 = *Littoraria irrorata*).

Taxonomic history: Of the three collections mentioned by Philippi (1846a) in the original description of *aspera*, only that from Sitka has been located, but the locality is obviously erroneous (Carpenter, 1857a). Philippi apparently included the closely similar southern species *N. dubiosa* in his concept of the taxon, since his figure (Philippi, 1847) of *N. aspera* appears to represent *N. dubiosa*. To fix the concept of this taxon, a lectotype is designated from the extant syntypes, and the type locality is here restricted to Mazatlán.

This species was the first of the *N. aspera* group to be described and the name has remained one of the most familiar in the eastern Pacific fauna. Examples of this species have never been figured or described under any other name, with the exception of Reeve's (1857) "*Littorina irrorata*" (an error first noted by von Martens, 1900). Nevertheless, most authors have had too broad a

Table 3
Summary of the most useful characters for the identification of the six species of the *Nodilittorina aspera* group.

Character	<i>N. aspera</i>	<i>N. tenuistriata</i>	<i>N. dubiosa</i>	<i>N. apicina</i>	<i>N. penicillata</i>	<i>N. paytensis</i>
1. Geographical range	S Baja California to S Mexico, Nicaragua	Nicaragua to N Peru	El Salvador to Colombia, Isla del Coco, Galápagos Is	S Baja California to N Ecuador	S Baja California, Gulf of California	Costa Rica to N Peru
2. Shell						
—spire profile	concave	straight	straight or concave	convex	straight	straight
—columella	concave	concave	concave	long, straight	concave	straight
—grooves above periphery of last whorl	7-10 deep wide grooves (up to 3 times rib width)	10-15 grooves (up to same width as ribs at periphery)	7-11 deep wide grooves (up to twice rib width) or incised lines mainly in stunted forms	9-12 incised lines or narrow grooves (rarely to half rib width)	8-11 incised lines	11-23 incised lines
—smooth form	in stunted forms	absent	broad blue-grey zone above periphery, line below periphery	rare	rare	frequent
—dark spiral bands (usually darkest on spire whorls)	broad black band above periphery on spire, black line below periphery	broad black band above periphery, black band below periphery	broad blue-grey zone above periphery, line below periphery	indistinct grey zone above periphery	1 narrow line above and 1 below periphery	broad brown band above periphery
—axial pattern	slightly oblique stripes	oblique axial lines	narrow oblique stripes	oblique or zigzag lines or stripes, or tessellation	oblique or waved lines	smudged brown dots
3. Penis						
—filament	smooth, tapering	wrinkled, tapering	broad, smooth, tapering	long, wrinkled, tapering	broad, smooth, pointed	wrinkled, tapering, pointed
—mamilliform gland	medium	medium	large	medium	medium	medium to large
—glandular disc	medium	large	small to medium	medium, forming a lobe	medium, forming a lobe	small to medium

concept of this taxon, including with it various others from the *N. aspera* complex. In the early literature, most authors discriminated two species in the complex, one larger and more strongly sculptured (to which the name *aspera* was applied), the other smaller and relatively smooth (see Taxonomic History of *N. apicina* and *N. penicillata*). For the first time, it is shown here that the larger, more sculptured shells comprise three species, *N. aspera* s.s., *N. dubiosa*, and *N. tenuistriata*. Of these, the last is relatively uncommon in Central America and has been specifically referred to (as *aspera*) only in the Peruvian literature (Alamo & Valdivieso, 1987, 1997; Paredes et al., 1999). The other two have, however, been widely confused, although their largely allopatric distribution assists when synonymies are compiled (see also Taxonomic History of *N. dubiosa*). The use of the name *aspera* for all species in the *N. aspera* group, regardless of sculpture and size, dates from Weinkauff (1883) and Tryon (1887, who also included the *N. modesta* group). This practice was followed by Keen (1971), Abbott (1974), and Reid (1989a).

Diagnosis: Shell large, spire whorls slightly rounded, spire profile often slightly concave; 5–7 primary spiral grooves; 7–10 grooves above periphery of last whorl; sculpture of deep grooves up to 3 times rib width on last whorl of large shells, but only incised lines on small shells; white with brown axial stripes and (most obvious on spire whorls) broad spiral black band just above periphery. Penis with gradually tapering filament; mamilliform gland and glandular disc of similar size, on prominent projection of base.

Material examined: 47 lots (including 23 penes, 2 sperm samples, 4 pallial oviducts, 4 radulae).

Shell (Figures 11A–H): Mature shell height 5.0–22.0 mm. Shape high turbate (H/B = 1.27–1.83, SH = 1.43–2.00); spire whorls slightly rounded, suture distinct; spire profile usually slightly concave, giving slight onion shape; periphery of last whorl weakly angled. Columella concave, hollowed and slightly pinched at base; small eroded parietal area. Sculpture of (4) 5–7 primary spiral grooves on spire whorls; ribs subequal, or slightly wider at suture and periphery; 7–10 grooves above periphery of last whorl, secondary sculpture usually absent, but rarely 1–2 narrow secondary ribs develop posteriorly; on last whorl grooves enlarge to 1–3 times width of intervening ribs, which become narrow, sharply raised cords; in dwarf forms, the typical wide grooves do not develop, grooves remain as impressed lines, or become faint; spiral microstriae absent. Protoconch 0.31 mm diameter, 2.5 whorls. Color white, with slightly oblique or waved axial brown stripes; on lower half of spire whorls a broad grey to black spiral band; on last whorl axial pattern may become less distinct except at suture, and broad grey band above periphery may also become faint; a narrow black

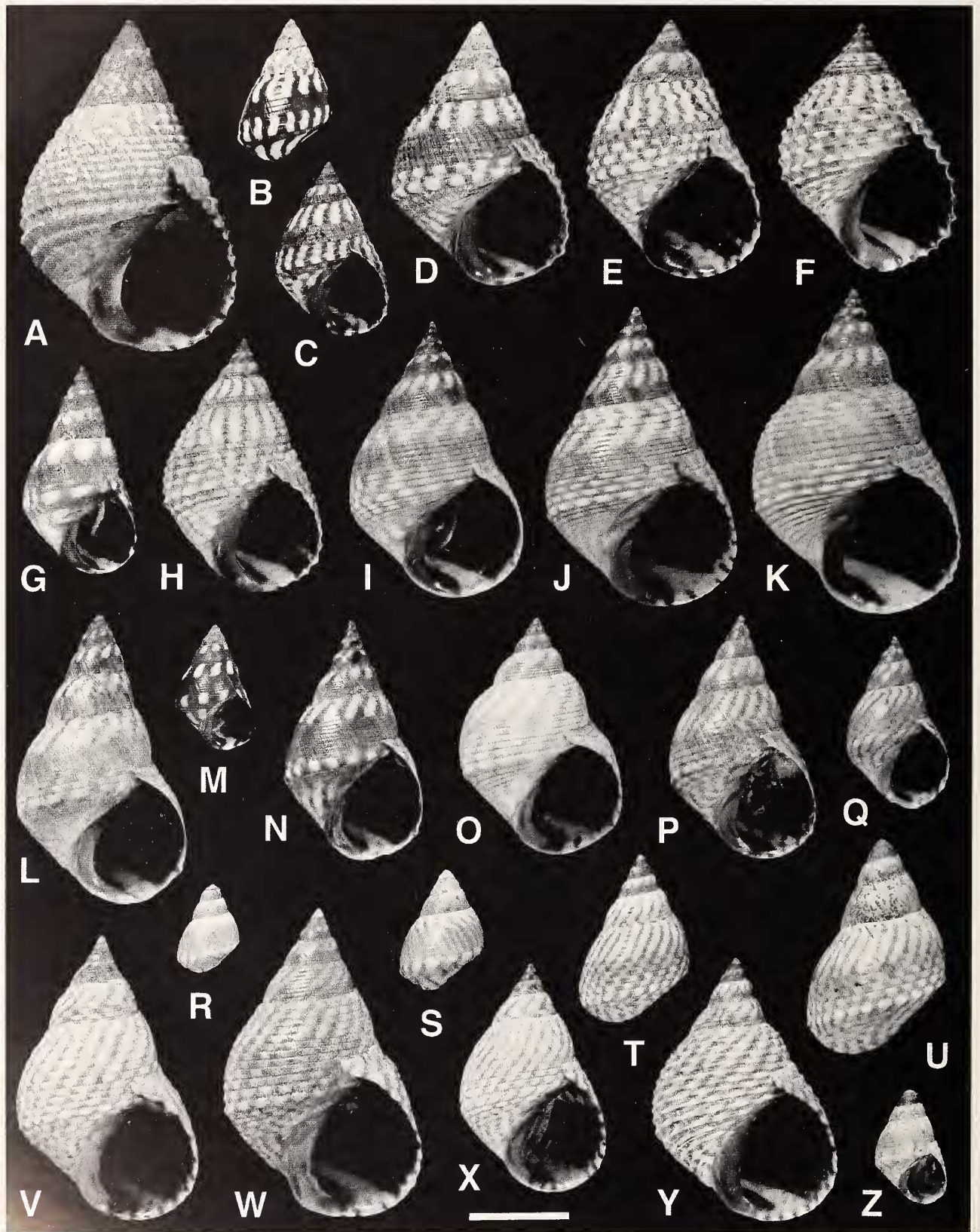
band is also present on base just below periphery; dwarf shells (Figure 11B) usually show striking pattern of black axial stripes and band above and below periphery; aperture brown, with 2 pale spiral bands at base and shoulder; columella brown.

Animal: Head grey to black, no unpigmented stripe across snout, tentacle pale at base and around eye, with two longitudinal black stripes, and black spot at tip; sides of foot pale grey to black. Opercular ratio 0.33–0.40. Penis (Figures 13A–F): filament moderately long, gradually tapering, smooth, thickened and glandular at base, 0.6–0.8 total length; sperm groove open to tip; mamilliform gland and glandular disc of similar size, on well developed projection of base; penis unpigmented or only slightly pigmented at base. Euspermatozoa not seen; paraspermatozoa (Figures 15J, K) 18–20 μm , oval, with large round granules, single stout rod-pieces (sometimes composed of smaller rod-shaped elements) fill cells or project slightly. Pallial oviduct (Figure 15A) with large copulatory bursa opening at half length of straight section and extending back to albumen gland. Spawn not observed; protoconch indicates planktotrophic development.

Radula (Figures 9E, F): Relative radular length 10.2–15.7. Rachidian: length/width 1.50–1.79; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps elongate, rounded at tip. Outer marginal: 7–9 cusps.

Habitat: Clustered in crevices and on bare rock in littoral fringe; above water level at margins of shallow pools at top of eulittoral; largely restricted to exposed and moderately exposed coasts in oceanic situations; recorded on granite and concrete; usually abundant. Overlapping with *N. apicina*, but extending farther into littoral fringe.

Range (Figure 17): Southwestern Baja California to Oaxaca (Mexico), Islas Revillagigedo, Nicaragua. Range limits: Laguna San Ignacio, Baja California Sur (USNM 130599, 1 specimen); Bahía Magdalena, Baja California Sur (USNM 264566, 819879, 1 specimen each); Punta Lobos, Todos Santos, Baja California Sur (personal observation); 7 km N of San José del Cabo, Baja California Sur (BMNH 2001209); Punta Doble, Sonora (KLK, 1 specimen); Topolobampo, Sinaloa (BMNH 20001210, 1 specimen); Mazatlán, Sinaloa (BMNH 20001211); Bahía Ventosa, Golfo de Tehuantepec, Oaxaca (USNM 60449, 4 specimens); Salina Cruz, Golfo de Tehuantepec, Oaxaca (LACM 67-97-30, 3 specimens); Bahía Henslow, Isla Socorro, Islas Revillagigedo (KLK, 1 specimen); Corinto, Nicaragua (LACM 149775, 149776, 1 and 6 specimens); Nicaragua (CAS 122365, 2 specimens). This species is apparently very rare in the Gulf of California, from which only two specimens are known. It is, however, common on the southwestern coast of Baja California and from Mazatlán southward. Material from Nicaragua is scarce in collections; the two lots in LACM are apparently re-



liable and further supported by von Martens' (1900) figure of a specimen from El Salvador. Only a single specimen has been seen from Isla Socorro, although the name appears in lists from the island (Mille-Pagaza et al., 1994; Emerson, 1995).

Remarks: Since the original description of this species (Philippi, 1846a; see Taxonomic History above) the name has been applied to all large eastern Pacific littorinids with sharp ribs separated by wide grooves, and therefore also included large shells of *N. dubiosa* (distributed from El Salvador to Colombia). This similarity is, however, superficial and there are small but consistent differences in shell coloration, penial anatomy and habitat (see Remarks on *N. dubiosa*). The new species *N. tenuistriata* is separated from *N. aspera* by its finer sculpture (7–10 primary spiral grooves on spire whorls, 10–15 narrow grooves above periphery of last whorl), but similarities in shell coloration, paraspermatozoa, and habitat suggest a close relationship (see Remarks of *N. tenuistriata*). The known geographical distribution of *N. tenuistriata* just meets that of *N. aspera* at Corinto (Nicaragua) and extends to Peru; their distinguishing shell characters remain distinct at the one known locality of sympatry.

The distinctive coloration of *N. aspera* remains rather constant throughout its range. However, adult size varies widely and only shells of moderate and large size develop the strong sculpture of narrow ribs by which this species (together with *N. dubiosa*) has previously been characterized. Dwarf specimens (Figure 11B) are found in shallow pools at the top of the eulittoral zone, and in these small shells the sculpture is weak or almost absent. Dwarf specimens show a striking black pattern on a white ground. Similar variation is seen in dwarf examples of *N. apicina* from the same microhabitat; in both species occasional shells show an abrupt change to a more normal sculpture and pattern, implying an ecophenotypic component to the variation.

The radula is extraordinarily long, sometimes exceeding 15 times the length of the shell.

Nodilittorina tenuistriata Reid, sp. nov.

(Figures 9G, 11I–O, 13G–L, 15B, L, M, 17)

Littorina (*Austrolittorina*) *aspera*—Alamo & Valdivieso, 1987:25, fig. 35. Alamo & Valdivieso, 1997:17, fig. 35. Paredes et al., 1999:22. (All not Philippi, 1846).

Etymology: Latin: “finely striated,” describing the characteristic sculpture.

Types: Holotype BMNH 20000312 (Figure 11I). 28 paratypes BMNH 20000310 (Figure 11L, M). 100 paratypes BMNH 20000314 (ethanol). 4 paratypes USNM 894293. Type locality: Punta Chocolatera, Peninsula Santa Elena, Guayas Province, Ecuador.

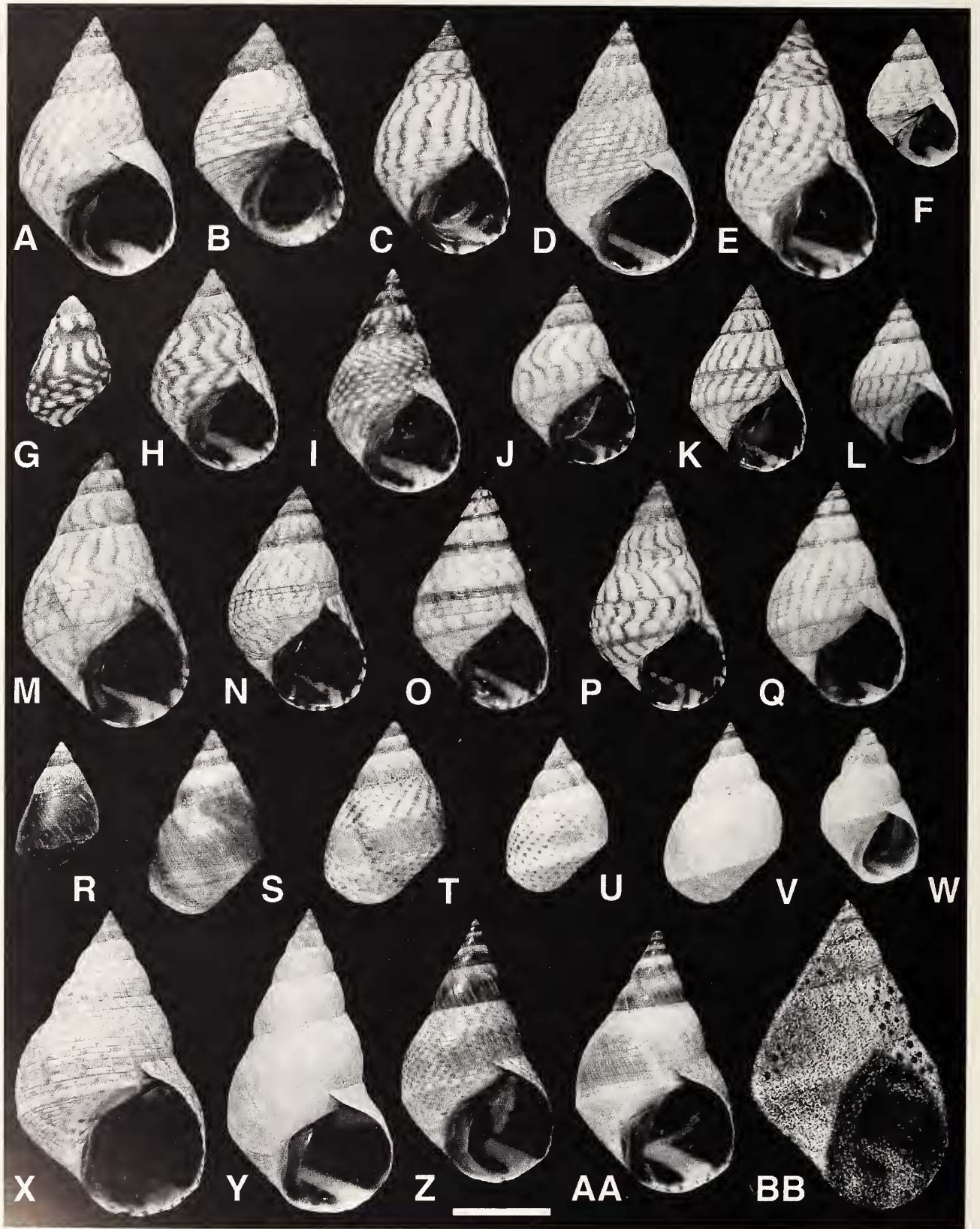
Taxonomic history: This species has been almost entirely ignored in the literature. It has a wide distribution from Nicaragua to Peru. However, in Central America it is relatively uncommon, and no authors working in the area have distinguished it from the abundant *N. dubiosa*, whereas the littorinids of Colombia and Ecuador have scarcely been studied. Only in Peru (where *N. dubiosa* does not occur) has this species been specifically referred to, and then identified as *aspera* (Alamo & Valdivieso, 1987, 1997; Paredes et al., 1999).

Von Martens (1900) introduced the name *Littorina philippii* var. *latistrigata* for shells superficially similar to this species, white with oblique black axial stripes and spiral black band, although the sculpture was described as faint. The type locality was given as Punta Arenas, western Costa Rica. Examination of two syntypes in MNB has confirmed that they belong to the Caribbean species *N. interrupta*, characterized by waved or zigzag axial stripes, fine or obsolete sculpture, and raised dark brown inner lip of the aperture adjacent to the columella. Von Martens' type locality must be regarded as erroneous, but the species does occur on the eastern coast of Costa Rica.

Diagnosis: Shell large or small, whorls moderately rounded or slightly shouldered, spire profile usually

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Figure 11. Shells of *Nodilittorina aspera* group: *N. aspera* (A–H), *N. tenuistriata* Reid, sp. nov. (I–O), and *N. dubiosa* (P–Z). A. Lectotype of *Littorina aspera* Philippi, 1846; locality unknown (BMNH 1968217/1). B, G. Bahía Santa María, Baja California Sur, Mexico (BMNH 20001212). C, E, H. Puerto Angel, Oaxaca, Mexico (C, H, BMNH 20001213; E, BMNH 20001214). D. Boca de Tomatlán, Jalisco, Mexico (BMNH 20001215). F. Playa de los Muertos, Puerto Vallarta, Jalisco, Mexico (BMNH 20001216). I. Holotype of *N. tenuistriata* Reid, sp. nov.; Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 2000312). J, O. Tarcoles, Costa Rica (BMNH 20001224). K. Muisne, Esmeraldas, Ecuador (BMNH 20001125). L, M. Paratypes of *N. tenuistriata* Reid, sp. nov.; Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 2000313). N. Same, Esmeraldas, Ecuador (BMNH 20001226). P. Isla San José, Islas Perlas, Panama (USNM 588051). Q. Punta Pitt, Isla San Cristobal, Galápagos Islands (BMNH 20001227). R. Coco, W of Liberia, Costa Rica (BMNH 20001228). S. San Juan del Sur, Nicaragua (USNM 23304). T, Y. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001229). U. Nicaragua (USNM 46973). V. Isla San José, Islas Perlas, Panama (USNM 587787). W. Bahía Chatham, Isla del Coco, Costa Rica (KLK). X. Tarcoles, Costa Rica (BMNH 20001230). Z. Lectotype of *Littorina dubiosa* C. B. Adams, 1852; Isla Taboga, Panama (MCZ 186573). Scale bar = 5 mm.



straight; 7–10 primary spiral grooves; 10–15 grooves above periphery of last whorl; sculpture of numerous fine grooves (10–15 above periphery of last whorl); white with oblique, grey-brown, axial lines and broad spiral grey to black band just above periphery (indistinct on last whorl). Penis with wrinkled filament roundly tapered at tip; mamilliform gland and large glandular disc borne on long projection of base.

Material examined: 31 lots (including 17 penes, 9 sperm samples, 4 pallial oviducts, 5 radulae).

Shell (Figures 11I–O): Mature shell height 5.0–19.6 mm. Shape high-turbinate to elongate (H/B = 1.39–1.78, SH = 1.47–1.95); spire whorls moderately rounded, suture distinct; spire profile usually straight, sometimes slightly concave; last whorl slightly shouldered, periphery angled. Columella concave, hollowed, and slightly pinched at base; eroded parietal area. Sculpture of 7–10 primary spiral grooves on spire whorls; primary ribs subequal, slightly wider toward suture; 10–15 (17) grooves above periphery of last whorl; peripheral rib raised and twice as wide as ribs above and below; secondary sculpture may be absent, or single narrow secondary riblets appear in grooves near suture and periphery; sculpture never becomes obsolete; on last whorl grooves close to periphery enlarge to 0.5–1 times width of intervening ribs, but others remain narrow; spiral microstriae absent. Protoconch not seen. Ground color white to pale blue-grey, with oblique brown, grey, or black stripes, interrupted by broad grey to black spiral band just above periphery and another on base; spiral bands become paler on last whorl, remaining as blue-grey zones; in dwarf forms (Figure 11M) a striking pattern of black stripes and bands on white ground; aperture brown, external pattern showing through, with 2 pale spiral bands at base and shoulder; columella brown.

Animal: Head grey to black, no unpigmented stripe across snout, tentacle pale around eye and sometimes at inside of base, with two longitudinal black stripes meeting at black tip; sides of foot grey or black speckled.

Opercular ratio 0.34–0.40. Penis (Figures 13G–L): filament moderately long, tapering toward rounded tip, with annular wrinkles on lower half, glandular, 0.6–0.8 total length; sperm groove open to tip; glandular disc large (usually larger than mamilliform gland), projecting as a lobe, borne with mamilliform gland on long projection of base (as long as filament, in well relaxed specimens); penis unpigmented or only slightly pigmented at base. Euspermatozoa 54–75 μm ; paraspermatozoa (Figures 15L, M) oval with single (sometimes 2–3 if narrow) blunt or rounded rod, 10–34 μm , projecting from cell, cytoplasm packed with large spherical granules. Pallial oviduct (Figure 15B) with large copulatory bursa opening at half length of straight section and extending back to albumen gland. Spawn not observed.

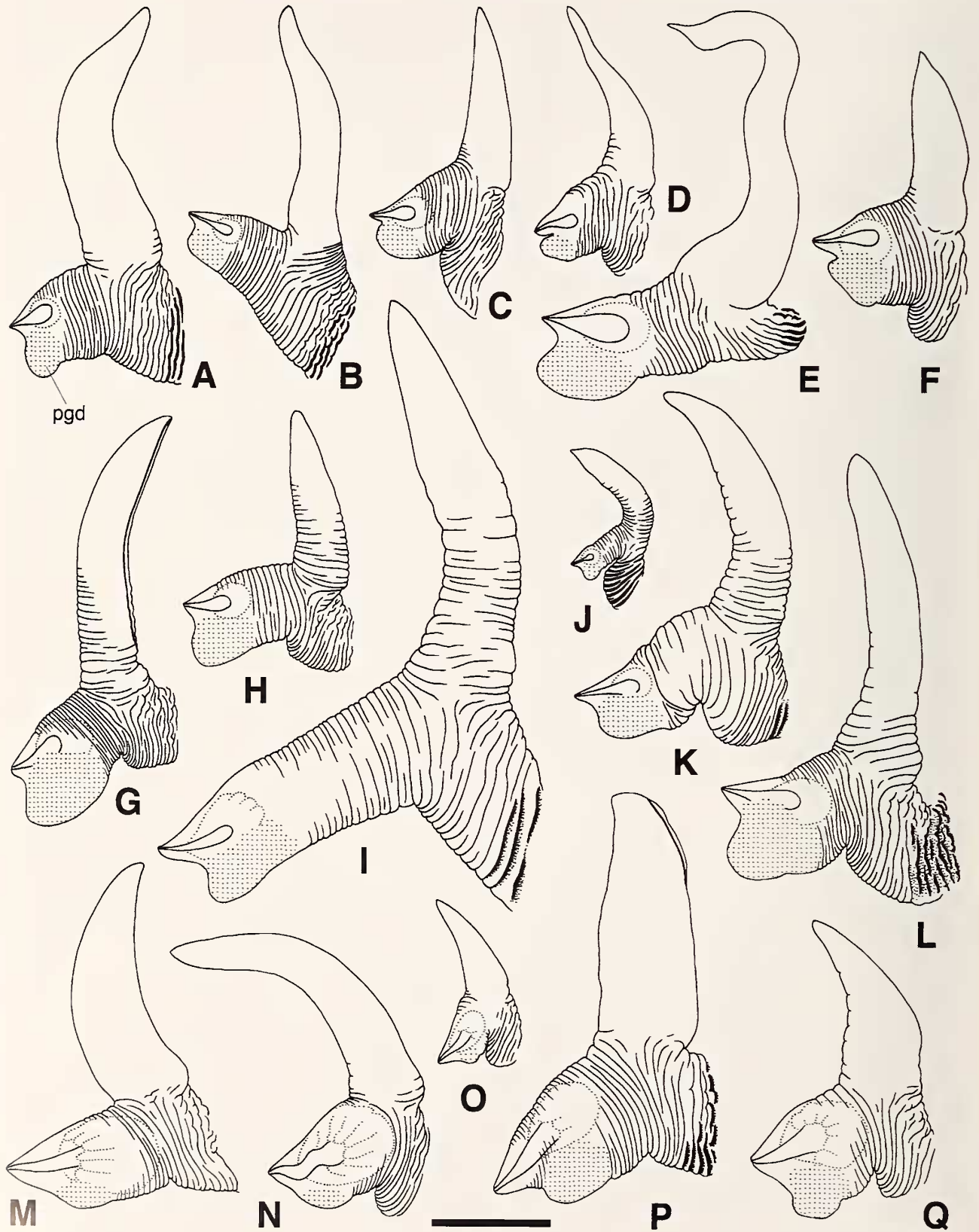
Radula (Figure 9G): Relative radular length 3.6–7.7. Rachidian: length/width 1.38–1.64; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps elongate, rounded at tip. Outer marginal: 6–7 cusps.

Habitat: Common on cliffs on exposed oceanic coasts; in littoral fringe, especially at sites of freshwater seepage; rare on rocks and piers on sheltered or muddy coasts; recorded on volcanic conglomerate, sandstone, mudstone, soil, concrete. Various microsympatric with *N. dubiosa*, *N. apicina*, and *N. paytensis* in different parts of its range, but extends higher up the shore than these.

Range (Figure 17): Nicaragua to northern Peru. Range limits: Corinto, Nicaragua (LACM 149776, 1 specimen); Playa del Coco, Costa Rica (G. J. Vermeij Collection); Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001220); Fort Amador, Panama (USNM 732997, 1 specimen); Isla Gorgona, Colombia (USNM 819732, 3 specimens); Atacames, Esmeraldas, Ecuador (BMNH 20001221); Peninsula Santa Elena, Guayas, Ecuador (Punta Chocolatera, BMNH 20000314; Anconcito, BMNH 20001222); Paita, Piura, Peru (Alamo & Valdivieso, 1987, 1997; as *Littorina aspera*). This species is moderately common in Costa Rica, but much more so in Ecuador. Only a single specimen has been recorded from

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Figure 12. Shells of *Nodilittorina aspera* group (continued): *N. apicina* (A–I), *N. penicillata* (J–Q), and *N. paytensis* (R–BB). A. Same, Ecuador (BMNH 20001236). B. Lectotype of *Littorina philippii* Carpenter, 1857; Mazatlán, Sinaloa, Mexico (BMNH 1857.6.4.1682/1). C, E. Puerto Marques, Acapulco, Guerrero, Mexico (BMNH 20001237). D. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001238). F. Lectotype of *Littorina apicina* Menke, 1851; Mazatlán, Sinaloa, Mexico (SMF 314713/4). G. Boca de Tomatlán, Jalisco, Mexico (BMNH 20001239). H. La Manzanilla, 10 km N of Melaque, Colima, Mexico (BMNH 20001240). I. Atacames, Esmeraldas, Ecuador (BMNH 20001235). J, M, Q. Topolobampo, Sinaloa, Mexico (BMNH 20001247). K. Cabo San Lucas, Baja California Sur, Mexico (BMNH 20001244). L. Lectotype of *Littorina penicillata* Carpenter, 1864; Cabo San Lucas, Baja California Sur, Mexico (USNM 4058). N–P. San Felipe, Baja California Norte, Mexico (BMNH 20001245). R. Punta Carnero, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001256). S–U. Ballenita, Guayas, Ecuador (BMNH 20001257). V. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001252). W. Mancora, Peru (USNM 663988). X. Muisne, Esmeraldas, Ecuador (BMNH 20001258). Y–AA. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001259). BB. Lectotype figure of *Littorina paytensis* Philippi, 1847; Paita, Peru (Philippi, 1847: *Littorina* pl. 3, fig. 25). Scale bar = 5 mm.



Panama despite abundant littorinid collections from the area.

Remarks: This species shows a range of shell variation comparable with that seen in *N. aspera* and *N. apicina*; dwarf specimens are not only smaller but also show weaker sculpture, a striking black and white color pattern, and a slightly convex (domed) profile (Figure 11M). Some large specimens show early whorls of this dwarf form (Figure 11L; note change in spire profile and coloration), suggesting that ecophenotypic plasticity may be responsible. Habitat details for dwarf forms are lacking, but by analogy with these other species it is likely that they are found in unfavorable conditions, such as pools with fluctuating salinity high on the shore. Dwarf forms are presumably produced when growth is slow, whereas rapid growth results in shells that are paler, with concave spire profile and larger adult size.

For much of its range, *N. tenuistriata* is sympatric with *N. dubiosa*, and there is therefore no doubt that these two are distinct (for discrimination, see Remarks on *N. dubiosa*). Their typical habitats differ, *N. tenuistriata* being more frequent on exposed coasts, and *N. dubiosa* on relatively sheltered shores; nevertheless, they can be micro-sympatric on shores of moderate exposure, for example in Costa Rica. Interestingly, this species is very rare in the Gulf of Panama, possibly connected with eutrophic conditions there. This species exhibits an oceanic type of distribution. Curiously, on oceanic coasts it is most abundant at the very top of the shore where there is freshwater seepage from cliffs or hillsides.

Its relationship to *N. aspera*, recorded from Mexico to Nicaragua, is more problematic. The shell shape, size, and color pattern (with a broad peripheral dark band, especially on spire and in dwarf shells) are closely similar. Nevertheless, all shells (including dwarf forms) can be readily separated by their sculpture, which is of finer and more numerous grooves in *N. tenuistriata* (7–10 primary grooves on spire whorls, 10–15 narrow grooves above periphery of last whorl) than in *N. aspera* (5–7 primary grooves on spire whorls, 7–10 wide grooves above periphery of last whorl). Anatomically, there is a small, but apparently consistent, difference in the penis: the filament

of *N. tenuistriata* bears annular wrinkles; it is also less obviously tapering than in *N. aspera* and the basal projection is often longer. The relative radular length is considerably greater in *N. aspera* (but this may be subject to variation according to rate of wear and requires further study). The paraspermatozoa are similar (although since most of the available specimens of *N. aspera* were immature, few sperm cells have been seen). Both species show a preference for exposed oceanic coasts. The similarities suggest a close relationship, and the differences could possibly be explained by geographical variation within a single species. However, a single sample has been seen from Corinto (Nicaragua; LACM 149776) which contains six examples of typical *N. aspera* and one shell tentatively identified as *N. tenuistriata*. This shell is atypical, lacking the dark spiral band and showing a slightly convex profile; nevertheless, the large size (16.7 mm), white ground color, and fine sculpture apparently preclude any other species. The resemblance is closest to some shells of *N. tenuistriata* from the nearest known localities to the south, in Costa Rica (Figure 11O). In any case, this shell (and its sympatric *N. aspera*) gives no suggestion of a merging of the shell characters of the two forms at this point of contact of their ranges. For these reasons, the two are believed to be distinct, although further sympatric records and genetic evidence are desirable to test this conclusion.

A commensal polyclad flatworm was found in the mantle cavity of one specimen (Punta Chocolatera, Guayas, Ecuador; BMNH), as also reported here for *N. modesta*, *N. conspersa*, and *N. apicina*.

Nodilittorina dubiosa (C. B. Adams, 1852)

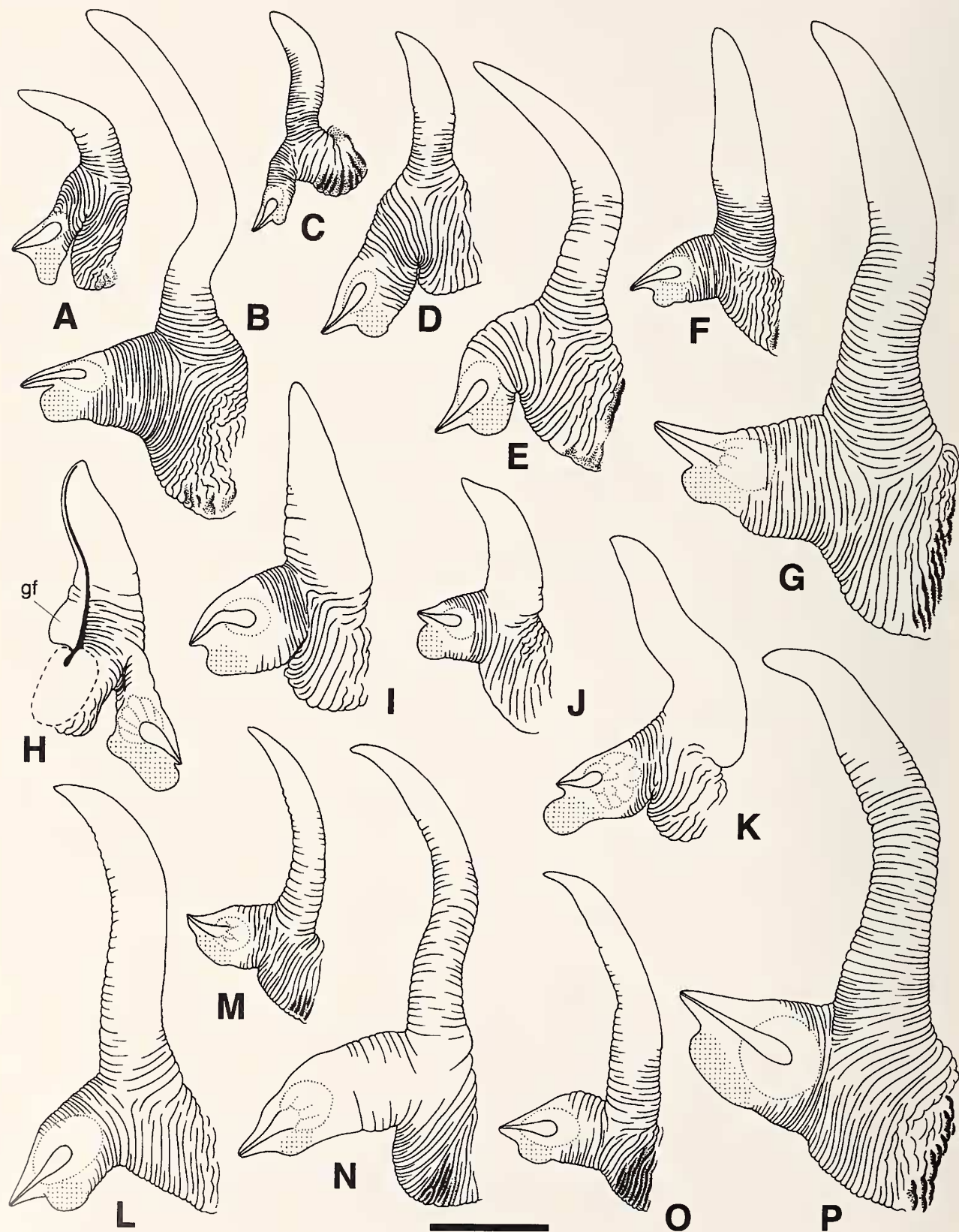
(Figures 9D, 11P–Z, 13M–Q, 15C, I, N, 17)

Littorina aspera—Philippi, 1847:2:200, *Littorina* pl. 4, fig. 13 (in part, includes *N. aspera*). Carpenter, 1857a:230, 326 (in part, includes *N. aspera*). Carpenter, 1864b:623 (in part, includes *N. aspera*). Weinkauff, 1882:60–61, pl. 8, figs. 2, 3 (in part, includes *N. aspera*). Weinkauff, 1883:220 (in part, includes *N. aspera*, *N. apicina*, *N. penicillata*).

Littorina aspera—C. B. Adams, 1852a:394–395 (in part, in-

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Figure 13. Penes of *Nodilittorina aspera* group: *N. aspera* (A–F), *N. tenuistriata* Reid, sp. nov. (G–L), and *N. dubiosa* (M–Q). A, B. Puerto Marques, Acapulco, Guerrero, Mexico (BMNH 20001217; shell H = 10.6 mm, 11.3 mm). C, F. Cabo San Lucas, Baja California Sur, Mexico (BMNH 20001218, shell H = 8.9 mm, 10.2 mm). D, E. Puerto Angel, Oaxaca, Mexico (D, BMNH 20001213; shell H = 11.1 mm; E, BMNH 20001214, shell H = 12.7 mm). G, H. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001223; shell H = 12.9 mm, 10.5 mm). I. Muisne, Esmeraldas, Ecuador (BMNH 20001225; shell H = 11.7 mm). J, L. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20000314; shell H = 5.0 mm, 11.3 mm). K. Atacames, Esmeraldas, Ecuador (BMNH 20001221; shell H = 10.3 mm). M. Tarcoles, Costa Rica (BMNH 20001230; shell H = 10.5 mm). N. Paitilla Beach, Panama City, Panama (USNM 733196; shell H = 9.5 mm). O. Coco, W of Liberia, Costa Rica (BMNH 20001228; shell H = 3.9 mm). P, Q. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001229; shell H = 11.3 mm, 8.6 mm). Abbreviation: pgd, penial glandular disc (stipple). Shading conventions as in Figure 3. Scale bar = 1 mm.



cludes *N. aspera*). C. B. Adams, 1852b:170–171 (in part, includes *N. aspera*). Carpenter, 1857a:186, 273 (not Philippi, 1846). Mörch, 1860:69 (not Philippi, 1846). Carpenter, 1863:352 (in part, includes *N. aspera*). Biolley, 1907:23 (not Philippi, 1846). Morrison, 1946:10 (not Philippi, 1846). Keen, 1958:282, fig. 173 left (in part, includes *N. aspera*). Hertlein, 1963:239 (as *aspersa*; not Philippi, 1846). Keen, 1971:365, fig. 181 (part) (in part, includes *N. aspera*, *N. penicillata*, *N. apicina*, *N. modesta*, *N. interrupta*). Montoya, 1983:332 (in part, includes *N. aspera*).

Littorina (Melarhaphie) aspera—von Martens, 1900:577, 587, ? pl. 43, fig. 16 (in part, includes *N. aspera*, *N. apicina*).

Littorina (Austrolittorina) aspera—Abbott, 1974:69 (in part, includes *N. aspera*, *N. apicina*, *N. penicillata*).

Nodilittorina (Nodilittorina) aspera—Reid, 1989a:99, fig. 11k (egg capsule) (in part, includes *N. aspera*). Kaiser, 1997:27.

Nodilittorina aspera—Finet, 1994:18.

Littorina parvula?—C. B. Adams, 1852a:398–399 (*Littorina parvula* Philippi, 1849, is a *nomen dubium*, see synonymy of *N. apicina*). C. B. Adams, 1852b:174–175.

Littorina dubiosa C. B. Adams, 1852a:398–399, 537 (Taboga [Taboga Island], Panama; lectotype (Turner, 1956: 118, pl. 13, fig. 13) MCZ 186573, seen, Figure 11Z herein; approx. 300 paralectotypes MCZ 139045, seen; 17 paralectotypes BMNH 1865.11.22.33, seen). C. B. Adams, 1852b:174–175, 313.

Littorina ? parvula var. *dubiosa*—Carpenter, 1857a:273.

Littorina aspera dubiosa—Turner, 1956:45–46, pl. 13, fig. 13.

Littorina dubiosa dubiosa—Keen, 1958:282, fig. 175.

Littorina philippii—Carpenter, 1863:352–353 (in part, includes *N. apicina*; not Carpenter, 1857 = *N. apicina*).

Taxonomic history: This species exhibits a range of shell sculpture from smooth to strongly ribbed. The ribbed shells have in the past been invariably identified as *aspera*, a name now restricted to a similar but largely allopatric species occurring mainly in Mexico (see also Taxonomic History of *N. aspera*). The fact that the species was named at all is owing to the rather common occurrence in Central America of a dwarf, smooth form that is superficially very different from larger ribbed shells. These smooth shells have frequently been confused with *N. apiciua* (see Taxonomic History of that

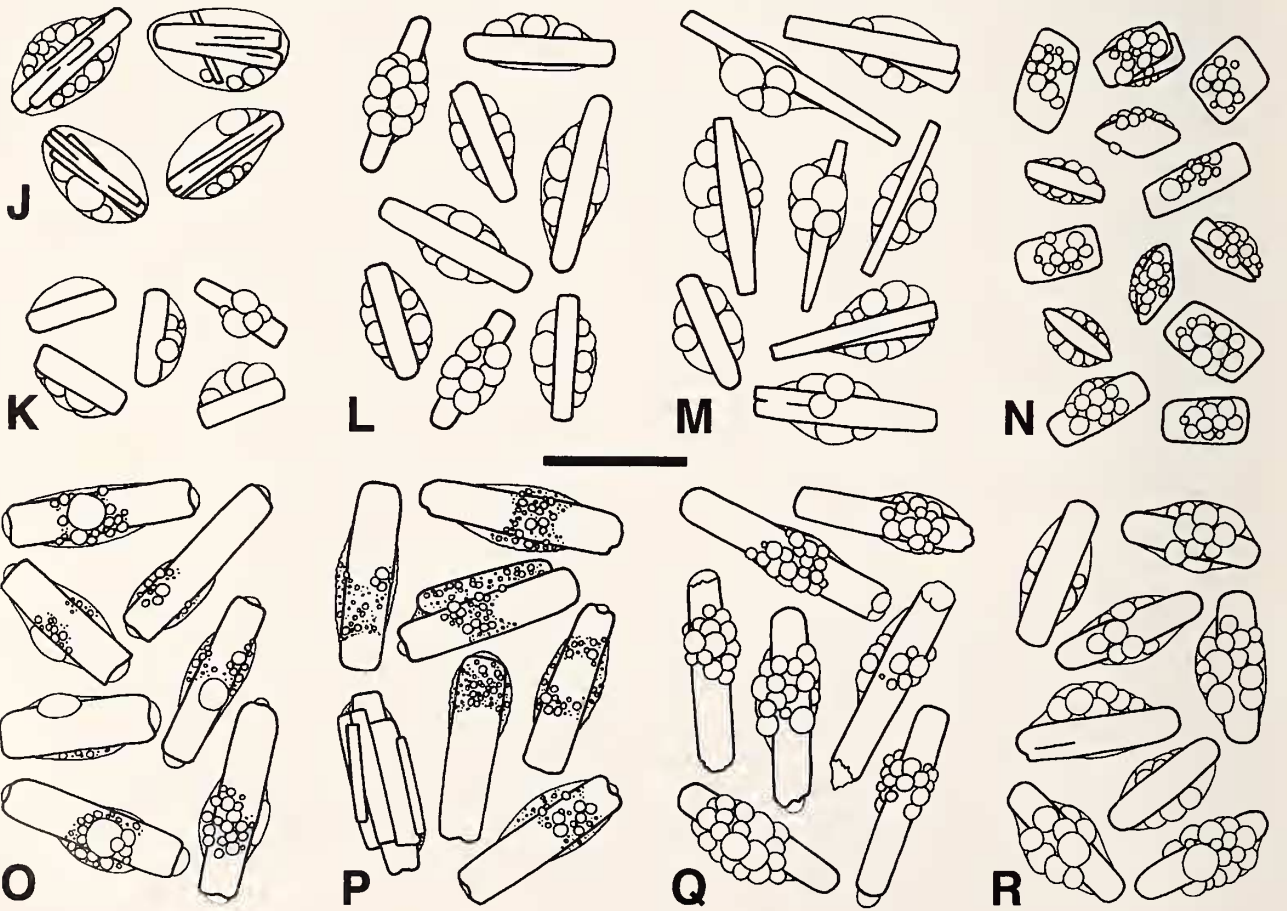
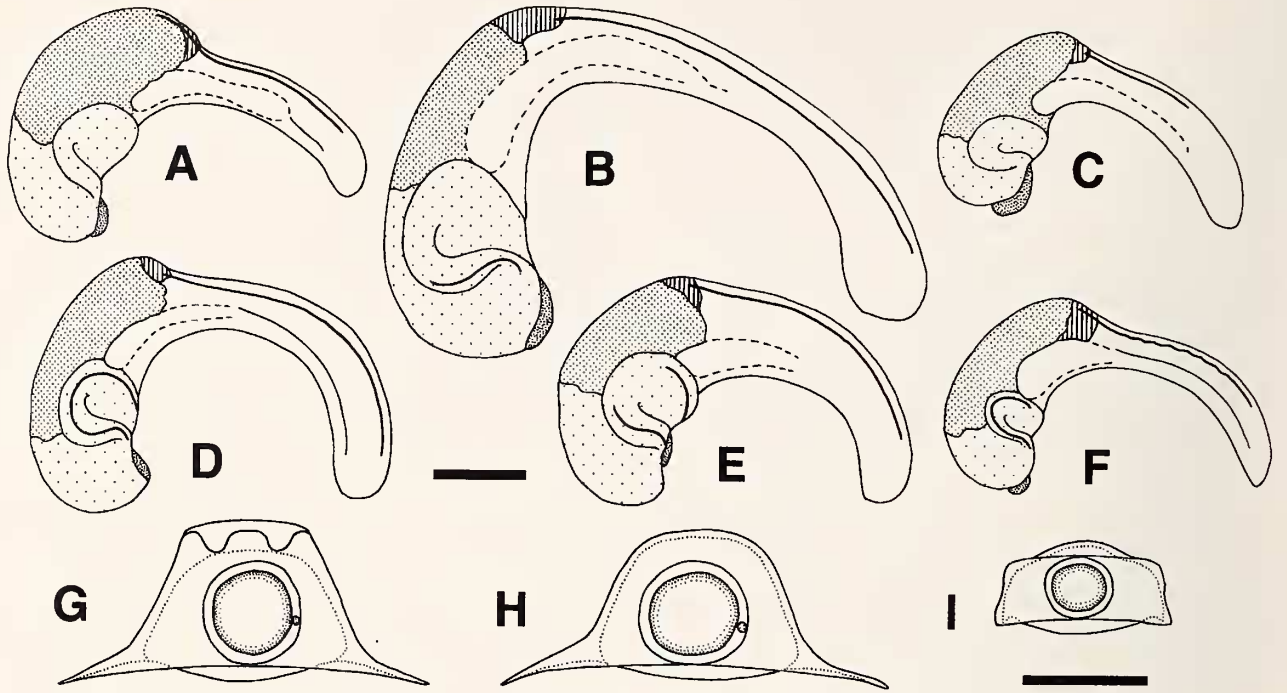
species). In fact, C. B. Adams (1852a) introduced his new species under the heading “*Littorina parvula*?” (here considered a *nomen dubium*, possibly a synonym of *N. apicina*) and prefaced the description with the qualification “If our shell is distinct from Philippi’s species, it may take the name of *L. dubiosa*. . . .” (This conditional proposal does not prevent availability of the name; ICZN, 1999, Art. 11.5.1.) The shells on which he based his new taxon do indeed bear a superficial resemblance to *N. apicina*, but that species is rare in Panama and is not represented among the syntypes of *L. dubiosa*, or in the large collection of littorinids from Panama in the C. B. Adams Collection in the BMNH. Adams himself identified larger shells of *N. dubiosa* from Panama as *Littorina aspera*. Since its description, the name *dubiosa* has been used as valid only twice (Turner, 1956; Keen, 1958).

Diagnosis: Shell large or small, spire whorls slightly rounded, spire profile often slightly concave; 6–8 primary spiral grooves; 7–11 grooves above periphery of last whorl; sculpture of deep grooves up to 2 times rib width on last whorl of large shells, but grooves narrow or faint on small shells; fawn with oblique brown axial stripes and (on spire whorls only) a broad spiral zone of blue-grey just above periphery. Penis with stout, gradually tapering filament; large mamilliform gland (larger than small glandular disc) almost filling short projection of base.

Material examined: 55 lots (including 21 penes, 5 sperm samples, 5 pallial oviducts, 1 spawn sample, 4 radulae).

Shell (Figures 11P–Z): Mature shell height 3.9–19.4 mm. Shape high-turbinata (H/B = 1.32–1.77, SH = 1.57–1.92); spire whorls slightly rounded, suture distinct; spire profile sometimes slightly concave, giving slight onion shape; periphery of last whorl weakly angled. Columella concave, hollowed, and slightly pinched at base; small eroded parietal area. Sculpture of (5) 6–8 primary spiral grooves on spire whorls; ribs subequal, or slightly wider at suture and periphery; 7–11 grooves above periphery of last whorl, secondary sculpture usually absent, but rarely single narrow secondary riblets appear in grooves, in-

Figure 14. Penes of *Nodilittorina aspera* group (continued): *N. apicina* (A–G), *N. penicillata* (H–K), and *N. paytensis* (L–P). A. Bahía Santa María, Cabo San Lucas, Baja California Sur, Mexico (BMNH 20001232; shell H = 7.2 mm). B. Mazatlán, Sinaloa, Mexico (BMNH 20001241; shell H = 9.9 mm). C, D. Playa de los Muertos, Puerto Vallarta, Jalisco, Mexico (BMNH 20001242; shell H = 3.8 mm, 5.6 mm). E. Puerto Marques, Acapulco, Guerrero, Mexico (BMNH 20001237; shell H = 7.8 mm). F. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001243; shell H = 6.0 mm). G. Same, Esmeraldas, Ecuador (BMNH 20001236; shell H = 11.8 mm). H, K. Punta San Felipe, Baja California Norte, Mexico (BMNH 20001250; shell H = 8.2 mm, 7.7 mm). I. Topolobampo, Sinaloa, Mexico (BMNH 20001247; shell H = 10.6 mm). J. Cabo San Lucas, Baja California Sur, Mexico (BMNH 20001244; shell H = 7.6 mm). L. Ballenita, Guayas, Ecuador (BMNH 20001257; shell H = 9.5 mm). M. Anconcito, Guayas, Ecuador (BMNH 20001254; shell H = 5.3 mm). N. Atacames, Esmeraldas, Ecuador (BMNH 20001253; shell H = 10.0 mm). O. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001252; shell H = 8.0 mm). P. Same, Esmeraldas, Ecuador (BMNH 20001260; shell H = 10.9 mm). Abbreviation: gf, glandular flange. Shading conventions as in Figures 3, 13. Scale bar = 1 mm.



creasing number of grooves above periphery to 13–15; development of sculpture is variable; on last whorl of large shells grooves enlarge to 1–2 times width of intervening ribs, which become raised, rounded cords; sometimes only grooves just above and below periphery become enlarged, others remaining as incised lines; in dwarf forms all grooves may be faint, or grooves become obsolete, remaining only near periphery and suture; spiral microstriae absent. Protoconch not seen. Ground color cream to fawn, with narrow oblique brown stripes; typically, on lower half of spire whorls a broad blue-grey background zone (not a discrete dark band) which becomes indistinct on last whorl where (in corresponding region) brown pattern may appear as a fine tessellation; in dwarf and smooth shells ground color is white to cream, with broad blue-grey band just above periphery and a blue-grey line below periphery, usually with oblique or wavy axial stripes superimposed (although these may be faint or absent); aperture brown, external pattern showing through, with 2 pale spiral bands at base and shoulder; columella brown.

Animal: Head black, only rarely an unpigmented stripe across snout, tentacle pale at base and around eye, with two longitudinal black stripes and black spot at tip; sides of foot speckled black. Opercular ratio 0.37–0.41. Penis (Figures 13M–Q): filament moderately long, gradually tapering, smooth, thickened, and glandular, 0.6–0.8 total length; sperm groove open to tip; mamilliform gland larger than glandular disc, often swollen and almost filling the short projection of base; penis unpigmented or only slightly pigmented at base. Euspermatozoa 64 μm ; paraspermatozoa (Figure 15N) with single (rarely double) broad rectangular or trapezoidal rod-pieces, 11–16, μm filling cell, with few large round granules. Pallial oviduct (Figure 15C) with large copulatory bursa opening at half length of straight section and extending back to albumen gland. Spawn (Figure 15I) a simple biconvex capsule 140 μm diameter, with upper ring and slight lower flange, containing single ovum 40 μm diameter.

Radula (Figure 9D): Relative radular length 5.6–7.8.

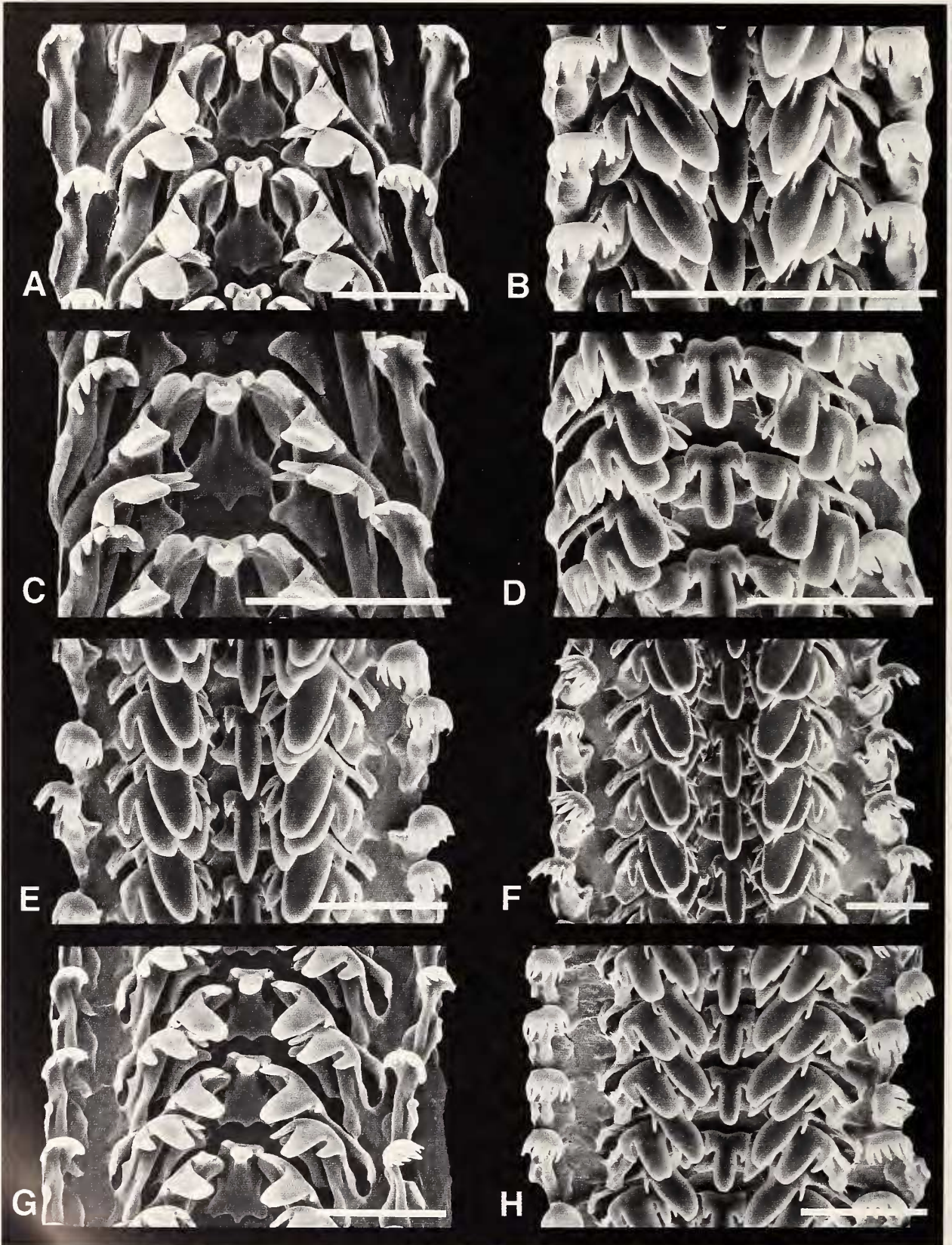
Rachidian: length/width 1.36–1.90; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps elongate, rounded at tip. Outer marginal: 7–9 cusps.

Habitat: Abundant on moderately exposed to sheltered shores; found even in somewhat turbid embayments and close to stream outflows; therefore shows a continental distribution pattern on the mainland. However, the species also occurs on Isla del Coco and there is a single record from the Galápagos. Occurs on rocks (including volcanic conglomerate, tuff, sandstone) in littoral fringe and at top of eulittoral zone. Dwarf specimens found in pools at top of shore. Rare on exposed coasts, where small specimens nestle among barnacles and in crevices. Microsympatric with *N. apicina* on moderately exposed shores, but extends to higher levels. On sheltered shores (particularly in Gulf of Panama) *N. dubiosa* is often the only member of the *N. aspera* group to be found. Ecological studies of “*Littorina aspera*” in Panama by Markel (1971), Garrity & Levings (1981), and Garrity (1984) were based largely on this species, but may have included others in the *N. aspera* complex.

Range (Figure 17): El Salvador (and perhaps Guatemala) to Colombia, Isla del Coco, Galápagos Islands. Range limits: Guatemala (LACM 149773, 1 specimen); Punta Amapala, El Salvador (USNM 780445, 10 specimens); San Juan del Sur, Nicaragua (USNM 23304); Punta San Francisco, Bahía Solano, Colombia (USNM 819739); Ladrilleros, Colombia (USNM 807724); Isla Gorgona and Isla Gorgonilla, Colombia (USNM 819729, 3 specimens); Isla del Coco, Costa Rica (KLK; 2 collections, 15 specimens); Punta Pitt, Isla San Cristobal, Galápagos (BMNH 20001227, 4 specimens). The species is rare in the Galápagos Islands, with only a single verified collection; records in faunal lists from the islands (Schwengel, 1938; Finet, 1985, 1994; Kaiser, 1993, 1997) are based on likely misidentification and on literature records: the two lots in LACM quoted by Finet (1994) are *N. conspersa* and an incorrectly localized sample of a mixture of *N. aspera* and *N. penicillata*. The unlocalized record from Guatemala is at least 150 years old and requires verification.

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Figure 15. Pallial oviducts (A–F), egg capsules (G–I), and paraspermatozoa (J–R) of *Nodilittorina aspera* group: *N. aspera* (A, J, K), *N. tenuistriata* Reid, sp. nov. (B, L, M), *N. dubiosa* (C, I, N), *N. apicina* (D, O, P), *N. penicillata* (E, Q), *N. paytensis* (F–H, R). A. J. Mazatlán, Sinaloa, Mexico (BMNH 20001219; shell H = 11.0 mm). B. Same, Esmeraldas, Ecuador (BMNH 20001226; shell H = 14.2 mm). C. Punta Amapala, El Salvador (USNM 332140; shell H = 10.2 mm). D. Puerto Marques, Acapulco, Guerrero, Mexico (BMNH 20001237; shell H = 11.5 mm). E, Q. Punta San Felipe, Baja California Norte, Mexico (BMNH 20001250; shell H = 10.5 mm). F. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001259; shell H = 10.8 mm). G, H. Ballenita, Guayas, Ecuador (BMNH 20001257). I. N. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 20001229). K. Puerto Marques, Acapulco, Guerrero, Mexico (BMNH 20001217). L. Atacames, Esmeraldas, Ecuador (BMNH 20001221). M. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 2000314). O. Playa de los Muertos, Puerto Vallarta, Jalisco, Mexico (BMNH 20001242). P. Same, Esmeraldas, Ecuador (BMNH 20001236). R. Same, Esmeraldas, Ecuador (BMNH 20001260). Shading conventions as in Figure 4. Scale bars: A–F = 1 mm; G–I = 0.1 mm; J–R = 20 μm .



but would be of interest since it lies in the Central American Gap (see Discussion).

Remarks: This species displays a confusing variation in shell size, coloration, and sculpture. As a result, the small, smooth, or weakly sculptured examples have in the past been classified with *N. apicina*, whereas the large, striped, strongly ribbed shells have been included with *N. aspera*. As in some other eastern Pacific *Nodilittorina* species, this shell variation is correlated with microhabitat, the dwarf forms (Figures 11R, S, Z) occurring in high-level saline pools and on exposed coasts, and the larger shells on more sheltered shores where conditions for growth are presumably more favorable. Unlike *N. aspera* and *N. tenuistriata*, the dwarf forms are not darkly patterned.

On moderately exposed shores (for example in Costa Rica) *N. dubiosa* is frequently sympatric with *N. apicina*, and discrimination between them is sometimes difficult. In the latter, the sculpture is of incised lines only (never wide grooves), the color paler (white ground color, often with a zigzag or finely tessellated pattern), the columella long and straight, and the overall shape more oblique. In contrast, when present, the grooves on the shell of *N. dubiosa* become wide at least near the periphery of the last whorl (or over the whole whorl), the ground color is cream to fawn (usually with a regular lined pattern), and the columella slightly curved. Identification of males can be confirmed by the penis, which in *N. apicina* has a long, wrinkled filament and protruberent glandular disc, and in *N. dubiosa* a smooth, tapering filament and much larger mamilliform gland. The form of the paraspermatozoa also differs.

Larger examples of *N. dubiosa* share with the more northern species, *N. aspera*, the unusual feature of wide grooves (up to twice the width of the intervening raised ribs) on the last whorl, besides a tendency to an onion-shaped profile, and for these reasons the species was at first believed to be simply a southern form of *N. aspera*. However, there is a difference in the penis, the mamilliform gland of *N. dubiosa* being much larger, almost filling the basal projection. Unfortunately, only two samples of sperm were available from *N. aspera*, but in these the long rod-pieces differed from the broader or trapezoidal rod-pieces in five samples from *N. dubiosa*. Close examination of the shells reveals that their color patterns are distinct, *N. aspera* showing coarser axial stripes, white ground color, and a strong dark spiral band above

the periphery of at least the spire whorls, in contrast to the cream or fawn ground color with diffuse peripheral blue-grey band, and finer axial stripes of *N. dubiosa*. The typical habitats of the two are also suggestive, on exposed coasts in *N. aspera*, and mainly on moderately sheltered shores in *N. dubiosa*. For these reasons, the two are here regarded as separate species. Their known distributions overlap slightly, in El Salvador and Nicaragua, but they have not yet been recorded at the same locality in order to confirm that their characters remain distinct. Additional, if indirect, evidence for their separate status is that there is a third species, *N. tenuistriata*, which has been found in sympatry with both *N. aspera* and *N. dubiosa*, and is itself the more likely sister-species of *N. aspera*. *Nodilittorina tenuistriata* is easily separated from *N. dubiosa* by its finer sculpture (7–10 primary spiral grooves on spire whorls, 10–15 narrow grooves above periphery of last whorl), broad dark spiral band above the periphery, and more rounded whorls; it also occurs on more exposed shores than *N. dubiosa*.

Since the typical habitat on relatively sheltered shores and tolerance of turbidity and freshwater influence suggest a continental distribution, the records of *N. dubiosa* on Isla del Coco and the Galápagos are unexpected. The provenance of these specimens is completely reliable. The specimens from Isla del Coco are dry shells, but these are entirely typical (Figure 11W). The four from the Galápagos are elongate and weakly sculptured, with an unusually prominent dark band above the periphery (Figure 11Q); the two dissected specimens were female so that the important characters of the penis were not available. The shape of the columella shows that these are not *N. apicina*, and the weak sculpture and brownish coloration suggest that they are not *N. tenuistriata*. The occurrence of *N. dubiosa* on Isla del Coco and the Galápagos Islands could be related to strong currents that originate in the Gulf of Panama from February to April and flow toward the southwest (Finet, 1991).

Nodilittorina apicina (Menke, 1851)

(Figures 12A–I, 14A–G, 15D, O, P, 16A–D, 17)

? *Littorina parvula* Philippi, 1849:149 (Panama; types lost; *nomen dubium*).

Littorina [*aspera* var.] *apicina* Menke, 1851:164 (Mazatlan [Mexico]; lectotype (here designated, 7.1 × 4.8 mm)

Figure 16. Radulae of *Nodilittorina apicina* (A–D), *N. paytensis* (E), *N. peruviana* (F), and *N. araucana* (G, H). A, B. Playa de los Muertos, Puerto Vallarta, Jalisco, Mexico (BMNH 20001242; flat. shell H = 8.7 mm; at 45°; shell H = 5.0 mm). C, D. Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001243; two views of radula, flat and at 45°; shell H = 7.1 mm). E. Punta Chocolatera, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001259; at 45°; shell H = 9.1 mm). F. Playa la Lisera, Arica, Tarapacá, Chile (BMNH 20001271; at 45°; shell H = 12.1 mm). G, H. Las Cruces, Valparaíso, Chile (BMNH 20001263; two views of radula, flat and at 45°; shell H = 7.8 mm). Scale bars = 50 μm.

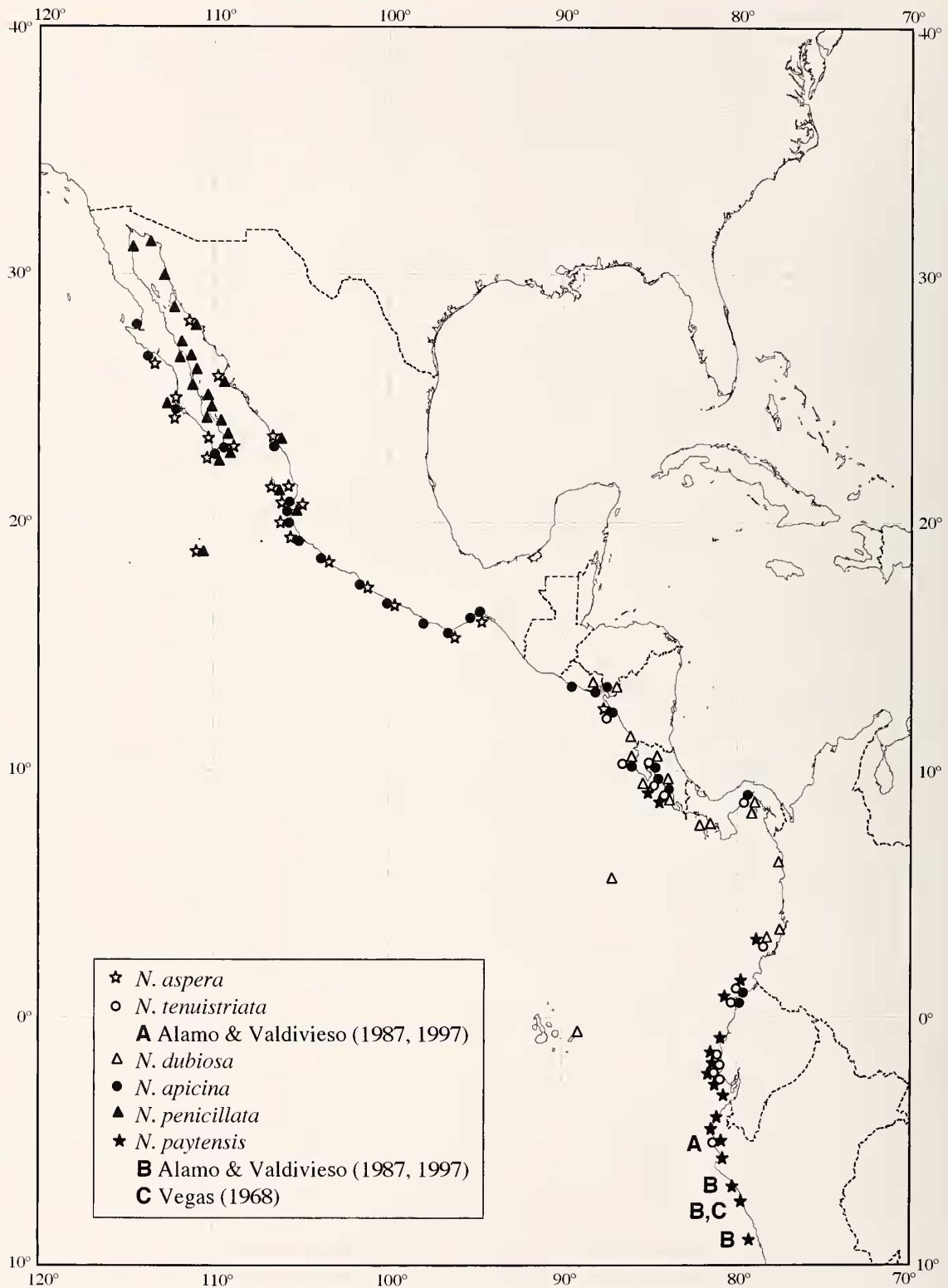


Figure 17. Geographical distribution of species of the *Nodilittorina aspera* group (records based on material examined and quoted literature sources). There are in addition an unlocalized record of *N. aspera* from El Salvador (von Martens, 1900) and another of *N. dubiosa* from Guatemala (LACM 149773).

SMF 314713a, Figure 12F; 3 paralectotypes SMF 314713/3; types seen).

Litorina (Melaraphe) philippii Carpenter, 1857b:349–350 (Mazatlan [Mexico]; lectotype (here designated, 10.9 × 7.3 mm) BMNH 1857.6.4.1682/1, Figure 12B; 109 paralectotypes BMNH 1857.6.4.1671–1685 (100 shells and 9 separate opercula; one shell figured by Keen, 1968, pl. 57, fig. 54; one shell is *N. aspera*); types seen).

Litorina philippii—Carpenter, 1857a:257, 326, 364. Carpenter, 1864b:546, 550, 623 (in part, includes *N. penicillata*, *N. dubiosa*). Weinkauff, 1882:104 (in part, includes *N. penicillata*).

Littorina (Melaraphe) aspera var. *philippii*—Tryon, 1887:249, pl. 44, fig. 84.

Littorina (Melaraphe) philippii—von Martens, 1900:577, 584, pl. 43, fig. 12 (in part, includes *N. dubiosa*, *N. penicillata*, *N. modesta*).

Littorina philippii—Carpenter, 1863:352–353 (in part, includes *N. dubiosa*). Pilsbry & Lowe, 1932:124.

Littorina dubiosa philippii—Keen, 1958:282, 623, fig. 175b. Keen, 1968:410, pl. 57, fig. 54.

Littorina aspera—Weinkauff, 1883:220 (in part, includes *N. aspera*, *N. dubiosa*, *N. penicillata*).

Littorina aspera—Keen, 1971:365, fig. 181 (part) (in part, includes *N. aspera*, *N. penicillata*, *N. dubiosa*, *N. modesta*, *N. interrupta*).

Littorina (Austrolittorina) aspera—Abbott, 1974:69 (in part, includes *N. aspera*, *N. dubiosa*, *N. penicillata*).

Littorina (Melaraphe) philippii var. *subsuturalis* von Martens, 1900:577, 585, pl. 43, fig. 17 (San José, W. Guatemala; five syntypes MNB, seen).

Taxonomic history: *Litorina parvula* was only briefly described, and not figured, by Philippi (1849), and no types have been traced. The color pattern of undulating black lines, impressed spiral lines (7 on last whorl) and small size (7.6 × 4.9 mm) suggest the present species, but do not exclude others that are similar. The material was collected by the author's brother, E. B. Philippi, from "Panama," but he visited both the eastern Pacific Ocean and Caribbean Sea, so the description might even apply to one of the several black and white *Nodilittorina* species of the Caribbean. This is regarded as a *nomen dubium*. The type material of *Litorina apicina*, recently rediscovered in the Bronn collection in SMF, confirms the precise description given by Menke (1851). The name was proposed preliminarily, within his account of *Litorina aspera*. (Translation from the German: "Without separating this form presently as a distinct species, I call it preliminarily *L. apicina*." This is here interpreted as introduction of an infraspecific name and not as publication in synonymy, which would invalidate the name for it has not been used since; ICZN, 1999, Art. 11.6.) Menke (1851) applied the name to small shells (7.6 × 4.8 mm) that he separated from the young of *Litorina aspera* by the more tumid shape, lack of dark spiral band, and evenly spaced ribs separated by narrow grooves; these characters are precisely those that separate this species from *N. aspera*, which is the only other black and white littorinid common at Mazatlán. In the Reigen Collection, Car-

penter (1857b) had a large amount of material also from Mazatlán and he recognized that this species was distinct from *N. aspera* at the same locality. Nevertheless, he rejected Menke's name, arguing that it applied to young *aspera* and was in any case inappropriate for a species which was almost always eroded; on these dubious grounds he introduced *Litorina philippii*. Carpenter's (1857b) species is represented by 101 shells from the Reigen Collection in BMNH, of which only one is *N. aspera*, and a lectotype is here selected. The choice of *apicina* rather than *philippii* as the valid name for this species is in accordance with the principle of priority; although the younger name has been used more frequently in the literature, it has not been used sufficiently often for precedence to be reversed (ICZN, 1999, Art. 23.9) and not at all since 1968. Three of the five syntypes of *L. philippii* var. *subsuturalis* have an unusually dark peripheral band, but the form of the columella and of the spiral sculpture confirms that all belong to *N. apicina* (and not to *N. dubiosa*).

A number of authors (Carpenter, 1857a, b, 1863, 1864b; Weinkauff, 1882; von Martens, 1900; Pilsbry & Lowe, 1932; Keen, 1958) have discriminated a smaller, smooth-shelled species from the larger, more strongly sculptured shells named *aspera*. The names *parvula*, *apicina*, *philippii*, and *dubiosa* have been applied to this smaller species, but the grouping is often not a natural one since most species in the *N. aspera* group can develop a relatively smooth shell. In some geographical areas, a distinction based on sculpture alone does indeed correctly separate sympatric species. Thus, at Mazatlán, the large, ribbed shells are *N. aspera* s.s., while small, smoother ones are *N. apicina* (the only other member of the *N. aspera* group to occur there, *N. penicillata*, is rare), as correctly recognized by both Menke (1851) and Carpenter (1857a, b; as *philippii*). Elsewhere, the smooth-shelled forms include *N. penicillata* and weakly sculptured examples of *N. dubiosa*, which have therefore often been included with the present species (Carpenter, 1863, 1864b; Weinkauff, 1882; von Martens, 1900; Keen, 1958). Weinkauff (1883) first synonymized these smooth species with *aspera*, as also done by Keen (1971) and Abbott (1974), and *N. apicina* has not since been recognized as distinct.

Diagnosis: Shell of moderate size, spire whorls moderately rounded, spire profile distinctly convex; columella long, straight; 5–7 primary spiral grooves; 9–12 grooves above periphery of last whorl; sculpture of incised lines or narrow grooves; white with grey-brown to black oblique or zigzag axial lines; no dark spiral bands, but often an indistinct greyish zone from periphery to shoulder, where pattern tends to form tessellation rather than axial lines. Penis with long, wrinkled filament; mamilliform gland and protruberant glandular disc on projection of base.

Material examined: 56 lots (including 32 penes, 9 sperm samples, 4 pallial oviducts, 6 radulae).

Shell (Figures 12A–I): Mature shell height 2.9–14.9 mm. Shape obliquely high-turbinate to moderately tall ($H/B = 1.33\text{--}1.71$, $SH = 1.31\text{--}1.94$); spire whorls moderately rounded, suture distinct; spire profile usually convex, giving oblique shape; periphery of last whorl weakly angled. Columella long, straight, slightly hollowed, and pinched at base; small eroded parietal area. Sculpture of 5–7 primary spiral grooves on spire whorls; these remain as incised lines, or become wider toward periphery of last whorl (occasionally up to half width of peripheral rib), only rarely become obsolete; grooves number 9–12 above periphery of last whorl, or occasionally up to 15 if some secondary grooves appear; ribs may be subequal, but usually 3–4 posterior ribs are slightly wider, and peripheral rib is slightly larger and raised; spiral microstriae absent. Protoconch not seen. Color white, with variable dark pattern; commonly brown oblique or zigzag axial lines, often forming grey-brown tessellation in greyish zone from periphery halfway to suture; sometimes strong black oblique axial stripes, occasionally anastomosing in peripheral zone to give irregular black band (dwarf shells from exposed localities only); sometimes a fine pallid beige or brown tessellation throughout, darkening to grey in zone from periphery halfway to suture; this indistinct greyish zone with darker pattern is typical, but distinct dark spiral lines or bands are almost always absent (rarely, an anterior spiral band is present on upper spire whorls only); aperture brown, with pattern showing through and 2 pale spiral bands, at base and shoulder; columella brown.

Animal: Head black, sometimes a thin unpigmented stripe across snout, tentacle pale at base and around eye, with two longitudinal black lines, sometimes fusing distally or with black spot at tip; sides of foot grey to black. Opercular ratio 0.31–0.41. Penis (Figures 14A–G): filament long, gradually tapering, rounded at tip, lower half of filament with annular wrinkles and not clearly differentiated from wrinkled penial base, filament about 0.5–0.7 total length; sperm groove open to tip; mamilliform gland and large glandular disc on projection of base, disc protrudes as a lobe; penis unpigmented or only slightly pigmented at base. Euspermatozoa 54–68 μm ; paraspermatozoa (Figures 15O, P) of single, long, stout, parallel-sided rod-pieces, 21–32 μm , often with rounded or pointed terminal caps, attached cytoplasm usually thin, with small indistinct granules, often one large granule (perhaps the nucleus) visible. Pallial oviduct (Figure 15D) with large copulatory bursa opening at three-quarters of the length of straight section and extending back to albumen gland. Spawn not observed.

Radula (Figures 16A–D): Relative radular length 2.8–4.8. Rachidian: length/width 1.42–2.0; major cusp elongate, rounded, or pointed at tip. Lateral and inner marginal: major cusps elongate; rounded, blunt or pointed at tip. Outer marginal: 6–8 cusps.

Habitat: Clustered in crevices and at margins of pools, in upper eulittoral and lower littoral fringe; sometimes among barnacles and mussels in mid-eulittoral zone; exposed and moderately sheltered coasts; recorded on granite, basalt, sandstone, mudstone, and concrete; usually common to abundant. Although for most of its range this species is found only in relatively exposed, oceanic situations, there are no records from offshore islands and it is sometimes found in embayments and lagoons (e.g., Laguna Ojo de Liebre and Ventosa Bay, Mexico; Golfo de Nicoya, Costa Rica). Overlapping with, but zoned slightly below *N. dubiosa* and *N. aspera* in Central America and Mexico, respectively; in Ecuador microsympatric with *N. paytensis*, but below *N. tenuistriata*.

Range (Figure 17): Western Baja California to northern Ecuador. Range limits: Laguna Ojo de Liebre, Baja California Sur (USNM 130598, 2 specimens); Punta Abrejos, Baja California Sur (USNM 862105); Bahía Magdalena, Baja California Sur (USNM 264566); Cabo San Lucas, Baja California Sur (BMNH 20001231); Bahía Santa María, E of Cabo San Lucas, Baja California Sur (BMNH 20001232); Mazatlán, Sinaloa (BMNH 20001233); Bahía Ventosa, Golfo de Tehuantepec, Oaxaca (USNM 60449); Salina Cruz, Oaxaca (LACM 149771); La Libertad, El Salvador (LACM 149774, 30 specimens); Punta Amapala, El Salvador (USNM 780445); Coyolita, Golfo de Fonseca, Honduras (USNM 749642); Corinto, Nicaragua (CAS 122359); Fort Amador, Panama (USNM 732997, 11 specimens); BMNH 20001234, 1 specimen); Atacames, Esmeraldas, Ecuador (BMNH 20001235); Punta Galera, Esmeraldas, Ecuador (USNM 711369). The species is common throughout most of its range, but is rare in the Gulf of Panama (only two records), perhaps connected with eutrophic and largely sheltered conditions there.

Remarks: Shape and sculpture are relatively constant in this species, but it displays some geographical variation in color pattern. In specimens from Mexico, the pattern is usually of dark axial stripes on a white ground, whereas in Central America and Ecuador the coloration is greyish or pallid, with a finer and more diffuse tessellation. In the former group, the most pronounced black and white striped pattern is often found in dwarf shells (Figure 12G) from shallow pools in the upper eulittoral zone; abrupt transitions to a paler and more tessellated pattern can sometimes be seen, suggesting phenotypic plasticity in the expression of coloration. At two localities (Puerto Vallarta, Jalisco; Puerto Quepos, Costa Rica), a commensal flatworm occurs occasionally in the mantle cavity (see Remarks on *N. modesta* group).

This species has the widest geographical range of all

the eastern Pacific *Nodilittorina* species and is the only one found both in central Mexico and south of Costa Rica. Over its range it is sympatric with several other species, and confusion is most likely with *N. aspera* and *N. penicillata* in Mexico, and with *N. dubiosa*, *N. paytensis*, and *N. tenuistriata* in Central and South America. Its most characteristic features are the relatively long and straight columella, the somewhat oblique shape (slightly *Succinea*-like), the relatively narrow grooves (not more than half width of ribs, distinguishing it from the more strongly sculptured examples of *N. aspera* and *N. dubiosa*), and the lack of a strong dark spiral band or line above the periphery (as present in *N. penicillata*, *N. aspera*, *N. tenuistriata* and usually in *N. paytensis*). Similarities of shell, paraspermatozoa, and geographical proximity suggest that its closest relative may be *N. penicillata*.

Nodilittorina penicillata (Carpenter, 1864)

(Figures 9H, 12J–Q, 14H–K, 15E, Q, 17)

Littorina (philippii, var.) penicillata Carpenter, 1864a:477 (Cape St Lucas [Cabo San Lucas, Baja California], Mexico; lectotype (here designated), 8.6 × 5.3 mm) USNM 4058, seen, Palmer, 1963:pl. 61, fig. 7, Figure 12L herein; 2 paralectotypes USNM 678691; 31 paralectotypes USNM 862110 (3 of these are *N. aspera*); 20 paralectotypes MCZ 086976; 1 paralectotype ANSP 212152; 26 paralectotypes BMNH 1865.11.6.70; 19 paralectotypes BMNH 19991559; all paralectotypes seen).

Littorina philippii var. *penicillata*—Weinkauff, 1882:104.

Littorina (Melaraphe) aspera var. *penicillata*—Tryon, 1887: 250, pl. 44, fig. 85.

Littorina (Melaraphe) philippii var. *penicillata*—von Martens, 1900:577, 584–585, pl. 43, fig. 14.

Littorina penicillata—Pilsbry & Lowe, 1932:124.

Littorina dubiosa penicillata—Keen, 1958:282, fig. 175a. Palmer, 1963:334–335, pl. 61, fig. 7.

Littorina (Austrolittorina) penicillata—Rosewater, 1970: 423.

Nodilittorina (Nodilittorina) penicillata—Reid, 1989a:99 (doubtfully included in synonymy of *N. aspera*).

Littorina aspera—Weinkauff, 1883:220 (in part, includes *N. aspera*, *N. dubiosa*, *N. apicina*).

Littorina aspera—Keen, 1971:365, fig. 181 (part) (in part, includes *N. apicina*, *N. aspera*, *N. dubiosa*, *N. modesta*, *N. interrupta*).

Littorina (Austrolittorina) aspera—Abbott, 1974:69 (in part, includes *N. aspera*, *N. dubiosa*, *N. apicina*).

Taxonomic history: This species was first described by Carpenter (1864a) as a variety of *L. philippii* (= *N. apicina*), characterized by its distinctive color pattern. It is represented by a large type series, of which the specimen figured by Palmer (1963) is here selected as the lectotype. Of the 79 known paralectotypes three are *N. aspera*, perhaps included inadvertently. Subsequent authors initially accepted this status as a color variety of a supposed smooth-shelled species named *philippii* or *dubiosa* (Weinkauff, 1882; von Martens, 1900; Keen, 1958; Palmer,

1963). Others synonymized it with *aspera*, which was believed to be a single widely variable species (Weinkauff, 1883; Tryon, 1887; Keen, 1971; Abbott, 1974). However, several authors have listed it as a distinct species; though the evidence has not been discussed, they were presumably impressed by the restriction of the distinctive color form to the Gulf of California and its sympatric occurrence with typical *N. aspera* (Pilsbry & Lowe, 1932; Rosewater, 1970; doubtful status in Reid, 1989a).

Diagnosis: Shell of moderate size, spire whorls moderately rounded; 6–9 primary spiral grooves; 8–11 grooves above periphery of last whorl; sculpture of incised lines only; white with oblique or waved grey to brown axial lines, one spiral dark line above periphery and one below. Penis with broad, pointed filament, thickened at base; mamilliform gland and large glandular disc on projection of base.

Material examined: 57 lots (including 15 penes, 2 sperm samples, 4 pallial oviducts, 4 radulae).

Shell (Figures 12J–Q): Mature shell height 3.9–15.3 mm. Shape moderately tall (H/B = 1.48–1.84, SH = 1.60–2.05); spire whorls moderately rounded, suture distinct; spire profile straight to slightly convex; periphery of last whorl weakly angled. Columella concave, hollowed and pinched at base; no eroded parietal area. Sculpture of 6–9 primary spiral grooves on spire whorls; these remain as incised lines, numbering 8–11 above periphery of last whorl, or occasionally become faint or obsolete on shoulder; rarely (only on largest shells) a secondary groove divides each primary rib; ribs subequal, except peripheral rib which is twice as wide; spiral microstriae absent. Protoconch not seen. Color bluish white, with brown, grey, or black pattern of fine wavy or oblique axial lines; two narrow spiral lines of blue-grey or black, one on third rib above peripheral rib, one in groove immediately below peripheral rib, occasionally other dark lines appear in grooves between these prominent lines, or sometimes spiral lines may become obsolete on last whorl (spiral line above periphery remains visible on spire); aperture dark chestnut brown with 2 pale spiral bands, at base and shoulder, where external pattern shows through; columella blackish brown.

Animal: Head dark grey to black, sometimes a thin unpigmented stripe across snout, tentacle pale at base and around eye, with two longitudinal black lines and black spot at tip; sides of foot grey to black. Opercular ratio 0.41–0.51. Penis (Figures 14H–K): filament broad, pointed at tip, with thickened flange at base on medial side, smooth and clearly differentiated from wrinkled penial base, about 0.6–0.8 total length; sperm groove open to tip; mamilliform gland and large glandular disc on stout projection of base; penis unpigmented. Euspermatozoa 57–64 µm; paraspermatozoa (Figure 15Q) of single, long, stout, parallel-sided rod-pieces, 24–35 µm, with cluster

of large spherical granules attached. Pallial oviduct (Figure 15E) with large copulatory bursa opening halfway along straight section and extending back to albumen gland. Spawn not observed.

Radula (Figure 9H): Relative radular length 3.9–8.5. Rachidian: length/width 1.38–1.67; major cusp elongate, pointed to rounded at tip. Lateral and inner marginal: major cusps elongate, rounded at tip. Outer marginal: 8–9 cusps.

Habitat: Clustered in crevices and at margins of saline pools, in littoral fringe; sheltered and moderately exposed coasts; recorded on granite, conglomerate, basalt, and muddy rocks; usually common to abundant. Sympatric with *N. aspera* and *N. apicina* in southernmost Baja California, but extends to higher levels on the shore.

Range (Figure 17): Gulf of California, southern Baja California, to Mazatlán, Islas Tres Marías, Puerto Vallarta, and Islas Revillagigedo. Range limits: Bahía Magdalena, Baja California Sur (USNM 819877, 3 specimens); Cabo San Lucas, Baja California Sur (BMNH 2001244); Bahía Coyote, Bahía Concepción, Baja California Sur (USNM 558627, 1 specimen); San Felipe, Baja California Norte (BMNH 20001245); Puerto Peñasco, Sonora (USNM 701417); Puerto Libertad, Sonora (USNM 809245, 1 specimen); S end Isla del Tiburón, Sonora (USNM 264910, 6 specimens); San Carlos, 20 km W of Guaymas, Sonora (BMNH 20001246); Topolobampo, Sinaloa (BMNH 20001247); Mazatlán, Sinaloa (BMNH 1857.6.4.1670, 3 specimens; BMNH 20001248, 2 specimens); Isla María Cleofas, Islas Tres Marías (KLK, 1 specimen); Playa de los Muertos, Puerto Vallarta, Jalisco (BMNH 20001249, 1 specimen); Isla Socorro, Islas Revillagigedo (KLK, 2 specimens). This species has a curious distribution, being abundant in most parts of the Gulf of California (from Cabo San Lucas northward, including San Felipe, Guaymas, and Topolobampo), with the apparent exception of the area between Bahía Concepción and San Felipe (this gap is probably real, since the smaller species *N. albicarinata* is well represented by collections from this part of the Gulf). Only nine specimens have been seen from localities south of the Gulf of California, where it is a rare immigrant (von Martens, 1900, noted its rarity at Mazatlán).

Remarks: The shell characters are relatively constant in this species, which is most easily recognized by the pattern of fine “pencilled” axial and two spiral lines. In other species with dark spirals, a wider band is present, occupying the lower half of each spire whorl and a zone just above the periphery on the last whorl. This species most resembles *N. apicina*, and the two can be found commonly together in the vicinity of Cabo San Lucas (southernmost Baja California) and occasionally on the Mexican mainland. They can always be distinguished by color pattern, which in *N. apicina* from these areas is of

strong axial stripes with no spiral lines. These two are likely sister species, as suggested by similarity of shell sculpture, paraspermatozoa, and parapatric geographical distribution.

Nodilittorina paytensis (Philippi, 1847)

(Figures 12R–BB, 14L–P, 15F–H, R, 16E, 17)

Littorina paytensis Philippi, 1847:2:166, *Littorina* pl. 3, fig. 25 (Payta in Peruvia [Paita, Piura, Peru]; types presumed lost; lectotype (here designated) Philippi, 1847: *Littorina* pl. 3, fig. 25, central shell, Figure 12BB herein). Weinkauff, 1882:68, pl. 9, figs. 1, 4. Weinkauff, 1883:218.

Littorina (Melaraphe) paytensis—H. & A. Adams, 1854: 314. Tryon, 1887:250, pl. 45, figs. 90, 91 (in part, includes *N. araucana*).

Littorina paytensis—Vegas, 1968:8. Keen, 1971:366, fig. 184 (possible subspecies of *L. modesta*). Peña, 1971b: 47, pl. 1, fig. 5. Finet, 1985:13 (possible subspecies of *L. modesta*). Finet, 1994:18, 127 (possible synonym of *N. araucana*).

Littorina (Littorinopsis) paytensis—Rosewater, 1970:423. Alamo & Valdivieso, 1987:25, fig. 37. Alamo & Valdivieso, 1997:17, fig. 37. Paredes et al., 1999:22.

Littorina modesta paytensis—Vermeij, 1973:324.

Nodilittorina paytensis—Bandel & Kadolsky, 1982:3.

Nodilittorina (Nodilittorina) paytensis—Reid, 1989a:99 (doubtfully included in synonymy of *N. araucana*).

Littorina araucana—Dall, 1909:231, 285 (in part, includes *N. araucana*). Hertlein & Strong, 1955b:273–274 (in part, includes *N. araucana*).

Taxonomic history: Since it is found mainly in Colombia, Ecuador and northern Peru, where the malacological fauna has been poorly studied, this species has seldom appeared in the literature. With limited availability of specimens, some authors of revisions and lists have maintained it as a distinct species (Weinkauff, 1882, 1883; Rosewater, 1970; Keen, 1971) and in the Peruvian literature it has been correctly identified (Vegas, 1968; Peña, 1971b; Alamo & Valdivieso, 1987, 1997; Paredes et al., 1999). Surprisingly, since its shells are similar to others in the confusing *N. aspera* group, it has never been synonymized with other members. Instead, it has been suggested as a possible southern subspecies of the *N. modesta* group (Keen, 1971; Vermeij, 1973; Finet, 1985), probably on account of the spotted shell pattern. Others have synonymized it with *N. araucana* from Peru and Chile (Tryon, 1887; Dall, 1909; Hertlein & Strong, 1955b; doubtfully by Reid, 1989a, and Finet, 1994).

Diagnosis: Shell moderately large, whorls slightly rounded, spire profile straight; 7–11 primary spiral grooves; sculpture of numerous fine grooves (11–23 above periphery of last whorl), but often obsolete on last whorl; white to cream, with pattern of smudged brown dots and broad spiral grey to black-brown band just above periphery (paler on last whorl). Penis with wrinkled filament taper-

ing to point; large mamilliform gland and small glandular disc borne on projection of base.

Material examined: 51 lots (including 18 penes, 6 sperm samples, 4 pallial oviducts, 1 spawn sample, 5 radulae).

Shell (Figures 12R-AA): Mature shell height 3.2–15.9 mm (to 19.7 mm, Peña, 1971b). Shape high-turbinate to elongate ($H/B = 1.35\text{--}1.87$, $SH = 1.52\text{--}2.11$); spire whorls slightly rounded, suture distinct; spire profile straight; periphery angled, becoming rounded on last whorl. Columella almost straight, slightly hollowed and pinched at base; eroded parietal area. Sculpture of 7–11 primary spiral grooves on spire whorls; primary ribs subequal, or slightly narrower posteriorly (especially if division begins on penultimate whorl); most or all ribs become divided on last whorl, giving 11–23 grooves above periphery, irregularly spaced; grooves remain as incised lines only (rarely enlarging to half width of ribs near periphery) and often become obsolete on shoulder or throughout last whorl; peripheral rib twice as wide as others, but not raised; spiral microstriae absent. Protoconch 0.34 mm diameter, 2.7 whorls. Color very variable; ground color white to cream; usually with broad black-brown spiral band on lower half of spire whorls, becoming blue-grey and diffuse on last whorl; sometimes brown band continues to last whorl, extending to just above or just below periphery, but no separate spiral band present on base; sometimes spiral band is blue-grey and diffuse throughout teleoconch; most shells have pattern of fine smudged brown dots arranged in oblique axial series (occasionally fused to give fine zigzag lines) across whole surface, usually pale on spire and darkening on last whorl; dots sometimes pale or absent; occasionally shells are dark black-brown throughout, with only paler zone at suture and on base, where dots and flames of orange-brown are visible; aperture brown, with 2 pale spiral bands at base and shoulder; columella brown.

Animal: Head grey to black, no unpigmented stripe across snout, tentacle pale around eye and usually at inside of base, with two broad longitudinal black stripes meeting at black tip; sides of foot grey or black speckled. Opercular ratio 0.34–0.39. Penis (Figures 14L–P): filament moderately long, tapering toward pointed tip, with annular wrinkles for most of length, opaque and glandular at base, 0.6–0.8 total length; sperm groove open to tip; glandular disc small, smaller than large mamilliform gland, borne on projection of base; penis unpigmented or only slightly pigmented at base. Euspermatozoa 57–61 μm ; paraspermatozoa (Figure 15R) oval, with single stout rod-pieces with rounded ends, 9–23 μm , projecting from cell, cytoplasm packed with large spherical granules. Pallial oviduct (Figure 15F) with copulatory bursa opening near posterior end of straight section and extending back to albumen gland. Spawn (Figures 15G, H) an asymmetrically biconvex pelagic capsule 300 μm diameter, with

thin projecting circumferential flange, usually a thickened ring on upper side, containing single ovum 84 μm diameter. Protoconch indicates planktotrophic development.

Radula (Figure 16E): Relative radular length 2.9–7.2. Rachidian: length/width 1.33–1.75; major cusp elongate, pointed or rounded at tip. Lateral and inner marginal: major cusps elongate, rounded at tip. Outer marginal: 5–8 cusps.

Habitat: Abundant in uppermost eulittoral and lower littoral fringe, on exposed and semi-sheltered coasts; rare on sheltered muddy shores; recorded on cliffs and outcrops of sandstone, mudstone, concrete, and volcanic conglomerate. Juveniles appear to settle among barnacles. In Ecuador microsymbiotic with *N. apicina* on exposed coasts, but zoned mainly below *N. tenuistriata*. Recorded also on mangroves and driftwood, on sandy beaches with rocks, in northern Peru (Peña, 1971a, b), but specimens from wood are smaller than from rocks, and this is evidently an atypical habitat.

Range (Figure 17): Costa Rica, southern Colombia to northern Peru. Range limits: Tarcoles, 20 km SW of San Mateo, Costa Rica (BMNH 20001251, 2 specimens); Playa de Manuel Antonio, Puerto Quepos, Costa Rica (BMNH 20001252, 30 specimens); Isla Gorgona and Isla Gorgonilla, Colombia (USNM 819737, 1 specimen); Atacames, Esmeraldas, Ecuador (BMNH 20001253); Anconcito, Peninsula Santa Elena, Guayas, Ecuador (BMNH 20001254); Isla Muerta, Golfo de Guayaquil, Ecuador (USNM 819730); Bahía de Sechura, Piura, Peru (BMNH 20001255, 6 specimens). There are in addition three literature records of localities farther south in Peru: Pimentel, Lambayeque (Peña, 1970; Alamo & Valdivieso, 1987, 1997), Pacasmayo, La Libertad (Vegas, 1968; Alamo & Valdivieso, 1987, 1997) and Islas Guañape, La Libertad (Alamo & Valdivieso, 1987, 1997); these may be reliable, but should be treated with caution owing to possible confusion with *N. araucana*. These records to the south of the normal limit of the TEP (3–6°S, see Discussion) might be connected with the expansion of the tropical zone during El Niño events (see Paredes et al., 1998). This species is abundant only in Ecuador and far northern Peru. Farther north there are isolated records only from Isla Gorgona and Costa Rica; nevertheless, at Puerto Quepos it was moderately common, suggesting a possibly self-sustaining population (personal observation). It has not been found in the Gulf of Panama, despite extensive collecting. The species was listed as present in the Galápagos Islands by Finet (1985, 1991), on the basis of two lots in USNM (USNM 819206, 703292, both from Darwin Station, Santa Cruz, total 9 specimens). These are subsamples of a larger lot (17 specimens, G. J. Vermeij Collection), referred to in an ecological paper by Vermeij (1973). All three lots have been examined and the identification confirmed. Nevertheless, this record from the

Galápagos is considered unreliable (as also concluded by Finet, 1994), since considerable collecting effort at this locality and elsewhere has not found the species in the islands. Vermeij also collected on the mainland of Ecuador at about the same time, and confusion of labels may have occurred.

Remarks: Of the other species in the *N. aspera* group, *N. paytensis* most closely resembles *N. apicina* and *N. penicillata* in details of shell sculpture and coloration, penial shape, and paraspermatozoa.

The variation in shell color in *N. paytensis* is more extreme than in other members of the *N. aspera* group. Sometimes both dark brown and grey-white shells can be found together on the shore, and brown juveniles may become pale as adults. Notably, at Punta Carnero on the Peninsula Santa Elena in southern Ecuador all shells were dark brown, or almost black, and of small size (less than 8.5 mm; Figure 12R), whereas from nearby Anconcito, shells of similar size were pale. Furthermore, abrupt color change can occur during the course of growth (Figures 12S, T), so that an ecophenotypic component to the variation seems likely. The shells of *N. paytensis* from Costa Rica are white with a slight grey zone on the spire whorls and only faint grey dots toward the end of the last whorl (Figure 12V), quite distinct from other species found there. Anatomically, the animals from Costa Rica are identical to those from Ecuador.

Although so variable in shell color, the species is nevertheless most readily recognized by the pattern of small brown dots on the last whorl, combined with a broad brown or blue-grey band on the spire, which is seen in most shells. Dots are also seen in sympatric *N. conspersa*, but in that species the ground color of the shell is entirely white, and grooves are much wider and fewer in number, so that no confusion should arise. Of the other sympatric species, confusion is likely with *N. apicina*, although this is less common in Ecuador, which is separated by its pattern of oblique axial stripes, breaking up into fine tessellation over the mid-part of the last whorl, and lack of secondary grooves; shells can, however, be very similar. Identification of males of *N. apicina* can be confirmed by the longer rod-pieces of the paraspermatozoa and the form of the penis, which has a more projecting glandular disc and rounded tip to the filament. The usual black (or grey) and white color of *N. tenuistriata* is generally distinctive, but pale examples might be confused with *N. paytensis*; the shell of *N. tenuistriata* is usually larger and broader than that of *N. paytensis*, with similarly narrow ribs but stronger grooves (which never become obsolete) on the last whorl, and the penial glandular disc is larger. Small shells and juveniles (less than 6 mm) with dark coloration (e.g., Figure 12R) can easily be confused with brown adult *N. santelenae*, with which they can be microsympatric among barnacles. Separation is achieved by the rounded periphery and more patulous shape of *N.*

santelenae, which has fine microstriae and may develop raised ribs, contrasting with the smooth, glossy surface and incised spiral lines of *N. paytensis*.

There has been a history of confusion of *N. paytensis* with the southern *N. araucana*; these two are restricted to the Panamic and Peruvian Provinces respectively, but in the transitional zone they may occur sympatrically (e.g., records of both from Paíta and Pimentel by Peña, 1970). The shell of the latter species is smaller with a more rounded periphery and slightly produced anterior lip; the color pattern is also variable but never shows axial series of dots; most usefully, the interior of the aperture shows a single pale basal band (two in *N. paytensis*) and in addition penial shape is diagnostic.

Remaining *Nodilittorina* Species

The remaining species in the eastern Pacific Ocean (*N. araucana*, *N. peruviana*, *N. galapagensis*, *N. fernandezensis*) form a heterogeneous group. The two southern species, *N. araucana* and *N. peruviana*, share some similarities in their shell shape, sculpture, and color pattern, but anatomical characters differ significantly. The Galápagos endemic, *N. galapagensis*, is the only nodulose species in the region and has a unique penial shape. The last species, *N. fernandezensis*, is endemic to the Islas Juan Fernández and Desventuradas off Chile, and is clearly related to a group of species in the southern Pacific rather than to any others in the eastern Pacific.

Nodilittorina araucana (d'Orbigny, 1840)

(Figures 16G, H, 18A–J, 19A–C, F, H, J, K, 20)

- Littorina araucana* d'Orbigny, 1840:393–394; Atlas (1840) pl. 53, figs. 8–10 (Valparaíso, Chile, also entire coast as far as Arica, Pérou [Valparaíso, Chile, to Arica, Chile]; here restricted to Valparaíso, the locality of the types; lectotype (here designated, 7.0 × 4.7 mm) BMNH 1854.12.4.365/1, seen, Figure 18I; 12 paralectotypes BMNH 1854.12.4.365/2, seen, 1 is probably not this species). Hupé, 1854:138. Reeve, 1857:sp. 88, pl. 16, fig. 88. Dall, 1909:231, 285 (in part, includes *N. paytensis*). Keen, 1971:365.
- Littorina araucana*—Philippi, 1847:2:197, *Littorina* pl. 4, fig. 5. Küster, 1856:17, pl. 2, figs. 21, 22 (1856). Weinkauff, 1878:30 (as *auracana*). Weinkauff, 1883:219. Strebler, 1907:155–156.
- Littorina (Melaraphe) araucana*—H. & A. Adams, 1854:314.
- Littorina (Austrolittorina) araucana*—Rosewater, 1970:423. Dell, 1971:205. Marincovich, 1973:25, figs. 48, 49. Alamo & Valdivieso, 1987:25. Alamo & Valdivieso, 1997:17.
- Nodilittorina (Nodilittorina) araucana*—Reid, 1989a:99 (*N. paytensis* a doubtful synonym). Skoglund, 1992:15 (*N. paytensis* a doubtful synonym).
- Nodilittorina araucana*—Finet, 1994:18, 127 (*N. paytensis* doubtfully included). Reid & Osorio, 2000:123, fig. 7C.
- Littorina thersites* Reeve, 1857:sp. 78, pl. 15, figs. 78a, b (Valparaíso [Chile]; 4 syntypes BMNH 1968317, Figure

18C, seen). Weinkauff, 1882:69, pl. 9, figs. 5, 8. Weinkauff, 1883:219. Dall, 1909:231.

Littorina (Melaraphe) thersites—Tryon, 1887:252, pl. 45, fig. 18 (doubtfully placed in synonymy of *L. (M.) neritoides*).

Littorina (Melaraphe) paytensis—Tryon, 1887:250, pl. 45, figs. 95, 96 (in part, includes *N. paytensis*).

Taxonomic history: The shell of this species is highly variable; d'Orbigny's (1840) species was based on elongate, faintly striated, brown shells, and that of Reeve (1857) on low-spined, grooved, blue-grey shells, although both collections were from Valparaíso. One of the paralectotypes of *L. araucana* is probably not this species; it bears fine oblique axial stripes over the whole whorl width, but is too eroded for certain identification. The name *thersites* has seldom been used; Weinkauff (1882, 1883) and Dall (1909) both accepted it as a distinct species, whereas Tryon (1887) doubtfully placed it in the synonymy of the European *Melaraphe neritoides*. In Peru and Chile *N. araucana* is well known. The only taxonomic confusion has arisen from its superficial similarity to some shells of *N. paytensis*, a species that was doubtfully included in the synonymy of *N. araucana* by Reid (1989a, followed by Finet, 1994); Tryon (1887) disregarded priority and used the name *paytensis* for this species.

Diagnosis: Shell small, whorls rounded, spire profile straight to slightly convex, periphery rounded; slightly produced anterior lip; six to 10 primary spiral grooves; sculpture of numerous fine grooves (up to 29 in total on last whorl), but often obsolete on last whorl; white to dark brown, pale basal band; single pale basal band within brown aperture. Penial filament broad, with subterminal opening of sperm groove; mamilliform gland and small glandular disc borne on projection of base.

Material examined: 52 lots (including 16 penes, 6 sperm samples, 6 pallial oviducts, 2 spawn samples, 4 radulae).

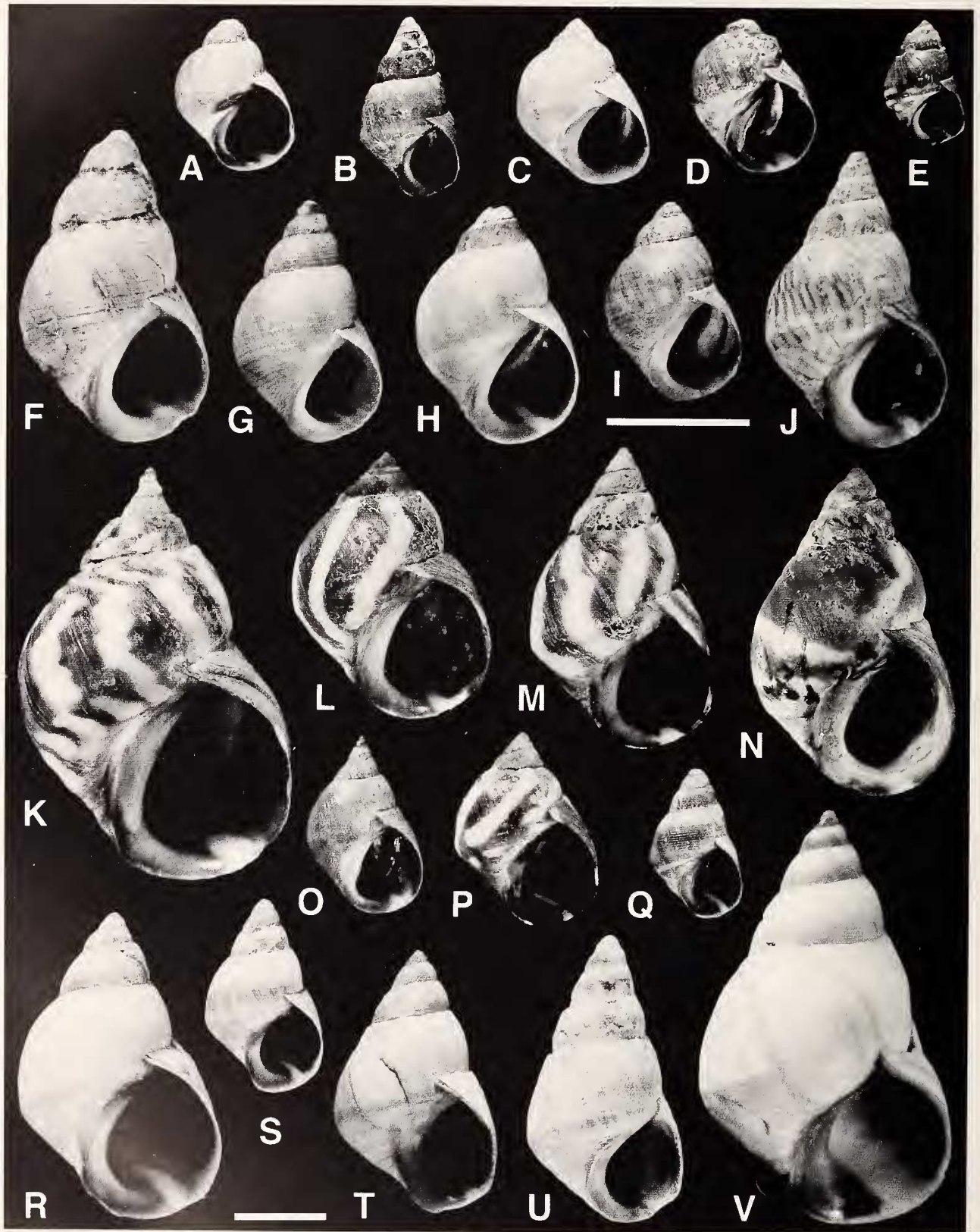
Shell (Figures 18A–J): Mature shell height 1.5–13.8 mm. Shape globular to elongate (H/B = 1.13–1.89, SH = 1.39–2.38); spire whorls rounded, suture distinct; spire profile straight to slightly convex; periphery usually rounded, sometimes angled. Columella concave to straight, slightly hollowed and pinched at base, anterior lip often slightly produced; small eroded parietal area. Sculpture of 6–10 primary spiral grooves on spire whorls, slightly more closely spaced posteriorly; secondary sculpture may start early, on last whorl up to 29 grooves in total (including base), irregularly spaced, grooves usually remain as incised lines, exceptionally equal to width of intervening ribs, peripheral rib may be slightly raised; more frequently sculpture becomes obsolete above periphery on last whorl, or over entire whorl; spiral microstriae absent; spire frequently eroded. Periostracum relatively thick, slightly overhanging apertural edge. Protoconch 0.37 mm diameter, about 3 whorls. Color white

to blue-grey to black-brown; dark brown shells may be paler near suture and on base, with white basal band; definite color pattern usually limited to white basal band, occasionally broken up into spots, and rarely with coarse white marbling over entire base; exceptionally 1–2 white spiral bands above periphery at end of last whorl and 2 below (including normal basal band); axial pattern rarely present, never showing distinct opisthocline oblique stripes, but limited to differentially colored growth lines, or slightly wavy lines along prosocline growth increments; aperture brown, with single pale spiral band at base; columella brown.

Animal: Head and tentacles black, pale only around eye; sides of foot dark grey to black. Opercular ratio 0.38–0.50. Penis (Figures 19A–C): filament broad, glandular at base, sometimes reddish at tip, 0.6–0.7 total penial length; sperm groove appears to end subterminally at about 0.7 filament length (although in fact it continues as a shallow trace to the tip), so that filament abruptly narrows behind tapered tip; glandular disc small, smaller than moderate mamilliform gland, borne on projection of base; penis with black pigment at base. Euspermatozoa 64–71 μm (80–100 μm , Jordan & Ramorino, 1975); paraspermatozoa (Figures 19J, K) oval to fusiform, 16–40 μm (35 μm , Jordan & Ramorino, 1975), packed with spherical granules that become smaller toward one (often pointed) end; no rod-pieces visible. Pallial oviduct (Figure 19H) with slight flexure in path of egg groove through opaque capsule gland, copulatory bursa sometimes very large, opening near posterior end of straight section, extending back almost to albumen gland. Spawn (Figure 19F) an asymmetrically biconvex pelagic capsule, 210–256 μm diameter, with broad vertical peripheral rim, single ring on domed upper surface, containing single ovum 68–84 μm diameter (Jordan & Ramorino, 1975). Development planktotrophic (Jordan & Ramorino, 1975).

Radula (Figures 16G, H): Relative radular length 1.5–3.5. Rachidian: length/width 1.23–1.45; major cusp moderately elongate, rounded at tip. Lateral and inner marginal: major cusps elongate, rounded or blunt at tip. Outer marginal: 7–8 cusps.

Habitat: Throughout most of its range, this species is abundant and characteristic of the bare littoral fringe and uppermost barnacle zone, on both exposed and sheltered rocky coasts (Alveal, 1970, 1971; Romo & Alveal, 1977; Santelices et al., 1977; Ruiz & Giampaoli, 1981). However, at the southern extreme of its range, in the Chilean Archipelago, it has been reported to occur commonly both in the littoral fringe and throughout the eulittoral zone (Dell, 1971; Alveal & Romo, 1977; Brattström, 1990; Reid & Osorio, 2000), among barnacles, tufts of red algae *Hildenbrandia* and *Iridaea*, filamentous green algae, beds of *Mytilus* and *Perumytilus*, and in shallow pools of the upper eulittoral. Most of these southern ob-



servations have been made on sheltered shores, whereas on exposed shores in the region the zonation is apparently more typical, among the uppermost barnacles and *Hildenbrandia* (Reid & Osorio, 2000). The species is often sympatric with *N. peruviana*, with which it may overlap in the upper barnacle zone, but *N. araucana* extends to higher levels in the littoral fringe (Guiler, 1959b; Alveal, 1970, 1971; Santelices et al., 1977; Brattström, 1990). Of these two species, *N. araucana* has been said to be the more common in exposed sites (Romo & Alveal, 1977), but Marinovich (1973) reported that it was absent on the most wave-exposed coasts in the vicinity of Iquique.

Range (Figure 20): Peru and Chile. Range limits: Paita, Piura, Peru (Alamo & Valdivieso, 1987, 1997; in view of possible confusion with *N. paytensis* this record might be doubted); Salaverry, La Libertad, Peru (USNM 667199); Forelius Peninsula, Aisen, Chile (BMNH 20001261). Dall (1909) gave the range as Isla Chiloé to Nicaragua, and this northern limit has been quoted by others (Carcelles & Williamson, 1951; Dell, 1971; Alamo & Valdivieso, 1987, 1997); it is undoubtedly incorrect and may partly be explained by the fact that Dall (1909) included *N. paytensis* in his concept of *araucana*, although even that species is not recorded farther north than Costa Rica.

Remarks: This species covers a range of latitude from at least 8 to 47°S, and therefore extends throughout the Peruvian Province, including the transitional zone with the southern Magellanic Province. Shell form, sculpture, and color are remarkably variable, and indeed Reeve (1857) described the low-spired, striated, blue-grey form as a species distinct from the taller, smoother brown shells originally described by d'Orbigny (1840). Nevertheless, such variation is common among *Nodilittorina* species, as repeatedly shown in those from the eastern Pacific. Furthermore, intergradation between extreme forms is found at most localities, as also noted by Marinovich (1973). It is not known if there are microenvironmental correlates of the shell variation within localities. However, there appears to be a geographical component to color variation. Of the material examined in the present

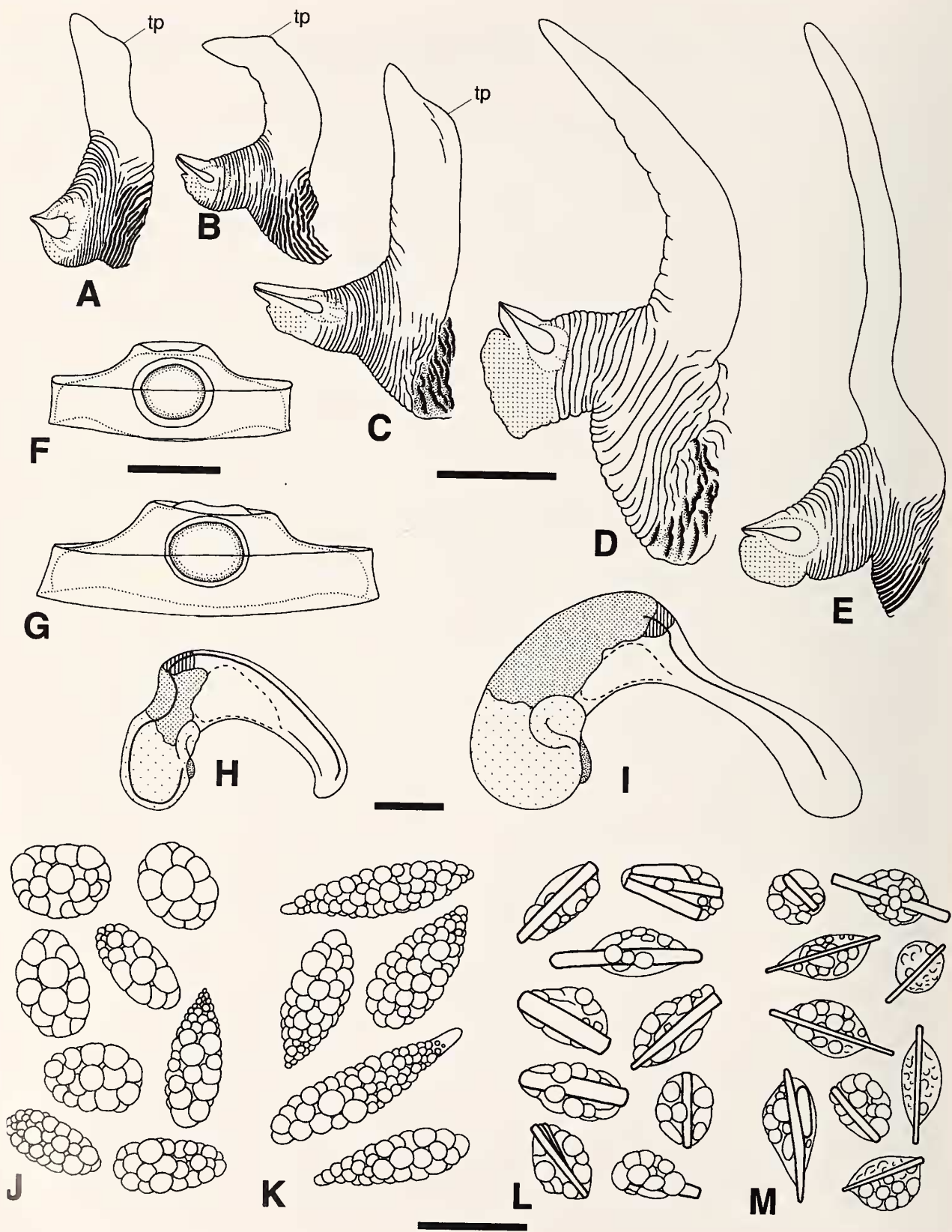
study all 19 collections from south of Valparaíso consisted entirely of brown shells. Only at Valparaíso (33°S) and northward were some blue-grey to white shells found (in 50% of the 26 samples seen), usually mixed with shells of variably brown hue. One possible explanation is that at lower latitudes there is climatic selection in favor of pale shells, which reach lower temperatures in sunlight (see Markel, 1971, for temperature measurements of dark *N. dubiosa* and white *N. conspersa*). Hughes (1979) described a supposedly intraspecific geographical cline from dark brown to blue-grey shells with decreasing latitude along the east coast of South Africa, although it is now known that two distinct species are involved (dark *N. knysnaensis* and pale *N. africana*; unpublished observations). Note that in dry museum collections the brown color of the shell fades to beige.

This species is unlikely to be confused with its frequently sympatric but much larger congener *N. peruviana*, except when the latter is small and lacking its striking zebra pattern (see Remarks on *N. peruviana*). Similarity to *N. paytensis*, with which it is occasionally sympatric in northern Peru, has been discussed in the Remarks on that species.

The relationships of *N. araucana* are unclear. Some features, such as the tendency toward a smooth shell, rather irregular pattern (even if often restricted to the base), shape of the aperture, and form of the spawn resemble the sympatric *N. peruviana*. However, in other respects *N. araucana* does not appear to be closely related to other *Nodilittorina* species from Central and South America. The peculiar subterminal opening of the sperm groove and slight flexure in the capsule gland are unusual, while the form of the paraspermatozoa is, so far as is known, unique in the genus. A similar penial shape is seen in *N. riisei* (Mørch) from the Caribbean and also in *N. unifasciata* from Australia (but the slight flexure of the egg groove in the capsule gland of *N. araucana* does not closely resemble the large loop in this position in members of *Austrolittorina*, see Remarks on *N. fernandezensis*).

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Figure 18. Shells of *Nodilittorina araucana* (A–J), *N. peruviana* (K–P), and *N. fernandezensis* (Q–V). A. Tubul, Bío-Bío, Chile (BMNH 20001262). B. Isla Acuaco, Aisen, Chile (BMNH 19990379). C. Syntype of *Littorina thersites* Reeve, 1857; Valparaíso, Chile (BMNH 1968317). D. Mollendo, Arequipa, Peru (BMNH 1938.7.11.56). E. Las Cruces, Valparaíso, Chile (BMNH 20001263). F, G. Coquimbo, Chile (BMNH 1886.6.9.259, 260). H. Los Vilos, Coquimbo, Chile (BMNH 20001264). I. Lectotype of *Littorina araucana* d'Orbigny, 1840; Valparaíso, Chile (BMNH 1854.12.4.365/1). J. Taltal, Antofagasta, Chile (USNM 713998). K. Valparaíso, Chile (BMNH 20001267). L. Locality unknown (BMNH 20001268). M. Locality unknown (BMNH 20001269). N. Lectotype of *Phasianella peruviana* Lamarck, 1822; Callao, Lima, Peru (MHNG 1096/86-1). O. Salaverry, La Libertad, Peru (USNM 667199). P. Las Cruces, Valparaíso, Chile (BMNH 20001270). Q. Isla Alejandro Selkirk, Archipiélago de Juan Fernández (BMNH 20001278). R, S. Punta San Carlos, Isla Robinson Crusoe (Más a Tierra), Archipiélago de Juan Fernández (BMNH 20001279). T. Holotype of *Littorina unifasciata fernandezensis* Rosewater, 1970; Bahía Cumberland, Isla Más a Tierra, Archipiélago de Juan Fernández (USNM 368900). U. Locality unknown (BMNH 1914.5.8.6). V. Isla San Felix, Islas Desventuradas (BMNH 20001280). Scale bars A–J = 5 mm; K–V = 5 mm.



Nodilittorina peruviana (Lamarck, 1822)

(Figures 16F, 18K–P, 19D, E, G, I, L, M, 20)

Phasianella peruviana Lamarck, 1822:53 (les côtes de Pérou, près de Callao [Callao, Peru]; lectotype (here designated) MHNG 1096/86-1, 16.7 × 11 mm, Figure 18N; 1 paralectotype MHNG 1096/86-2; 1 lost paralectotype figured by Delessert, 1841:pl. 37, fig. 9a, b). Delessert, 1841:pl. 37, fig. 9a, b. Deshayes & Milne Edwards, 1843:243.

Littorina peruviana—Gray, 1839:138, pl. 36, fig. 8 (includes *Littorina striata* King & Broderip, 1832 in synonymy). d'Orbigny, 1840:393, pl. 53, figs. 5–7. Hupé, 1854:137–138. Stearns, 1893b:444. Dall, 1909:172–173, 231, 285, pl. 23, fig. 7. Vegas, 1968:7–8. Keen, 1971:366, fig. 185. Finet, 1985:9, 13.

Littorina (Melaraphe) peruviana—H. & A. Adams, 1854:314. Tryon, 1887:249, pl. 44, fig. 78.

Littorina peruviana—Weinkauff, 1883:221.

Littorina (Austrolittorina) peruviana—Rosewater, 1970:423. Marincovich, 1973:26, fig. 50. Basly, 1983:18, pl. 4, fig. 34. Alamo & Valdivieso, 1987:25, fig. 36. Alamo & Valdivieso, 1997:17, fig. 36.

Nodilittorina peruviana—Bandel & Kadolsky, 1982:14. Finet, 1994:18.

Nodilittorina (Echinolittorina) peruviana—Reid, 1989a:99. Skoglund, 1992:15. Kaiser, 1997:27.

Turbo zebra Wood, 1828:20, pl. 6, *Turbo* fig. 33 (S. America; restricted to Arica, Chile, the locality of the syntypes; 18 syntypes, BMNH 1968367, seen).

Littorina zebra—Philippi, 1847:2:165, *Littorina* pl. 3, fig. 16. Küster, 1856:18–19, pl. 2, figs. 25–27 (1853). Weinkauff, 1878:31.

Littorina zebra—Reeve, 1857:sp. 61, pl. 12, fig. 61a, b. Troschel, 1858:134, pl. 11, fig. 2 (radula).

Littorina zebra var. *nana* Nevill, 1885:140 (Valparaíso [Chile]; *nomen nudum*).

Taxonomic history: This well known species is sufficiently distinctive that it has not been confused with any other. In the early literature the junior synonym *zebra* was commonly employed by German and English authors (an exception was Gray, 1839), but following the revisions of Weinkauff (1883) and Tryon (1887) the earlier *peruviana* prevailed.

Diagnosis: Shell large, whorls rounded, spire profile concave near apex, periphery rounded; slightly produced anterior lip; spiral sculpture usually absent; white with few broad irregular waved axial black stripes; single pale basal

band within brown aperture. Penial filament long; mamilliform gland and large glandular disc borne on projection of base.

Material examined: 63 lots (including 11 penes, 5 sperm samples, 4 pallial oviducts, 4 radulae).

Shell (Figures 18K–P): Mature shell height 6.0 mm (Jordan & Ramorino, 1975)–23.8 mm. Shape high turbinate (H/B = 1.31–1.88, SH = 1.46–1.93); spire whorls rounded, suture distinct; spire profile concave near apex, but often eroded; periphery rounded, or only slightly angled in some juveniles. Columella long, concave to straight, slightly hollowed and pinched at base, anterior lip often slightly produced; no eroded parietal area. Spiral sculpture usually absent, even on early whorls; sometimes 1–4 (rarely 6–8) faint incised lines above periphery; occasionally a slightly enlarged rib forms an angle at periphery; spiral microstriae absent. Periostracum relatively thick, sometimes slightly overhanging apertural edge. Protoconch not seen. Color white with dark brown or black broad, waved or irregular axial stripes; sometimes entirely black or with only an interrupted white basal band; aperture purplish black, with single pale spiral band at base; columella brown to black.

Animal: Head and tentacles black, pale around eye and sometimes at inside of tentacle base; sides of foot dark grey to black. Opercular ratio 0.36–0.43. Penis (Figures 19D, E): filament long when fully relaxed, 0.7–0.8 total length, sperm groove open to tip; glandular disc large, often projecting, borne with mamilliform gland on projection of base; penis unpigmented or slightly pigmented at base. Euspermatozoa 57–64 μm (65–80 μm , Jordan & Ramorino, 1975); paraspermatozoa (Figures 19L, M) oval, 11–18 μm (25 μm , Jordan & Ramorino, 1975), filled with large round granules, often an apparent nucleus visible, rod-pieces variable within individuals, single or multiple, short and rectangular or long slender and projecting, up to 28 μm long. Pallial oviduct (Figure 19I) with copulatory bursa opening near posterior end of straight section and extending back to albumen gland. Spawn (Figure 19G) an asymmetrically biconvex pelagic capsule, 336–421 μm diameter, with broad and slightly oblique peripheral rim, 1–2 rings on domed upper surface, containing single ovum 84–89 μm diameter (Jordan

Figure 19. Penes (A–E), egg capsules (F, G), pallial oviducts (H, I), and paraspermatozoa (J–M) of *Nodilittorina araucana* (A–C, F, H, J, K) and *N. peruviana* (D, E, G, I, L, M). A. Isla Acuaco, Aisen, Chile (BMNH 19990379; shell H = 7.2 mm). B, C, H, J. Las Cruces, Valparaíso, Chile (BMNH 20001263; shell H = 7.0 mm, 6.7 mm, 8.2 mm). D. Playa La Lisera, Arica, Tarapacá, Chile (BMNH 20001271; shell H = 11.9 mm). E, I. Caleta Catarindo, Arequipa, Peru (BMNH 20001272; shell H = 11.9 mm, 13.0 mm). F. Montemar, Valparaíso, Chile (after Jordan & Ramorino, 1975). G. Montemar, Valparaíso, Chile (after Jordan & Ramorino, 1975). K. Concepción, Bío-Bío, Chile (BMNH 20001265). L, M. Las Cruces, Valparaíso, Chile (BMNH 20001270). Abbreviation: tp, termination of deep part of penial sperm groove (continues as a shallow trace to tip). Shading conventions as in Figures 3, 4, 13. Scale bars: A–E = 1 mm; F, G = 0.1 mm; H, I = 1 mm; J–M = 20 μm .

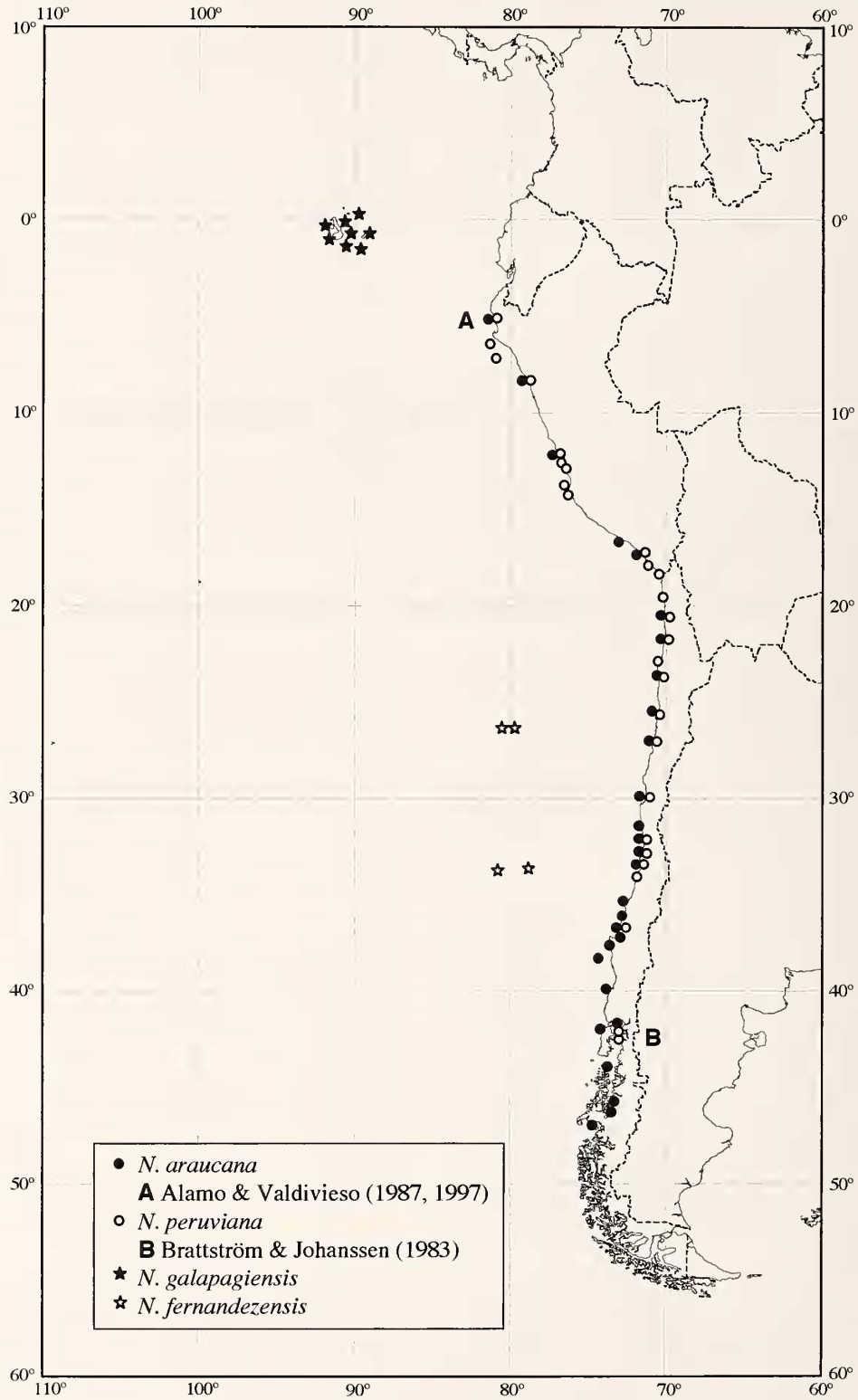


Figure 20. Geographical distribution of *Nodilittorina araucana*, *N. peruviana*, *N. galapagensis*, and *N. fernandezensis* (records based on material examined and quoted literature sources).

& Ramorino, 1975). Development planktotrophic (Jordan & Ramorino, 1975).

Radula (Figure 16F): Relative radular length 2.8–3.4. Rachidian: length/width 1.34–1.41; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps elongate, rounded at tip. Outer marginal: 7–10 cusps.

Habitat: Abundant on rocky coasts, both exposed and sheltered, but favoring strong wave-exposure; typically in upper part of barnacle zone, extending into littoral fringe in areas with heavy spray; also among *Perumytilus*; often sympatric with *N. araucana*, but zoned slightly below that species (Guiler, 1959a, b; Vegas, 1963; Alveal, 1970, 1971; Marinovich, 1973; Paredes, 1974; Romo & Alveal, 1977; Santelices et al., 1977; Brattström, 1990). The algal diet has been studied by Santelices & Ugarte (1987).

Range (Figure 20): Peru and Chile. Range limits: Paita, Piura, Peru (USNM 6029, 2 specimens; Stearns, 1891; Vegas, 1963; Peña, 1970; Alamo & Valdivieso, 1987, 1997); Isla Lobos de Tierra, Piura, Peru (USNM 538007, 4 specimens; Alamo & Valdivieso, 1987, 1997); Isla Lobos de Afuera, Lambayeque, Peru (USNM 753012, 4 specimens); Navidad, Santiago, Chile (ZMA); Río Bío-Bío, Concepción, Chile (BMNH 20001266, 1 specimen); Isla Chiloé, Chile (USNM 348499, 2 specimens); Golfo de Ancud, 41°49'S, Chile (Brattström & Johanssen, 1983). Records include islands such as Isla Lobos de Afuera (60 km from the mainland). This species appears to be scarce south of the Santiago Region, from which only three museum specimens have been seen, whereas *N. araucana* is relatively frequently represented from the same area. Brattström (1990) observed that it was uncommon in Seno Reloncaví (southern Chile). The northernmost record from Paita is based on an old sample in USNM, but the locality is confirmed by the authors quoted above. This locality is close to the northern limit of the influence of the cold Peru Current (see Discussion). Two old collections from the Galápagos Islands (USNM 60661; USNM 132798) are apparently the basis for the records by Stearns (1893b) and Dall (1909) that have been quoted by subsequent authors (Keen, 1971; Finet, 1985; Alamo & Valdivieso, 1987, 1997). Finet (1994) doubted the provenance of the specimens, yet curiously accepted the literature records based on them. He therefore counted the species as one of only three "purely Peruvian" members of the Galápagos fauna (Finet, 1991, 1994). Occurrence in the Galápagos has not been verified by any recent records, despite considerable collecting effort, and is here regarded as unlikely. Dall (1909) also mentions the species from Nicaragua and Panama, where it certainly does not occur.

Remarks: The large size and strikingly colored, smooth shell of this species are so distinctive that confusion of typical specimens with any other species is not likely. Juveniles can be confused with the smaller sympatric *N.*

araucana if they have entirely black shells; such shells are recognized by the delicate apertural edge (indicating that they are juvenile) and their distinctively concave spire profile.

The possible relationships of this species are unclear. While the shell shows some similarity to that of *N. araucana* in its frequently smooth surface, apertural shape, and irregular pattern, and in egg capsule morphology, the anatomical differences in paraspermatozoa and penial shape are likely to be more significant. *Nodilittorina peruviana* is similar to the members of the *N. aspera* group in the form of the penis, oviduct, and paraspermatozoa, but these are all of types common throughout the genus and so do not necessarily indicate close relationship.

Nodilittorina galapagensis (Stearns, 1892)

(Figures 7L–Q, 20, 21A–F, K, M, N, 22A, B)

Hamus lemniscatus—Wimmer, 1880:32 (not *Littorina lemniscata* Philippi, 1846 = *N. miliaris* (Quoy & Gaimard, 1833)).

Tectarius lemniscatus—Stearns, 1893b:397, 444 (not Philippi, 1846).

Hamus trochoides—Wimmer, 1880:32–33 (not *Littorina trochoides* Gray, 1839 = *N. trochoides*).

Tectarius trochoides—Stearns, 1893b:397, 444 (not Gray, 1839).

Littorina (*Tectarius*) *galapagensis* Stearns, 1892:87–88 (James Island [Isla Santiago, Galápagos]; holotype USNM 102509, Stearns, 1892:pl. 51, fig. 7, Figure 7L herein, seen). Stearns, 1893b:396–397, pl. 51, fig. 7.

Tectarius galapagensis—Pilsbry & Vanatta, 1902:553. Dall, 1909:232. Hertlein & Strong, 1939:371. Hertlein & Strong, 1955a:137.

Nodilittorina (*Nodilittorina*) *galapagensis*—Rosewater, 1970:424. Reid, 1989a:99. Skoglund, 1992:15. Kaiser, 1993:106. Kaiser, 1997:27.

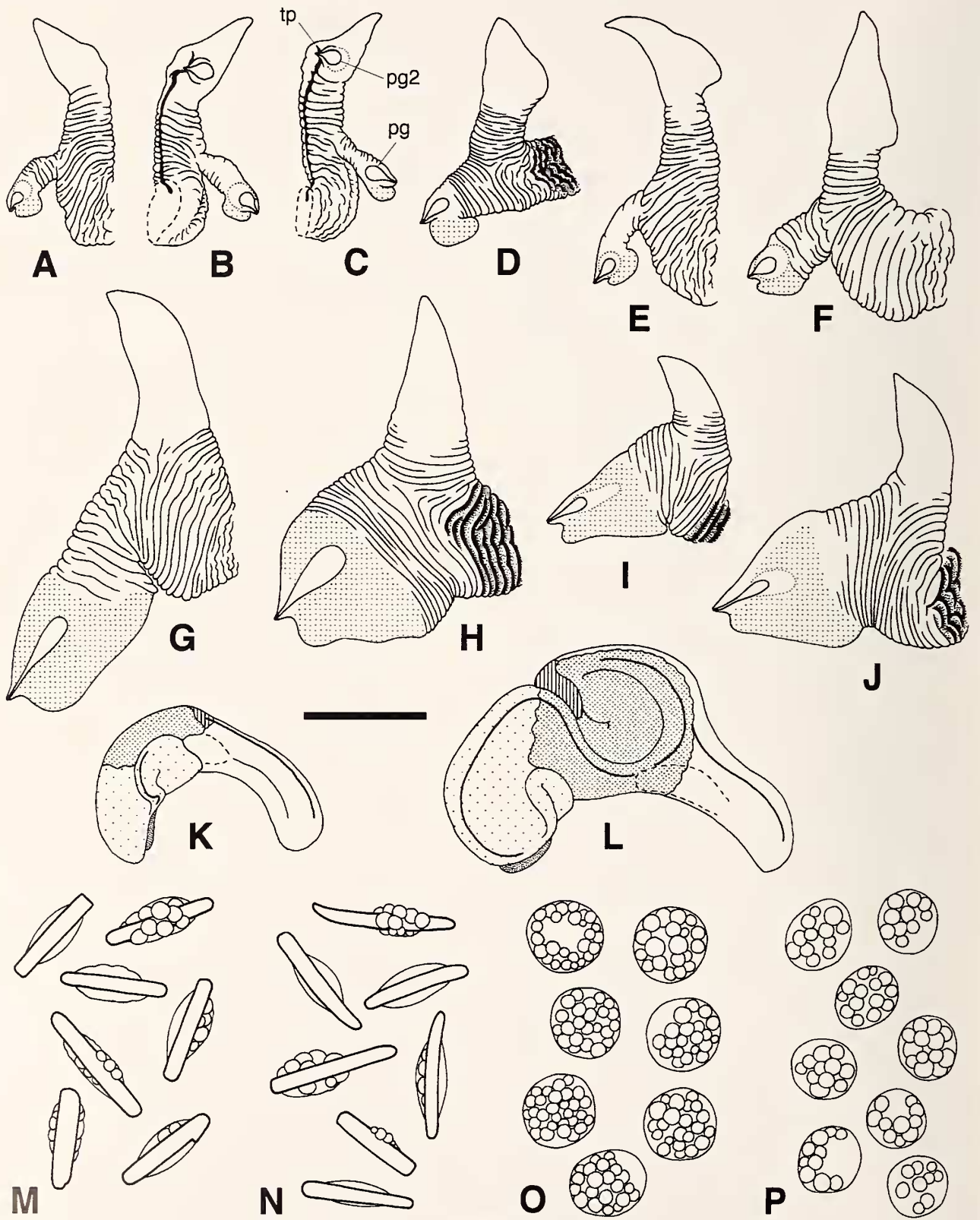
Nodilittorina galapagensis—Keen, 1971:367, fig. 190. Hertz, 1977:29, fig. Taviani, 1979:14, figs. 10A, B, 11. Finet, 1985:13. Finet, 1994:18.

Tectarius atyphus Stearns, 1891:326 (*nomen nudum*).

Littorina (*Tectarius*) *atyphus* Stearns, 1892:88–89 (Manta, Ecuador; holotype USNM 48396, seen).

Tectarius atyphus—Stearns, 1893a:350, pl. 50, fig. 5.

Taxonomic history: This nodulose shell was confused with similar forms from the Atlantic and West Pacific by Wimmer (1880; quoted by Stearns, 1893b). It is surprising that Stearns (1892) should have described this species twice, as *galapagensis* and *atyphus*, in the same publication. However, he possessed only single specimens of each, and the latter was a more elongate, less nodulose beachworn shell, said to have originated from Manta on the mainland of Ecuador. Only Stearns (1891, 1892, 1893a) employed the name *atyphus*; subsequent authors (following Pilsbry & Vanatta, 1902, as first revisers) have recognized its synonymy with *N. galapagensis*. Like other members of *Nodilittorina* with nodulose sculpture, this has in the past sometimes been placed in the genus *Tectarius* (= *Hamus*; see Rosewater, 1972; Reid, 1989a).



Diagnosis: Shell small; sculpture of nodulose or granulose cords; dark brown to black with white band on base, nodules whitish, especially on base. Penial filament with hooked tip, subterminal opening of sperm groove; small mamilliform gland and small glandular disc borne on narrow projection of base; a second mamilliform gland on medial side of filament, behind tip.

Material examined: 33 lots (including 12 penes, 3 sperm samples, 4 pallial oviducts, 4 radulae).

Shell (Figures 7L–Q): Mature shell height 3.5–13.1 mm. Shape turbinate to high turbinate ($H/B = 1.23\text{--}1.79$, $SH = 1.58\text{--}2.19$); spire whorls usually rounded, suture distinct, sometimes flattened and with indistinct suture; spire profile straight; periphery rounded or angled, marked by nodulose rib. Columella short, concave, hollowed, and slightly pinched at base, anterior columellar lip slightly flared; small eroded parietal area. Sculpture of 3 spiral rows of nodules (at periphery, shoulder and, smaller, near suture); base with 2–5 nodulose or granulose cords; nodules usually large, but may be reduced in size to give granulose rather than nodulose appearance to shell, occasionally reduced to mere undulations on fine spiral riblets numbering about 20 on last whorl; entire surface covered with fine spiral microstriae grading into riblets. Protoconch 0.26 mm diameter, 2.8 whorls. Color dark brown to black, nodules often paler brown or, on base, whitish; spiral cream band on base and often a pale line on shoulder, sometimes also at suture; aperture dark brown, pale spiral band at base; columella purplish brown.

Animal: Head black; tentacle with 2 broad black longitudinal stripes, pale around eye, at tip and at inside of tentacle base; sides of foot black. Opercular ratio 0.44–0.60. Penis (Figures 21A–F): filament wrinkled at base, about 0.5–0.6 total length, dilated distally with hooklike tip, opening of sperm groove subterminal on raised projection; small glandular disc and small mamilliform gland on narrow projection of base; second mamilliform gland on medial surface of distal part of filament, surrounded by glandular subepithelial tissue; penis unpigmented. Euspermatozoa 39–43 μm ; paraspermatozoa (Figures 21M, N) oval with single long straight (or slightly curved) blunt projecting rod-pieces, 16–25 μm , cyto-

plasm filled with large round granules. Pallial oviduct (Figure 21K) with copulatory bursa opening near posterior end of straight section and extending back to albumen gland. Spawn not observed. Protoconch indicates planktotrophic development.

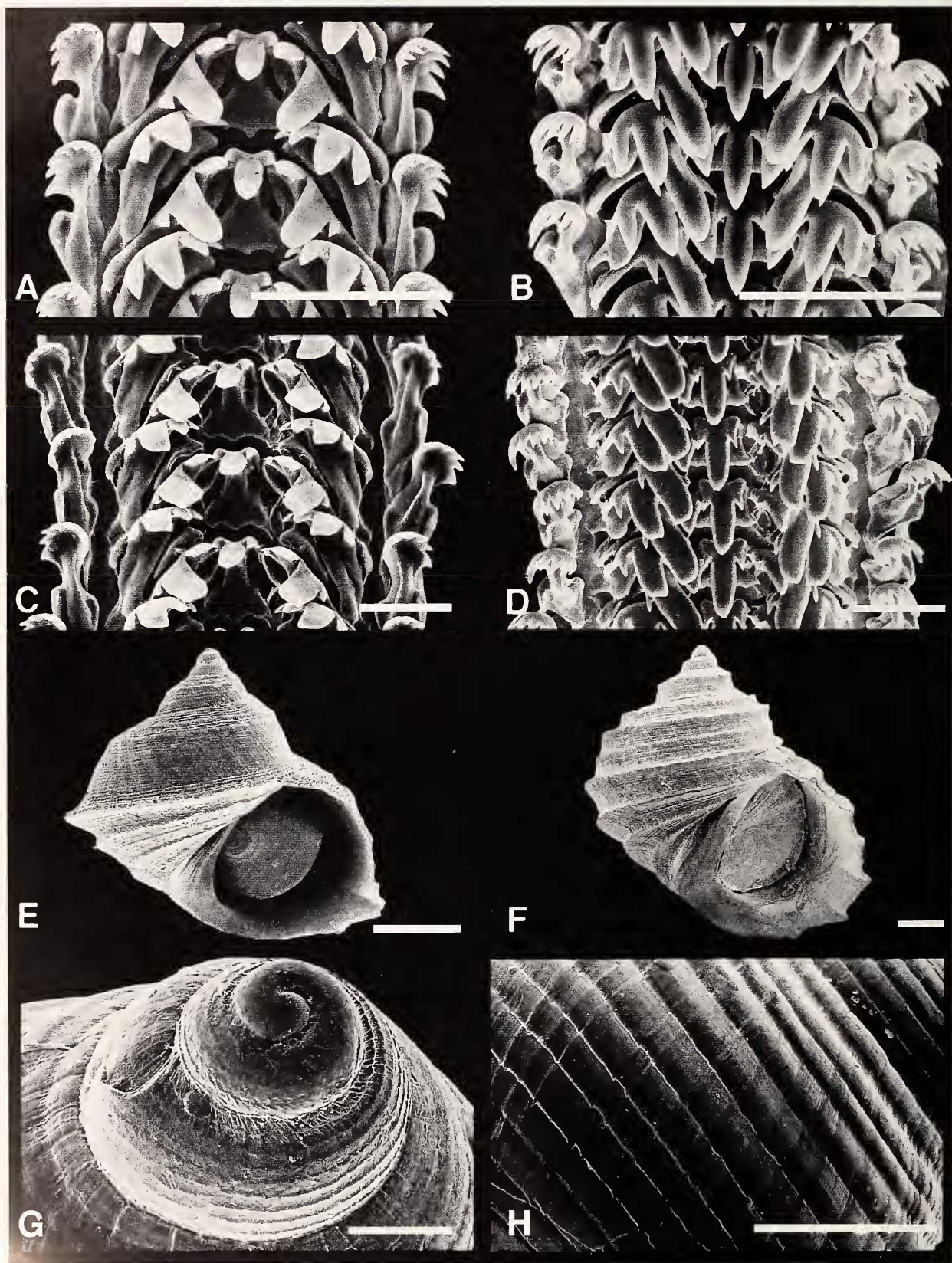
Radula (Figures 22A, B): Relative radular length 1.6–5.5. Rachidian: length/width 1.39–1.57; major cusp elongate, pointed or slightly rounded at tip. Lateral and inner marginal: major cusps elongate, rounded or pointed at tip. Outer marginal: 9–10 cusps.

Habitat: Abundant on boulders, rocks and cliffs of lava, also on volcanic tuff and on concrete; on bare surfaces in littoral fringe and uppermost eulittoral zone, also in crevices and at edges of saline pools; on exposed and sheltered shores. This is the only abundant littorinid of the littoral fringe in the Galápagos Islands; sympatric *N. conspersa*, *N. atrata*, and *N. porcata* are all found at lower levels. For descriptions of zonation see Cinelli & Colantoni (1974, as *Tectarius galapagensis*); these authors also record occurrence on mangrove trunks.

Range (Figure 20): Probably endemic to the Galápagos Islands; a single record from mainland Ecuador (Stearns, 1891, 1892) has not been confirmed. Range limits: Caleta Iguana, Isla Isabela (USNM 796177); NE side Isla Fernandina (LACM AHF 153–34); Punta Egas, Isla Santiago (USNM 807237); Isla Bartolomé (USNM 707612); Isla Genovesa (personal observation); Puerto Ayora, Isla Santa Cruz (USNM 769823; BMNH 20001273); Punta Pitt, Isla San Cristobal (personal observation); Bahía Gardner, Isla Española (CDRS); Punta Cormorant, Isla Santa María (personal observation). Stearns (1891, 1892) recorded a single specimen from Manta on the mainland of Ecuador (as *Tectarius atyphus*; USNM 48396), said to have been collected there by W. H. Jones. Since then, no further specimens are known to have been collected on the mainland. It is possible that some error of labeling occurred, for in the same month (August 1884) the navy surgeon visited both Manta and the Galápagos Islands.

Remarks: Specimens with well developed nodules cannot be mistaken for any other littorinid from the region. Small, relatively smooth specimens might be confused with brown shells of the sympatric *N. atrata* and *N. por-*

Figure 21. Penes (A–J), pallial oviducts (K, L), and paraspermatozoa (M–P) of *Nodilittorina galapagensis* (A–F, K, M, N) and *N. fernandezensis* (G–J, L, O, P). A–D, K, M, N. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (BMNH 20001273; shell H = 6.0 mm, 4.6 mm, 6.5 mm, 8.8 mm; A, B, two views). E, F. Punta Estrada, Isla Santa Cruz, Galápagos Islands (E, BMNH 20001274, shell H = 7.4 mm; F, BMNH 20001276, shell H = 6.9 mm). G, Punta San Carlos, Isla Robinson Crusoe (Más a Tierra), Archipiélago de Juan Fernández (BMNH 20001279; shell H = 12.8 mm). H, Isla San Ambrosio, Islas Desventuradas (BMNH 20001281; shell H = 17.0 mm). I, J, L, O, P. Bai del Oeste, Isla Robinson Crusoe (Más a Tierra), Archipiélago de Juan Fernández (BMNH 20001282; shell H = 7.5 mm, 10.7 mm, 13.7 mm). Abbreviations: pg, mamilliform penial gland in normal position; pg2, second mamilliform penial gland; tp, termination of penial sperm groove. Shading conventions as in Figures 3, 4, 13. Scale bars: A–L = 1 mm; M–P = 20 μm .



cata, but both of these usually have a lower spire and a large pseudo-umbilicus. Stearns (1892, 1893a, b) described nodulose and granulose forms under different names, and the variability in development of nodules was noted by Taviani (1979).

The nodulose shell is very distinctive and unlike that of any other eastern Pacific species, while it superficially resembles such nodulose Atlantic species as *N. dilatata*, *N. miliaris*, and *N. granosa* (Philippi). However, sculpture is so variable within many *Nodilittorina* species that it appears to be an unreliable guide to relationships. Of more significance is the penis which, with its unusual subterminally opening sperm groove and unique second mamilliform gland, does not closely resemble that of any other species.

Nodilittorina (*Austrolittorina*) *fernandezensis*
(Rosewater, 1970)

(Figures 18Q–V, 20, 21G–J, L, O, P, 22C, D)

Littorina penitaria "Wood" Nevill, 1885:142 (San Juan Fernandez [Juan Fernandez Islands]; *nomen nudum*).

Littorina mauritiana—Odhner, 1922:223. Rozbaczylo & Castilla, 1987:176. (Both not *Phasianella mauritiana* Lamarek, 1822 = *Littoraria mauritiana*.)

Littorina (*Austrolittorina*) *unifasciata fernandezensis* Rosewater, 1970:471–472, pl. 359, figs. 9–12, pl. 361, fig. B (radula) (east shore of Cumberland Bay, Isla Más a Tierra, Juan Fernandez Islands [Chile]; holotype USNM 368900, Rosewater, 1970, pl. 359, figs. 11, 12, Figure 18T herein, seen; 25 paratypes USNM 679256, seen; 11 paratypes DMNH 039221, not seen).

Nodilittorina (*Nodilittorina*) *fernandezensis*—Reid, 1989a:99.

Nodilittorina fernandezensis—Ramírez & Osorio, 200:1–13.

Taxonomic history: Although Nevill (1885) ascribed the name *penitaria* to W. Wood on the basis of a museum label of unknown provenance, it was apparently never published. The name was rejected as a *nomen nudum* by Rosewater (1970), although arguably the locality alone, as given by Nevill (1885), was sufficient to unambiguously identify the species, since no other member of the family occurs there. This species is abundant on the islands of the Juan Fernández and Desventuradas archipelagos, but these are so remote that it is very rare in museum collections and has scarcely been mentioned in the literature. Odhner (1922) misidentified it as *mauritiana*,

a member of the genus *Littoraria* with a superficially similar greyish white shell. Rosewater (1970) introduced the name as a subspecies of the Australian *N. unifasciata*, correctly recognizing *N. fernandezensis* as a member of the *Austrolittorina* group.

Diagnosis: Shell large, whorls rounded, spire profile straight, periphery only slightly angled; aperture finely lirate; spiral sculpture of fine microstriae only; white with broad indistinct blue-grey zone above periphery; single pale basal band within brown aperture. Penial filament small, pointed; small mamilliform gland and large glandular disc borne on projection of base.

Material examined: 16 lots (including 15 penes, 3 sperm samples, 5 pallial oviducts, 4 radulae).

Shell (Figures 18Q–V): Mature shell height 5.4–21.3 mm. Shape high turbate (H/B = 1.37–1.87, SH = 1.42–2.09); spire whorls rounded, suture distinct; spire profile straight; periphery weakly angled, last whorl slightly flattened. Columella concave, weakly hollowed, slightly pinched at base; sometimes a small eroded parietal area; aperture finely lirate within outer edge. Spiral sculpture of 10–14 weak primary grooves above periphery on early whorls, but by last whorl these become less distinct and only slightly stronger than numerous fine spiral microstriae across whole surface, so shell appears superficially smooth. Periostracum relatively thick, slightly overhanging apertural edge. Protoconch not seen. Color white with broad indistinct zone of blue-grey above periphery; smaller shells often with brownish axial growth marks, or pale brown with basal white band; aperture dark brown, with single pale spiral band at base; columella brown.

Animal: Head and sides of foot black. Opercular ratio 0.37–0.60. Penis (Figures 21G–J): filament small, pointed, 0.4–0.5 total length (but available specimens not relaxed), terminal opening of sperm groove; mamilliform gland small, narrow, embedded in enlarged penial glandular disc, together borne on stout projection of base; penis slightly pigmented at base. Posterior 0.25 of prostate is swollen, reddish, closed as a duct; anterior part is thinner and an open groove. Euspermatozoa 66–71 μ m; paraspermatozoa (Figures 21O, P) round, packed with granules, no visible rod-piece or nucleus, 11–15 μ m diameter. Pallial oviduct (Figure 21L) with single loop of

Figure 22. Radulae of *Nodilittorina galapagensis* (A, B) and *N. fernandezensis* (C, D); juvenile shells of *N. porcata* (E; note periostracal hairs on basal ribs) and *N. parcipicta* (F); protoconch of *N. modesta* (G); sculpture of *N. modesta* (H; note absence of microsculptural striae). A, B. Punta Estrada, Isla Santa Cruz, Galápagos Islands (BMNH 20001276; two views of radula, flat and at 45°; shell H = 6.9 mm). C, D. Punta San Carlos, Isla Robinson Crusoe (Más a Tierra), Archipiélago de Juan Fernández (BMNH 20001279; two views of radula, flat and at 45°; shell H = 12.8 mm). E. Puerto Ayora, Isla Santa Cruz, Galápagos Islands (BMNH 20001169). F. 7 km N of San José del Cabo, Baja California Sur, Mexico (BMNH 20001179). G, H. Puerto Vallarta, Jalisco, Mexico (BMNH 20001197). Scale bars A–D, G = 50 μ m; E, F, H = 0.5 mm.

albumen gland followed by large single loop of opaque capsule gland, terminating in reddish translucent portion; copulatory bursa opening at mid-point of straight section, extending back into capsule gland. Spawn not observed; form of oviduct indicates pelagic spawn and likely planktotrophic development.

Radula (Figures 22C, D): Relative radular length 2.3–5.0. Rachidian: length/width 1.14–1.27; major cusp elongate, rounded at tip. Lateral and inner marginal: major cusps elongate, rounded or blunt at tip. Outer marginal: 7–9 cusps.

Habitat: Volcanic rocks; abundant on rocks and in crevices, in highest intertidal zone, at densities of 65–430 per m² (Ramírez & Osorio, 2000). No other littorinids occur with this species.

Range (Figure 20): Found only on the Islas Juan Fernández and Islas Desventuradas off the coast of Chile. Range limits: Isla Robinson Crusoe (Isla Más a Tierra), Archipiélago de Juan Fernández (BMNH 20001279); Isla Alejandro Selkirk, Archipiélago de Juan Fernández (BMNH 20001278); Isla San Félix, Islas Desventuradas (BMNH 20001280); Isla San Ambrosio, Islas Desventuradas (BMNH 20001281).

Remarks: The large, thick white shells of this species cannot be confused with any other in the eastern Pacific. However, medium and small examples are superficially similar to some pale specimens of *N. araucana* and *N. paytensis*. The former is distinguished by its lack of spiral microstriae, lack of lirae within the aperture, and (when present) stronger primary grooves. *Nodilittorina paytensis* also lacks external microstriae and apertural lirae, has two pale stripes within the aperture, and almost always a pattern of small brown dots. Much more similar, and sometimes indistinguishable except by anatomical characters, are the New Zealand species *N. antipodum* (Philippi) and the Australian *N. unifasciata*; where the locality is unknown, details of penial shape separate these three.

Despite the superficial similarity to *N. araucana* and *N. paytensis*, the present species is not closely related to either of these. Rosewater (1970) recognized its relationships when he described it as a subspecies of the temperate Australian *N. unifasciata* (which he placed in *Littorina*, and included *antipodum* as another subspecies). Likely anatomical synapomorphies of these three species include the short and stout penial filament (although *N. antipodum* and *N. unifasciata* have a slightly subterminal opening of the sperm groove), the narrow mamilliform penial gland often partly embedded in the large penial glandular disc and, most importantly, the additional loop of the egg groove through the opaque capsule gland. This last character state unites a group of littorinids comprising, in addition to these three, *N. cincta* (Quoy & Gaimard) from New Zealand, *N. praetermissa* (May) and *N. acutispira* (E. A. Smith) from southeastern Australia, and

from South Africa *N. africana* (Philippi) and *N. knysnaensis* (Philippi). All eight species are here assigned to *Austrolittorina* Rosewater, 1970 (type species *Littorina unifasciata*). This is provisionally recognized as a subgenus, although in the absence of strong synapomorphies for *Nodilittorina* it is not yet clear that this is correct, and the relationship of *Austrolittorina* with the rest of the genus requires examination with molecular data. Another possible member of the *Austrolittorina* group is the eastern Australian endemic *N. pyramidalis*; this shares the form of the pallial oviduct, but shows an unusual penial shape and is the only one with a nodulose shell. (It may be noted that since *N. pyramidalis* is the type species of *Nodilittorina* (subsequent designation by Abbott, 1954) its relationships and those of *Austrolittorina* have important consequences for the nomenclature of the entire genus; see Remarks on *Nodilittorina*.) As originally constituted, Rosewater's subgenus contained many more species (including e.g., *N. aspera*, *N. peruviana*, smooth-shelled Atlantic *Nodilittorina* species, and *Littoraria tessellata* (Philippi)), and three more species were added later (Ponder & Rosewater, 1979). In revisions of the generic classification of Littorinidae, both Bandel & Kadolsky (1982) and Reid (1989a) considered *Austrolittorina* a synonym of *Nodilittorina*. The subgenus *Austrolittorina* is here used in a restricted sense, and this group shows an austral distribution in temperate and warm temperate latitudes of the Southern Hemisphere.

The shell of *N. fernandezensis* is among the thickest and most solid of all *Nodilittorina* species, but nevertheless the large available samples show an unusually high frequency of scarring and repair on the shell (Figures 18R, T, V). This is more pronounced than in the similar *N. unifasciata*. Whether the shell damage is caused by unusually strong wave action, mobile boulders, or a powerful predator is unknown.

DISCUSSION

Intraspecific Shell Variation

Using shell characters alone it would have been impossible to resolve the taxonomy of the three species complexes of *Nodilittorina* in the eastern Pacific. However, having defined the species largely by means of diagnostic penial shapes it was possible to reexamine the confusing range of shell types and thus to discover taxonomically useful characters. The key to interpreting shell variation is that, in each species group, the more obvious shell characters such as size, shape, development of ribs, and color show parallel variation within species, and that it is the more subtle differences in numbers of grooves and color pattern that discriminate between them. Using suitable characters, identification is in fact possible using shells alone in almost all cases.

The degree of intraspecific variation (in shape, sculpture and color in the *N. porcata* group; in sculpture in the

N. aspera and *N. modesta* groups and *N. galapagensis*; and in shape and color in *N. araucana*) is remarkable, even among the notoriously polymorphic littorinids. In the well studied temperate genus *Littorina*, extreme intra-specific variability is associated with benthic spawn and a non-planktotrophic mode of development, whereas those species with pelagic egg capsules and planktotrophic development are less variable, at least on a local scale (review by Reid, 1996). The classic explanation for these observations is that the restricted gene flow in non-planktotrophic species permits local genetic adaptation in response to differing selection regimes, resulting in distinctive shell forms or "ecotypes" that are characteristic of different microhabitats on the shore (e.g., Janson, 1983; Seeley, 1986; Johannesson et al., 1993; Trussell, 1997). Controlled rearing has confirmed that some shell traits are indeed heritable (Boulding & Hay, 1993; Johannesson & Johannesson, 1996; Parsons, 1997a). Striking local variation is also known in some planktotrophic littorinids, such as the polymorphism of striated and nodulose forms of *Littorina striata* (Reid, 1996; de Wolf et al., 1997), *Nodilittorina hawaiiensis* (Rosewater & Kadolsky) (Struhsaker, 1968), and *N. australis* (Gray) (Johnson & Black, 1999). Although selection has sometimes been invoked to account for this (Struhsaker, 1968), it would have to be very strong to explain the local-scale variation in the face of high gene flow. Alternative explanations also invoking a genotypic basis might involve non-random larval settlement or some means of limiting dispersal during the pelagic stage. However, there is now increasing evidence from laboratory rearing and field translocation that direct environmental effects on the phenotype play an important role. Examples of ecophenotypic effects include the influences of food availability (mediated via its effect on growth rate) on shell shape (Kemp & Bertness, 1984; Boulding & Hay, 1993; Johnson & Black, 1998) and shell sculpture (Boulding et al., 1993), and the influence of crab predators and water temperature on shell thickness (Trussell, 1996, 2000). Although these demonstrations mostly involve non-planktotrophic littorinids, ecophenotypic effects have also been invoked to explain cases of local variation that are correlated with microhabitat in planktotrophic species (Chapman, 1995; Reid, 1996; Johnson & Black, 1999). Indeed it is argued that in widely dispersed species occupying a range of habitats, phenotypic plasticity should be a favored strategy (Parsons, 1997b).

The evidence for phenotypic plasticity of shell traits in the eastern Pacific *Nodilittorina* species is largely indirect. In common with all known members of the genus, they produce pelagic egg capsules and undergo planktotrophic development. (Although this has not been confirmed by direct observation of spawn and protoconchs in every species, it is predicted from the universal association of a large capsule gland in the pallial oviduct with planktotrophy in members of the Littorininae; Reid,

1989a.) Assuming that this results in high gene flow, the cases of shell variation between microhabitats on the same shore are difficult to explain except by phenotypic plasticity. The most striking examples are the contrasts between the smooth shells of *N. atrata* and *N. santelenae* from mid-shore rock pools and ribbed or carinate shells among barnacles on rocks close by. A possible explanation might be that faster growth under the more favorable conditions in pools results in a smoother shell (as shown in *Littorina sitkana* Philippi by Boulding et al., 1993). Other examples are the dwarf shells of *N. aspera*, *N. tenuistriata*, and *N. apicina* found in small high-shore rock pools that are smaller, smoother, and more darkly patterned than larger shells on open rock surfaces at the same localities. Occasional individuals can be found in which shell shape and sculpture changes abruptly during the course of growth (Figure 11L), supporting the suggestion of plasticity. Similarly, examples of sudden color change (Figures 1G, M) imply likely environmental effects on shell coloration. Although abrupt color change has been observed following translocation between microhabitats in *Littoraria* species (Reid, 1986), there has been no experimental study of phenotypic plasticity in shell color in other littorinids. Among other gastropods, effects of diet upon shell banding patterns have been reported in the trochid *Austrocochlea* (Underwood & Creese, 1976), whereas in neritids this is influenced by cation ratios (Neumann, 1959) and perhaps by salinity (Gundersen & Minton, 1997).

Other Taxonomically Useful Characters

In addition to their important role in the initial characterization of species, anatomical characters may be required to confirm otherwise doubtful identifications. The simple feature of pigmentation of the head can be useful. Although most of the species show either the typical *Nodilittorina* pattern of head pigmentation, black with a pair of longitudinal black lines on each tentacle, or alternatively are entirely black, in *N. modesta* there are transverse black lines on the tentacles. This provides a useful character for its distinction from the other species in the *N. modesta* group, *N. conspersa*. Tentacle pattern has also been used as a taxonomic character separating two similar *Littorina* species, *L. scutulata* Gould and *L. plena* Gould (Reid, 1996).

As is well known in the Littorinidae, penial shape is the most useful of the taxonomic characters and has frequently provided the first evidence for the discovery of "sibling" species. Since even allopatric sister-species usually show diagnostic penial differences, it has been suggested that penial shape is part of the "specific mate recognition system" (Paterson, 1985) of *Littorina* (review by Reid, 1996). Although the descriptions of eastern Pacific *Nodilittorina* species largely support this idea, the differences among members of species complexes are of-

ten more subtle than those among closely related groups of *Littorina* (Reid, 1996) or *Littoraria* (Reid, 1986, 1999a). Consequently, penial shape is sometimes not entirely diagnostic as, for example, in the *N. porcata* and *N. aspera* species groups (Figures 3, 13, 14). A similar case is known in the sympatric pair *Littorina saxatilis* (Olivi) and *L. arcana* Hannaford Ellis, in which penial shape shows some overlap (Hannaford Ellis, 1979), although genetic results confirm their species status (review by Reid, 1996). It is likely that the shape of the penis during copulation is different from that in relaxed, fixed specimens (see Bingham, 1972, in *Littoraria irrorata* (Say)), perhaps aiding species recognition, or alternatively other unknown recognition cues may be important in *Nodilittorina*. As in *Littoraria* (Reid, 1986), though not in *Littorina* (Reid, 1996), the paraspermatozoa often show marked differences between *Nodilittorina* species, even within species groups (e.g., *N. aspera* group, Figure 15), but the significance of this is unknown.

Among the Littorinidae as a whole, oviduct structure is closely tied to the type of spawn and larval development (Reid, 1989a, 1996). The pallial oviducts of the eastern Pacific *Nodilittorina* species are mostly rather uniform, as expected from their similar (whether known or presumed) life histories. Only that of *N. fernandezensis* is strikingly different from the rest, to which it is probably not closely related (as discussed below). There are small differences between the species groups, but these are not useful for identification within these groups. The egg capsules have been described in five of these species; while these are notably different, it remains to be seen whether this will be the case within species groups. Interestingly, the capsule and contained egg are relatively small in the tropical *N. dubiosa* (capsule 140 μm diameter, ovum 40 μm diameter) and *N. atrata* (160 μm , 40 μm) from Costa Rica, and larger in *N. paytensis* in Ecuador (300 μm , 84 μm) and in Chilean *N. araucana* (210–256 μm , 68–84 μm) and *N. peruviana* (336–421 μm , 84–89 μm). These data are limited, but a similar trend of increasing egg and capsule size in colder water has been documented in *Littorina* (Reid, 1996), although there is no convincing explanation.

Among other gastropods, radulae may provide useful characters for species discrimination, but this is not usually the case among littorinids (e.g., Reid, 1986, 1996), nor is it so among the eastern Pacific *Nodilittorina*. It has recently been claimed that the radulae of some littorinids show phenotypic plasticity according to the substrate on which they graze (Padilla, 1998; Reid & Mak, 1999). *Nodilittorina* species are almost always found on rocks so that potential plasticity is not easily studied, but in a sample of *N. albicarinata* from grasses the radulae did not differ from the normal form. The members of the *N. porcata* group, all of which are relatively small in size, share a similar radular tooth form with pointed cusps, which on the five central teeth in each row are more uniform in

size than the elongated major cusps seen in the remaining species. In species of *Littorina* both juveniles and small adults show relatively pointed cusps; this has been suggested to be an allometric effect (Reid, 1996) which might also account for the pattern in small *Nodilittorina* species. At up to 15 times the length of the shell, the radula of *N. aspera* is the longest yet reported in this family.

Phylogenetic Relationships

Although anatomical details are available for all the approximately 60 species of *Nodilittorina* worldwide, attempts at cladistic analysis of morphological characters have so far been uninformative (unpublished observations), a result of relative uniformity in some structures and apparent homoplasy in others. The pallial oviduct is similar in most species (with the exception of the *Austrolittorina* group; there is also some variation in the position of the copulatory bursa), connected with the similar pelagic spawn and planktotrophic development throughout the genus. The radula likewise shows little variation (beyond a trend toward narrowing of the rachidian tooth in some species), which may be related to the high-intertidal rock-dwelling habitat of most of these largely tropical species. The penis too is rather uniform, with a single mamilliform gland and glandular disc in most species and only subtle interspecific variations in overall shape, while there is likely homoplasy in loss of glandular elements. Shell shape and sculpture, however, are too variable within species to provide convenient characters for phylogenetic analysis. In contrast, in the probable sister-genus *Littorina* (which occupies a broad latitudinal temperature range, a range of rock and algal substrates, shows a wide diversity of reproductive modes, and much variation in numbers of penial glands) the analysis of anatomical characters has provided a well resolved cladogram, subsequently supported by molecular data (Reid, 1989a; Reid et al., 1996; Reid, 1996). As noted earlier (see Remarks on the genus *Nodilittorina*) it is not even certain that the genus is monophyletic as presently constituted. In *Nodilittorina* it is likely that only molecular data will satisfactorily resolve phylogenetic relationships. Meanwhile, there are some useful groupings based on morphological resemblance rather than formal cladistic analysis.

The most obvious of these in the eastern Pacific is perhaps the *N. aspera* group, in which resemblances are so close that five of the six species have at one time been considered conspecific (see Remarks on *N. aspera* group). This group shares a spirally sculptured shell without nodules, and a striking shell pattern (usually with a more or less developed dark peripheral band), but penis, pallial oviduct, and radula are each of a form common in the genus. Egg capsules have been described only in *N. dubiosa* and *N. paytensis*, and show some similarity in the absence or slight development of spiral rings on the cu-

pola (compare with figures and references in Reid, 1989a; Mak, 1995; Rudman, 1996). There is a possible parallel in the *N. ziczac* complex in the western Atlantic, comprising between five (Reid, 1989a) and seven (Bandel & Kadolsky, 1982) species. These likewise have strongly patterned shells of similar shape and sculpture, but they exhibit a diversity of penial shapes, radulae, and egg capsules and so may not be a natural group. It is possible that shell similarities between the *N. aspera* and *N. ziczac* complexes are convergent since they are not unique in the genus (e.g., *N. punctata* (Gmelin), *N. peruviana*, and some western Pacific species) and there are no apparent anatomical synapomorphies. Since the eastern Pacific and western Atlantic formed a single marine region until the appearance of the Panamanian Isthmus during the Pliocene, some relationship between their modern faunas is to be expected. Nevertheless, the available evidence gives little indication of this.

A second species complex in the eastern Pacific, the *N. porcata* group, is well defined and probably monophyletic, based on the unique or unusual features of the umbilicate shell, strong expression of likely phenotypic plasticity in sculpture, absence of penial glandular disc, twisted tip to the penial filament, flexure in the straight section of pallial oviduct, pointed radular cusps, and similar mid-shore habitat. The small size, umbilicate shell, and mid-shore or rock pool habitat recalls the pair *N. meleagris* and *N. mespillum* in the Atlantic and Caribbean. Rosewater (1981) introduced the subgenus *Fossarilittorina* for these two species (with *N. meleagris* as type species) and added *N. atrata*, *N. porcata*, and *N. albicarinata*. In this case, a relationship with the Atlantic species is supported by the possible synapomorphies of umbilicate shell, absence of penial glandular disc, flexure in the oviduct, and radular cusps (although none of these is individually unique, their combination is not found elsewhere in the genus). Furthermore, paraspermatozoa and egg capsules (known only in *N. atrata* and *N. meleagris*; personal observation) are closely similar. The most significant difference is in the penis which, in the Atlantic species, lacks all glandular projections and has a superficially closed sperm duct (Reid, 1989a). The former condition is found as a rare abnormality in the eastern Pacific species (*N. atrata* and *N. parcipicta*), and the latter is a minor anatomical modification found elsewhere in littorinids, so while these characters are likely synapomorphies of *N. meleagris* and *N. mespillum* they do not preclude a sister-group relationship with the *N. porcata* complex.

The two species of the *N. modesta* group are undoubtedly sister-species, sharing almost identical shells, a unique simple and vermiform penis, a unique synapomorphy of projection of the renal oviduct into the spiral of the albumen gland, and similar extra denticles on the rachidian tooth. The relationships of this clade are nevertheless obscure. As a result of a cladistic analysis of the Littorini-

dae, Reid (1989a) tentatively placed *N. modesta* (then considered a single species) together with *N. meleagris* and *N. mespillum* in the subgenus *Fossarilittorina*. However, the only synapomorphy was the absence of mamilliform penial glands which, as suggested above, is weak and liable to convergence, since mamilliform glands are readily lost (also noted in *Littorina*, Reid, 1996; and *Peasiella*, Reid, 1989b).

Nodilittorina fernandezensis, endemic to the oceanic islands off Chile, is the only one of the eastern Pacific *Nodilittorina* species to show a clear relationship with a group of species to the west. As discussed in the Remarks on the species, it is placed in the subgenus *Austrolittorina* (type species *N. unifasciata*) together with at least seven species from southern Australia, New Zealand, and South Africa. This subgenus is defined by the synapomorphy of the additional loop of the egg groove through the opaque capsule gland (elsewhere in *Nodilittorina* shared only with *N. pyramidalis*, a species of uncertain relationships but possibly belonging to the same clade) and additionally characterized by similarities of penial shape and weak shell color pattern.

The remaining eastern Pacific *Nodilittorina* species cannot at present be convincingly linked with other groups within the genus (see Remarks on *N. araucana*, *N. peruviana*, and *N. galapagensis*).

With the exception of *Austrolittorina*, subgeneric names have not been used here for the tentative groupings suggested. In an earlier review of the genus, Bandel & Kadolsky (1982) remarked on the pervasive homoplasy and likewise did not designate subgeneric groups. In the only formal cladistic analysis, Reid (1989a) accepted three subgenera *Fossarilittorina*, *Echinolittorina*, and *Nodilittorina*. The doubt surrounding the first has been discussed earlier. The latter two were distinguished only by the relative position of the copulatory bursa in the pallial oviduct, but new observations (presented here and unpublished) suggest that this distinction is not clear cut. Molecular data are urgently required to address these phylogenetic questions.

Distribution Patterns and Faunal Provinces

The attempt to define faunal provinces is an unfashionable part of marine zoogeography, having been superseded by studies of regional biodiversity and the phylogenetic approach to historical biogeography. Nevertheless, the twin concepts of faunal provinces and the boundaries between them are heuristically useful, serving as a framework for distributional data, highlighting dispersal processes, and influencing sampling for systematic and genetic studies. Provinces have been defined either by an arbitrary level of endemism (10% was taken by Briggs, 1974) or by coincidence of many end-points of ranges. However, the distributions of taxonomic groups respond to environmental barriers in different ways, according to

their biogeographic history, dispersal capabilities, habitat requirements, and physiological tolerances. Therefore, it is not useful to seek a universal classification of marine faunal provinces, except in the broadest terms.

The recognition of marine faunal provinces in the eastern Pacific Ocean has a long and complex history. Since their distributions are relatively well known, studies of mollusks have played an important part (e.g., Carpenter, 1857b; Dall, 1909; Newell, 1948; Olsson, 1961; Valentine, 1966; Bernard et al., 1991). There is general agreement that the tropical region extends from the Gulf of California south to northernmost Peru, including the oceanic islands (Islas Revillagigedo, Isla del Coco, Isla de Malpelo, and Galápagos). This has been named the Eastern Pacific Zoogeographic Region (Briggs, 1974), but is now commonly referred to as the Tropical Eastern Pacific or TEP (Hastings, 2000). Although Briggs (1974) classified the Gulf of California (Sea of Cortez) as part of the warm-temperate region to the north, its chief affinities lie with the TEP, and its designation as tropical is not now disputed (Brusca, 1980; Hastings, 2000). The northern limit of the TEP on the Pacific coast of Baja California is set by the influence of the cold southerly California Current. However, this limit is not sharply defined, since this coast is complex, with lagoons and bays providing refugia for tropical species, whereas exposed coasts and upwelling zones harbor a temperate fauna. This is best regarded as a transitional zone between the TEP and warm-temperate Californian Province, lying approximately between Punta Eugenia and Bahía Magdalena (Brusca & Wallerstein, 1979; Brusca, 1980) or extending farther south to Cabo San Lucas (Bernard et al., 1991). The southern limit of the TEP also corresponds to a steep temperature gradient, where the cold northerly Peru (Humboldt) Current sweeps offshore, between the Golfo de Guayaquil and Punta Aguja (3–6°S) (Keen, 1971; Brusca & Wallerstein, 1979; Bernard et al., 1991; Hastings, 2000). To the south the Peruvian Province (or Peru-Chilean, Briggs, 1974) is of warm-temperate character and extends down the coast of Peru and Chile to merge with the Magellanic Province in a broad transitional zone between 30–46°S (Viviani, 1979; Brattström & Johansen, 1983; although Bernard et al., 1991, combined these as a single Chilean Province).

The provincial classification of the oceanic islands of the eastern Pacific is problematic, since the faunas are generally impoverished relative to the mainland and are often poorly studied. In addition they may include a proportion of rare species that are immigrants from either the Indo-West Pacific or from the mainland, and that do not become established. The classification of the tropical islands is discussed below. Of particular interest are the warm-temperate oceanic islands off Chile, the Islas Desventuradas, and Islas Juan Fernández. Their molluscan faunas are little known (Odhner, 1922; Rozbaczylo & Castilla, 1987; Bernard et al., 1991), but some species are

shared with the Peruvian Province. However, in a list by Rozbaczylo & Castilla (1987) 72% of the 39 recorded mollusks (excluding cephalopods) were given as endemic. In a later compilation of the bivalves, 26% of the 31 species from the Juan Fernández Archipelago were recorded as endemic, none was shared with the Indo-West Pacific, only three were shared with the still more poorly known Islas Desventuradas, and no endemics were noted on those islands (Bernard et al., 1991). Although these two island groups are only 600 km from the mainland and 800 km apart, the islands appear to be isolated from the continent by the Peru Current flowing northward parallel to the Chilean coast (Bernard et al., 1991). The single littorinid found there, *N. fernandezensis*, is endemic and appears to be conspecific on the two island groups. As noted earlier, its relationships are undoubtedly with a southern-temperate group from Australia, New Zealand, and South Africa (subgenus *Austrolittorina*). Similar trans-Pacific relationships of mollusks at subtropical and warm-temperate latitudes (for example, of Islas Juan Fernández and Isla de Pascua with Australia and New Zealand) have been noted before (Rehder, 1980; Lindberg & Hickman, 1986; Bernard et al., 1991). The distances are too great for transport of pelagic larvae (except teleplanic forms) in oceanic currents, but rafting of adults has been suggested for a trans-Pacific oyster (Ó Foighil et al., 1999). Alternatively, trans-Pacific dispersal of shallow-water species may have been facilitated by the presence of little-known or uncharted reefs in these latitudes in the South Pacific Ocean; at times of low sea level these may have emerged as islands to act as stepping stones for littoral species (P. Bouchet, personal communication). In a recent list of 51 fishes of the Juan Fernández Islands, Pequeño & Sáez (2000) found that 25.5% were endemic, 29.4% shared only with the Islas Desventuradas, and that slightly more species were shared with Pacific islands to the west than with the mainland to the east (19.6% compared with 15.6%). It seems appropriate that the Islas Juan Fernández and Desventuradas should together be included in a distinct Juan Fernández Province, as proposed by Briggs (1974), although whether this is classified as part of the warm-temperate region of the South American mainland (Briggs, 1974) or of the tropical Indo-West Pacific region (Pequeño & Sáez, 2000) is debated.

Opinions about the subdivision of the TEP region into smaller faunal provinces are diverse and dependent upon the group studied. Molluscan workers have, with few exceptions, emphasized the faunal uniformity of the TEP (named the "Panamic Province" in molluscan texts) and have not identified distributional boundaries within it (Dall, 1909; Keen, 1958, 1971; Olsson, 1961; Bernard et al., 1991; Emerson & Chaney, 1995; Roy et al., 1998). This is so even when considering the molluscan fauna of the Galápagos Islands with endemism estimated as 18–23% (Finet, 1991; Kay, 1991). However, Keen (1958) remarked on Panamic "subprovinces" in the northern

Gulf of California and Gulf of Panama, and Vermeij (1991) suggested that the Mexican coast and Gulf of California have acted as refuges from extinction for mollusks that were formerly more widespread within the TEP. Working with echinoderms, Maluf (1988) found high overall faunal similarity within the TEP from Cabo San Lucas to Peru, but recognized the Gulf of California (Cortez Province) as distinct (based on species shared with the Californian Province, and despite low endemicity of only 2%) and also the Galápagos Province (endemicity 16%). Using decapods, Correa-Sandoval & Rodríguez-Cortés (1998) accepted a Cortez Province with 24% endemicity, distinct from Mexican and Panamic Provinces to the south, contrary to an earlier study in which Cortez and Mexican Provinces were united (Hendrickx, 1992). Based on analysis of the depauperate zooxanthellate coral fauna of the TEP, Glynn & Ault (2000) found similarities among the Islas Revillagigedo, Gulf of California, and southern Mexico, suggesting a provincial difference from the group of southern localities (Central America, Ecuador, Galápagos). However, it has been studies of shore fishes that have led to the clearest subdivision of the TEP. Although with differences of detail, most workers have divided the region into four provinces: Cortez, Mexican, Panamic, and Galápagos (Hubbs, 1952; Briggs, 1955, 1974; Springer, 1958; Walker, 1960; Hastings, 2000), separated mainly by gaps of open ocean and of inhospitable coastline without rocky substrates. The limits of these provinces can be defined as follows (where authors disagree, the boundaries have been selected for maximum agreement with the distributions of *Nodilittorina* reported here; see Figure 23). The Cortez Province includes the entire Gulf of California as far south as La Paz on the eastern coast of Baja California (Hubbs, 1952; Briggs, 1974) and Topolobampo (Sinaloa) on the mainland (Briggs, 1974; Hastings, 2000). The northern boundary of the Mexican Province is disputed; Hastings (2000) restricted this province to the mainland south of Mazatlán, while extending the Cortez Province around the tip of Baja California to the junction with the Californian Province. Here, however, the southwestern coast of Baja California (Punta Eugenia to La Paz) is included with the Mexican mainland south of Mazatlán (Hubbs, 1952; Springer, 1958; Walker, 1960; Briggs, 1974). The southern limit of the Mexican Province is near Salina Cruz in the Golfo de Tehuantepec (Southern Mexico) (Briggs, 1955, 1974; Springer, 1958; Hastings, 2000). Here, the Islas Revillagigedo are classified in the Mexican Province, although included in the Panamic Province by Briggs (1974). The Panamic Province (Panamanian of Briggs, 1974) is restricted to the region south of the Golfo de Fonseca (between El Salvador and Nicaragua) (Springer, 1958; Hastings, 2000) and includes Isla del Coco (Cocos Island) and Isla de Malpelo.

The distributions of *Nodilittorina* species and, for comparison, of *Littoraria* species (from Reid, 1999a) are sum-

marized in Table 4. There is a close correspondence with the faunal provinces as defined on the basis of shore fishes. Of the 18 species of *Nodilittorina*, only four extend their distributions (with apparently self-sustaining populations) through large parts of two adjacent provinces (*N. atrata* and *N. conspersa* in Panamic and Galápagos; *N. albicarinata* in Cortez and Mexican; *N. apicina* in Mexican and Panamic). For these littorinids, the barriers between the provinces are evidently remarkably effective. Oceanographic conditions clearly play some part. The steep temperature gradients at the northern and southern boundaries of the TEP have been mentioned, but temperature limitation is probably not significant within the TEP where temperatures exceed 20–25°C throughout the year (Bernard et al., 1991; Correa-Sandoval & Rodríguez-Cortés, 1998). During El Niño events the latitudinal extent of the TEP widens, which may account for occasional records of Panamic mollusks beyond their normal limits in northern Peru (Paredes et al., 1998). The Galápagos Islands are isolated from the mainland of Ecuador by 1000 km of open ocean, although under the influence of the Peruvian Current and of the Panama Current (from January to April) (Finet, 1991). Within the TEP the major currents are the northward Costa Rica Current (stronger in the summer, when it reaches the Gulf of California), the Panama Bight Gyre and the Panama Current (Bernard et al., 1991; Correa-Sandoval & Rodríguez-Cortés, 1998; Glynn & Ault, 2000) but, while significant for dispersal, these are not obviously connected with provincial boundaries. The influence of oceanographic conditions related to productivity, upwelling, and freshwater inflow are not understood. The distinction between “oceanic” and “continental” distributions among littorinids and other mollusks has often been noted (Reid, 1986, 1989b, 1999a) and may in some way be connected with the high productivity, turbidity, and runoff on continental margins. It may therefore be significant that the Panamic Province includes three areas of upwelling (in the Gulfs of Tehuantepec, Papagayo, and Panama) and has by far the highest freshwater input in the TEP, resulting in high algal productivity and turbidity (Glynn & Ault, 2000; Oceanic Primary Productivity Study, Rutgers University), thus providing a typically “continental” habitat for shallow-water mollusks. The Gulf of California is also an area of high oceanic productivity, whereas the Pacific coast of Baja California and most of the Mexican Province (with the exception of a periodic upwelling off the coast of Jalisco) provide typically “oceanic” conditions of low productivity and clear water (Santamaría-del-Angel et al., 1994; Barnard et al., 1999; Glynn & Ault, 2000; Oceanic Primary Productivity Study, Rutgers University). However, by far the most important determinant of provincial boundaries along the contiguous TEP coastline appears to be simply the availability of suitable intertidal habitat.

As recognized by workers on shore fishes that, like *Nodilittorina* species, require rocky substrate, the Cortez



Figure 23. Faunal provinces of the Tropical Eastern Pacific Region (TEP), based on distribution of shallow-water fauna of rocky substrates, principally fish and *Nodilittorina* species (modified from Springer, 1958; Briggs, 1974; Hastings, 2000). Cross-hatched areas are transitional zones between TEP and (to the north) the Californian Province and (to the south) the Peruvian Province.

Table 4

Distributional ranges of Littorinidae (*Nodilittorina* and, from Reid, 1999, *Littoraria*) from Baja California to Chile, listed by marine faunal provinces (Figure 23; see text for definitions). For *Nodilittorina*, "species groups" are tentatively suggested as possible monophyletic groups, based on likely synapomorphies and overall similarity. Species are listed in the provinces in which they have all or a significant part (i.e., likely self-sustaining populations) of their distributions. Occasional rare records are indicated by +.

Species groups	Californian	Cortez	Mexican	Panamic	Galápagos	Peruvian	Juan Fernández
<i>N. atrata</i>				<i>N. atrata</i>	<i>N. atrata</i>		
<i>N. porcata</i>					<i>N. porcata</i>		
<i>N. sauteleuae</i>				<i>N. sauteleuae</i>			
<i>N. fuscolineata</i>				<i>N. fuscolineata</i>			
<i>N. parcipicta</i>		+	<i>N. parcipicta</i>				
<i>N. albicarinata</i>	+	<i>N. albicarinata</i>	<i>N. albicarinata</i>				
<i>N. modesta</i>		+	<i>N. modesta</i>	+			
<i>N. conspersa</i>			+	<i>N. conspersa</i>	<i>N. conspersa</i>		
<i>N. aspera</i>		+	<i>N. aspera</i>	+			
<i>N. tenuistriata</i>				<i>N. tenuistriata</i>			
<i>N. dubiosa</i>				<i>N. dubiosa</i>	+		
<i>N. apicina</i>	+		<i>N. apicina</i>	<i>N. apicina</i>			
<i>N. penicillata</i>		<i>N. penicillata</i>	+				
<i>N. paytensis</i>				<i>N. paytensis</i>		+	
<i>N. araucana</i>						<i>N. araucana</i>	
<i>N. peruviana</i>						<i>N. peruviana</i>	
<i>N. galapagensis</i>					<i>N. galapagensis</i>		
<i>N. fernandezensis</i>							<i>N. fernandezensis</i>
<i>L. pintado pullata</i>			<i>L. pintado pullata</i>	<i>L. pintado pullata</i>			
<i>L. varia</i>				<i>L. varia</i>			
<i>L. zebra</i>				<i>L. zebra</i>			
<i>L. variegata</i>		<i>L. variegata</i>	<i>L. variegata</i>	<i>L. variegata</i>			
<i>L. rosewateri</i>		<i>L. rosewateri</i>	<i>L. rosewateri</i>	<i>L. rosewateri</i>			
<i>L. aberrans</i>				<i>L. aberrans</i>			

and Mexican Provinces are separated by a stretch of predominantly muddy coastline with mangroves and deltas that extends for 700 km from Guaymas to Mazatlán (Briggs, 1955, 1974; Springer, 1958). An isolated rock outcrop occurs at Topolobampo (Sinaloa), and this is now taken as the southern limit of the Cortez Province for shore fishes, separated from the Mexican Province by the "Sinaloan Gap" of 370 km (Hastings, 2000; Figure 23). A similar barrier, the Central American Gap, separates the Mexican and Panamic Provinces, consisting of over 1200 km of sand, mud, and mangrove lagoons between the Golfo de Tehuantepec and the Golfo de Fonseca (Springer, 1958; Briggs, 1974; Hastings, 2000; Figure 23). Likely stepping stones are found in El Salvador at Los Cobanos and La Libertad, where, respectively, *N. atrata* and *N. apicina* have been found (see also Glynn & Ault, 2000). The boundary between the Cortez and Mexican Provinces in the vicinity of La Paz, Baja California, cannot be explained so easily. Rocky shores are more or less contin-

uous, but perhaps the greater wave exposure and lower oceanic productivity in southeastern Baja California are significant; these conditions are more similar to the mainland coast of the Mexican Province than to the Gulf of California. Those *Nodilittorina* species restricted to the Mexican Province are characteristic of wave-exposed coasts (*N. parcipicta*, *N. modesta*, *N. aspera*) and those of the Cortez Province of sheltered shores (*N. albicarinata*) or a range of exposure (*N. penicillata*).

In addition to the Sinaloan and Central American Gaps, there is another large expanse of sedimentary shore and mangroves, extending more than 500 km between Cabo Corrientes (Colombia) and San Lorenzo (Ecuador). The biogeographic implications do not appear to have been mentioned previously and the area can be termed the Colombian Gap (Figure 23). There is some evidence from the distributions of *Nodilittorina* species that this gap also presents a barrier to dispersal. Of the six species occurring commonly in the Panamic Province north of this gap,

only four are also common south of it in Ecuador (*N. atrata*, *N. conspersa*, *N. tenuistriata*, *N. apicina*). Of the other two, *N. fuscolineata* is likely a chance immigrant in Ecuador, whereas *N. dubiosa* has not been recorded south of Isla Gorgona, which is a stepping stone of rocky shore within the gap. Conversely, *N. sauteleuae* is endemic to Ecuador and northern Peru. The status of *N. paytensis* is uncertain; it is abundant in Ecuador and northern Peru, but there are only three records from Colombia and Costa Rica, only one of which was of a large population; it may therefore be another species virtually endemic to the tropical region south of the Colombian Gap. This gap is evidently a less effective barrier for littorinids than the two farther north, perhaps owing to the presence of stepping stones, but is still significant for some. These data as yet provide little evidence upon which to subdivide the Panamic Province, although the possibility should be considered when the poorly known Ecuadorean fauna is studied. It should also be noted that as natural coastlines are altered by clearing of mangroves and building of marine structures to act as artificial stepping stones, these three gaps in the rocky-shore fauna of the TEP may become less effective, permitting permanent range extensions into adjacent provinces (Glynn & Ault, 2000).

While the correspondence between littorinid distributions and the provinces of the TEP is striking, the habitat and water gaps delimiting the provinces clearly do not present impassable barriers. In fact there are eight known cases of species that are recorded as rare arrivals in adjacent provinces (Table 4; not including two extensions into the temperate Californian and Peruvian Provinces). The dispersal capabilities of tropical littorinids are not known in detail. Only a single species, *N. hawaiiensis*, has been successfully reared in the laboratory, taking on average 24 days from spawning to metamorphosis at 25°C (Struhsaker & Costlow, 1968, as "*Littorina picta*"). From similarities in oviduct structure and protoconch throughout the genus, planktotrophic development in the *Nodilittorina* species of the TEP is predicted to be similar to that of this Indo-Pacific species. At this rate of development, a moderate current speed of only 40 km per day would be sufficient to transport pelagic eggs and larvae for 1000 km. Therefore it is not remarkable that mainland species reach the Galápagos Islands, or that species can span the Central American Gap. More surprising is that these barriers are so effective and that immigrants do not become established. While environmental conditions or competitive effects might be invoked, it should also be noted that establishment of self-sustaining populations of planktotrophic-developing species at a large distance from the source population is difficult, since pelagic eggs and larvae are swept away from founding individuals and settle only at very low density (Johannesson, 1988). Thus wide habitat gaps may indeed be effective barriers to colonization, although not to occasional immigration. In as-

sessing the causes of provinciality within the TEP, it is interesting to compare the distributions of *Nodilittorina* with those of the only other native littorinid genus, *Littoraria* (Table 4; Reid, 1999a). Of the six endemic *Littoraria* species, only one (*L. pintado pullata* (Carpenter)) occurs on rocky shores and this is restricted to the Mexican Province (the southern tip of Baja California and Mexican mainland), but also including Clipperton Atoll (at the boundary between the Indo-West Pacific and TEP) and Isla del Coco (classified as part of the Panamic Province). However, the five remaining species inhabit mangrove trees and (in some cases) salt marsh vegetation. Of these five, three are strictly Panamic, whereas two (*L. variegata* (Souleyet) and *L. rosewateri*) extend the length of the TEP from the Gulf of California to Peru. These species are more widespread than any of the rocky-shore *Nodilittorina* species, perhaps because the mangrove habitat is more continuous (and provides more opportunities for dispersal by rafting). For these mangrove-associated species the significant barrier is the expanse of rocky shore without open-coast mangrove habitats (Glynn & Ault, 2000) along almost the entire mainland coast of the Mexican Province (Reid, 1999a). Significant barriers to dispersal, and hence the designation of "provincial boundaries," can therefore differ among ecological (and taxonomic) groups of animals.

To the west of the TEP lies the great expanse (at least 5400 km) of open ocean that constitutes the Eastern Pacific Barrier, the most effective oceanic barrier to the dispersal of shallow-water fauna in the world's oceans (Grigg & Hey, 1992). Even this barrier is not impermeable to animals with sufficiently long pelagic stages and it acts as a largely unidirectional (west to east) filter bridge (Glynn & Ault, 2000). Recently, three littorinid species from the Indo-West Pacific (IWP) Province have been recorded from the TEP for the first time, from Clipperton Atoll, Isla del Coco, and Costa Rica (Reid & Kaiser, 2001). So far, no trans-Pacific *Nodilittorina* species have been found in the TEP. The most isolated of the oceanic islands in the TEP is Clipperton Atoll, with the highest representation of IWP fauna in the TEP (Emerson, 1991; Robertson & Allen, 1996; Glynn & Ault, 2000). Of the TEP *Nodilittorina* species only *N. modesta* is found at Clipperton Atoll, where it is an occasional immigrant.

This review of provinciality in the rocky-shore fauna of the TEP holds potentially important implications for systematic malacology in the region. The prevailing concept in the malacological literature of a uniform "Panamic Province" from the Gulf of California to northern Peru (i.e., equivalent to the TEP region) is based largely on two influential studies of bivalves (Olsson, 1961; Bernard et al., 1991). Since bivalves are predominantly a subtidal, soft-bottom group, this may explain why the provinciality of the TEP has not been more widely noticed previously. As revisionary work progresses on the

shallow-water gastropods of hard substrates, it is likely that genera in addition to *Nodilittorina* will show a more marked provincial diversity than is currently recognized. Already Vermeij (2001) has indicated examples in the genera *Neorapana*, *Stramonita*, and *Nerita*. Even in some infaunal bivalve genera, careful systematic work has revealed provincial endemics as well as genuinely widespread species (Coan, 1983; Roopnarine, 1996). In future, when sampling supposedly widespread species from the TEP for systematic and genetic purposes, samples should be included from the four TEP provinces described here (Figure 23) and long known in other animal groups.

Historical Biogeography and Speciation

In the absence of both a rigorous phylogenetic hypothesis and a fossil record, discussion of historical biogeography and patterns of speciation can only be speculative. The Pliocene history of Central America is dominated by the uplift and (at 3.1–2.8 Ma) final closure of the Isthmus of Panama (Coates & Obando, 1996). This vicariant event separated the biota of the TEP and tropical western Atlantic and had profound evolutionary consequences, being followed by a marked impoverishment of the tropical American marine fauna. The causes and timing of the extinctions are still debated, but they had a more pronounced effect in the Caribbean. As a result, during the later Pliocene many of the taxa formerly widespread in tropical America became restricted to the Pacific side of the isthmus, far outnumbering those that survived only on the Atlantic side (Vermeij & Petuch, 1986; Vermeij, 1991, 1993). Nevertheless, overall molluscan diversity has remained comparable in both oceans, perhaps because extinction in the western Atlantic was balanced by speciation and immigration (Allmon et al., 1993, 1996; Jackson et al., 1993). However, when inter-oceanic comparisons have been made within single molluscan clades with a good fossil record, they have revealed both higher extinction in the western Atlantic and higher diversification in the TEP, resulting in the modern higher diversity of the latter (e.g., chionine Veneridae, Roopnarine, 1996; *Strombina*, Jackson et al., 1996; *Thais*-like muricids and others, Vermeij, 2001). Among littorinids, there is evidence of higher modern diversity in the TEP than in the western Atlantic within a clade of mangrove-associated members of *Littoraria*, but in the absence of a fossil record this cannot yet be ascribed to differential diversification or extinction (Reid, 1999a).

Against this background, the perceived higher diversity of the genus *Nodilittorina* in the Caribbean than in the TEP under previous classifications of the group was surprising. The most recent listing (Reid, 1989a) gave five species in the TEP (*N. porcata*, *N. albicarinata*, *N. modesta*, *N. aspera*, *N. galapaguisis*) and eight (*N. meleagris*, *N. mespillum*, *N. angustior* (Mørch), *N. dilatata*, *N. interrupta*, *N. riisei*, *N. tuberculata*, *N. ziczac*) in the Ca-

ibbean. The revision of *Nodilittorina* species in the TEP shows that this is not in fact the case, the recognized total for the entire TEP region being 15 species (Table 4). Despite the relatively recent separation of the TEP and Caribbean faunas, the possible phylogenetic relationships between *Nodilittorina* species on either side of the Isthmus remain obscure. As suggested earlier, the *N. porcata* group may perhaps be a sister-radiation to the Caribbean pair, *N. meleagris* and *N. mespillum*, and the *N. aspera* group shows some similarity to the *N. ziczac* group in the Caribbean. Nevertheless, the lack of clear trans-isthmian relationships implies that significant diversification and/or extinction in the two regions has taken place since their separation.

Preliminary studies of the distributions of sister-species pairs in Littorinidae suggest that the prevailing mode of speciation has been allopatric (Reid, 1994, 1996). The distributional data for *Nodilittorina* in the eastern Pacific support this conclusion, since species pairs and triplets that are likely most closely related are largely allopatric (Table 4). Whether speciation in these cases has proceeded by vicariance of an originally more extensive range by imposition of a barrier to gene flow, or by dispersal across a pre-existing barrier (founder or peripatric speciation) cannot yet be ascertained (except in the case of Galápagos and Juan Fernández endemics, for which only founder speciation is possible). If, as argued earlier, habitat gaps are the main determinants of range limits for these species in the TEP, then knowledge of the age of the coastal landforms will be important. The observation that dispersal across these barriers is relatively frequent might suggest that founder events have played a part.

This diverse group of rocky-shore gastropods, with precisely known geographical distributions, could provide a model system for the study of speciation in the TEP. First, however, a robust phylogenetic hypothesis is required and, for this, molecular data are now being sought.

Acknowledgments. Field work in Costa Rica was undertaken during the tenure of a postdoctoral fellowship at the National Museum of Natural History, Smithsonian Institution. In Costa Rica I thank the Consejo Nacional de Investigaciones Científicas y Tecnológicas for permission to use the Laboratorio de Investigaciones Marinas at Punta Morales, the Organization for Tropical Studies for transport, and W. A. Szelistowski for assistance in the field. I am most grateful to S. A. Jeffcoat for help during field work in Mexico. Collections in southern Chile were made during an expedition jointly organized by The Natural History Museum and Raleigh International, funded by the British Government's Darwin Initiative for the Survival of Species. Fieldwork in Ecuador was assisted by a grant from the Percy Sladen Memorial Fund of the Linnean Society of London. In Ecuador a field trip was kindly arranged by M. Cruz and E. Mora, assisted by A. Calles, M. F. Arroyo, and D. Merino. In the Galápagos, facilities at the CDRS were provided by R. H. Bustamante. A visit to USNM to examine the collections was funded by the short-term visitor program of the Smithsonian Institution.

Loans of specimens were kindly arranged by R. Germon (USNM), L. T. Groves (LACM), A. J. Baldinger (MCZ), E. J.

Kools (CAS), K. Davis (ANSP), and R. Janssen (SMF), and from the personal collections of K. L. Kaiser and G. J. Vermeij. Additional specimens were collected by R. Bieler, J. Dyson, Y. Finet, R. N. Hughes, D. Kadolsky, C. Richardson, D. G. Robinson, C. F. Sacchi, R. S. Scheltema, and D. Voltolina. I thank G. J. Vermeij for helpful comments on the manuscript and Y. Finet (MHNG) for the photograph of the lectotype of *N. peruviana*. For their assistance with electron microscopy I thank C. Jones and A. Ball, for help with electronic images of maps J. Chimonides, and for expert photography H. Taylor, N. Hayes, and P. Crabb (all BMNH).

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