博士論文

Evolutionary history, species diversity and biogeography of amphidromous neritid gastropods in the Indo-West Pacific

（インド・西太平洋域における両側回遊性アマオブネ科腹足類の
進化史および種多様性と生物地理に関する研究）

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Chapter 1: General Introduction

1-1: Amphidromy in tropical and subtropical freshwater fauna

Island biodiversity has been a major topic of debate in evolutionary ecology and conservation biology. Islands generally form unique ecosystems because they are isolated from other islands and continents (Grant 1998). With such patchy and fragmented conditions, the role of immigration and extinction in relation to area size and proximity to source areas has been elaborated in the theory of island biogeography (MacArthur & Wilson 1963, 1967; Locos & Schluter 2000; Emelson & Kolm 2005). When an island is colonized by dispersal from other islands and continents, the physical and genetic separation of populations often leads to an important evolutionary consequence—speciation (Mayr 1970; Turelli *et al.* 2001; Thorpe *et al.* 2008). The speciation process due to geographic isolation is further promoted by the founder effect (Comes *et al.* 2008). Adaptive radiation and speciation may also occur on isolated islands with unoccupied niches (Grant 1998). Island fauna and flora thus tend to be unique, but many endemic and locally adapted species occupy limited geographic areas and have small population sizes and specific habitat requirements. Island biodiversity is now being threatened by human activities including habitat destruction and introduction of invasive species, which have resulted in local or global extinction and consequently a loss of ecological stability (Whittaker & Fernández-Palacios 2007).

In tropical and subtropical regions worldwide, numerous continental and oceanic islands exist and many such islands have freshwater streams (Falkland 1991). In general, island streams are smaller than continental rivers, having relatively high gradients and short distances from headwaters to stream mouth (McDowall 2007). Such streams are too short, thus in the tropics they become raging torrents during the rainy season, while during drought they may be dried up (McDowall 2007; Kano et al. 2011). These environmental conditions present a serious problem for primary freshwater animals that spend the whole lives in streams and rivers, even if they could somehow colonize the islands by rare, stochastic dispersal events (Strong et al. 2008; McDowall 2010). Amphidromous animals, on the other hand, flourish in the streams of tropical and subtropical islands (McDowall 2010; Kano *et al.* 2011).

Amphydromy or amphidromous life cycle has been defined by McDowall (2010) as follows: (1) spawning occurs in freshwater, where egg development also takes place; (2) hatched larvae are immediately transported to sea in the flows of streams; (3) they spend a few weeks to a few months at sea, feeding and growing; (4) there is a return migration to freshwater by small post-larvae to well-grown juveniles; (5) they then mature and spawn, thus completing the cycle. Since the introduction of the term as a subcategory of diadromy by Myers (1949), this life cycle has been found in many different animal lineages (Table 1-1), such as fishes (e.g. Gobiidae, Eleotridae and Plecoglossidae), crustaceans (e.g. Atyidae and Palaemonidae) and gastropod molluscs (Neritidae, Neritiliidae, Stenothyridae, Thiaridae and Acochlididae; Fig. 1-1). Most amphidromous animals are microalgal herbivores, feeding on stream periphyton (e.g. McDowall 2007; Bauer 2011; Kano et al. 2011). The intensities of competition as well as predation in upstream freshwater environments may be lower than in most marine environments; this is particularly the case on islands due to the inaccessibility for non-diadromous competitors and predators (Holthuis 1995; McDowall 2010). The short and steep conditions of the island streams are also favorable for the amphidromous animals. These conditions provide easier access of amphidromous larvae to the ocean and easier access of settled juveniles to upper streams.

The females of most amphidromous species reproduce a larger number of smaller eggs than those of non-diadromous, direct developing species do (McDowall 2010; Kano et al. 2011; Bauer 2011). These reproductive traits, known as r-strategy, involve a greater risk of offspring mortality than the so-called K-strategy of direct developers but often give an advantage in heterogeneous or unstable environments (e.g. Strathmann 1985). The rate of larval transport to new habitats can be significantly enhanced by the presence of such numerous larvae. Also, the hatched larvae of amphidromous species have a planktotrophic stage that enables exploitation of the trophic riches of the marine phytoplankton during the long pelagic life (McDowall 2007). The mechanisms of amphidromy thus allow larval dispersal and (re)colonization of streams in remote islands, where habitats may be ephemeral and there is a risk of local extirpation (McDowall 2010). Correspondingly, recent studies have revealed low genetic variations among distant populations (Bebler & Foltz 2004; Cook et al. 2006; Hoareau et al. 2007; Crandall et al. 2010; Castelin et al. 2013). For instance, two species of amphidromous neritid gastropods show high gene flow over several thousands of kilometers among South Pacific archipelagos (Crandall et al. 2010). An amphidromous prawn *Macrobrachium lar* similarly reveals a low level of genetic structure across the West Pacific and between Indian and Pacific Ocean basins (Castelin et al. 2013). For these reasons, amphidromy plays a key ecological role and is the most prevalent life history strategy in low-latitude island streams (McDowall 2007, 2010; Kano et al. 2011; Watanabe et al. 2013). For example, amphidromous life cycle is represented by 50% of the total fish fauna on the West Pacific islands (Thuesen et al. 2011).

This predominance of the amphidromous life cycle in tropical island streams exhibits a clear contrast to the general lack or rarity of a planktonic stage in other freshwater realms. Species with pelagic early development comprise less than 10% of the freshwater, free-living invertebrate fauna worldwide, while the proportion is about 80% for tropical, shallow-water marine invertebrates (Thorson 1950; Holthuis 1995). The general paucity of planktonic development in freshwater ecosystems may be attributable to the fact that continental rivers, ponds and lakes are often less rich in phytoplankton as their diet than in the sea (Holthuis 1995). Also, running water sweeps swimming larvae downstream, possibly too far away from adult habitats in long rivers (Holthuis 1995; McDowall 2010). The risk of long-distance dispersal and cost of long upstream migration may not be advantage the above benefits if the natal habitat is rich and stable enough. Some amphidromous species reproduce long distances upstream in rivers, but the newly hatched larvae may be at risk of irreversible larval starvation during migration to sea (Iguchi and Mizuno 1999). Indeed, many lineages with amphidromous taxa have given rise to species with direct development, predominantly on the continents and continental islands (e.g. Hayashi 1999, 2007; McDowall 2004, 2007, 2010).

Despite such critical importance of amphidromous animals in heterogeneous stream environments on tropical and subtropical islands, fundamental studies on their taxonomy, phylogeny, ontogeny and ecology are still badly needed (Dudgeon et al. 2006; McDowall 2007, 2010; Kano et al. 2011). Islands generally have a limited capacity to buffer against environmental hazards and they possess a low resilience to disturbance (Smith et al. 2003; Van der Velde et al. 2007). Economic developments in tropical countries, such as agriculture, fisheries, industrialization and tourism, may lead to environmental impacts on water resources, along with pollution, degradation, erosion and loss of biodiversity (e.g. Dudgeon et al. 2006). However, our taxonomic knowledge in many parts of the tropics is inadequate to document extinctions and widespread undetected extinctions of inconspicuous species have already taken place (Harrison & Stiassny 1999; Stiassny 2002; Dudgeon et al. 2006). This is particularly true to invertebrate animals, including gastropod and bivalve molluscs. There have been more documented extinctions of non-marine molluscs than of mammals and birds combined, although this is not reflected in the priorities of conservation agencies (IUCN 1996; Ponder & Walker 2003). Indeed, the lack of taxonomic information for many tropical groups may disrupt to estimate or accurately project extinction rates of freshwater biodiversity (Dudgeon et al. 2006). Amphidromous animals do not seem to be an exception to this trend, regardless of their high dispersal capability that apparently makes them less prone to local destruction and species extinction. McDowall (1999) proposed that the transition from fresh to marine habitats is particularly critically threatened, because it is in the coastal zone where urban and industrial development has the largest impacts on the hydrological situation and environmental quality. For example, the New Zealand grayling fish *Prototroctes oxyrhynchus* has become extinct in New Zealand by the early 1930s due to deforestation and competition with invasive species (McDowall 1996). Summing up, comprehensive approaches to the natural history of amphidromous species are the first step in elucidating the formation and maintenance mechanisms—and in promoting conservation—of freshwater ecosystems on tropical and subtropical islands.

1-2: Neritidae as a model group for understanding tropical stream ecosystems

Neritidae is one of eight families in the gastropod superorder Neritimorpha (= Neritopsina). The members of Neritidae, a small to medium sized snails and limpets, are widely distributed to various environments ranging from intertidal rocky shores, seagrass beds and mangrove forests to estuaries and streams in tropical to temperate regions worldwide. Freshwater species are among the most dominant animals in tropical streams and most of them have amphidromous life cycles (Kano 2006; McDowall 2010; Kano et al. 2011). For their large biomass, they are used for food in tropics (Kurozumi et al. 1990; Poutiers 1998; Scott & Kenny 1998). With their exceptional longevity that occasionally exceeds 20 years, netritid snails are known to crawl upstream for long distances, sometimes to tens of kilometers (Schneider & Lyons 1993; Shigemiya & Kato 2001; Kano 2009; Kano et al. 2011). Amphidromous neritids produce a large number of small-sized eggs, and they disperse across the ocean as planktotrophic larvae whose pelagic period may extend over several months (Holthuis 1995; Kano 2006; Crandall et al. 2010). Their geographic distribution ranges are relatively wide to enormous; some species are known to distribute from the east coast of Africa to French Polynesia (Kawaguchi 2007; Kano et al. 2011). Population genetic analyses have revealed that the dispersal potential of amphidromous neritids is often as high as that of entirely marine species in the same family (Myers et al. 2000; Bebler & Foltz 2004; Crandall et al. 2010).

Shell-bearing gastropods including neritids have many advantages in understanding various aspects of life history strategies and diversity, thanks to the appositional growth of the exoskeleton that records the ontogenetic history of each individual (Jablonski and Lutz 1983). Their early developmental mode, i.e. planktotrophic or non-planktotrophic, can be inferred from the morphology of larval shell at the apex of the adult shell (Shuto 1974; Lima and Lutz 1990; Rex and Etter 1998; Kano 2006). Also, the growth lines of the adult shell may be used as an indicator of age (Shigemiya & Kato 2001). A huge number of neritid specimens have been collected and deposited in museums since the age of European colonization in various tropical regions of the world (Kabat & Finet 1992). Shell specimens are often well represented and preserved as they are not too small or too large (several millimeters to a few centimeters) and can be deposited in a dry condition. Such specimens enable us to assess species compositions in the past and present (e.g. Cowie & Cook 2001; Cowie & Robinson 2003). Furthermore, fossils of freshwater neritids have been recovered from different ages since the Jurassic (Kano et al. 2002; Symonds & Pacaud 2010).

These characteristics potentially make the Neritidae a promising and valuable model group in the study of amphidromy in low-latitude island streams. However, this group does not form an exception to our poor current state of knowledge on the natural history of freshwater invertebrates. In the lines below, I present a summary of what is and is not known for these gastropods.

1-3: Origin and evolution of amphidromous taxa

A good phylogeny with resolved relationships among genera and species based on comprehensive taxon sampling provides vital information on the origin and evolutionary transitions of life history strategies as well as past dispersal events. However, such a phylogeny analysis has not been obtained for the Neritidae and relationships are not well understood among the amphidroumous and other taxa. A previous study based on the detailed morphological examination and cladistic analyses has shown that the freshwater species are not monophyletic, having invaded stream habitats multiple times during their evolution (Holthuis 1995). Direct development also seems to have occurred parallelly in the same family (Holthuis 1995; Kano 2006; Frey & Vermeij 2008). However, the robustness of the tree topology was not tested and the history of their radiation has remained largely elusive, and the selection of study species and number of characters were not suitable and sufficient enough to reveal deep nodes and relationships. Multi-gene sequences of both nuclear and mitochondrial genes from comprehensively sampled taxa would better estimate the neritid phylogeny, allowing us to map ecological, ontogenetic and morphological traits onto the tree as the first step in inferring the evolutionary history of the family. Resolving this phylogeny would help in understanding general evolutionary trends in the amphidromous animals on tropical and subtropical islands, such as the historical origins of migration, acquisition of direct development and adaptive specialization of morphological traits in the stream environments.

1-4: Morphology, ecology and evolution of planktotrophic larvae

Information on larval dynamics and dispersal in the ocean is vitally important for understanding the life cycles of amphidromous animals. Although such study should be very difficult without identifying larvae, our knowledge on the larval morphology of amphidromous species is particularly poor for invertebrates (e.g. Kikkawa et al. 1995; Nakahara et al. 2007). In fact, the collection of these amphidromous larvae has never been observed in the ocean beyond brackish river mouths. Rearing experiments on larvae are also very limited (Holthuis 1995), and thus their dispersal abilities are inferred mainly from population genetic analyses (e.g. Cook et al. 2006; Crandall et al. 2010; Castelin et al. 2013). As mentioned earlier, an important advantage of shell-bearing gastropods is that the accretionary growth of the shell throughout their ontogeny leaves the larval shell at the apex of the adult shell as the protoconch (Jablonski and Lutz 1983). The presence or absence of larval feeding (planktotrophy) can be inferred from the protoconch morphology, and also the settlement size of larvae has been studied through the measurement of the protoconch on adult shells (e.g. Shuto 1974; Lima and Lutz 1990; Rex and Etter 1998; Kano 2006). Moreover, the pelagic larval duration may be inferred from settlement size or the size of the protoconch in gastropods (Scheltema 1971; Hadfield and Switzer-Dunlap 1984; Kohn and Perron 1994).

The apex of a gastropod shell is often worn and eroded and such inference is not feasible in acidic freshwater streams. In the Neritimorpha, however, the operculum of the larval shell remains as the opercular nucleus in almost all adult specimens and can instead be used for the same purpose (Kano 2006). The diameter of the opercular nucleus often differs among genera or families while the intraspecific variation is negligible (Kano 2006). This makes the size of the opercular nucleus further useful as a taxonomic key for the identification of neritid larvae as well as newly settled juveniles (Kano 2006). Moreover, the multispiral protoconchs of planktotrophic neritimorphs are extremely uniform in shape with the operculum closely fit into the aperture (Bandel 1982; Kano 2006; Page and Ferguson 2013). The size of the protoconch, which roughly corresponds to the body size at settlement, may be therefore potentially correlated with, and inferred from, the size of the nucleus retained in the adult operculum. Interspecific variation in settlement size has been often attributed to the ecological characteristics of individual species in aquatic animals (e.g. Lesoway and Page 2008). Comprehensive data on settlement size in neritids from different types of habitats is of particular importance to better understand the evolutionary trends of larval ecology in amphidromous animals.

1-5: Species and population diversity, taxonomy and biogeography

Over 1,000 species names have been proposed for neritid gastropods, of which approximately 600 were given for limnic species (Reeve 1855–1856; Martens 1863–1879, 1881; Tryon

1888; Kabat & Finet 1992). Most of the limnic taxa are living in tropical to subtropical island streams with the amphidromous life cycle, but the preconceived idea that islands harbor isolated, endemic faunas apparently led to an overestimation of the global diversity and description of so many species until the mid-20th century. Later on and in recent years, taxonomists tend to lump and many names have been regarded as the junior synonyms of only about 50 species in the entire Indo-West Pacific region (e.g. Komatsu 1986; Starmühlner 1986; Tsuchiya 2000; Haynes 2001, 2005). However, this may well be an underestimation, because neritid shells sometimes exhibit quite subtle differences between species in their shape, color and markings and it is often accompanied by considerable intraspecific variation (Kano et al. 2011). Thus species identification is difficult without understanding the exact ranges of within-species variation in these characters by using independent criteria, such as DNA barcoding.

Ocean currents and adult habitat suitability seem to be among the most important determinants of distribution of amphidromous neritid species (Crandall et al. 2010) and astonishing dispersal ability has been estimated by population genetics (e.g. Cook et al. 2009). However, the distribution areas of most species are not clearly demonstrated due to the lack of our knowledge on their taxonomy. Previous discussion on the biogeography of tropical freshwater neritids has therefore been rather incomplete and possibly biased due to the currently fragmented and unsatisfactory information on how these species widespread in the ocean basins. Kawaguchi (2007) indeed shows, in his unpublished masters dissertation, that the total number of freshwater neritid species has been badly underestimated in Japan to half of the actual species richness by examining their molecular and morphological traits. Such multidisciplinary analysis, but with more comprehensive taxon sampling from all over the Indo-West Pacific, must shed new light on the understanding of the patterns of the species distribution, composition and diversity in island streams.

1-6: Aim, scope and outline of thesis

In the present dissertation, I explore the natural history of limnic neritids as a model group to understand the role and importance of amphidromy in low-latitude islands by taking the following three approaches in three chapters. Chapter 2 on evolutionary systematics provides a comprehensive, well-supported phylogeny of Neritoidea (including Neritidae, Phenacolepadidae and Neritiliidae) based on four gene sequences from 60 species representing most extant genera in this super family. The topics discussed there include how morphological and ecological traits have evolved in the Neritidae. Chapter 3 on larval ecology and evolution explores the global patterns of settlement size in planktotrphic neritimorphs in consideration with their phylogenetic and ecological backgrounds. Chapter 4 on taxonomy employs morphological characters and genetic markers to clarify the species diversity and distributions of amphidromous neritids in the Indo-West Pacific. Species taxonomy and biogeography are assessed and revised with comprehensively accumulated samples and museum specimens including type material. Finally in Chapter 5, I discuss the formation and maintenance mechanisms and conservation of diversity in the ecosystems of tropical and subtropical island streams that are dominated by amphidromous fauna.

Table 1-1. Taxonomic groups that include amphidromous species.

	Family	Reference
Teleostei		
Osmeriformes	Plecoglossidae	Nishida (2000); Watanabe et al. (2013)
	Galaxiidae (= Aplochitonidae)	McDowall (2004); Cross et al. (2013)
	Retropinnidae (= Prototroctidae)	McDowall (1988); Koster et al. (2013)
Clupeiformes	Clupeidae	McDowall (1988)
Scorpaeniformes	Cottidae	McDowall (2007)
Perciformes	Pinguipedidae (= Mugiloididae)	McDowall (1988)
	Eleotridae	McRae (2007); McDowall (2010)
	Gobiidae	Lord et al. (2010)
	Rhyacichthyidae	McDowall (1988)
Decapoda		
Brachyura	Varunidae	Vogt (2013)
Caridea	Atyidae	Hayashi (2007)
	Palaemonidae	Bauer (2011); Castelin et al. (2013)
	Xiphocarididae	Bauer (2011)
Gastropoda		
Neritimorpha	Neritidae	Holthuis (1995); Kano et al. (2011)
	Neritiliidae	Kano & Kase (2003); Kano et al. (2011)
Caenogastropoda	Stenothyridae	Strong et al. (2008)
	Thiaridae	Köhler & Glaubrecht (2003); Strong et al. (2008)
Heterobranchia	Acochlididae	Brenzinger et al. (2011)

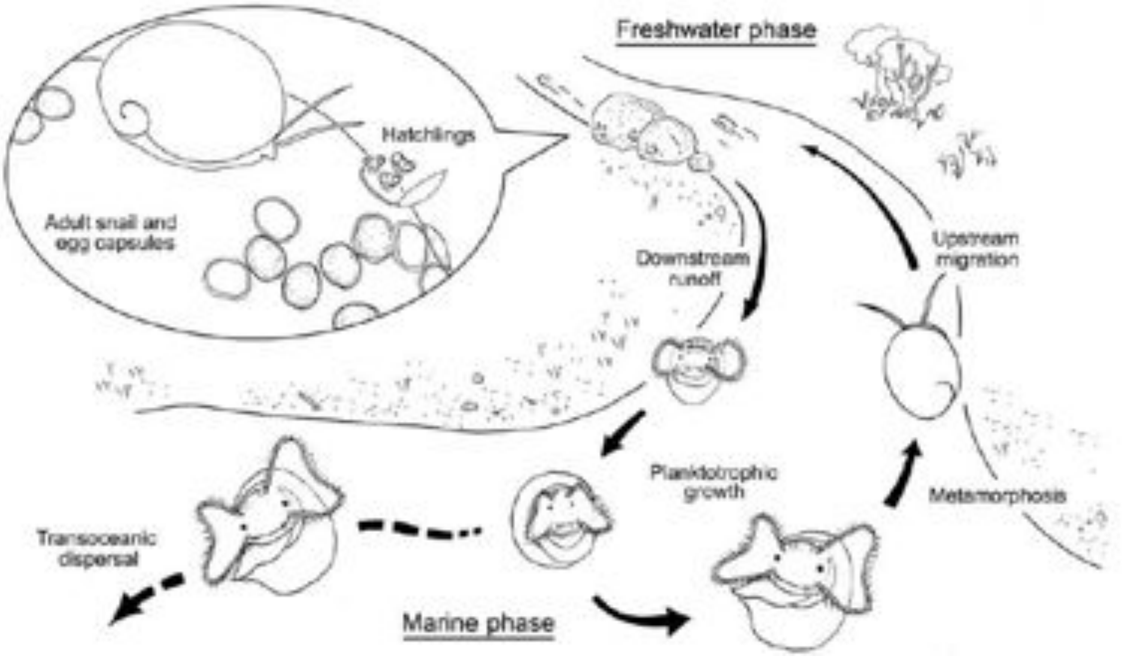


Figure 1-1. Schematic illustration for the amphidromous life cycle of the freshwater Neritidae and Neritiliidae (after Kano et al. 2011). (1) Mother snails lay egg capsules on rocks in the freshwater reaches of rivers. (2) Hatched larvae are swept downstream to the ocean. (3) The swimming marine larvae feed on phytoplankton and grow up. Most larvae apparently remain in the vicinity of the river mouth, but some may travel great distances with ocean currents and the luckiest of them may happen to drift to an estuary on a remote island. (4) Metamorphosis to crawling juveniles occurs at estuaries of rivers. (5) Young snails crawl upstream to the freshwater where they spend the rest of their life. Certain species migrate surprisingly long distances with over 10 years of longevity.

Chapter 2: Molecular phylogeny of the superfamily Neritoidea (Gastropoda: Neritimorpha)

2-1: Introduction

The class Gastropoda has been commonly divided into six superorders (Bouchet & Rocroi 2005). Of these, Neritimorpha is represented by a small group of snails, limpets and slugs, comprising over 2,000 living species (Kano et al. 2002). Their fossil record extends back at least to the Middle Devonian of ca. 375 million years ago (Knight et al. 1960). The superorder has been classified into four aquatic (Neritopsidae, Neritiliidae, Neritidae and Phenacolepadidae) and four terrestrial families (Hydrocenidae, Helicinidae, Ceresidae and Proserpinidae; Kano et al. 2002; Richling 2004). The aquatic families except Neritopsidae show similar anatomical and conchological conditions and they collectively constitute the superfamily Neritoidea (Holthuis 1995; Robertson 2007). Neritoid gastropods have adapted to various environments from the deep-sea to freshwater streams and evolved new morphological traits in accordance with their habitats (Kano et al. 2002).

The nominotypical family Neritidae contains a few hundred species that belong to marine (e.g. *Nerita*, *Puperita* and *Smaragdia*) or limnic genera (e.g. *Neritodryas*, *Theodoxus*, *Clithon*, *Neritina* and *Septaria*; Holthuis 1995; Kano et al. 2002). In tropical and subtropical regions, neritids flourish in intertidal and shallow subtidal zones as well as streams and brackish estuarine environments (Scott & Kenny 1998). They are small to relatively large, ranging from 3 to 40 mm in shell diameter. Most marine species have a hemispherical shell, while limnic species show considerable variation in shell morphology, such as high-spired conical, spiny, flat planispiral with wing-like edges of the inner lip, or completely limpet-like. Limnic species usually have an amphidromous life cycle and few undergo a direct or a lecithotrophic development (Holthuis 1995; Kano 2006).

Phenacolepadidae comprise approximately a hundred species inhabiting dysoxic, sulphide-rich environments in tropical to warm-temperate shallow seas. They are found on the under-surface of deeply embedded stones and decaying wood in soft sediments (e.g. the genera *Phenacolepas*, *Cinnalepeta* and *Plesiothyreus*) and at deep-sea hydrothermal vents and seeps (*Shinkailepas*, *Olgasolaris* and *Bathynerita*) worldwide (Kano et al. 2002). Although most phenacolepadids are limpets with a whitish shell of 3–30 mm, *Bathynerita naticoidea* has a hemispherical shell resembling those of neritid species and lives at oil and gas seeps in the Gulf of Mexico (Clarke 1989). The blood of phenacolepadids is red as they have erythrocytes that contain haemoglobin to increase the capacity of blood to transport oxygen (Fretter 1984; Sasaki 2001). Although phenacolepadids have such unique characters, they share many synapomorphies with neritids in internal anatomy (Kano & Kase 2002). A previous molecular phylogenetic analysis of the Neritimorpha using 28S rRNA sequences also strongly supports the monophyly of these two families (Kano et al. 2002).

The third family, Neritiliidae, comprises a few dozens of minute to small species in the limnic genera *Neritilia* and *Plathynerita* and in *Pisulina* and several other genera inhabiting submarine caves (Kano & Kase 2008). Because all limnic species are amphidromous and some species of the cave genera have a planktotrophic larval stage, they can be dispersed a great distance by ocean currents (e.g. Kano & Kase 2002, 2004, 2008; Kano 2006). Neritiliids show many differences from the Neritidae and Phenacolepadidae in anatomical and radular characters despite their close resemblance to neritids in shell morphology (Kano & Kase 2002).

The phylogenetic reconstruction of the Neritoidea was first attempted and described by Holthuis (1995: Ph.D. Thesis) based on 13 operational taxonomic units (OTUs) and 57 morphological characters, including the reproductive system, radula, shell and operculum. Later on, in their Masters dissertations Kawaguchi (2007) and Watanabe (2010) determined the nucleotide sequences of the mitochondrial (cytochrome oxidase *c* subunit I: COI) and nuclear (internal transcribed spacer 1 and 2: ITS1, 2) genes, respectively, for the species identification of neritid gastropods through phylogenetic reconstruction with these markers. However, those unpublished phylogenies were rather poorly resolved with low support values for branches, because the selection of study species and number of characters or sequence lengths were not suitable and sufficient enough to reveal deep nodes and relationships among neritoid genera in the family Neritidae (Kawaguchi 2007; Watanabe 2010). As a result, fundamentally different tree topologies were inferred from those mitochondrial, nuclear and morphological datasets (Holthuis 1995; Kawaguchi 2007; Watanabe 2010). Quintero-Galvis and Raquel-Castro (2013) recently published a phylogeny of the Neritidae based on the partial sequences of COI and 16S rRNA (16S) genes, but again support values for nodes were very low due to insufficiently long sequences and biased taxonomic sampling for phylogenetic inference. Multi-gene sequences from both nuclear and mitochondrial genes and more comprehensive taxon sampling are needed to better estimate the phylogeny and evolutionary history of the Neritoidea.

Interestingly, the limnic species of the Neritidae did not form a monophyletic clade in the morphological analyses by Holthuis (1995), and thus multiple freshwater invasions have been suggested. Direct (benthic) development also seems to have occurred parallelly in the same family (Holthuis 1995; Kano 2006). The reconstruction of a comprehensive and robust phylogeny at genus and species levels is significant to map ecological, ontogenetic and morphological traits onto the tree as the first step in inferring the evolutionary history of the Neritoidea. This reconstruction is also important in understanding general evolutionary trends in the amphidromous animals of tropical islands, such as the historical origins of migration, acquisition of direct development and adaptive specialization of morphological traits in the stream environments.

Further importance of resolving the evolutionary history and acquisition of amphidromy (i.e. freshwater invasion) in neritoids that are very abundant in tropical and subtropical streams relates to the understanding of the origin and history of the island stream biota. In this chapter, I show a well-resolved phylogeny based on the partial sequences of three mitochondrial (COI, 16S and 12S) and one nuclear (28S rRNA) genes (ca. 4,500 bp in total length) from 20 genera and 60 species that represent most living genera of the Neritoidea. The evolutionary consequences of transitions of habitat types, modes of development and morphological traits are discussed by the maximum-likelihood reconstruction of these characters on the inferred topology.

2-2: Materials and Methods

Taxonomic sampling

Sixty neritoid specimens were collected and selected for the present molecular analysis to increase the total phylogenetic diversity of OTUs (Table 2-1). Results from morphology-based classifications were adopted for this purpose (Warén & Bouchet 1993, 2001; Holthuis 1995; Kano & Kase 2000, 2002, 2004, 2008; Kano et al. 2011), and as many recognized genera and subgenera as possible were included in the analysis. Besides, the COI barcode of the Indo-West Pacific Neritidae was referred to for the selection of the OTUs (see Chapter 4). Familial and generic assignments tentatively followed Holthuis (1995), Kano et al. (2002), Bouchet & Rocroi (2005) and Frey & Vermeij (2008) for this selection of OTUs. Holthuis (1995) used the Neritinae for the genus *Nerita* and “Theodoxinae” as the subfamily name for ten other recognized genera (*Neritodryas*, *Fluvinerita*, *Theodoxus*, *Smaragdia*, *Clithon*, *Vitta*, *Puperita*, *Neritina*, *Neripteron* and *Septaria*) of the Neritidae in her morphological analysis, while Theodoxinae Bandel, 2001 may be a junior synonym of the Neritininae Poey, 1842 (Bouchet & Rocroi 2005). These specimens were sampled from intertidal to subtidal rocky shores, mud flats, mangrove swamps and coastal ponds (*Nerita*, *Puperita*, *Chinnalepeta*, *Plesiothyreus* and *Phenacolepas*), seagrass beds (*Smaragdia*), brackish to freshwater streams, rivers and ponds (*Neritilia*, *Plethynerita*, *Theodoxus*, *Clithon*, *Vitta*, *Neritina*, *Neripteron*, *Septaria* and *Neritodryas*), submarine caves (*Pisulina*), and hydrothermal vents and a cold seep (*Bathynerita*, *Olgasolaris* and *Shinkailepas*) in worldwide locations (Table 2-1). Two species of Neritopsidae (*Neritopsis radula* and *Titiscania shinkishihataii*) were also included as outgroup taxa in the data set. The Neritopsidae represent the earliest offshoot of the superorder Neritimorpha (Holthuis 1995; Kano et al. 2002).

Most snails were boiled in 70–90ºC water for 10–30 sec after sampling (*Niku-nuki* method: see Fukuda et al. 2008) and the animals were extracted from the shells and then preserved in pure ethanol. Other snails were relaxed in 7.5% magnesium chloride, or shells were cracked prior to ethanol-preservation. The identification of specimens was based on original descriptions and revisional papers, as well as the photographs of type specimens whenever available. However, some snails seemed to represent undescribed species and rigorous assignment was difficult in such cases. Voucher material has been deposited at the Atmosphere and Ocean Research Institute, The University of Tokyo, Japan (AORI), or Muséum National d'Histoire Naturelle, Paris, France (MNHN). All shell, operculum, radula and cephalic part of the animal were kept undamaged in most specimens for future taxonomic studies.

DNA extraction, amplification and sequencing

DNA was extracted with Qiagen DNeasy kit from the preserved foot tissue of specimens. Table 2-2 summarizes the primers used in this study. Two fragments of the mitochondrial COI gene were amplified using the primer pairs (1) LCO1490 and HCO2198 and (2) COIf, COIf-A, COIf-B, COIf-D, COIf-G, COIf-J or COIf-L and COIa-NER for each species. PCR reactions were carried out in a final volume of 25 μl [2.5 μl genomic DNA template (ca. 100 ng), 17.5 μl ddH2O, 2.5 μl Takara ExTaq buffer, 2 μl dNTPs (2.5 μM each), 0.3 μl of each primer (20 μM), and 0.13 μl Takara ExTaq enzyme]. After an initial denaturation for 2 min at 94.5˚C, the reaction solution was run for 35 cycles with the following parameters: denaturation for 40 sec at 94.5˚C, annealing for 40 sec at 42˚C, followed by extension for 60 sec at 72˚C. A final extension was performed for 5 min at 72˚C. If COI amplification was unsuccessful under these conditions, primers were replaced with LCOmod and HCOmod or LCO-SMA and HCO-SMA, or alternatively nested PCR strategy was employed using the downstream COIa-NER primer for the first run. Three more fragments of nucleotide sequences from one nuclear and two mitochondrial genes were determined for the same 62 OTUs using the following primer pairs: 900F and Lg2, FL and na2, Fa and 28Sr2 for the 28S gene; 16SarL and 16SbrH for the 16S gene; 12S1 and 12S2 for the 12S gene. PCR reactions for 28S, 16S and 12S were carried out with following modifications: annealing temperatures at 50°C and extension for 90 sec, annealing at 50°C and extension for 60 sec; annealing temperatures at 48–52°C and extension for 90 sec. The PCR products were visualized by electrophoresis on 1.5% TBE agarose gel, which was stained with ethidium bromide and photo-documented.

Successful PCR products were purified by ExoSAP-IT (USB) treatment in a total volume of 3.8 μl using approximately 1.5 μl of the PCR amplicon and 0.3 μl ExoSAP-IT enzyme with ddH2O. After enzyme incubating at 37°C for 40 min, the ExoSAP-IT was inactivated by heating at 80°C for 15 min. Both strands were directly cycle-sequenced using the amplification primers with a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) on an ABI 3130 automated sequencer at AORI. The accuracy of each sequence fragment was checked by a BLAST search and comparison with homologous sequences from closely related taxa.

Sequence analysis and phylogenetic reconstruction

Sequences of the three rRNA (28S, 16S and 12S) genes were aligned individually by ProAlign 0.5 (Löytynoja & Milinkovitch 2003) with the band-width set to 500. Regions with posterior probabilities below 70% were regarded as alignment-ambiguous sites and were excluded in the succeeding analyses. The COI sequences were aligned by eye in MacClade 4.08 (Maddison & Maddison 2005), as there was no indels. Nucleotide composition, variable and parsimony informative positions, and transition-transversion rates were estimated using MEGA 5 (Tamura et al. 2011).

Phylogenetic trees were reconstructed from five datasets using the Bayesian inference. The first four datasets consisted of independent gene sequences; the fifth dataset concatenated sequences from all four genes. Bayesian analyses were performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). The GTR + G and GTR + I + G models were chosen for the 12S gene and the remaining genes, respectively, on the basis of the Akaike information criterion (AIC; Akaike 1974) implemented in Kakusan4 (Tanabe 2007; Tanabe 2011). The shape, proportion of invariant sites, state frequency and substitution rate parameters were estimated for each codon position separately in the amino-acid coding COI gene. Each gene was allowed to have different parameters in the concatenated dataset, hence the dataset involving all four genes had six partitions of parameters. Two parallel runs were made for 5,000,000 generations (with a sample frequency of 1,000) using the default value of four Markov chains. The first 1,150 trees for each run were discarded to ensure the four chains reached stationarity by referring to the average standard deviation of split frequencies (Ronquist & Huelsenbeck 2003). Consensus trees and posterior probabilities (PP) were computed from the remaining 7,700 trees (3,850 trees x 2 runs). Posterior probabilities equal to or above 95% were considered significant support. The phylogenetic trees were graphically edited in FigTree v1.3.1 (Rambaut 2007: http://tree.bio.ed.ac.uk/software/).

The same five datasets were also analyzed using the maximum likelihood (ML) method in RAxML 7.4.2 (Stamatakis 2006). Bootstrap runs consisted of 1,000 pseudoreplicates with the GTR + G model for 12S dataset and with the GTR + I + G model for all other datasets, six partitions and parameters estimated from the data, following the software manual. Bootstrap probabilities (BP) equal to or above 75% were considered significant support.

In order to better understand the relationships among genera or subfamilies in the Neritidae, a separate phylogenetic reconstruction was made only for the clade of the Neritidae and Phenacolepadidae based on a new alignment of the four genes (COI, 16S, 12S and 28S). The Neritiliidae were used as outgroup taxa and the two species of Neritopsidae were not included in this analysis. Sequences of the three rRNA genes were aligned and edited individually by ProAlign with the same parameters as above. The Baysian and ML trees were reconstructed in MrBayes and RAxML in the same manner as described in the former lines.

Divergence time estimates

The divergence dates among neritoid species were calculated using the same four-gene dataset and a relaxed molecular clock model in the program BEAST 1.8.0 (Drummond et al. 2012). The GTR + I + G model was applied and parameters were unlinked across the six partitions. Sixty taxa including the Neritidae, Phenacolepadidae and Neritiliidae were constrained as a monophyletic group according to the results from the above Bayesian and ML analyses. Branch lengths and dates were estimated with an uncorrelated model in which the rate at each branch was drawn from an underlying log-normal distribution. The Yule model was used as the tree prior as recommended in the manual.

The tree was time-calibrated by setting priors on the ages of five neritimorph clades based on paleontological evidence. (1) Bandel & Frýda (1999) proposed that the ancient Neritimorpha split to form the Neritopsidae and all remaining extant neritimorph families, at some time near the Paleozoic–Mesozoic boundary (see also Kano et al. 2002). Following this hypothesis, I assumed a normal distribution centered at 248 million years ago (Mya) and a 95% highest probability density (HPD) interval of 223–275 Mya for the first split among the Neritimorpha. (2) The first divergence within *Nerita* was set to take place at 56 Mya in the Late Paleocene (95% HPD: 51–61 Mya). This was based on the appearances of two fossil species of the genus with different shell shapes in this period (Squires 1992; Squires & Saul 2002; see Frey & Vermeij 2008). (3) The oldest records of the extant freshwater genera *Clithon* and *Dostia* (= part of "*Neripteron*"; see below) from the Early Eocene (Symonds & Pacaud 2010) were used for two clades with similar shell shapes. The two clades include (a) *Clithon* + *Vitta* + *Vittina* + *"Neritina"* sp. from Vanuatu and (b) *Neritina pulligera* + *Neritina petitii* + *Neritina asperulata* + *Dostia* + *Septaria* except "*Septaria*" sp. from Palau, respectively, and the first split within each group was constrained at 52 Mya (95% HPD: 48–56 Mya). (4) The first occurrence of the definite *Plesiothreus* species from the Middle Eocene (Bartonian) shallow-water deposit of France (Knight et al. 1960; Tracey et al. 1993) was used to constrain the divergence date between *Plesiothreus newtoni* and *Cinnalepeta pulchella* + *Phenacolepas crenulatus* at 39.5 Mya (95% HPD: 36–42 Mya). (5) The split between *Plathynerita* and *Neritilia* was estimated to have occurred at 44.5 Mya (95% HPD: 40–48 Mya) based on the fossil records of *Plathynerita bisinuata* and undescribed *Neritilia* species, both in the Early to Middle Eocene of France (Lozouet 2004, fig. 2; Lozouet & Kano in preparation).

BEAST runs consisted of 200,000,000 generations (with a sample frequency of 1,000) that produced 200,000 estimates of divergence dates. The convergence and mixing of the chains were assessed in the program Tracer v.1.5.0 and first 20,000 estimates were discarded as burn-ins.

Ancestral character-state reconstruction of ecological and morphological traits

The ancestral states of morphological and ecological traits were reconstructed for neritoid gastropods by parsimony and Maximum likelihood methods in Mesquite 2.75 (Maddison & Maddison 2011). For the ML reconstruction, a Markov one-parameter model was used with the varying parameter being the rate of change in states. Neritoid species occupy a wide range of different aquatic habitats (Kano et al. 2002; Kano 2006), which can be divided into three groups by salinity, i.e. marine, brackish and freshwater environments. These habitat groups were mapped onto the best ML tree inferred from the four-gene dataset with all 62 species (see above). Other ecological traits including the early developmental mode and presence or absence of amphidromy, as well as the shell shape (snail *vs*. limpet), were also mapped onto the tree to infer the evolutionary history of the Neritoidea and to reveal possible convergent acquisition of the same state as a consequence of parallel adaptive radiation to freshwater habitats.

2-3: Results

Sequence data

The newly-generated partial COI sequences had a length of 1,276 bp excluding primer regions. Of these, 32 bp near the primers were only ambiguously determined and were excluded from the succeeding analyses, resulting in the final alignment of 1,244 bp. This alignment comprised 529 (42.5%) variable sites and 510 (41.0%) parsimony informative characters. The original alignment for the newly determined partial 16S sequences had 526 characters, of which 140 sites received PP of 70% in the ProAlign analysis and were excluded as alignment-ambiguous sites in the phylogenetic reconstruction. The remaining 386 sites contained 154 (39.9%) variable and 129 (33.4%) informative sites. Sequences of the partial 12S gene amplified ranged from 540 to 586 bp in length excluding the primers and poorly determined sequences near both ends. The ProAlign alignment run identified 244 sites as alignment-ambiguous among the original dataset of 628 characters. The remaining 384 sites had 190 (49.5%) variable and 160 (41.7%) parsimony informative sites. The partial 28S rRNA sequences amplified for neritoid species ranged from 2,044 (in *Dostia dilatatum*) to 2,111 bp (*Nerita albicilla*). The two outgroup species had shorter sequences and it was 2,039 bp in *Titiscania shinkishihataii*. The initial alignment generated by ProAlign had

2,163 characters after the exclusion of poorly determined sites near the amplification primers. Alignment ambiguous regions were also excluded in the subsequent analyses and the final dataset comprised 1,983 sites, of which 171 (8.6%) were variable and 132 (6.7%) parsimony informative. The concatenated four-gene matrix had a total length of 3,997 bp for the phylogenetic reconstruction.

The exclusion of the two neritopsid species resulted in slightly longer alignments of the rRNA genes. The final alignment of the concatenated four-gene matrix consisted of 4,175 sites, including 1,244 sites of COI, 439 sites of 16S, 482 sites of 12S and 2,010 sites 28S gene. The respective numbers of variable and parsimony informative sites in each gene fragment were as follows: 508 and 497 sites in COI; 186 and 160 sites in 16S; 244 and 212 sites in 12S; 143 and 105 sites in 28S.

Phylogenetic analyses

The Bayesian analyses of the five datasets yielded the consensus trees shown in Figures 2-1 to 2-5. The ML analyses produced tree topologies that were very similar to those of the Bayesian trees and retrieved most clades with a significant PP support (≥ 95%). The Neritoidea were recovered as a robust monophyletic clade in all analyses (PP = 100%, BP = 100%). In the following lines, internal relationships within the Neritoidea are presented by referring to traditionally used generic names for OTUs (e.g. Holthuis 1995); those names are enclosed in quotations when the genetic assignment is revised and new combination is compelled by the present molecular analysis (see below).

The COI phylogeny (Fig. 2-1) recovered a monophyletic Neritiliidae as well as Phenacolepadidae with the highest PP value and strong BP support (BP = 85% and 100%, respectively). Phenacolepadidae appeared as the first offshoot in the Neritoidea albeit with insignificant PP and BP values (PP = 80%, BP = 58%). Several robust clades were found in the COI tree: *Pisulina* + *Plathynerita* + *Neritilia* (PP = 98%, BP = 78%), *Bathynerita* +

Olgasoralis + *Shinkailepas* (PP = 100%, BP = 100%), *Olgasoralis* + *Shinkailepas* (PP = 98%, BP = 79%), *Phenacolepas* + *Plesiothyreus* + *Chinnalepeta* (PP = 100%, BP = 95%), *Nerita* (PP = 100%, BP = 88%), *Neritodryas* + "*Septaria*" sp. from Palau (PP = 100%, BP = 96%), *Clithon* (PP = 100%, BP = 88%), "*Vitta*" *variegata* + "*Vitta*" *cumingiana* (PP = 96%, BP = 71%), "*Puperita*" + *Vitta virginea* (PP = 100%, BP = 99%) and "*Neripteron*" + *Septaria porcellana* + *Septaria suffreni* + *Septaria tessellata* + *Septaria clypeolum* (PP = 100%, BP = 95%). Each of *Septaria* and *Neritina* were recovered as polyphyletic groups.

The 16S dataset recovered only few clades with a high enough nodal support under either or both of the Bayesian and ML criteria (Fig. 2-2): Neritiliidae (PP = 100%, BP = 92%), *Neritilia* (PP = 99 %, BP = 77%), *Nerita* (PP = 100%, BP = 97%), *Neritodryas* + "*Septaria*" sp. (PP = 100%, BP = 100%), *Bathynerita* + *Shinkailepas* + *Olgasoralis* (PP = 96%, BP = 81%) and *Shinkailepas* + *Olgasoralis* (PP = 99%, BP = 91%). The 12S dataset yielded the Bayesian tree shown in Figure 2-3. Neritiliidae and Phenacolepadidae were recovered as monophyletic clades, respectively (PP = 100%, BP = 100% for the former and PP = 98%, BP = 73% for the latter). Neritiliidae appeared as the first offshoot in the Neritoidea with significant support values (PP = 100%, BP = 94%). Neritidae and Phenacolepadidae collectively formed a well-supported clade (PP = 100%, BP = 94%). All ingroup clades with significant support in the 16S trees were also supported in the 12S analyses (PP ≥ 97% or BP ≥ 76%) except the genus *Nerita*.

The nuclear 28S dataset recovered nine clades with significant PP and/or BP support (Fig. 2-4): Neritiliidae (PP = 100%, BP = 100%), Phenacolepadidae (PP = 99%, BP = 85%), *Bathynerita* + *Shinkailepas* + *Olgasoralis* (PP = 100%, BP = 96%), *Shinkailepas* + *Olgasoralis* (PP = 97%, BP = 93%), *Phenacolepas* + *Plesiothyreus* + *Chinnalepeta* (PP = 100%, BP = 99%), *Nerita* (PP = 100%, BP = 98%), *Neritodryas* + "*Septaria*" sp. (PP = 100%, BP = 99%), *Clithon* (PP = 100%, BP = 77%) and "*Puperita*" + *Vitta virginea* (PP = 86%, BP = 81%).

Figure 2-5 shows a Bayesian tree reconstructed from the concatenated four-gene sequences with a length of 3,997 bp. As the independent gene trees were mostly congruent to each other in terms of robust clades, support values for many nodes were increased in this combined gene tree. Of the three families of Neritoidea, the monophyletic Neritiliidae (PP = 100%, BP = 100%) had the basal position relative to the Neritidae and Phenacolepadidae (PP = 100%, BP = 98%). Phenacolepadidae was supported as a monophylum (PP = 100%, BP = 100%), while the monophyly of the Neritidae was meaningfully supported only by the ML analysis (PP = 85%, BP = 81%). Two ingroup clades of the Neritiliidae received significant support: *Pisulina* + *Plathynerita* + *Neritilia* (PP = 99%, BP = 77%) and genus *Neritilia* (PP = 100%, BP = 100%). In the Phenacolepadidae, five ingroup clades were consistently recovered in both Bayesian and ML analyses: *Bathynerita* + *Olgasoralis* + *Shinkailepas* (PP = 100%, BP = 100%), *Olgasoralis* + *Shinkailepas* (PP = 100%, BP = 95%), *Phenacolepas* + *Plesiothyreus* + *Chinnalepeta* (PP = 100%, BP = 100%), *Plesiothyreus* + *Chinnalepeta* + *Phenacolepas crenulatus* (PP = 100%, BP = 90%) and *Phenacolepas unguiformis* + *Phenacolepas galathea* (PP = 100%, BP = 98%).

The monophyly of Theodoxinae (= Neritininae) *sensu* Holthuis (1995), which comprises all neritid genera but *Nerita*, was supported in this combined tree but with lower statistical values (PP = 85%, BP = 70%). This ambiguously clustered group was divided into *Neritodryas* + "*Septaria*" sp. and the remaining 38 OTUs; the latter formed a strongly supported monophyletic group (PP = 100%, BP = 94%). Within this large monophylum (= newly defined the Neritininae; see Discussion), *Theodoxus* and "*Neritina*" *granosa* split first (PP = 100%, BP = 86%). The monophyly of the following genera was highly supported in the Neritidae: *Nerita* (PP = 100%, BP = 100%), *Smaragdia* (PP = 100%, BP = 99%) and *Clithon* (PP = 100%, BP = 99%). *Neritina* and *Septaria* were shown to be polyphyletic and each genus was divided into four clades: "*Neritina*" *granosa*, "*Neritina*" sp. from Vanuatu, "*Neritina*" *bruguieri* and four other species of *Neritina*, and "*Septaria*" sp., "*Septaria*" *luzonica*, "*Septaria*" *cumingiana* + "*Septaria*" *sanguisuga* and other taxa. The monophyly of "*Septaria*" sp. + *Neritodryas* sp. (both from Palau) and "*Neripteron*" *spiralis* + four species of *Septaria* were supported with the highest PP (BP = 99% and BP = 86%, respectively), and thus *Neritodryas* and *Neripteron* were consistently paraphyletic. Seven other species of "*Neripteron*" arranged in a clade (PP = 100%, BP = 98%). The monophyly of *Clithon* + "*Puperita*" + "*Vitta*" + "*Neritina*" sp. from Vanuatu was supported by a high enough PP (99%), but with a moderate BP (62%). "*Vitta*" *variegata* + "*Vitta*" *cumingiana* was monophyletic (PP = 100%, BP = 96%), while *Vitta virginea* was robustly clustered with "*Puperita*" *pupa* in both Bayesian and ML analyses (PP = 100%, BP = 100%), rendering the former genus polyphyletic. The genera *Neritina*, "*Neripteron*" and *Septaria* collectively formed a terminal clade of the Neritidae (PP = 100%, BP = 92%) if the above-mentioned "*Neritina*" sp., "*Neritina*" *granosa* and "*Septaria*" sp. were considered to represent separate groups.

Separate Bayesian and ML analyses based only on 60 neritoid taxa yielded higher support values for some of internal nodes in the clade Phenacolepadidae + Neritidae (Figs 2-6, 2-7). For example, a cluster composed of three *Neritina*, five *Septaria* and eight "*Neripteron*" was newly recognized with high PP (100%) and BP (82%) values. The monophyly of *Clithon* + "*Puperita*" + "*Vitta*" + "*Neritina*" sp. also received a higher PP support (100%). A clade made of all Neritininae but four basal lineages (*Neritodryas* + "*Septaria*" sp., "*Neritina*" *granosa*, *Theodoxus* and *Smaragdia*) were newly supported with a high enough PP (99%) albeit with a moderate BP (53%).

Divergence time estimates

The concatenated four-gene dataset with 62 OTUs was further utilized to explore divergence dates among neritoid species. Figure 2-8 illustrates a chronogram inferred from five neritimorph calibration priors based on fossil records. The mean divergence date for the split of the Neritiliidae from the clade of the Neritidae and Phenacolepadidae was calculated at 190.0 Mya (Early Jurassic) with the 95% HPD interval of 141.3–242.2 Mya that spans an age range of the Cretaceous to Triassic. The same set of the five priors yielded the Neritidae–Phenacolepadidae split at 116.6 Mya (95% HPD: 92.1–144.0 Mya) in the Early Cretaceous. The earliest divergence within the Neritidae was calculated at 107.0 (84.5–131.7) Mya, also in the Early Cretaceous. The first splits within two major clades with amphidromous species, namely the Neritiliidae and Neritininae + *Neritodryas* (new subfamily), were estimated to have occurred at 97.3 (75.7–120.6) Mya and 107.0 (67.4–133.5) Mya in the Late Cretaceous, respectively.

Ancestral character-state reconstruction

The reconstruction of ancestral states for ecological and morphological characters was made with reference to the best ML phylogram and is shown in Figures 2-9 to 2-11. As to habitat shifts, two independent invasion of the freshwater environment by marine ancestors were suggested by parsimony (not shown); however, ML reconstruction did not clarify the ancestral condition in the superfamily for this character and hence the number of freshwater invasions (Fig. 2-9). On the other hand, both parsimony and likelihood reconstructions unequivocally showed that there have been two reinvasions of marine environments by the ancestors of *Smaragdia* and "*Puperita*" *pupa* within the Neritidae. The marine origins of these two lineages were supported by proportional likelifood values (PL) of 0.95 (for *Smaragdia*) and 0.96 ("*Puperita*" *pupa*). Likewise, transition from planktotrophic to direct development among limnic neritids, hence the loss of amphidromy, was strongly suggested in *Theodoxus* and a subclade of *Neritodryas* with PL of over 0.99 (Fig. 2-10).

Reconstruction of shell forms by parsimony unequivocally suggested that the limpet-like or patelliform shells have acquired at least six times independently by ancestors with hemispherical (neritiform) shells. Of these, four transitions have occurred in the Neritininae, resulting in very similar, convergent shell shapes that characterize the genus *Septaria* in the current classification (PL ≥ 0.96; Fig. 2-11).

2-4: Discussion

Phylogeny and classification of Neritoidea

In the present phylogenetic analyses of the superfamily Neritoidea, Neritiliidae were recovered as the first offshoot and the sister group of Neritidae + Phenacolepadidae with the maximum posterior probability (Fig. 2-5). This and some other basal nodes are consistently recovered in the previous, morphology-based phylogeny and classification by Holthuis (1995). However, there are a number of incongruent neritid clades in the present and previous trees. Of these, the genera *Neritina*, *Vitta*, *Neripteron* and *Septaria* in a traditional sense are first shown to be non-monophyletic in the present molecular phylogeny (Fig. 2-6). In the following lines, I revise the generic positions of the species in those polyphyletic or paraphyletic groups and then discuss relationships among genera in the new taxonomic framework.

The genus *Neritina* of the traditional classification was found to include at least four independent lineages, probably reflecting the rather uncharacteristic, plesiomorphic condition of their shells (see Chapter 4). These lineages are represented in my molecular phylogeny by (1) "*Neritina*" *granosa* (Fig. 2-6: *Neritina* A), (2) "*Neritina*" sp. from Vanuatu (*Neritina* B), (3) "*Neritina*" *bruguieri* (*Neritina* C), and (4) *Neritina pulligera* + *Neritina petitii* + *Neritina asperulata* (*Neritina* D). The genus was originally established by Lamarck (1816) for *Nerita pulligera* (= *Neritina pulligera*), thus the last clade bears this generic name. "*Neritina*" *granosa* from Hawaii putatively represents the first offshoot of the subfamily Neritininae and is very distantly related to the proper members of *Neritina*. Interestingly, a few authors have been classified this species under the subgenus *Neritona* Martens, 1869 along with three other species from the Philippines, Indonesia and Melanesia based on their opercula with a uniquely serrated lower apophysis (Mienis 1991; Haynes 2005). *Neritona* therefore merits a full generic status and "*Neritina*" *granosa* and the three other species herein transferred to this genus (Fig. 2-7; Table 2-3). "*Neritina*" sp. from Vanuatu was robustly clustered with *Clithon*, *"Puperita"* and *"Vitta"*, while the internal relationship was not resolved in this clade (Fig. 2-6). "*Neritina*" *bruguieri* from Okinawa, Japan was recovered as a singleton lineage outside a clade composed of the true *Neritina* and some species of *Septaria* and "*Neripteron*". These seems to be no generic name available for the last two species and new genera are needed to accommodate them (Fig. 2-7).

The genus *Septaria* Férrusac, 1807 is similarly in a puzzled state (Fig. 2-6). Again, four lineages were widely scattered in the Neritidae: (1) "*Septaria*" sp. from Palau (Fig. 2-6: *Septaria* A), (2) "*Septaria*" *cumingiana* + "*Septaria*" *sanguisuga* (*Septaria* B), (3) "*Septaria*" *luzonica* (*Septaria* C), and (4) *Septaria porcellana* + *Septaria suffreni* + *Septaria tessellata* + *Septaria clypeolum* (*Septaria* D). Of these, the Palauan species is nested within the genus *Neritodryas* and should be transferred to the latter genus, regardless of their fundamentally different shell shapes (see below). The clade "*Septaria*" *cumingiana* + "*Septaria*" *sanguisuga* represents a divergence before the split between *Neritina* and other flat to patelliform groups; these two species with two apophyses in the operculum can now be assigned to *Laodia* Gray, 1868 with its type species *Navicella cumingiana* (= *Laodia cumingiana*). The clade of the four species (Fig. 2-6: *Septaria* D) includes the type of the genus (*Patella porcellana*, i.e. *Septaria porcellana*) and may therefore represent the exclusive members of *Septaria*, while support values for this node were insufficient in all trees (Figs 2-5, 2-6). Meanwhile, they constitute a strongly supported clade with "*Neripteron*" *spiralis*, which is the sister species of "*Neripteron*" *auriculata* (Chapter 4), a senior synonym of the type of *Neripteron* Lesson, 1831 (see Table 2-3). Given that the shell shape is a plastic character in the evolutionary history of the Neritoidea (Fig. 2-11), it seems reasonable to assign the latter two species with depressed but coiled shells into the genus *Septaria* together with the aforementioned four species (Fig. 2-7). The synonymization of *Neripteron* under *Septaria* gives rise to the need of a generic name for seven species in a highly supported ternimal clade ("*Neripteron*" *violacea* + "*Neripteron*" *subalata* + "*Neripteron*" *bicanaliculata* + "*Neripteron*" *florida* + "*Neripteron*" *guamensis* + "*Neripteron*" *dilatatum* + "*Neripteron*" *siquijorense*). *Dostia* Gray, 1847 is the suitable name with the type species *Neritina crepidularia* (a junior synonym of *Dositia violacea*). Lastly, the phylogenetic position of "*S*." *luzonica* was not rigorously determined in this study: it represents the sister clade of either *Neritina* or *Dostia* + *Septaria* (Fig. 2-6). An analysis of COI sequences with more dense taxon sampling supports the former topology with meaningful support credibility (Chapter 4). I therefore tentatively place this species in *Neritina* (Fig. 2-7).

Species that have formerly been classified in the genus *Vitta* Mörch, 1852 comprise two distinct clades: one in the Central America (herein represented by *Vitta virginea* only) and the other in the Indo-West Pacific ("*Vitta*" *cumingiana* and "*Vitta*" *gagates*; Figs 2-5, 2-6). The type species *Nerita virginea* (= *Vitta virginea*) belongs to the former group, while *Vittina* Baker, 1923 is available for the latter group with its type species *Nerita royssiana*, a junior synonym of *Vittina communis* that is very closely related to *Vittina cumingiana* (Chapter 4). Very interestingly, *Vitta virginea* is more closely allied to the Caribbean rocky-shore species *Puperita pupa* than to the limnic *Vittina* in the Pacific, suggesting reinvasion of the marine habitat in the former ocean basin (see below). The monotypic genus *Puperita* Gray, 1857 indeed occupies a terminal position within the American *Vitta* in a more densely sampled COI tree (Fukumori, unpublished data) and is therefore synonymized herein under the older *Vitta*. The monophyly of the newly-defined *Vitta* + *Vittina* was weakly supported in the COI tree (Fig. 2-1) but rejected or not supported in other reconstruction (e.g. Figs 2-5, 2-7). The two genera seem to be valid both in the phylogenetic relationship and geographic and morphological differentiation (Chapter 4).

Theodoxinae *sensu* Holthuis (1995), which comprises all neritid genera but *Nerita*, was ambiguously recovered with one of the combined four-gene datasets (Fig. 2-5). On the other hand, the reconstruction from the other dataset with only neritoid OTUs resulted in a basal trichotomy within the Neritidae, involving *Nerita*, *Neritodryas* and a clade with all other genera of the family (Fig. 2-6). The last clade made up of 12 revised neritid genera is, however, unanimously recovered with very high support values (e.g. PP = 100%, BP = 94% in Fig. 2-7). *Neritodryas* possesses a unique composition of layers in the operculum that is shared only with *Nerita* (Kano 2006), possibly suggesting the sister relationship between the two genera, while there exist anatomical characteristics that instead imply the affinity between *Neritodryas* and other non-marine genera (Holthuis 1995). In any case, the phylogenetic, morphological and paleontological evidence show a long independent evolutionary history of *Neritodryas* and this genus merits a new subfamily in the Neritidae (Table 2-3). The remaining 12 neritid genera constitute the redefined Neritininae. The discrepancies between the topologies from the present molecular study and morphological investigation by Holthuis (1995) may be attributable to parallel acquisition of similar conchological and anatomical conditions accompanied by multiple habitat shifts. These characters seem to be relatively vulnerable to convergent evolution (see below).

The present molecular phylogeny involves all but only one extant genus in the Neritidae. Unfortunately, the monotypic genus *Fluvinerita* with *F. tenebricosa* known only from Jamaica in the Caribbean Sea was not available despite my effort to locate a specimen for DNA extraction in various collections. *Fluvinerita* shows a number of similarities to the members of the Indo-West Pacific *Neritodryas* in conchological, radular and reproductive characters, and these morphological resemblance led Holthuis (1995) convicted that they form a robust monophyletic group. These two groups also share the benthic early development (Holthuis 1995) that further suggests their kinship and a single loss of planktotrophy in their common ancestor (but see below). However, the discontinuity of their geographic distributions and presumed lack of oceanic dispersal may render the phylogenetic connection somewhat questionable. Future molecular phylogenetic analyses with this enigmatic species, along with detailed morphological examination on the various neritid lineages in the light of the present topology, would settle the generic classification of this large and common gastropod family, provide diagnoses for each genus and advocate global evolutionary transitions in (and correlation between) the shape and function of conchological and anatomical characters.

Habitat shifts, evolution of amphidromy and reinvasion of the sea

The present likelihood reconstruction of ancestral states suggests rather vaguely that the limnic lineages have evolved independently in the Neritiliidae and Neritidae from a marine ancestor (Fig. 2-9). The ambiguity of the polarity seems to result from the lack of reference on habitats outside Neritimorpha. The likelihood reconstruction showed near-equal probabilities for marine, brackish or freshwater condition for the common ancestor of the superorder, but outgroup comparison favors the marine ancestory as shown by most living species of basal gastropod lineages and Paleozoic fossil records (Ponder & Lindberg 1997). More recent fossils of Neritoidea also suggest that the superfamily originated as a marine group and habitat shift to streams and rivers occurred succeedingly (e.g. Scott & Kenny 1998; Kano et al. 2002). The independent invasion of the stream habitat by the Neritiliidae and Neritidae while retaining planktotrophic early development indicates parallel acquisition of the amphidromous life cycle, as has already been suggested by previous studies (Holthuis 1995; Kano & Kase 2002). More interestingly, two reinvasions of the marine environment by amphidromous ancestors are newly demonstrated in the present study (Fig. 2-9).

Most neritid species except those in two genera (*Nerita* and *Smaragdia*) and one species (*Vitta pupa*) live in freshwater or brackish-water conditions. The non-monophyletic nature of the limnic Neritidae has been pointed out by Holthuis (1995), while the polarity or the number of habitat shifts could not be estimated in the latter work due to the lack of a resolved phylogeny. Provided that the direction of the habitat transition from the marine to freshwater and brackish water is irreversible and the best ML topology shows the true phylogenic relationship, invasion of the limnic environment should have occurred at least eight times in the Neritidae. *Smaragdia* species living in seagrass beds worldwide and *Vitta* *pupa* on Caribbean intertidal rocky shores, however, have more plausibly undergone the reverse habitat shift from the freshwater to the marine environment (Fig. 2-9). This evolutionary hypothesis involves only three transitions in the Neritidae and maximizes parsimony with least steps. Indeed, the physiological tolerance of many freshwater and brackish water species to a wide salinity range during the life history favors the latter view (e.g. Kumazawa et al. 1991; Kano et al. 2013). Brackish species of *Clithon* and *Dostia* are exposed to nearly full seawater in estuaries and stream mouths during high tide (Table 2-1; Kano et al. 2011). A particularly euryhaline nature can be seen in *Dostia guamensis*; this species commonly inhabits the under-surfaces of rubble on the brackish riverbed, while seagrass beds harbor the same species in intertidal flats along with the species of *Smaragdia* (Kano et al. 2003; Masuda & Uchiyama 2004; see also Chapter 4). An even more intriguing example involves the discovery of *Septaria spiralis* in sunken pieces of wood on the continental floor in Vanuatu (Kano et al. 2013). This species, also represented in the present molecular analysis, is typically found on driftwood in brackish estuaries but is apparently able to survive in the full salinity for an extended period of time.

Amphidromy apparently plays an essential role in such euryhaline nature at maturity as well as the evolutionary habitat shifts and reinvasion of the sea. Amphidromous nerites live in freshwater conditions as adults, while their larvae obligatorily experience a planktotrophic stage in the ocean (Kano 2006; Kano et al. 2011, 2013). Most species of marine neritids including *Vitta pupa* and *Smaragdia* spp. share this planktotrophic phase (Fig. 2-10; Holthuis 1995). The amphidromous life cycle has probably facilitated the physiological tolerance to varying salinity levels not only in the ontogeny of a single individual but also in an evolutionary timescale and therefore the multiple habitat transitions.

The molecular clock-based divergence time estimate for neritoids suggests that the Neritininae and *Neritodryas* represent relatively old lineages with their origins sometime in the mid to late Cretaceous (75–120 Mya; Fig. 2-8). Fossils belonging to the Recent freshwater genera have been recovered from the Eocene deposits of Hampshire Basin in

England and Paris Basin in France (Symonds & Pacaudo 2010). Although the timing of freshwater invasion and evolutionary antiquity of amphidromy by the two lineages cannot be determined due to the lack of identifiable fossil specimens from the Cretaceous or the Paleocene, different groups of Neritimorpha have invaded the limnic environment already in the Jurassic by and the Early Cretaceous (Bandel & Riedel 1994; Bandel & Kiel 2003). Surprisingly, each of the Jurassic *Schwardtina* and *Deianira* and Cretaceous *Mesoneritina* seems to represent independent invasion of non-marine waters through independent acquisition of the amphidromous life cycle (see Chapter 3). This paleontological evidence along with the present molecular phylogeny further demonstrates the amazing flexibility in habitat shifts through the evolutionary history of neritimorph gastropods.

Parallel evolution of limpet form in stream environment

Although the shell shape varies in many aspects in Neritoidea, e.g. smooth or spined, the snail–limpet dichotomy has been most frequently and clearly made by previous workers. Some species of *Neritona* and *Dostia* have a very flat shape and a large aperture of the shell, while these semi-limpets bear a fully functional operculum for the protection of the animal. The “full” limpets with an unfunctional, internal operculum between the pedal muscle and visceral hump have been collectively assigned to the genus *Septaria*, for which even the independent family Septariidae has been adopted by some conchologists (see Holthuis 1995 for review). The present molecular phylogeny reveals that the limpet shells have evolved at least four times in the Neritidae (Fig. 2-11). Those limpet species in *Septaria*, *Laodia*, *Neritina* and *Neritodryas* are surprisingly similar to each other in terms of the shape, coloration, color pattern and texture of the shell (Fig. 2-7) and the shape and position of the operculum as well as in the general body plan (Haynes 1991). However, unignorable differences have already been detected in the soft anatomy, particularly in the reproductive tract, among these lineages (Holthuis 1995).

Limpets in general have a larger surface area of the foot sole and accordingly an increased strength of adhesion to the substrate than snails do; this shape also works to hold their body closer to the substrate and to increase fitness against strong waves and currents (Vermeij 1993; Ponder & Lindberg 1997). Such morphological characteristics seem to be particularly adaptive in the upstream migration in the fast-flowing streams by the amphidromous snails of the Neritidae (Kano 2009). Indeed, larger individuals of *Vitta lattisima* with a larger foot are shown to have a stronger adhesion and a higher tolerance against downstream currents, hence a better chance of upstream migration, than smaller conspecific individuals (Schneider & Lyons 1993). *Laodia*, *Neritina luzonica* and *Neritodryas* sp. (= "*Septaria*" sp. from Palau) all inhabit fast-flowing streams and well fit with this explanation, although one limpet species of *Septaria* (*S. tessellata*) lives in brackish estuaries and lower reaches of streams with less strong water velocity (Haynes 1991; Kano et al. 2011). The latter species represents a terminal clade of the genus and it might have secondarily shifted its habitat from the upper stream while retaining the body plan (Fig. 2-11).

The limpets in the genus *Septaria* are nested within the clade of semi-limpets including *S. spiralis* and species of *Dostia* (Fig. 2-7). Those semi-limpets may possibly represent transitional conditions of shell morphology in the evolutionary pathway towards the "full" limpet. Semi-limpets, including *Neritona granosa* and *Vitta lattisima*, are also considered adaptive against strong downstream currents even if not to the level of those limpets (Vermeij 1969; Schneider & Lyons 1993). The cause, process and effect of shell evolution have attracted significant research interests (Vermeij 1993) and the present case in the Neritidae would provide a rare and unusual opportunity to test various hypotheses and to further understand the evolutionary changes of gastropod body plan.

Origins of benthic development

Although the majority of neritoids have the planktotrophic larval stage, a few dozens of species are reported to have either direct or lecithotrophic early development. These taxa include all *Theodoxus*, *Fluvineria tenebricosa* and some of *Nerita* and *Neritodryas* species in the Neritidae (Holthuis 1995; Kano 2006) as well as several submarine-cave dwelling species in the Neritiliidae (Kano & Kase 2008). The marine genus *Nerita* has been intensely examined phylogenetically based on the partial DNA sequences of the mitochondria COI and 16S rRNA and nuclear ATP synthetase subunit alpha genes (Frey & Vermeij 2008). Character mapping on their topology for ontogenetic conditions (Holthuis 1995; Kano 2006) suggests multiple losses of the planktotrophic larva within this genus. For example, *Nerita japonica* and *Nerita helicinoides* are phylogenetically distantly related to each other (Frey & Vermeij 2008) while they both lack a feeding larval stage and hatch as either a benthic juvenile or a lecithotrophic veliger (Nakano & Nagoshi 1980; Paruntu & Tokeshi 2003; Kano 2006). Similarly, neritiliids in submarine caves have lost planktotrophy multiple times as suggested by the presence of two different types of paucispiral protoconchs in *Pisulina* and *Micronerita* (Kano & Kase 2008). The adaptive significance of the non-planktotrophy, which is always accompanied by larger eggs and hence more investment per egg by the mother than in planktotrophs, may be associated with preference to the so-called K-selected reproductive strategy in certain environmental conditions. For example, the K-selected strategy predominates in submarine caves, which are characterized by low levels of primary production and durophagus predation (Kase & Hayami 1992; Kano & Kase 2008).

On the other hand, a fundamentally different mechanism has been proposed for the multiple loss of planktotrophy in the limnic Neritidae by Holthuis (1995). Water flows one direction in streams and planktonic larvae may face critical risk to be flushed out beyond their habitats and thus the acquisition of direct development theoretically has a significant adaptive advantage in terms of reproductive investment and subsistence and survival of local populations (Holthuis 1995). All members of the freshwater to brackish genus *Theodoxus* in the temperate Europe and northern Africa hatch as benthic juveniles by feeding on sibling eggs in the same egg capsule (Andrews 1935; Holthuis 1995; Kano 2006). Interestingly, *Theodoxus* inhabits both running and still waters; *Theodoxus fluviatilis* is common in ponds and lakes in European countries (Bunje 2005). This radiation to the closed freshwater system is obviously a consequence of the loss of amphidromy and acquisition of benthic development.

Neritodryas species from streams and mangrove swamps in the tropical Indo-West Pacific seem to include both planktotrophic and non-planktotrophic species. The type species *Neritodryas cornea* as well as *Neritodryas ampullaria* have very wide geographic ranges; the presence of the feeding larva that survive only in saline water, hence the amphidromous life cycle, has been experimentally verified for the latter species (Sato & Kano unpublished). All other congeneric species are most plausibly non-planktotrophic, judging from the morphology of their protoconchs and larval opercula as well as geographic distributions (Kano 2006; Kano et al. 2011). Such non-planktotrophs in *Neritodryas* are more likely direct developers than pelagic lecithotrophs, as survival fitness of the latter strategy must be crucially lower in the running freshwater (Holthuis 1995). Here it is interesting to note that the present phylogeny and ancestral-state reconstruction strongly suggest that the benthic development has evolved from an ancestral amphidromous species within the genus *Neritodryas* (Fig. 2-10). The three direct-developing species included in the analysis constitute a highly supported terminal clade (Fig. 2-6). As mentioned earlier, *Fluvinerita tenebricosa* from Jamaica shares many features with *Neritodryas* including the benthic development and the two genera have been considered as the reciprocal sister clades (Holthuis 1995). However, the present topology suggests either the single loss of amphidromy and divergence of *Fluvinerita tenebricosa* from a direct-developing *Neritodryas* (hence the synonymy of *Fluvinerita*), or parallel losses of the larval stage in the two valid genera. Their geographic disparity favors the latter hypothesis, although possibility of transoceanic dispersal as juveniles or adult snails has been demonstrated at least for the brackish species of the Neritidae (Kano et al. 2013).

In conclusion, direct development may have an adaptive advantage in sustaining the local populations of limnic neritids, particularly in stable environments exemplified by the lakes and large rivers in the European continent where *Theodoxus* species predominate. However, there are only one or two transitions to this mode of early ontogeny among the limnic genera of tropical and subtropical regions. This contrasts to the apparently more frequent acquisition of non-planktotrophic development at rocky shores and in submarine caves by the other lineages of the Neritoidea. Retention of amphidromy obviously has many more advantages in inhabiting and surviving the varying environment of freshwater streams in small islands through the oceanic dispersal and recruitment of larvae (see also Chapter 4).

Table 2-1. Species used in the present analyses, arranged systematically, with collection sites of specimens. Subfamilial and generic classification follows previous, morphology-based hypotheses (e.g. Holthuis 1995); species with enclosed generic names are transferred to different genera in the present study (see Table 2-3; Fig. 2-7).

Species	Locality and habitat	DNA No.
Neritiliidae		
Neritilia rubida (Pease, 1865)	Honiara, Solomons; freshwater stream	177
Neritilia vulgaris Kano & Kase, 2002	Honiara, Solomons; freshwater stream	178
Pisulina adamsiana Nevill & Nevill, 1869	Blue Hole, Palau; submarine cave	9
Platynerita rufa Kano & Kase, 2002	Upolu, Samoa; freshwater stream	171
Neritiliidae n. gen., n. sp.	Honiara, Solomons; stream mouth	179
Phenacolepadidae		
Bathynerita naticoidea Clarke, 1989	Green Canyon, Gulf of Mexico; cold seep	168
Olgasoralis tollmanni Beck, 1992	Lau Basin, Papua New Guinea; hydrothermal vent	285
Shinkailepas kaikatensis Okutani et al., 1989	Kaikata Seamount, Japan; hydrothermal vent	98
Cinnalepeta pulchella (Lischke, 1871)	Kamikoshiki Is., Kagoshima, Japan; coastal pond	34
Phenacolepas crenulata (Broderip, 1834)	Ishigaki Is., Okinawa, Japan; tidal flat	103
Phenacolepas galathea (Lamarck, 1819)	Ishigaki Is., Okinawa, Japan; tidal flat	104
Phenacolepas unguiformis (Gould, 1859)	Kanagawa, Japan; intertidal rocky shore	118
Plesiothyleus newtoni Sowerby III, 1894	Kochi, Japan; tidal flat	92
Neritidae: Neritinae		
Nerita (*Theliostyla*) *albicilla* Linnaeus, 1758	Okinawa Is., Japan; intertidal rocky shore	69
Nerita (*Argonerita*) *histrio* Linnaeus, 1758	Okinawa Is., Japan; tidal flat	1452
Nerita (*Linnerita*) *litterata* Gmelin, 1791	Cocos Islands, Australia; intertidal rocky shore	30
Nerita (*Ilynerita*) *planospira* Anton, 1838	Phuket, Thailand; mangrove swamp	1449
Neritidae: Neritininae (= Theodoxinae *sensu* Holthuis, 1995)		
Clithon corona (Linnaeus, 1758)	Iriomote Is., Okinawa, Japan; freshwater stream	134
Clithon peguensis (Blanfold, 1867)	Phang Nga, Thailand; freshwater stream	1448
Clithon oualaniensis (Lesson, 1831)	Iriomote Is., Okinawa, Japan; stream mouth	127
"*Neripteron*" *bicanaliculata* (Récluz, 1843)	Okinawa Is., Japan; stream mouth	162
"*Neripteron*" *dilatatum* (Lesson, 1830)	Iriomote Is., Okinawa, Japan; stream mouth	157
"*Neripteron*" *florida* (Récluz, 1850)	Santo Is., Vanuatu; stream mouth	661
"*Neripteron*" *guamensis* (Quoy & Gaimardi, 1834)	Amami Is., Japan; stream mouth	161
"*Neripteron*" *siquijorense* (Récluz, 1843)	Iriomote Is., Okinawa, Japan; stream mouth	37
"*Neripteron*" *spiralis* (Reeve, 1855)	Iriomote Is., Okinawa, Japan; estuary	158
"*Neripteron*" *subalata* (Souleyet, 1842)	Okinawa Is., Japan; stream mouth	916

Species	Locality and habitat	DNA No.
"*Neripteron*" *violacea* (Gmelin, 1791)	Northern Territory, Australia; estuary	1289
Neritina asperulata (Récluz, 1843)	Ishigaki Is., Okinawa, Japan; freshwater stream	148
Neritina powisiana (Récluz, 1843)	Santo Is., Vanuatu; freshwater stream	666
Neritina pulligera (Linnaeus, 1767)	Ishigaki Is., Okinawa, Japan; freshwater stream	145
"*Neritina*" *bruguieri* (Récluz, 1841)	Iriomote Is., Okinawa, Japan; freshwater stream	151
"*Neritina*" *granosa* Sowerby I, 1825	Oahu Is., Hawaii; freshwater stream	1260
"*Neritina*" sp.	Santo Is., Vanuatu; freshwater stream	663
Neritodryas cornea (Linnaeus, 1758)	Santo Is., Vanuatu; on a tree near stream	652
Neritodryas dubia (Gmelin, 1791)	Luzon Is., Philippines; mangrove swamp	705
Neritodryas ampullaria (Lesson, 1831)	Iriomote Is., Okinawa, Japan; freshwater stream	123
Neritodryas sp.	Babeldaob Is., Palau; freshwater stream	1710
"*Puperita*" *pupa* (Linnaeus, 1767)	Grand Cayman, Caribbean; intertidal rocky shore	33
Septaria clypeolum (Récluz, 1842)	Kagoshima, Kyushu Is., Japan; stream mouth	583
Septaria porcellana (Linnaeus, 1758)	Ishigaki Is., Okinawa, Japan; freshwater stream	164
Septaria suffreni (Récluz, 1842)	Upolu, Samoa; freshwater stream	184
Septaria tessellata (Lamarck, 1816)	Amami Is., Japan; stream mouth	581
"*Septaria*" *cumingiana* (Récluz, 1843)	Ishigaki Is., Okinawa, Japan; freshwater stream	163
"*Septaria*" *luzonica* (Récluz, 1842)	Panglao Is., Philippines; freshwater stream	1004
"*Septaria*" *sanguisuga* (Reeve, 1856)	Upolu, Samoa; freshwater stream	183
"*Septaria*" sp.	Babeldaob Is., Palau; freshwater stream	1711
Smaragdia bryanae (Pilsbry, 1917)	Oahu Is., Hawaii; seagrass bed	1258
Smaragdia pulcherrima (Angas, 1871)	Ishigaki Is., Okinawa, Japan; seagrass bed	1272
Smaragdia rangiana (Récluz, 1841)	Ishigaki Is., Okinawa, Japan; seagrass bed	277
Smaragdia souverbiana (Montrouzier, 1863)	Miyako Is., Okinawa, Japan; seagrass bed	278
Smaragdia tragena (Iredale, 1936)	Moorea, French Polynesia; seagrass bed	1442
Smaragdia viridis (Linnaeus, 1758)	Grand Cayman, Cayman Islands; seagrass bed	78
Smaragdia sp. 1	Miyazaki, Kyushu Is., Japan; seagrass bed	1336
Smaragdia sp. 2	Cocos Islands, Australia; seagrass bed	260
Smaragdia sp. 3	Cocos Islands, Australia; seagrass bed	1040
Theodoxus fluviatilis (Linnaeus, 1758)	Stockholm, Sweden; freshwater pond	287
Vitta virginea (Linnaeus, 1758)	Grand Cayman, Caribbean; freshwater stream	993
"*Vitta*" *cumingiana* (Récluz, 1843)	Okinawa Is., Japan; stream mouth	435
"*Vitta*" *gagates* (Lamarck, 1822)	Amami Is., Japan; freshwater stream	432
Neritopsidae (Outgroup)		
Neritopsis radula (Linnaeus, 1758)	Ie Is., Okinawa, Japan; submarine cave	85
Titiscania shinkishihataii Taki, 1955	Hachijo Is., Japan; rocky shore	279

Table 2-2. Nucleotide sequences of primers used in this study.

Name	Sequence	Direction	Reference
COI			
LCO1490	5′-GGTCAACAAATCATAAAGATATTGG-3′	Forward	Folmer et al. (1994)
HCO2198	5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Reverse	Folmer et al. (1994)
LCOmod	5′-TCTACTAATCATAAGGAYATYGGNAC-3′	Forward	Kano (2008)
HCOmod	5′-ACTTCTGGGTGTCCRAARAAYCARAA-3′	Reverse	Kano (2008)
LCO-SMA	5′-ATATTATGTTTGGTGTTTGATCTG-3′	Forward	Present study
HCO-SMA	5′-CATACCCAAGGTACCAAATG-3′	Reverse	Present study
COIf	5′-CCTGCAGGAGGAGGAGAYCC -3′	Forward	Present study
COIf-A	5′-CCTGCTGGTGGAGGTGAYCC-3′	Forward	Present study
COIf-B	5′-CCTGCTGGTGGTGGAGAYCC -3′	Forward	Present study
COIf-D	5′-CCTGCCGGAGGGGGTGAYCC -3′	Forward	Present study
COIf-G	5′-CCAGCTGGRGGGGGTGATCC -3′	Forward	Present study
COIf-J	5′-CCAGCAGGAGGCGGGGATCC -3′	Forward	Present study
COIf-L	5′-CCAGCGGGTGGRGGTGATCC-3′	Forward	Present study
COIa-NER	5′-CATTTAGTGTAGCAATCAGGRTARTC-3′	Reverse	Kano & Kase (2004)
16S rRNA			
16SarL	5′-CGCCTGTTTATCAAAAACAT-3′	Forward	Palumbi et al. (1991)
16SbrH	5′-CCGGTCTGAACTCAGATCAYGT -3′	Reverse	Palumbi et al. (1991)
12S rRNA			
12S1	5′-CCTACCTGGTTGATCCTGCCAG-3′	Forward	Present study
12S2	5′-GGATCTATTGGAGGGCAAGT-3′	Forward	Present study
28S rRNA			
900F	5′-CCGTCTTGAAACACGGACCAAG-3′	Forward	Williams & Ozawa (2006)
Lg2	5′-ATGGAACCCTTCTCCACTTCAG-3′	Reverse	Present study
FL	5′-AAGTGGAGAAGGGTTCCATGT-3′	Forward	Present study
na2	5′-AGCCAATCCTTATCCCGAAG-3′	Reverse	Kano et al. (2002)
Fa	5′-CGTACCCATATCCGCAGCA-3′	Forward	Present study
r2	5′-TGACAGCTGTACCGCCCCA-3′	Reverse	Present study

Table 2-3. New subfamilial and generic classification of the family Neritidae. Type species for each genus is provided with its senior synonym in brackets if present. All available names listed in Holthuis (1995) and Bouchet & Rocroi (2005). *Neripteron* and *Puperita* are synonymized herein.

Genus	Type species
Neritinae Rafinesque, 1815	
Nerita Linnaeus, 1758	*Nerita peloronta* Linnaeus, 1758
New subfamily	
Neritodryas Martens, 1869	*Nerita cornea* Linnaeus, 1758
Fluvinerita Pilsbry, 1932	*Nerita alticola* Pilsbry, 1932 [= *Fluvinerita tenebricosa* (C.B. Adams, 1851)]
Neritininae Poey, 1852	
Clithon Montfort, 1810	*Nerita corona* Linnaeus, 1758
Dostia Gray, 1847	*Neritina crepidularia* Lamarck, 1822 [= *Dostia violacea* (Gmelin, 1791)]
Laodia Gray, 1868	*Navicella cumingiana* Récluz, 1843
Neritina Lamarck, 1816	*Nerita pulligera* Linnaeus, 1767
Neritona Martens, 1869	*Neritina labiosa* Sowerby I, 1836
Septaria Férussac, 1807	*Patella borbonica* Bory de St. Vincent, 1803 [= *Septaria porcellana* (Linnaeus, 1758)]
Syn.: *Neripteron* Lesson, 1831	*Neritina taitense* Lesson, 1831 [= *Septaria auriculata* (Lamarck, 1816)]
Smaragdia Issel, 1869	*Nerita viridis* Linnaeus, 1758
Theodoxus Montfort, 1810	*Nerita fluviatilis* Linnaeus, 1758
Vitta Mörch, 1852	*Nerita virginea* Linnaeus, 1758
Syn.: *Puperita* Gray, 1857	*Nerita pupa* Linnaeus, 1758
Vittina Baker, 1923	*Nerita roissyana* Récluz, 1841 [= *Vittina communis* (Quoy & Gaimard, 1834)]
New genus A	"*Neritina*" n. sp. from Vanuatu
New genus B	"*Neritina*" *bruguieri* (Récluz, 1841)

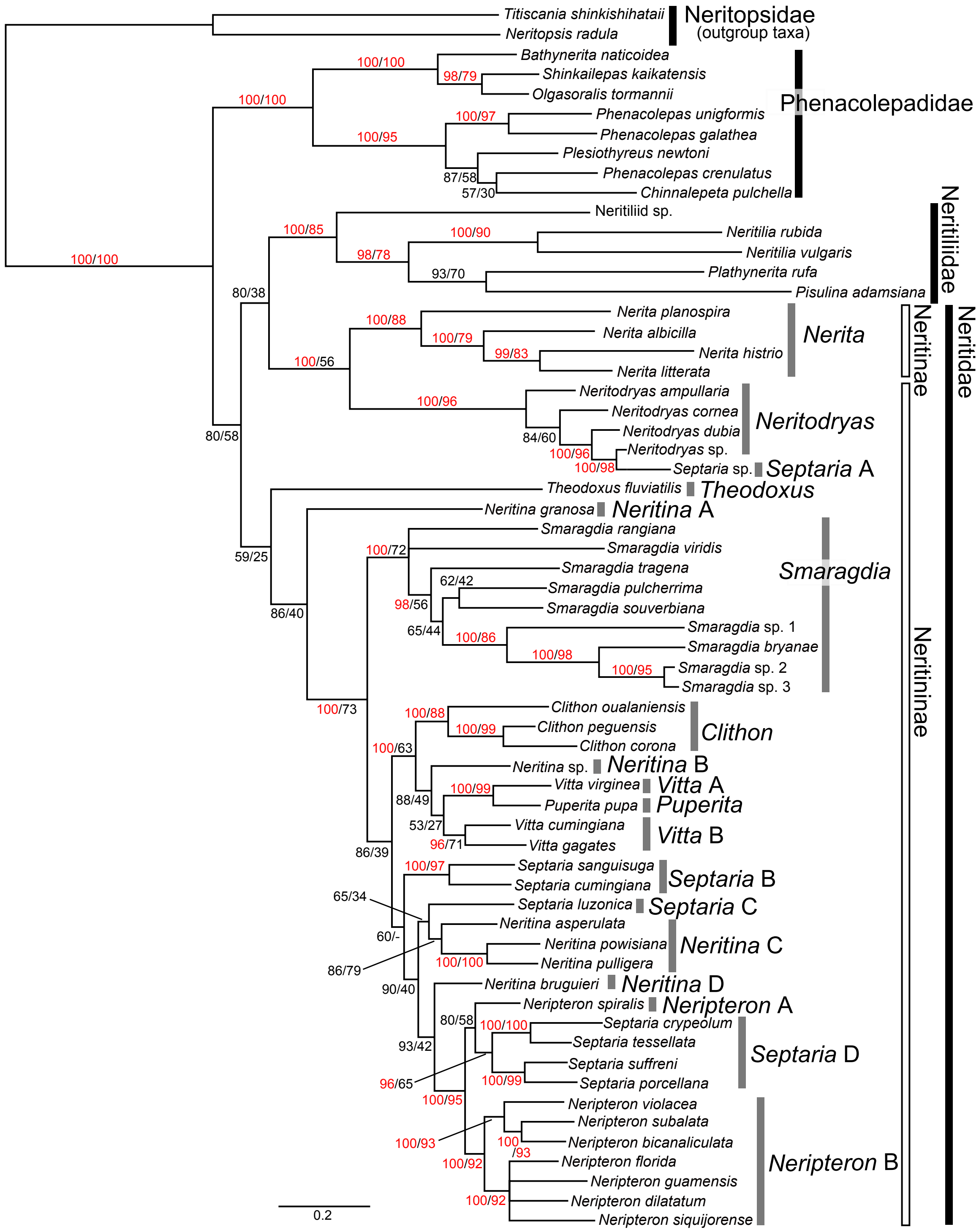


Figure 2-1. Bayesian phylogeny of Neritoidea inferred from 1,244 sites of mitochondrial COI gene. Numbers on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values (BP, right), both shown as percents. Significant support shown in red (PP ≥ 95%, BP ≥ 75%).

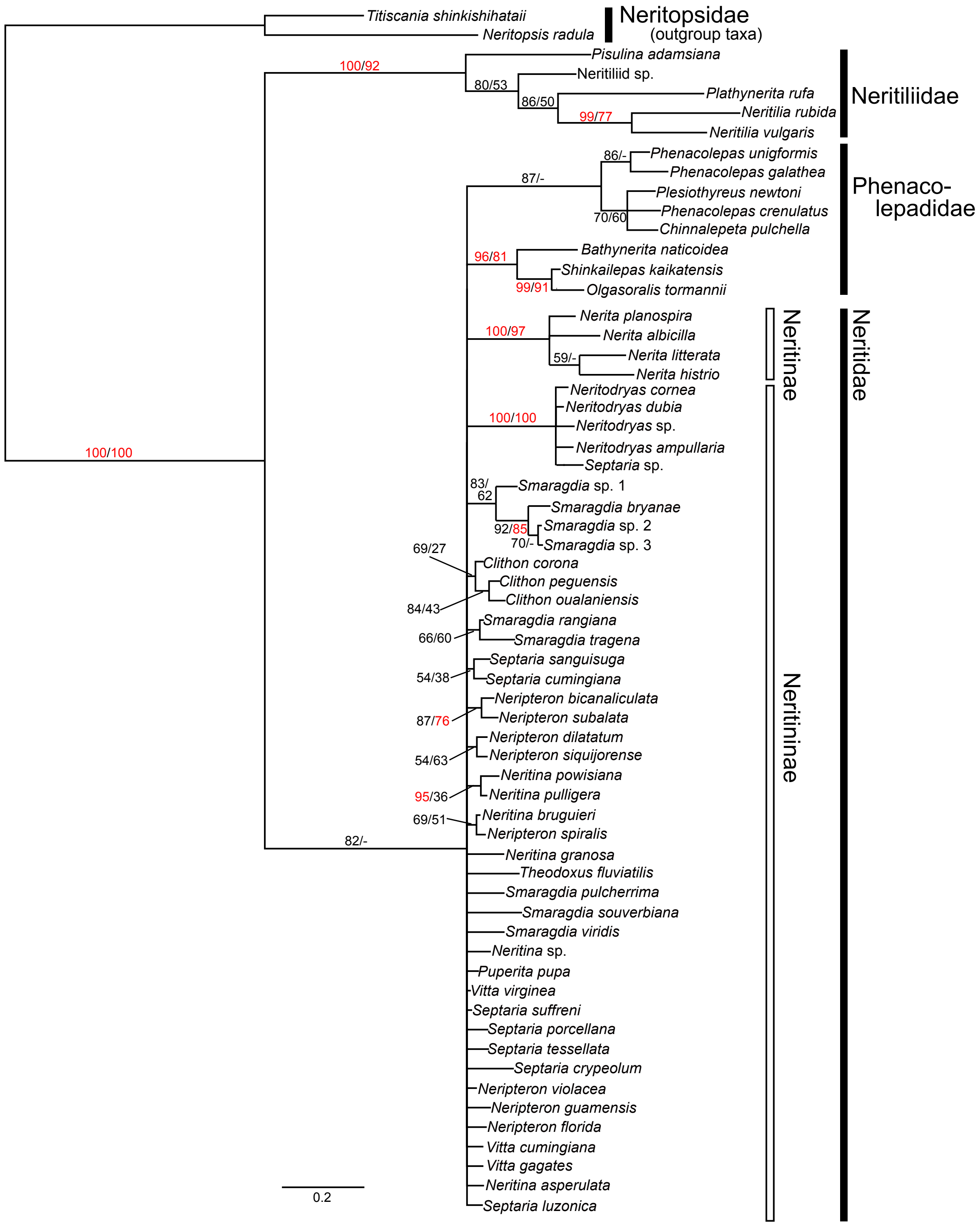


Figure 2-2. Bayesian phylogeny of Neritoidea inferred from 386 sites of mitochondrial 16S gene. Numbers on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values (BP, right), both shown as percents. Significant support shown in red (PP ≥ 95%, BP ≥ 75%).

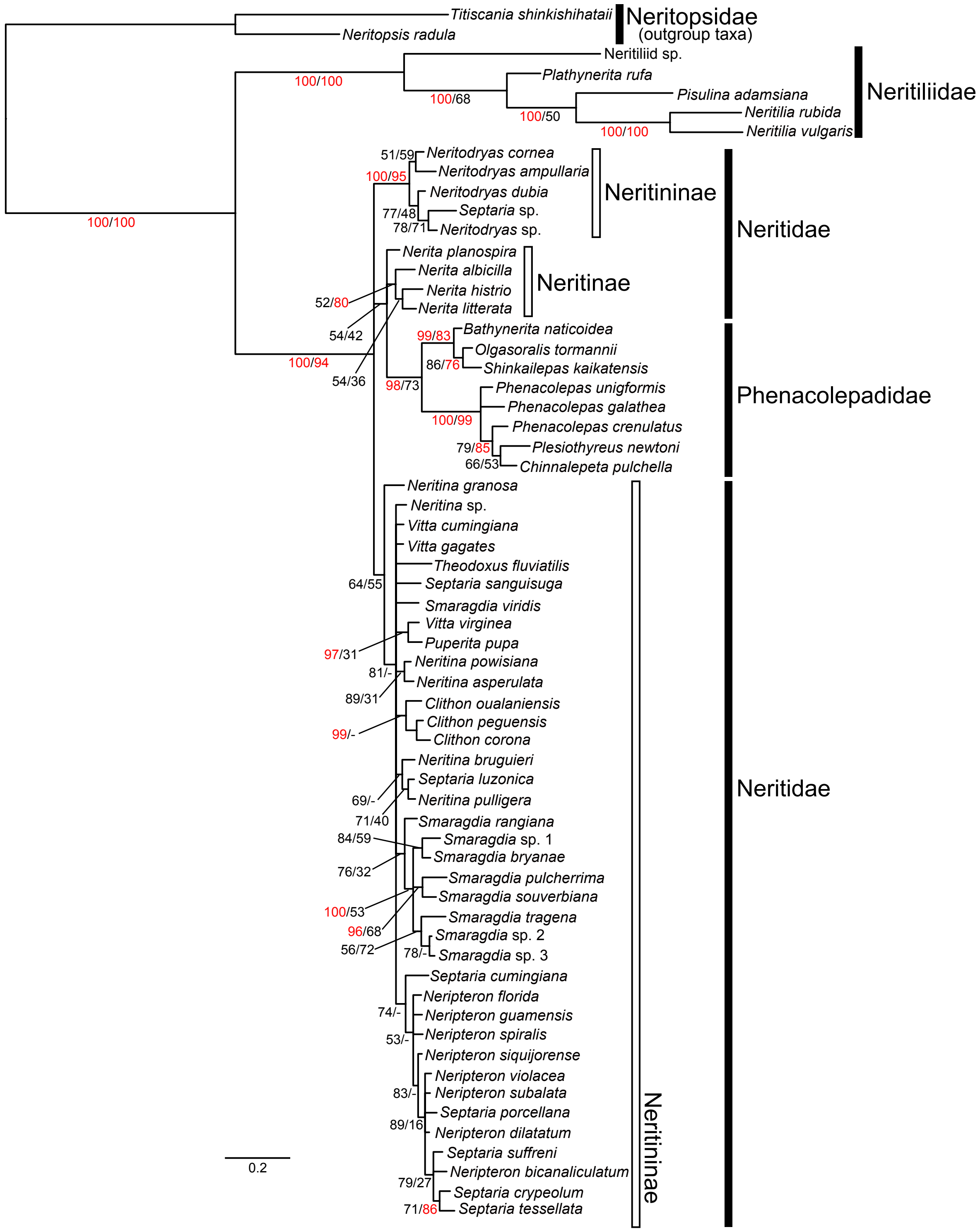


Figure 2-3. Bayesian phylogeny of Neritoidea inferred from 384 sites of mitochondrial 12S gene. Numbers on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values (BP, right), both shown as percents. Significant support shown in red (PP ≥ 95%, BP ≥ 75%).

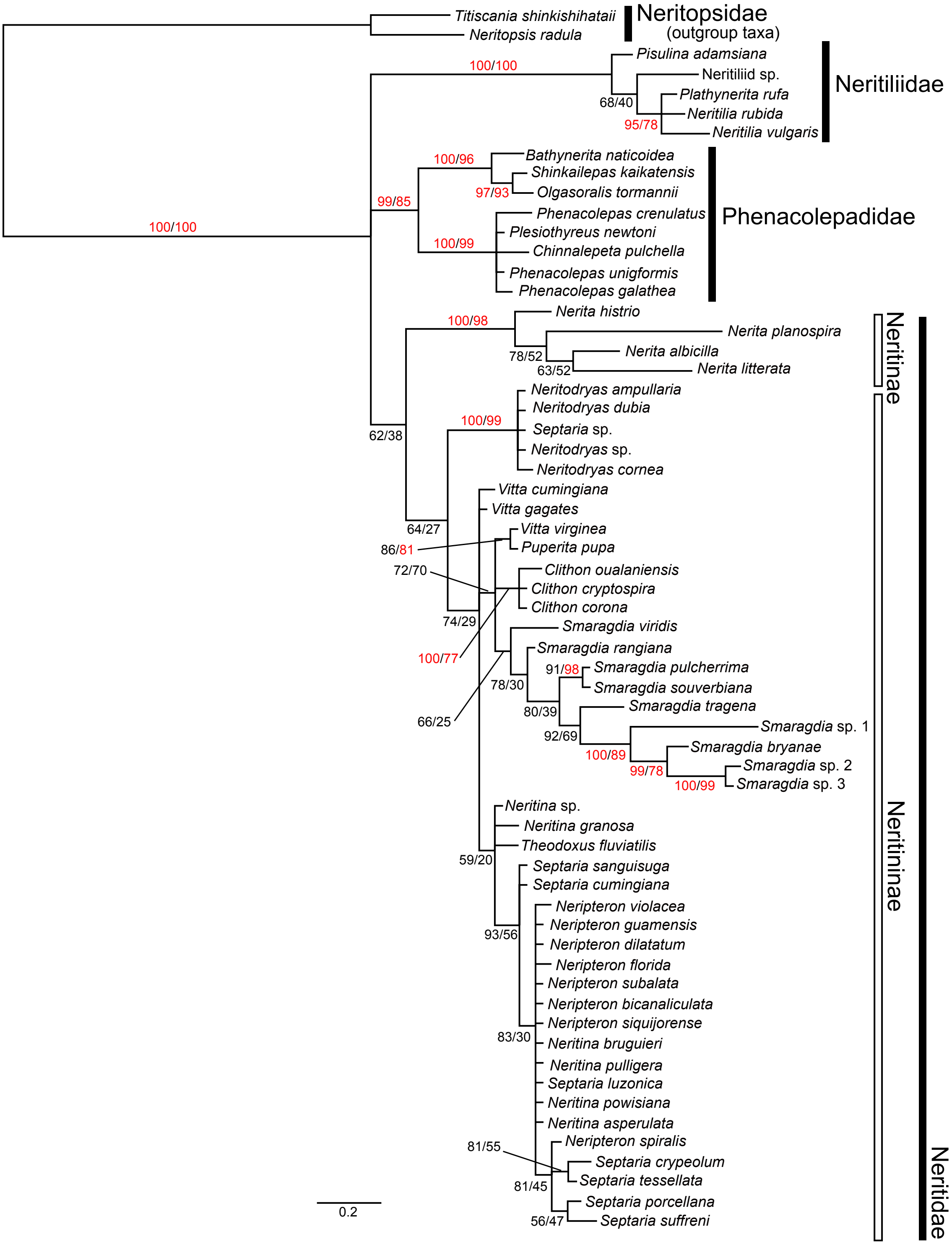


Figure 2-4. Bayesian phylogeny of Neritoidea inferred from 1,983 sites of nuclear 28S gene. Numbers on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values (BP, right), both shown as percents. Significant support shown in red (PP ≥ 95%, BP ≥ 75%).

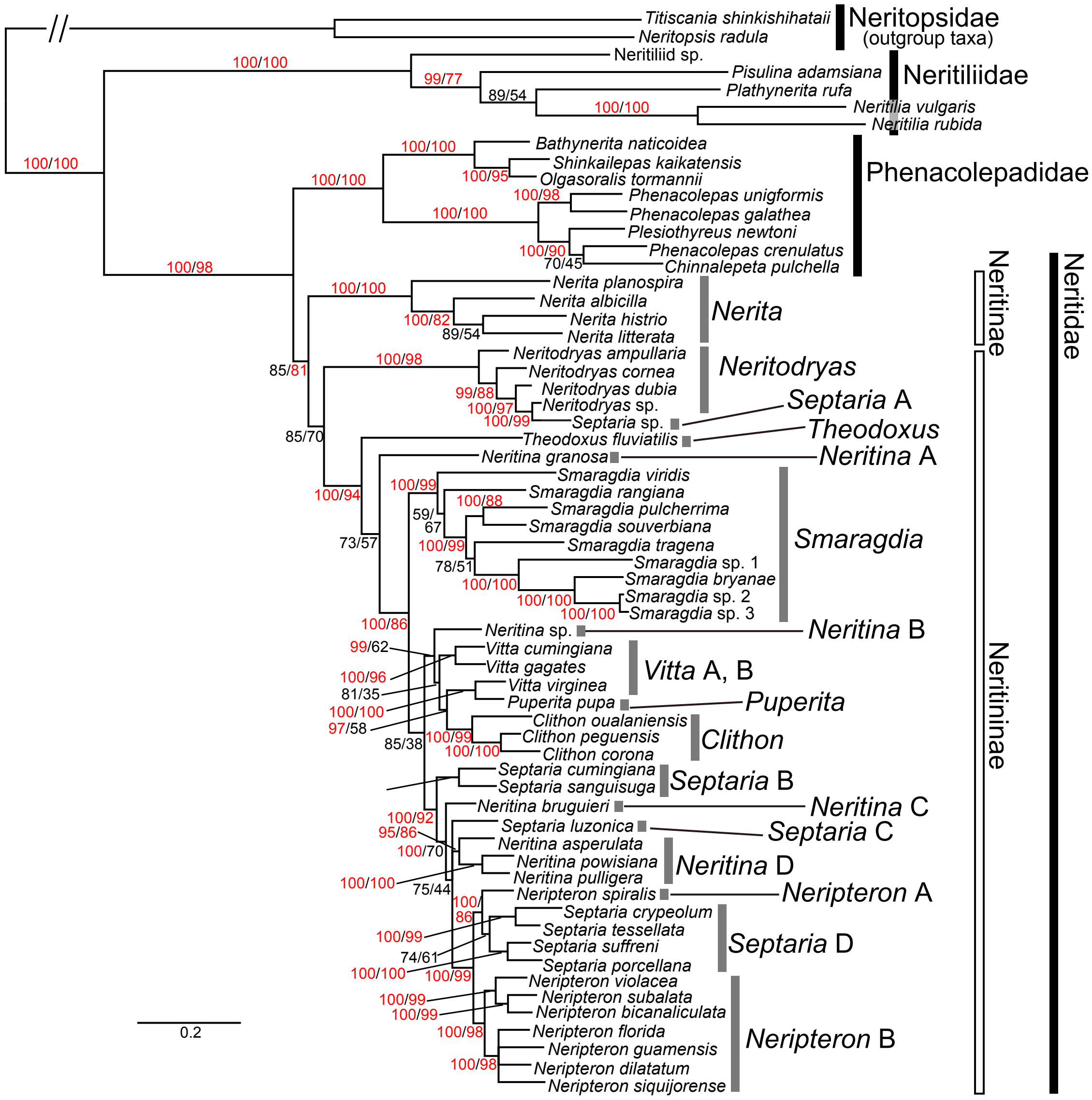


Figure 2-5. Bayesian phylogeny of Neritoidea inferred from concatenated four-gene dataset (COI + 16S + 12S + 28S, 3,997 sites). Numbers on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values (BP, right), both shown as percentage. Significant support shown in red (PP ≥ 95%, BP ≥ 75%). Neritopsidae are included as outgroup taxa.

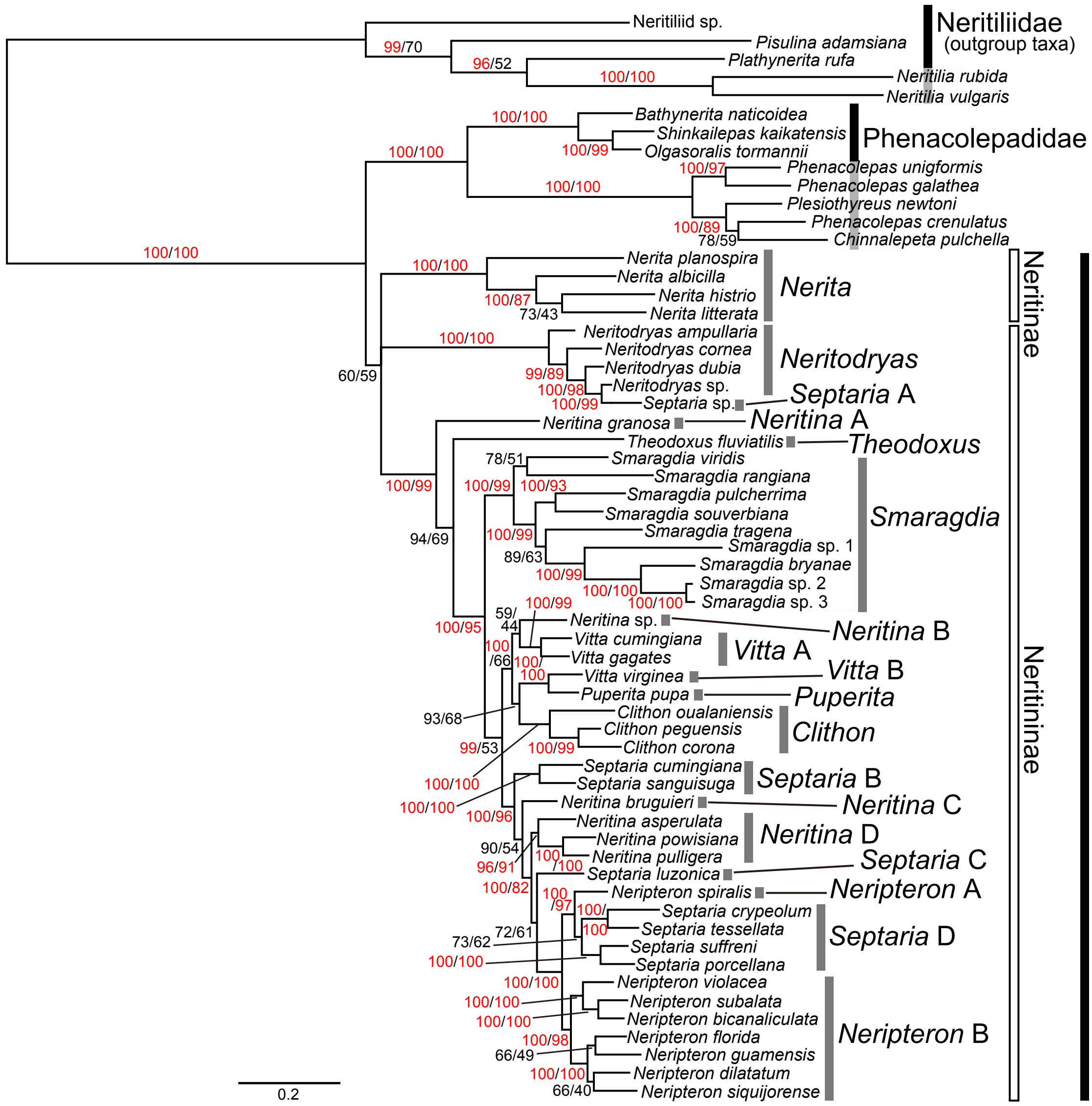


Figure 2-6. Bayesian phylogeny of Neritoidea inferred from concatenated four-gene dataset (COI + 16S + 12S + 28S, 4,175 sites). Numbers on branches denote posterior probabilities (PP, left) and likelihood-based bootstrap values (BP, right), both shown as percentage. Significant support shown in red (PP ≥ 95%, BP ≥ 75%). Neritiliidae are used as outgroup taxa.

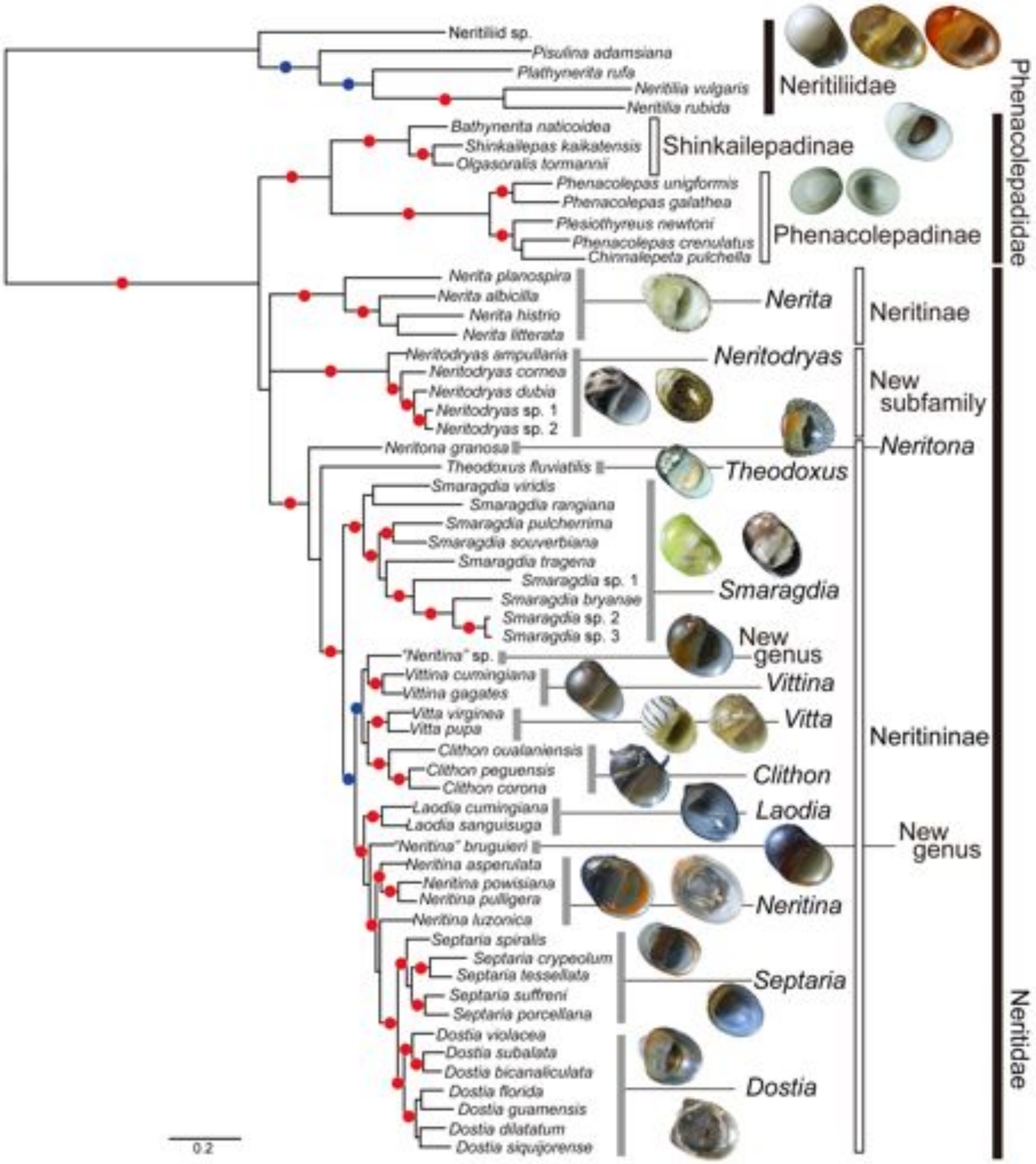


Figure 2-7. New subfamilial and generic classification for Neritidae. Tree topology is derived from Bayesian analysis of four-gene dataset without Neritopsidae (Fig. 2-6). Nodes with significant support in both Bayesian and likelihood reconstructions are marked by red circles (PP ≥ 95%, BP ≥ 75%); those supports only by meaningful posteriors are indicated with blue circles. In total of three subfamilies and 15 genera are recognized in Neritidae (see text), including a new subfamily for *Neritodryas* and two new genera for "*Neritina*."

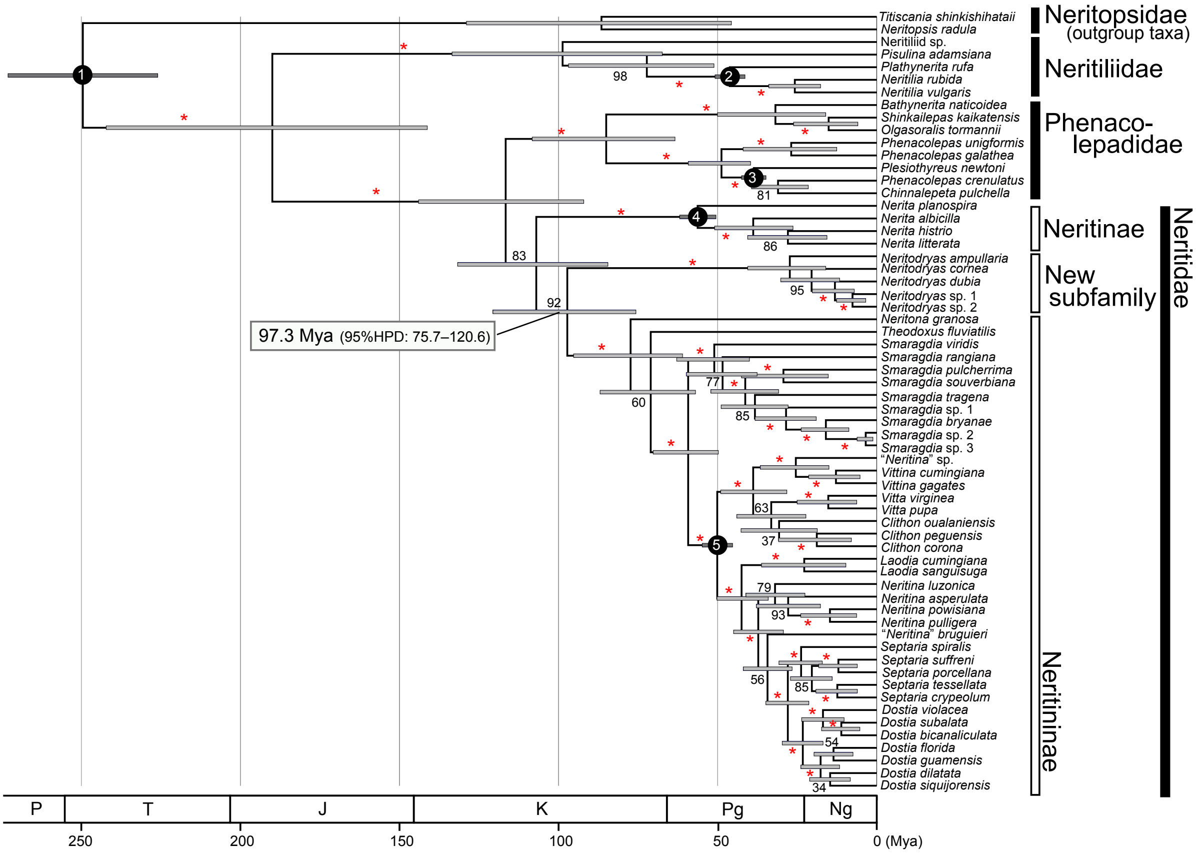


Figure 2-8. Divergence time chronogram of Neritoidea inferred from a Bayesian relaxed-clock analysis in BEAST. Five calibration points at nodes 1–5 were set as priors based on fossil records. Numerals on branches indicate posterior probabilities as percentage; asterisks denote 100% support. Horizontal bars show 95% HPD intervals of priors (dark grey) and estimated ages (light grey).

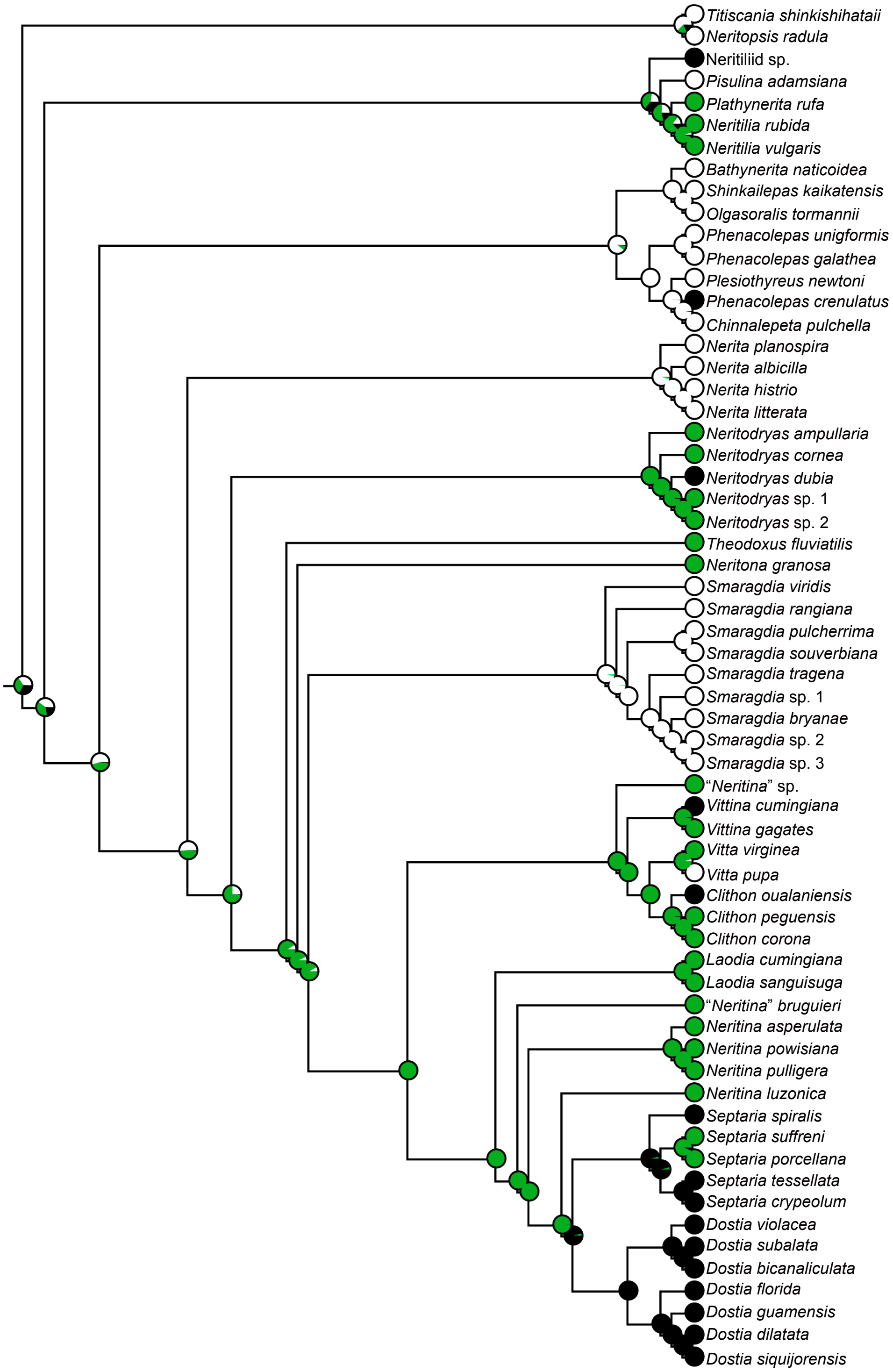


Figure 2-9. Reconstruction of habitat shifts in Neritoidea by Mk1 model in Mesquite. Tree topology was obtained by likelihood analysis of concatenated four-gene dataset in RAxML. Pie charts at nodes indicate proportion of each of three habitat types: marine (white), brackish (black) and freshwater (green).

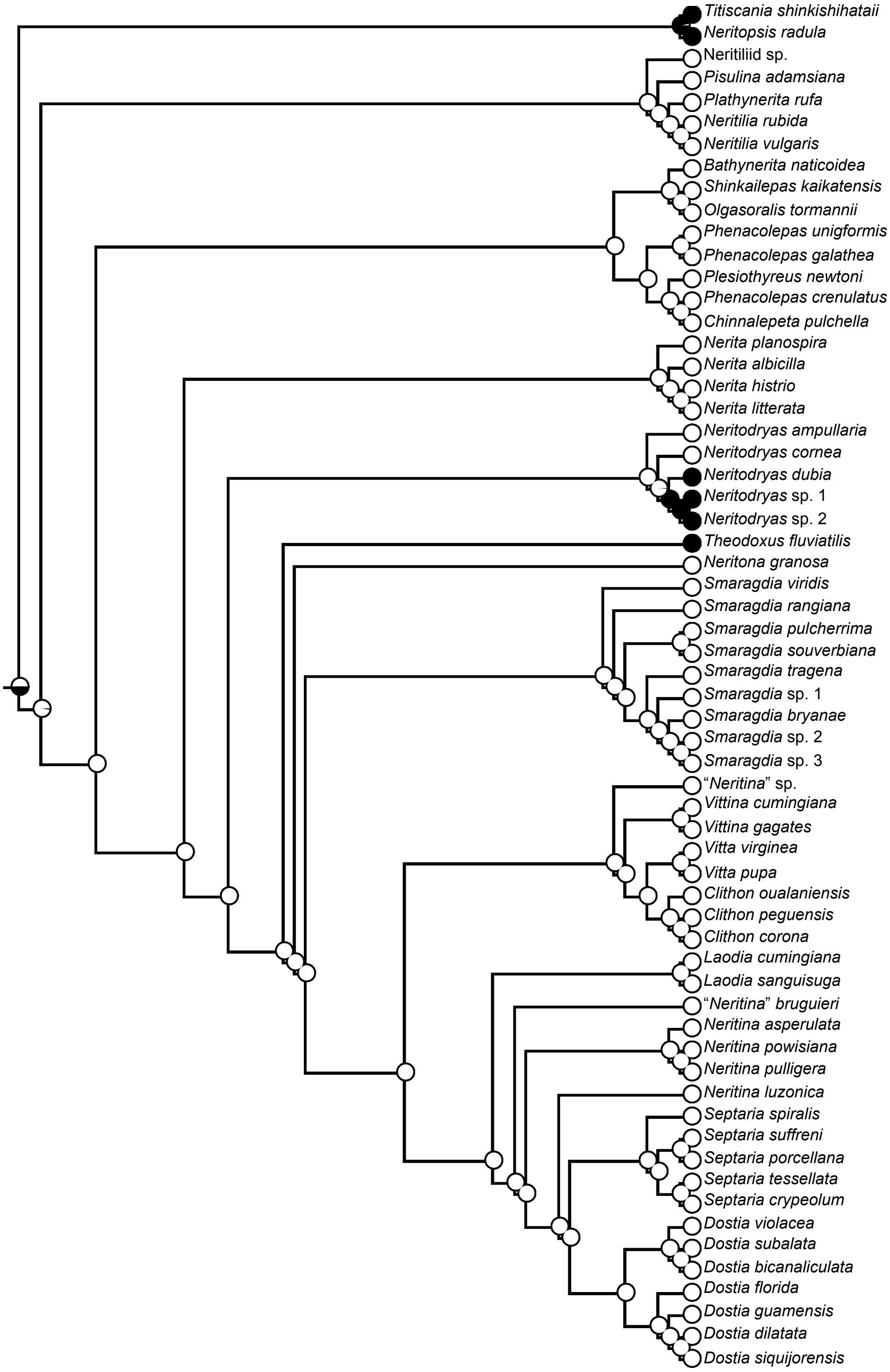


Figure 2-10. Ancestral state reconstruction for early ontogeny of Neritoidea in Mesquite (Mk1 model). Tree topology was obtained by likelihood analysis of concatenated four-gene dataset in RAxML. Pie charts at nodes indicate proportion of each of two developmental modes: planktotrophic (white) and non-planktotrophic (black). Loss of planktotrophy occurred twice in *Neritodryas* and *Theodoxus*.

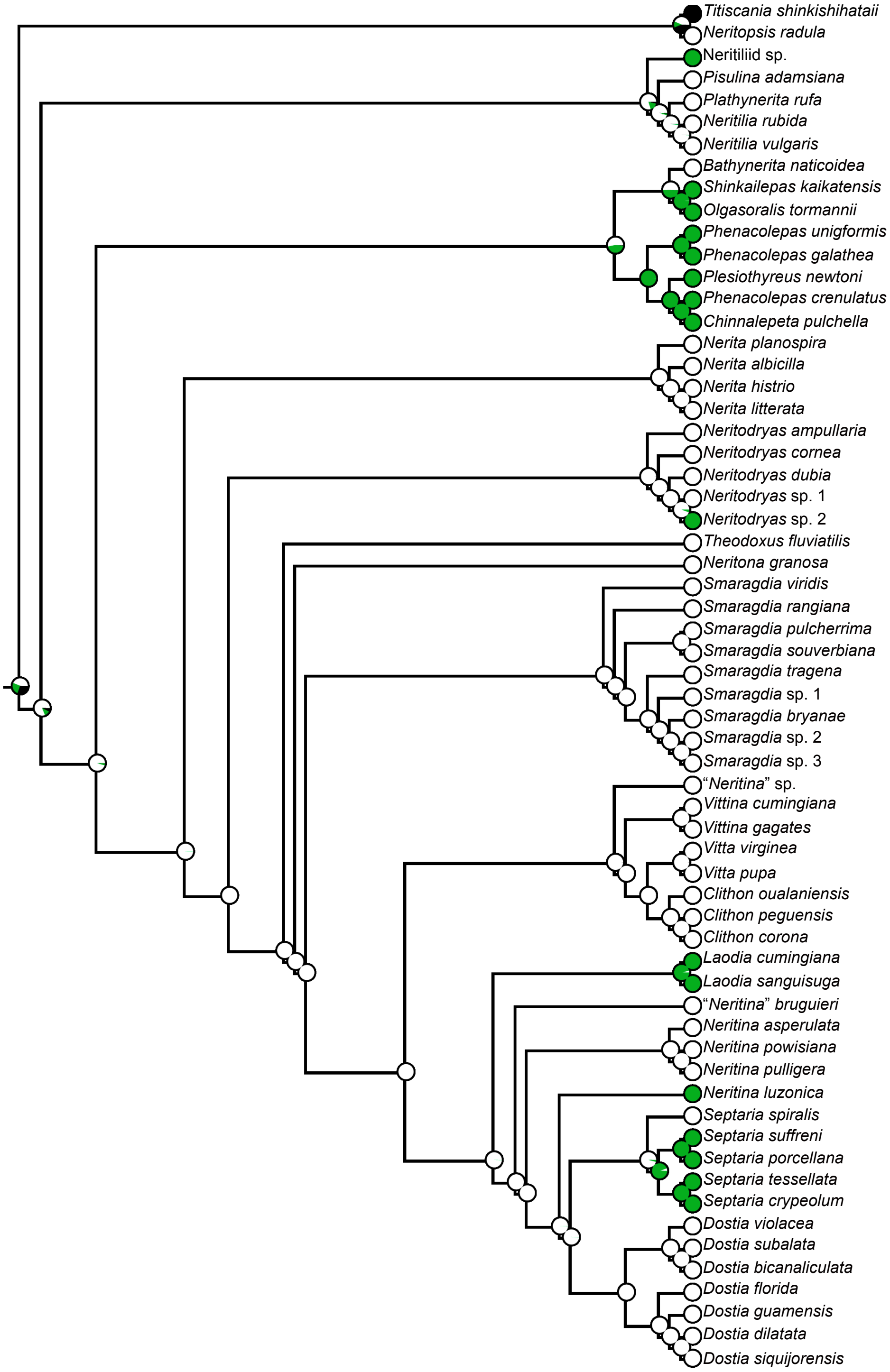


Figure 2-11. Ancestral state reconstruction for body plan of Neritoidea in Mesquite (Mk1 model). Tree topology was obtained by likelihood analysis of concatenated four-gene dataset in RAxML. Pie charts at nodes indicate proportion of each of three morphologies: neritiform snail with contractile body (white), limpet without functional operculum (green) and shell less slug (black). Patelliform has evolved four times in Neritidae.

Chapter 3: Evolutionary ecology of settlement size in planktotrophic neritimorph gastropods

3-1: Introduction

Body size during larval development is one of the most important attributes of aquatic invertebrates with complex life cycles from both ecological and evolutionary standpoints (Marshall & Keough 2007). In particular, special attention has been paid to the size at metamorphosis, which can be affected by selection on the initial size of offspring as well as the optimal size for changing form or habitat (Strathmann 1993). Intraspecific variation of settlement size is not only associated with maternal effects, but also influences post-settlement mortality and growth rate in planktotrophic species (Phillips 2002; Giménes 2010). Larger size at metamorphosis enables adaptation to harsh environmental conditions, including exposure to desiccation, predation and starvation (Spight 1976; Moran & Emlet 2001). On the other hand, interspecific variation of settlement size has been often attributed to the ecological characteristics of the species. For example, predatory caenogastropods that feed on moving prey after metamorphosis tend to have larger settlement sizes than grazing herbivores or carnivores feeding on sessile animals (Lesoway & Page 2008). Settlement size is related to the sediment characteristics of settling areas in bivalves, possibly because their fragile larvae need to be larger than sediment grains (Cardoso *et al*. 2006). However, phylogenetic constraints and ancestral conditions have rarely been taken into consideration when discussing size differences with respect to various ecological traits (Hadfield & Switzer-Dunlap 1984; Kohn & Perron 1994; Levitan 2000; Collin 2003). Settlement size is often used in taxonomic studies to diagnose genera and families that may contain species with different diets and habitats (e.g. Kano & Kase 2002; Knowlton & Vargo 2004).

Shell-bearing gastropods are ideal subjects for the interspecific comparison of settlement size, because they flourish in almost all aquatic environments from intertidal to hadal waters as well as in freshwater ponds and streams (Kano *et al.* 2002), and because a calcified shell is a reliable indicator of overall body size and its rigidity allows accurate measurement (Lesoway & Page 2008). The metamorphosis of their planktotrophic larvae, which often become competent to metamorphose at some earlier point in their development, is generally instigated by particular chemical or physical cues (Pechenik 1990). Larvae of some species continue to grow when lack of environmental induction forces a delay of metamorphosis, resulting in a high level of intraspecific size variation at settlement (Pechenik 1980; Lesoway & Page 2008). In contrast, most gastropod species arrest growth during the competent period and as a consequence show small intraspecific variation of body size at settlement (see Lesoway & Page 2008 for review). This uniformity of settlement size is advantageous for studying the evolution of selection on an optimal size at settlement in aquatic gastropods.

Another and even more important advantage of shell-bearing gastropods is that the accretionary growth of the shell throughout their ontogeny leaves the larval shell at the apex of the adult shell as the protoconch (Jablonski & Lutz 1983). Instead of the direct observation of larvae, settlement size has been studied through the measurement of the protoconch on adult shells in both Recent and fossil species (e.g. Shuto 1974; Rex & Etter 1998). The presence or absence of feeding (planktotrophy) can also be inferred from the protoconch morphology. The protoconch consists of both embryonic and larval shells in species with planktotrophic development; in non-planktotrophic species, on the other hand, there is no larval shell and the protoconch consists exclusively of a relatively large embryonic shell formed prior to hatching. The protoconch as a whole is accordingly multispiral in the former species and paucispiral in the latter species (e.g. Bouchet & Warén 1979; Jablonski & Lutz 1983; Lima & Lutz 1990). However, the apex of a gastropod shell is often worn and eroded. Microorganisms that bore into calcium carbonate as well as larger invertebrates do extensive damage to the shells of marine mollusks; abiotic agents also influence erosion, especially in animals inhabiting environments that are harsh physically or chemically, including rocky shores with strong surf, acidic freshwater streams, mangrove swamps, and deep-sea hydrothermal vents and seeps (Kano 2006). The original shape of the protoconch in those taxa remains intact for only a short period after metamorphosis, so it can be extremely difficult to infer the developmental mode by examining the protoconch on juvenile or adult shells.

Neritimorpha (= Neritopsina), a gastropod superorder, comprises several hundred living species in four aquatic families (Neritopsidae, Neritiliidae, Neritidae and Phenacolepadidae; Kano *et al.* 2002) and four terrestrial ones (Bouchet & Rocroi 2005). This group has undergone a major adaptive radiation and currently occupies a great variety of habitats, including rocky shores, seagrass beds, submarine caves, mangrove swamps, freshwater streams, subterranean waters and deep-sea vents and seeps, in addition to terrestrial and arboreal ecosystems (Ponder & Lindberg 1997; Kano *et al.* 2002). Aquatic neritimorphs often have a prolonged planktotrophic larval phase of a few or several months (Scheltema 1971; Holthuis 1995; Kano 2006; Lesoway & Page 2008). Their larvae are characterized by spherical, strongly convoluted shells, which make them easily distinguishable from other gastropod larvae (e.g. Scheltema 1971; Page & Ferguson 2013). However, the protoconch is eroded in most metamorphosed individuals except those in shallow subtidal waters due to the unfavorable conditions as mentioned above.

Meanwhile, this snail group provides a rare opportunity to assess the interspecific variation and adaptive significance of settlement size with unique morphological characteristics. Kano (2006) has shown that the operculum of the larval shell remains as the opercular nucleus in almost all adult opercula of neritimorphs. The form of the nucleus reflects the type of larval development as the protoconch does, while the organic composition of the nucleus makes it tolerant to erosion and thus advantageous, compared to the protoconch, in this ecologically diverse group. Species with planktotrophic larvae are characterized by the paucispiral nucleus with a small initial region or embryonic operculum (nucleus type A;

see Kano 2006, fig. 4). Non-planktotrophic species have three types of the opercular nucleus: paucispiral with a large initial region (type B), paucispiral without a distinct initial region (type C), and concentric without conspicuous growth lines (type D). This method is applicable to almost all species and individuals in the Neritimorpha except less than two dozen species in three genera, namely *Neritopsis*, *Titiscania* and *Neritodryas*, due to the erosion of the opercular nucleus, total absence of the adult operculum, and methodological difficulty in peeling off the calcareous layer overlying the nucleus, respectively (Kano 2006). The measurements of the opercular nucleus may also be a useful estimate of settlement size. The neritimorph protoconch is extremely uniform in shape and sculpture and the operculum fits closely into the shell aperture in all aquatic species of the superorder (Bandel 1982; Kano 2006; Page & Ferguson 2013). Thus, settlement size may be potentially correlated with, and inferred from, the size of the nucleus, which is retained in the adult operculum.

The major goal of this chapter is to reveal the phylogenetic and ecological patterns of the interspecific variation of settlement size in the gastropod superorder Neritimorpha through the measurement of adult opercula. By taking advantage of this snail lineage, I aim to provide the most comprehensive data on the settlement size of marine invertebrates in terms of taxonomic sampling and coverage of different habitats. I selected 88 planktotrophic species from almost all extant genera and measured the diameter of the larval operculum retained as the nucleus of the adult operculum. The diameters of the protoconch and operculum in post-settlement juveniles were also measured to investigate whether the two measurements are correlated and whether the latter can be used as a reliable indicator of settlement size across the superorder. Finally, the adaptive significance of the various settlement sizes in this clade is discussed in phylogenetic and ecological contexts. The usefulness of the opercular nucleus and protoconch for identifying species and phylogenetic lineages is also illustrated in the taxonomy and paleontology of neritimorph gastropods as well as ecological studies on their larval dispersal and recruitment.

3-2: Materials and methods

Selection of study taxa

In this study, I selected specimens of 88 planktotrophic species belonging to 17 genera that represent all four families of the recent aquatic Neritimorpha (Table 3-1). The species were collected from rocky shores, seagrass beds, sand flats, mangrove swamps, estuaries, freshwater streams, submarine caves, deep-sea hydrothermal vents and cold seeps. Familial and generic assignments follow Holthuis (1995), Kano *et al.* (2002), Frey (2010a) and the Chapter 2 of this dissertation. As this chapter was originally written and published (Fukumori & Kano 2014) before the detailed reconstruction of neritimorph phylogeny shown in the Chapter 2, a few taxa were assigned to a certain subfamily based on previous systematic investigations, not on the present molecular tree. Such taxa include the species of *Smaragdia*, which have traditionally been classified in their independent subfamily Smaragdiinae and were here in excluded from Neritininae. Species identification was confidently made based on molecular and morphological data, while scientific names used for the Neritidae are provisional as the nomenclature of this large group requires a major revision (see Chapter 4). In this study, I defined that the word Neritininae used in this study indicates seven genera of the Neritininae except for *Smaragdia*.

Measurement of opercular nucleus

Up to 23 (an average of 5.2) opercular nuclei were observed and measured for each species. Conspecific individuals from multiple localities worldwide were also selected when samples were available. The diameter of the opercular nucleus (Fig. 3-1, *nd*; see Kano 2006, fig. 1) was measured to 5-μm precision by tracing the outline of horizontally placed nuclei using a stereomicroscope (Nikon SMZ1500) equipped with a drawing tube. For *Nerita* specimens, I used forceps and needles to peel off the outer calcareous layer to reveal the opercular nuclei as described in Kano (2006). I gathered the nucleus sizes of 42 individuals from previous studies (Kano 2006, table 2; Kano 2009, online supplementary fig. 1) for seven species in four genera in addition to the measured values in the present study (total 368 individuals for 88 species in 18 genera). For the rare planktotrophic *Neritopsis*, the apertural size of the protoconch was measured in a juvenile shell of an unidentified species through an application of micro-CT techniques (Y. Kano *et al.* in preparation) and was used instead of the measurement of the opercular nucleus.

Comparison between sizes of opercular nucleus and protoconch

Forty-five post-settlement juveniles were used to test the correlation between the larval shell size at settlement and the diameter of the opercular nucleus. I used only small juveniles that had less than 0.5 volution of the teleoconch for precise measurement of the protoconch (Fig. 3-1, *pd*). The protoconch was measured to 5-μm precision in the same way as for the opercular nucleus in adult specimens; the juvenile shells were placed in a small hole made in a rubber plate, except the single shell of *Neritopsis* sp. that was measured by micro-CT scanning.

Comparison of settlement size distribution among lineages and habitats

Phylogenetic trends of settlement size in the Neritimorpha were examined by a size comparison among six lineages (Neritopsidae, Neritiliidae, Phenacolepadidae, Neritinae, Neritininae and *Smaragdia*). Each lineage represents a monophyletic clade (Fig. 3-2) that occupies a wide range of different habitats (Kano *et al.* 2002). These habitats can be divided into three groups, i.e. marine, brackish and freshwater, for the comparison of nucleus diameter among habitats. (1) The marine group refers to species from (near) euhaline habitats including the rocky shore, sand flat, mangrove swamp, seagrass bed, submarine cave, deep-sea hydrothermal vent and cold seep. (2) The brackish group includes species living in the mixohaline water of the estuary and stream mouth. Members of this group may be able to tolerate occasional exposure to both fully marine or freshwater conditions. (3) Freshwater group refers to limnic species that mainly occur in the upper and middle reaches of the stream and river, while some show tolerance to low-salinity brackish water. Opercular size distribution was compared among the six lineages or three habitat groups. The mean and standard deviation of the nucleus size for each group was calculated by averaging the mean size of species.

Relationship between settlement size and geographic range

The relationship between settlement size and geographic distribution area was examined for 60 representative species to assess the effect of settlement size in determining the distribution in the sea, i.e. whether a larger larva results in a wider geographic range through a presumably longer planktonic period. The 60 species were selected from the 88 study species for the nucleus measurements based on the availability of the information on the distribution range and nucleotide sequences in previous literature or my data library (see Chapter 4). Morphological species with multiple evolutionarily-significant units (ESUs) were excluded, or only one ESU from such morphospecies was selected to include the specimens used for the measurement of the nucleus and protoconch. The distribution range was represented by the distance between two remotest known occurrences of the species via a straight line at a 50-km level of precision. The size of the larval shell at settlement was estimated from that of the opercular nucleus when an adequate protoconch was not available for measurement of each species (see Results).

Statistical analyses

Pearson's correlation test was used to assess whether the diameters of protoconch and opercular nucleus are correlated and whether the settlement size and geographic distribution area of species are related. Analysis of variance and Tukey-Kramer test were used to statistically compare the distributions of the settlement size among lineages and habitats. All test were conducted with R (R development Core Team 2008).

3-3: Results

Size of opercular nucleus

Table 3-1 summarizes the diameter of the opercular nucleus in the study species of planktotrophic neritimorphs. The diameter of the nucleus revealed a broad size range (*nd*: 175–570 μm). Contrary to the small intraspecific variation, there was considerable interspecific variation in the diameter, as previously shown in Kano (2006) with a smaller dataset. Among the study species, *Neritina petitii* was found to have the widest intraspecific variation with its range corresponding to 10.7% of the mean, and only four species (*Nerita insculpta*, *Clithon subpunctata*, *Neritina delestennei*, *Neritina petitii*) showed intraspecific variation exceeding 10%. Overall, the average of intraspecific variation was 5.2% of the mean for each species. The diameter often differed considerably among species within the same genus, without an overlap of size ranges (Table 3-1).

The dimensions of the opercular nucleus differed among six lineages. *Smaragdia* represented the largest average diameter (482 ± 59 μm; range: 405–570 μm) and included the species with the largest opercular nucleus in Neritimorpha (*Smaragdia rangiana*: up to 570 μm). Phenacolepadidae were the second largest (452 ± 51 μm; 340–520 μm). Within this family, the reciprocal sister clades Phenacolepadinae and Shinkailepadinae showed different ranges of the nucleus size. The former shallow water group, here represented by

Phenacolepas and *Cinnalepeta*, had smaller nuclei (405 ± 36 μm; 340–445 μm) than those of *Shinkailepas*, *Olgasolaris* and *Bathynerita* from deep-sea chemosynthetic environments (489 ± 16 μm; 460–520 μm). Neritopsidae and Neritinae showed moderate sizes. *Neritopsis* from a submarine cave had a nucleus of 350 μm wide. Neritinae, which comprise the monotypic genus *Nerita* from intertidal rocky shores and mangrove swamps, showed a size range of 300–450 μm (375 ± 39 μm); the smallest nucleus was found in *Nerita histrio* and the largest in *Nerita melanotragus*.

Neritininae had smaller nuclei than the above four groups (298 ± 26 μm; 235–360 μm). Among seven neritinine genera, exclusively marine or brackish water taxa (*Dostia, Vitta pupa*) tend to have slightly larger nuclei than freshwater (*Laodia*, *Neritina*, *Vitta* except *V. pupa*) or fresh/brackish water genera (*Clithon, Vittina* and *Septaria*). The fully marine species *Vitta pupa* (= "*Puperita*" *pupa*) had a nucleus diameter of 310 ± 5 μm (305–315 μm); 7 species of the brackish water genus *Neripteron* showed a similar range (305 ± 27 μm; 255–360 μm). There was no difference between the exclusively freshwater *Laodia*, *Neritina* and *Vitta* except *V. pupa* and the fresh/brackish water *Clithon, Vittina* and *Septaria*. *Laodia*, *Neritina* and *Vitta* except *V. pupa* showed the respective sizes of 258 ± 6 μm (255–265), 295 ± 13 μm (279–310 μm) and 261 ± 17 μm (245–280 μm); *Clithon*, *Vittina* and *Septaria* were 301 ± 28 μm (260–345 μm), 313 ± 8 μm (295–330 μm) and 261 ± 22 μm (235–325 μm), respectively. At the species level, the largest nucleus for Neritininae was found in *Dostia guamensis* (360 μm) and the smallest in *Septaria tessellata* (235 μm), both of which are brackish dwellers.

Neritiliidae had the smallest opercular nuclei (194 ± 16 μm; 175–230 μm) among neritimorph gastropods. The nuclei were larger in the submarine-cave genus *Pisulina* (217 ± 8 μm; 210–230 μm) than those in freshwater *Platynerita* (185–200 μm; 193 ± 6 μm) and *Neritilia* (184 ± 1 μm; 175–190 μm).

Size of protoconch

I measured the diameter of 45 protoconchs in post-settlement juveniles. The specimens belonged to four families or subfamilies and at least nine genera: Neritopsidae (*Neritopsis*), Neritiliidae (*Neritilia*), Phenacolepadidae (*Shinkailepas*), Neritininae (*Clithon*, *Dostia*, *Neritina*, *Vittina* and *Septaria*) and *Smaragdia* ("Smaragdiinae"). Of these, 28 specimens were identified at the species level based on the teleoconch morphology; ten live-caught juveniles of six species (Table 3-2) enabled us to also measure the size of the in-situ operculum. The remaining 18 empty shells were identified to five species (Table 3-2), and the diameters of their larval opercula were extrapolated from the mean diameters of opercular nuclei for each species obtained in the above measurement of adult specimens. Measurements were also taken for the protoconch and larval operculum for 16 live-caught specimens that were identified only at the generic or higher level for the inclusion in the comparisons of the two sizes (results shown in Fig. 3-3).

The diameter of the protoconch varied greatly among neritimorph species, ranging from 345 μm in *Neritilia vulgaris* to 855 μm in an unidentified neritoid species from submarine caves in Palau and Yap, western Pacific. The intraspecific variation was small (<5% in up to 6 individuals for each species), conforming to Kano (2006) and Lesoway & Page (2008). There is noticeable phylogenetic variation: *Smaradia* and Phenacolepadidae had the largest protoconchs (675–815 μm and 675–715 μm, respectively), Neritopsidae and Neritininae were intermediate (580 μm and 415–560 μm, respectively), and Neritiliidae represent the smallest size class (345–360 μm). This phylogenetic pattern of the protoconch size agrees closely with that of the size of the opercular nucleus (= larval operculum) described above. The comparison of the two sizes in each species showed a strong correlation (Pearson's correlation test: $r = 0.982$, $P < 0.00001$), which suggests nearly uniformly shaped larval shells and opercula at metamorphic competence across the planktotrophic Neritimorpha. The approximate size of the protoconch (y) can therefore be estimated from the size of the nucleus (x) with a formula $1.29x + 80.55$ (Fig. 3-3).

Comparison of settlement size distribution among lineages and habitats

The diameter of the opercular nucleus, hence the size of the larval shell at settlement, differed significantly among families or subfamilies (analysis of variance: $P < 0.00001$; Fig. 3-4), with the exception of Neritopsidae, which was represented by a single specimen and therefore was excluded from the analysis. Tukey-Kramer test detected significant differences ($P < 0.0001$) between all groups except between Phenacolepadidae and *Smaragdia* ($P = 0.419$).

Moreover, settlement size differed significantly between the marine group and freshwater or brackish group (Fig. 3-5; Tukey-Kramer test: $P < 0.000001$). No significant difference was detected between the freshwater and brackish water groups ($P = 0.336$), nor among the three habitats in an omnibus test (analysis of variance: $P = 0.13$).

Comparison of settlement size and geographic range

There was no correlation between settlement size and geographic distribution area of species among all study taxa or within any of the five phylogenetic groups (Fig. 3-6; Table 3-3). Distances between the two remotest known occurrences of species in each group were: 700–18,950 km for Neritiliidae (n = 4), 2,250–17,150 km for Phenacolepadidae (n = 7), 1,550–19,950 km for Neritinae (n = 19), 6,600–16,500 km for *Smargdia* (n = 5) and 1,600–15,250 km for Neritininae (n = 24). Species that have either small or large settlement size can have narrow to wide distribution ranges. Pearson's correlation tests did not result in a significant *P*-value for all species or species within each phylogenetic group ($P > 0.2$).

3-4: Discussion

Inference of settlement size from measurement of adult operculum

In this study, I demonstrate that settlement size can be precisely estimated by measuring the diameter of the opercular nucleus in the planktotrophic species of the gastropod superorder Neritimorpha. There is a strong correlation between settlement size and diameter of the nucleus (Fig. 3-3), confirming nearly uniformly shaped protoconchs and larval opercula across the group (Bandel 1982; Kano 2006; Page & Ferguson 2013). The opercular nucleus retains its original shape in nearly all fully-grown specimens, while the protoconch is worn and eroded in the majority of metamorphosed individuals (Kano 2006). Moreover, the flat opercular nucleus is easier to measure than that of a globular protoconch, where the overlapping growth of the teleoconch makes the measurement even more difficult. This finding enables me to generate the largest data set so far on larval settlement sizes within a group of marine invertebrates that recruit into very different post-metamorphic habitats.

The size of the opercular nucleus is fairly constant within a species, with a range of intraspecific variation less than 10.7% of the average diameter in each species, in agreement with preliminary results by Kano (2006). Observations during rearing of planktotrophic larvae have shown determinate growth in *Nerita melanotragus* (treated as *N. atramentosa*): their shell growth is arrested during the delayed period unlike some caenogastropods that continue to grow when lack of environmental induction forces a delay of metamorphosis (Lesoway & Page 2008). The constant intraspecific sizes at settlement obtained in the present study strongly suggest the determinate larval growth in all planktotrophic species of the superorder. My results support the evolutionary hypothesis by Lesoway & Page (2008) that the capacity for continued growth during the delay period, as exhibited by some caenogastropods, is a derived innovation among feeding gastropod larvae.

Interestingly, Przeslawski (2011) has shown that the egg capsule of *N. melanotragus* sometimes persists for much longer than would be expected with strict planktotrophy. Their larvae occasionally hatch as crawling juveniles with smaller body sizes than the settlement size of feeding larvae (Przeslawski 2011), possibly representing the first reported case of gastropod poecilogony outside the Heterobranchia (see Bouchet 1989). In the present study, however, the opercular nucleus and estimated settlement size were fairly constant among the three specimens of this species and only negligible intraspecific variation (< 2.2%) was detected among 119 specimens in the genus *Nerita* (Table 3-1). Possible explanations for the incongruence between the direct observation and inference from the operculum include a higher mortality for the smaller metamorphosed hatchlings, and poecilogony as the species-specific character of *N. melanotragus*. The proportion of adults that hatched as crawling juveniles can be estimated by measuring a sufficient number of nuclei in the fully-grown opercula of the species (Fukumori *et al.* in preparation).

Settlement size as an identification trait for juveniles and larvae

The diameter of the opercular nucleus often differs substantially among species, in contrast to the small intraspecific variation (Table 3-1). The presence of significant interspecific variation of settlement size makes the protoconch and opercular nucleus very useful for identifying juveniles, which are typically nondescript with few suitable taxonomic characters, to genus or species. This is particularly the case in the tropical West-Pacific islands where the species diversity of neritids is the highest (Frey & Vermeij 2008; Kano *et al.* 2011).

Settlement size can also be used as an identification trait for neritimorph larvae. Larval shells of Neritimorpha that reached their final size are distinguished from immature larvae by the flared outer lip of the aperture (Bandel 1982; Kano 2006; Page & Ferguson 2013). The usefulness of this character is enhanced by the proportionally long delay period in their entire larval life. For example, the larvae of *Nerita melanotragus* tripled in shell length 45 days after hatching, but showed no further growth until the end of culture period of 69 days (Lesoway & Page 2008). While the exact duration of the delay period is not known for this and other neritimorph species, Underwood (1974) found the first newly settled juveniles nearly half a year after the first sighting of egg capsules of *N. melanotragus* at his study site, suggesting roughly four to five months of pelagic life including three to four months of the delay period. Likewise, the hatched planktotrophic larvae of the Caribbean species *Smaragdia viridis* were estimated to require about 25 days of the onset of metamorphic competence and the fully-grown larvae were kept at least 30 days in laboratory culture (Scheltema 1971). The delay period of this species may be much longer as the larvae were collected west of Azores Islands, to which the journey may take several months in the North Atlantic Drift (Scheltema 1971).

Taxonomic identification of the juveniles and larvae can be more effectively practiced in combination with information from other morphological characteristics as well as molecular data. Besides the unique, uniformly multispiral and globose shape, neritimorph larvae sometimes have distinct coloration. Certain species of *Smaragdia* have a bright green shell and soft tissue before and after metamorphosis (Scheltema 1971). *Shinkailepas* species consistently have a grayish-purple protoconch (Fig. 3-1; Beck 1992). Settlement size and other morphological criteria are indispensable for the identification of living neritimorph larvae for ecological and behavioral studies, while such characters can also facilitate the screening of specimens for DNA barcoding (see Garland & Zimmer 2002; Barber & Boyce 2006). A promising application of the present finding is to study the larval behavior and dispersal of limnic (amphidromous) and deep-sea hydrothermal vent species in the field, which to date have been inferred from larval rearing, comparison of spawning times and settlement dates, and genetic population analyses (e.g. Holthuis 1995; Crandall *et al.* 2010; Young *et al.* 2012).

Phylogenetic constraints on settlement size for neritimorph subclades

The present study reveals that the settlement size of the planktotrophic Neritimorpha primarily reflects phylogenetic constraints rather than adaptive consequences of ecological radiation within each lineage. The Neritiliidae have the smallest settlement sizes among the Neritimorpha regardless of different habitats they occupy (Fig. 3-4). Within the Neritidae, the species of Neritininae are smaller than the *Smaragdia* at settlement and the Neritinae show intermediate sizes. Members of its sister family Phenacolepadidae (Fig. 3-2) have the second largest average size at settlement among the six lineages, next to the *Smaragdia*. The planktotrophic larva of the archetypal family Neritopsidae (Kano *et al.* 2002) is moderate in size (580 μm) and possibly represents the ancestral condition for the extant Neritimorpha. While radically different larval shell morphologies in other gastropod clades (Scheltema 1971; Bandel 1982) prevent outgroup comparison for this character, early neritimorphs from the fossil record show that moderate protoconch sizes were common (e.g. Bandel & Frýda 1999; Bandel & Kiel 2003). Assuming the condition in *Neritopsis* is the shared ancestral state, body size at metamorphosis may have decreased twice in the lineages leading to the Neritiliidae and Neritininae and increased twice in the clades of Phenacolepadidae and *Smaragdia*. The small settlement size as derived conditions is also favored by parsimony, as the large and moderate-sized larvae distribute polyphyletically in the evolutionary tree of the extant Neritimorpha (see Figs 3-2 and 3-4).

Interspecific variation in settlement size among planktotrophic species has been addressed by a limited number of studies on echinoid echinoderms and gastropod and bivalve mollusks (e.g. Levitan 2000; Collin 2003). Many of these studies focused on the post-metamorphic effects of maternal provisioning, and found no relationship between egg size and settlement size (Hadfield & Switzer-Dunlap 1984; Kohn & Perron 1994; Levitan 2000; but see Marshall & Keough 2007). In particular, there has been almost no research of how environmental conditions affect settlement sizes of different planktotrophic species. Podolsky & Moran (2006) provided a rare but very interesting empirical account by examining six geminate pairs of bivalve species in the eastern Pacific and western Atlantic, where settlement size tends to be larger in the former ocean with higher productivity. This paucity of data reflects difficulties not only in measuring settlement size for a sufficient number of species, but also in obtaining reliable phylogenetic hypotheses. Inherited developmental programs may impose limits on realized growth and differentiation of larvae (Hadfield & Miller 1987). Therefore, the question about selection on settlement size can be addressed only when the influence of ancestry on observed differences is clarified (Levitan 2000; Marshall & Keough 2007; Lesoway & Page 2008). The present results that show ancestry is a major determinant at family and subfamily levels in Neritimorpha, further emphasizes the importance of phylogenies in understanding current selection for optimal size for changing form and habitat.

The more or less defined settlement size (hence the protoconch size) for a given clade enables me to infer the phylogenetic position of many neritimorph fossils. The fossil record of the superorder extends back at least to the middle Devonian and possibly as early as the Ordovician (Bandel & Frýda 1999). The first divergence among the extant families may have occurred in the late Paleozoic (Kano *et al.* 2002), so that the protoconch size may be used for the phylogenetic inference of Mesozoic and Cenozoic fossils. The familial or subfamilial positions of many Cretaceous and Paleogene taxa have not been conclusively determined by the traditional teleoconch characters. On the other hand, the preservation condition of such fossils is often complete enough to allow the examination of the protoconch (e.g. Bandel & Kiel 2003; Lozouet 2004), probably in part because many of the pre-Neogene species inhabited shallow subtidal waters, where physical and chemical erosion has been less extensive than in intertidal or limnic waters (Kano 2006). Future studies on the fossil material would shed new light on the evolutionary history of Neritimorpha by referring to the present data on settlement size.

Adaptive significance of smaller settlement size for amphidromous taxa

Besides the phylogenetic constraints, difference in the habitats of the adult individuals seemingly influences settlement size in Neritimorpha, particularly among different families and subfamilies. The freshwater and brackish species have significantly smaller sizes at metamorphosis than those of marine species (Fig. 3-5), while this may reflect a phylogenetic bias as two subclades, Neritiliidae and Neritininae, represent all freshwater species and most brackish ones among the living Neritimorpha (Table 3-1; Fig. 3-2). I propose that the acquisition of small settlement size is an adaptive consequence of ecological radiation to limnic habitats in each lineage.

All limnic species of Neritiliidae and Neritininae except a few direct developers have an amphidromous life cycle (Kano 2006; Kano *et al.* 2011). Amphidromy is a strategy involving migration of juveniles from the sea into freshwater, where growth from juvenile to adult, attainment of sexual maturity, and spawning all occur (McDowall 2007). The neritimorph larvae with this life cycle apparently spend a few months in the ocean as their marine relatives do, resulting in the widespread geographic distribution of the species regardless of the exclusively limnic nature in the following ontogenetic stage (Kano 2006; Crandall *et al.* 2010). However, the longer larval life as marine plankton may increase the risk of expatrial dispersal far from the mouth of the natal river or any other estuarine environment that is suitable for settlement: if the growth period of larvae is shortened, many individuals are likely to remain near the natal river (McDowall 2010). Given the proportional growth of the larval shell, the smaller settlement size of the amphidromous neritimorphs (Fig. 3-5) may reflect the shorter growth period from hatching to metamorphic competence in comparison with marine taxa with larger settlement sizes. On the other hand, the presence of the considerably long delay period (see above) may still allow the larvae to disperse over a long distance if needed and to colonize new habitats on remote islands on an evolutionary timescale (e.g. Crandall *et al.* 2010). The smaller settlement size of amphidromous species than that of fully marine relatives has not been reported in other amphidromous animal groups such as palaemonid prawns (Knowlton & Vargo 2004), possibly due to the absence or insufficiently long delay period. However, ontogenetic data are obviously too scarce for further consideration outside Neritimorpha.

Further support for the smaller settlement size in amphidromous taxa is given by the fossil record of two additional lineages of the limnic Neritimorpha bearing small protoconchs. Bandel & Riedel (1994) studied the Late Cretaceous fauna of Ajka in Hungary and concluded that this fauna flourished in freshwater to more or less brackish estuarine paleoenvironments. This fauna includes five neritimorph species, one of which (*Schwardtina cretacea*) belongs to a lineage close to the Recent terrestrial family Hydrocenidae, while three others in the genus *Deianira* (family Deianiridae) are morphologically similar enough to presume a phylogenetic relationship to another living terrestrial family Helicinidae (Bandel & Riedel 1994; Kano *et al*. 2002). The last species, *Mesoneritina ajkaensis*, shares the typical globose shell shape of Neritidae, but it probably represents an independent invasion into the limnic habitat prior to the Eocene radiation of extant amphidromous neritids in the subfamily Neritininae (Kano *et al*. 2002; Bandel & Kiel 2003; Symonds 2006). Notably, *Schwardtina* and *Deianira* bear among the smallest multispiral protoconchs (= planktotrophic larval shells) in fossil neritimorphs investigated so far, while the size is unknown in *Mesoneritina*. The maximum diameters of the protoconchs are 280 μm and 300–350 μm in *S. cretacea* and *Deianira* species, respectively (Bandel & Riedel 1994). Comparable protoconch sizes (*pd*) can be found only in the two amphidromous lineages among the extant species (Neritiliidae and Neritininae; Figs 3-3 and 3-4) and none of the other extinct lineages. Planktotrophy of riverine gastropod larvae is directly associated with an amphidromous life cycle as a result of downstream transport and scarcity of planktonic food in the running freshwater ecosystem (Holthuis 1995). Thus, the consistently small protoconchs in the four amphidromous lineages (two recent and two extinct) but nearly none in living and fossil marine taxa suggest the presence of strong evolutionary constraints that led to a hypothesized decreased settlement size for neritimorph species with this life strategy. Such constraints may have resulted from a reduced risk of being wafted away from the estuaries of their natal streams, given that small metamorphs spend less time achieving metamorphic competence.

Submarine-cave species of Neritiliidae represents the only few marine taxa with settlement sizes that are comparable to those of amphidromous species. In addition to *Pisulina adamsiana* investigated herein, a few more cave-dwelling neritiliids that have been represented exclusively by dead shells bear small protoconchs with diameters ranging from 360 μm (*Laddia traceyi*) to 530 μm (*Siaesella fragilis*; Kano & Kase 2008). The phylogenetic relationships among the neritiliid taxa and evolutionary transition between the two apparently contrasting habitats remain speculative due to the lack of material for anatomical and molecular analyses (Kano & Kase 2002, 2008). The small settlement size of the cave species may represent retention of the character state of the common ancestral species with an amphidromous life cycle, possibly in the underground water system (Kano & Kase 2004).

The larger sizes at metamorphosis in *Smaragdia* and Phenacolepadidae than in other lineages (Fig. 3-4) are more difficult to attribute to evolutionary consequences of adaptive differentiation. It is known that juveniles of benthic marine invertebrates are highly vulnerable while a larger body size provides a better survival rate against changing physiological and ecological pressures (e.g. Spight 1976; Gosselin & Qian 1997). One possible cause for the larger settlement size of *Smaragdia* is generally higher predation pressure in subtidal waters than in intertidal or limnic habitats (Vermeij 1993). *Smaragdia* species are specialized marine herbivores that utilize seagrasses as both food and habitat (Rueda *et al*. 2011; Unabia 2011). Another possibility is individuals that are too small may have difficulty in breaking the tough cell wall of seagrass leaves, regardless of their modified radular teeth for this feeding habit (e.g. Rueda *et al*. 2011). The Phenacolepadidae have acquired erythrocytes to increase the capacity of blood to transport oxygen in highly reducing environments, such as the underside of deep-buried stones in tidal flats and deep-sea hydrothermal vents, gas seeps and sunken-wood communities (Kano *et al*. 2002; Kano & Haga 2011; Young *et al*. 2012). The reduced dissolved oxygen and increased concentration of hydrogen sulfide and other toxic compounds might have favored larger settlers with more tolerance to harsh environmental conditions.

Settlement size and geographic distribution range

In general, the duration of the planktonic period is positively related to the larval dispersal distance of marine benthos (e.g. Todd *et al.* 1998; Shanks *et al.* 2003; Siegel *et al.* 2003; Shanks 2009) and consequently to their genetic homogeneity and geographic distribution range of species (Paulay & Meyer 2006; Weersing & Toonen 2009). The pelagic larval duration may theoretically be inferred from settlement size or the size of the protoconch in gastropods (Scheltema 1971; Hadfield & Switzer-Dunlap 1984; Kohn & Perron 1994). The simplest expectation would therefore be that species with a larger settlement size have a wider geographic distribution. However, no such correlation was found for the planktotrophic species of neritimorph gastropods, or any of the five subclades of the superorder that occupy different habitats as adults (Fig. 3-6).

When the neritimorph larvae reach the defined settlement size for each species (Table 3-1), they can be induced to metamorphose by certain external cues from their adult habitats, such as their food sources; without such cues, they remain as plankton (Lesoway & Page 2008). It is therefore probable that their long delay period up to a few or several months (see above) obscures the relationship between settlement size and distribution range. Another possibility for the absence of the correlation is that even the species with presumably shortest pelagic periods (e.g. neritiliids) may be good enough dispersers across oceanic basins (Kano & Kase 2003, 2008). Rafting on driftwood as adults has also been documented for a few estuarine species of the Neritidae (Kano *et al.* 2013). Interspecific variation in size at hatching may pose a further obstacle in estimating the dispersal ability of larvae from settlement size. The hatching size of neritimorphs tends to differ among species (Kano 2006) so that the duration of the growth period theoretically differs among species with the same settlement size. This possibility has not been explored in this or in previous studies. Future investigation on the diameter of the embryonic operculum in Neritimorpha may help to better understand the general relationship between the larval duration and biogeography of benthic animals. In conclusion, the inference of larval dispersal from the size at metamorphosis may be justified when various factors are considered, including the delay period and size at hatching, as well as other life history characteristics (e.g. larval behavior; Shanks 2009; see also Becker *et al*. 2007) and accurate species taxonomy (Paulay & Meyer 2006).

Concluding remarks

Gastropods offer many advantages for exploring hypotheses about phylogenetic and ecological patterns of the body size at ontogenetic life-history transitions including larval metamorphosis and settlement. The calcified shell is a major advantage because it is usually a reliable indicator of overall body size and its rigidity allows accurate measurement (Lesoway & Page 2008). Furthermore, all ontogenetic phases of shell secretion are retained in well-preserved adult shells of both extant and fossil gastropods (Bandel 1982; Jablonski & Lutz 1983; Lima & Lutz 1990). The present study revealed even more pronounced advantages in neritimorph gastropods thanks to the wide range of their habitat exploitation, resolved phylogeny and retention of the larval operculum in almost all adult individuals as a rigorous indicator of the size at metamorphosis.

The settlement size of the planktotrophic Neritimorpha primarily reflects phylogenetic constraints, while parallel acquisitions of small settlement sizes are also suggested in limnic habitats. The smaller size may possibly reduce the risk of being wafted away from the estuaries of their natal streams through less time achieving metamorphic competence, while the ability to make occasional long-distance trips is retained by the presence of a sufficiently long delay period. This delay period also seems to obscure the possible correlation between settlement size and geographic distribution range of neritimorph species, both marine and amphidromous. Interspecific variation in size at hatching may pose a further obstacle in estimating the dispersal ability of larvae from settlement size. Future investigation on the size at hatching using the opercula of neritimorphs and scanning electron microscopy may help to better understand the general relationship between the larval duration and biogeography of benthic animals. The same approach can be used to investigate the presence or absence of poecilogony in non-heterobranch mollusks and to assess the body size effect of hatchlings on the sizes at metamorphosis and maturity in a large number of species from different ecological and phylogenetic backgrounds.

The final publication of the Chapter 3 is available at link.springer.com (http://link.springer.com/article/10.1007/s00227-013-2330-5).

Table 3-1. Neritimorph species used in present study, habitat, collection site and diameter of opercular nucleus (*nd*).

Species	Habitat[*1]	Collection site	*nd*[*2]
Neritopsidae			
Neritopsis sp. cf. *aqabaensis* Bandel, 2007	Submarine cave (M)	Bali Is., Indonesia	350 (1, 350)[*3]
Neritiliidae			
Neritilia rubida (Pease, 1865)	Stream (F)	Ishigaki Is., Okinawa, Japan	183 ± 7 (8, 175–190)[*4]
Neritilia vulgaris Kano & Kase, 2002	Stream (F)	Iriomote Is., Okinawa, Japan	184 ± 6 (11, 175–190)[*4]
Platynerita rufa Kano & Kase, 2002	Stream (F)	Amami Is., Japan	193 ± 6 (8, 185–200)[*4]
Pisulina adamsiana Nevill & Nevill, 1869	Submarine cave (M)	Sipadan Is., Sabah, Malaysia	217 ± 8 (6, 210–230)[*4]
Phenacolepadidae			
Phenacolepadinae			
Phenacolepas cytherae (Lesson, 1831)	Sand flat (M)	Kuroshima Is., Okinawa, Japan	429 ± 9 (4, 430–445)
Phenacolepas unguiformis (Gould, 1859)	Rocky shore (M)	Kanagawa, Honshu Is., Japan	438 ± 6 (4, 420–440)
Phenacolepas sp.	Sand flat (M)	Iriomote Is., Okinawa, Japan	359 ± 13 (5, 340–370)
Cinnalepeta pulchella (Lischke, 1871)	Coastal pond (B)	Kami-Koshiki Is., Kyushu, Japan	392 ± 10 (9, 375–405)[*4]
Shinkailepadinae			
Shinkailepas briandi Warén & Bouchet, 2001	Hydrothermal vent (M)	Lucky Strike, Mid-Atlantic Ridge	505 ± 13 (10, 485–510)
Shinkailepas kaikatensis Okutani et al., 1989	Hydrothermal vent (M)	Kaikata Seamount, Japan	475 ± 8 (7, 460–480)
Shinkailepas myojinensis Sasaki et al., 2003	Hydrothermal vent (M)	Kaikata Seamount, Japan	505 ± 5 (6, 500–510)
Olgasoralis tollmanni Beck, 1992	Hydrothermal vent (M)	Lau Basin, Papua New Guinea	492 ± 10 (6, 480–505)
Bathynerita naticoidea Clarke, 1989	Cold seep (M)	Green Canyon, Gulf of Mexico	470 ± 0 (2, 470)
Neritidae			
Neritinae			
Nerita (*Nerita*) *peloronta* Linnaeus, 1758	Rocky shore (M)	Grand Cayman, Cayman Islands	368 ± 9 (5, 355–380)
Nerita (*Nerita*) *versicolor* Gmelin, 1791	Rocky shore (M)	Grand Cayman, Cayman Islands	369 ± 5 (4, 365–375)
Nerita (*Amphinerita*) *incerta* von dem Busch in Philippi, 1844	Rocky shore (M)	Amami Is., Japan	401± 9 (6, 390–415)
Nerita (*Amphinerita*) *insculpta* Récluz, 1841	Rocky shore (M)	Iriomote Is., Okinawa, Japan	378 ± 12 (9, 360–395)
Nerita (*Argonerita*) *argus* Récluz, 1841	Rocky shore (M)	Tahiti Is., French Polynesia	393± 8 (6, 380–400)
Nerita (*Argonerita*) *chameleon* Linnaeus, 1758	Rocky shore (M)	Yonaguni Is., Okinawa, Japan	318 ± 15 (4, 300–330)
Nerita (*Argonerita*) *histrio* Linnaeus, 1758	Sand flat (M)	Iriomote Is., Okinawa, Japan	316 ± 6 (10, 305–325)
Nerita (*Argonerita*) *ocellata* Le Guillou, 1841	Rocky shore (M)	Amami Is., Japan	415 ± 11 (4, 400–425)
Nerita (*Ilynerita*) *planospira* Anton, 1838	Mangrove swamp (M)	Iriomote Is., Okinawa, Japan	340 ± 7 (8, 330–350)
Nerita (*Linnerita*) *litterata* Gmelin, 1791	Rocky shore (M)	Okinawa Is., Japan	328 ± 10 (4, 315–340)
Nerita (*Linnerita*) *polita* Linnaeus, 1758	Rocky shore (M)	Hachijo Is., Japan Russell Is., Solomon Islands	326 ± 6 (11, 320–335)
Nerita (*Lisanerita*) *melanotragus* Smith, 1884	Rocky shore (M)	N of Auckland, New Zealand	447 ± 6 (3, 440–450)
Nerita (*Lisanerita*) *morio* Sowerby, 1833	Rocky shore (M)	Pitcairn Is., Pitcairn Islands	427 ± 10 (3, 415–435)
Nerita (*Ritena*) *costata* Gmelin, 1791	Rocky shore (M)	Okinoerabu Is., Japan	352 ± 11 (6, 340–370)
Nerita (*Ritena*) *picea* Récluz, 1841	Rocky shore (M)	Maui Is., Hawaii Islands, USA	379 ± 6 (7, 370–385)
Nerita (*Ritena*) *plicata* Linnaeus, 1758	Rocky shore (M)	Yonaguni Is., Okinawa, Japan	387 ± 10 (9, 375–410)
Nerita (*Theliostyla*) *albicilla* Linnaeus, 1758	Rocky shore (M)	Yonaguni Is., Okinawa, Japan	438 ± 12 (7, 425–450)
Nerita (*Theliostyla*) *tessellata* Gmelin, 1791	Rocky shore (M)	Grand Cayman, Cayman Islands	362 ± 10 (6, 350–370)
Nerita articulata Gould, 1847	Mangrove swamp (M)	Phuket Is., Thailand Langkawi Is., Malaysia	385 ± 11 (7, 370–400)
Neritininae			
Smaragdia bryanae (Pilsbry, 1917)	Seagrass bed (M)	Mauritius; Santo Is., Vanuatu Hawaii Is., Hawaii Islands, USA	432 ± 10 (3, 420–440)
Smaragdia pulcherrima (Angas, 1871)	Seagrass bed (M)	Ishigaki Is., Okinawa, Japan	557 ± 3 (3, 555–560)
Smaragdia rangiana (Récluz, 1841)	Seagrass bed (M)	Ishigaki Is., Okinawa, Japan Panglao Is., Bohol, Philippines	552 ± 9 (23, 535–570)
Smaragdia souverbiana (Montrouzier, 1863)	Seagrass bed (M)	Savanne, Mauritius Ryukyu Isls., Okinawa, Japan	442 ± 10 (5, 430–455)
Smaragdia tragena (Iredale, 1936)	Seagrass bed (M)	Santo Is., Vanuatu Moorea Is., French Polynesia	505 ± 0 (2, 505)
Smaragdia viridis (Linnaeus, 1758)	Seagrass bed (M)	Discovery Bay, Jamaica	523 ± 4 (2, 520–525)
Smaragdia sp. 1	Seagrass bed (M)	Miyazaki, Kyushu Is., Japan	405 (1, 405)

Table 3-1. cont.

Species	Habitat[*1]	Collection site	*nd*[*2]
Smaragdia sp. 2	Seagrass bed (M)	Cocos Islands, Australia Miyazaki, Kyushu Is., Japan	440 ± 13 (3, 425–450)
Clithon corona (Linnaeus, 1758)	Stream (F)	Ishigaki Is., Okinawa, Japan Phuket Is., Thailand	300 ± 7 (6, 290–310)
Clithon coronatus (Leach, 1815)	Stream (F)	Grand Port, Mauritius	340 (1, 340)
Clithon diadema (Récluz, 1841)	Stream (F)	Kagoshima, Kyushu Is., Japan Okinawa Is., Japan Bohol Is., Philippines Santo Is., Vanuatu	282 ± 8 (8, 275–300)
Clithon faba (Sowerby, 1836)	Stream mouth (B)	Miyazaki, Kyushu Is., Japan Okinawa Is., Japan	263 ± 3 (3, 260–265)
Clithon leachii (Récluz, 1841)	Stream mouth (B)	Okinawa Is., Japan	270 ± 0 (3, 270)
Clithon nouletianus (Gassies, 1863)	Stream mouth (B)	Okinawa Is., Japan	343 ± 3 (3, 340–345)
Clithon olivaceus (Récluz, 1843)	Stream (F)	Ishigaki and Iriomote Isls., Japan Agat, Guam, Micronesia	318 ± 13 (3, 305–330)
Clithon oualaniensis (Lesson, 1831)	Stream mouth (B)	Phuket Is., Thailand Wakayama, Honshu Is., Japan	294 ± 6 (6, 290–305)
Clithon pauluccianus (Gassiers, 1870)	Stream mouth (B)	Okinawa Is., Japan	326 ± 5 (6, 320–330)
Clithon peguensis (Blanfold, 1867)	Stream (F)	Phang Nga, Thailand	310 ± 5 (3, 305–315)
Clithon retropictus (Martens, 1878)	Stream (F)	Chiba, Honshu Is., Japan Miyazaki, Kyushu Is., Japan Ryukyu Isls., Okinawa, Japan	277 ± 4 (9, 270–280)
Clithon rugatus (Récluz, 1842)	Stream (F)	Ishigaki Is., Japan	270 ± 5 (3, 265–275)
Clithon sowerbianus (Récluz, 1843)	Stream mouth (B)	Miyazaki, Kyushu Is., Japan Yakushima Is., Kyushu, Japan Okinawa Is., Japan	280 ± 10 (3, 270–290)
Clithon spinosus (Sowerby, 1825)	Stream (F)	Tahiti Is., French Polynesia	335 ± 4 (4, 330–340)
Clithon subpunctatus (Récluz, 1844)	Stream (F)	Okinawa Is., Japan	333 ± 12 (6, 315–350)
Clithon sp. 3	Stream (F)	Okinawa Is., Japan	282 ± 8 (3, 275–290)
Dostia bicanaliculata (Récluz, 1843)	Estuary (B)	Okinawa Is., Japan	257 ± 3 (3, 255–260)
Dostia dilatata (Lesson, 1830)	Stream mouth (B)	Okinawa Is., Japan	323 ± 6 (3, 320–330)
Dostia guamensis (Lamarck, 1816)	Stream mouth (B)	Okinawa Is., Japan	353 ± 8 (5, 340–360)
Dostia siquijorensis (Récluz, 1843)	Estuary (B)	Palawan Is., Philippines Iriomote Is., Okinawa, Japan	325 ± 5 (5, 320–330)
Dostia subalata (Soulayet, 1842)	Estuary (B)	Iriomote Is., Okinawa, Japan	301 ± 2 (5, 300–305)
Dostia violacea (Gmelin, 1791)	Estuary (B)	Phuket Is., Thailand	287 ± 3 (3, 285–290)
Dostia sp. 1	Estuary (B)	Fukuoka, Kyushu Is., Japan Miyazaki, Kyushu Is., Japan	303 ± 11 (5, 285–310)
Laodia cumingiana (Récluz, 1843)	Stream (F)	Ishigaki Is., Okinawa, Japan	258 ± 6 (3, 255–265)
Neritina asperulata (Récluz, 1843)	Stream (F)	Ishigaki Is., Okinawa, Japan Cebu Is., Philippines Guadalcanal Is., Solomon Islands Santo Is., Vanuatu	307 ± 7 (10, 295–315)[*4]
Neritina canalis Sowerby, 1825	Stream (F)	Tahiti Is., French Polynesia	297 ± 10 (3, 285–305)
Neritina delestennei (Récluz, 1843)	Stream (F)	Ryukyu Isls., Okinawa, Japan	293 ± 9 (10, 280–310)
Neritina iris Mousson, 1849	Stream (F)	Ryukyu Isls., Okinawa, Japan	280 ± 8 (6, 265–285)
Neritina petitii (Récluz, 1841)	Stream (F)	Ryukyu Isls., Okinawa, Japan Guadalcanal Is., Solomon Islands Santo Is., Vanuatu	279 ± 10 (9, 270–300)[*4]
Neritina powisiana (Récluz, 1843)	Stream (F)	Guadalcanal Is., Solomon Islands	310 (1, 310)
Neritina pulligera (Linnaeus, 1767)	Stream (F)	Ryukyu Isls., Okinawa, Japan	283 ± 8 (13, 270–295)
“*Neritina*” *burguieri* (Récluz, 1841)	Stream (F)	Ryukyu Isls., Okinawa, Japan	307 ± 3 (3, 305–310)
“*Neritina*” sp.	Stream (F)	Guadalcanal Is., Solomon Islands	255 (1, 255)
Septaria auriculata (Lamarck, 1816)	Estuary (B)	Miyazaki, Kyushu Is., Japan Okinawa Is., Japan	307 ± 6 (3, 300–310)
Septaria lecontei (Récluz, 1853)	Estuary (B)	Northern Territory, Australia	278 ± 11 (2, 270–285)
Septaria porcellana (Linnaeus, 1758)	Stream (F)	Miyazaki, Kyushu Is., Japan Ryukyu Isls., Okinawa, Japan	284 ± 7 (5, 275–290)

Table 3-1. cont.

Species	Habitat[*1]	Collection site	*nd*[*2]
Septaria spiralis (Reeve, 1855)	Estuary (B)	Okinawa Is., Japan	320 ± 5 (3, 315–325)
Septaria tessellata (Lamarck, 1816)	Estuary (B)	Phang Nga, Thailand	241 ± 6 (6, 235–250)
		Kagoshima, Kyushu Is., Japan	
		Okinawa Is., Japan	
Vitta latissima (Broderip, 1832)	Stream (F)	Gobernadora Is., Panama	280 (1, 280)
Vitta pupa (Linnaeus, 1767)	Rocky shore (M)	Grand Cayman, Cayman Islands	310 ± 5 (3, 305–315)
Vitta virginea (Linnaeus, 1758)	Stream (F)	Trelawhy, Jamaica	247 ± 3 (3, 245–250)
Vittina cuvieriana (Récluz, 1841)	Stream (F)	Guadalcanal Is., Solomon Islands	320 ± 14 (2, 310–330)
		Santo Is., Vanuatu	
Vittina cumingiana (Récluz, 1843)	Estuary (B)	Okinawa Is., Japan	317 ± 6 (3, 310–320)
Vittina communis (Quoy & Gaimard, 1834)	Stream mouth (B)	Agat, Guam, Micronesia	308 ± 8 (3, 300–315)
		Santo Is., Vanuatu	
		Upolu Is., Western Samoa	
Vittina gagates (Lamarck, 1822)	Stream (F)	Phuket Is., Thailand	301 ± 5 (8, 295–310)
		Kagoshima, Kyushu Is., Japan	
		Iriomote Is., Okinawa, Japan	
Vittina lugubris (Sowerby, 1836)	Estuary (B)	Ishigaki Is., Okinawa, Japan	310 ± 14 (6, 295–330)
		Bohol Is., Philippines	
Vittina turrita (Gmelin, 1791)	Estuary (B)	(Purchased at aquarium store)	320 ± 0 (2, 320)

[*1] Marine (M), brackish (B) or freshwater (F). [*2] Mean ± SD in μm (number of specimens, range). [*3] Estimated from apertural size of protoconch. [*4] Kano (2006, 2009)

Table 3-2. Diameter of protoconch (*pd*, = diameter of larval shell) in selected neritimorph species.

Species	*pd**
Neritopsidae	
Neritopsis sp.	580 (1, 580)
Neritiliidae	
Neritilia vulgaris	353 ± 11 (2, 345–360)
Phenacolepadidae	
Shinkailepadinae	
Shinkailepas kaikatensis	683 ± 8 (3, 675–690)
Shinkailepas myojinensis	720 (1, 720)
Neritidae	
Neritininae	
Smaragdia rangiana	815 (1, 815)
Smaragdia souverbiana	693 ± 6 (4, 680–695)
Clithon retropictus	435 ± 4 (6, 430–440)
Dostia guamensis	560 (1, 560)
Dostia siquijorensis	508 ± 11 (2, 500–515)
Neritina asperulata	433 ± 4 (2, 430–435)
Septaria porcellana	462 ± 10 (6, 450–470)

*Mean ± SD in μm (number of specimens, range)

Table 3-3. Diameter of protoconch (nd = diameter of opercular nucleus; *pd*, = diameter of larval shell) and geographic distances of distributional areas in selected neritimorph species.

Species	Distance between remotest sites (km)	Larval operculum diameter (nd, μm)	Measured or estimated pd (μm)	Locality 1	Locality 2	Reference
Neritopsis sp.	1350	350	580[*1]	Rimatara, French Polynesia	Tuamotu, French Polynesia	Lozouet (2009)
Pisulina adamsiana	18950	217	360.48	Mozambique	Hawaii Is.	Kano & Kase (2000)
Platynerita rufa	700	193	329.52	Amami, Japan	Iriomote, Japan	This study
Neritilia rubida	5950	183	316.62	Jawa, Indonesia	Pohnpei, Micronesia	This study
Neritilia vulgaris	4600	184	353[*1]	Jawa, Indonesia	Amami, Japan	This study
Phenacolepas cytherae	17150	429	633.96	Dar es Salaam, Tanzania	Tahiti, French Polynesia	Christiaens (1988)
Phenacolepas sp.	6450	359	543.66	Iriomote, Japan	Santo, Vanuatu	This study
Cinnalepeta pulchella	6900	392	586.23	Jeju Is, Korea	Santo, Vanuatu	This study; Min (2004)
Shinkailepas briandi	2900	505	732	Menez Gwen, MAR	Logatchev, MAR	Warén & Bouchet (2001)
Shinkailepas kaikatensis	2250	475	683[*1]	Yoron, Japan	East Diamante, Marianas	This study
Olgasoralis tollmanni	4000	492	715.23	Manus, PNG	Lau, Tonga	This study
Bathynerita naticoidea	3700	470	686.85	Louisiana, USA	Barbados	Van Gaest et al. (2007)
Nerita picea	1550	379	569.46	Johnston Atoll	Hawaii Is.	Frey (2010b)
Nerita melanotragus	2500	447	657.18	Melbourne, Australia	Auckland, New Zealand	Frey (2010b)
Nerita tessellata	3000	362	547.53	Bermuda	Panama	Frey (2010b)
Nerita peloronta	3000	368	555.27	Bermuda	Panama	Frey (2010b)
Nerita versicolor	3000	369	556.56	Bermuda	Panama	Frey (2010b)
Nerita morio	4000	427	631.38	Tubuai, Austral Islands	Easter Is.	Speccer et al. (2007); Frey (2010b)
Nerita ocellata	4700	415	615.9	Jawa Is., Indonesia	Kagoshima, Japan	This study; Frey (2010b)
Nerita argus	5550	393	587.52	Solomon IsIs.	Tahiti	Frey (2010b)
Nerita articulata	6900	385	577.2	Quanzhou, China	Brisbane, Australia	Frey (2010b)
Nerita costata	7750	352	534.63	Sri Lanka	Townsville, Australia	Frey (2010b)
Nerita incerta	9000	401	597.84	Jakarta, Indonesia	American Samoa	Frey (2010b)
Nerita chameleon	10050	318	490.77	Mumbai, India	Brisbane, Australia	Frey (2010b)
Nerita histrio	12250	316	488.19	Sri Lanka	American Samoa	Frey (2010b)
Nerita planospira	12600	340	519.15	Mandobi, India	Fiji	Frey (2010b)
Nerita insculpta	12850	378	568.17	Calicut, India	American Samoa	Frey (2010b)
Nerita litterata	17150	328	503.67	Tanzania	Tahiti, French Polynesia	Frey (2010b)
Nerita albicilla	18400	438	645.57	Port Elizabeth, South Africa	Hawaii Is.	Frey (2010b)
Nerita polita	18750	326	501.09	South Africa	Hawaii Is.	Frey (2010b)
Nerita plicata	19950	387	579.78	Durban, South Africa	Galapagos Is.	Frey (2010b)
Smaragdia bryanae	16500	432	637.83	Mauritius	Hawaii Is.	This study
Smaragdia rangiana	13250	552	815[*1]	Mozambique	Santo, Vanuatu	This study
Smaragdia souverbiana	11350	442	693[*1]	Mauritius	Santo, Vanuatu	This study
Smaragdia tragena	14900	505	732	Reunion	Moorea, French Polynesia	This study
Smaragdia sp.1	6600	405	603	Kumamoto, Japan	Santo, Vanuatu	This study
Clithon diadema	6300	282	444.33	Okinawa Is., Japan	Santo, Vanuatu	This study[*2]
Clithon faba	5000	263	419.82	Mie, Japan	Papua New Guinea	This study[*2]
Clithon olivaceus	6400	318	490.77	Ishigaki, Japan	Santo, Vanuatu	This study[*2]
Clithon oualaniensis	8600	294	459.81	Karnataka, India	Cairns, Australia	This study[*2]; Boominathan et al. (2012)
Clithon paulussianus	6300	326	501.09	Amami, Japan	Santo, Vanuatu	This study[*2]
Clithon retropictus	2500	277	435[*1]	Taiwan	Chiba, Japan	This study[*2]
Clithon spinosus	1600	335	512.7	Raiatea, French Polynesia	Marquesas	Myers et al. (2000)
Dostia bicanaliculata	5500	257	412.08	Takua Pa, Thailand	Madang, PNG	This study[*2]
Dostia guamensis	15250	353	560[*1]	Mauritius	Makemo, French Polynesia	This study[*2]
Dostia siquijorensis	12000	325	508[*1]	Cocos Isls., Australia	Moorea, French Polynesia	This study[*2]
Dostia subalata	12000	301	468.84	Sri Lanka	Samoa	This study[*2]

Table 3-3. cont.

Species	Distance between remotest sites (km)	Larval operculum diameter (nd, μm)	Measured or estimated pd (μm)	Locality 1	Locality 2	Reference
Neritina canalis	8750	297	463.68	Guam	Marquesas	This study[*2]; Crandall et al. (2010)
Neritina petitii	7300	279	440.46	Okinawa Is., Japan	Fiji	This study[*2]; Haynes (2009)
Neritina powisiana	2550	310	480.45	Madang, PNG	Santo, Vanuatu	This study[*2]
Neritina pulligera	7900	283	445.62	Amami, Japan	Samoa	This study[*2]
Septaria porcellana	11350	284	462[*1]	Mauritius	Santo, Vanuatu	This study[*2]
Septaria tessellata	9550	241	391.44	West Bengal, India	Santo, Vanuatu	This study[*2]; Chatterjee et al. (2008)
Vitta virginea	6700	247	399.18	Florida	Paranagua, Brazil	Russel (1941); Netto & Lana (1999)
Vitta pupa	2150	310	480.45	Florida	Panama	Russel (1941)
Vittina communis	7850	308	477.87	Okinawa Is., Japan	Samoa	This study[*2]
Vittina cuvieriana	2550	320	493.35	Madang, PNG	Santo, Vanuatu	This study[*2]
Vittina lugbris	12600	310	480.45	Takua Pa, Thailand	Tahiti, French Polynesia	This study[*2]
Vittina cumingiana	2300	317	489.48	Amami, Japan	Guam	This study[*2]
Vittina gagates	9200	301	468.84	Takua Pa, Thailand	Fiji	This study[*2]; Haynes (2009)

[*1]Measured *pd*. [*2] Chapter 4

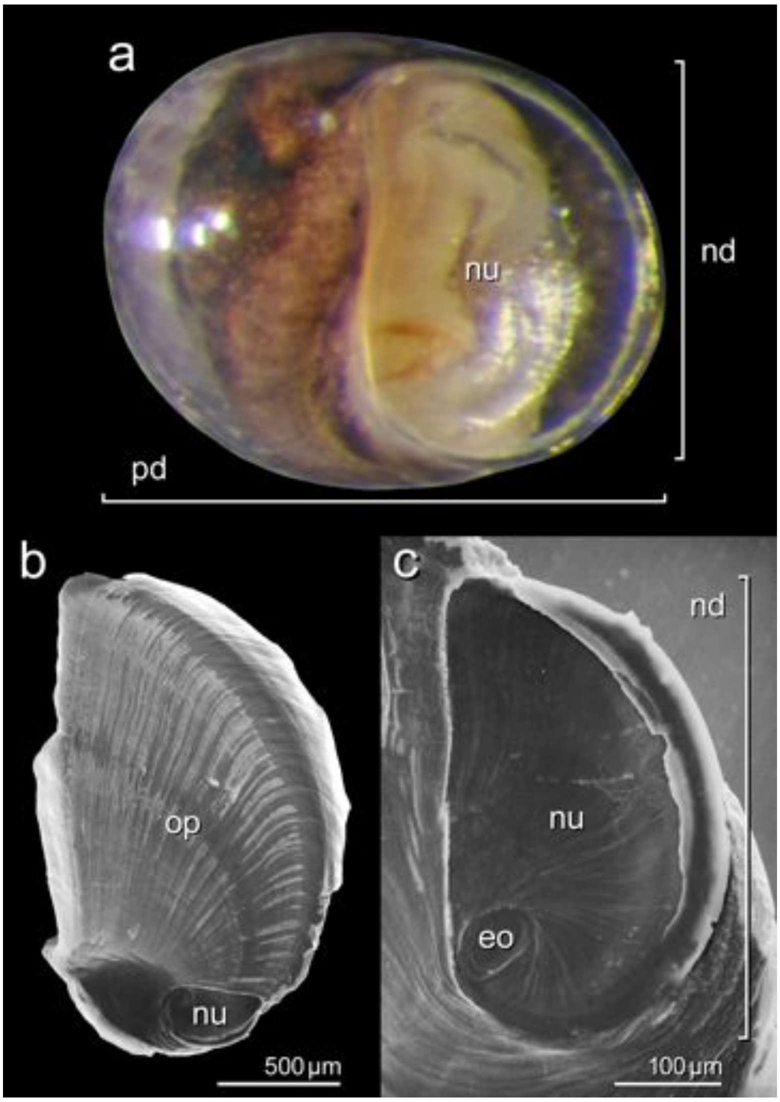


Figure 3-1. **a** Newly-settled juvenile of *Shinkailepas kaikatensis*, Myojin Knoll, Izu-Ogasawara Arc, Pacific. **b** SEM image of adult operculum of *Smaragdia souverbiana* (after Kano 2006, fig. 1A). **c** Close-up of nucleus in (b). *eo* embryonic operculum or initial region of opercular nucleus, *nd* diameter of larval operculum, *nu* opercular nucleus or larval operculum, *op* adult operculum, *pd* diameter of protoconch or settlement size.

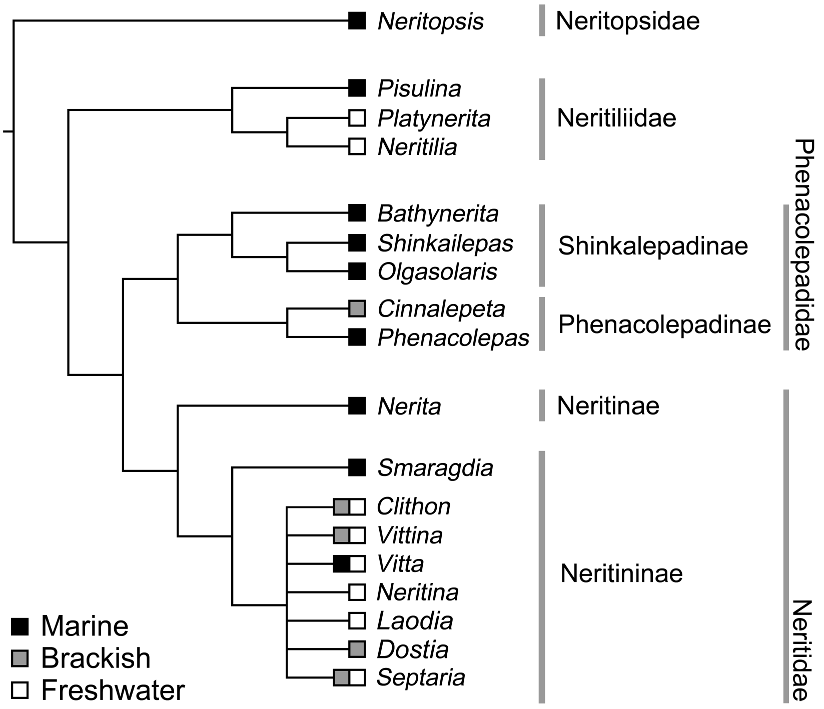


Figure 3-2. Phylogenetic relationships among living neritimorph clades with planktotrophic species, adopted from molecular phylogram (see Chapter 2). Information on habitat type is provided for each clade.

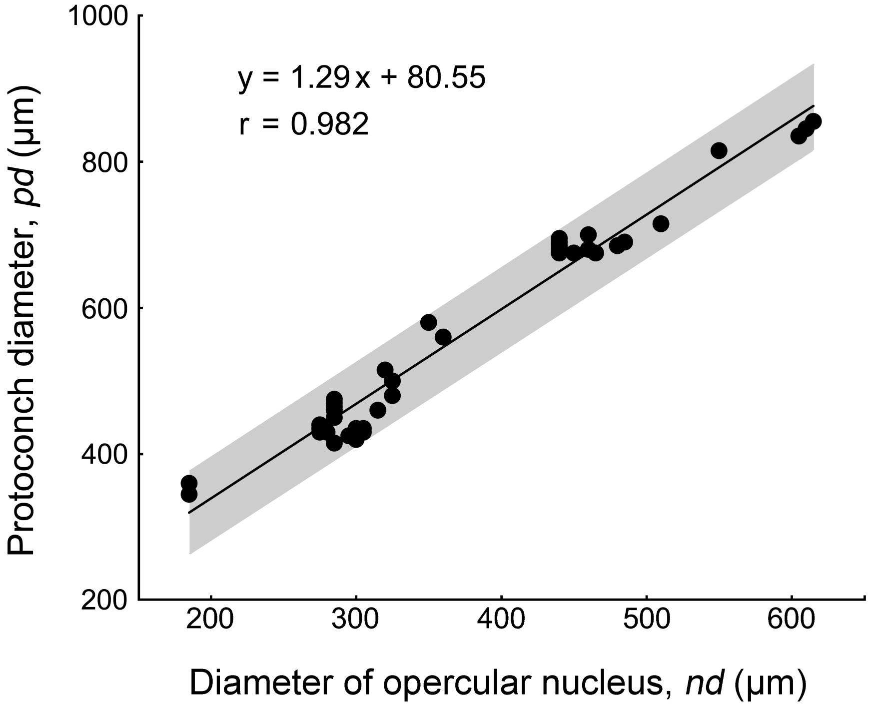


Figure 3-3. Correlation between diameters of opercular nucleus (*nd*) and protoconch (*pd*) (Pearson's correlation test: $p < 0.00001$), showing nearly uniform larval shells and opercula at metamorphic competence across planktotrophic Neritimorpha. Shaded area corresponds to a confidence interval of 95%.

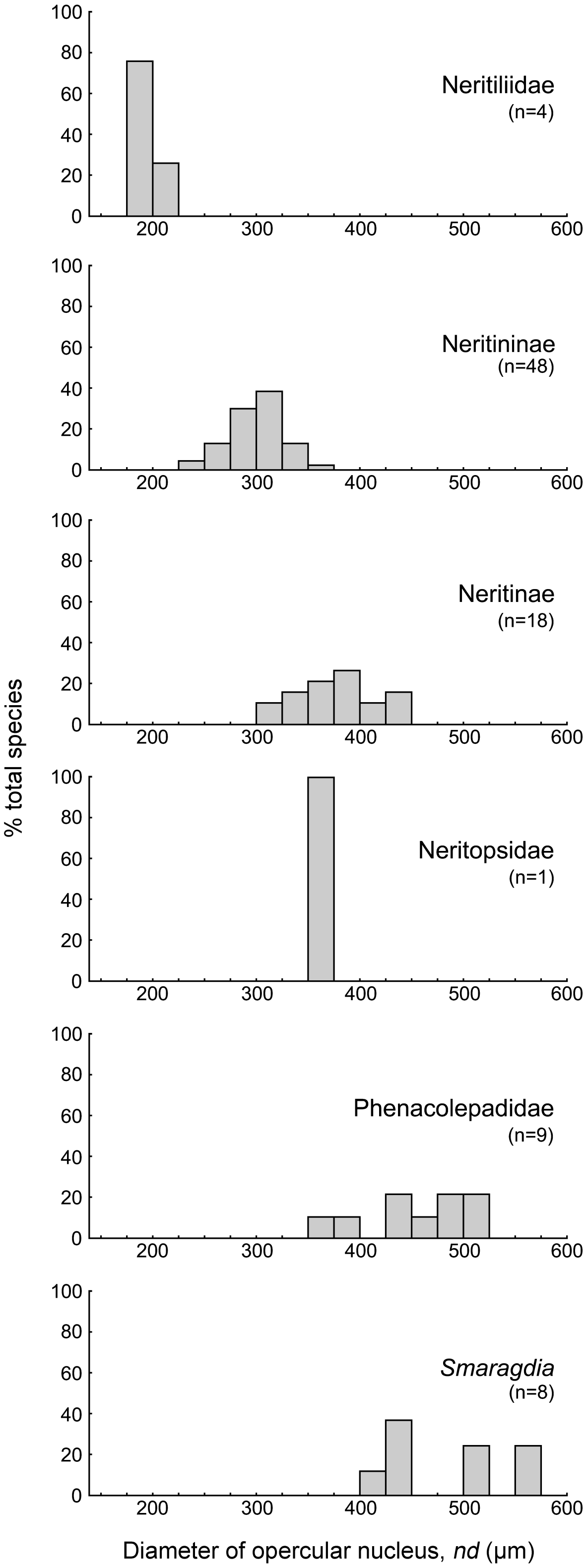


Figure 3-4. Frequency distributions of settlement size of planktotrophic species (represented by average diameter of opercular nucleus) for six neritimorph clades.

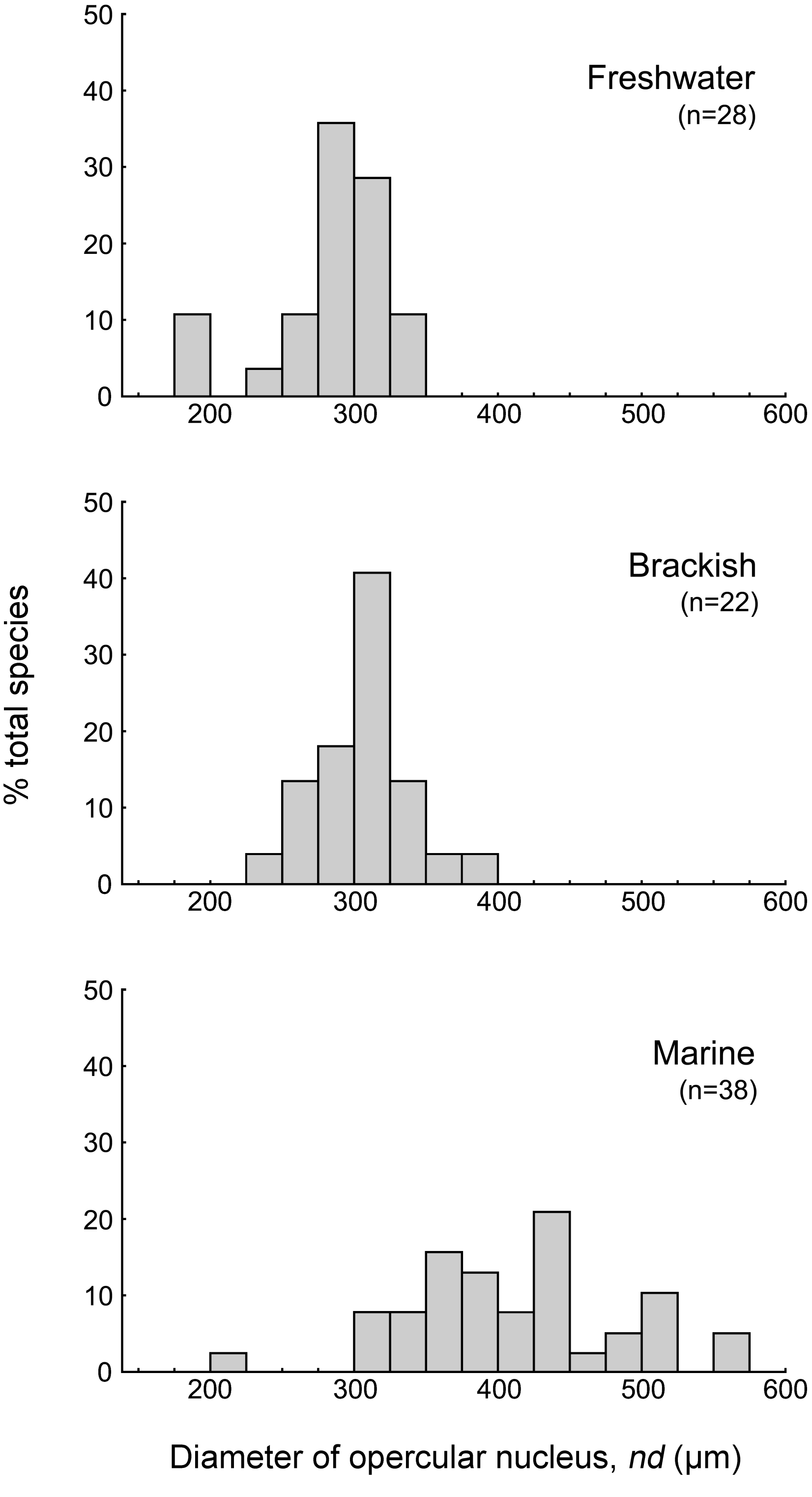


Figure 3-5. Frequency distributions of settlement size of planktotrophic species (represented by average diameter of opercular nucleus, *nd*) for marine, brackish and freshwater habitats of adult.

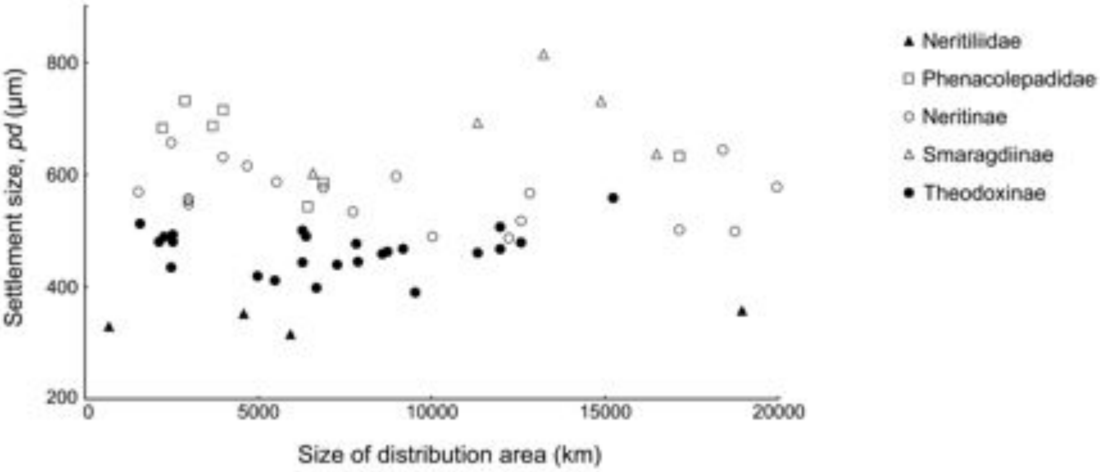


Figure 3-6. Relationship between settlement size (= diameter of protoconch) and geographic distribution area in planktotrophic species of Neritimorpha. Size of distribution range was represented by distance between two remotest known occurrences of species via a straight line.

Chapter 4: Taxonomy and biogeography of the amphidromous Neritidae in the Indo-West Pacific

4-1: Introduction

The tropical to subtropical Indo-West Pacific Ocean encompasses over 30,000 islands (Falkland 1991) that often support streams with relatively high gradients and short distances from headwaters to stream mouth (McDowall 2007). Many fishes, crustaceans and gastropods inhabiting these streams have an amphidromous life cycle, characterized by an extended planktonic period in the sea (McDowall 2010; Kano et al. 2011; Vogt 2013). Amphidromous animals are very abundant on oceanic islands in the numbers of both species and individuals, while they are comparatively less represented on large continental islands (McDowall 2010; Thuesen et al. 2011). Regardless, amphidromous taxa are the most important components of faunal communities in low-latitude island streams. However, the lack of proper and accurate taxonomy has rendered our knowledge on their ecology, distribution and species richness particularly limited in this Indo-West Pacific region, where biological diversity is generally highest among the world oceans (e.g. Bellwood & Meyer 2009). Most of previous taxonomic works suffered from insufficient sampling, enormous species richness and difficulties in assessing the homology and validity of morphological characters (e.g. Kano & Kase 2003; Smith et al. 2003; Page et al. 2005; Cook et al. 2008; Kano et al. 2011; Akihito et al. 2013).

Freshwater species of the Neritidae are one of the most dominant and diverse animal groups in the tropical and subtropical streams (Starmühlner 1986; Haynes 2000, 2005) and they mostly have an amphidromous life cycle (Kano 2006, 2009; Kano et al. 2011). Their hatched larvae are swept downstream to the ocean where the swimming larvae feed on phytoplankton and grow up in the pelagic period of a few or several months (Holthuis 1995; Lesoway and Page 2008; Kano et al. 2011). The combination of the long larval life and dispersal by ocean currents and their reproductive strategy involving the spawning of a large number of small eggs makes amphidromous neritids potentially capable of colonizing new habitats in very distant regions (McDowall 2007; Crandall et al. 2010; Kano et al. 2011). However, geographic distribution areas are not clearly demonstrated for most species, due essentially to the lack of our knowledge on their taxonomy. Although high dispersal ability has often been estimated by population genetic studies (e.g. Myers et al. 2000; Bebler & Foltz 2004; Cook et al. 2009), previous discussion on the biogeography of tropical freshwater neritids has been rather incomplete and possibly biased due to the currently fragmented and unsatisfactory information on how these species widespread in the ocean basins.

DNA barcoding is one of promising tools for species identification as sequence divergences are generally much lower among intraspecifc individuals than between closely related species (e.g. Hebert et al. 2003, 2004a; Barber & Boyce 2006). For instance, within-species genetic variation in cowry shells (Gastropoda: Cypraeidae) shows an average sequence divergence of 0.81% in the mitochondrial cytochrome *c* oxidase I (COI) gene, whereas the mean genetic divergence is 5.4% between sister species (Meyer 2003; Meyer & Paulay 2005). Similar values have been obtained in many animal groups, such as birds, insects and other marine invertebrates (Moore 1995; Hebert et al. 2004a, b; see also Meyer & Paulay 2005 for review). However, overlaps between intra- and interspecific genetic variations do occur, posing one of major problems with DNA barcoding. The reliance on finding a suitable marker, which possesses a short variable DNA region suitable to target a particular taxonomic group, flanked by two highly conserved regions of over 20 bp to anchor the primers also presents a considerable difficulty for the application of this tool in identifying unknown species (Lorenz et al. 2005; Taberlet et al. 2012). Some taxonomic groups are recalcitrant and it is difficult to find suitable universal primers for them (e.g. Lorenz et al. 2005). Identifying species by using a single gene marker such as COI may also be problematic due to the possible presence of introgression and incomplete lineage sorting (Will et al. 2005; Rubinoff 2006; Valentini et al. 2008). It is therefore proposed that DNA barcoding should be used in conjunction with other information including morphology, behavior and ecology, as well as nuclear gene markers (Meyer & Paulay 2005; Hickerson et al. 2006; Song et al. 2008).

In his unpublished master's dissertation, Kawaguchi (2007) has shown that the total number of freshwater neritid species have been badly underestimated in southwestern Japan to half of the actual species richness by examining their morphological traits and COI sequences. Similarly underestimated species richness may well be expected in other regions, for which attempt has not been made previously. An integrated systematic study involving DNA sequencing and traditional morphological investigation based on extensively sampled specimens from all over the Indo-West Pacific most probably provide crucial information for the understanding of the general patterns in the distribution, composition and richness of species as well as intraspecific differentiation, not only for the Neritidae but also tropical and subtropical amphidromous taxa in general.

Freshwater streams in tropical regions had been largely ignored in organized biodiversity investigations since after voyages in the Age of Exploration and colonization by European countries. However, recent scientific expeditions have extensively sampled and documented fauna and flora in several regions, including those of freshwater ecosystems (e.g. Bouchet et al. 2008, 2009a, b). Among such expeditions, SANTO 2006 was held in Espiritu Santo, Vanuatu and organized by Muséum national d'Histoire naturelle, Paris, France (MNHN; Bouchet et al. 2011). This expedition brought together over 150 scientists, volunteers and students originating from 25 countries and provided a comprehensive sampling and large biological information (Bouchet et al. 2008, 2011). Collected material includes a large number of specimens of the limnic Neritidae (Kano et al. 2011). Slightly less extensive sampling of neritids was also conducted in Solomon Islands, 900 km northwest of Vanuatu, during a joint field survey by Yasunori Kano and Katharina Jörger, while similar field trips have been made to many other Indo-West Pacific islands by the former malacologist (see Material and methods). These materials can be effectively used and compared with tens of thousands of Japanese specimens collected in the past 20 years (see Kawaguchi 2007). Of particular interest here is the comparison of species composition and richness between Japan and two eastern Melanesian countries, Vanuatu and Solomons, which are about 5,000–6,000 km away across the equator (Fig. 4-1). Species diversity for shallow-water marine animals is similar high in the subtropical Okinawan islands of Japan and in the two Melanesian countries (e.g. Bellwood & Meyer 2009). The comparison in freshwater neritids would provide deeper understanding of the distribution patterns and oceanic dispersal abilities of amphidromous animals at a large geographic scale.

The use of correct species names for each recognized species is the next step in establishing the taxonomy of the amphidromous Neritidae. Fresh- and brackish-water neritids were first described by Linnaeus (1758) and many succeeding authors in 18th and 19th centuries introduced nearly 600 names for living species from all over the world (e.g. Lamarck 1816; Reeve 1855–1856; Martens 1863–1879, 1881; see Kabat & Finet 1992; Petit 2009, 2011). Species names under prevailing usage for limnic neritids have so many problems concerning their stability as only few previous authors have referred to the type material or even to the original description. For example, Kabat & Finet (1992) noted that a number of obvious mistakes by Martens (1863–1879, 1881) have been repeated by subsequent authors who did not check the primary references. Although shell morphology provides useful taxonomic characters for shell-bearing molluscs, only few previous workers dealt with type specimens of these neritids and they all suffered from the lack of solid idea as to the homology and validity of the conchological characters for species identification (e.g. Komatsu 1986; Kabat & Finet 1992; Kabat & Boss 1997; Haynes 2001). Extensive investigation on the numerous old types scattered into a number of European museums and DNA sequencing and assessment of morphological traits using newly collected material are all vital parts in assigning species names to recognized biological species.

The goals of this study are (1) to recognize all neritid species in the limnic environments of the tropical to subtropical Indo-West Pacific islands through meticulous investigation on morphological and COI sequence data, (2) to assign species names to the recognized biological species based on thorough examination of type material and literature survey, (3) to demonstrate levels and patterns of their diversity and distributions within the area, and (4) to assess the dispersal capability of amphidromous species from biogeographic and genetic evidence.

4-2: Material and Methods

Taxonomic sampling and selection of specimens for DNA sequencing

Approximately 20,000 specimens of limnic species of Neritidae had been collected from the streams, rivers, ditches, estuaries and mangrove swamps of tropical and subtropical islands in the Indo-West Pacific (Fig. 4-1), treated and preserved for DNA extraction and deposited at the Benthos Laboratory of Atmosphere and Ocean Research Institute, The University of Tokyo, Japan (AORI), Muséum national d'Histoire naturelle, Paris, France (MNHN), Museum für Naturkunde, Berlin, Germany (ZMB), and Australian Museum, Sydney, Australia (AMS). Most snails were boiled in 70–90ºC water for 0.1–0.5 min and the animals were extracted from the shells and preserved in 70–99% ethanol. Other snails were relaxed in 7.5% magnesium chloride, or shells were cracked prior to ethanol-preservation.

The specimens used in this study were selected to represent the most comprehensive phylogenetic diversity for limnic neritids in the region (Table 4-1). Prior to genetic analysis, all specimens were examined morphologically and sorted into morphotypes (morphological species). This sorting was made in a “splitter” approach, to reflect the slightest differences in the shape, ornamentation and coloration of the shell and operculum. The DNA sequencing was conducted for a few specimens from each morphotype to maximize the diversity of obtained sequences in the limited time and expense. Also, the sequenced specimens were selected from as many different and remote geographic localities of each morphotype as possible for the understanding of genetic variation between and within biological species and evolutionary significant units (ESUs: populations having independent evolutionary histories; Moritz 1994; Meyer & Paulay 2005). The DNA numbers of specimens used in this study are shown in Table 4-1.

DNA extraction, amplification and sequencing

DNA was extracted with Qiagen DNeasy kit from the preserved foot tissue of specimens. Most of shell, operculum, radula and cephalic part of the animals were kept undamaged for future, more detailed taxonomic and morphological studies. The shells of the sequenced specimens representing each species are shown in Appendix 1. A fragment of the mitochondrial COI gene was amplified using the universal primer pairs LCO1490 (5′- GG TCA ACA AAT CAT AAA GAT ATT GG -3′) and HCO2198 (5′- TAA ACT TCA GGG TGA CCA AAA AAT CA -3′; Folmer et al. 1994) for each specimen. PCR reactions were carried out in a final volume of 25 μl [2.5 μl genomic DNA template (ca. 100 ng), 17.5 μl ddH_2O, 2.5 μl Takara ExTaq buffer, 2 μl dNTPs (2.5 μM each), 0.3 μl of each primer (20 μM), and 0.13 μl Takara ExTaq enzyme]. After an initial denaturation for 2 min at 94.5°C, the reaction solution was run for 35 cycles with the following parameters: denaturation for 40 sec at 94.5°C, annealing for 40 sec at 42°C, followed by extension for 60 sec at 72°C. A final extension was performed for 5 min at 72°C. If amplification was unsuccessful under these conditions, one or both of the primers were replaced LCOmod (5′- TCT ACT AAT CAT AAG GAY ATY GGN AC -3′) and/or HCOmod (5′- ACT TCT GGG TGT CCR AAR AAY CAR AA -3′; Kano 2008), or alternatively, nested PCR strategy was employed with the downstream primer COIa-NER (5′- CAT TTA GTG TAG CAA TCA GGR TAR TC -3′; Kano & Kase 2004) for the first run. The PCR products were visualized by electrophoresis on 1.5% TBE agarose gel, which was stained with ethidium bromide and photo-documented.

Successful PCR products were purified by ExoSAP-IT (USB) treatment in a total volume of 3.8 μl using approximately 1.5 μl of the PCR amplicon and 0.3 μl ExoSAP-IT enzyme with ddH_2O. After enzyme incubating at 37 °C for 40 min, the enzyme was inactivated by heating at 80 °C for 15 min. Both or a single strand was directly cycle-sequenced using the amplification primer(s) with a BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) on an ABI 3130 automated sequencer at AORI. The accuracy of each sequence fragment was checked by a BLAST search and comparison with sequences from the same morphological species. Homologous COI sequences from 181 neritid specimens determined in Kawaguchi (2007) were also included in the succeeding analyses after assigning the specimens into the recognized morphotypes.

Sequence analysis and phylogenetic reconstruction

The obtained sequences of the COI gene were aligned by eye in MacClade 4.08 (Maddison & Maddison 2005) as there was no indels. Nucleotide composition, variable and parsimony informative positions and transition-transversion rates were estimated using MEGA 5 (Tamura et al. 2011). Sequence divergences among individuals were quantified by using the Kimura 2-Parameter (K2P) distance model and graphically displayed as a neighbor-joining (NJ) tree by using MEGA 5.2.1 (Tamura et al. 2011). The reliability of the inferred branches was tested by bootstrap resampling of the sequences with 1,000 pseudo-replicates; bootstrap probabilities (BP) equal to or above 75% were considered significant support.

Also reconstructed was a Bayesian phylogenetic tree based on the same COI dataset in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). For this Bayesian analysis, a general time-reversible model was used with an invariant site frequency and gamma-shape parameter estimated from the data (GTR + I + G). The shape, proportion of invariant sites, state frequency and substitution rate parameters were separately estimated for each codon position.

Two parallel runs were made for 5,000,000 generations (with a sample frequency of 1,000) using the default value of four Markov chains. The first 2,000 trees for each run were discarded to ensure the four chains reached stationarity by referring to the average standard deviation of split frequencies (Ronquist & Huelsenbeck 2003). The consensus tree and posterior probabilities (PP) were computed from the remaining 6,000 trees (3,000 trees x 2 runs). Posterior probabilities equal to or above 95% were considered significant support. The phylogenetic tree was graphically edited in FigTree v1.3.1 (Rambaut 2007: http://tree.bio.ed.ac.uk/software/).

Species recognition and assignment of scientific names

Closely related monophyletic ESUs in the NJ and Baysian trees were compared in view of the geographic distribution and shell morphology of the sequenced specimens for the assessment of presence or absence of reproductive isolation. If a given pair of the closest ESUs has any noticeable, constant morphological difference and overlapping distribution ranges, each of them can be regarded as a reproductively isolated biological species. Some pairs of ESUs with deep genetic divergence but showing neither recognizable morphological difference nor a geographic overlap were provisionally treated as a single species in the present analysis. Many studies have been reported the overestimation of species diversity caused by intraspecific polymorphism of the barcoding marker between allopatric or parapatric populations, and the importance of morphological data has been stressed for studies involving specimens from a wide geographic area (e.g. Meyer & Paulay 2005; Hickerson et al. 2006; Valentine et al. 2009).

The assignment of species names to the recognized species was based on original descriptions, few revisional papers with photographs of type specimens, and investigation of types themselves. An extensive survey on the primary types of the Neritidae was conducted at collections in MNHN, ZMB, AMS, Natural History Museum, London, UK (BMNH), Senckenberg Naturmuseum, Frankfurt, Germany (SMF), Muséum d'Histoire Naturelle, Geneva, Switzerland (MHNG), and Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ). This survey allowed the accumulation of photographs of primary types (holotypes, lectotypes and syntypes) that represent information on 280 scientific names for the limnic Neritidae (Appendix 2). The literature survey on the original description was conducted in conjunction above investigation on the types; for some names represented by syntypes that contain more than one biological species, the description and figure provided by the author were used to select specimen(s) that should bear the name (e.g. *Clithon exclamesionis, C. nouletianus, Vittina gagates, V. zigzag* and *Septaria auriculata*). If the original description is too short and lacks an illustration of any of syntypes, the use of the name by the first reviewer was followed. Some biological species recognized among recent samples seemed to be undescribed but formal description will be published elsewhere. Generic classification was based on a separate, more solid phylogeny of the family using multi-gene sequences (see Chapter 2).

Genetic and geographic distances

Pairwise K2P distances and coalescent depth for the COI dataset were used to characterize intraspecific variation. The two most genetically distant individuals within each species were chosen to bookend genetic diversity and recover coalescent depth (maximum intraspecific variability). The interspecific divergence was characterized by genetic distance between the two closest individuals from a species and its closest species.

The dispersal ability of amphidromous neritids across the ocean was accessed by the comparison of genetic and geographic distances between individuals within species. For comparative purposes, 137 sequences of the same COI gene were also obtained from the planktotrophic species of marine neritids (*Nerita* and *Smaragdia*). Previously published sequences (Frey & Vermeij 2008) were also included for the same purpose. The genetic distance between each pair of individuals was quantified by using the K2P distance model. The geographic distance was represented by a straight line between the two localities of each pair at precision of 50 km. The genetic and geographic distances were categorized into and compared between three habitat groups on the salinity preference of component species as adults. These include freshwater, brackish water and marine groups. (1) The freshwater group mainly occurs in the upper and middle reaches of the stream and river, while some show tolerance to low-salinity brackish water. (2) The brackish group includes species living in the mixohaline water of the estuary and stream mouth. (3) The marine group refers to species from (near) euhaline habitats including the rocky shore, sand flat, mangrove swamp and seagrass bed.

Biogeographic patterns of limnic neritids

Geographic distribution range was documented for each recognized species to evaluate the global patterns of species diversity of limnic neritids. To delineate the distribution range, locality data were gathered from tens of thousands of specimens deposited at AORI and museums (MNHN, BMNH, ZMB, SMF, MHNG, AMS and MCZ). Previous literature records were also used for this accumulation of locality data but only when specimens were figured in those papers for rigorous species identification. The compiled locality data were used to count the number of the limnic neritid species within each country or island(s) where the species richness seems to be reasonably well documented, i.e. Mauritius, Thailand, Indonesia, Philippines, Japan (mainland and Nansei Islands), Palau, Guam, Papua New Guinea, Australia, Solomon Islands, Vanuatu, Samoa, Hawaii and French Polynesia, roughly from west to east. The species number was also separately counted for each of representative prefectures, islands and island groups in Japan, i.e. the prefectures of Ishikawa, Chiba, Mie, Wakayama, Kochi, Fukuoka, Miyazaki and (mainland) Kagoshima, and Amami Island, Okinawa Island, Yaeyama Islands and Ogasawara Islands, where suitable habitats exist and sufficient enough specimens were collected.

Based on the same data, species composition was compared in more detail between two regions, namely southwestern Japan and two eastern Melanesian countries, Vanuatu and Solomon Islands, where field samplings were most intensively made and a large majority of distributed species seem to be represented by the specimens sequenced for the COI gene. The Japanese specimens have been accumulated in the past 20 years, mainly from the subtropical islands of Amami, Okinawa, Ishigaki and Iriomote. Material from Santo Island, Vanuatu was collected during the Santo 2006 expedition organized by P. Bouchet and loaned from MNHN, and from Solomon Islands was mainly sampled during a field survey on Guadalcanal Island in 2007 by Y. Kano. The total number of specimens approximated 2,000 for the two eastern Melanesian countries. Using these specimens, the numbers of species occurring in both southwestern Japan and the Melanesian countries and those represented only in either of the regions are counted to compare the similarity and endemicity of limnic neritid faunas in these distant geographic regions across the equator and Equatorial Currents. Genetic distances between intraspecific specimens in the two regions were also assessed to demonstrate the presence or absence of connectivity at a shorter time scale.

4-3: Results

Sequence data

The primer pair designed by Folmer et al. (1994) for the amplification of a partial COI fragment worked well for the most of neritid specimens used in this study, whereas the sequences of *Dostia guamensis*, *Laodia cumingiana* and *Laodia sanguisuga* were amplified successfully only by the modified primers, presumably due to mismatches between the primer and target sequences. A total of 462 partial COI sequences were generated or obtained from previous studies, and all had a length of 658 bp excluding the primer regions. Of these, 13 bp near the primers were only ambiguously determined and were excluded from the succeeding analysis, resulting in the final alignment of 645 bp. This alignment comprised 250 (38.8%) variable sites and 244 (37.8%) parsimony informative characters. The proportion of nucleotides throughout all sequences was T = 39.5%, C = 16.7%, A = 21.1%, and G = 22.7%, respectively (GC = 39.4%).

Comparison of genetic distances between and within species

One hundred and five ESUs were identified among 462 individuals based on their COI gene sequences; the numbers of individuals per ESUs varied between 1 and 23, with a mean of 5 (Figs. 4-2, 4-3). Kimura 2-parameter distances among the individuals ranged from 0 to 25.3%; the largest distance was found between the specimen #2079 of *Neritodryas cornea* and #996 of *Dostia mauritii*. In the Neritininae (see Chapter 2), the divergence between *Neritona granosa* (#1260) and *Clithon pauluccianus* (#366) showed the highest value of 22.2 %. The average genetic distances within each ESU represented by multiple individuals ranged from 0 to 2.1% with an average of 0.65% (Fig. 4-4). The recognized 105 ESUs were classified into 86 species by their morphology: 32 ESUs had shells and opercula that could not be distinguished from those of other ESUs, which were often recovered from allopatric localities. Thirteen species were composed of more than one ESU (up to six). The mean of average genetic distances within each species with more than one individual was 1.1% with a distribution shown in Figure 4-4. Of the 70 species represented by multiple individuals, 46 (65.7%) had an average intraspecific distance of less than 1.0%. The average distance was largest in *Clithon castaneus* (5.4%), which was represented by only three specimens from different countries (Table 4-1; Fig. 4-2).

There was a broad overlap between levels of interspecific divergence and intraspecific variation in limnic neritids, while the mean of the former (6.9%) was larger than that of the latter (1.7%) by about three times (Fig. 4-5). The interspecific divergence (minimum distance between the closest pairs of species) ranged from 2.6% to 14.2 %. Intraspecific variation (distance between the two remotest individuals in the same species) was no more than 8.9%; a majority of species (57 in 70: 81.4%) had the variation lower than 2.6%, the smallest interspecific divergence in the liminic Neritidae of the Indo-West Pacific region. The intraspecific variations of three direct developers (n ≥ 2) of the genus *Neritodryas* ranged from 0.0% to 4.0%. The genetic distance between two specimens of *Neritodryas dubia* from Luzon and Panglao Islands, Philippines was 3.4%. *Neritodryas* sp. 1 from Babeldaob Island, Palau had up to 4.0% intraspecific distances and six ESUs, and mean genetic distances within ESU ranged from 0.0% to 0.4%. The two specimens of *Neritodryas* sp. 2 from Babeldaob Island, Palau shared the same haplotype.

Relationship between genetic and geographic distances

Intraspecific genetic distances in each group were 0–8.9% (average: 1.1%), 0–7.6% (1.9%) and 0.2–8.2% (1.7%) for the freshwater, brackish and marine groups, respectively. Maximum pairwise geographic distances between the collection sites of two specimens in each group were 11,400 km for the freshwater group (N = 502) and 16,350 km for the brackish (N = 1120) and marine groups (N = 142). Sequence differences within species to geographic distances between the collection points for neritid specimens were compared and found these were unrelated (Fig.4-6). The maximum pairwise geographic distances between the collection sites of two specimens with the same haplotype were 6,400 km (the specimen #145 and #927 of *Neritina pulligera* and #147 and #665 of *N. petitii* from Ishigaki Island and Vanuatu) and 10,450 km (#144 and #1298 of *Vittina lugubris* from Ishigaki and French Polynesia) for the freshwater and brackish groups, respectively.

Biogeographic patterns of limnic neritid species

Summary of the compiled locality data revealed that species richness peaks in the Coral Triangle (38–42 species), a region bounded by the Philippines, Indonesia and Papua New Guinea, and declines with increasing distance from this region, both latitudinally and longitudinally (Table 4-2; Figs. 4-7, 4-8). This agrees well with the pattern shown in many shallow-water marine taxa in the Indo-West Pacific (Hoeksema 2007).

Nine species inhabit the islands of French Polynesia at the eastern edge of distribution of limnic neritids in the West Pacific (Fig. 4-7). Of these, only one species (*Clithon spinosus*) is endemic to these islands, while others have more wide-ranging distributions extending to the west (Table 4-2). The Coral Triangle harbors seven of these species (*Clithon variabilis*, *Vittina lugubris*, *Neritina canalis*, *Dostia dilatata*, *D. guamensis*, *D. siquijorensis* and *Septaria auriculata*). *Dostia guamensis* and *S. auriculata* living in stream mouths and estuaries are also found from Mauritius, spanning nearly the entire the Indo-West Pacific with a distance of over 15,000 km. In Mauritius, the westernmost locality where enough specimens were accumulated for the present study, seven species are recognized and three of which (*Clithon coronatus*, *Vittina zigzag* and *Dostia mauritii*) are endemic to the western Indian Ocean islands; two species (*Neritina delestennei* and *S. porcellana*) extend their distributions to the Coral Triangle besides the above mentioned *D. guamensis* and *S. auriculata*.

Of the 86 species recognized in this study, only four are direct developers that lack a marine larval phase. The four non-diadromous species all belong to the genus *Neritodryas* and are narrowly distributed in the tropical western Pacific (Table 4-2). *Neritodryas dubia* has the widest distribution among the four, ranging from the Philippines to Vanuatu. The narrowest known ranges were observed in *Neritodryas* sp. 1 (represented by six ESUs) and *Neritodryas* sp. 2 (only one ESU) that were collected only from the waterfalls of Babeldaob Island, Republic of Palau (Figs. 4-2, 4-3).

The species richness in Japan peaks in the southernmost Yaeyama Islands with 38 species and latitudinally declines with increasing distance from these islands toward the north

(Fig. 4-8). The mainland of Okinawa has 34 species and Amami Island harbors 27 species. The richness is much lower in the mainland Japan including Kyushu, Shikoku and Honshu Islands, but again showing the same tendency with higher numbers of species in southern prefectures, particularly those along the Pacific coast and encountering the warm Kuroshio Current. Of these, only one species (*Dostia* sp. 1) is confined to the temperate water of the mainland Japan and does not occur in Amami or Okinawan islands. The limnic Neritidae do not distribute in Tohoku and Hokkaido districts in the northern part of Japan. The subtropical Ogasawara Islands harbor only eight species in a few, small permanent streams.

The large gap of the richness between the Nansei Islands (including Yaeyama, Okinawa and Amami) and the main islands of Japan is less pronounced when specimens from two ditches in Kagoshima and Miyazaki Prefectures are taken into account. The one in Ibusuki, Kagoshima (31°17'N, 130°37'E) harbors 23 species in warm sewage water received from hot springs since the late Edo era of about 150 years ago (Fig. 4-9). The other in Hitotsuse, Miyazaki (32°03'N, 131°27'E) has 14 species and warm drainage water from an eel farm since around a dozen years ago (see Miura & Jitsumasa 2010). These species numbers are twice to three times higher than those from nearby streams, rivers and estuaries with natural conditions.

The comparison of species composition between Japan and two eastern Melanesian countries was made by using 203 sequenced specimens, of which 144 were from the former and 59 were from the latter region. The Japanese specimens comprised 41 ESUs in 39 species (Table 4-2). *Vittina lugubris* among the 39 species showed the largest intraspecific variation of the COI sequence within this region (5.0%), followed by *Septaria spiralis* (3.9%). The two Melanesian countries had a total of 36 ESUs, all of which represented distinct species with unique conchological characteristics; the pairwise COI distances within the species did not exceed 0.6%. There existed two more taxa (*Neritodryas dubia* and *Neritona labiosa*) represented only by empty shells in this region and these increased the total number of species to 38. In the two regions combined there were 55 species, 22 of which were shared in both Japanese and Melanesian waters (Table 4-2). Two allopatric ESUs with no recognizable morphological difference existed within each of *Neritina asperulata* and *Dostia dilatatum* (Figs. 4-2, 4-3).

4-4: Discussion

Recognition of biological species in limnic Neritidae

The present integrative analysis of molecular and morphological data recognized 87 species (including *Neritona labiosa* represented only by empty shells in Vanuatu and Solomon Islands) of the limnic Neritidae in the Indo-West Pacific. Many species and ESUs were newly recognized or defined in this study, and higher species richness was observed for individual regions than documented in previous studies (see below). The present analysis also demonstrated that the intraspecific genetic variability of limnic neritids represented by the COI gene sequence was generally lower than the minimum divergence between the closest pairs of species. The correspondence between the ESUs defined exclusively by the COI distance and species that also accounted for morphology was relatively high (84.5%), although there was a considerable overlap between the ranges of genetic distances within and between species (Fig. 4-5). These findings further validate the previous guidelines that recommend the use of DNA barcoding in conjunction with other data including morphology and ecology (Meyer & Paulay 2005; Hickerson et al. 2006; Song et al. 2008).

Comprehending the range of intraspecific variation in morphology helps highlight traits that are taxonomically more useful than others. For example, the present study demonstrated that the color of inner lip of the shell aperture provided an important criterion for species identification of *Neritina* specimens as the general shell shape does, while this was not always the case in different genera. On the other hand, a number of other characters such as shell spines were highly plastic within many of *Clithon* species, often among specimens from the same locality (Appendix 1). Species identification based on such characters with extensive intraspecific variation indeed has produced widespread confusion that is shared by virtually all previous taxonomic and faunistic studies of the group. Thorough understanding of characters with interspecific differentiation and/or intraspecific variations including ontogenetic changes is therefore crucially important for the species taxonomy of limnic neritids.

The mitochondrial COI gene is universally regarded as the most appropriate marker for animal DNA barcoding, because its sequence evolves with an accelerated nucleotide substitution rate and conserves within species (Meyer 2003; Xia et al. 2012). However, the mitochondrial DNA typically shows maternal inheritance within sexually reproducing organisms, differing in the transmission patterns from nuclear genes (e.g. Sato & Sato 2011). Thus, comparison of genetic variation between mitochondrial and nuclear markers may be helpful in species identification (Meyer & Paulay 2005). Watanabe (2010), in his master's thesis, has assessed the nuclear ITS2 region for the identification of limnic neritids by using 27 individuals from the two COI ESUs of *Vittina lugubris* (see also Kawaguchi 2007). The tree topologies based on the COI and ITS2 sequences differ from each other and all individuals are therefore recognized to form a single species, regardless the different proportions of color patterns exhibited in the shells of the two ESUs (Watanabe 2010). However, it is also suggested that the ITS2 sequences are possibly insufficiently long (319 sites) and variable for such a purpose. Future use of different nuclear markers certainly helps us better understand their reproductive isolation as do ecological and behavioral studies.

The previous lack of knowledge on the range of intraspecific morphological variation and differences between species seemed to have hindered proper recognition of many of limnic neritid species in faunistic and biogeographic researches. Indeed, the species richness in Japan and two eastern Melanesian countries has been badly underestimated in former studies (e.g. Starmühlner 1976; Haynes 1993, 2000; Tsuchiya 2000). Starmühlner (1976) sampled limnic neritids in Vanuatu and Solomon Islands and classified them to 14 species.

Haynes (1993, 2000) later on revised neritid taxonomy and reassessed the species richness of the region as having a total of 28 species (22 in each country). These 28 species unfortunately were mentioned only by their names without accompanying figures of specimens and direct comparison of taxonomic criteria is not possible, although approximately 30% among 38 species recognized in this study (Table 4-2) seemed to be ignored and more were erroneously classified and identified. For Japanese islands, Kawaguchi (2007) has shown that at least 36 species inhabit freshwater to brackish environments and many of which were ignored in previous studies (Kuroda 1963; Komatsu, 1986; Tsuchiya, 2000; Masuda & Uchiyama, 2004). Two species in the genus *Clithon* and one in *Dostia* were further added by the present study, resulting in the total number of 39. No such taxonomic attempt involving the extensive filed sampling and combined molecular and morphological analyses has been made for other regions. Future studies are clearly needed to clarify the species composition of the limnic Neritidae in each region and more new taxa will continue to be discovered, particularly in the least investigated East Malaysia, southern part of the Philippines and Indonesia.

The biogeography and diversity of freshwater invertebrates are generally poorly known in tropical streams due to the same impediments in species-level taxonomy that include enormous species richness, inaccessibility to a sufficient number of properly preserved specimens and lack of knowledge on taxonomic characters and character states (e.g. Jacobsen et al. 2008). Difficulty in species identification also comprises one of the reasons for the paucity of ecological studies for those stream invertebrates (Dudgeon 2003). The present advances in the taxonomy of the limnic Neritidae will allow for subsequent ecological and conservation studies for the group. A huge number of neritid shells have been collected and deposited in museums since the age of European explorations in various tropical regions of the world (Kabat & Finet 1992). Such specimens enable us to assess species compositions in the past and present (e.g. Cowie & Cook 2001; Cowie & Robinson 2003) with the now available knowledge on the intraspecific variability of shell morphology.

Assignment of valid names to biological species

Through examination of type material and literature investigation, 68 names are presumed as valid and assigned to the above limnic neritids while 19 recognized species have remained unidentified to any of existing names (Table 4-1). The latter unidentified neritids may represent undescribed or new species; before preparing formal description, however, more attention and time are required to locate missing type specimens that represent some 300 names among 600 introduced for the limnic species from all over the world.

A few different types of issues have also been realized regarding those names by the specimen examination and literature survey. Many species names were newly synonymized, naturally including those used by recent authors as valid names. The valid name of a taxon is the oldest available name applied to it (International Code of Zoological Nomenclature, Art. 23), but sometimes the use of the older names would threaten stability and cause confusion than the use of the younger names (e.g. Petit 2011). For example, *Neritodryas subsulcata* (Sowerby, 1836) is a name for a widely distributed species in the Indo-West Pacific and has been considered valid by many authors for a long time (e.g. Haynes 1988, 1990; Smith 2003; Kano 2006; Symonds & Pacaud 2010). However, this represents a junior synonym of *Neritodryas ampullaria* (Lesson, 1831), which has seldom appeared in the literature since its original description. Unfortunately, the status of the name is not met the condition for the reversal of precedence as follows: the junior synonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least ten authors in the immediately preceding 50 years and encompassing a span of not less than ten years (ICZN, Art. 23.9.1). The older *N. ampullaria* should therefore be used for the stability of species name.

The present survey on the types of limnic neritids also revealed that most species were described based on a series of syntypes, which collectively constituted the name-bearing type.

However, many of the type series were found to include two or more biological species recognized in this study. When stability or universality is threatened, or confusion is likely to be caused for example by the presence of multiple resembling species, a lectotype may subsequently be selected and designated as the single name-bearing type from the type series (ICZN, Art. 74.1). Unfortunately and ironically, however, previous designation of lectotypes has created unnecessary confusion to the taxonomy of the limnic Neritidae, by selecting the name-bearing specimens without paying enough attention to reproductive isolation or intention of the original authors (e.g. Kabat & Finet 1992). Designation of new lectotypes will be made elsewhere as part of revisionary papers by reflecting the present results from genetic and morphological data.

Dispersal ability of amphidromous neritids

Most species of amphidromous neritids exhibited relatively to very small genetic diversity despite their wide geographic ranges, suggesting dispersal capability comparable to those of confamilial species in fully marine environments (Fig. 4-6). Conspecific individuals sometimes shared the same haplotypes over several thousands of kilometers (Table 4-2; Fig. 4-2). Such homogeneity and shared haplotypes suggest gene flow between far distant populations due to their high dispersal ability in ocean currents. Population genetic studies on marine neritid species with a long larval period have unanimously shown that they have high levels of homogeneity for the COI gene among distant populations (Waters et al. 2005; Hurtado et al. 2007; Crandall et al. 2008). For amphidromous species, Meyrs et al. (2000) and Crandall et al. (2010) have assessed the larval dispersal of *Clithon spinosus* among French Polyneian islands and *Dostia dilatata* and *Neritina canalis* among South Pacific archipelagos, respectively, both again using the COI gene sequences. All three species have pelagic duration equivalent to that of marine relatives and high dispersal capability can be expected (see Chapter 3). The former two amphidromous species indeed show panmictic haplotype distributions within the investigated areas; the last one has generic differentiation between Society Islands, Marquesas and other areas, which are separated by more than a thousand kilometers (Myers et al. 2000; Crandall et al. 2010). Judging from the results in this study that show the genetic variation within an ESU or a species is relatively to very small (Fig. 4-6), most if not all amphidromous neritids also disperse and colonize over distances of several hundreds or thousands of kilometers as marine confamilials do. More detailed population genetic studies covering the entire distribution ranges of species (Table 4-2) would reveal the causes and consequences of different ontogenetic, ecological and morphological characteristics to their geographic distributions and population structures.

The comparison of species compositions between two distant geographic regions demonstrated high faunistic homogeneity of limnic neritids across wide areas in the western Pacific Ocean. As mentioned earlier, 39 and 38 species out of 87 recognized (including *Neritona labiosa*) in this study were obtained from Japan and the two eastern Melanesian countries, i.e. Solomon Islands and Republic of Vanuatu, respectively (Table 4-2). These two regions having comparable richness shared a large proportion of taxa (22 species, which represent nearly 60% of richness in both regions). The similarity of these faunal assemblages in limnic environments parallels to the general tendency in marine neritid faunas. In the marine genus *Nerita*, 12 species are shared between Japan (16 species) and the two eastern Melanesian countries (18 species; Frey & Vermeij 2008; Frey 2010b). Comparable biogeographic patterns are found in many marine gastropod families in the tropical to subtropical Indo-West Pacific with high dispersal capability (e.g. Meyer 2003; Williams & Reid 2004). Such similarity of species compositions in the remote areas and lack of clear genetic differentiation in most of the shared species provide further evidence for high dispersal capability of amphidromous neritids regardless of their limnic adult habitats.

Surprisingly, even wider distribution from southwestern Indian coasts to French Polynesia was found in two (*Dostia guamensis* and *Septaria auriculata*) out of 87 limnic neritid species (Table 4-2; Fig. 4-2). However, the faunal composition and species richness on the southwestern Indian islands, here represented by Mauritius as an extensively investigated locality, was rather different from and lower than those of West Pacific regions (Fig. 4-7). The COI sequences of the above two widely distributed species also show some differentiation between Mauritius and Pacific localities (Fig. 4-2). Among other, non-neritid amphidromous animals, the freshwater shrimp *Macrobrachium lar* has the same wide-ranging distribution from the southwestern Indian coasts to French Polynesia, which can be explained by the presence of a marine larval period for three months (Castelin et al. 2013). However, the populations of this species are also differentiated between southwestern Indian and Pacific oceans as demonstrated by the sequences of both mitochondrial 16S and nuclear 28S genes (Castelin et al. 2013).

In the South Pacific, the populations of *Dostia dilatata* have been connected between the distantly located Vanuatu and French Polynesia through larval dispersal via many intermediate, high volcanic islands as stepping stones (Crandall et al. 2010). However, amphidromous neritids tend to have lower gene flow where only low islands of coral atoll origin are available, because of the absence of a suitable freshwater habitat (Crandall et al. 2012). The cause of small number of shared neritid species between the southwest Indian and western Pacific streams most probably is the lack of high islands with enough precipitation and freshwater streams in the middle of the Indian Ocean. Such islands in the Indian Ocean are distributed in the western part of the ocean basin (e.g. Seychelles, Réunion, Comoro, Mauritius and Madagascar), which are all distant from the West Pacific (Falkland 1991). The same mechanism nicely explains the very few number of limnic neritid species in the islands of Hawaii (Fig. 4-7). Some of these high volcanic islands receive high precipitation and provide perfect habitats for amphidromous neritids, while only three species distribute there; two of them are Hawaiian endemics and the other is the most highly dispersible *Septaria auriculata* (Table 4-2). Nearby islands of Hawaii are all atolls and the closest and yet very far stream habitats locate in the 3,500 km-apart Marquesas and 4,000 km-away Samoa (Fig. 4-1).

Biogeographic patterns of species richness

Summary of the compiled locality data for limnic neritids revealed that species richness peaks in the Coral Triangle, a region bounded by the Philippines, Indonesia and Papua New Guinea. The numbers of limnic neritid species declined with increasing distance from this region, both latitudinally and longitudinally. This agrees well with the pattern shown in many shallow-water marine taxa in the Indo-West Pacific (Hoeksema 2007). The biodiversity of tropical marine fish, corals and other invertebrates is unanimously high in the Indo-Australian Archipelago, encompassing the Coral Triangle (e.g. Bellwood & Hughes 2001; Hughes et al. 2002; Meyer 2003; Hoeksema 2007; Renema et al. 2008; Bellwood & Meyer 2009; Frey 2010b). The total species richness of 13 tropical fish families, for example, ranges from nearly 600 at sites around Indonesia and about 500 in southwestern Japan to approximately 200 in French Polynesia (Glynn et al., 1996; Hughes et al., 2003). The species numbers of the marine neritid genus *Nerita* similarly decline from over 20 in Indonesia and 16 species in Japan to only 5 in French Polynesia (Frey & Vermeij 2008; Frey 2010b). Limnic neritids were most diverse in the Philippines where 42 species are recorded, despite the sampling effort there might not have been sufficient (Fig. 4-7). Okinawan and Indonesian islands and Papua New Guinea that surround the Philippines follow with 38 species (Fig. 4-8), while the nearby Palau and Guam are less diverse (21 and 14 species, respectively) probably due to limited numbers of different habitats on those small islands. The species numbers at the peripheries of the Indo-West Pacific are as low as seven in Mauritius, nine in French Polynesia and three in Hawaii as mentioned above.

The latitudinal cline is also clearly seen in the species richness of limnic neritids. Only five species are found in the warm-temperate region in Honshu Island, Japan (Fig. 4-9; see also Kawaguchi 2007). The number increases toward the south; it is eight in the mainland Kagoshima that represents the southernmost tip of the temperate Japan; 27 on the northernmost subtropical island Amami, 34 on Okinawa Island and then 38 on the southernmost Yaeyama Islands. The much lower diversity on Oagasawara Islands (8 species) can undoubtedly be explained by the scarcity of suitable freshwater and brackish-water habitats. On the other hand, the fewer numbers along the Sea of Japan coast (Fig. 4-9) than on the Pacific side of the mainland is clearly attributable to the different levels of influence of the warm Kuroshio Current from that carries the long-lived planktotrophic larvae of the amphidromous Neritidae from the southern islands.

Provided that there are suitable habitats and supply of larvae, air temperature seems to be the crucial determinant of their species richness. Two ditches in Ibusuki, Kagoshima and Miyazaki of southern Kyushu receive warm water from hot springs or an eel farm and harbor surprisingly high numbers of neritid species (23 and 14, respectively; Fig. 4-9). These numbers provide clear contrast with the diversity in the streams and estuaries of the same area in natural conditions (eight and six) and are rather close to that of the subtropical Amami Island (Fig. 4-8). The annual mean air temperature was 21.4–22.4ºC on Amami in the past ten years with the annual minimum dropping only to 5.1–8.9ºC (Japan Meteorological Agency 2013: data available at http://www.data.jma.go.jp). The annual mean was not too low in Ibusuki and Miyazaki at 17.8–19.1ºC and 17.5–18.4˚C, respectively, while the annual minimum was much lower and ranged from -2.2ºC to -5.7ºC in the former and from -0.7ºC to -2.3ºC in the latter city. These low temperatures in the winter certainly hinder the survival of many species that live in the streams of southern islands as well as in the two ditches with artificial input of warm drainage water. Interestingly, these subtropical species have indeed been recorded as juvenile or subadult specimens from natural rivers and estuaries in Kyushu and Honshu islands, but only in the fall and early winter (Miura et al. 2006; Ekawa & Noda 2010). Such sporadic occurrences certainly represent abortive migration, which involves larval settlement in the summer, growth in the fall and then fatally low temperatures in January and February of the winter.

Air temperature: limiting factor in the present and past

The findings of the higher diversity in the artificial warm ditches and the abortive migration provide further insights on the dispersal of the amphidromous Neritidae and the determination mechanisms of the global diversity of the family in limnic environments. The origins of the warm condition go back only to the late Edo era of about 150 years ago at most for the ditch in Kagoshima and to around a dozen years ago for the one in Miyazaki. However, these ditches harbor so many subtropical species, one of which (*Septaria clypeolum*) occurs on the 600-km away Okinawa Island and southward but not on Amami Island. The juvenile and subadult specimens found in Wakayama, Honshu Island include species that occur naturally as adults only on the 800-km away Amami and other subtropical islands to the south (e.g. *Dostia siquijorensis*; Ekawa & Noda 2010). These combined suggest that (1) the larvae of amphidromous neritids are transported for at least several hundred kilometers in ocean currents, and (2) there are numerous such dispersing larvae in the Kuroshio and certainly also in other currents originating from the Coral Triangle. Finally, (3) such numerous larvae allow colonization and establishment of population in a remote stream in at least a dozen years since the time when the habitat is available for adult individuals.

The distributions of the four direct-developing species of the limnic Neritidae are restricted to the tropical islands near the equator, most probably due to the global cooling in the Quaternary glacial periods. The water temperature of streams and rivers is directly affected by the annual fluctuation of air temperature, contrasting generally more stable conditions in marine environments. The south Pacific coasts of the mainland Japan are washed by the warm Kuroshio Current that keeps the water temperature relatively high even in the winter. There exists a marine species of Neritidae with benthic early development (*Nerita japonica*; Kano 2006) along these coasts, whereas Japanese islands including the subtropical ones lack any direct-developing species of the family in limnic waters. The air (and stream-water) temperature of temperate and subtropical regions in the Last Glacial

Maximum (LGM) was globally several degrees lower than today, while it was only ca. 2ºC lower over the tropical western Pacific (Kitoh & Murakami 2002). Several degrees lower means that the islands of Amami and Okinawa were approximately as cold as the mainland Japan in LGM. The species richness of the limnic Neritidae there was presumably as low as in the mainland Japan today and its currently diverse fauna should have a recent origin after LGM at around 21,000 years ago. Only the frequent, abundant and long-distance dispersal of the amphidromous Neritidae should have enabled the colonization and establishment of the diverse fauna in a relatively short time on an evolutionary scale. In conclusion, the Neritidae as well as many other amphidromous animal lineages with their origins in the tropics may have rapidly changed distribution ranges according to the fluctuating climate and shaped the present-day regional diversity almost entirely by dispersal but rarely by speciation through small-scale vicariance.

Table 4-1. Limnic Neritidae of the Indo-West Pacific used in this study, with collection sites and DNA numbers. Generic assignment follows the classification in Chapter 2.

Species and collection site	DNA No.
***Neritodryas* Martens, 1869**	
Neritodryas ampullaria (Lesson, 1831)	
Iriomote Is., Okinawa, Japan	123
Amami Is., Japan	521
Babeldaob Is., Palau	1740, 1745
Santo Is., Vanuatu	650
Neritodryas cornea (Linnaeus, 1758)	
Timor Is., East Timor	2079, 2085
Santo Is., Vanuatu	652
Neritodryas dubia (Gmelin, 1791)	
Luzon Is., Philippines	1323
Panglao Is., Philippines	705
Santo Is, Vanuatu	–
Neritodryas notabilis Riech, 1935	
Santo Is., Vanuatu	651
Neritodryas sp. 1	
Babeldaob Is., Palau	1710, 1712, 1714, 1716, 1718, 1738–1743, 1745–1751, 1753, 1902, 1903, 1921–1925, 1928–1955, 1970–1991
Neritodryas sp. 2	
Babeldaob Is., Palau	1711, 1736
***Neritona* Martens, 1869**	
Neritona granosa (Sowerby, 1825)	
Hawaii Is., Hawaii	1260
Neritona labiosa (Sowerby, 1836)	
Guadalcanal Is., Solomon Islands	–
Santo Is., Vanuatu	–
***Clithon* Montfort, 1810**	
Clithon castaneus (Hombron & Jaquinot, 1854)	
Flores Is., Indonesia	1307
Viti Levu, Fiji	1311
Upolu, Western Samoa	262
Clithon chlorostoma (Sowerby I, 1833)	
Upolu, Western Samoa	264
Cook Is., South Pacific	1444
Tahiti, French Polynesia	1299
Clithon corona (Linnaeus, 1758)	
Kagoshima, Kyushu, Japan	356
Amami Is., Japan	406
Okinawa Is., Japan	849
Ishigaki Is., Okinawa, Japan	138
Iriomote Is., Okinawa, Japan	134–137
Pingtung, Taiwan	1919
Cebu Is., Philippines	405, 1037
Timor Is., East Timor	2089
Clithon coronatus (Leach, 1815)	
Grand Port, Mauritius	182
Clithon diadema (Récluz, 1841)	
Kagoshima, Kyushu, Japan	846
Okinawa Is., Japan	847
Palawan Is., Philippines	850, 992
Panglao Is., Philippines	1043
Bali Is., Indonesia	854
Santo Is., Vanuatu	639, 997
Clithon elephas (Mabille, 1895)	
Santo Is., Vanuatu	640, 1002
Clithon exclamesionis (Mabile, 1895)	
Agat, Guam, Micronesia	360
Queensland, Australia	1917
Guadalcanal Is., Solomon Is.	967
Santo Is., Vanuatu	642, 1000
Clithon faba (Sowerby I, 1836)	
Phang Nga, Thailand	1900
Nha Trang, Vietnam	414
Mie, Honshu, Japan	301
Miyazaki, Kyushu, Japan	188, 932, 988
Kagoshima, Kyushu, Japan	990
Amami Is., Japan	298
Panglao Is., Philippines	1005
Timor Is., East Timor	2080
Port Moresby, Papua New Guinea	1314
Clithon interruptus (Récluz, 1843)	
Okinawa Is., Japan	694, 2010
Clithon leachii (Récluz, 1841)	
Amami Is., Japan	314, 412, 413
Okinawa Is., Japan	299, 367, 853, 1271
Iriomote Is., Okinawa, Japan	128, 297, 317, 318, 319
Yonaguni Is., Okinawa, Japan	300, 315, 354
Clithon navigatoria (Reeve, 1855)	
Queensland, Australia	1320, 1916
Clithon nouletianus (Gassies, 1863)	
Miyazaki, Kyushu, Japan	189
Amami Is., Japan	126
Okinawa Is., Japan	125
Palawan Is., Philippines	364
Guadalcanal Is., Solomon Is.	966
Santo Is., Vanuatu	649
Clithon olivaceus (Récluz, 1843)	
Ishigaki Is., Okinawa, Japan	696
Iriomote Is., Okinawa, Japan	139
Agat, Guam, Micronesia	370
Santo Is., Vanuatu	928
Clithon oualaniensis (Lesson, 1831)	
Phuket Is., Thailand	2019
Ehime, Shikoku, Japan	439
Miyazaki, Kyushu, Japan	190

Iriomote Is., Okinawa, Japan	127
Panglao Is., Philippines	365
Santo Is., Vanuatu	647
Clithon pauluccianus (Gassies, 1870)	
Okinawa Is., Japan	124
Yonaguni Is., Okinawa, Japan	366
Santo Is., Vanuatu	644
Clithon peguensis (Blanfold, 1867)	
Phang Nga, Thailand	1303, 1448
Clithon pritchardi (Dohrn, 1861)	
Viti Levu, Fiji	2095
Clithon retropictus (Martens, 1878)	
Kochi, Shikoku, Japan	130
Iriomote Is., Okinawa, Japan	131
Clithon rugatus (Récluz, 1842)	
Iriomote Is., Okinawa, Japan	132
Palawan Is., Philippines	362
Flores Is., Indonesia	1253
Guadalcanal Is., Solomon Islands	913
Clithon siderea (Gould, 1847)	
Panglao Is., Philippines	1044
Guadalcanal Is., Solomon Is.	965
Santo Is., Vanuatu	648
Clithon sowerbianus (Récluz, 1843)	
Kagoshima, Kyushu, Japan	353
Amami Is., Japan	351, 352, 410, 411
Okinawa Is., Japan	313, 852
Iriomote Is., Okinawa, Japan	129
Palawan Is., Philippines	361, 999
Flores Is., Indonesia	1252
Clithon spinosus (Sowerby I, 1825)	
Tahiti, French Polynesia	1281
Clithon subpunctatus (Récluz, 1844)	
Amami Is., Japan	408
Iriomote Is., Okinawa, Japan	133
Cebu Is., Philippines	363
Agat, Guam, Micronesia	369
Clithon variabilis (Lesson, 1831)	
Pohnpei Is., Caroline Islands	409, 968
Santo Is., Vanuatu	643, 912
Upolu, Western Samoa	265–267
Marquesas Is., French Polynesia	1446
Clithon sp. 1	
Pingtung, Taiwan	1901
Mindanao Is., Philippines	969
Santo Is., Vanuatu	645, 646
Clithon sp. 2	
Sulawesi Is., Indonesia	1908
Clithon sp. 3	
Amami Is., Japan	407
Okinawa Is., Japan	302, 355, 856
Clithon sp. 4	
Bali Is., Indonesia	859
Flores Is., Indonesia	1249
Clithon sp. 5	
Cebu Is., Philippines	368
Guadalcanal Is., Solomon Is.	963, 964
Clithon sp. 6	
Sulawesi Is., Indonesia	1317, 1326
Clithon sp. 7	
Phuket Is., Thailand	1339
Kedah, Malaysia	1324
Flores Is., Indonesia	1322
***Vittina* Baker, 1923**	
Vittina communis (Quoy & Gaimard, 1834)	
Okinawa Is., Japan	359
Agat, Guam, Micronesia	437
Santo Is., Vanuatu	929
Upolu, Western Samoa	263
Vittina cumingiana (Récluz, 1842)	
Amami Is., Japan	140
Okinawa Is., Japan	435
Agat, Guam, Micronesia	436
Vittina cuvieriana (Récluz, 1841)	
Guadalcanal Is., Solomon Is.	958
Santo Is., Vanuatu	653
Vittina gagates (Lamarck, 1822)	
Amami Is., Japan	432
Iriomote Is., Okinawa, Japan	141
Agat, Guam, Micronesia	434
Pohnpei Is., Caroline Islands	433
Queensland, Australia	1915
Santo Is., Vanuatu	654
Vittina lugubris (Lamarck, 1822)	
Phang Nga, Thailand	1454
Kagoshima, Kyushu, Japan	258, 357, 358
Amami Is., Japan	428, 1009, 1210
Okinawa Is., Japan	143, 429, 430, 858
Ishigaki Is., Okinawa, Japan	142, 144
Iriomote Is., Okinawa, Japan	857, 860, 1220
Pingtung, Taiwan	1918
Cebu Is., Philippines	320, 431, 855, 1213, 1214
Bohol Is., Philippines	1212
Babeldaob Is., Palau	1737
Timor Is., East Timor	2081
Guadalcanal Is., Solomon Is.	1215
Santo Is., Vanuatu	655, 1216–1219
Viti Levu, Fiji	1285
Huahine, French Polynesia	1298
Tahiti, French Polynesia	1300
Vittina serrulata (Récluz, 1842)	
Sulawesi Is., Indonesia	1308
Jawa Is., Indonesia	1312
Vittina turrita (Gmellin, 1791)	
Purchased (Indonesia?)	931, 1211
Vittina zigzag (Lamarck, 1822)	
Sananne, Mauritius	438

Laodia Gray, 1868

Laodia sanguisuga (Reeve, 1856)	
Upolu, Western Samoa	183
Laodia cumingiana (Récluz, 1843)	
Ishigaki Is., Okinawa, Japan	163
Iriomote Is., Okinawa, Japan	209, 589
Palawan Is., Philippines	587
Sulawesi Is., Indonesia	1302

***Neritina* Lamarck, 1816**

Neritina asperulata (Récluz, 1843)	
Amami Is., Japan	520
Ishigaki Is., Okinawa, Japan	148
Iriomote Is., Okinawa, Japan	149
Cebu Is., Philippines	518
Babeldaob Is., Palau	1920
Flores Is., Indonesia	1251
Agat, Guam, Micronesia	510
Santo Is., Vanuatu	664, 667
Neritina canalis Sowerby I, 1825	
Agat, Guam, Micronesia	1036
Santo Is., Vanuatu	662
Upolu, Western Samoa	187
Moorea, French Polynesia	2015
Neritina delestennei Récluz, 1853	
Grand Port, Mauritius	504
Grand Port, Mauritius	1038
Amami Is., Japan	505
Ishigaki Is., Okinawa, Japan	146
Panglao Is., Philippines	1042
Agat, Guam, Micronesia	507
Neritina iris Mousson, 1849	
Amami Is., Japan	511
Iriomote Is., Okinawa, Japan	150
Palawan Is., Philippines	506, 512
Babeldaob Is., Palau	1715
Timor Is., East Timor	2083
Queensland, Australia	1914
Pohnpei Is., Caroline Islands	513
Guadalcanal Is., Solomon Is.	960
Neritina luzonica (Récluz, 1841)	
Panglao Is., Philippines	1004
Babeldaob Is., Palau	1713
Neritina petitii (Récluz, 1841)	
Ishigaki Is., Okinawa, Japan	147, 508
Iriomote Is., Okinawa, Japan	577
Santo Is., Vanuatu	665
Neritina powisiana (Récluz, 1843)	
Guadalcanal Is., Solomon Is.	959
Santo Is., Vanuatu	666
Neritina pulligera (Linnaeus, 1767)	
Amami Is., Japan	502
Ishigaki Is., Okinawa, Japan	145
Iriomote Is., Okinawa, Japan	1927
Palawan Is., Philippines	503
Babeldaob Is., Palau	1752
Timor Is., East Timor	2088
Queensland, Australia	1912
Agat, Guam, Micronesia	519
Santo Is., Vanuatu	927
Upolu, Western Samoa	261
Neritina sp. 1	
Sulawesi Is., Indonesia	1321
Flores Is., Indonesia	1250
Neritina sp. 2	
Ishigaki Is., Okinawa, Japan	152
Iriomote Is., Okinawa, Japan	153
Sulawesi Is., Indonesia	1325
Agat, Guam, Micronesia	516
Pohnpei Is., Caroline Islands	509, 517
Neritina sp. 3	
Sarawak, Malaysia	1305
Neritina sp. 4	
Phang Nga, Thailand	1451
Neritina sp. 5	
Queensland, Australia	1290

***Dostia* Gray, 1842**

Dostia bicanaliculata (Récluz, 1843)	
Phang Nga, Thailand	1456
Amami Is., Japan	566
Okinawa Is., Japan	162
Ishigaki Is., Okinawa, Japan	697
Cebu Is., Philippines	567
Queensland, Australia	1913
Dostia cariosa (Gray, 1827)	
Oahu Is., Hawaii	1259, 1261
Dostia dilatata (Broderip, 1833)	
Amami Is., Japan	568
Iriomote Is., Okinawa, Japan	157
Palawan Is., Philippines	570
Agat, Guam, Micronesia	569
Santo Is., Vanuatu	930, 998
Upolu, Western Samoa	207
Moorea, French Polynesia	2014
Dostia florida (Récluz, 1850)	
Santo Is., Vanuatu	661, 914
Dostia guamensis (Quoy & Gaimard, 1834)	
Svanne, Mauritius	563
Kagoshima, Kyushu, Japan	560
Amami Is., Japan	161, 561
Babeldaob Is., Palau	1717
Makemo, French Polynesia	1280
Dostia mauritii (Sowerby, 1849)	
Le Cap, Mauritius	996
Dostia melanostoma (Troschel, 1837)	
Phuket Is., Thailand	1338
Dostia siquijorensis (Récluz, 1843)	
Phang Nga, Thailand	2021
Cocos Is., Australia	995

Miyazaki, Kyushu, Japan	191
Iriomote Is., Okinawa, Japan	37, 564
Palawan Is., Philippines	565
Santo Is., Vanuatu	660
Moorea, French Polynesia	1453
Dostia subalata (Souleyet, 1842)	
Miyazaki, Kyushu, Japan	848
Amami Is., Japan	571–573
Okinawa Is., Japan	916, 2016
Ishigaki Is., Okinawa, Japan	256
Iriomote Is., Okinawa, Japan	156
Pingtung, Taiwan	2017
Cebu Is., Philippines	575
Bohol Is., Philippines	576
Santo Is., Vanuatu	656
Upolu, Western Samoa	208
Dostia violacea (Gmelin, 1791)	
Phuket Is., Thailand	1447
Northorn Territory, Australia	1289
Dostia sp. 1	
Mie, Honshu, Japan	552
Oita, Kyushu, Japan	154
Miyazaki, Kyushu, Japan	551
Dostia sp. 2	
Queensland, Australia	2091
Dostia sp. 3	
Amami Is., Japan	155
Okinawa Is., Japan	851
Septaria Férrusac, 1807	
Septaria auriculata (Lamarck, 1816)	
Grand Port, Mauritius	559
Okinawa Is., Japan	159
Ishigaki Is., Okinawa, Japan	160
Agat, Guam, Micronesia	558
Santo Is., Vanuatu	657, 658
Upolu, Western Samoa	268, 269
Oahu Is., Hawaii	1297
Moorea, French Polynesia	2013
Septaria clypeolum (Récluz, 1843)	
Kagoshima, Kyushu, Japan	583
Okinawa Is., Japan	695
Panglao Is., Philippines	706
Madang, Papua New Guinea	1893
Septaria lecontei (Récluz, 1853)	
Northan Territory, Australia	1286, 1309
Septaria porcellana (Linnaeus, 1758)	
Baie du Cap, Mauritius	586
Sananne, Mauritius	588
Phuket Is., Thailand	1340
Oita, Kyushu, Japan	578
Kagoshima, Kyushu, Japan	584
Amami Is., Japan	582
Ishigaki Is., Okinawa, Japan	164, 165
Palawan Is., Philippines	579
Babeldaob Is., Palau	1744
Timor Is., East Timor	2087
Agat, Guam, Micronesia	580
Pohnpei Is., Caroline Islands	585
Santo Is., Vanuatu	668, 670
Septaria spiralis (Reeve, 1855)	
Kagoshima, Kyushu, Japan	673
Amami Is., Japan	553, 671, 672
Iriomote Is., Okinawa, Japan	158
Yonaguni Is., Okinawa, Japan	554
Palawan Is., Philippines	557
Cebu Is., Philippines	555
Agat, Guam, Micronesia	556
Santo Is., Vanuatu	659, 1898
Septaria suffreni (Récluz, 1842)	
Upolu, Western Samoa	184–186
Septaria tessellata (Lamarck, 1816)	
Phang Nga, Thailand	1455
Miyazaki, Kyushu, Japan	991
Amami Is., Japan	581
Okinawa Is., Japan	167
Palawan Is., Philippines	193
Santo Is., Vanuatu	669
Septaria sp.	
Viti Levu, Fiji	1310
New genus 1	
“*Neritina*” *bruguieri* (Récluz, 1841)	
Iriomote Is., Okinawa, Japan	151
Yonaguni Is., Okinawa, Japan	514
Agat, Guam, Micronesia	515
Guadalcanal Is., Solomon Is.	962
Santo Is., Vanuatu	961
New genus 2	
“*Neritina*” *haemastoma* (Martens, 1878)	
Maluku, Indonesia	1288
“*Neritina*” *sayana* (Récluz, 1844)	
Sulawesi Is., Indonesia	1306
Flores Is., Indonesia	1248
“*Neritina*” sp.	
Guadalcanal Is., Solomon Is.	915
Santo Is., Vanuatu	663

Table 4-2. Habitat and geological distribution of limnic Neritidae in the Indo-West Pacific. Frequently used junior synonyms are shown under valid names; generic assignment follows the classification in Chapter 2. Occurrence in Japan and two Melanesian countries, Vanuatu and Solomon Islands, are highlighted (●, present; –, absent).

Species	Habitat[*1]	Distribution	Japan (N = 39)	Melanesia (N = 38)
***Neritodryas* Martens, 1869**				
Neritodryas ampullaria (Lesson, 1831)	Stream (F)	Japan to Vanuatu	●	●
= *Neritodryas subsulcata* (Sowerby I, 1836)				
Neritodryas cornea (Linnaeus, 1758)	Stream (F)	Philippines to Vanuatu	–	●
Neritodryas dubia (Gmelin, 1791)	Mangrove (B)	Philippines to Vanuatu	–	●
Neritodryas notabilis Riech, 1935	Stream (F)	PNG[*2] to Vanuatu	–	●
Neritodryas sp. 1	Stream (F)	Babeldaob Is., Palau	–	–
Neritodryas sp. 2	Stream (F)	Babeldaob Is., Palau	–	–
***Neritona* Martens, 1869**				
Neritona granosa (Sowerby, 1825)	Stream (F)	Hawaii Islands	–	–
Neritona labiosa (Sowerby, 1836)	Stream (F)	Phillippines to Melanesia	–	●
***Clithon* Montfort, 1810**				
Clithon castaneus (Hombron & Jaquinot, 1854)	Stream (F)	Indonesia to Samoa	–	–
Clithon chlorostoma (Sowerby I, 1833)	Stream mouth (B)	Samoa and French Polynesia	–	–
= *Clithon dispar* (Pease, 1868)				
Clithon corona (Linnaeus, 1758)	Stream (F)	Japan to Indonesia	●	–
= *Clithon brevispina* (Lamarck, 1822)				
Clithon coronatus (Leach, 1815)	Stream (F)	Southwest Indian Ocean	–	–
Clithon diadema (Récluz, 1841)	Stream (F)	Japan to Vanuatu	●	●
= *Clithon donovani* (Récluz, 1843)				
Clithon elephas (Mabille, 1895)	Stream (F)	Vanuatu[*3]	–	●
Clithon exclamesionis Mabile, 1895	Stream (F)	Guam to Vanuatu	–	●
Clithon faba (Sowerby I, 1836)	Stream mouth (B)	Thailand to Japan and PNG	●	–
Clithon interruptus (Récluz, 1843)	Stream (F)	Japan to Philippines	●	–
Clithon leachii (Récluz, 1841)	Stream mouth (B)	Japan to Philippines	●	–
Clithon navigatorius (Reeve, 1855)	Stream (F)	Australia	–	–
Clithon nouletianus (Gassies, 1863)	Stream mouth (B)	Japan to New Caledonia	●	●
Clithon olivaceus (Récluz, 1843)	Stream (F)	Japan to Vanuatu	●	●
Clithon oualaniensis (Lesson, 1831)	Stream mouth (B)	Thailand to Japan and Vanuatu	●	●
Clithon pauluccianus (Gassies, 1870)	Stream mouth (B)	Japan to New Caledonia	●	●
Clithon peguensis (Blanfold, 1867)	Stream (F)	India to Thailand	–	–
Clithon pritchardi (Dohrn, 1861)	Stream (F)	Fiji[*3]	–	–
Clithon retropictus (Martens, 1878)	Stream (F)	Japan to Philippines	●	–
Clithon rugatus (Récluz, 1842)	Stream (F)	Japan to Solomon Islands	●	●
= *Clithon squarrosus* (Récluz, 1843)				
Clithon siderea (Gould, 1847)	Stream mouth (B)	Philippines to Vanuatu	–	●

Clithon sowerbianus (Récluz, 1843)	Stream mouth (B)	Japan to Indonesia	●	–
Clithon spinosus (Sowerby I, 1825)	Stream (F)	French Polynesia	–	–
Clithon subpunctatus (Récluz, 1844)	Stream (F)	Japan to Guam and Philippines	●	–
Clithon variabilis (Lesson, 1831)	Stream (F)	Pohnpei to French Polynesia	–	●
= *Clithon aspersus* (Sowerby II, 1849)				
= *Clithon recluzianus* (Le Guillou, 1841)				
= *Clithon soulayetanus* (Récluz, 1842)				
Clithon sp. 1	Stream mouth (B)	Taiwan to Vanuatu	–	●
Clithon sp. 2	Stream (F)	Indonesia[*3]	–	–
Clithon sp. 3	Stream (F)	Japan to Philippines	●	–
Clithon sp. 4	Stream (F)	Indonesia[*3]	–	–
Clithon sp. 5	Stream (F)	Philippines to Fiji	–	●
Clithon sp. 6	Stream (F)	Indonesia to Vanuatu	–	●
Clithon sp. 7	Stream (F)	Thailand to Indonesia	–	–
***Vittina* Baker, 1923**				
Vittina communis (Quoy & Gaimard, 1834)	Stream mouth (B)	Japan to Samoa	●	●
= *Vittina royssiana* (Récluz, 1841)				
Vittina cumingiana (Récluz, 1842)	Stream mouth (B)	Japan to Guam	●	–
Vittina cuvieriana (Récluz, 1841)	Stream (F)	PNG to Vanuatu	–	●
= *Vittina adumbrata* (Reeve, 1855)				
Vittina gagates (Lamarck, 1822)	Stream (F)	Thailand to Japan and Fiji	●	●
= *Vittina variegata* (Lesson, 1831)				
Vittina lugubris (Lamarck, 1822)	Estuary (B)	Thailand to Japan and FP[*4]	●	●
= *Vittina coromandeliana* (Sowerby I, 1836)				
Vittina serrulata (Récluz, 1842)	Stream (F)	Indonesia	–	–
Vittina turrita (Gmellin, 1791)	Estuary (B)	Malaysia to Indonesia	–	–
Vittina zigzag (Lamarck, 1822)	Stream (F)	Southwest Indian Oceacn	–	–
***Laodia* Gray, 1868**				
Laodia sanguisuga (Reeve, 1856)	Stream (F)	Fiji and Samoa	–	–
Laodia cumingiana (Récluz, 1843)	Stream (F)	Japan to Indonesia	●	–
***Neritina* Lamarck, 1816**				
Neritina asperulata (Récluz, 1843)	Stream (F)	Japan to Vanuatu	●	●
Neritina canalis Sowerby I, 1825	Stream (F)	Guam to French Polynesia	–	●
Neritina delestennei Récluz, 1853	Stream (F)	Mauritius to Japan	●	–
Neritina iris Mousson, 1849	Stream (F)	Japan to Australia	●	●
Neritina luzonica (Récluz, 1841)	Stream (F)	Philippines to PNG	–	–
Neritina petitii (Récluz, 1841)	Stream (F)	Japan to Fiji	●	●
Neritina powisiana (Récluz, 1843)	Stream (F)	PNG to Vanuatu	–	●
Neritina pulligera (Linnaeus, 1767)	Stream (F)	Japan to Samoa	●	●
Neritina sp. 1	Stream (F)	Indonesia[*3]	–	–
Neritina sp. 2	Stream (F)	Japan to Indonesia	●	–
Neritina sp. 3	Stream (F)	Malaysia[*3]	–	–
Neritina sp. 4	Stream (F)	Thailand[*3]	–	–
Neritina sp. 5	Stream (F)	Australia[*3]	–	–
***Dostia* Gray, 1842**				
Dostia bicanaliculata (Récluz, 1843)	Estuary (B)	Thailand to Japan and PNG	●	–

Dostia cariosa (Gray, 1827)	Stream mouth (B)	Hawaiian Islands	–	–
Dostia dilatata (Broderip, 1833)	Stream mouth (B)	Japan to French Polynesia	●	●
Dostia florida (Récluz, 1850)	Stream mouth (B)	Solomon Islands and Vanuatu	–	●
Dostia guamensis (Quoy & Gaimard, 1834)	Stream mouth (B)	Mauritius to French Polynesia	●	–
Dostia mauritii (Sowerby, 1849)	Stream mouth (B)	Southwest Indian Ocean	–	–
Dostia melanostoma (Troschel, 1837)	Estuary (B)	Thailand and Malaysia	–	–
Dostia siquijorensis (Récluz, 1843)	Stream mouth (B)	India to French Polynesia	●	●
Dostia subalata (Souleyet, 1842)	Estuary (B)	Sri Lanka to Japan and Samoa	●	●
Dostia violacea (Gmelin, 1791)	Estuary (B)	Thailand to Australia	–	–
Dostia sp. 1	Estuary (B)	Korea and Japan	●	–
Dostia sp. 2	Estuary (B)	PNG to Australia	–	–
Dostia sp. 3	Estuary (B)	Japan[*3]	●	–
***Septaria* Férrusac, 1807**				
Septaria auriculata (Lamarck, 1816)	Stream (F)	Mauritius to Hawaii and FP[*4]	●	●
Septaria clypeolum (Récluz, 1843)	Estuary (B)	Japan to Australia	●	–
Septaria lecontei (Récluz, 1853)	Estuary (B)	PNG to Australia	–	–
Septaria porcellana (Linnaeus, 1758)	Stream (F)	Mauritius to Japan and Vanuatu	●	●
Septaria spiralis (Reeve, 1855)	Estuary (B)	Japan to Vanuatu	●	●
Septaria suffreni (Récluz, 1842)	Stream (F)	Fiji and Samoa	–	–
Septaria tessellata (Lamarck, 1816) = *Septaria lineata* (Lamarck, 1816)	Estuary (B)	India to Japan Vanuatu	●	●
Septaria sp.	Estuary (B)	Fiji[*3]	–	–
New genus 1				
“Neritina” bruguieri (Récluz, 1841)	Stream (F)	Japan to Vanuatu	●	●
New genus 2				
“Neritina” haemastoma (Martens, 1878)	Stream (F)	Philippines to Indonesia	–	–
“Neritina” sayana (Récluz, 1844)	Stream (F)	Philippines to Indonesia	–	–
“Neritina” sp.	Stream (F)	Solomon Islands and Vanuatu	–	●

[*1] Freshwater (F) or brackish (B). [*2] Papua New Guinea. [*3] Available data apparently insufficient for documenting distribution range. [*4] French Polynesia.

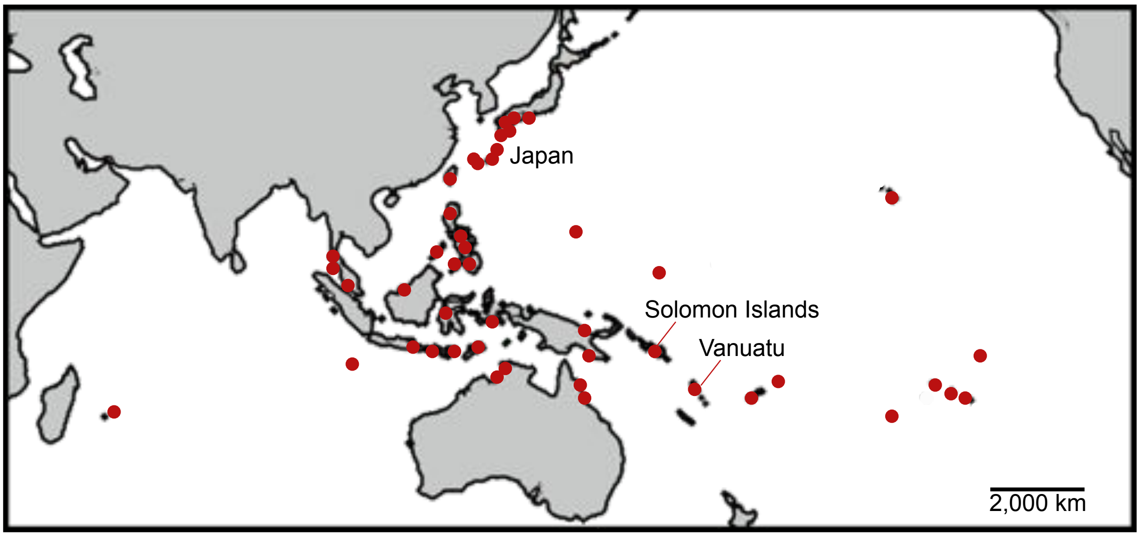
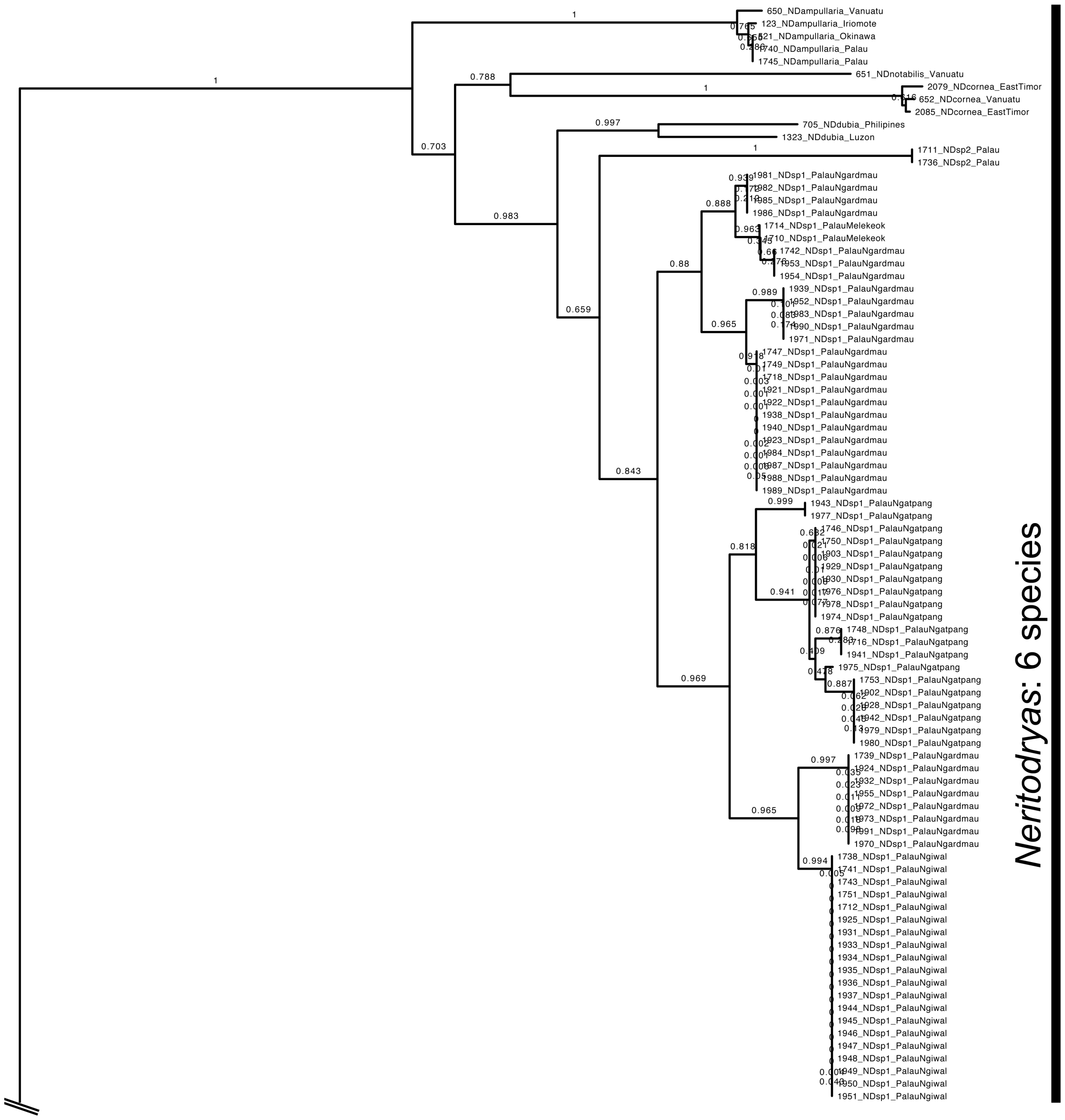


Figure 4-1. Collection sites of limnic neritid specimens used in this study. Most extensive sampling was made in southern Japan and two Melanesian countries (Solomon Islands and Vanuatu), which are separated by approximate distances of 5,000–6,000 km.



continued

Figure 4-2 (*Neritodryas*). Neighbor-Joining (NJ) phylogeny of limnic Neritidae from the Indo-West Pacific based on partial COI sequences. Numbers on branches denote NJ bootstrap values.

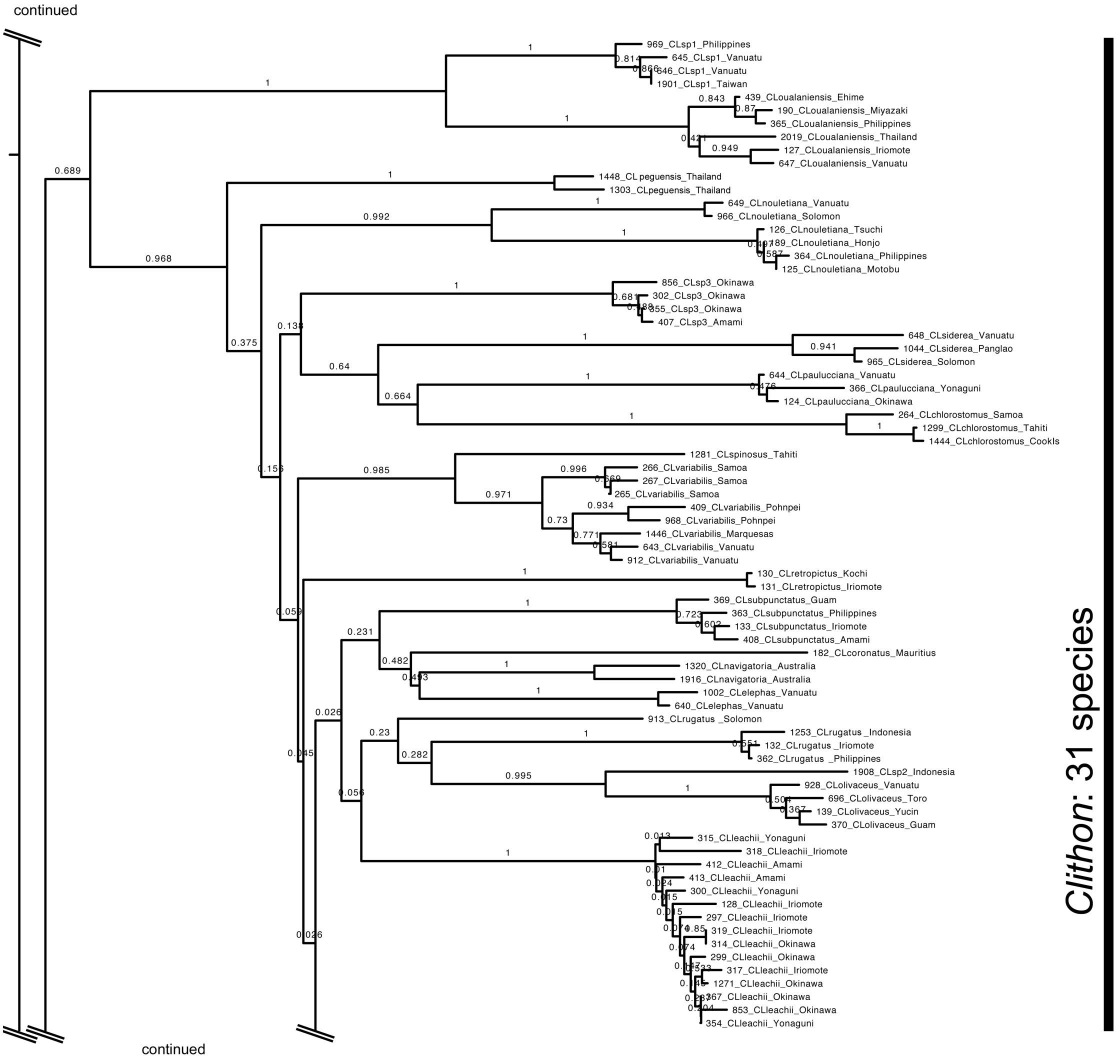


Figure 4-2 (continued; part of *Clithon*).

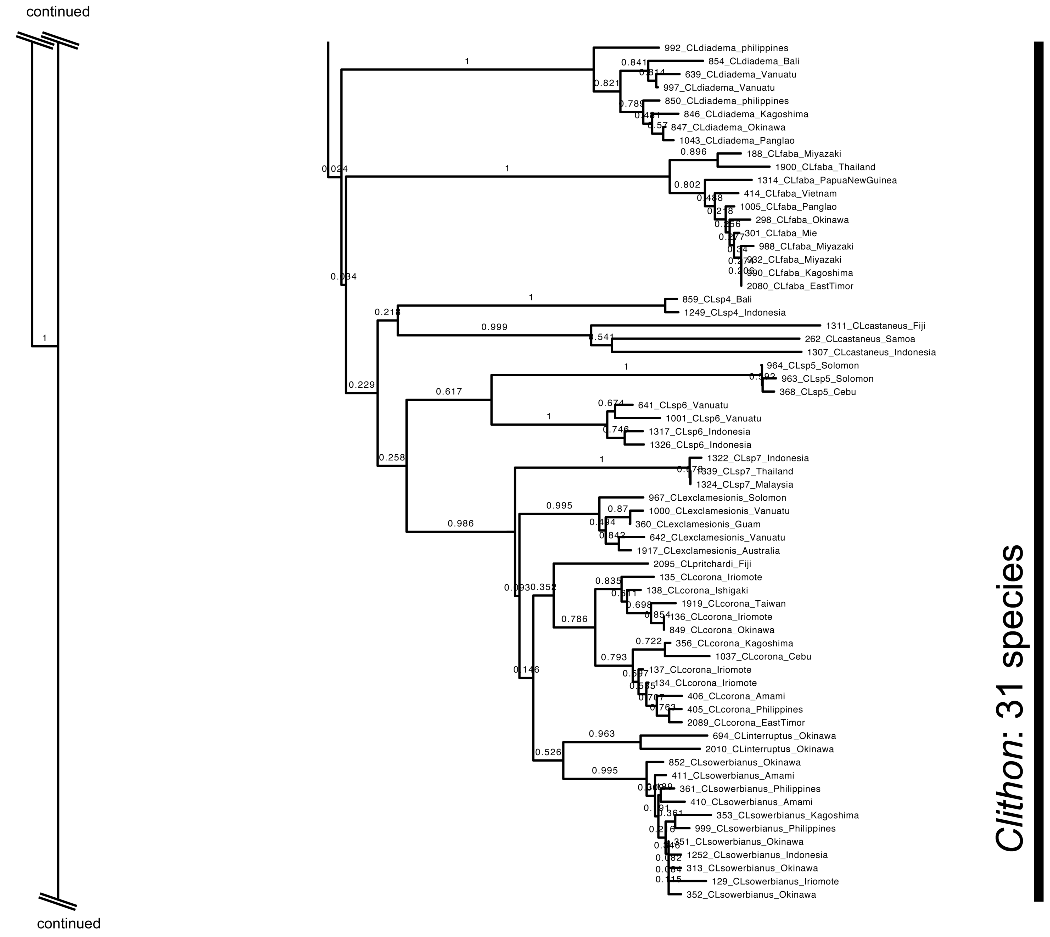


Figure 4-2 (continued; part of *Clithon*).

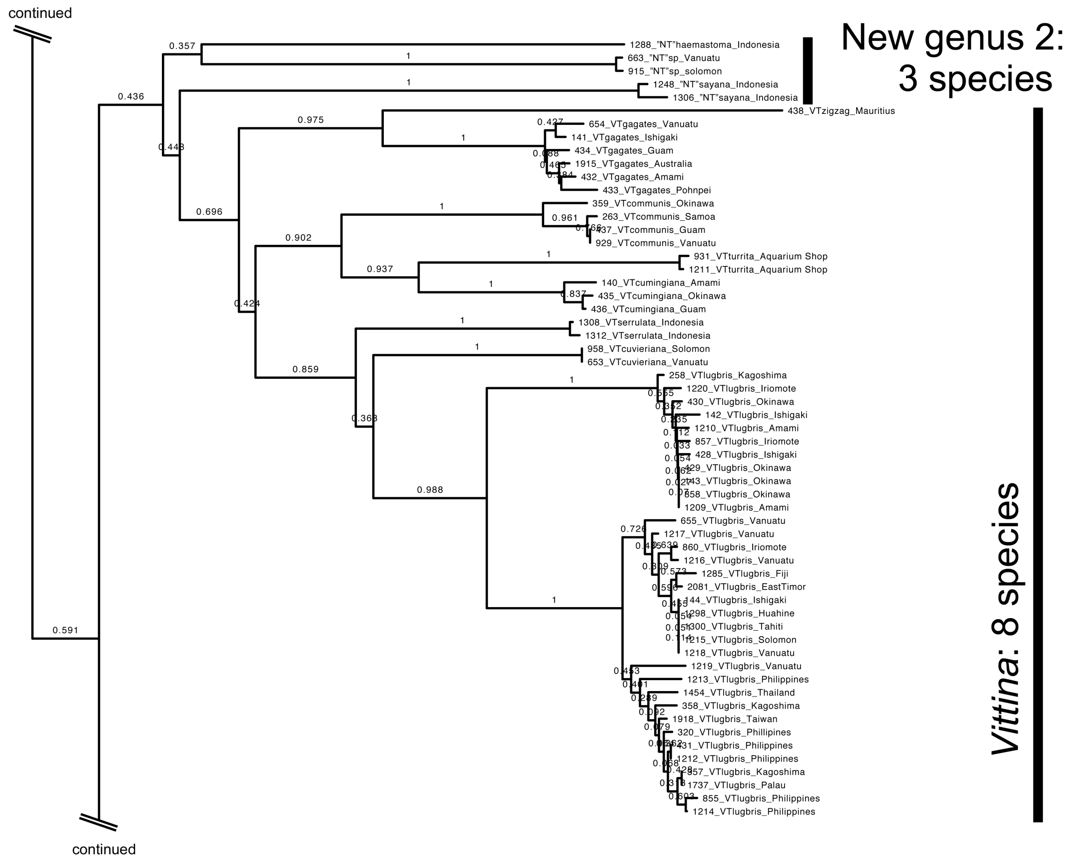


Figure 4-2 (continued; New genus 2 and *Vittina*).

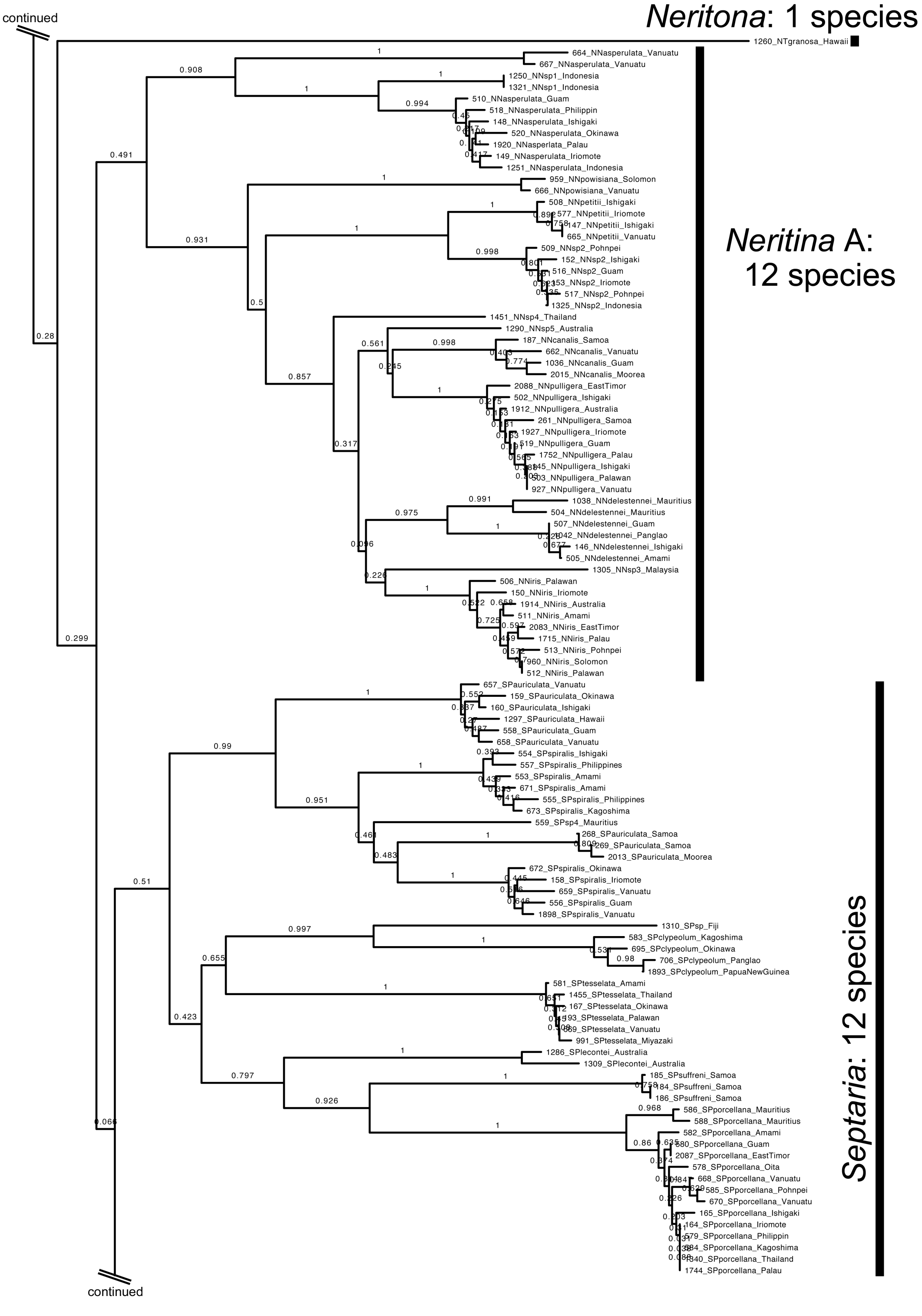


Figure 4-2 (continued; *Neritona*, *Septaria* and part of *Neritina*).

Figure 4-2 (continued; New genus 1, *Laodia*, *Dostia* and part of *Neritina*).

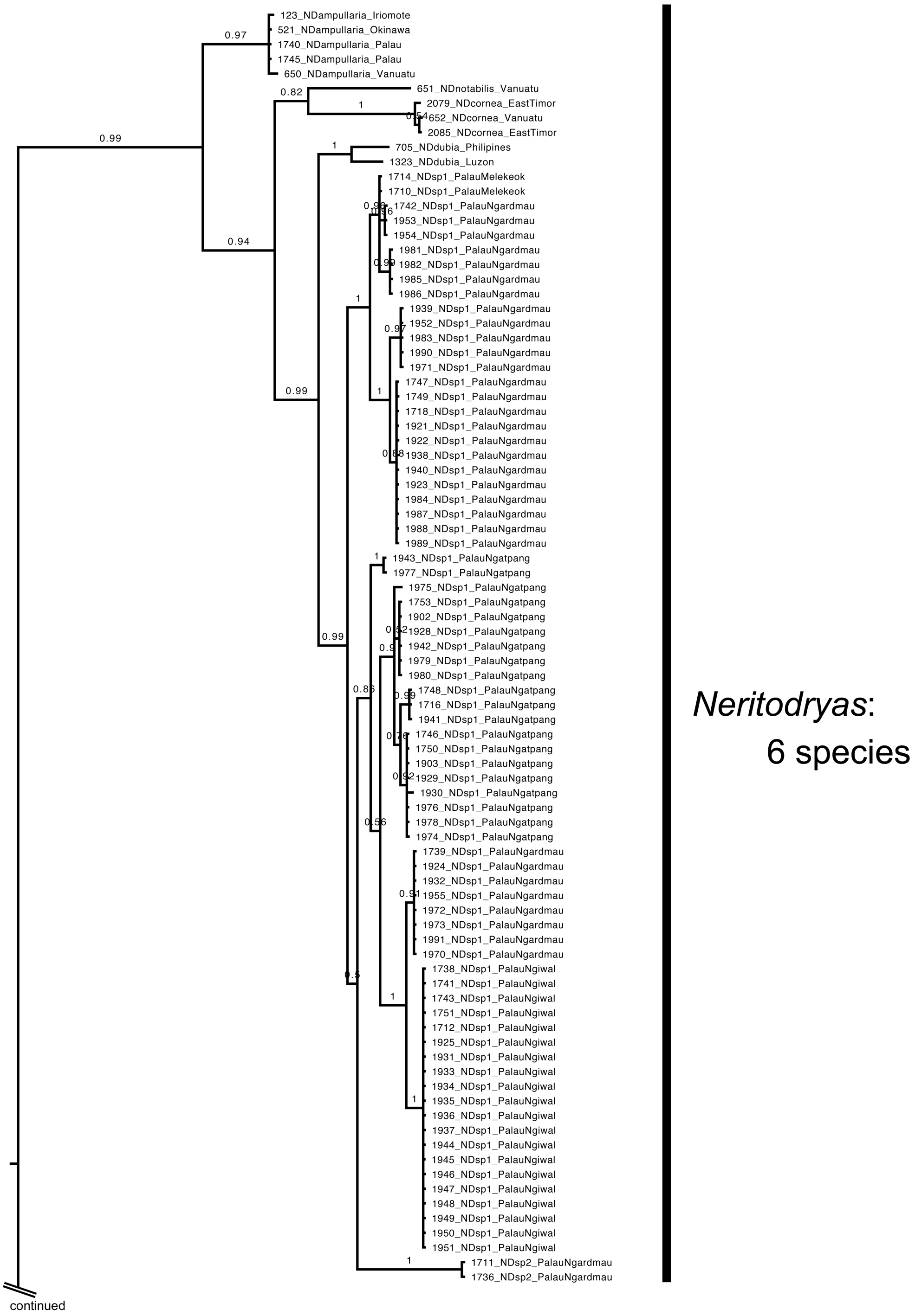


Figure 4-3 (*Neritodryas*). Bayesian phylogeny of limnic Neritidae from the Indo-West Pacific based on partial COI sequences. Numbers on branches denote posterior probabilities.

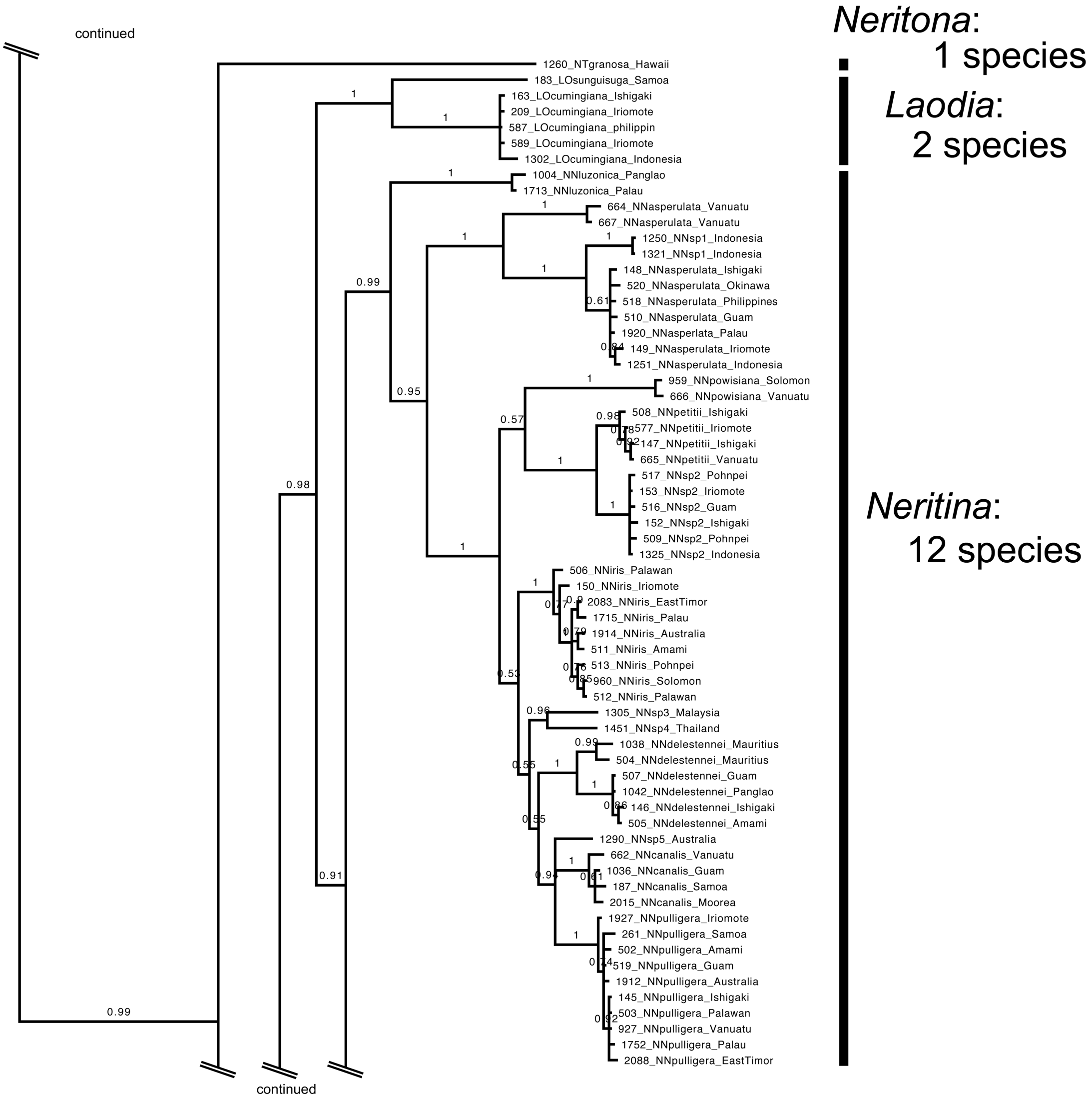


Figure 4-3 (continued: *Neritona*, *Laodia* and *Neritina*).

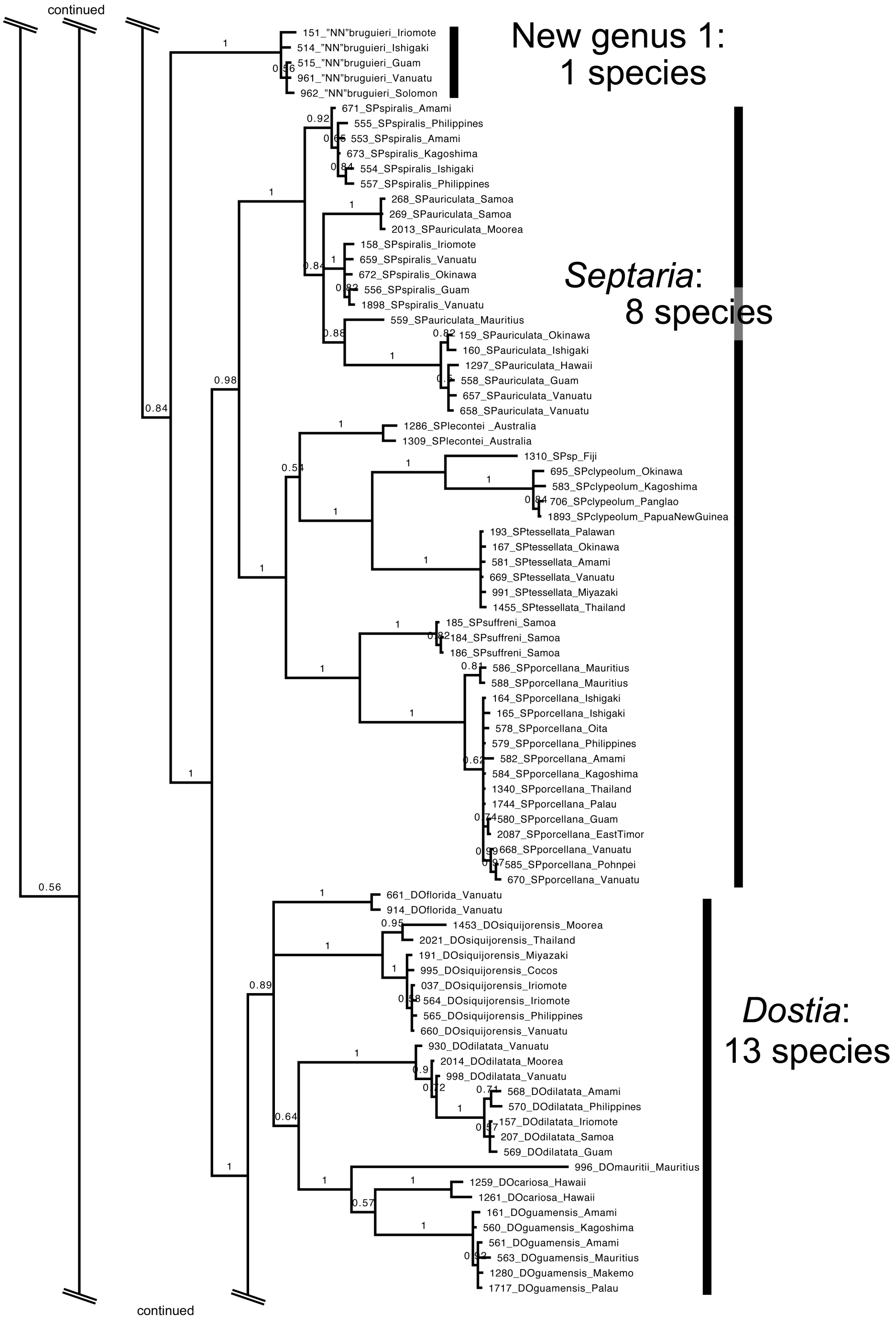


Figure 4-3 (continued: New genus 1, *Septaria* and part of *Dostia*).

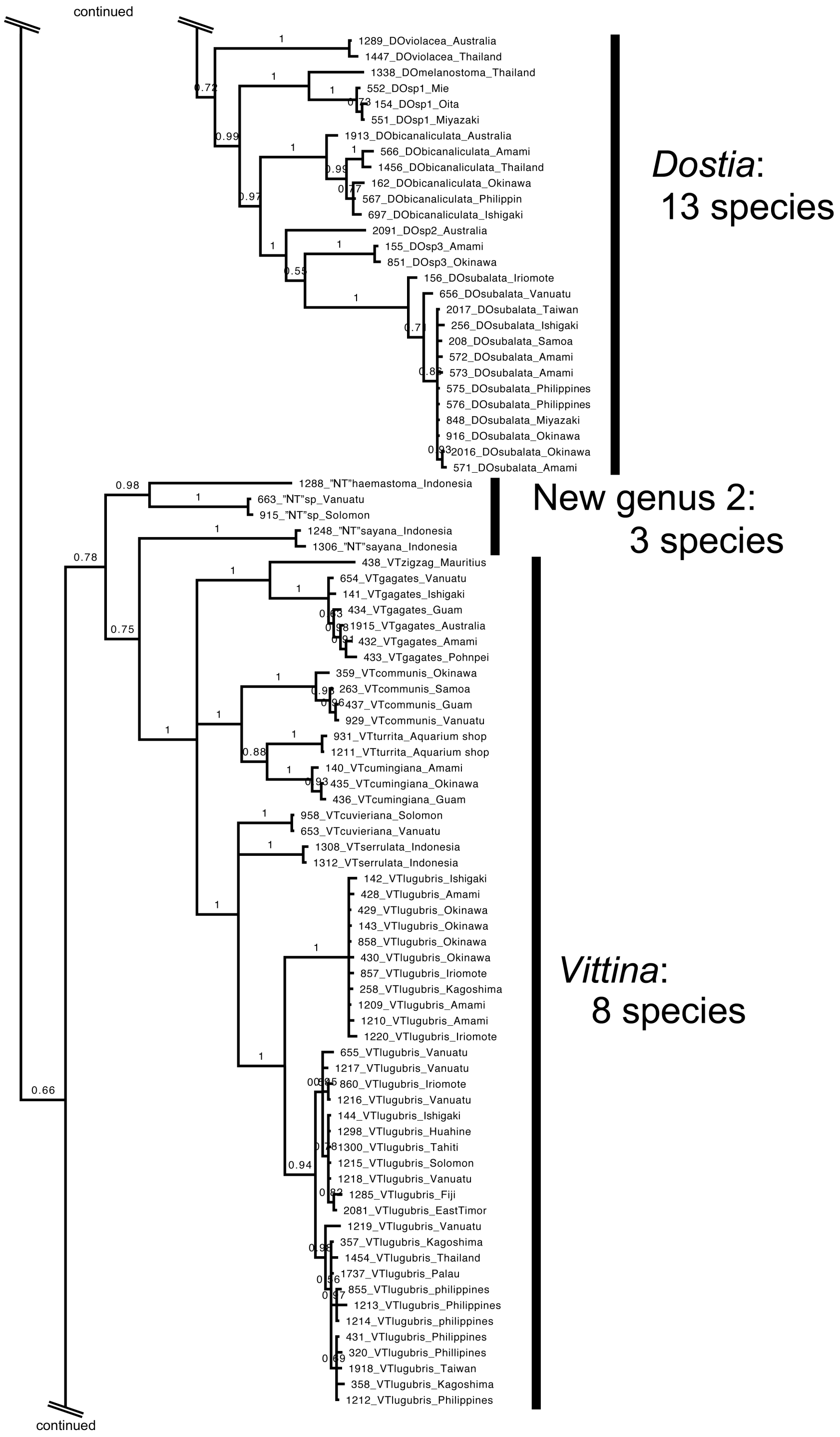


Figure 4-3 (continued: New genus 2, *Vittina and* part of *Dostia*).

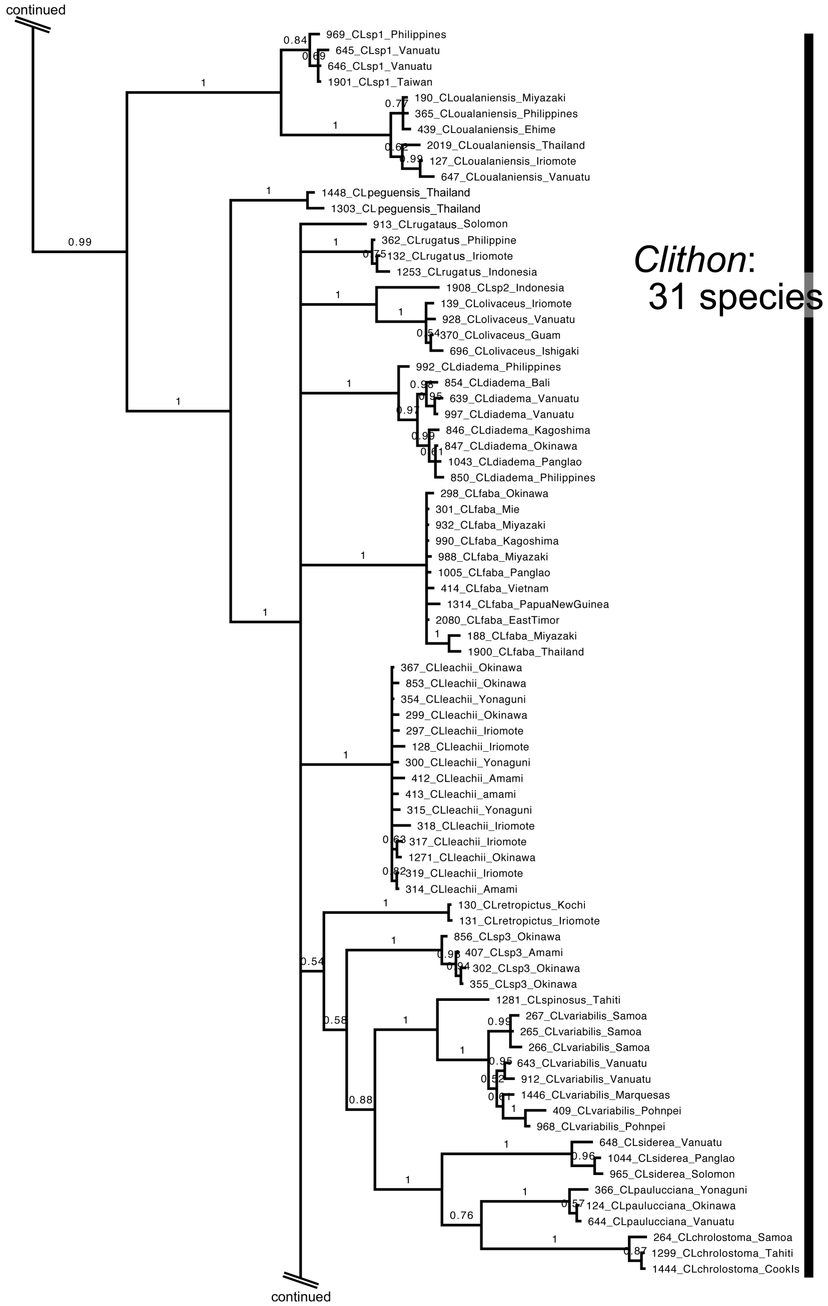


Figure 4-3 (continued: part of *Clithon*).

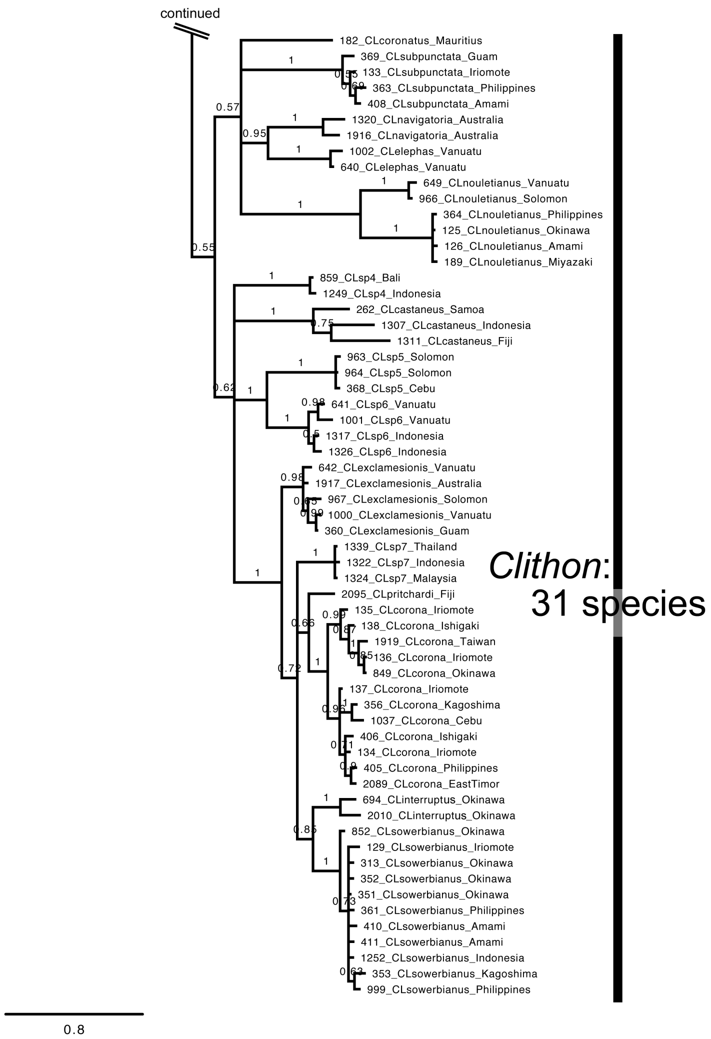


Figure 4-3 (continued: part of *Clithon*).

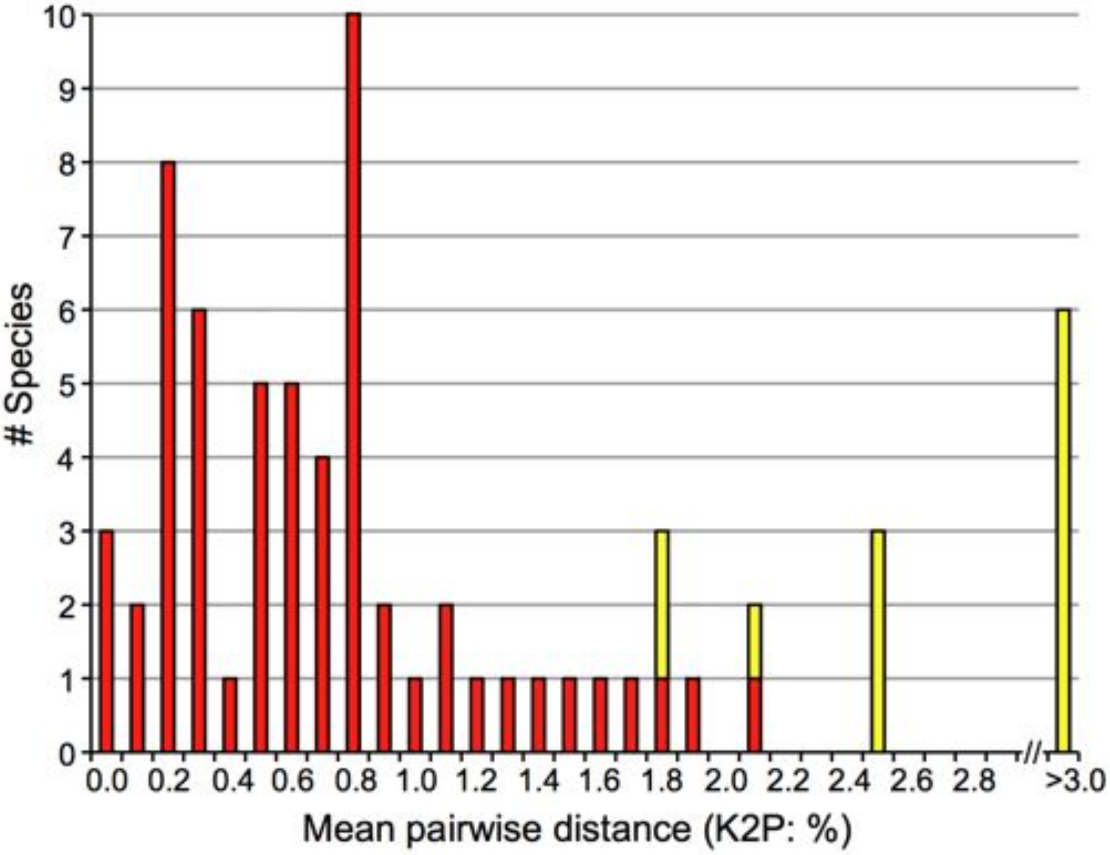


Figure 4-4. Mean Kimura 2-parameter (K2P) genetic distances of COI gene within 70 limnic neritid species recognized and represented by more than one sequence in this study. Red and yellow bars denote species with a single and multiple evolutionary significant units (ESUs), respectively.

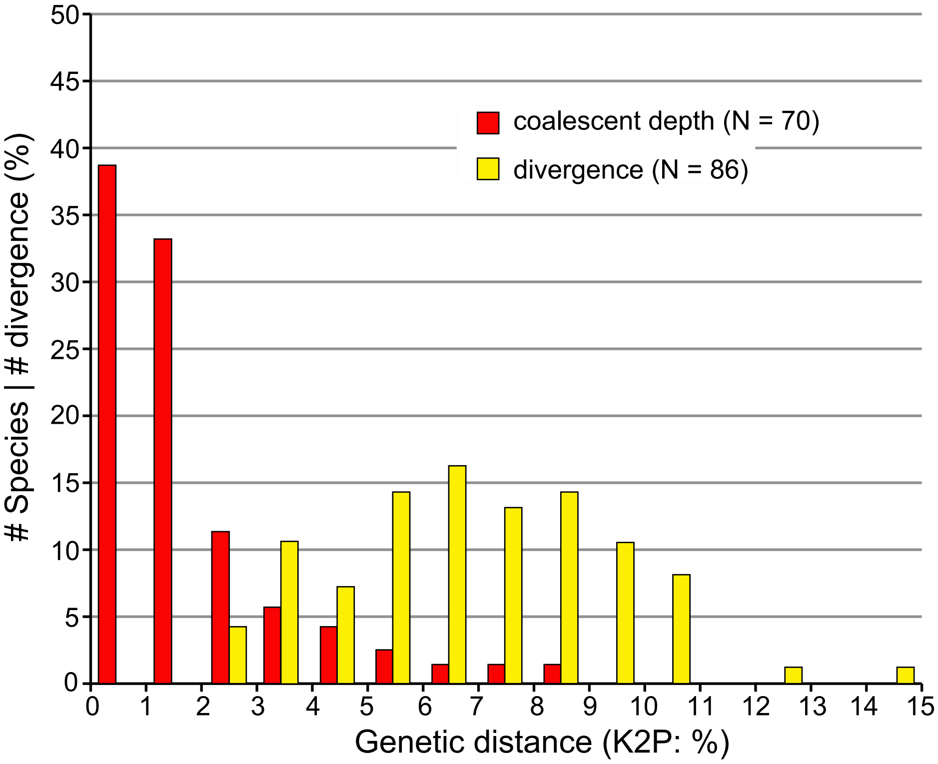


Figure 4-5. Relative distributions of intraspecific variability (coalescent depth: red) and minimum divergence between the closest species (yellow) of COI gene for limnic neritids in the Indo-West Pacific.

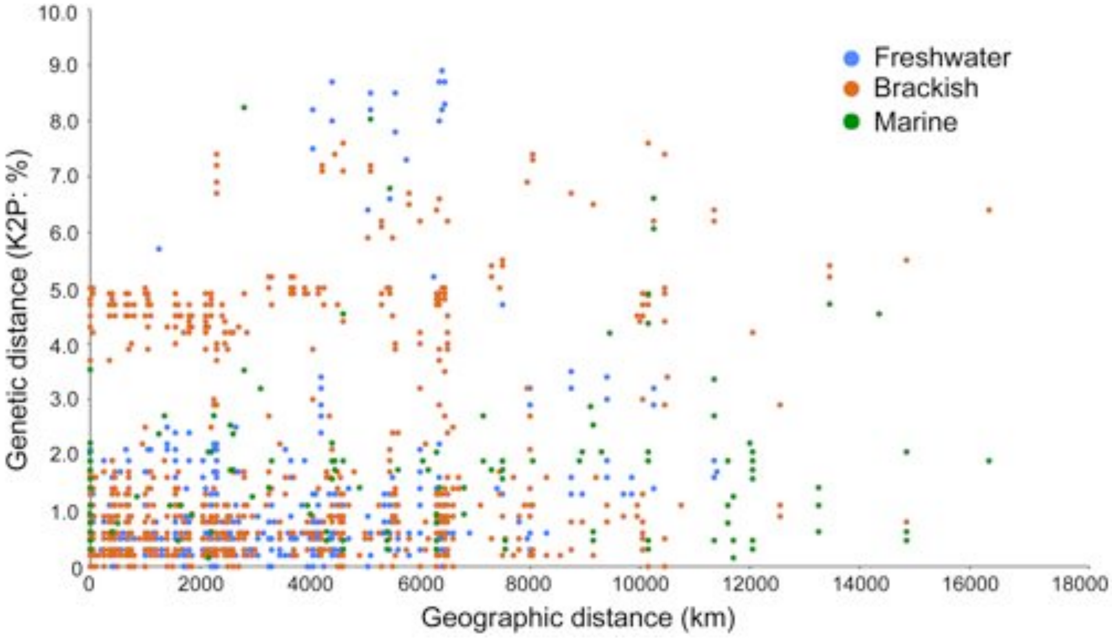


Figure 4-6. Genetic and geographic distances between intraspecific individuals of the Indo-West Pacific Neritidae with planktotrophic early development, shown for three habitat groups of adults (freshwater, brackish and marine). Genetic distance is derived from pairwise comparison of COI sequences under Kimura 2-parameter (K2P) model. Geographic distance is shown in kilometers between collection sites via a straight line.

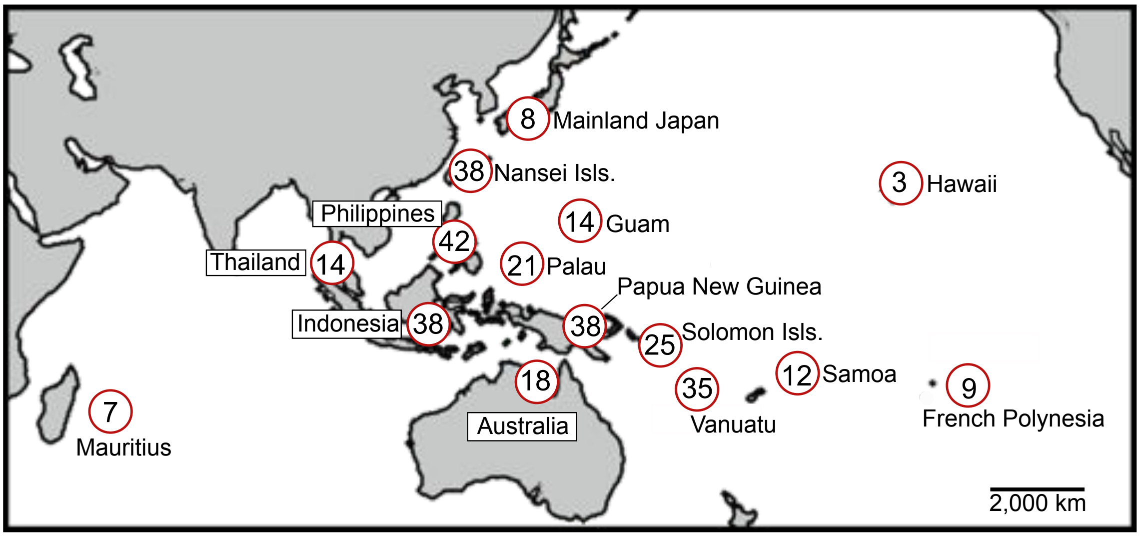


Figure 4-7. Species richness of freshwater and brackish-water Neritidae in the Indo-West Pacific as indicated by total number of species within each of 15 regions.

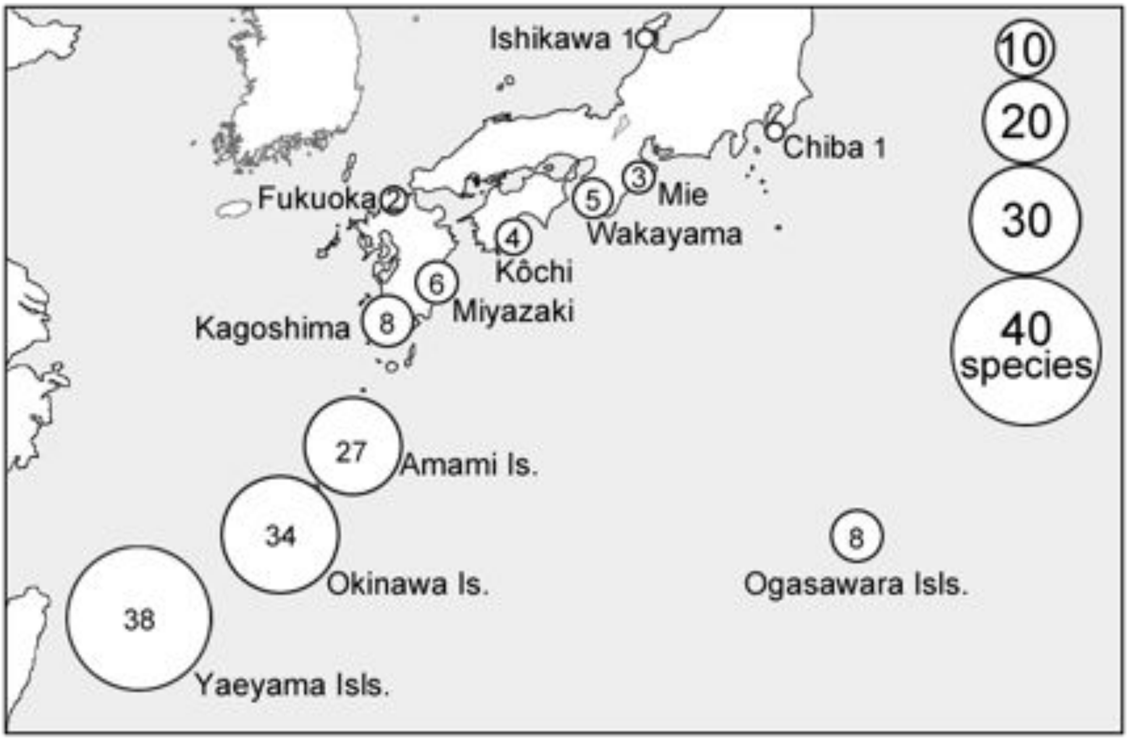


Figure 4-8. Species richness of freshwater and brackish-water Neritidae in Japan as indicated by total number of species that naturally occur within each prefecture, island or island group.

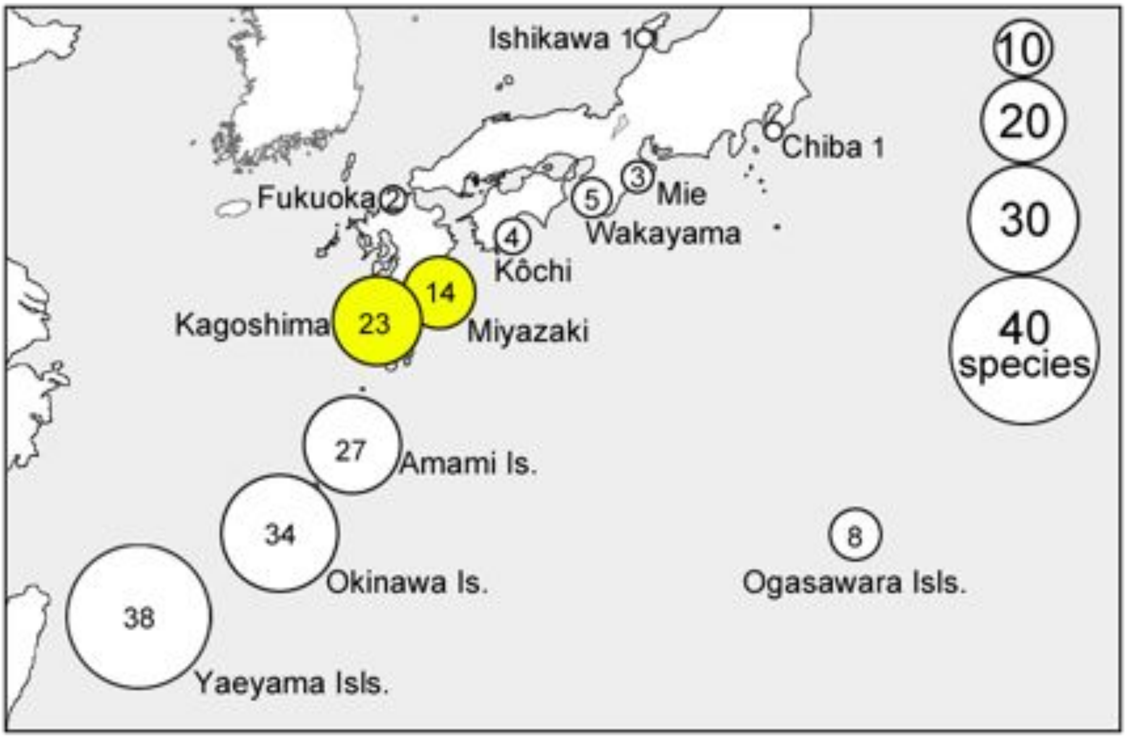


Figure 4-9. Species richness of freshwater and brackish-water Neritidae in Japan as indicated by total number of species within each prefecture, island or island group. Note that numbers for Miyazaki and Kagoshima include species occur only in warm drainages from a hot spring or an eel farm, respectively.

Chapter 5: General Discussion

For the present thesis, I studied the natural history of limnic gastropods of the family Neritidae as a model group for understanding the role and importance of amphidromy in the tropical and subtropical island streams. On the basis of the results in this study, I discuss the formation and maintenance mechanisms and conservation of diversity in the island stream ecosystems, which are most often dominated by amphidromous fauna.

5-1: Formation and maintenance mechanisms of island stream fauna

In tropical and subtropical regions in the Indo-Pacific, numerous continental and oceanic islands exist and they often support streams with relatively high gradients and short distances from headwaters to stream mouth (McDowall 2007). Such streams are too short, thus in tropics they become raging torrents during the rainy season, while during drought they may be dried up. These environmental conditions present a serious problem for primary freshwater animals that spend the whole lives in streams and rivers, even if they could somehow colonize the islands by rare, stochastic dispersal events (Strong et al. 2008; McDowall 2010). Amphidromous animals, on the other hand, flourish and are very abundant on oceanic islands in the numbers of both species and individuals. Their hatched larvae are swept downstream to the ocean where the swimming larvae feed on phytoplankton and grow up in the pelagic period of a few or several months (Holthuis 1995; Kano et al. 2011). The females of most amphidromous species reproduce a larger number of smaller eggs than those of non-diadromous, direct developing species do (McDowall 2010; Bauer 2011). These reproductive traits (r-strategy) often give an advantage in heterogeneous or unstable environments (e.g. Strathmann 1985). The combination of the long larval life and dispersal by ocean currents and their reproductive strategy involving the spawning of a large number of small eggs makes amphidromous animals potentially capable of expanding new habitats in very distant regions (McDowall 2007).

Freshwater gastropods of the family Neritidae (superorder Neritimorpha) are one of the most dominant and diverse animal groups in the tropical and subtropical streams (Kano et al. 2011). Shell-bearing gastropods including neritids have many advantages in understanding various aspects of life history strategies and diversity, due to the appositional growth of the exoskeleton that records the ontogenetic history of each individual (Jablonski and Lutz 1983). Their early developmental mode, i.e. either planktotrophic or non-planktotrophic, can be inferred from the form of opercular nucleus, which is retained in the adult operculum (Kano 2006). In the Chapter 3, I observed the nucleus for 47 species of the limnic Neritidae as well as 27 of marine confamilial species and 14 other aquatic neritimorph taxa and verified that they all have planktotrophic larvae. Only four species among limnic neritids investigated and probably a few others (Holthuis 1995), all of which are distributed in the tropics, have benthic development and spend the whole life in the freshwater environment (Chapters 3 and 4). I also found that size at various ontogenetic stages of neritimorphs could be rigorously estimated by measuring the adult opercula, and with this unique feature I generated the largest data set so far on larval settlement sizes within a group of marine invertebrates that recruit into different post-metamorphic habitats (Fig. 3-3). Most interestingly, parallel evolution towards smaller sizes was shown to occur exclusively in four independent clades (two living and two extinct) of amphidromous snails with a marine larval period followed by a limnic adult phase. The smaller settlement size may possibly reduce the risk of being wafted away from the estuaries of their natal streams through less time achieving metamorphic competence (Fig. 3-5).

Does such smaller metamorphic sizes regulate and limit the dispersal ability of amphidromous neritids across the ocean? In the Chapter 4, I assessed the level and consequence of their larval dispersal by the comparison of genetic and geographic distances between individuals within species. The results show that most species of amphidromous neritids exhibit relatively to very small genetic diversity despite their wide geographic ranges (Fig. 4-6). Conspecific individuals sometimes share the same haplotypes of the mitochondrial COI gene over several thousands of kilometers (Table 4-2; Fig. 4-2), corroborating results from previous population genetic studies for smaller geographic areas (Meyrs et al. 2000; Crandall et al. 2010). Such homogeneity and shared haplotypes suggest gene flow between far distant populations due to their high dispersal ability in ocean currents (Fig. 4-6). Presumably, the ability to make occasional long-distance trips is retained by the presence of a sufficiently long delay period, which seems to obscure the possible correlation between settlement size and geographic distribution range of neritimorph species, both fully marine and amphidromous (Fig. 3-6).

High dispersal capability of amphidromous neritids was also clearly seen in their high faunistic homogeneity across wide areas in the western Pacific Ocean. In general, larval dispersal is among the most important determinants for the geographic distribution range of benthic marine animal species (Paulay & Meyer 2006; Weersing & Toonen 2009). The species compositions of freshwater neritids were compared between Japan and two eastern Melanesian countries, namely the Republic of Vanuatu and Solomon Islands, which are approximately 5,000–6,000 km away across the equator and equatorial ocean currents. Extensive sampling and documentation of the neritid faunas demonstrated that the limnic environments in the two regions harbor comparable species diversity and share a large proportion of taxa, representing nearly

60% of richness in both regions (Table 4-2; Fig. 4-7). Such similarity of species compositions in the remote areas and lack of clear genetic differentiation in most of the shared species provide further evidence for the high dispersal capability of amphidromous neritids, regardless of their limnic adult habitats. These neritids produce a large number of small-sized eggs (Holthuis 1995; Kano et al. 2011). The rate of larval transport to new habitats can be significantly enhanced by the presence of such a high fecundity. The mechanisms of amphidromy thus allow larval dispersal and (re)colonization of streams in remote islands, where habitats may be ephemeral and there is a risk of local extirpation (McDowall 2010). This way, amphidromy plays a key ecological role and is the most prevalent life history strategy in low-latitude island streams (McDowall 2007, 2010; Kano et al. 2011; Watanabe et al. 2013).

Clearly, amphidromy has evolved many times independently in various vertebrate and invertebrate lineages (Table 1-1). In the Chapter 2, I reconstructed Bayesian and maximum-likelihood phylogenetic trees based on a total of ca. 4 kbp DNA sequences from three mitochondrial and one nuclear genes in order to explore the relationships among families, subfamilies and genera in the extant Neritoidea (Fig. 2-7). The likelihood reconstruction of ancestral states suggests that the limnic lineages have evolved independently in the Neritiliidae and Neritidae from fully marine ancestors (Fig. 2-9). Their independent invasion of the stream habitat, while retaining planktotrophic early development, clearly indicates parallel acquisition of the amphidromous life cycle. These invasions occurred in the middle or late Cretaceous (Fig. 2-8), while three more such habitat shifts, again accomplished by amphidromy, seem plausible for the extinct lineages of the Neritimorpha since the Jurassic time (Chapter 3). The evolutionary scenarios for the shrimps family Atyidae also suggest that they have invaded and adapted to freshwater habitats in the mid Cretaceous or perhaps earlier (Rintelen et al. 2012). Because of the elevated atmospheric CO_2 and CH_4 concentration, the global climate during the Cretaceous was warm and equable, and ocean-continent temperature gradients were lower than today (Hay 2008). Thus, amphidromous animals may have flourished in low-latitude island streams since at least the late Cretaceous, as seen in today's stream faunas in the tropical Indo-West Pacific. The intensities of competition as well as predation in upstream freshwater environments may be lower than in most marine environments; this is particularly the case on islands due to the inaccessibility for non-diadromous competitors and predators (Holthuis 1995; McDowall 2010). The multiple invasions of freshwater by different lineages may have been pushed not only by vacant ecological niches but also by escape from marine competition and predation, which have been extensive since the Mesozoic Marine Revolution in the Jurassic and Cretaceous eras (Vermeij 1993).

5-2: Contributions to taxonomy and conservation of limnic neritids

Recognizing species is the most important aspect when considering conservation targets (Mace 2004). However, our taxonomic knowledge in many parts of the tropics is inadequate to document species diversity and extinctions, and widespread undetected extinctions of inconspicuous species have already taken place (Harrison & Stiassny 1999; Stiassny 2002; Dudgeon et al. 2006). Amphidromous taxa are the most important components of faunal communities in low-latitude island streams, and yet they are no exception where fundamental studies on their taxonomy and ecology are still badly needed (McDowall 2007, 2010; Kano et al. 2011). Most of previous taxonomic works suffered from insufficient sampling, enormous species richness and difficulties in assessing the homology and validity of morphological characters (e.g. Kano & Kase 2003; Smith et al. 2003; Page et al. 2005; Cook et al. 2008; Kano et al. 2011; Akihito et al. 2013). In the Chapter 4, I revised the species classification, diversity and distributions of the limnic Neritidae in the tropical to subtropical Indo-West Pacific and recognized 87 such species through meticulous investigation on morphological and genetic (COI sequence) data. Many species and ESUs are newly recognized or defined, and this new systematics indeed revealed that species richness in each region has been badly underestimated in most, if not all, previous studies (e.g. Starmühlner 1976; Haynes 1993, 2000; Tsuchiya 2000). The combined molecular and morphological approach utilized in this study is efficient and effective for accurate identification and for the understanding of their geographic and ecological distributions, which are vitally needed for the establishment of the management plan for species diversity.

Many amphidromous species have been identified as conservation priorities because threats to these habitats continue to grow with economic development in tropical to subtropical regions (e.g. IUCN 1994, 2001; Ministry of The Environment, Japan 2003, 2005, 2012; Okinawa Prefecture 2005; Japanese Association of Benthology 2012). However, the risk of extinction for amphidromous species such as most freshwater neritids, which are widely distributed in the low-latitude islands of the Indo-West Pacific (Chapter 4), may be lower than that for narrowly distributed endemic species with benthic development. In the Red Data Book of Kagoshima Prefecture (2003), for example, many of the species were ranked as critically endangered, probably based on a preconceived idea that the southwestern subtropical islands of Amami harbor isolated, endemic neritid faunas without the marine larval dispersal. On the other hand, the habitat characteristics of the adult are limited to pristine stream environments in certain taxa. For example, *Neritodryas ampullaria* lives only in uppermost stream habitats near headwaters within dense forest vegetation (Kano et al. 2011) and their recent occurrences are restricted to a limited number of localities in Japan (Ministry of The Environment 2012). Such species seem to represent a more important component in biodiversity conservation than other amphidromous species in open streams, because forest vegetation and stream environments there are more likely to suffer from the impact of human activities (Van der Velde et al. 2007).

5-3: Future perspectives

This study provides the fundamental information on the taxonomy, evolution and ecology of limnic neritids. The knowledge of the natural history of amphidromous species will contribute for deeper understanding of island stream ecosystems predominated by these animals. Summary of the compiled locality data for limnic neritids reveals that species richness peaks in the Coral Triangle, a region bounded by the Philippines, Indonesia and Papua New Guinea (Fig. 4-7). However, taxonomic attempt involving extensive filed sampling and combined molecular and morphological analyses could not be made for East Malaysia, southern part of the Philippines and Indonesia. Future studies are clearly needed to clarify the species composition of the limnic Neritidae in each region and more new taxa will continue to be discovered, particularly in these least investigated. The formal description of the new genera and species also composes an important future procedure for the proper documentation of diversity in the limnic Neritidae.

Another promising application of the present finding is to study the larval behavior and dispersal of amphidromous species of the Neritidae in the field, which to date have been inferred from larval rearing, comparison of spawning times and settlement dates, and genetic population analyses. Needless to say, information on larval dynamics and dispersal in the ocean is vitally important for understanding the life cycles of amphidromous animals. However, the collection of planktonic larvae has never been reported for amphidromous invertebrate species in the ocean beyond brackish river mouths, probably because of our particularly poor knowledge on their larval morphology (e.g. Kikkawa et al. 1995; Nakahara et al. 2007). Settlement size can be used as an identification trait for neritimorph larvae, particularly to facilitate the screening of specimens for DNA barcoding (Garland & Zimmer 2002; Barber & Boyce 2006; Chapter 3).

Tropical and subtropical island biogeography has provided many elegant examples of the evolutionary and ecological mechanisms involved in generating biodiversity, including geological processes and colonization and isolation (Agnarsson & Kuntner 2012). As mentioned earlier, stream ecosystems on such low-latitude islands support high species richness and diversity of amphidromous species (McDowall 2004; Hayashi 2007). At a smaller scale, a different set of species occupies a different type of microhabitats in a short stretch of rivers (Kano et al. 2011). Yet, several species commonly occupy exactly the same type of microhabitat in the same stream, and the surprisingly high species diversity of limnic nerites cannot be solely explained by resource partitioning (Kano et al. 2011). In general, the presence of disturbance prevents competitive equilibrium in natural community, so that sympatric diversity is increased in the community (Krebs 2001). Seasonal natural disturbances are characteristic of tropical streams, so that the extinction or decrease of local population may happen frequently over evolutionary and ecological timescales. On the other hand, the presence of numerous larvae in the sea seems to allow them to reoccupy in vacant habitats (see above). This combination of natural disturbances and abundant larval recruitment may result in the high sympatric and syntopic diversity of amphidromous species. However, the biodiversity studies for tropical island stream ecosystems have suffered from absence or scarcity of fundamental ecological, behavioral and environmental studies of invertebrate species (e.g. Dudgeon et al. 2006). Further accumulation of ecological data on the freshwater stream animals on low-latitude islands, which has been greatly enabled for the Neritidae by the present study, is needed for evaluating the above hypothesis on the driving and maintenance mechanisms of the high species diversity.

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Appendix 1.

Specimens of limnic Neritidae from Indo-West Pacific, used for species taxonomy and DNA sequencing in Chapter 4

Numbers, place names and measured values under specimens denote DNA No. (#), collected location of specimen and maximum shell diameter (mm), respectively.

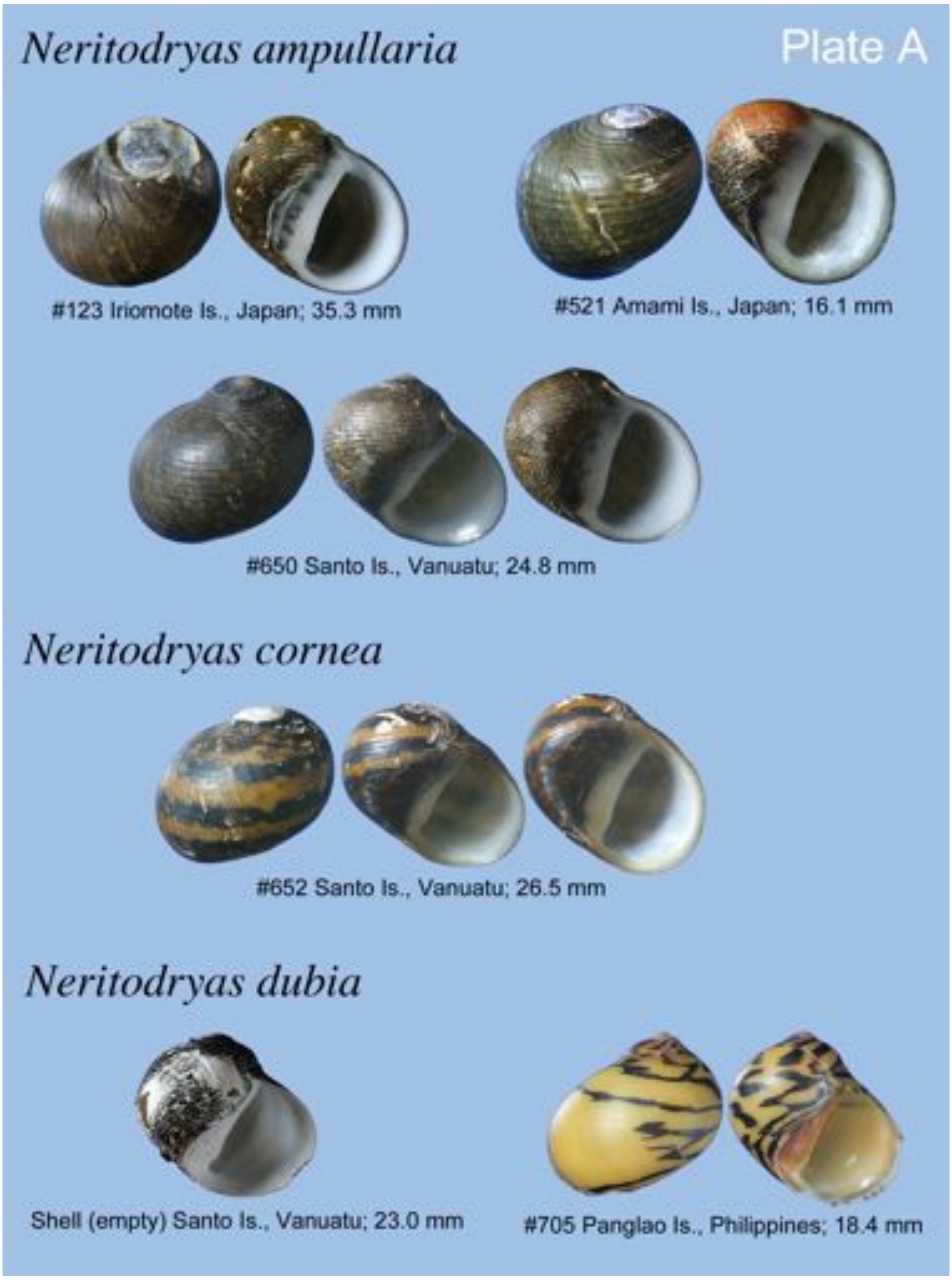


Plate A. *Neritodryas ampullaria*, *Neritodryas cornea* and *Neritodryas dubia*

Plate B. *Neritodryas notabilis*, *Neritodryas* sp. 1 and *Neritodryas* sp. 2

Plate C. *Clithon leachii*

Plate D. *Clithon nouletianus* and *Clithon diadema*

Plate E. *Clithon coronatus*, *Clithon pritchardi*, *Clithon pauluccianus* and *Clithon olivaceus*

Plate F. *Clithon oualaniensis*, *Clithon retropictus*, *Clithon rugatus* and *Clithon siderea*

Plate G. *Clithon corona* and *Clithon exclamesionis*

Plate H. *Clithon elephas* and *Clithon faba*

Plate I. *Clithon sowerbianus* and *Clithon subpunctatus*

Plate J. *Clithon variabilis*, *Clithon* sp. 1 and *Clithon* sp. 3

Plate K. *Clithon* sp. 4, *Clithon* sp. 5 and *Clithon* sp. 6

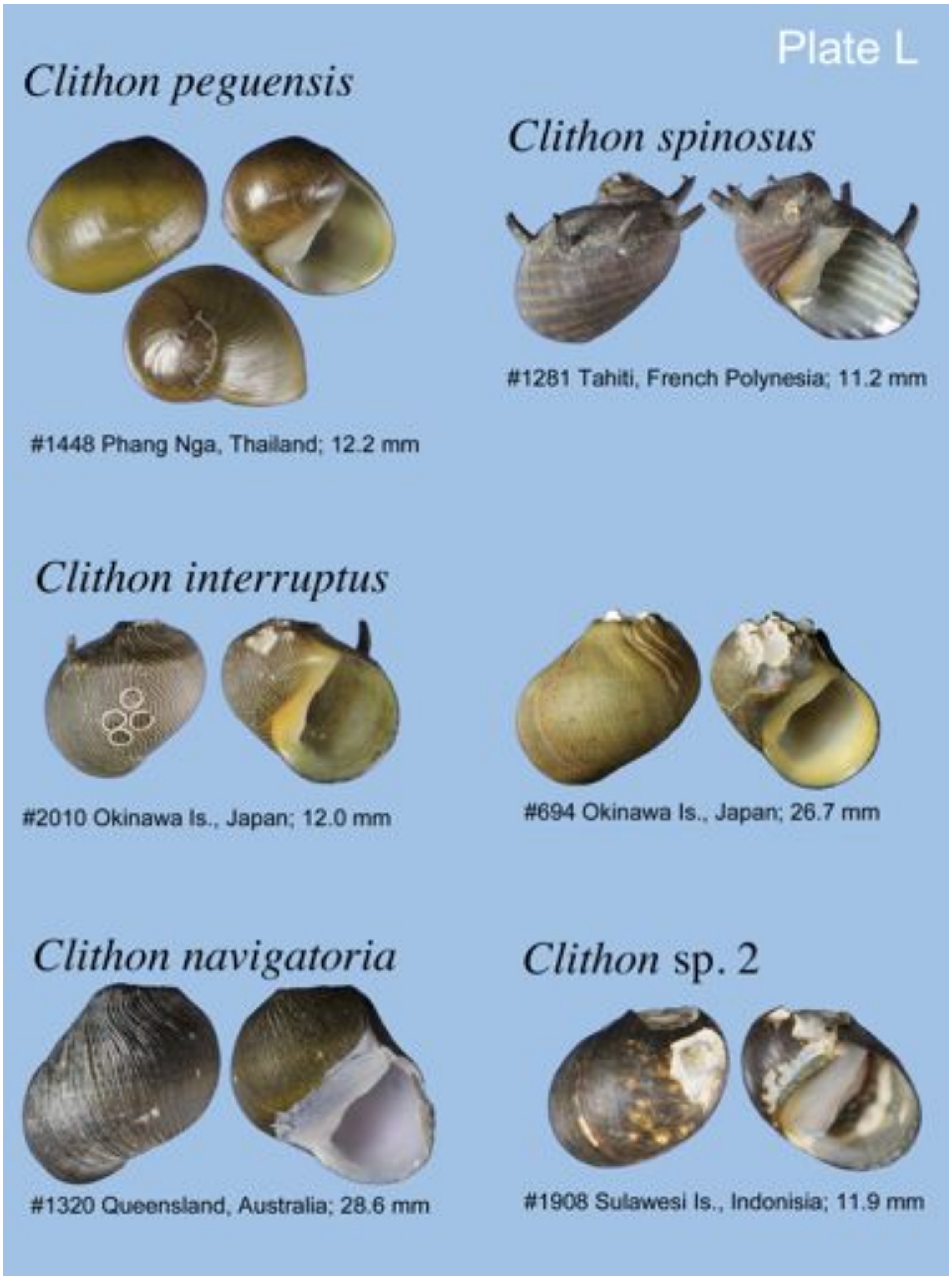


Plate L. *Clithon peguensis*, *Clithon spinosus*, *Clithon interruptus*, *Clithon navigatoria* and *Clithon* sp. 2

Plate M. *Clithon chlorostoma*, *Clithon castaneus* and *Clithon* sp. 7

Plate N. *Vittina communis*, *Vittina cumingiana* and *Vittina turrita*

Plate O. *Vittina cuvieriana*, *Vittina gagates* and *Vittina zigzag*

Plate P. *Vittina lugubris*

Plate Q. "*Neritina*" *haemastoma*, "*Neritina*" *sayana*, "*Neritina*" sp. and *Vittina serrulata*

Plate R. *Neritina* sp. 4, *Neritina* sp. 5, *Neritona granosa* and *Neritona labiosa*

Plate S. *Neritina asperulata*, *Neritina canalis* and *Neritina delestennei*

Plate T. *Neritina iris*, *Neritina petitii* and *Neritina* sp. 2

Plate U. *Neritina powisiana*, *Neritina pulligera*, *Neritina* sp. 1 and *Neritina* sp. 3

Plate V. *Dostia bicanaliculata*, *Dostia dilatata* and *Dostia guamensis*

Plate W. *Dostia florida*, *Dostia siquijorensis*, *Dostia mauritii* and *Dostia* sp. 1

Plate X. *Dostia subalata* and *Dostia* sp. 3

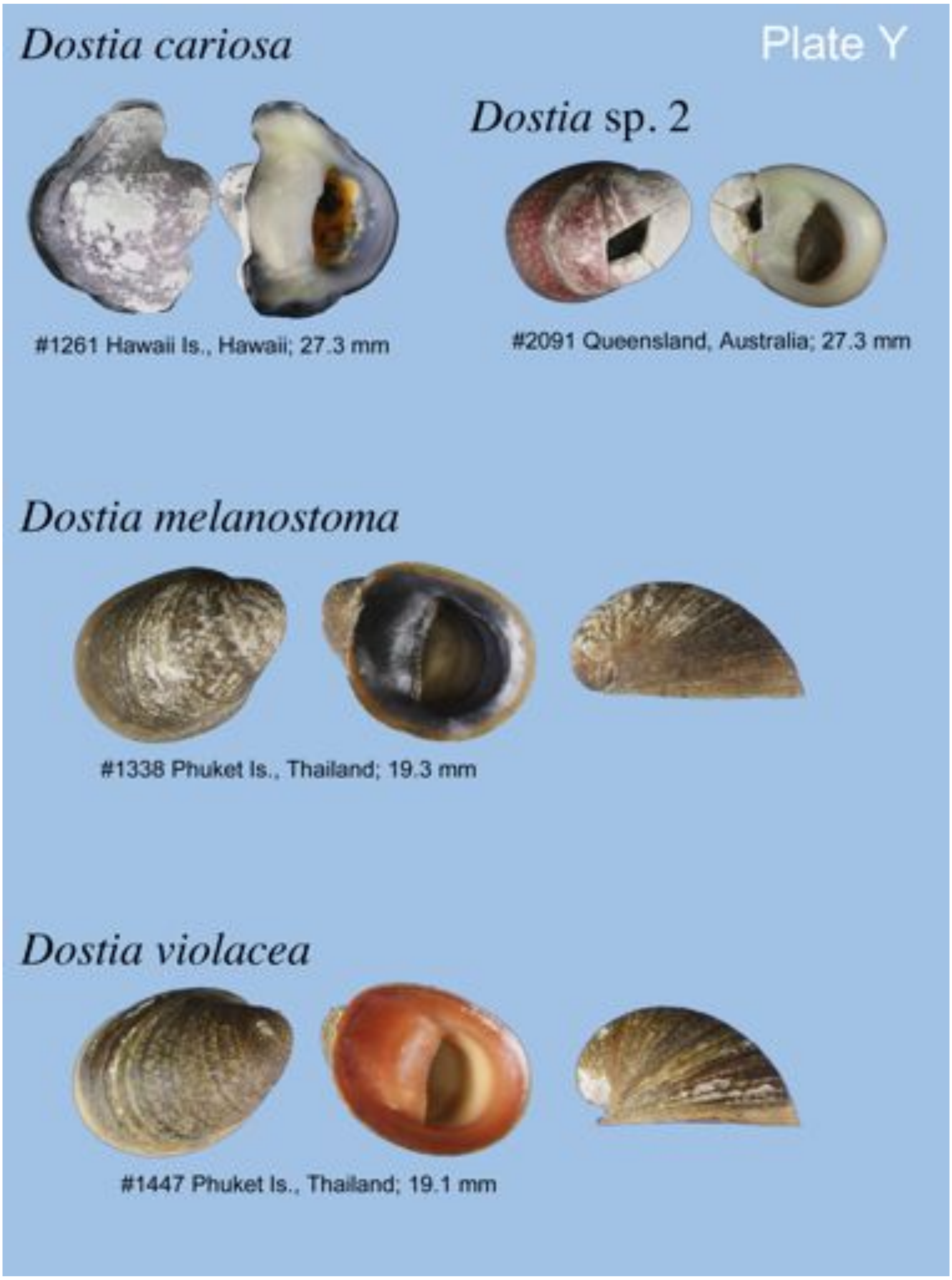


Plate Y. *Dostia cariosa*, *Dostia* sp. 2, *Dostia melanostoma* and *Dostia violacea*

Plate Z. *Laodia sanguisuga*, *Laodia cumingiana*, *Neritina luzonica* and "*Neritina*" *bruguieri*

Plate AA. *Septaria auriculata* and *Septaria spilaris*

Plate BB. *Septaria lecontei*, *Septaria suffreni*, *Septaria porcellana* and *Septaria clypeolum*

Plate CC. *Septaria tessellata* and *Septaria* sp.

Index for Appendix 1.

Genus	Species	Plate
Neritodryas	*ampullaria*	A
	cornea	A
	dubia	A
	notabilis	B
	sp. 1	B
	sp. 2	B
Neritona	*granosa*	R
	labiosa	R
Clithon	*castaneus*	M
	chlorostoma	M
	corona	G
	coronatus	E
	cryptospira	L
	diadema	D
	elephas	H
	exclamesionis	G
	faba	H
	interruptus	L
	leachii	C
	navigatoria	L
	nouletianus	D
	olivaceus	E
	oualaniensis	F
	pauluccianus	E
	pritchardi	E
	retropictus	F
	rugatus	F
	siderea	F
	sowerbianus	I
	spinosus	L
	subpunctatus	I
	variabilis	J
	sp. 1	J
	sp. 2	L
	sp. 3	J
	sp. 4	K
	sp. 5	K
	sp. 6	K
	sp. 7	M
Vittina	*communis*	N
	cumingiana	N
	cuvieriana	O
	gagates	O
	lugubris	P
	serrulata	Q
	turrita	N
	zigzag	O

Genus	Species	Plate
Laodia	*cumingiana*	Z
	sanguisuga	Z
Neritina	*asperulata*	S
	canalis	S
	delestennei	S
	iris	T
	luzonica	Z
	petitii	T
	powisiana	U
	pulligera	U
	sp. 1	U
	sp. 2	T
	sp. 3	U
	sp. 4	R
	sp. 5	R
Dostia	*bicanaliculata*	V
	cariosa	Y
	dilatata	V
	florida	W
	guamensis	V
	mauritii	W
	melanostoma	Y
	siquijorensis	W
	subalata	X
	violacea	Y
	sp. 1	W
	sp. 2	Y
	sp. 3	X
Septaria	*auriculata*	AA
	clypeolum	BB
	lecontei	BB
	porcellana	BB
	spilaris	AA
	suffreni	BB
	tessellata	CC
	sp.	CC
New genus 1 "*Neritina*"	*bruguieri*	Z
New genus 2 "*Neritina*"	*haemastoma*	Q
	sayana	Q
	sp.	Q

Appendix 2.

Type specimen catalog of the limnic Neritidae used for species taxonomy in Chapter 4.

Species names, authors, dates of publication and maximum shell diameters are shown with type specimen photos. Original publication, type series, abbreviations of museum name (see below), type locality and range of maximum shell diameter of type series are also shown in figure caption.

Abbreviations used: BMNH = British Museum (Natural history), London, UK; MCZ = Museum Comparative Zoology, Cambridge, USA; MHNG = Muséum National d'Histore Naturelle, Geneva, Switzerland; MNHN = Muséum National d'Histore Naturelle, Paris, France.

Type specimens, Paris Museum

Plate 1.

A, B

Nerita (*Clithon*) *adspersa* Récluz, 1853
Journal de Conchyliologie, 4: 319 (Pl.7, Fig.6)
1 syntype MNHN
Locality: ?
MSD: 16.5 mm

C

Neritina amphibia Lesson, 1831
Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825… for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 372–374 (Pl.16, Fig.1)
2 syntypes MNHN
Locality: New Ireland (Nouvelle-Irlande), Papua New Guinea
MSD: 21.2 mm

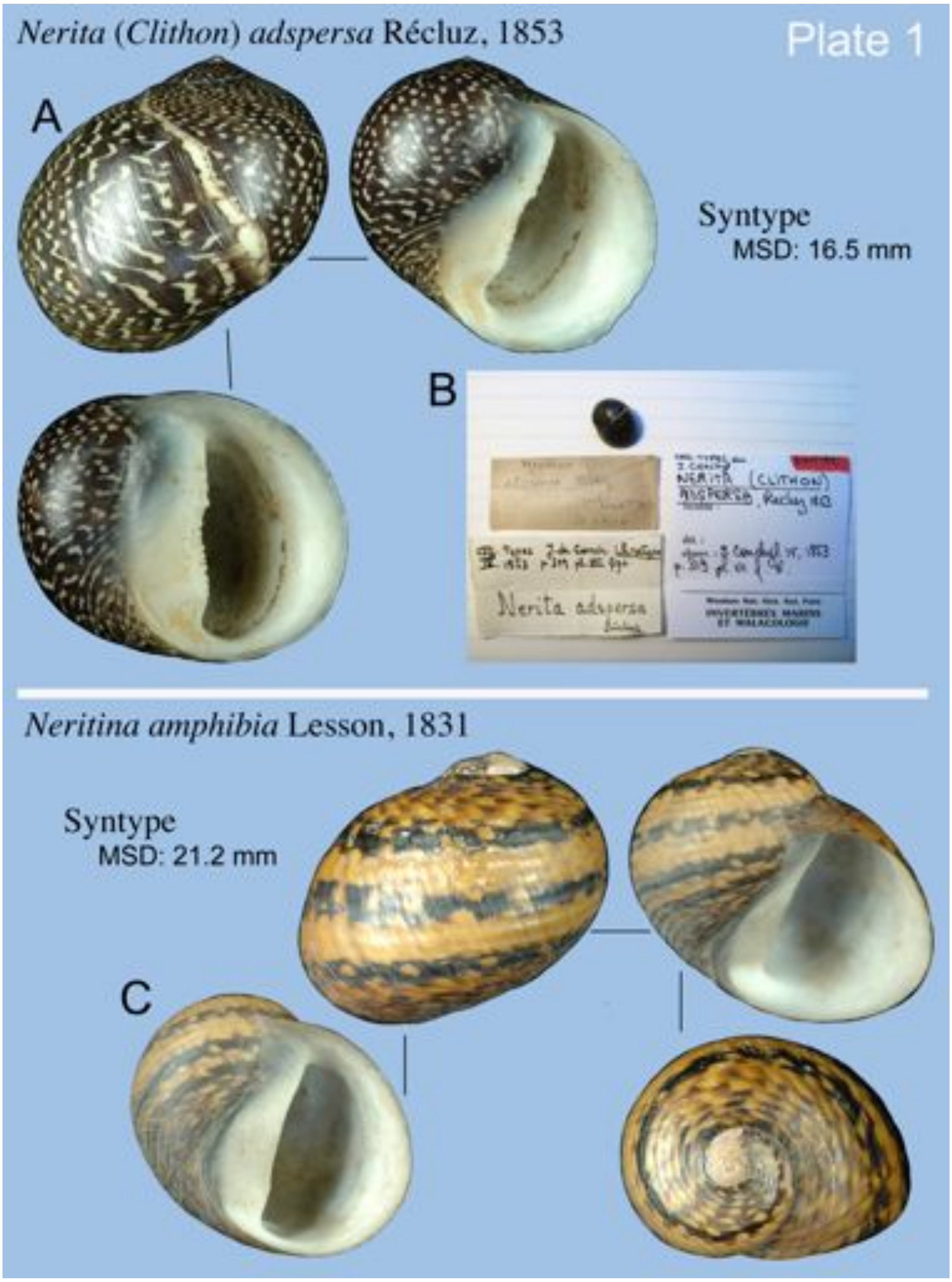


Plate 1

Nerita (*Clithon*) *adspersa* Récluz, 1853

Neritina amphibia Lesson, 1831

Plate 2.

A, B

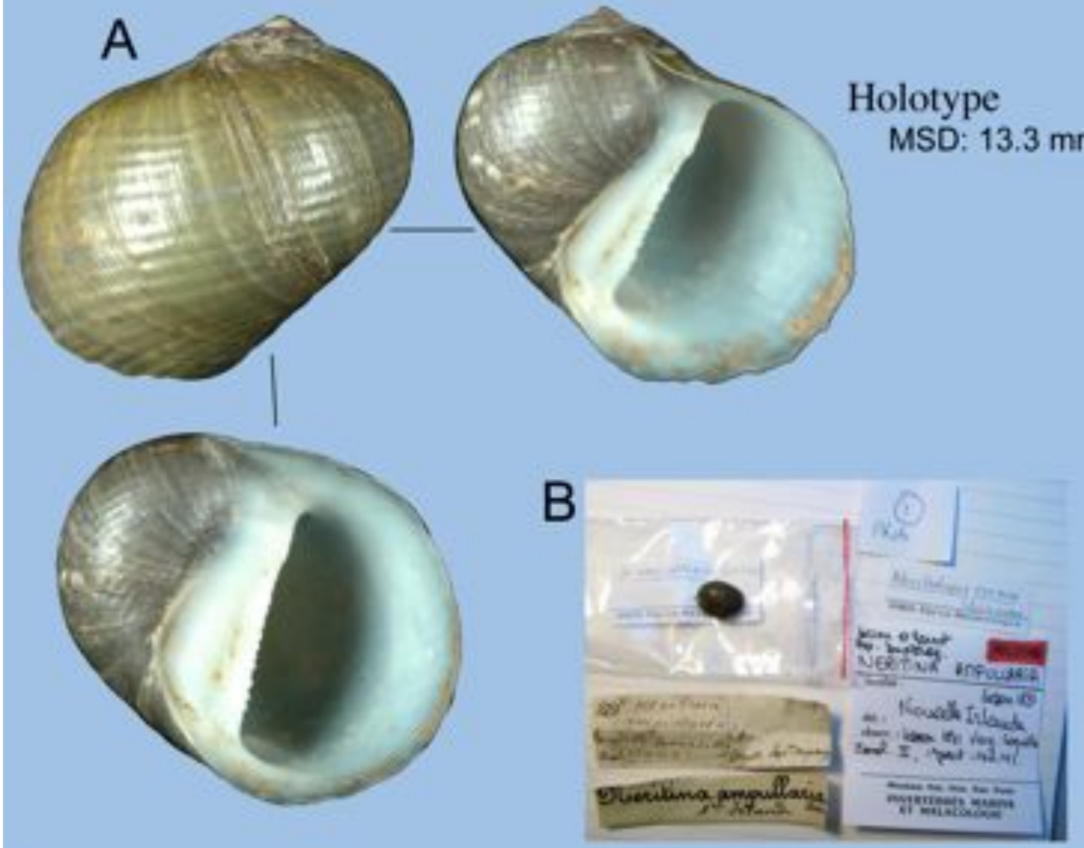
Neritina ampullaria Lesson, 1831
Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825…for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 376–377
Holotype MNHN
Locarity: New Ireland (Nouvelle-Irlande), Papua New Guinea
MSD: 13.3 mm

C

Navicella apiata Récluz, 1842
Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 376
3 syntypes MNHN
Locarity: Nuku Hiva, Marquesas Is., French Polynesia
MSD: 24.5 mm

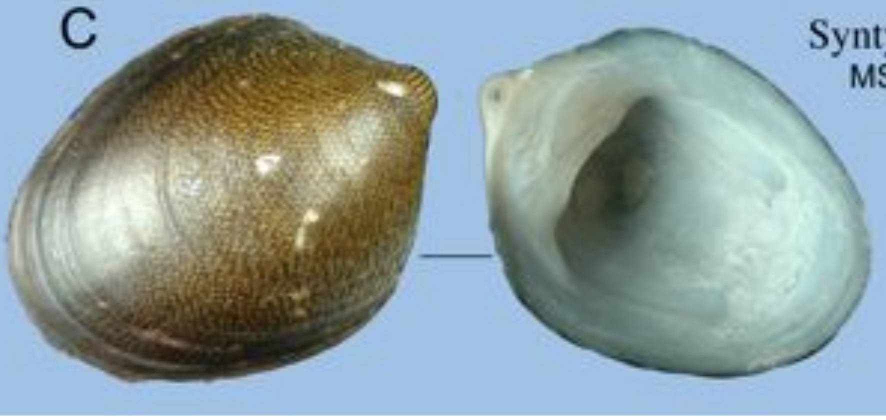
Plate 2

Neritina ampullaria Lesson, 1831



Holotype
MSD: 13.3 mm

Navicella apiata Récluz, 1842



Syntype
MSD: 24.5 mm

Plate 3.

A, B

Nerita (*Neritina*) *asperulata* Recluz, 1843
Proceedings of the Zoological Society of London for 1842, 10: 169
2 syntypes MNHN
Locality: Pasuquin, Ilocos Norte, Luzon, Philippines
MSD: 20.9 mm, 18.5 mm

C, D

Neritina auriculata Lamarck, 1816
Encyclopédie méthodique. Tableau Encyclopédique et méthodique des trois règnes de la nature. Vingt-troisième partie. Mollusques et polypes divers. V. Agasse, Paris: 11 p (Pl.455, Fig.6)
6 syntypes MNHN
Locality: Australia (Nouvelle-Hollande) and the surrounding islands
MSD: 15.1–15.6 mm

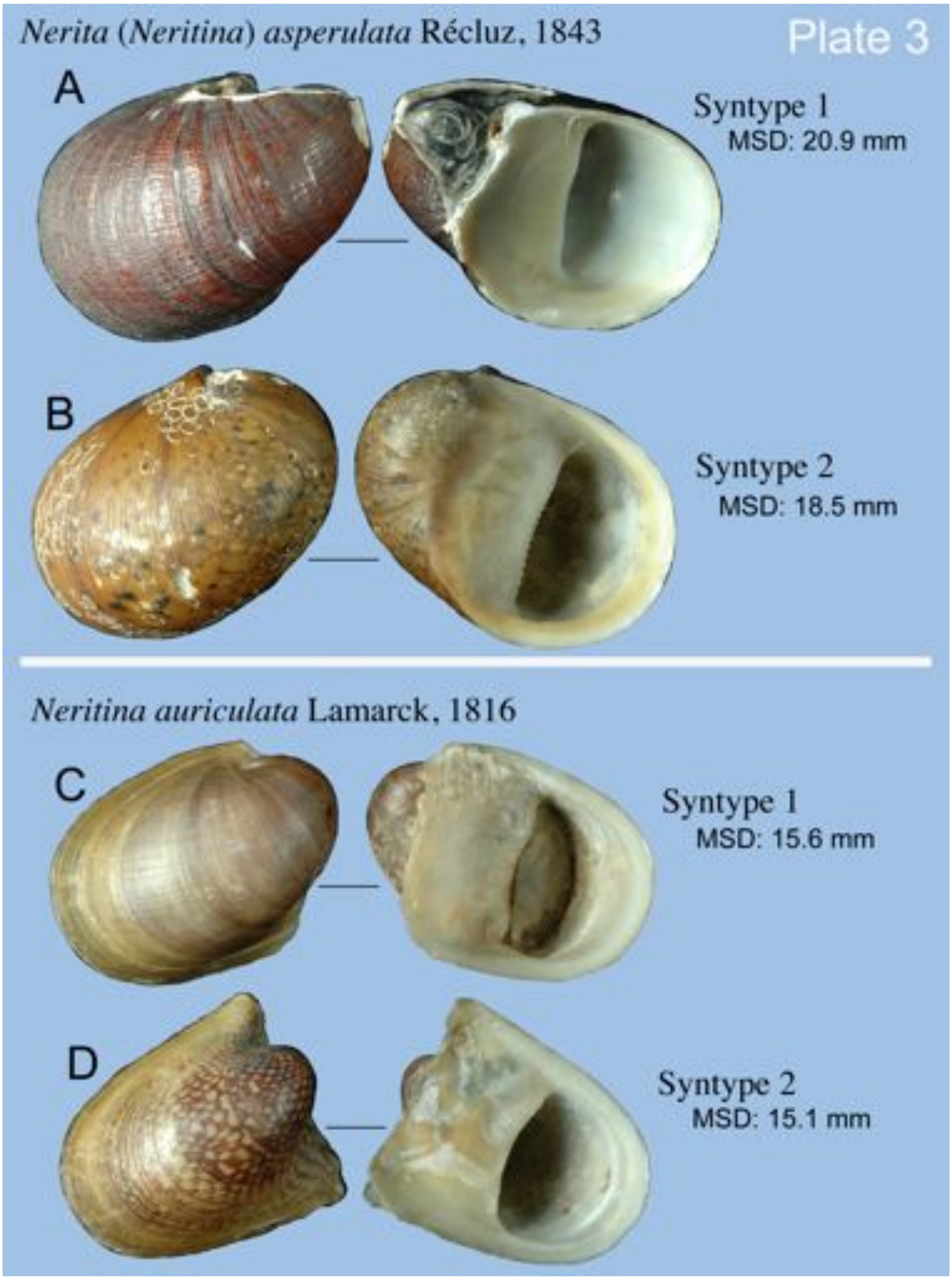

Nerita (Neritina) asperulata Récluz, 1843
Plate 3
A
Syntype 1
MSD: 20.9 mm
B
Syntype 2
MSD: 18.5 mm
Neritina auriculata Lamarck, 1816
C
Syntype 1
MSD: 15.6 mm
D
Syntype 2
MSD: 15.1 mm

Plate 4.

A

Nerita bahiensis Récluz, 1850
Journal de Conchyliologie 1(2): 146 (Pl.7, Fig.10)
Lectotype MNHN; 7 paralectotypes MHNG
Locality: Bahia, Brazil
MSD: 15.8 mm

B

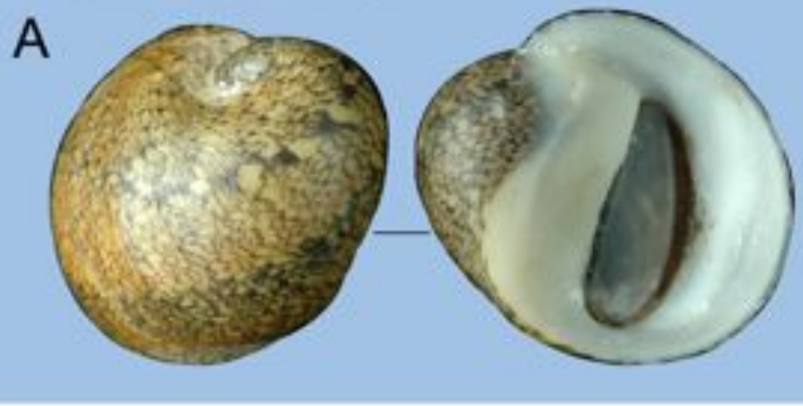
Nerita cardinalis Le Guillou, 1841
Revue Zoologique, par la Société Cuvierienne 4(11): 345
1 syntype MNHN
Locality: Aru Is. (Arrou Is.), Indonesia?
MSD: 16.7 mm

C

Nerita communis Quoy & Gaimard, 1834
Voyage de découvertes de l'Astrolabe. Exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont d'Urville. Zoologie. Tome troisième. J. Tastu, Paris. Vol. 1: 195 (Pl.65, Fig.12–14)
3 syntypes MNHN
Locality: Vanicoro, Solomon Is.
MSD: 18.2 mm

Nerita bahiensis Récluz, 1850

Plate 4



Lectotype
MSD: 15.8 mm

Nerita cardinalis Le Guillou, 1841

Syntype
MSD: 16.7 mm

Nerita communis Quoy & Gaimard, 1834

Syntype
MSD: 18.2 mm

Plate 5.

A

Navicella cumingiana Récluz, 1843

Proceedings of the Zoological Society of London, 10: 157

2 syntypes MNHN

Locality: Camaguing, Philippines

MSD: 15.9 mm

B

Nerita (*Neritina*) *cumingiana* Récluz, 1842

Revue Zoologique, par la Société Cuvierienne 5: 74–75

Lectotype MNHN; 4 paralectotypes MNHN; Paralectotype MCZ; 4 paralectotypes MHNG; 3 paralectotypes MHNG; 3 paralectotypes MHNG

Locality: Maluku Is., Indonesia (Les Philippines et les Moluques)

MSD: 28.4 mm (Lectotype), 21.6–29.3 mm (Paralectotypes)

C

Nerita (*Clithon*) *dacostae* Recluz, 1844

Proceedings of the Zoological Society of London for 1843, 11: 199

2 Syntypes MNHN

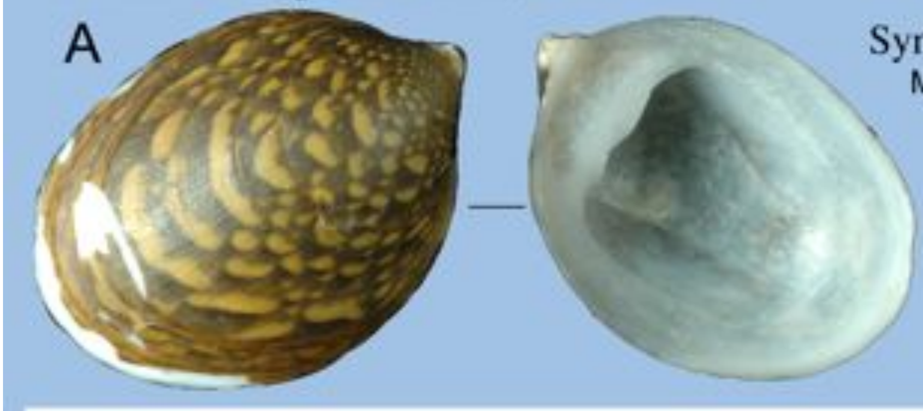
Locality: Negros Is., Philippines

MSD: 13.3 mm, 12.0 mm

Plate 5

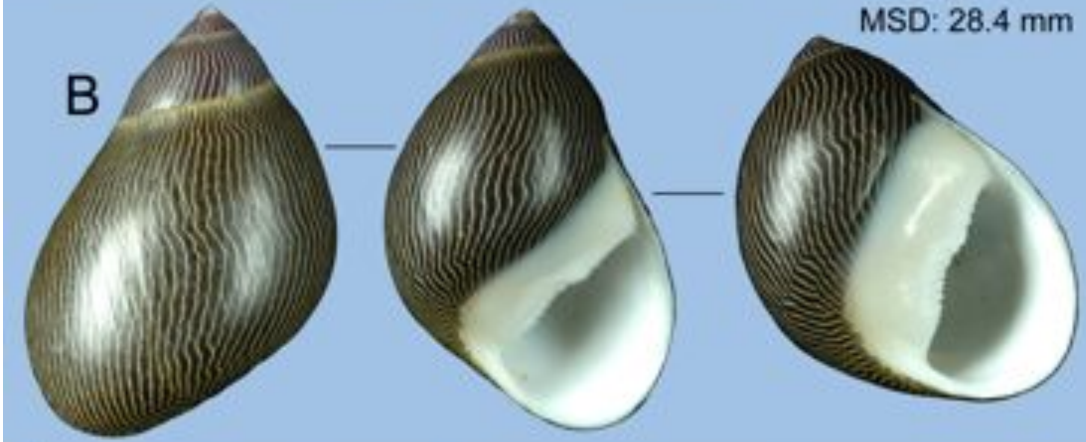
Navicella cumingiana Récluz, 1843

Syntype
MSD: 15.9 mm



Nerita (*Neritina*) *cumingiana* Récluz, 1842

Lectotype
MSD: 28.4 mm



Nerita (Clithon) dacostae Recluz, 1844

Syntype
MSD: 13.3 mm

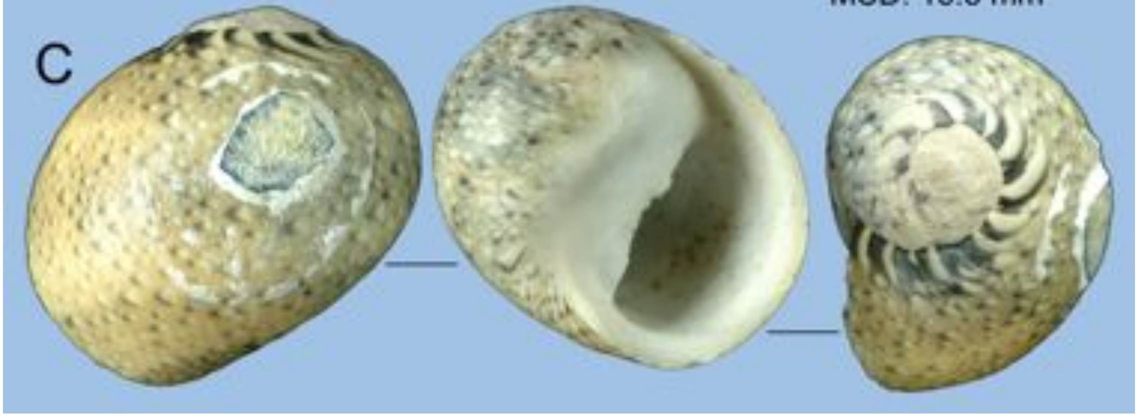


Plate 6.

A, B

Nerita deficiens Mabille, 1887

Molluscorum Tonkinorum diagnoses. A. Masson, Meulan, 18 p.

9 Syntypes MNHN

Locality: Viet Nam (Tonkin)

MSD: 14.6–19.0 mm

C

Navicella depressa Lesson, 1831

Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825…for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 386

2 syntypes MNHN

Locality: New Guinea (Nouvelle-Guinée)

MSD: 24.8 mm, 16.4 mm

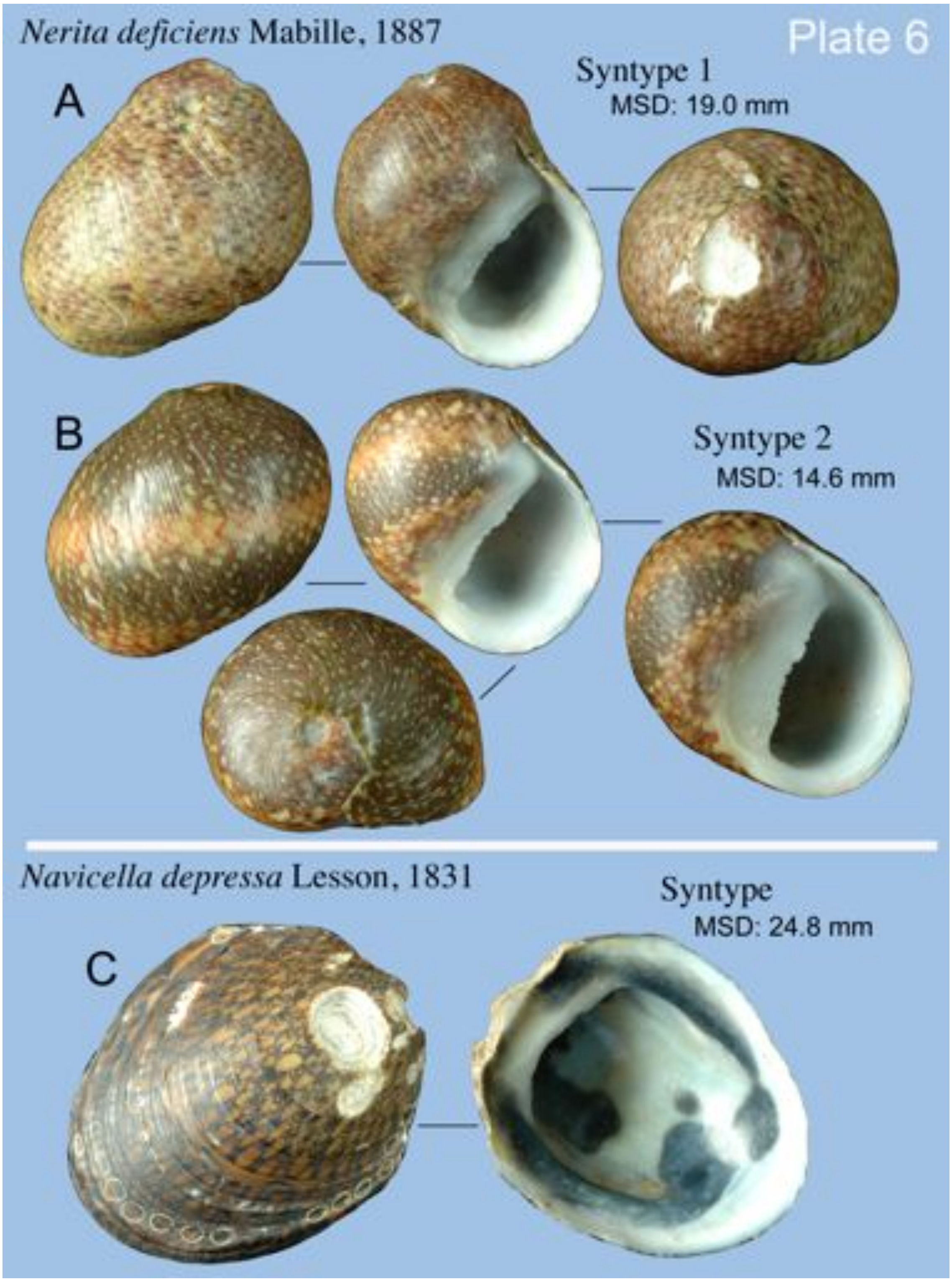

Nerita deficiens Mabille, 1887
Plate 6
Syntype 1
MSD: 19.0 mm
A
B
Syntype 2
MSD: 14.6 mm
Navicella depressa Lesson, 1831
Syntype
MSD: 24.8 mm
C

Plate 7.

A, B

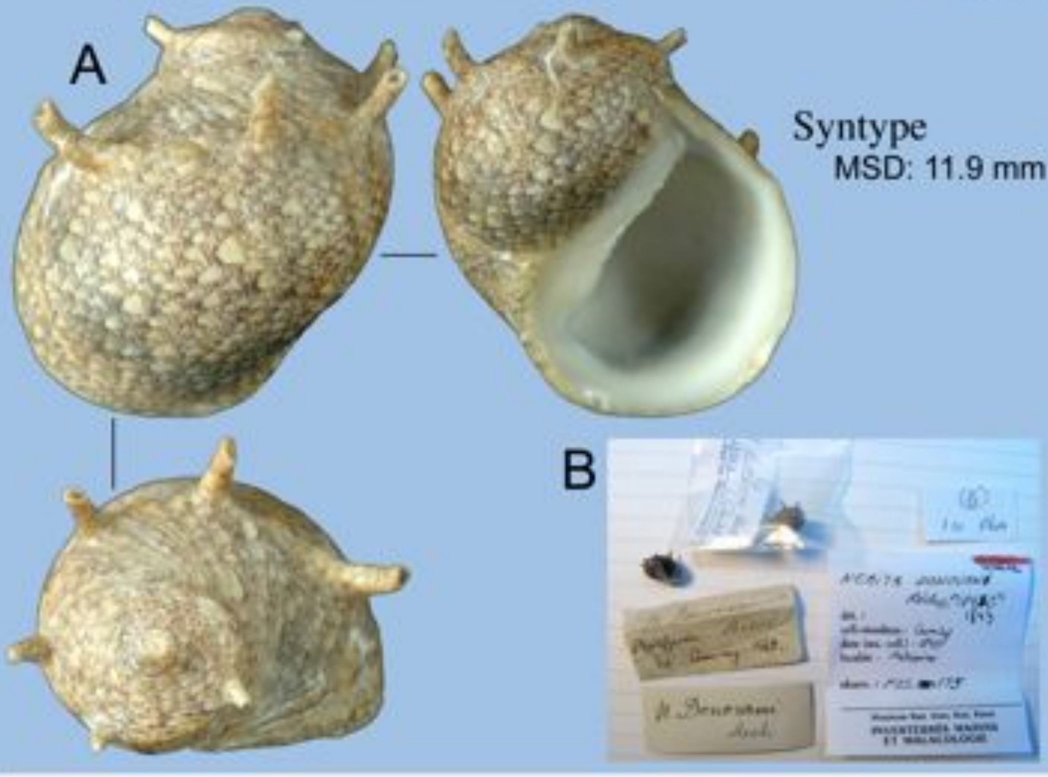
Nerita (*Clithon*) *donovani* Récluz, 1843
Proceedings of the Zoological Society of London for 1842, 10: 175
2 syntypes MNHN
Locality: Guimaras Is., Philippines
MSD: 11.0–11.9 mm

C

Neritina elephas Mabille, 1895
Bulletin Société Histoire Naturelle, Autun, 8: 398
10 syntypes MNHN
Locality: Vanuatu (Nouvelles-Hébrides)
MSD: 26.4–37.7 mm

Plate 7

Nerita (*Clithon*) *donovani* Récluz, 1843



Syntype
MSD: 11.9 mm

Neritina elephas Mabille, 1895

Syntype
MSD: 26.4 mm

Plate 8.

A

Neritina exaltata Récluz, 1850
Journal de Conchyliologie 1: 65–66 (Pl.3, Fig.3)
3 syntypes MNHN
Locality: Negros Is., Philippines
MSD: 21.6–22.5 mm

B, C

Neritina (*Clithon*) *exclamationis* Mabille, 1895
Bulletin Société Histoire Naturelle, Autun, 8: 397
4 syntypes MNHN
Locality: Vanuatu (Nouvelles-Hébrides)
MSD: 8.9 mm–13.9 mm

Plate 8

Neritina exaltata Récluz, 1850

Neritina (*Clithon*) *exclamationis* Mabille, 1895

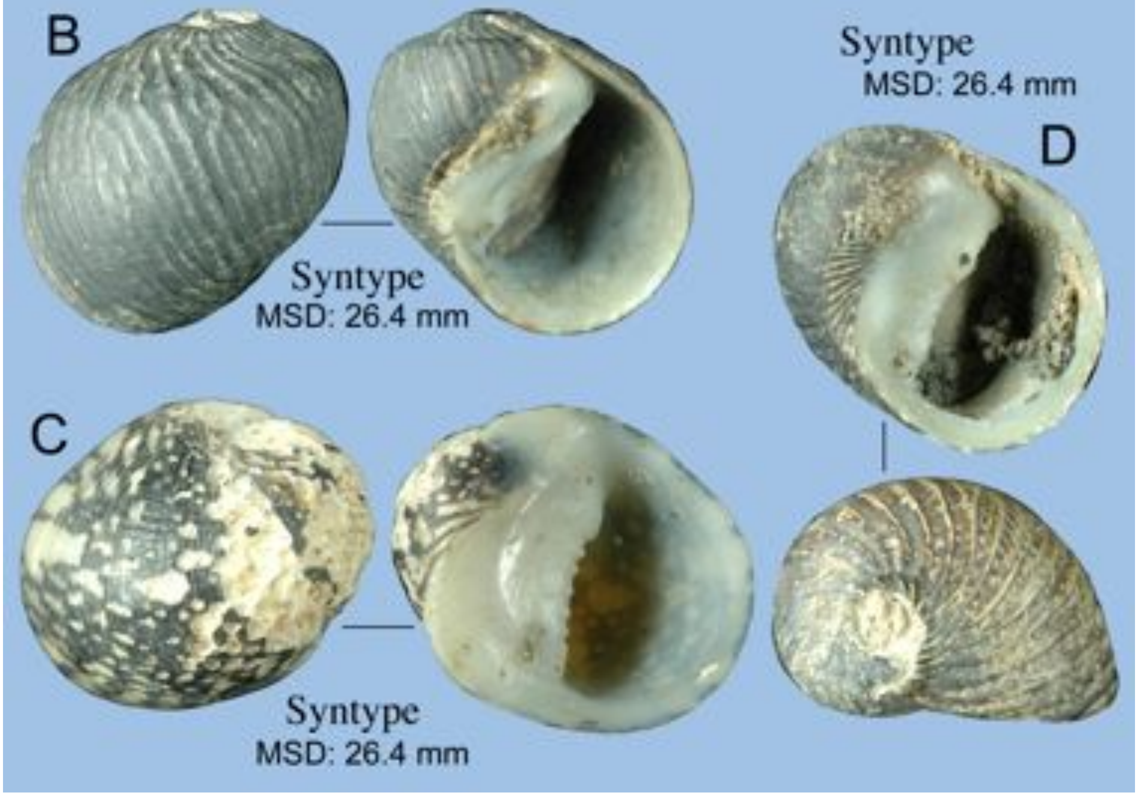


Plate 9.

A, B

Neritina florida Récluz, 1850

Journal de Conchyliologie 1: 160–161 (Pl.7, Figs.6–7)

2 syntypes

Locarity: Tahiti

MSD: 9.8 mm, 10.8 mm

C

Navicella francoisi Mabille, 1895

Bulletin Société Histoire Naturelle, Autun, 8: 400

1 syntype MNHN

Locality: Vanuatu (Nouvelles-Hébrides)

MSD: 29.1 mm

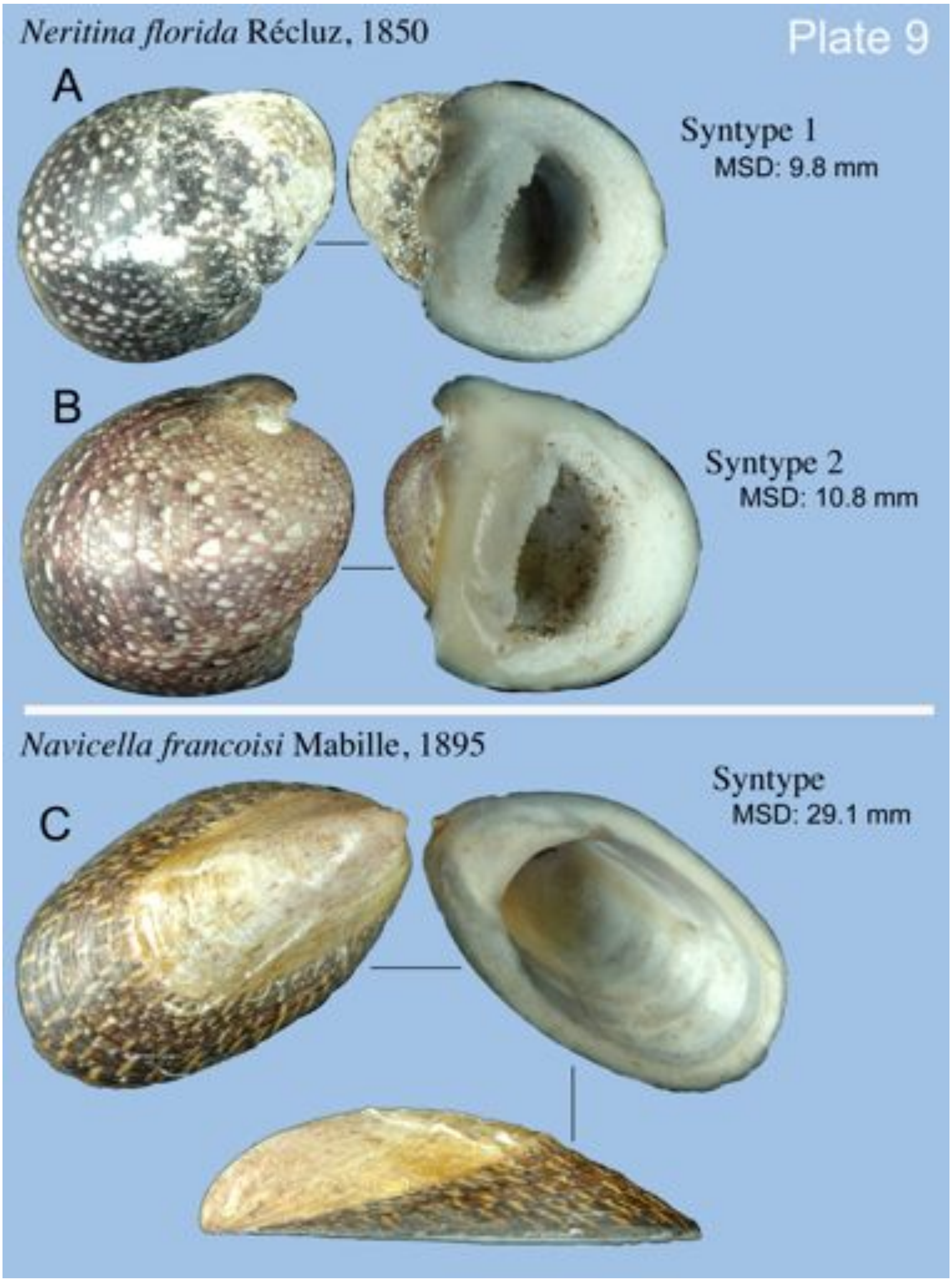


Plate 9

Neritina florida Récluz, 1850

Syntype 1
MSD: 9.8 mm

Syntype 2
MSD: 10.8 mm

Navicella francoisi Mabille, 1895

Syntype
MSD: 29.1 mm

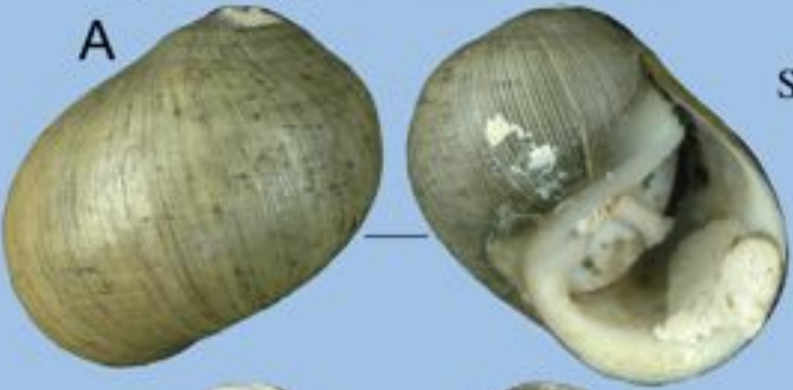
Plate 10.

A, B
Neritina (*Clithon*) *francoisi* Mabille, 1895
Bulletin Société Histoire Naturelle, Autun, 8: 397
4 syntypes
Locality: Vanuatu (Nouvelles-Hébrides)
MSD:

C
Neritina gagates Lamarck, 1822
Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l’auteur, au jardin du Roi: 185 p
2 possible syntypes MNHN;
Locality: ?
MSD: 21.5 mm, 22.3 mm

Neritina (*Clithon*) *francoisi* Mabille, 1895

Plate 10



Syntype 1
MSD: 27.2 mm

Syntype 2
MSD: 25.8 mm

Neritina gagates Lamarck, 1822

Syntype 1, 2
MSD: 22.3 (left), 21.5 mm

Plate 11.

A

Nerita gaimardi Souleyet, 1842

Revue Zoologique, par la Société Cuvierienne, 5: 269–270

2 syntypes MNHN

Locality: Da Nang (Tourane), Viet Nam

MSD: 11.7 mm, 12.6 mm

B

Nerita guamensis Quoy & Gaimardi, 1834

Voyage de découvertes de l'Astrolabe. Exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont d'Urville. Zoologie. Tome troisième. J. Tastu, Paris. Vol. 3: 191 (Pl.65, Fig.45)

Syntype MNHN

Locality: Guam

MSD: 11.8 mm

C

Neritina horrida Mabille, 1895

Bulletin Société Histoire Naturelle, Autun, 8: 399

12 syntypes MNHN

Locality: Vanuatu (Nouvelles-Hébrides)

MSD: 11.8–13.2 mm

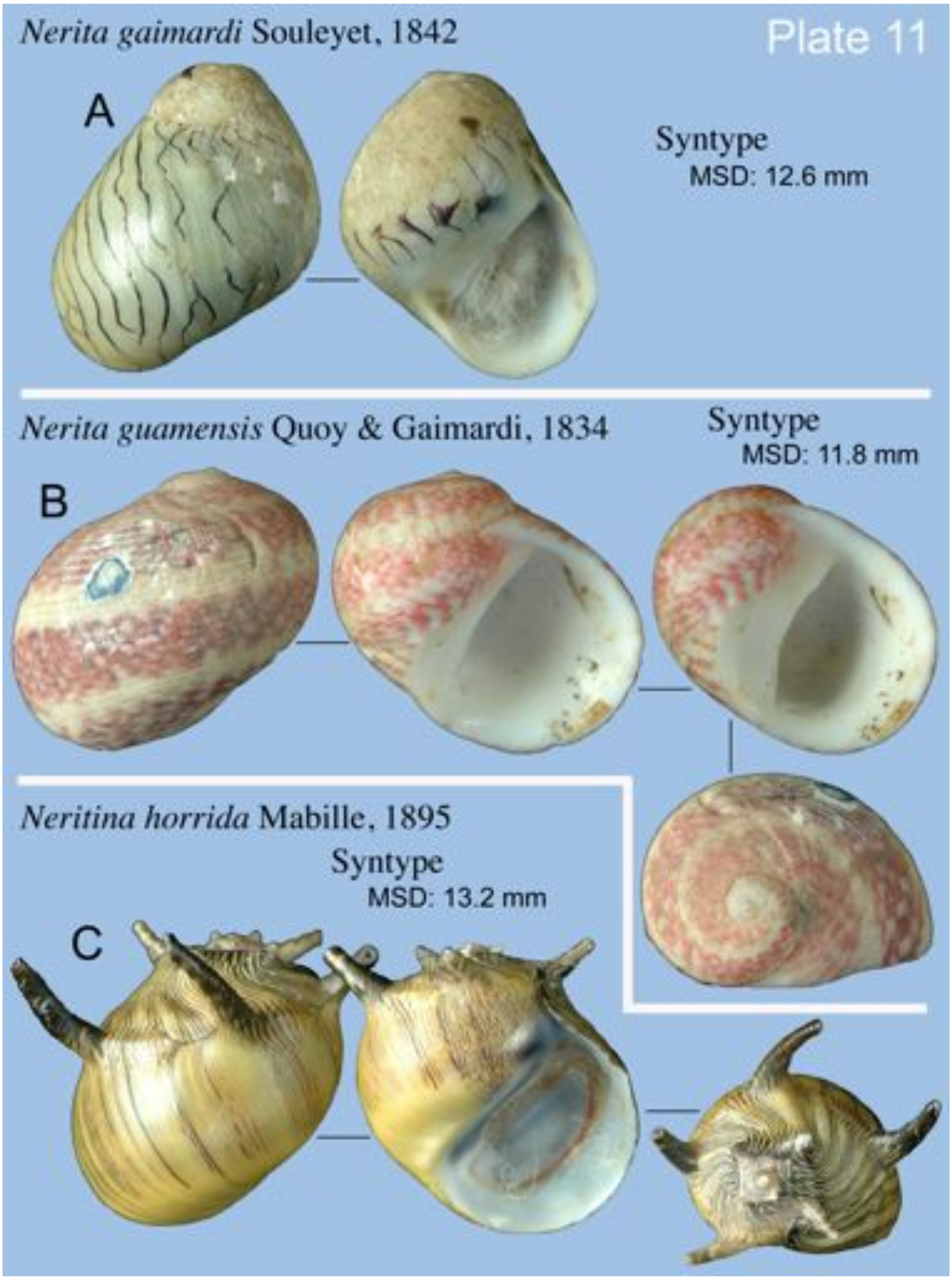

Nerita gaimardi Souleyet, 1842
Plate 11
A
Syntype
MSD: 12.6 mm
Nerita guamensis Quoy & Gaimardi, 1834
Syntype
MSD: 11.8 mm
B
Neritina horrida Mabille, 1895
Syntype
MSD: 13.2 mm
C

Plate 12.

A, B

Navicella hupeiana Gassies, 1863

Faune conchyliologique terrestre et fluvio-lacustre de la Nouvelle-Calédonie Part 1. Actes de la Société linnéenne de Bordeaux. 24: 114 (Pl.8, Fig.13)

2 syntypes MNHN

Locality: Balade, New Caledonia

MSD: 24.5 mm, 24.7 mm

C, D

Nerita indica Souleyet, 1842

Revue Zoologique, par la Société Cuvierienne, 5: 269

5 syntypes MNHN

Locality: Ganges, India

MSD: 15.1–20.5 mm

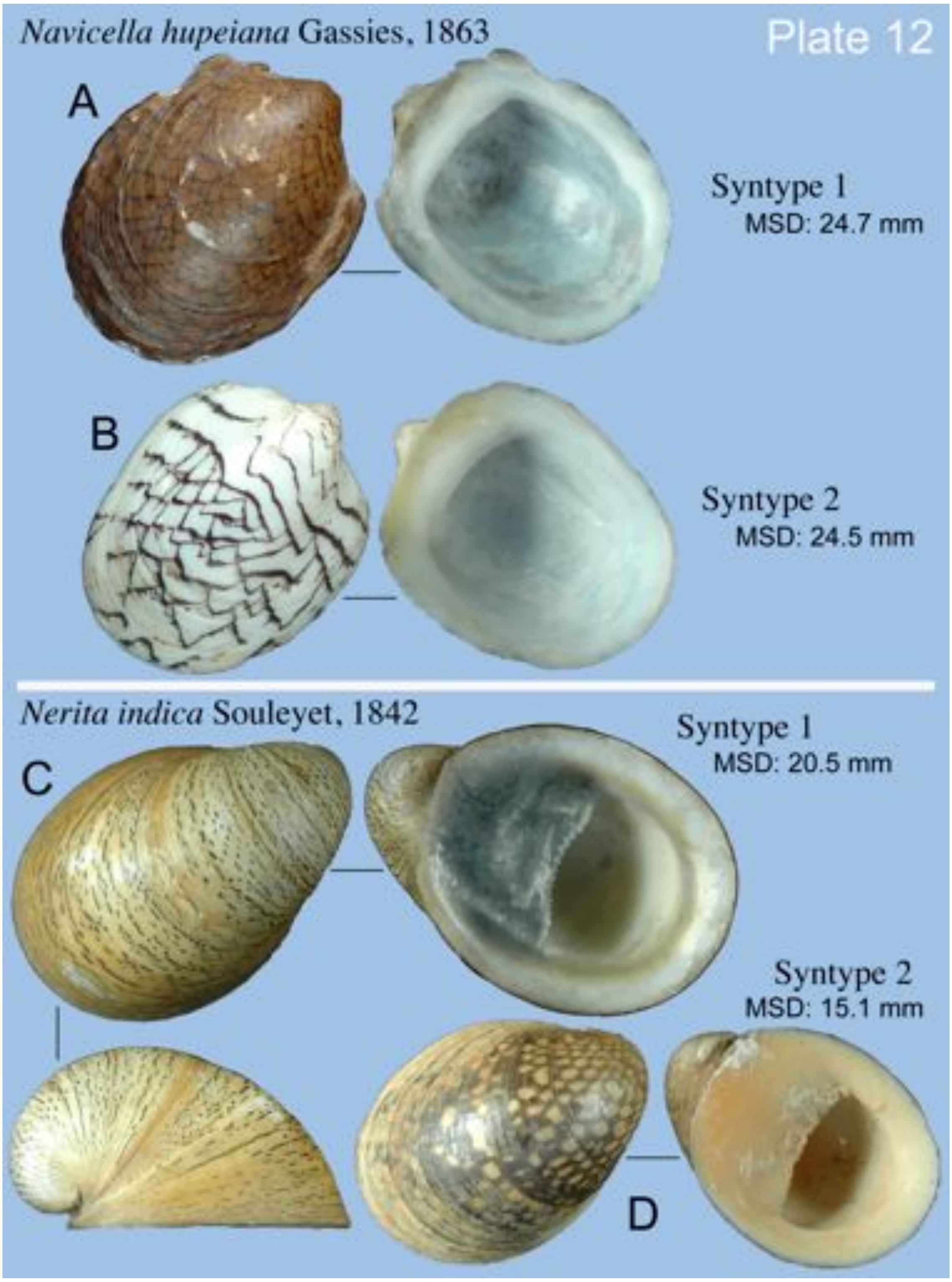

Navicella hupeiana Gassies, 1863
Plate 12
A
Syntype 1
MSD: 24.7 mm
B
Syntype 2
MSD: 24.5 mm
Nerita indica Souleyet, 1842
Syntype 1
MSD: 20.5 mm
C
Syntype 2
MSD: 15.1 mm
D

Plate 13.

A

Neritina pileolus Récluz, 1850

Journal de Conchyliologie 1: 66–67

(A replacement name for *Nerita intermedia* Deshayes, 1834, non *Nerita intermedia* Grateloup, 1828, nec *Neritina intermedia* Sowerby I, 1833)

Nerita intermedia Deshayes, 1834

Belanger C, Voyage aux Indes-Orientales par le nord de l'Europe: les provinces du Caucase, la Géorgie, l'Arménie et la Perse, pendant les années 1825, 1826, 1827, 1828 et 1829. A. Bertrand. Paris. 1834: 420 (Pl.1, Figs.6–7)

Nerita pileolus Récluz, 1850

Replacement name for *Nerita intermedia*, Deshayes 1834, non Grateloup, 1828, nec Sowerby, 1832.

Journal de Conchyliologie 1: 66–67

4 syntypes MNHN

Locality: Malabar Coast, India

MSD: 13.7 mm

B

Nerita keraudrenii Le Guillou, 1841

Revue Zoologique, par la Société Cuvierienne 4(11): 346

2 possible syntypes MNHN

Locality: Nuku Hiva, Marquesas Is., French Polynesia

MSD: 12.2 mm, 15.4 mm

C

Neritina lamarckii Deshayes, 1838

Lamarck JB, Histoire naturelle des animaux sans vertèbres. 2 éd. Milne-Edwards. Paris. Vol.8: 578

5 syntypes MNHN

Locality: Sandwich Is., Hawaii

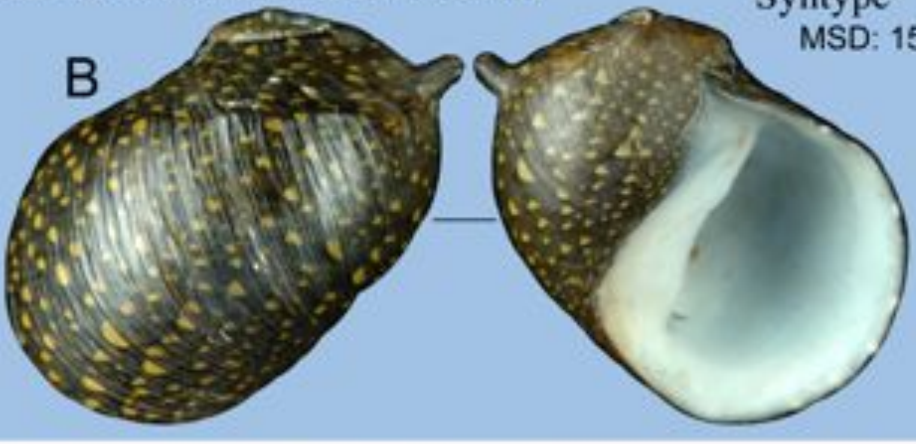
MSD: 24.1 mm

Plate 13

Neritina pileolus Récluz, 1850
Nerita intermedia Deshayes, 1834

Syntype
MSD: 13.7 mm

Nerita keraudrenii Le Guillou, 1841



Syntype
MSD: 15.4 mm

Neritina lamarckii Deshayes, 1838

Syntype
MSD: 24.1 mm

Plate 14.

A, B

Navicella laperousei Récluz, 1842
Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 378–379
2 syntypes MNHN (Guam)
Locality: Guam; Fiji; Samoa
MSD: 31.0 mm, 34.0 mm

C

Neritina lecontei Récluz, 1853
Journal de Conchyliologie 4: 257–259 (Pl.8, Fig.3)
7 syntypes MNHN
Locality: New Caledonia
MSD: 16.9 mm–26.7 mm

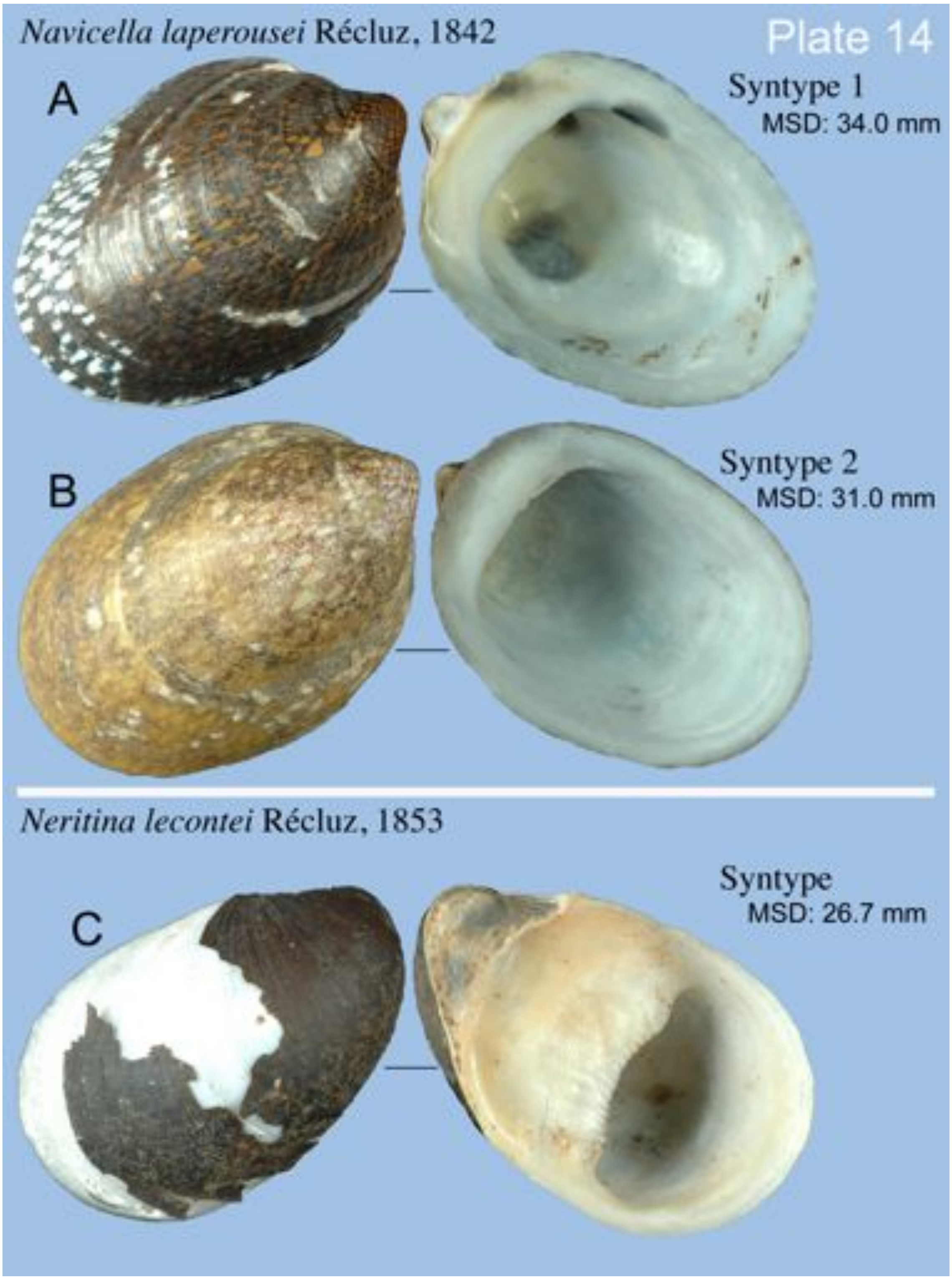

Navicella laperousei Récluz, 1842
Plate 14
A
Syntype 1
MSD: 34.0 mm
B
Syntype 2
MSD: 31.0 mm
Neritina lecontei Récluz, 1853
C
Syntype
MSD: 26.7 mm

Plate 15.

A

Nerita (*Clithon*) *longispina* Récluz, 1841

Replacement name for *Nerita coronata*, Leach 1815, non *Nerita corona*, Linnaeus, 1758, but this was an unnecessary replacement name.

Revue Zoologique, par la Société Cuvierienne, 4(10): 312–313

2 "syntypes" MNHN (merely Récluz own collection, Rodriguez Is., Indian Ocean)

Locality: ?

MSD: 21.0 mm

B, C

Navicella luzonica Récluz, 1842

Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 375

2 syntypes MNHN

Locality: Luzon Is., Philippines

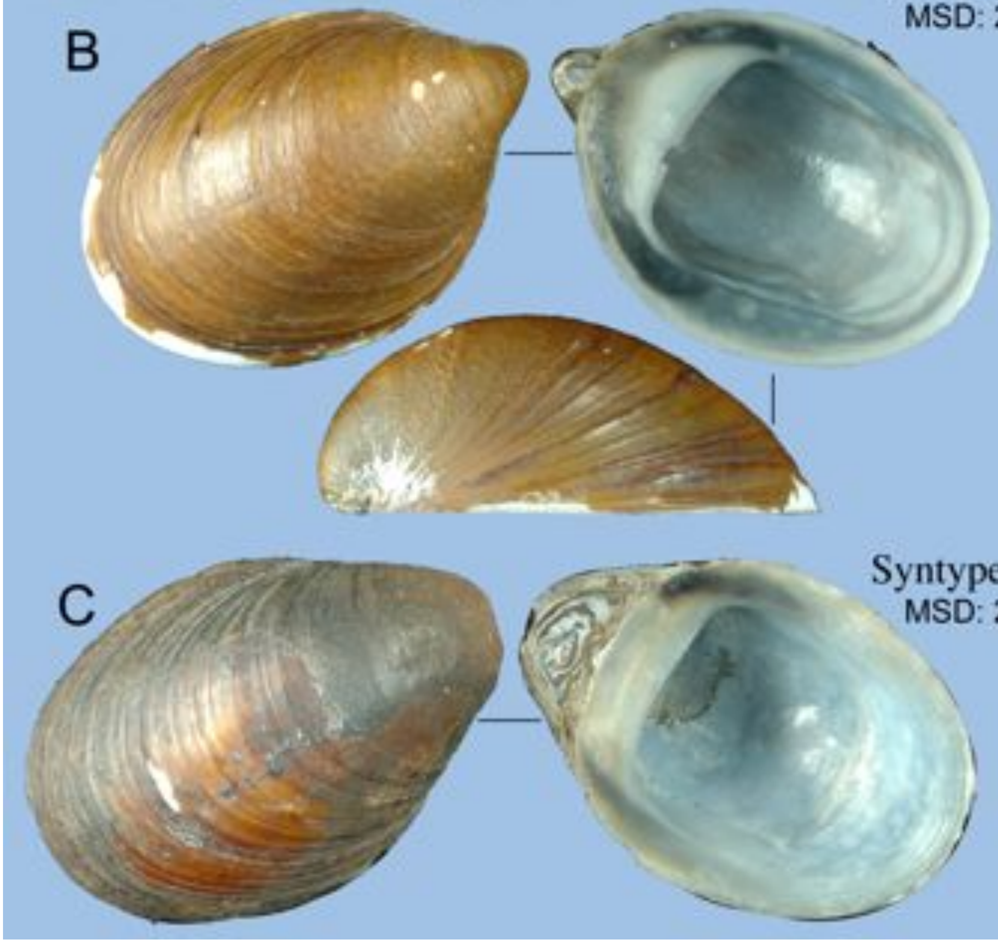
MSD: 20.7 mm, 23.6 mm

Plate 15

Nerita (*Clithon*) *longispina* Récluz, 1841

"Syntype"
MSD: 21.0 mm

Navicella luzonica Récluz, 1842



Syntype 1
MSD: 23.6 mm

Syntype 2
MSD: 20.7 mm

Plate 16.

A, B

Navicella macrocephala Récluz, 1842
Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 374
3 syntypes MNHN
Locality: Lebouka, Fiji
MSD: 15.2–24.4 mm

C

Neritina mauritiana Morelet, 1867
Journal de Conchyliologie 15: 440
1 syntype MNHN
Locality: Mauritius
MSD: 25.8 mm

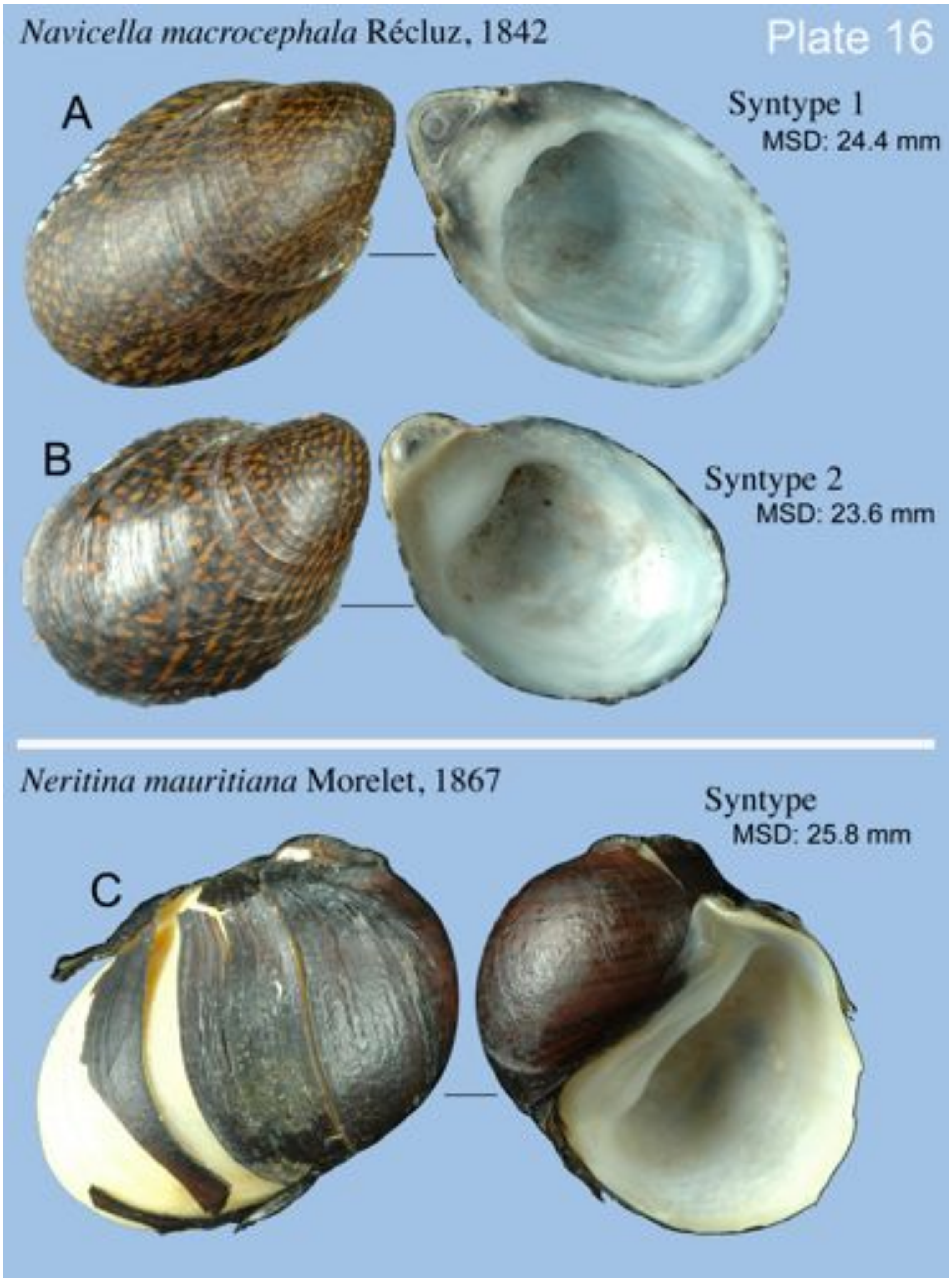

Navicella macrocephala Récluz, 1842
Plate 16
A
Syntype 1
MSD: 24.4 mm
B
Syntype 2
MSD: 23.6 mm
Neritina mauritiana Morelet, 1867
Syntype
MSD: 25.8 mm
C

Plate 17.

A, B

Nerita (*Clithon*) *montacuti* Récluz, 1843
Proceedings of the Zoological Society of London for 1842, 10: 174
1 syntype MNHN
Burias Is., Philippines
MSD: 15.6 mm

C, D

Neritina moquiniana Récluz, 1850
Journal de Conchyliologie 1(2): 156–157 (Pl.7, Fig.9)
1 syntype MNHN
Locality: Islands of the South Sea
MSD: 9.6 mm

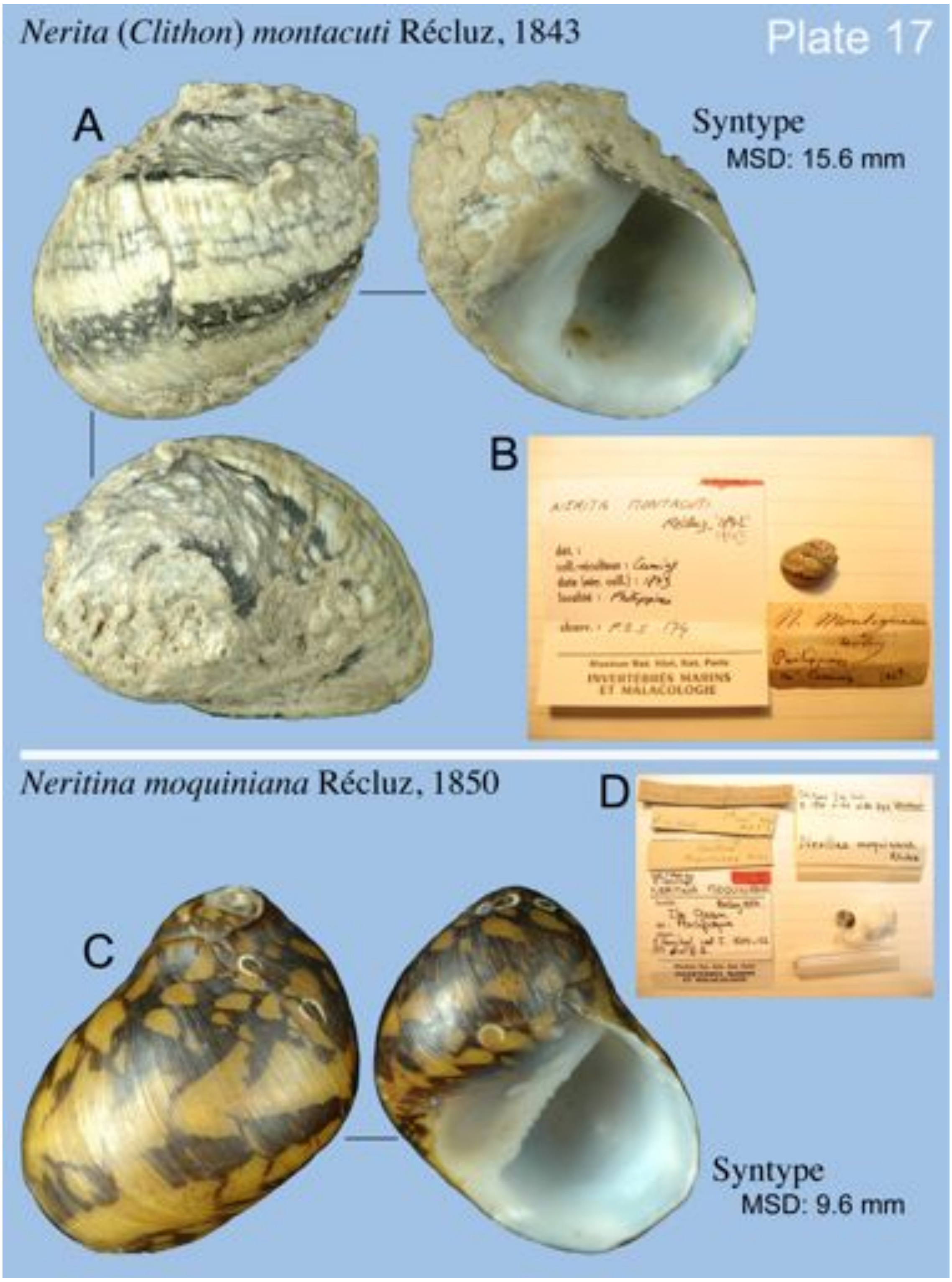


Plate 17

Nerita (*Clithon*) *montacuti* Récluz, 1843

Syntype
MSD: 15.6 mm

Neritina moquiniana Récluz, 1850

Syntype
MSD: 9.6 mm

Plate 18.

A, B, C

Neritina nouletiana Gassies, 1863

Faune conchyliologique terrestre et fluvio-lacustre de la Nouvelle-Calédonie Part 1. Actes de la Société linnéenne de Bordeaux. 24: 104–105 (Pl.8, Fig.5)

12 syntypes MNHN

Locality: Art Is., New Caledonia

MSD: 6.9–9.5 mm

D, E

Neritina oualaniensis Lesson, 1831

Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825… for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 379

3 syntypes MNHN

Locality: Kosrae (Oualan Island), Micronesia

MSD: 6.1–7.7 mm

Plate 18

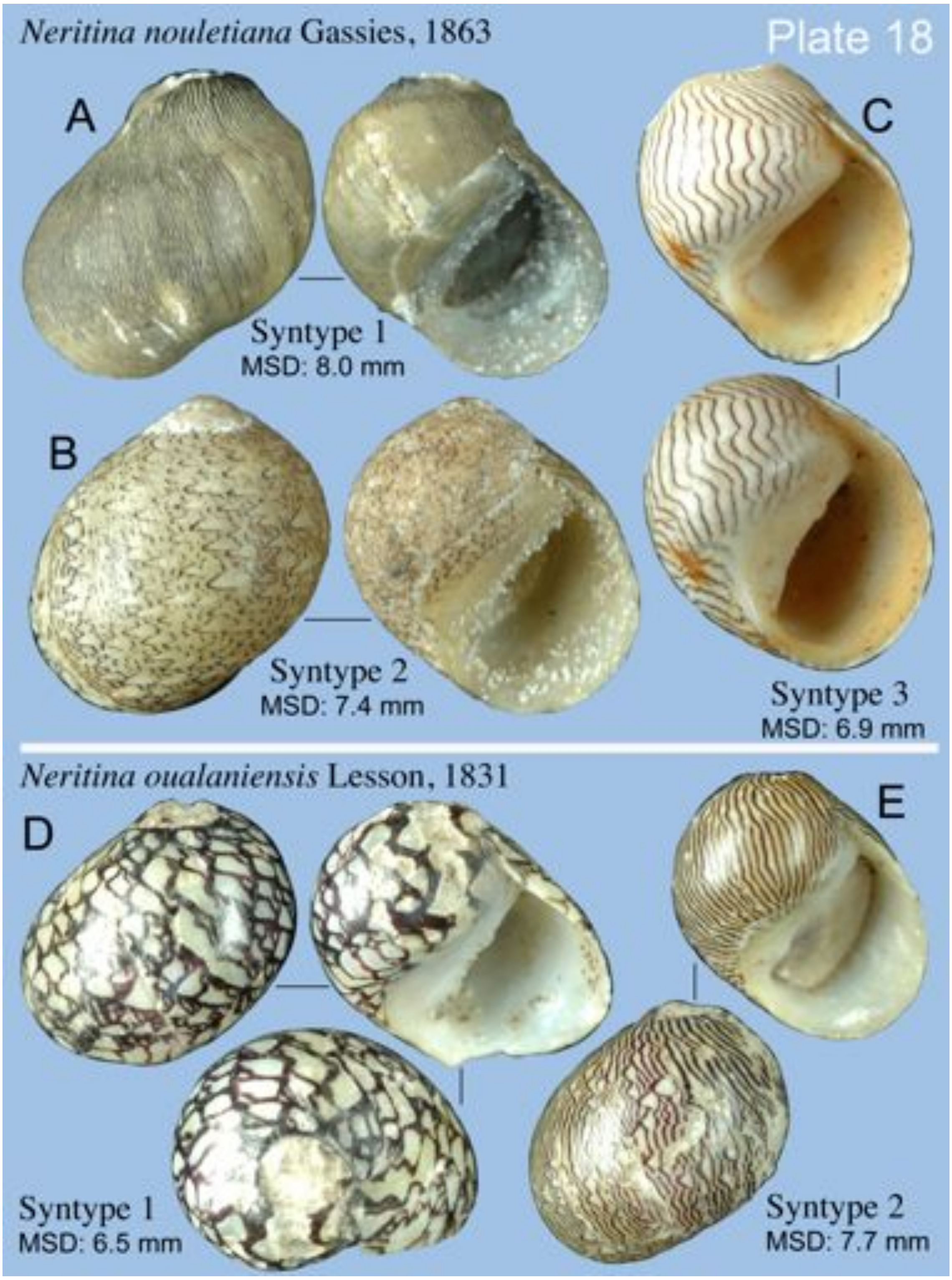

Neritina nouletiana Gassies, 1863
A
Syntype 1
MSD: 8.0 mm
B
Syntype 2
MSD: 7.4 mm
C
Syntype 3
MSD: 6.9 mm
Neritina oualaniensis Lesson, 1831
D
Syntype 1
MSD: 6.5 mm
E
Syntype 2
MSD: 7.7 mm

Plate 19.

A, B, C

Neritina perfecta Mabille, 1895
Bulletin Société Histoire Naturelle, Autun, 8: 397
17 syntypes MNHN
Locality: Vanuatu (Nouvelles-Hébrides)
MSD: 10.6–20.0 mm

D, E

Nerita (*Neritina*) *petitii* Récluz, 1841
Revue Zoologique, par la Société Cuvierienne, 4(9): 273–274
Holotype MNHN
Locality: Saint-Domingue?
MSD: 37.2 mm

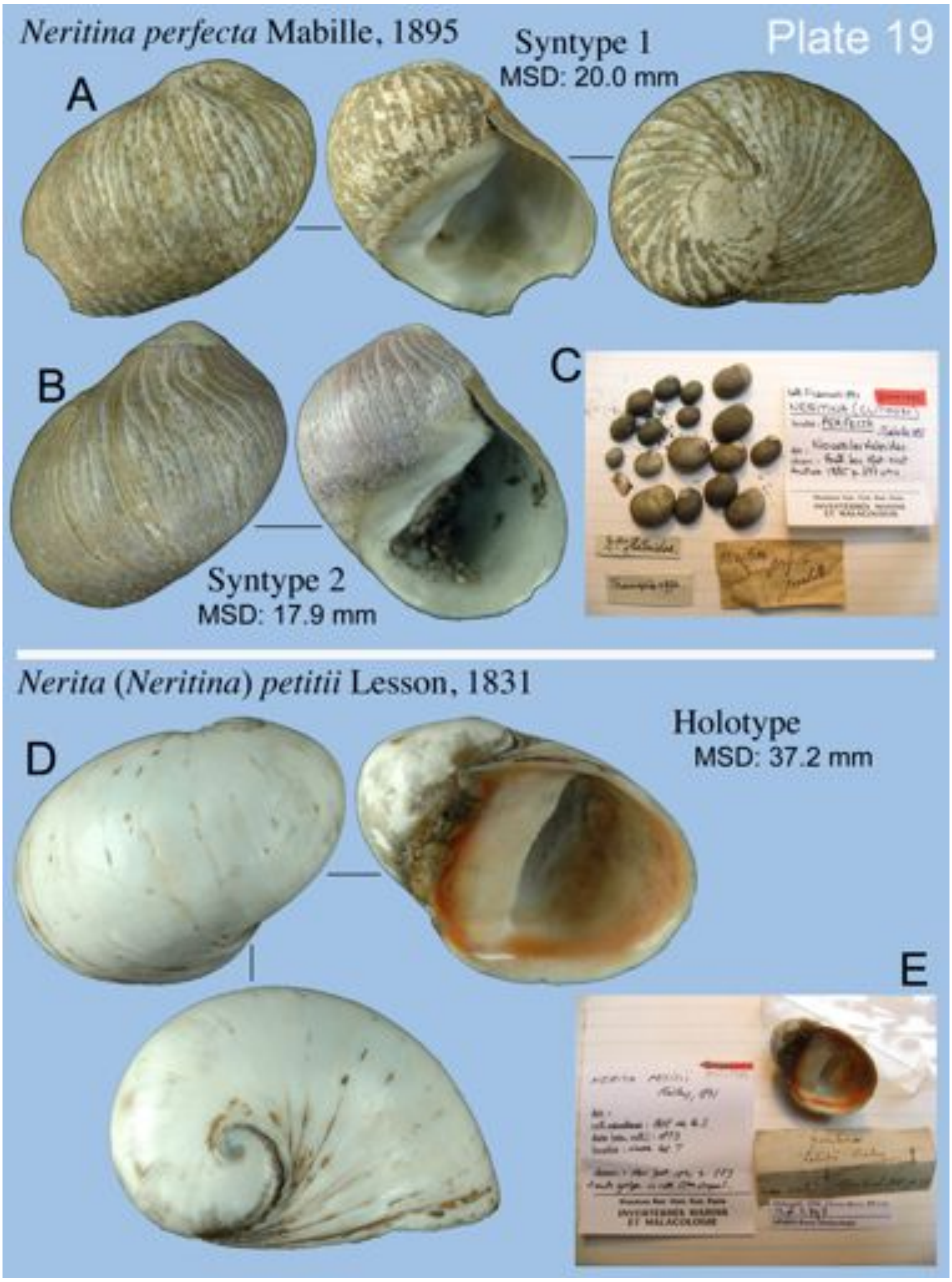

Neritina perfecta Mabille, 1895
Plate 19
Syntype 1
MSD: 20.0 mm
A
B
C
Syntype 2
MSD: 17.9 mm
Nerita (Neritina) petitii Lesson, 1831
Holotype
MSD: 37.2 mm
D
E

Plate 20.

A, B, C

Nerita recluziana Le Guillou, 1841
Revue Zoologique, par la Société Cuvierienne 4(11): 345
5 syntypes MNHN
Locality: Tahiti
MSD: 12.1–17.6 mm

D

Nerita reticulata Quoy & Gaimard, 1834
Voyage de découvertes de l'Astrolabe. Exécuté par ordre du Roi, pendant les années 1826–1827–1828–1829, sous le commandement de M.J. Dumont d'Urville. Zoologie. Tome troisième. J. Tastu, Paris. Vol. 3: 194 (Pl.65, Fig.4–5)
4 syntypes MNHN
Locality: Port Dorey, Papua New Guinea
MSD: 19.0–25.8 mm

Nerita recluziana Le Guillou, 1841

Plate 20

A

Syntype 1
MSD: 12.1 mm

B

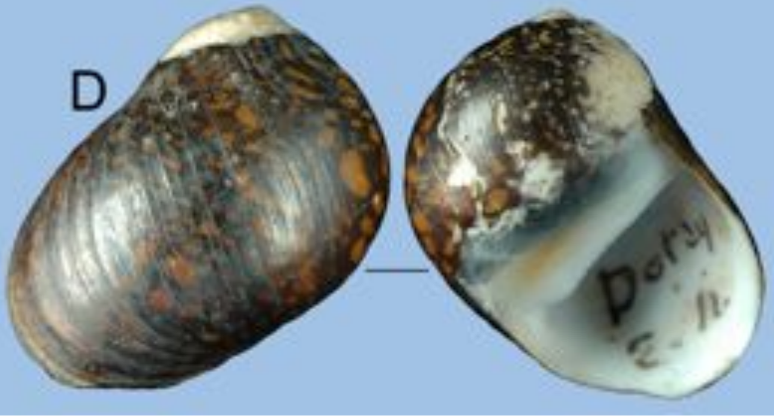
Syntype 4

C

Syntype 2,3,4 MSD: 11.0 (left), 14.0 (middle),17.9 mm

Nerita reticulata Quoy & Gaimard, 1834

D



Syntype
MSD: 25.8 mm

Plate 21.

A

Neritina sandwichensis Deshayes, 1838
Lamarck JB, Histoire naturelle des animaux sans vertèbres. 2 éd. Milne-Edwards. Paris.
Vol.8: 579
3 syntypes MNHN
Locality: Sandwich Is., Hawaii
MSD: 17.2–20.2 mm

B

Nerita (*Clithon*) *souleyetana* Récluz, 1842
Revue Zoologique, par la Société Cuvierienne 5: 182–183
2 syntypes MNHN
Locality: Tahiti, French Polynesia
MSD: 14.0–14.7 mm

C

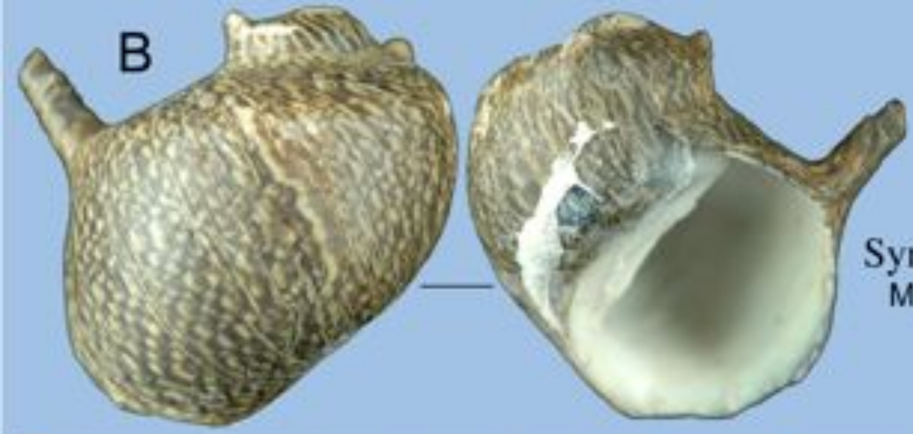
Nerita (*Clithon*) *sowerbiana* Récluz, 1843
Proceedings of the Zoological Society of London for 1842, 10: 174
3 syntypes
Locality: Sinait, North Ylocos, Luzon Is., Philippines
MSD: 15.9–16.6 mm

Plate 21

Neritina sandwichensis Deshayes, 1838

Syntype
MSD: 20.2 mm

Nerita (*Clithon*) *souleyetana* Récluz, 1842



Syntype
MSD: 14.0 mm

Nerita (*Clithon*) *sowerbiana* Récluz, 1843

Syntype
MSD: 16.0 mm

Plate 22.

A, B

Navicella splendens Mabille, 1895

Bulletin Société Histoire Naturelle, Autun, 8: 399

3 syntypes MNHN

Locality: Vanuatu (Nouvelles-Hébrides)

MSD: 23.2–31.5 mm

C

Nerita subalata Souleyet, 1842

Revue Zoologique, par la Société Cuvierienne, 5: 269

1 syntype MNHN

Locality: Luzon Is., Philippines

MSD: 10.7 mm

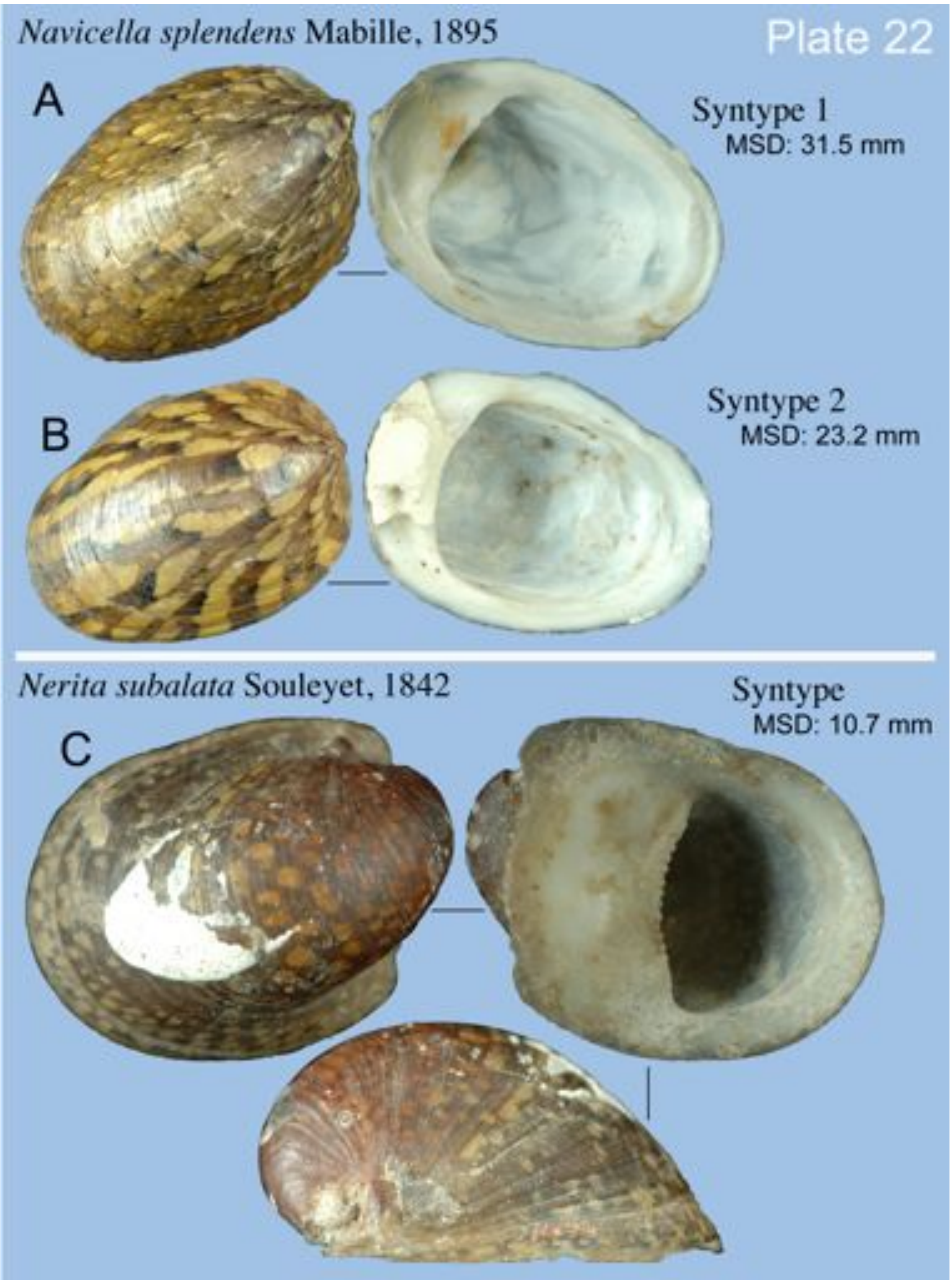


Plate 22

Navicella splendens Mabille, 1895

Syntype 1
MSD: 31.5 mm

Syntype 2
MSD: 23.2 mm

Nerita subalata Souleyet, 1842

Syntype
MSD: 10.7 mm

Plate 23.

A, B

Neritina subgranosa Mabille, 1895
Bulletin Société Histoire Naturelle, Autun, 8: 399
8 syntypes MNHN
Locality: Vanuatu (Nouvelles-Hébrides)
MSD: 11.0–12.2 mm

C

Neritina (*Neripteron*) *taitensis* Lesson, 1831
Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825… for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 385
1 syntype MNHN
Locality: Point Venus, Matavai, Tahiti
MSD: 14.0 mm

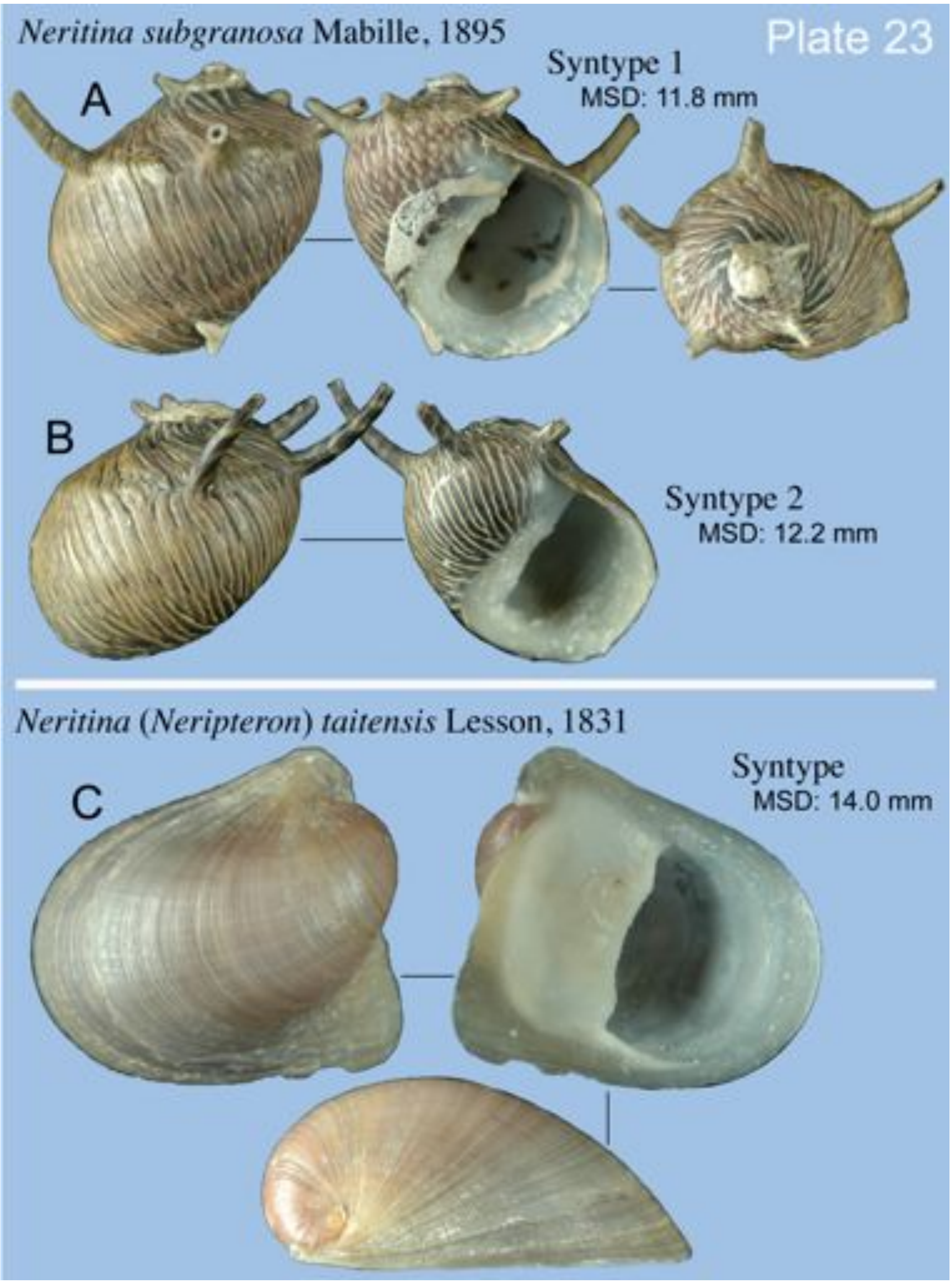


Plate 23

Neritina subgranosa Mabille, 1895

Neritina (*Neripteron*) *taitensis* Lesson, 1831

Plate 24.

A

Nerita tritonensis Le Guillou, 1841
Revue Zoologique, par la Société Cuvierienne 4(11): 345
1 syntype MNHN
Locality: Triton Bay, Indonesia
MSD: 9.1 mm

B

Neritina turbida Morelet, 1849
Testacea novissima insulae Cubanae et America Centralis Chez J.-B. Bailliére, Paris. Part1: 27
13 syntypes MNHN
Locality: Rio Machaquilan, Guatemala
MSD: 8.4–8.6 mm

C, D

Clithon undatus Lesson, 1831
Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825… for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 381 (Pl.13, Fig.13)
6 syntypes MNHN
Locality: Tahiti
MSD: 15.4–21.2 mm

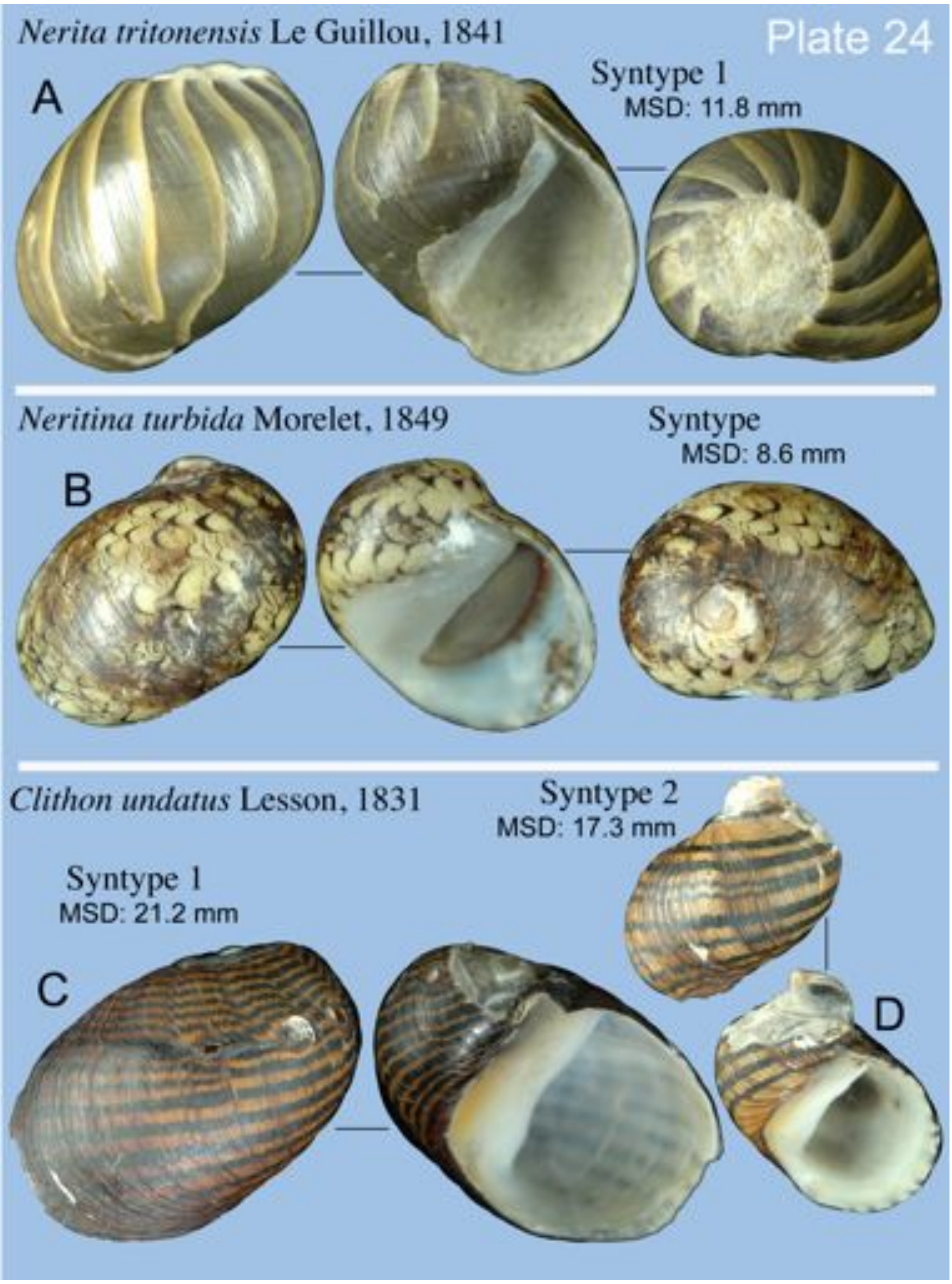

Nerita tritonensis Le Guillou, 1841
Plate 24
A
Syntype 1
MSD: 11.8 mm
Neritina turbida Morelet, 1849
Syntype
MSD: 8.6 mm
B
Clithon undatus Lesson, 1831
Syntype 2
MSD: 17.3 mm
Syntype 1
MSD: 21.2 mm
C
D

Plate 25.

A

Neritina (*Clithon*) *unidentata* Récluz, 1850
Journal de Conchyliologie 1(2): 158 (Pl.7, Fig.8)
2 syntypes MNHN
Locality: Tahiti
MSD: 10.6 mm, 12.9 mm

B

Clithon variabilis Lesson, 1831
Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825… for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 383–384
3 syntypes MNHN
Locality: New Ireland (Nouvelle-Irelande), Papua New Guinea; Mauritius (Maurice Is.)
MSD: 10.4 mm

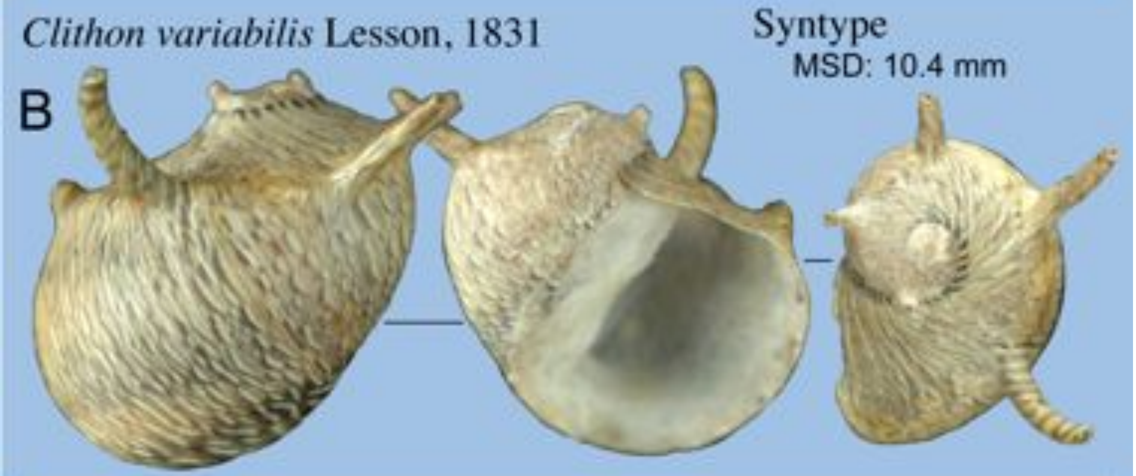
C, D

Neritina variegata Lesson, 1831
Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825… for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 378–379
4 syntypes MNHN
Locality: New Ireland (Nouvelle-Irelande), Papua New Guinea
MSD: 11.1–21.4 mm

Plate 25

Neritina (*Clithon*) *unidentata* Récluz, 1850

Clithon variabilis Lesson, 1831



Neritina variegata Lesson, 1831

Plate 26.

A, B

Nerita vestita Souleyet, 1842

Revue Zoologique, par la Société Cuvierienne, 5: 269

2 syntypes MNHN

Locality: Luzon Is., Philippines

MSD: 13.1 mm, 14.8 mm

C, D

Neritina waigiensis Lesson, 1831

Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825… for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 379–380

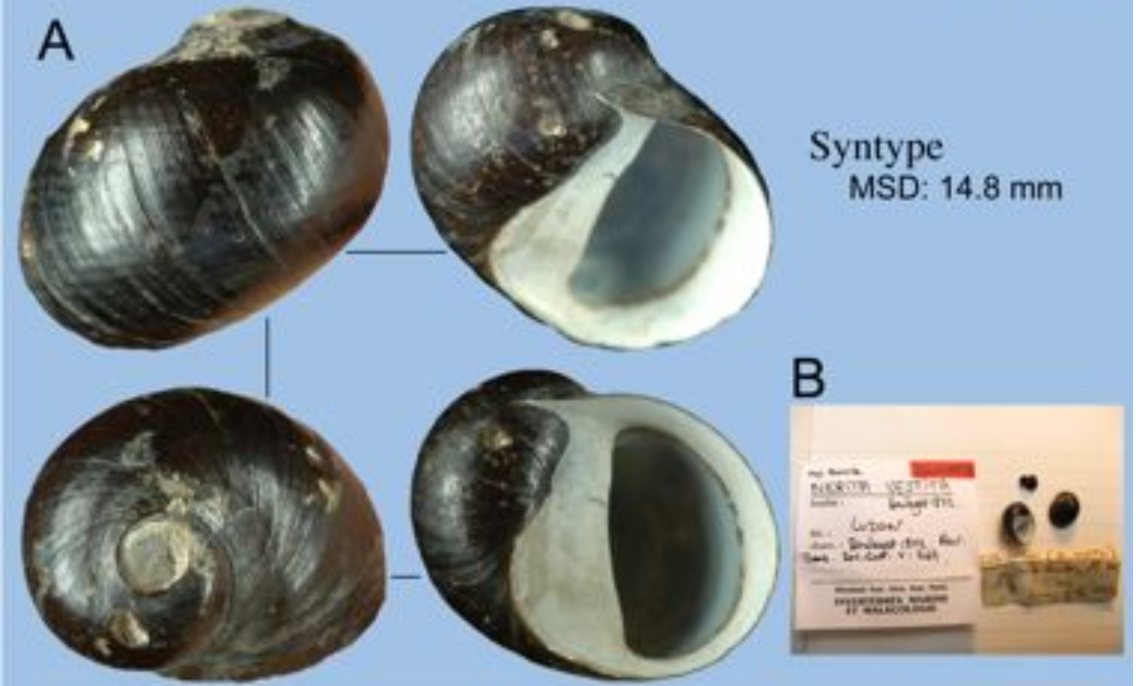
4 syntypes MNHN

Locality: New Ireland (Nouvelle-Irelande), Papua New Guinea

MSD: 18.0–19.8 mm

Plate 26

Nerita vestita Souleyet, 1842



Neritina waigiensis Lesson, 1831

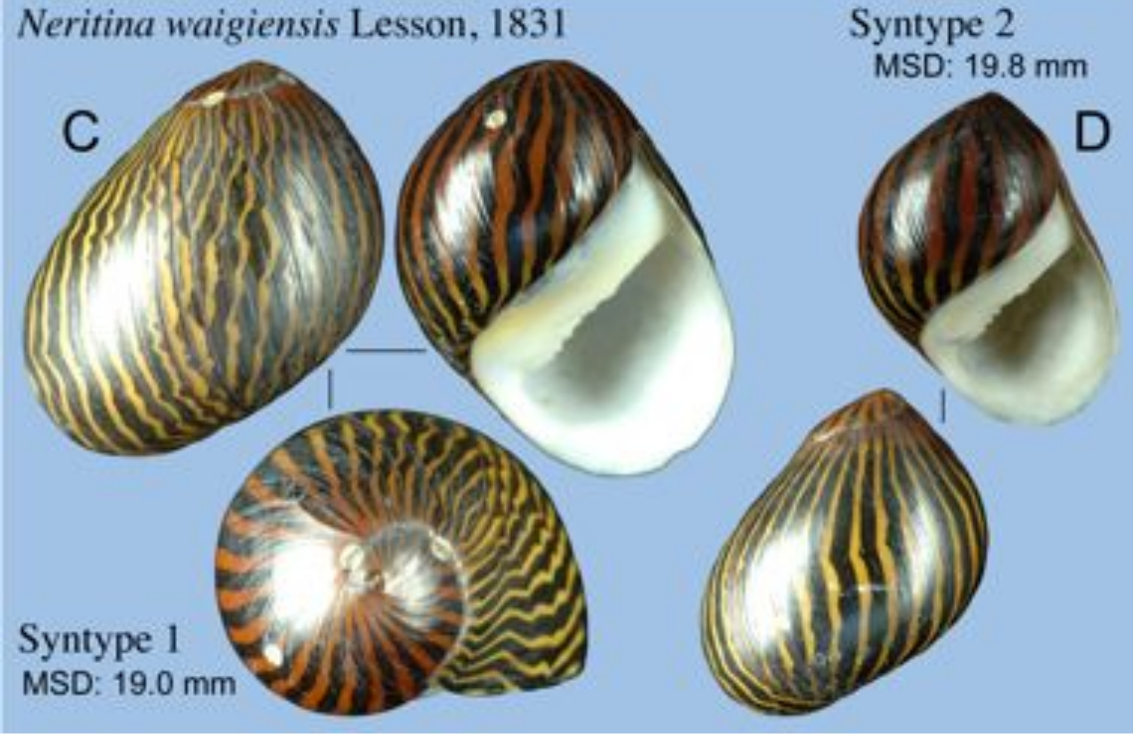


Plate 27.

A, B

Neritina wallisiarum Récluz, 1850

Journal de Conchyliologie 1(2): 161 (Pl.7, Figs.11–12)

Lectotype MNHN (New Caledonia); 1 Paralectotype MNHN (New Caledonia); 3 paralectotypes MHNG

Locality: Wallis Is. (the Territory of the Wallis and Futuna Islands); New Caledonia

MSD: 34.5 mm (Lectotype), 28.3 mm (Paralectotype)

C, D

Navicella zebra Lesson, 1831

Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825… for 1830–1831. Histoire naturelle. Zoologie. Vol. 2: 379–380

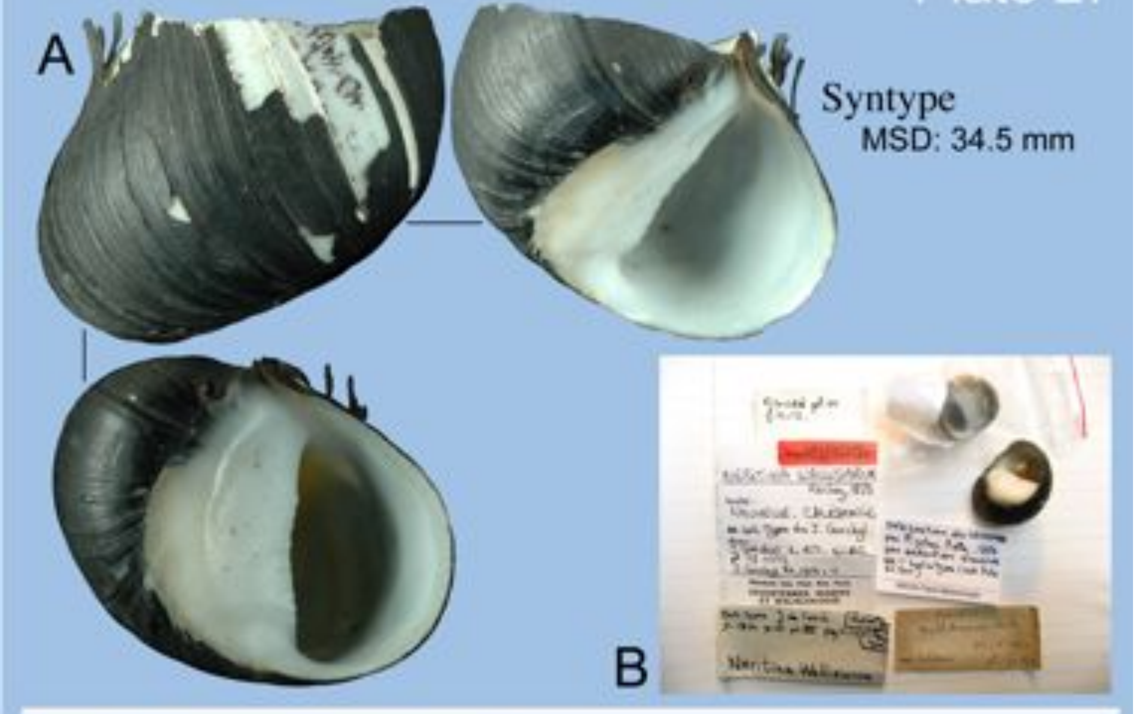
2 syntypes MNHN

Locality: New Ireland (Nouvelle-Irelande), Papua New Guinea

MSD: 10.9 mm, 13.0 mm

Plate 27

Neritina wallisiarum Récluz, 1850



Navicella zebra Lesson, 1831

Plate 28.

A, B, C
Nerita zebra Bruguière, 1792
Catalogue des coquilles envoyées de Cayenne, à la Société d'Histoire Naturelle de Paris, par M. Le Blond. Actes de la Société d'Histoire Naturelle de Paris 1: 126 (No.21)
2 syntypes MNHN
Locality: French Guinea (Cayenne)
MSD: 18.6 mm, 19.2 mm

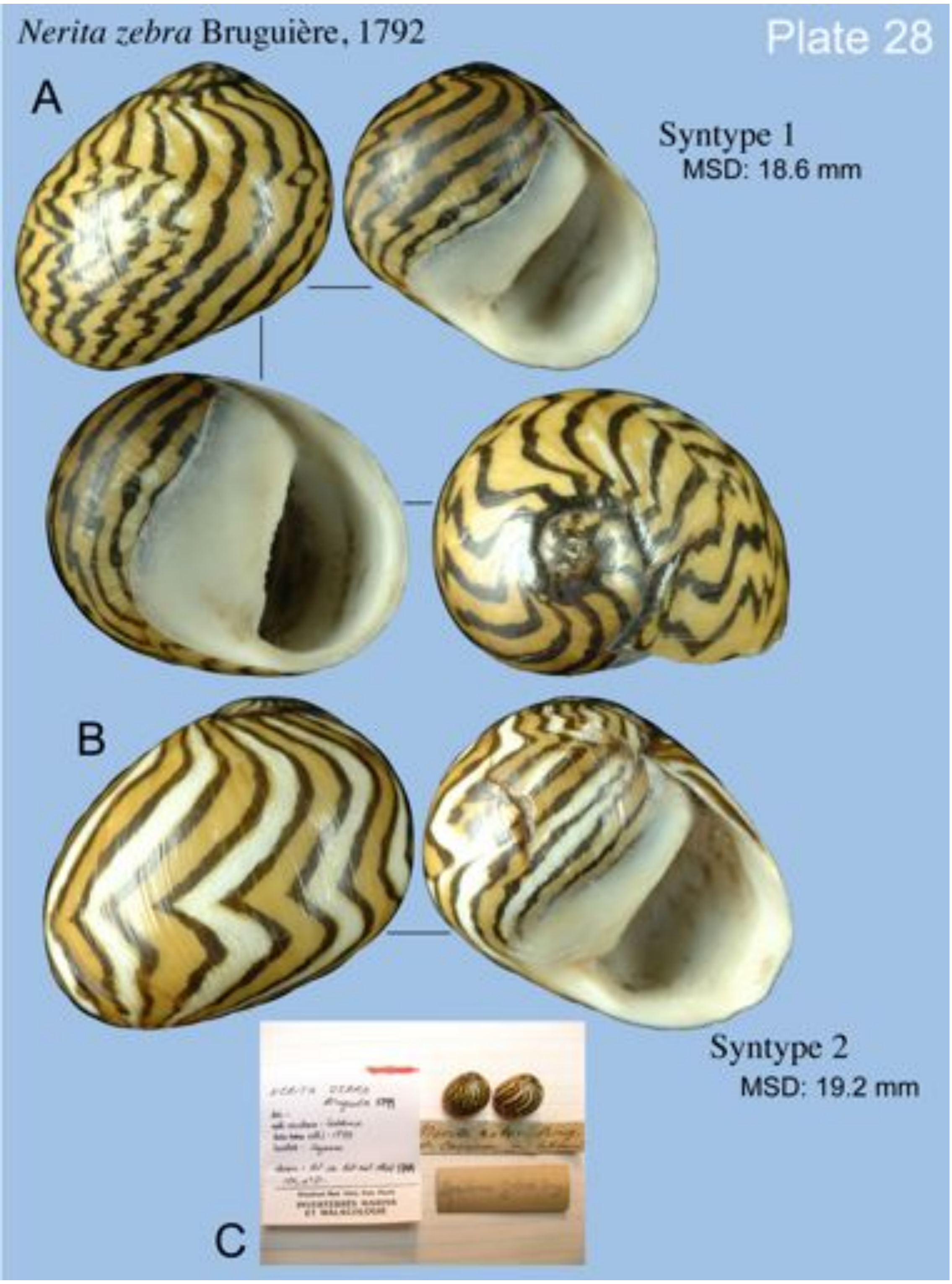

Nerita zebra Bruguière, 1792

Plate 28

Type specimens, London Museum

Plate 29.

A

Neritina adumbrata Reeve, 1855

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina. Natica. Navicella. Siphonaria. Nerita. Latia.* L. Reeve, London: [November 1855] Pl.12, Fig. 57a,b

Holotype BMNH

Locality: Solomon Is.

MSD: 22.3 mm

B

Neritina aequinoxialls Morelet, 1848

Revue Zoologique, par La Société Cuvierienne [1848]: 355

5 syntypes BMNH

Locality: Príncipe, São Tomé and Príncipe

MSD: 18.1–19.7 mm

C

Neritina africana Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina. Natica. Navicella. Siphonaria. Nerita. Latia.* L. Reeve, London: [January 1856] Pl.30, Fig. 138a,b

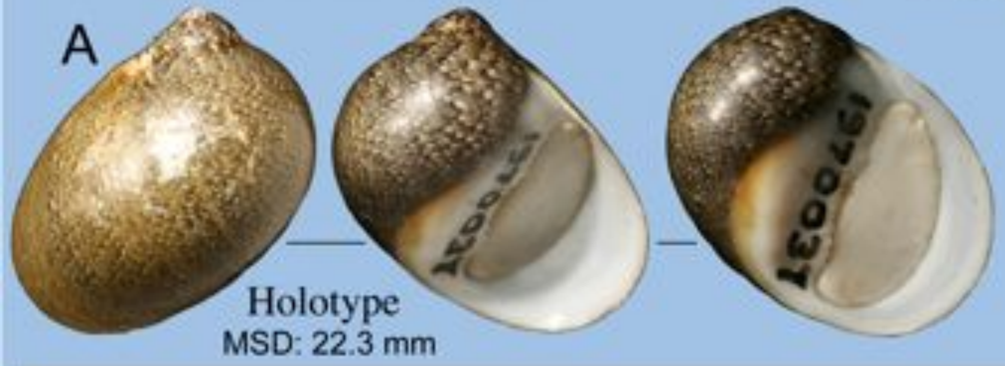
8 syntypes BMNH

Locality: Africa

MSD: 7.1 mm

Plate 29

Neritina adumbrata Reeve, 1855



Neritina aequinoxialls Morelet, 1848

Neritina africana Reeve, 1856

Plate 30.

A

Neritina aspersa Sowerby II, 1849 [Récluz MS.]

Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 524, pl. 110, Fig. 43–44

4 syntypes BMNH

Locality: Hawaiian Island

MSD: 14.7 mm (with spine)

B

Neritina atra Gray, 1831

Gray, John Edward. The Zoological Miscellany. Treuttel, Wurtz. No.1 [February, 1831]: 11

3 syntypes BMNH

Locality: Bioko (Fernando Pó), Cameroon

MSD: 22.7–23.0 mm

C

Neritina baconi Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [January 1856] Pl.28, Fig. 127a,b

3 syntypes BMNH

Locality: Swan River, Western Australia?

MSD: 10.0–11.4 mm

Plate 30

Neritina aspersa Sowerby II, 1849

A

Syntype
MSD: 14.7 mm

Neritina atra Gray, 1831

Syntype
MSD: 22.7 mm

B

Neritina baconi Reeve, 1856

Syntype
MSD: 11.4 mm

C

Plate 31.

A

Navicella bimaculata Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.1, Fig. 2a,b

5 syntypes BMNH

Locality: Mauritius

MSD: 18.0–26.3 mm

B

Navicella caerulescens Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.7, Fig. 29a,b

5 syntypes BMNH; 5 syntypes BMNH; 4 syntypes BMNH; Syntype BMNH;

Locality: Calcutta (in the streets of the city and in the Botanic Gardens)

MSD: 19.4–23.2 mm

C

Neritina californica Reeve, 1855

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [October 1855] Pl.4, Fig. 20a,b

2 syntypes BMNH

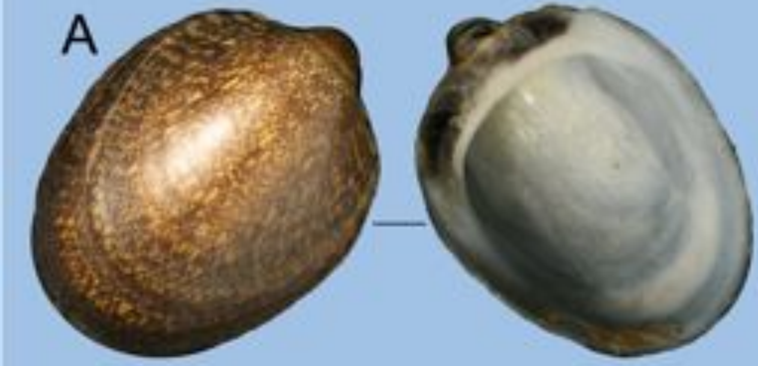
Locality: Gulf of California

MSD: 27.7 mm, 28.6 mm

Plate 31

Navicella bimaculata Reeve, 1856

A

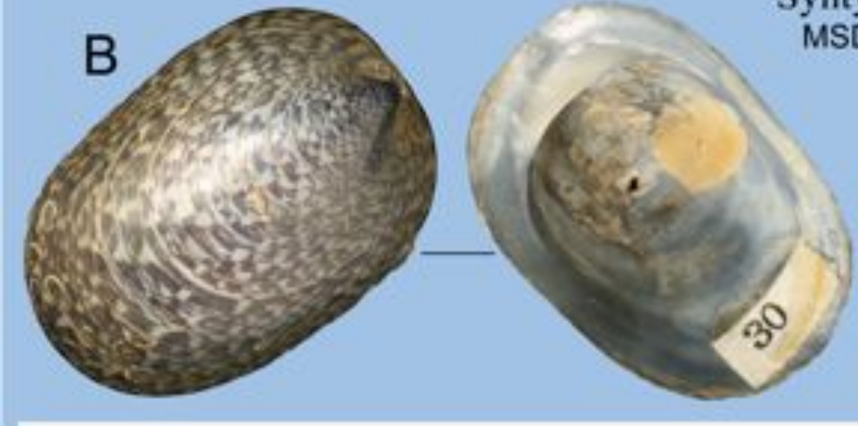


Syntype
MSD: 26.3 mm

Navicella caerulescens Reeve, 1856

Syntype
MSD: 19.9 mm

B



Neritina californica Reeve, 1855

Syntype
MSD: 28.6 mm

C

Plate 32.

A, B

Neritina cariosa Gray, 1827

[Names on plate legends] In: Encyclopaedia Metropolitana. London (1 December 1827): pl.5, Fig.12

Nerita cariosa Wood, 1828 (Type specimen may be objective synonym of *Neritina cariosa* Gray, 1827)

Wood, William. Supplement to the Index Testaceologicus, Or, A Catalogue of Shells, British and Foreign. Illustrated with 480 Figures. W. Wood. London: 45 (Pl.8, Fig.9), as *Neritina*

3 syntypes BMNH

Locality: ”Africa”?

MSD: 21.3–23.4 mm

C, D, E

Neritina chlorostoma Sowerby I, 1833

Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832 (13 March 1833): 201 (illustrated in Conchological Illustrations May 2, 1836: 97, fig. 34; Tahiti.)

4 syntypes BMNH

Locality: Tahiti

MSD: 11.7–13.6 mm

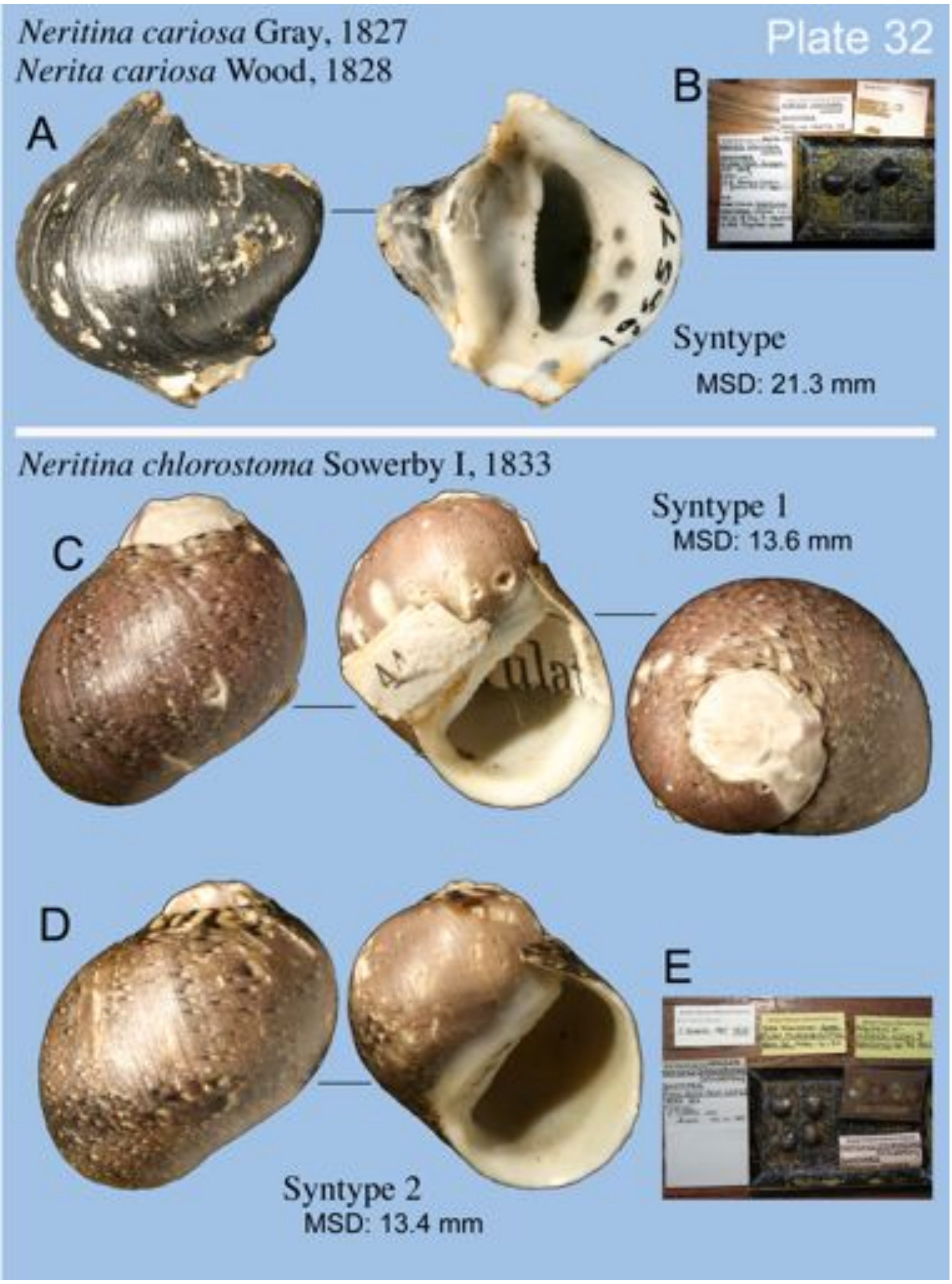

Neritina cariosa Gray, 1827
Nerita cariosa Wood, 1828
Plate 32
A
B
Syntype
MSD: 21.3 mm
Neritina chlorostoma Sowerby I, 1833
C
Syntype 1
MSD: 13.6 mm
D
E
Syntype 2
MSD: 13.4 mm

Plate 33.

A

Neritina christovalensis Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina. Natica. Navicella. Siphonaria. Nerita. Latia.* L. Reeve, London: [February 1856] Pl.33, Fig. 150a,b

Holotype BMNH

Locality: San Christoval, Solomon Is.

MSD: 12.7 mm

B, C, D

Navicella clypeolum Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 157–158

8 syntypes BMNH

Locality: mountain stream, Pasuguing, North Ylocos, Luzon, Philippines

MSD: 26.1–32.5 mm

Plate 33

Neritina christovalensis Reeve, 1856

Navicella clypeolum Récluz, 1843

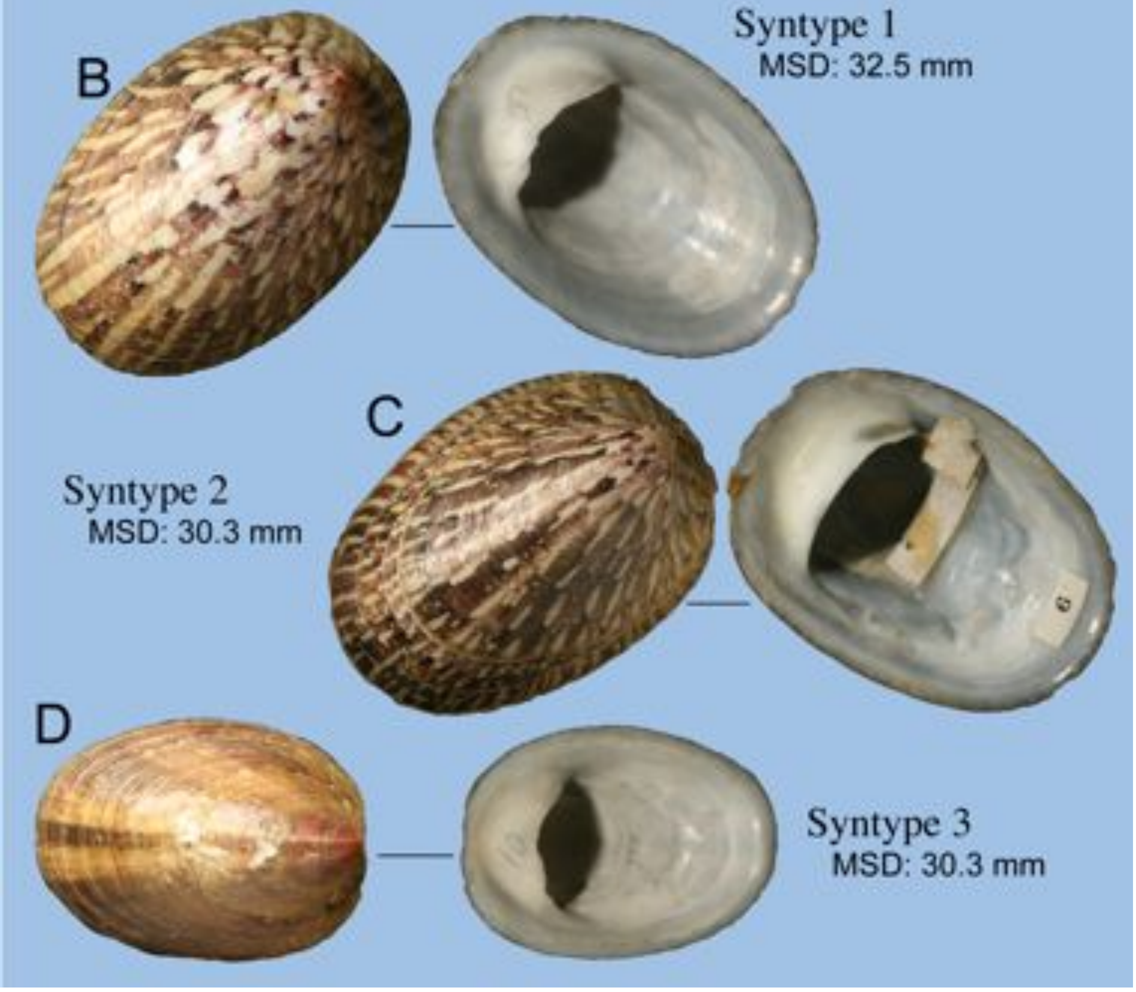


Plate 34.

A, B, C

Neritina comorensis Morelet, 1877
Journal de Conchyliologie, 25: 345
5 syntypes BMNH
Locality: Anjouan (Anjouan), Comoros
MSD: 9.0–11.4 mm

D

Nerita constellata Sowerby III, 1905
Annals and Magazine of Natural History, series 7, 16: 190
Holotype? BMNH
Locality: Sri Lanka (Ceylon)
MSD: 9.5 mm

D

Neritina cornata Reeve, 1855
Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [November 1855] Pl.13, Fig. 63a,b
3 syntypes BMNH
Locality: Philippines
MSD: 20.6–26.6 mm

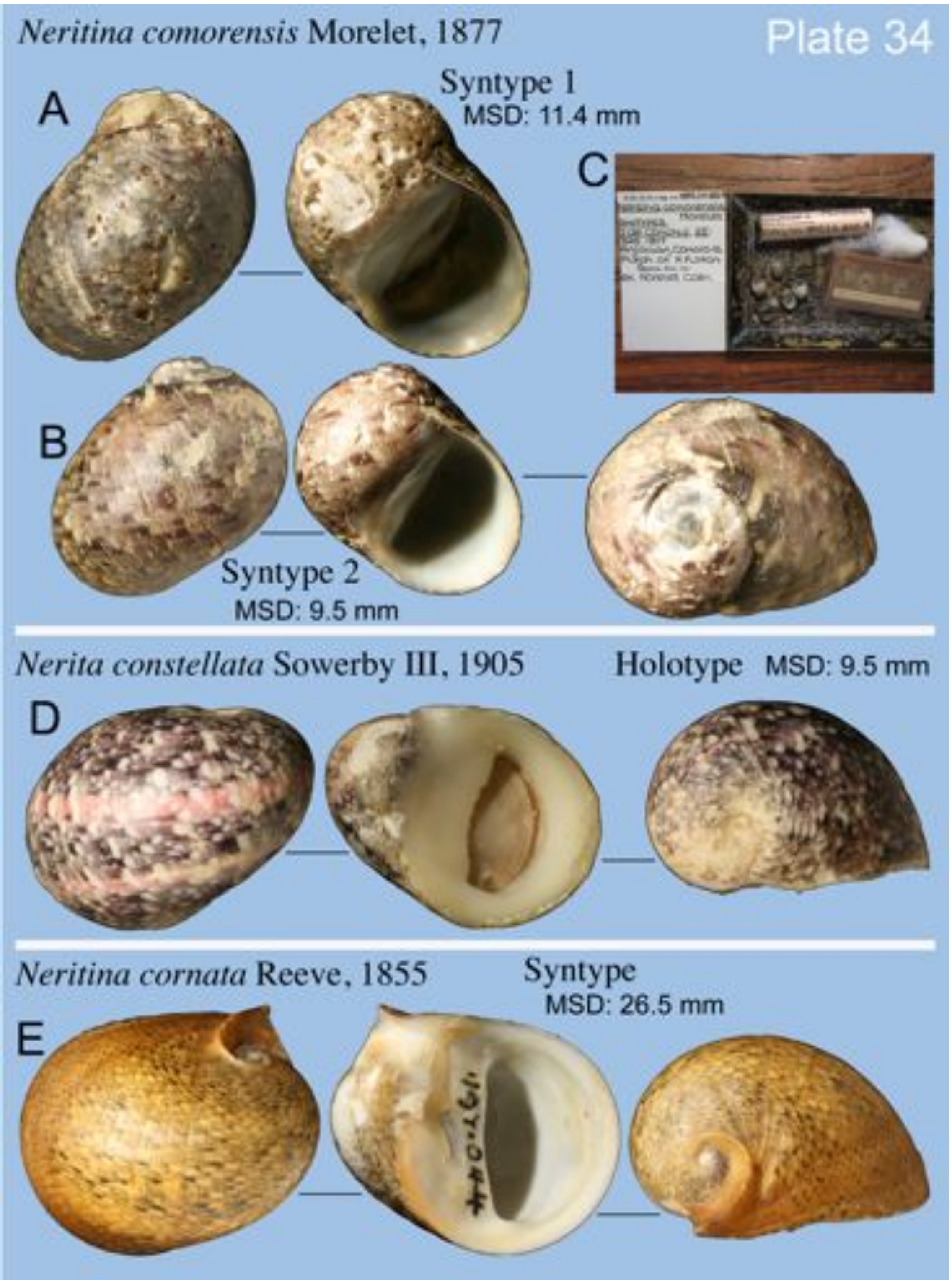

Neritina comorensis Morelet, 1877
Plate 34
A
Syntype 1
MSD: 11.4 mm
C
B
Syntype 2
MSD: 9.5 mm
Nerita constellata Sowerby III, 1905
Holotype
MSD: 9.5 mm
D
Neritina cornata Reeve, 1855
Syntype
MSD: 26.5 mm
E
1197.044

Plate 35.

A, B, C

Navicella crepiduloides Reeve, 1856
Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.5, Fig. 19a,b
5 syntypes BMNH
Locality: ?
MSD: 21.7–22.1 mm

D

Neiritna cristata Morelet, 1864
Journal de Conchyliologie, 12: 288
6 syntypes BMNH
Locality: Gabon, Africa
MSD: 18.1–21.3 mm

E, F

Navicella cumingiana Récluz, 1843
Proceedings of the Zoological Society of London for 1842, 10: 157
4 syntypes BMNH
Locality: mountain stream, Camaguing, Philippines
MSD: 28.6–34.0 mm

Navicella crepiduloides Reeve, 1856

Plate 35

Neiritna cristata Morelet, 1864

Navicella cumingiana Récluz, 1843

Plate 36.

A, B
Neritina cyanostoma Morelet, 1853
Journal de Conchyliologie 4: 373–374
6 syntypes BMNH
Locality: Vanuatu (Nouvelles-Hébrides)
MSD: 13.0–15.9 mm

C, D
Neritina dilatata Broderip, 1833
Proceedings of the Committee of Science and Correspondence of the Zoological Society of London for 1832, 2(25): 201 [13 March 1833]
4 syntypes BMNH
Locality: Tahiti
MSD: 15.9–20.7 mm

E
Nerita doingii Récluz, 1846
Journal de Conchyliologie for 1845, 13: 121
3 syntypes BMNH
Locality: Hanover Bay, Australia
MSD: 7.5–10.4 mm

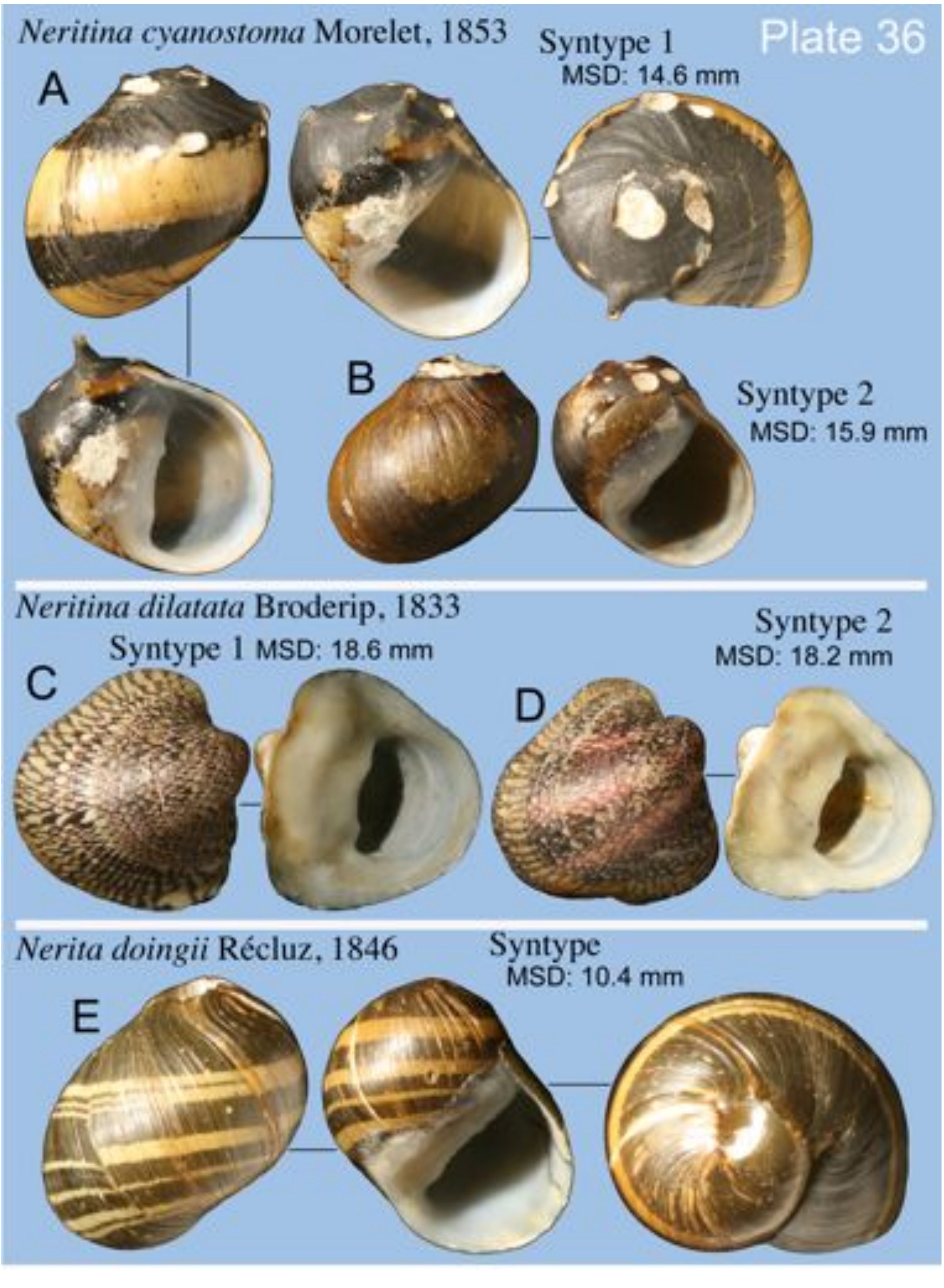


Plate 36
Neritina cyanostoma Morelet, 1853
Syntype 1
MSD: 14.6 mm
A
B
Syntype 2
MSD: 15.9 mm
Neritina dilatata Broderip, 1833
Syntype 1 MSD: 18.6 mm
Syntype 2
MSD: 18.2 mm
C
D
Nerita doingii Récluz, 1846
Syntype
MSD: 10.4 mm
E

Plate 37.

A

Theodoxus eudeli Sowerby III, 1917

Proceedings of the Malacological Society of London 12(6): 320, text-fig.

Figured syntype BMNH

Locality: Phu-Yen, Vietnam

MSD: 8.5 mm

B

Navicella excelsa Gassies, 1870

Journal de Conchyliologie 18: 150

Holotype BMNH

Locality: Pouébo, Jenjen, New Caledonia

MSD: 37.1 mm

C

Navicella eximia Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.6, Fig. 26a,b

4 syntypes BMNH

Locality: Ceylon (Layard)

MSD: 21.6–30.4 mm

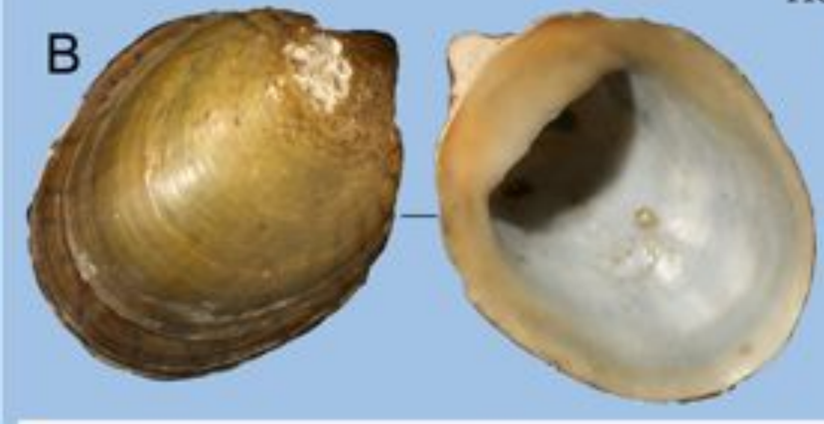
Plate 37

Theodoxus eudeli Sowerby III, 1917

Syntype
MSD: 8.5 mm

Navicella excelsa Gassies, 1870

Holotype
MSD: 37.1 mm



Navicella eximia Reeve, 1856

Syntype
MSD: 30.4 mm

Plate 38.

A, B

Neritina faba Sowerby I, 1836

Concholological Illustrations: Pl.90, Fig.10 [January 1]

4 syntypes BMNH

Locality: Singapore

MSD: 15.1–18.8 mm

C

Neritina flexuosa Gassies, 1878

Journal de Conchyliologie 26: 342

2 syntypes BMNH

Locality: Pouébo, New Caledonia

MSD: 7.8 mm, 8.2 mm

D

Neritina fraseri Reeve, 1855

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [November 1855] Pl.25, Fig. 113a,b

2 syntypes BMNH

Locality: “West Africa” Nosy-Be, Madagascar (East Africa)

MSD: 12.2mm, 12.8 mm

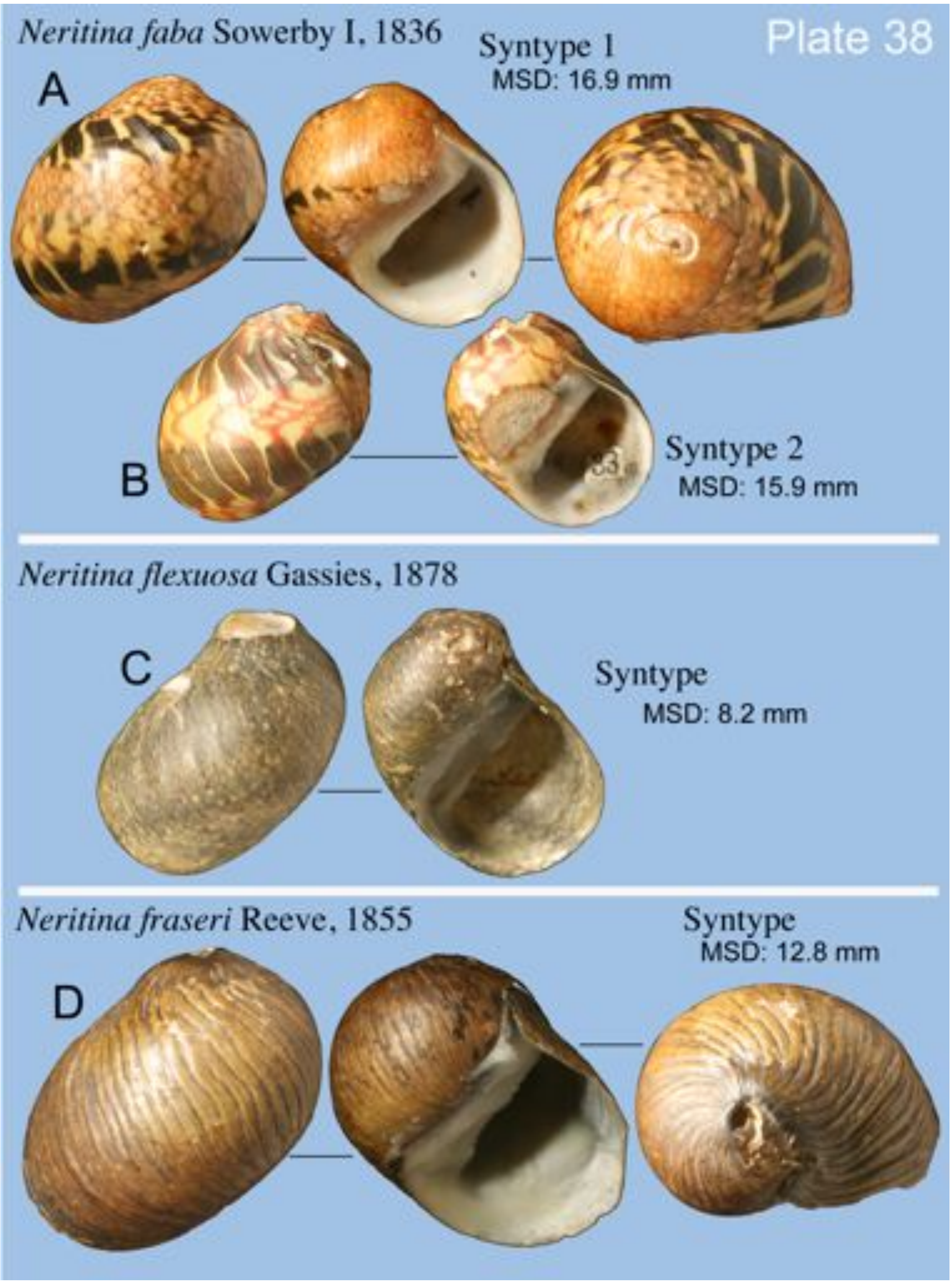


Plate 38
Neritina faba Sowerby I, 1836
Syntype 1
MSD: 16.9 mm
A
B
Syntype 2
MSD: 15.9 mm
Neritina flexuosa Gassies, 1878
C
Syntype
MSD: 8.2 mm
Neritina fraseri Reeve, 1855
Syntype
MSD: 12.8 mm
D

Plate 39.

A

Neritina fulgetrum Reeve, 1855

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [November 1855] Pl.23, Fig. 103a,b

Holotype BMNH

Locality: Madagascar?

MSD: 12.8 mm

B

Neritina granosa Sowerby I, 1825

A Catalogue of the shells contained in the collection of the late Earl of Tankerville arranged according to the Lamarckian Conchological System; together with an appendix, containing descriptions of many new species. Illustrated with several coloured plates. London: 45, App. 11

Syntype BMNH

Locality: South Sea Island

MSD: 31.9 mm

C

Neritina gravis Morelet, 1849

Testacea novissima insulae Cubanae et America Centralis Chez J.-B. Bailliére, Paris. Part1: 27

3 syntypes BMNH

Locality: Belize

MSD: 21.0–22.8 mm

Plate 39

Neritina fulgetrum Reeve, 1855

Neritina granosa Sowerby I, 1825

Neritina gravis Morelet, 1849

Plate 40.

A

Navicella haustrum Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.4, Fig. 18a,b

4 syntypes BMNH

Locality: New Caledonia

MSD: 29.1–29.7 mm

B

Navicella hupeana Gassies, 1863

Faune conchyliologique terrestre et fluvio-lacustre de la Nouvelle-Calédonie Part 1. Actes de la Société linnéenne de Bordeaux. 24: 114 (Pl.8, Fig.13)

2 syntypes BMNH

Locality: Balade, New Caledonia

MSD: 24.5 mm, 29.4 mm

C

Navicella insignis Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.5, Fig. 21a,b

Holotype BMNH

Locality: Sumatra, Indonesia

MSD: 29.9 mm

Plate 40

Navicella haustrum Reeve, 1856

Navicella hupeana Gassies, 1863

Navicella insignis Reeve, 1856

Plate 41.

A

Neritina intermedia Sowerby I, 1833
Proceedings of the Committee of Science and Correspondence of the Zoological Society of London for 1832, 2(25): 201 [13 March 1833]
4 syntypes BMNH
Locality: Bay of Montijo, Panama
MSD: 20.6–22.5 mm

B, C

Neritina latissima Broderip, 1833
Proceedings of the Committee of Science and Correspondence of the Zoological Society of London for 1832, 2(25): 200 [13 March 1833]
3 syntypes BMNH; syntype BMNH
Locality: Tahiti
MSD: 15.9–20.7 mm

D

Neritina layardi Reeve, 1855
Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [November 1855] Pl.24, Fig. 105a,b
3 syntypes BMNH; 4 syntypes BMNH
Locality: Sri Lanka (Ceylon)
MSD: 12.8–15.4 mm

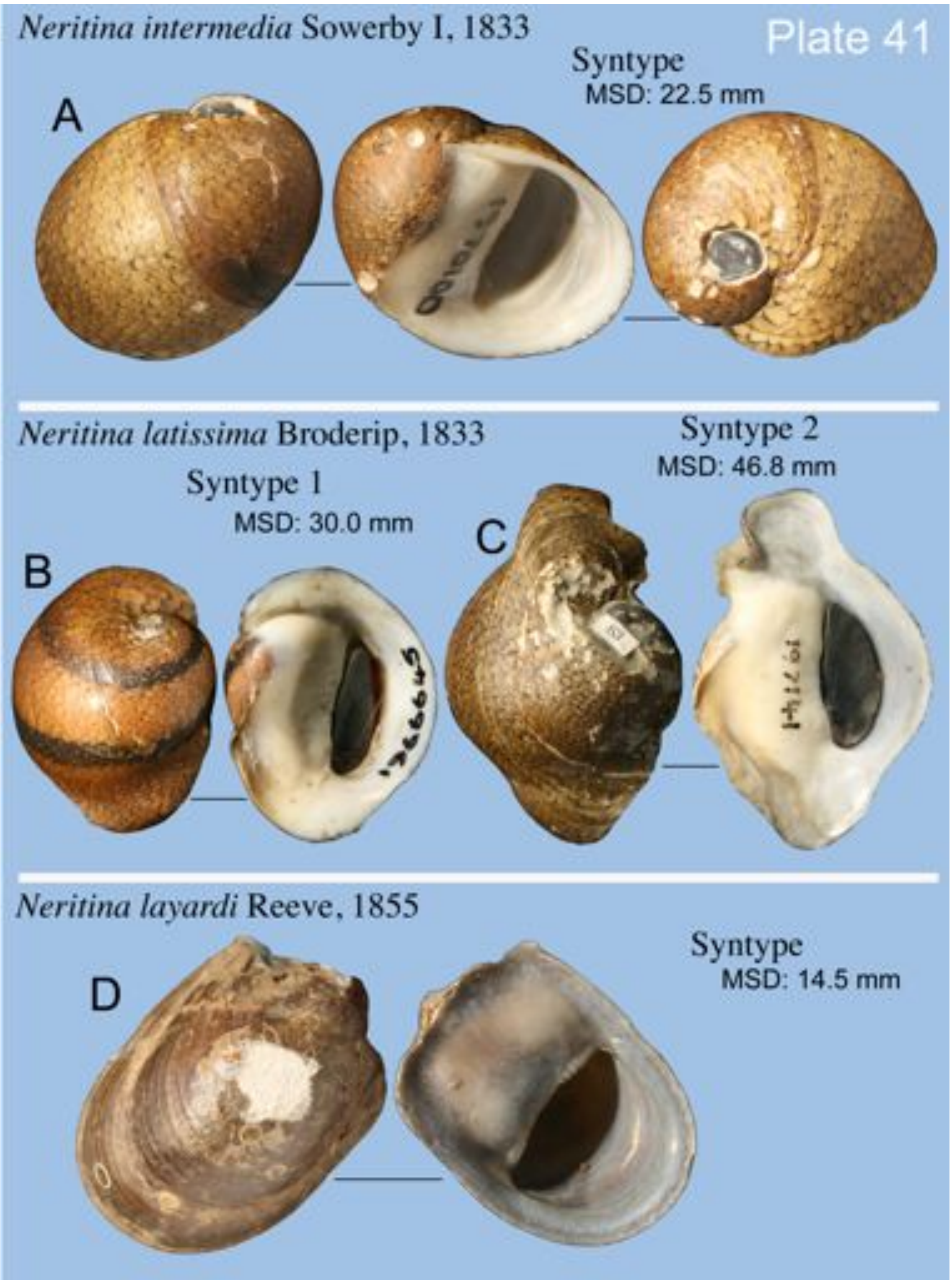


Plate 41
Neritina intermedia Sowerby I, 1833
Syntype
MSD: 22.5 mm
A
Neritina latissima Broderip, 1833
Syntype 1
MSD: 30.0 mm
B
Syntype 2
MSD: 46.8 mm
C
Neritina layardi Reeve, 1855
Syntype
MSD: 14.5 mm
D

Plate 42.

A

Neritina lenormandi Gassies, 1870

Journal de Conchyliologie 18: 150

Syntype BMNH (Tuo)

Locality: Tuo, New Caledonia; Kanala, New Caledonia

MSD: 24.4 mm

B

Neritina lentiginosa Reeve, 1855

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [November 1855] Pl.25, Fig. 110a,b

2 syntypes BMNH

Locality: Pacific Islands

MSD: 12.7 mm, 14.4 mm

C

Navicella lentiginosa Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.3, Fig. 9a,b

Holotype BMNH

Locality: ?

MSD: 23.0 mm

Plate 42

Neritina lenormandi Gassies, 1870

Syntype
MSD: 24.4 mm

Neritina lentiginosa Reeve, 1855

Syntype
MSD: 14.4 mm

Navicella lentiginosa Reeve, 1856

Holotype
MSD: 23.0 mm

Plate 43.

A

Neritina lifuensis A. Adams & Angas, 1864

Proceedings of the Scientific Meetings of the Zoological Society of London [1864]: 36

Holotype? BMNH

Locality: Lifu Is., Loyalty Islands

MSD: 24.8 mm

B, C

Navicella livida Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.3, Fig. 13a,b

2 syntypes BMNH

Locality: ?

MSD: 25.5 mm, 25.6 mm

D

Neritina macgillivrayi Reeve, 1855

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [October 1855] Pl.4, Fig. 16a,b

4 syntypes BMNH

Locality: Port Carteret, Solomon Is.

MSD: 28.0–45.5 mm

Neritina lifuensis A. Adams & Angas, 1864

Plate 43

Navicella livida Reeve, 1856

Neritina macgillivrayi Reeve, 1855

Plate 44.

A

Neritina madecassina Morelet, 1858

Morelet, Arthur. Séries conchyliologiques comprenant l'énumeration de mollusques terrestres et fluviatiles recueillis pendant le cours de différents voyages, ainsi que la description de plusieurs espèceś nouvelles. Chez Klincksieck. Paris. Vol. 1: 122

4 syntypes BMNH

Locality: Saint Marie, Madagascar

MSD: 17.0–20.1 mm

B

Navicella magnifica Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.4, Fig. 16a,b

Holotype BMNH

Locality: Hamond Is., Australian Seas

MSD: 43.4 mm

C

Neritina mauritiana Morelet, 1867

Journal de Conchyliologie 23: 228–229

Syntype BMNH

Locality: Ouagap, New Caledonia

MSD: 27.3–30.1 mm

Plate 44

Neritina madecassina Morelet, 1858

Syntype
MSD: 20.1 mm

Navicella magnifica Reeve, 1856

Holotype
MSD: 43.4 mm

Neritina mauritiana Morelet, 1867

Syntype
MSD: 30.1 mm

Plate 45.

A

Neritina montrouzieri Gassies, 1875

Journal de Conchyliologie 23: 228–229

Syntype BMNH

Locality: Ouagap, New Caledonia

MSD: 13.6 mm

B

Navicella moreletiana Gassies, 1866

Journal de Conchyliologie 14: 52–53

Holotype BMNH

Locality: Art Island, New Caledonia

MSD: 22.7 mm

C, D

Neritina morosa Gassies, 1870

Journal de Conchyliologie 18: 149

3 syntypes BMNH

Locality: New Caledonia

MSD: 6.9–8.2 mm

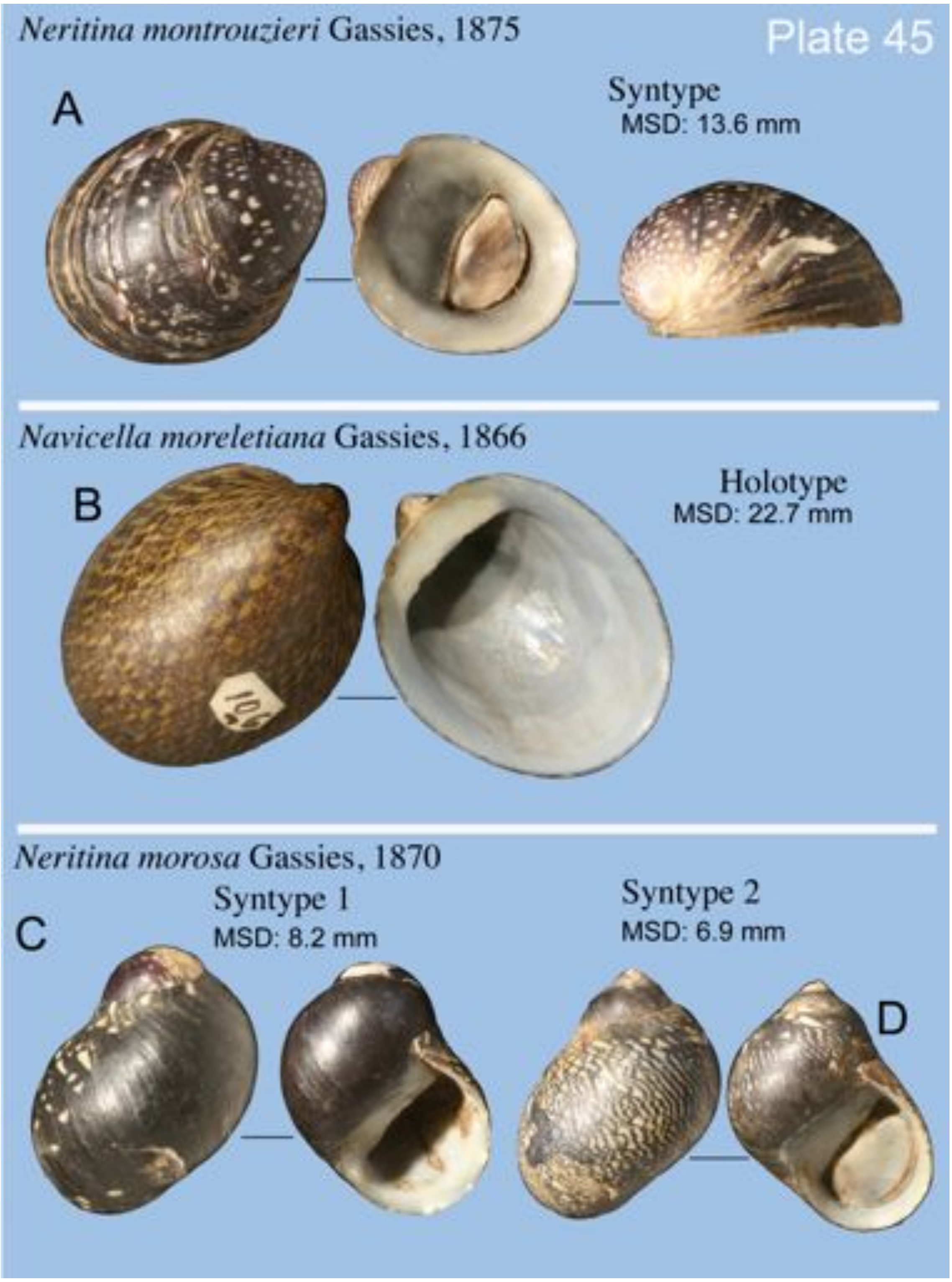

Neritina montrouzieri Gassies, 1875
Plate 45
A
Syntype
MSD: 13.6 mm
Navicella moreletiana Gassies, 1866
B
Holotype
MSD: 22.7 mm
Neritina morosa Gassies, 1870
Syntype 1
MSD: 8.2 mm
C
Syntype 2
MSD: 6.9 mm
D

Plate 46.

A

Navicella nana Montrouzier, 1879

Journal de Conchyliologie 27: 135

Syntype BMNH

Locality: New Caledonia

MSD: 6.8 mm

B

Neritina neglecta Pease, 1860

Proceedings of the Scientific Meetings of the Zoological Society of London [1860]: 435

Lectotype BMNH (designated by Kay 1965; junior synonym of *Nerita picea* Récluz, 1853); 3 paralectotypes BMNH (these specimens can be regarded as *Neritina cariosa* Gray, 1827)

Locality: Sandwich Is. (Hawaii)

MSD: 16.4 mm (lectotype), 15.4 mm (paralectotype)

C, D

Neritina nouletiana Gassies, 1863

Faune conchyliologique terrestre et fluvio-lacustre de la Nouvelle-Calédonie Part 1. Actes de la Société linnéenne de Bordeaux. 24: 104–105 (Pl.8, Fig.5)

7 syntypes BMNH

Locality: Art Is., New Caledonia

MSD: 6.9–11.0 mm

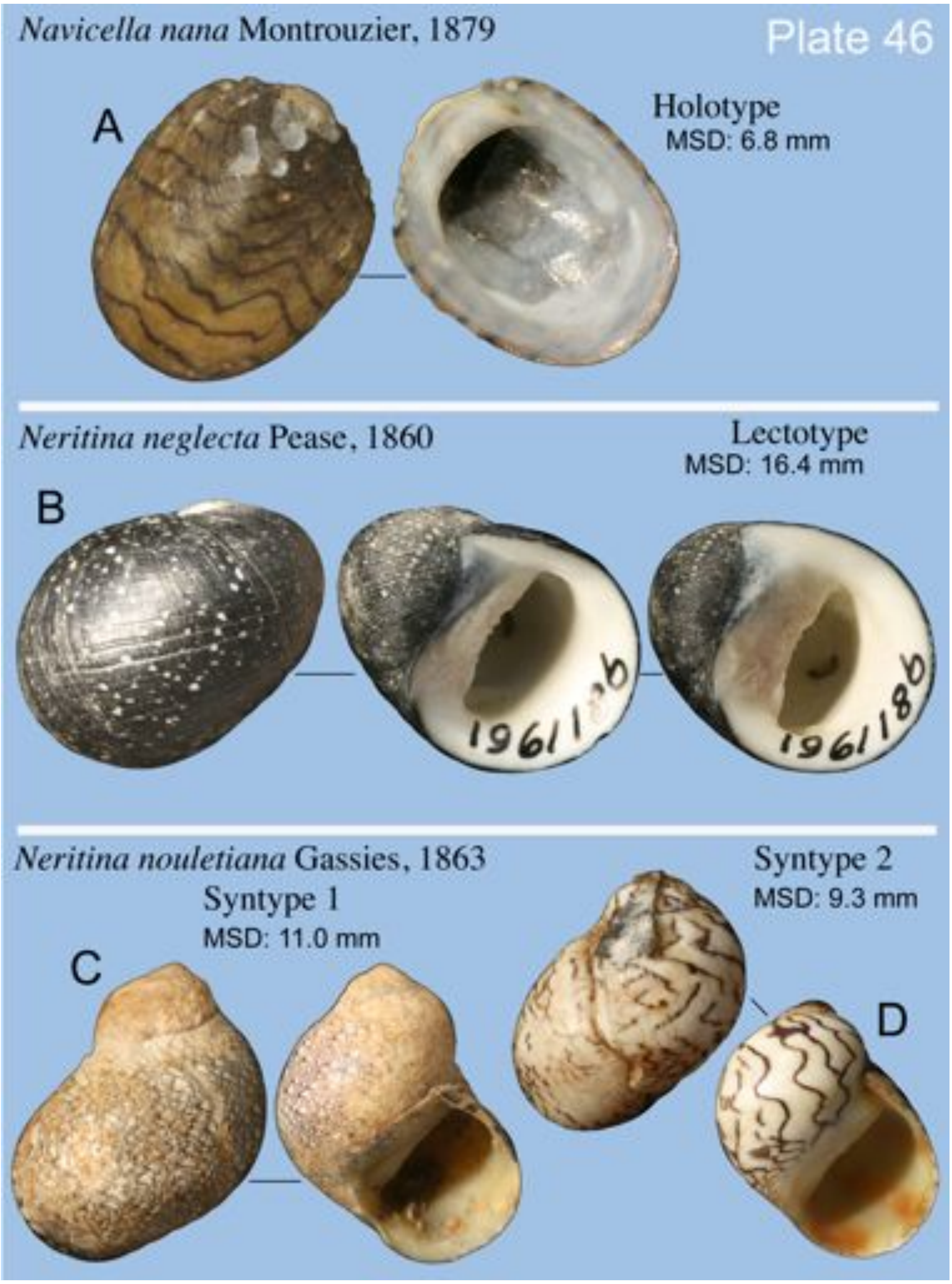


Plate 46
Navicella nana Montrouzier, 1879
A
Holotype
MSD: 6.8 mm
Neritina neglecta Pease, 1860
Lectotype
MSD: 16.4 mm
B
1961186
1961186
Neritina nouletiana Gassies, 1863
Syntype 1
MSD: 11.0 mm
C
Syntype 2
MSD: 9.3 mm
D

Plate 47.

A, B

Neritina novocaledonica Reeve, 1855

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [November 1855] Pl.24, Fig. 107a,b

4 syntypes BMNH

Locality: New Caledonia

MSD: 17.2–17.5 mm

C

Navicella orientalis Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.8, Fig. 33a,b

7 syntypes BMNH

Locality: Calcutta, India

MSD: 15.9 mm

D, E

Neritina paulucciana Gassies, 1870

Journal de Conchyliologie 18: 149–150

5 syntypes BMNH

Locality: Lifu Is., Loyalty Islands

MSD: 6.9–8.2 mm

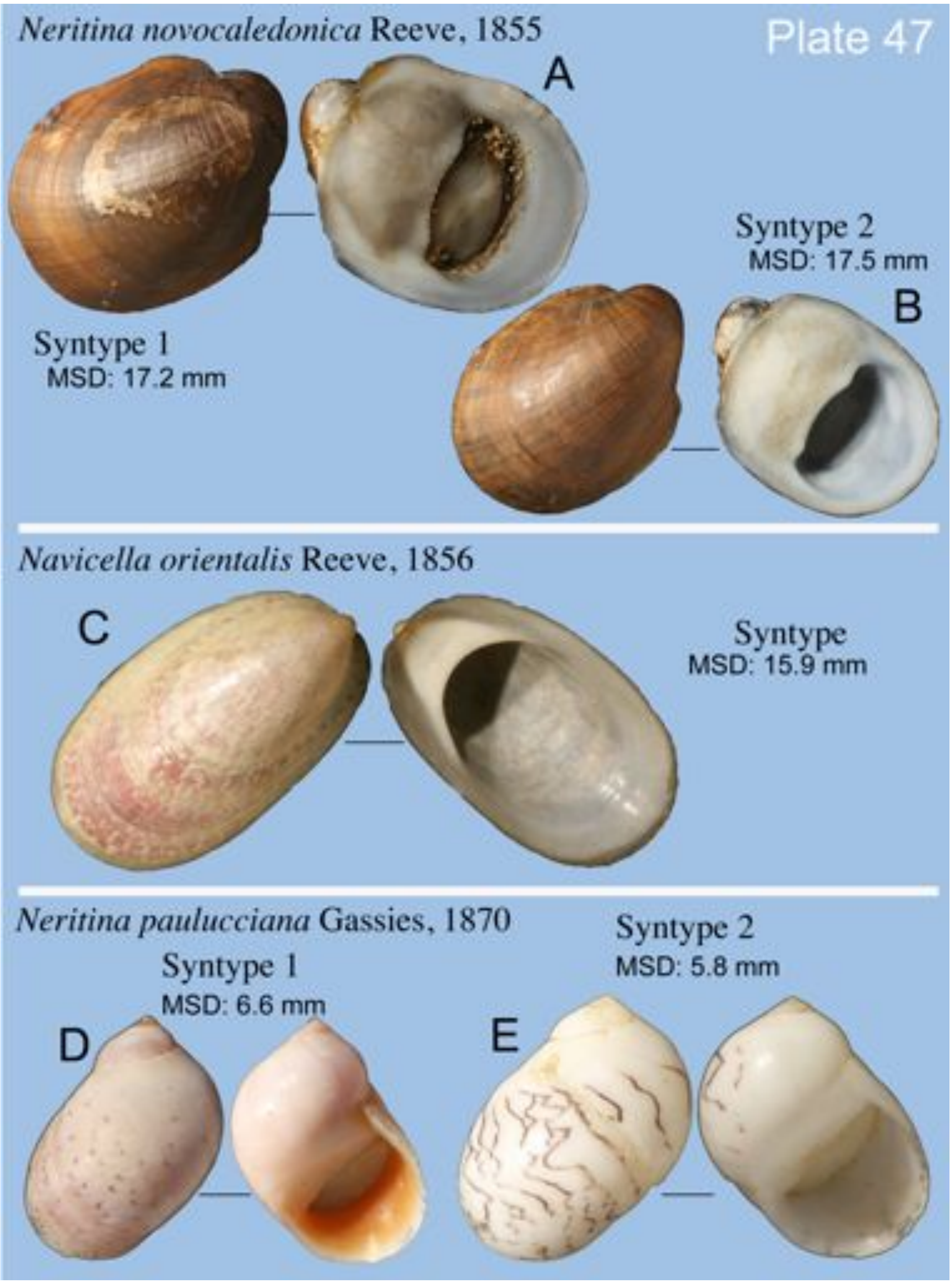

Neritina novocaledonica Reeve, 1855
Plate 47
A
Syntype 1
MSD: 17.2 mm
Syntype 2
MSD: 17.5 mm
B
Navicella orientalis Reeve, 1856
C
Syntype
MSD: 15.9 mm
Neritina paulucciana Gassies, 1870
Syntype 1
MSD: 6.6 mm
D
Syntype 2
MSD: 5.8 mm
E

Plate 48.

A, B

Neritina pazi Gassies, 1858
Journal de Conchyliologie 7: 71–72
2 syntypes BMNH
Locality: New Caledonia
MSD: 15.3 mm, 16.3 mm (with spine)

C, D

Neritina picta Sowerby I, 1833
Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832 (13 March 1833): 201 (illustrated in Conchological Illustrations September 29, 1835: 86, fig. 1; Panama)
4 syntypes BMNH; 3 syntypes BMNH; 2 syntypes BMNH; Syntype BMNH
Locality: Panama

E

Neritina pritchardi Dohrn, 1861
Proceedings of the Scientific Meetings of the Zoological Society of London [1861]: 206
4 syntypes BMNH
Locality: Fiji
MSD: 23.5 mm

Plate 48

Neritina pazi Gassies, 1858

Neritina picta Sowerby I, 1833

Syntypes

Neritina pritchardi Dohrn, 1861

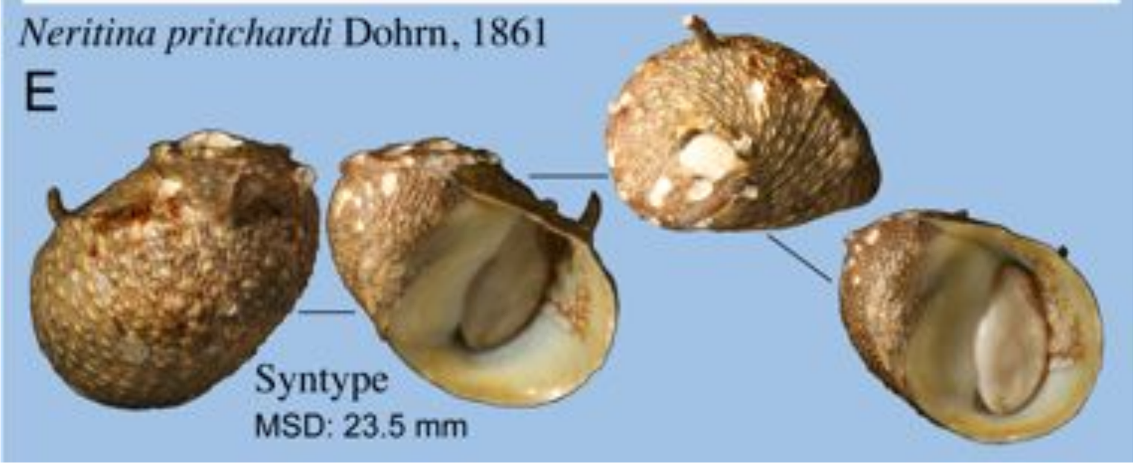


Plate 49.

A

Navicella psittacea Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856]

Pl.5, Fig. 23a,b

4 syntypes BMNH

Locality: Australian Island

MSD: 21.9 mm

B

Navicella pulchella Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856]

Pl.4, Fig. 25a,b

Holotype BMNH

Locality: ?

MSD: 24.0 mm

C, D

Navicella reticulata Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856]

Pl.5, Fig. 25a,b

4 syntypes BMNH

Locality: Sri Lanka (Ceylon)

MSD: 17.0–18.3 mm

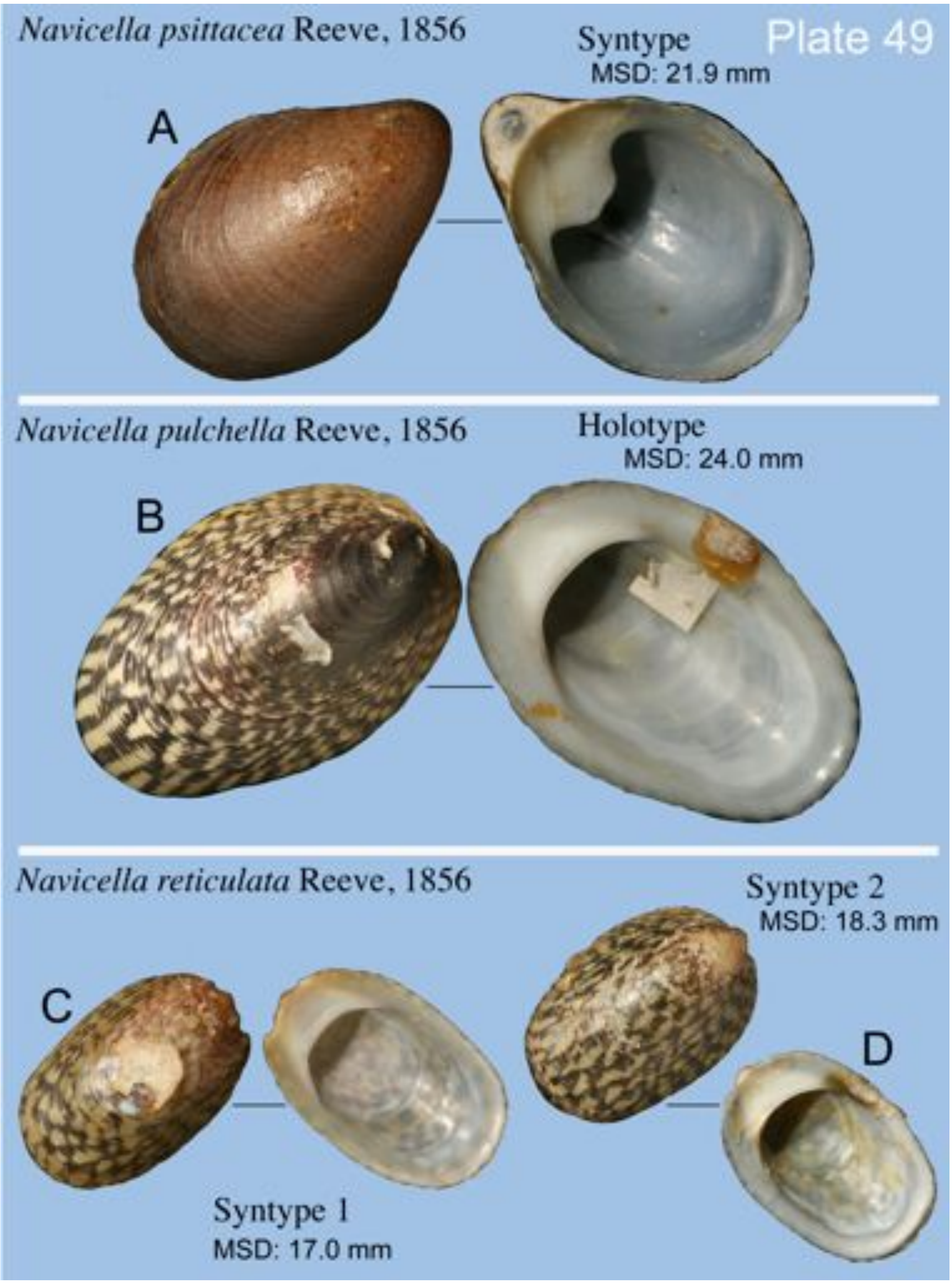


Plate 49
Navicella psittacea Reeve, 1856
Syntype
MSD: 21.9 mm
A
Navicella pulchella Reeve, 1856
Holotype
MSD: 24.0 mm
B
Navicella reticulata Reeve, 1856
Syntype 2
MSD: 18.3 mm
C
D
Syntype 1
MSD: 17.0 mm

Plate 50.

A, B

Nerita bensoni Récluz, 1850

(A replacement name for *Neritina reticulata* Sowerby, 1833, non *Neritina reticulata* Cristofori & Jan, 1832, Section II, Conchyliologia. Conspectus Methodicus Molluscorum, Testacea Terrestria et Fluviatilia. Mantissa in Secundam Partem Catalogi Testaceorum. Carmignani, Parmae: 4)

Journal de Conchyliologie 1: 150

Neritina reticulata Sowerby, 1833

Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832 (13 March 1833): 201 (illustrated in Conchological Illustrations September 29, 1835: 86, fig. 2; Lord Hood's Island)

6 syntypes BMNH

Locality: Marutea Atoll (Lord Hood's Island), French Polynesia

MSD: 10.4–12.4 mm

C, D

Neritina retusa Morelet, 1853

Journal de Conchyliologie 4: 372–373

3 syntypes BMNH

Locality: Vanuatu (Novas Hebridas)

E, F

Neritina rostrata Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [February 1856] Pl.33, Fig. 151a,b

5 syntypes BMNH

Locality: Sri Lanka (Ceylon)

Plate 50

Neritina bensoni Récluz, 1850
Neritina reticulata Sowerby I, 1833

Neritina retusa Morelet, 1853

Neritina rostrata Reeve, 1856

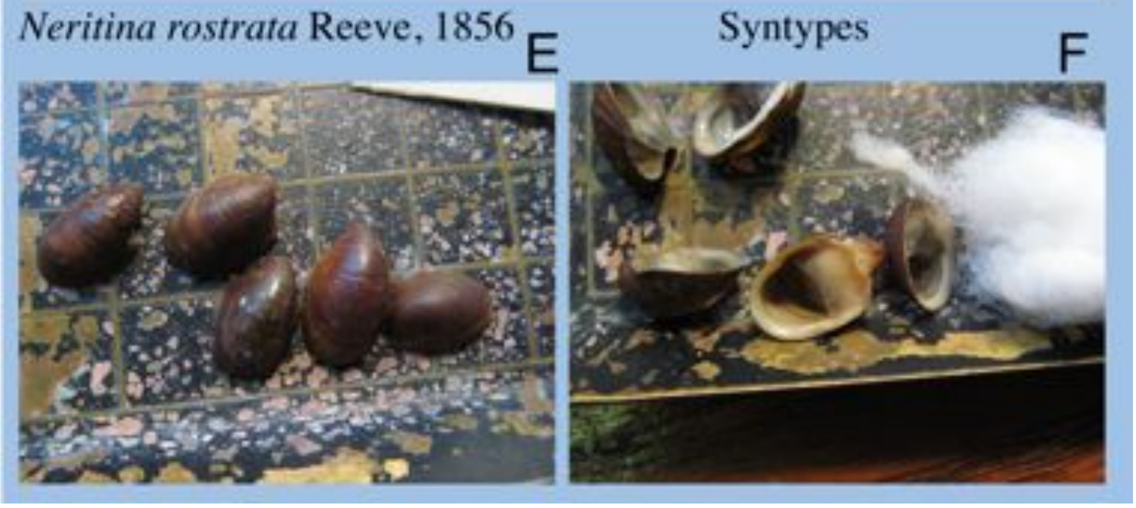


Plate 51.

A, B

Neritina sanguinea Sowerby II, 1849

Thesaurus Conchyliorum or monographs of genera of shells: 513, Pl.114, Fig.162

4 syntypes BMNH

Locality: New Ireland, Papua New Guinea

C

Navicella sanguisuga Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.4, Fig. 17a,b

4 syntypes BMNH

Locality: New Caledonia

MSD: 38.9 mm

D, E

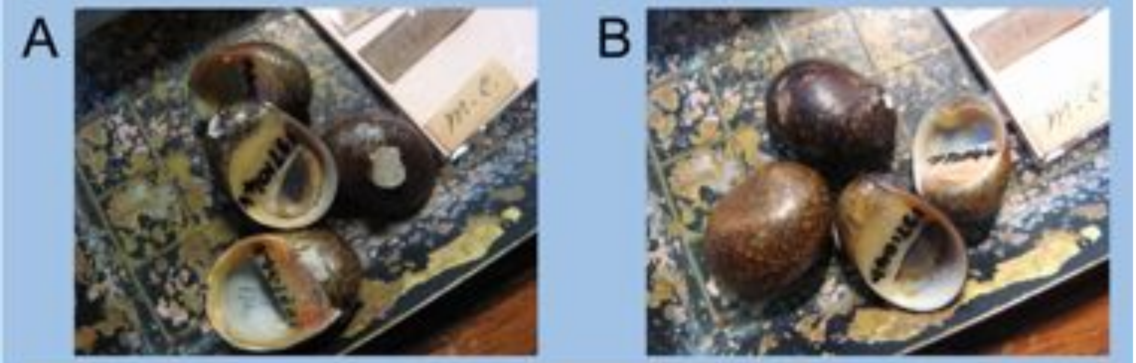
Neritina savesi Gassies, 1878

Journal de Conchyliologie 26: 345

2 syntypes BMNH

Locality: Tuo, New Caledonia

Neritina sanguinea Sowerby II, 1849 Syntypes Plate 51



Navicella sanguisuga Reeve, 1856 Syntype

MSD: 38.9 mm

Neritina savesi Gassies, 1878 Syntypes

Plate 52.

A, B

Navicella scarabaeus Reeve, 1856

Reeve, L.A. 1855–1856. Conchologia Iconica: or, illustrations of the shells of molluscous animals. Volume IX. Containing monographs of the genera Spondylus. *Neritina*. *Natica*. *Navicella*. *Siphonaria*. *Nerita*. *Latia*. L. Reeve, London: [June 1856] Pl.3, Fig. 12a,b

4 syntypes BMNH

Locality: Hammond Is., Australian Seas

MSD: 38.9 mm

C, D

Nerita smithii Wood, 1828

Wood, William. Supplement to the Index Testaceologicus, Or, A Catalogue of Shells, British and Foreign. Illustrated with 480 Figures. W. Wood. London: 45 (Pl.8, Fig.9), as *Neritina*

7 syntypes BMNH

Locality: ”Africa”? East India

E, F

Neritina solidissima Sowerby II, 1849

Thesaurus Conchyliorum or monographs of genera of shells: 541, Pl.116, Fig.273

4 syntypes BMNH

Locality: ?


Navicella scarabaeus Reeve, 1856
Plate 52
A
B
Syntype 1
MSD: 37.5 mm
Syntype 2
MSD: 45.6 mm
Nerita smithii Wood, 1828
Syntypes
C
D
Neritina solidissima Sowerby II, 1849
Syntypes
E
F
1971045
1971045

Plate 53.

A, B, C, D

Neritina spiniperda Morelet, 1858

Morelet, Arthur. Séries conchyliologiques comprenant l'énumeration de mollusques terrestres et fluviatiles recueillis pendant le cours de différents voyages, ainsi que la description de plusieurs espèceś nouvelles. Chez Klincksieck. Paris. Vol. 1: 121–122

3 syntypes BMNH (Nosy Be); 2 syntypes BMNH (Mayotte Is.)

Locality: Nosy Be, Madagascar; Mayotte Is.?, Comoros?

E, F

Neritina spinosa Sowerby I, 1825

A Catalogue of the shells contained in the collection of the late Earl of Tankerville arranged according to the Lamarckian Conchological System; together with an appendix, containing descriptions of many new species. Illustrated with several coloured plates. London. [February 1825]: 45 (illustrated in Conchological Illustrations, January 1, 1836: 90, fig. 9; Otaheite = Tahiti) [ex: Budgin MS]

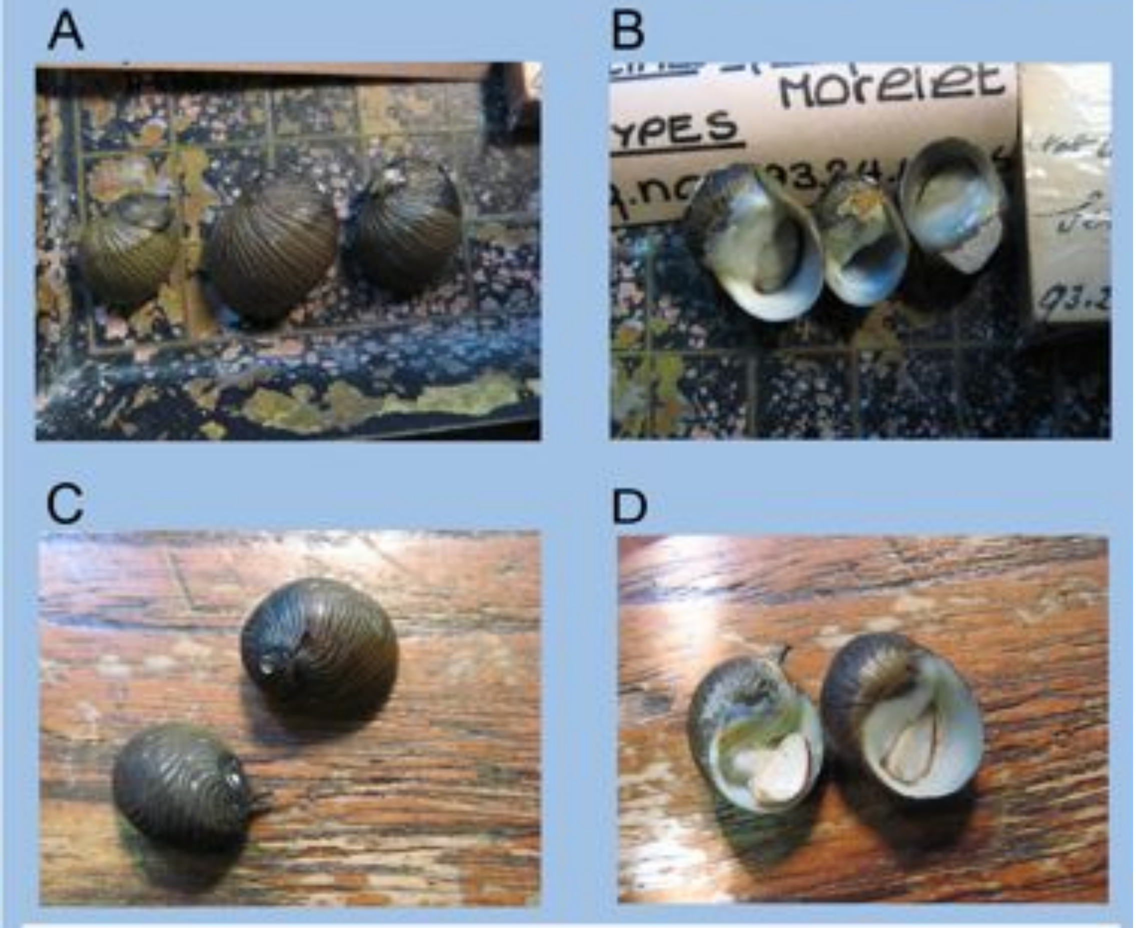
3 syntypes BMNH

Locality: Tahiti

Plate 53

Neritina spiniperda Morelet, 1858

Syntypes



Neritina spinosa Sowerby I, 1825

Syntypes

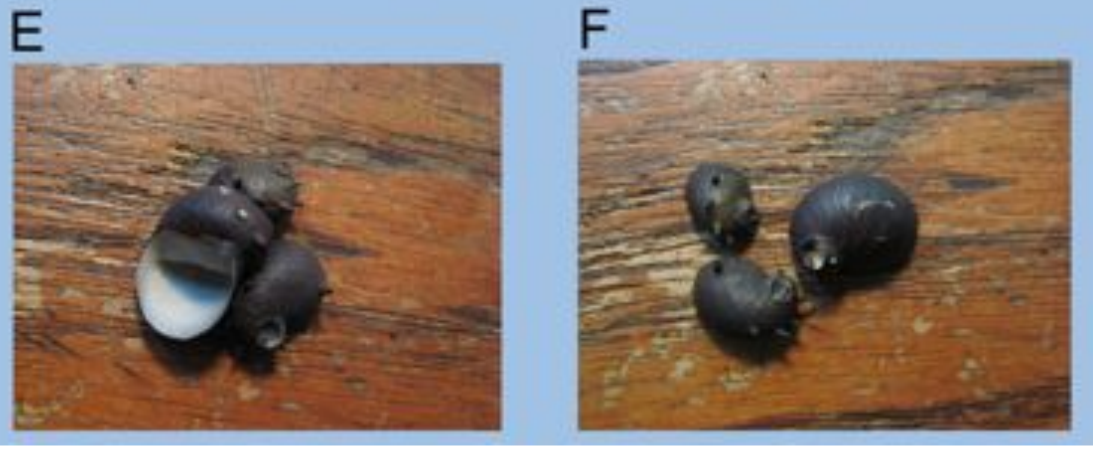


Plate 54.

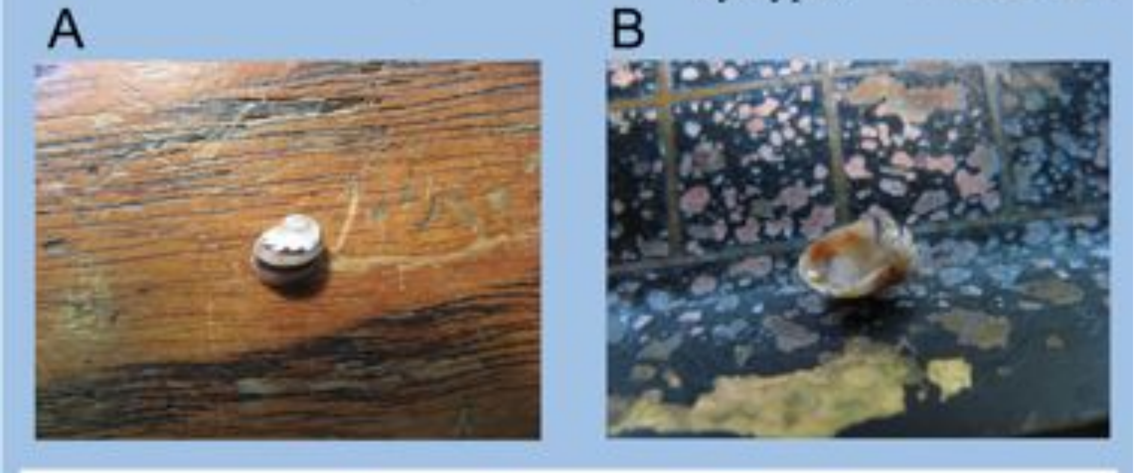
A, B

Neritina suavis Gassies, 1879
Journal de Conchyliologie 27: 134–135
Holotype BMNH
Locality: Lifu Is., Loyalty Is.

C, D, E, F

Neritina subrugata Baird in Brenchery, 1873
Julius L. Brenchley. Jottings during the Cruse of H.M.S. Curazoa among The South Sea Islands in 1865 by Julius L. Brenchley, M.A., F.R.G.S. with numerous illustrations and natural history notices. Longman, Green, and Co.. London. Shells: 438
6 syntypes BMNH
Locality: Upolu, Samoa

Neritina suavis Gassies, 1879 Syntypes Plate 54



Neritina subrugata Baird in Brenchery, 1873 Syntypes

Plate 55.

A, B

Neritina turbida Morelet, 1849

Testacea novissima insulae Cubanae et America Centralis Chez J.-B. Bailliére, Paris.

Part1: 27

3 syntypes BMNH

Locality: Guatemala

C, D, E

Navicella variabilis Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 155

10 syntypes BMNH

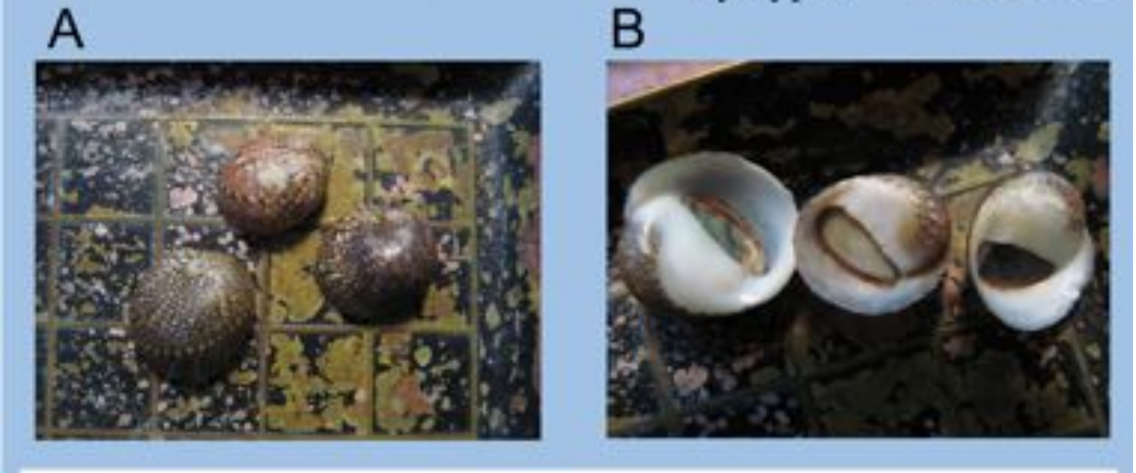
Locality: Cagayan, Misamis, Mindanao Is., Philippines

MSD: 23.0–31.2 mm

Neritina turbida Morelet, 1849

Syntypes

Plate 55



Navicella variabilis Récluz, 1843

Plate 56.

A

Nerita angulosa Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 173

Lectotype MCZ; 2 paralectotypes MNHN; 2 paralectotypes MHNG; 3 paralectotypes MHNG

Locality: Casan, Misamis, Mindanao Is., Philippines

MSD: 19.3 mm

B

Nerita apiata Récluz, 1843

Proceedings of the Zoological Society of London, 11: 72–73

Lectotype MCZ; 5 paralectotypes MNHN; 3 paralectotypes MHNG

Locality: Negros Is., Philippines

MSD: 14.2 mm (lectotypes), 9.1–11.9 mm (paralectotypes)

C

Nerita (*Clithon*) *avellana* Récluz, 1842

Revue Zoologique, par la Société Cuvierienne, 5: 76

Lectotype MCZ; Paralectotype MHNG; 4 paratypes MHNG

Locarity: Manilla, Philippines

MSD: 18.2 mm (lectotype), 10.4–16.6 mm (paralectotypes)

Plate 56

Nerita angulosa Récluz, 1843

Lectotype
MSD: 19.3 mm

Nerita apiata Récluz, 1843

Lectotype
MSD: 14.2 mm

Nerita (*Clithon*) *avellana* Récluz, 1842

Lectotype
MSD: 18.2 mm

Plate 57.

A

Nerita (*Neritina*) *bicanaliculata* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 171–172

Lectotype MCZ; 3 paralectotypes MNHN; 2 paralectotypes MHNG; 3 paralectotypes MHNG

Locality: Camiguing Is., Philippines

MSD: 13.9 mm

B

Nerita (*Clithon*) *bicolor* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 172

Lectotype MCZ; 4 paralectotypes MNHN; 2 paralectotypes MHNG; 3 paralectotypes MHNG

Locality: Agoo, Pangasin, Luzon, Philippines

MSD: 23.6 mm

C

Neritina dispar Pease, 1868

American Journal of Conchology for 1867, 3(4): 285 (Pl.24, Fig.3)

41 types? “Cotypes” MCZ

Locality: Rarotonga, Cook Is.

MSD: 4.8–8.5 mm

Plate 57

Nerita (*Neritina*) *bicanaliculata* Récluz, 1843

Lectotype
MSD: 13.9 mm

Nerita (*Clithon*) *bicolor* Récluz, 1843

Lectotype
MSD: 23.6 mm

Neritina dispar Pease, 1868

“Cotypes”
MSD: 8.5 mm

Plate 58.

A

Nerita (*Clithon*) *interrupta* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 173

Lectotype MCZ; 2 paralectotypes MNHN; 3 paralectotypes MHNG

Locality: Yba, Zambales, Luzon Is., Philippines

MSD: 20.5 mm (lectotype), 18.2–22.2 mm (paratypes; MHNG)

B

Nerita (*Clithon*) *olivacea* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 172

Lectotype MCZ; 3 paralectotypes MNHN; 2 paralectotypes MHNG; 3 paralectotypes MHNG

Locality: Agoo, Pangasinan, Luzon Is., Philippines

MSD: 27.2 mm (lectotype), 16.4–32.6 mm (paralectotypes)

C

Nerita (*Clithon*) *rugata* Récluz, 1842

Revue Zoologique, par la Société Cuvierienne, 5: 75–76

Lectotype MCZ; 4 paralectotypes MNHN

Locality: Philippines

MSD: 17.4 mm

Plate 58

Nerita (*Clithon*) *interrupta* Récluz, 1843

Lectotype
MSD: 20.5 mm

Nerita (*Clithon*) *olivacea* Récluz, 1843

Lectotype
MSD: 27.2 mm

Nerita (*Clithon*) *rugata* Récluz, 1842

Lectotype
MSD: 17.4 mm

Plate 59.

A

Nerita (*Neritina*) *squamaepicta* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 169

Neritina squamaepicta Sowerby, 1849 (?=*Nerita* (*Neritina*) *squamapicta* Récluz, 1843) [Récluz MS.]

Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 513, pl. 111, Figs. 79

Lectotype MCZ; 2 paralectotypes MNHN; 3 paralectotypes MHNG

Locality: Agoo, Pangasinan, Luzon Is., Philippines

MSD: 25.7 mm (lectotype), 28.4–34.2 mm (paralectotypes)

B

Nerita (*Clithon*) *squarrosa* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 174

Neritina squamosa Sowerby, 1849 (?=*Nerita* (*Clithon*) *squarrosa* Récluz, 1843) [Récluz MS.]

Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 527, pl. 109, Figs. 26–27

Lectotype MCZ; 3 paralectotypes MNHN; 3 paralectotypes MHNG

Locality: Jimamailan, Negros Is., Philippines

MSD: 25.7 mm (lectotype), 20.9–23.6 mm (paralectotypes)

C

Neritina siderea Gould, 1847

Proceedings of the Boston Society of Natural History, 2: 238

14 paratypes? (Fiji) 3 cotypes? (Fiji) 3 paratypes? (“Fiji” end of Upolu, Samoa) MCZ

Locality: Fiji

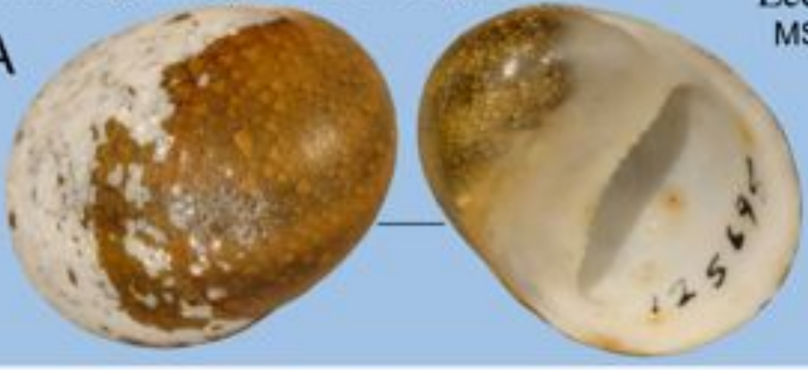
MSD: 3.7–7.2 mm

Plate 59

Nerita (*Neritina*) *squamaepicta* Récluz, 1843
Neritina squamaepicta Sowerby, 1849?

Lectotype
MSD: 25.7 mm

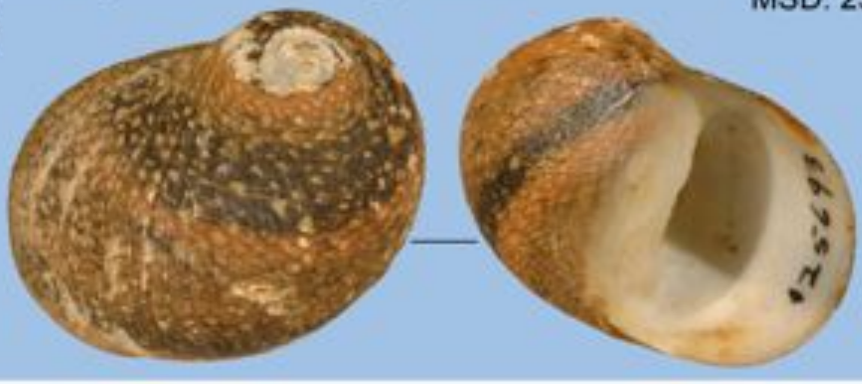
A



Nerita (*Clithon*) *squarrosa* Récluz, 1843
Neritina squamosa Sowerby, 1849?

Lectotype
MSD: 25.7 mm

B



Neritina siderea Gould, 1847

Paratype?
MSD: 6.1 mm

C

Type specimens, Senckenberg Museum

Plate 60.

A

Neritina andamanica Nevill, “1883”
Ex. Nevill, 1883?
3 syntypes? SMF; 3 syntypes? SMF
Locality: Andaman Is., India
MSD: 18.2–26.4 mm

B

Neritina chlorostoma Sowerby I, 1833 “*Neritina chlorostoma* Broderip, 1833”
Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832 (13 March 1833): 201 (illustrated in Conchological Illustrations May 2, 1836: 97, fig. 34; Tahiti)
3 syntypes SMF
Locality: Tahiti
MSD: 10.6–11.6 mm

C

Nerita (*Clithon*) *circumvoluta* Récluz, 1843
Proceedings of the Zoological Society of London for 1842, 10: 173
2 syntypes SMF
Locality: Philippines
MSD: 10.6 mm, 10.9 mm

Plate 60

"*Neritina andamanica* Nevill, 1883"

Syntype?
MSD: 26.4 mm

Neritina chlorostoma Sowerby I, 1833

Syntype
MSD: 10.6 mm

Nerita (*Clithon*) *circumvoluta* Récluz, 1843

Syntype
MSD: 10.9 mm

Plate 61.

A

Navicella cumingiana Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 157

2 syntypes SMF

Locality: Mauntain stream, Camaguing, Philippines

MSD: 15.1 mm, 15.2 mm

B

Neritina deltoidea Mousson, 1870 "*Neritina deltoidea* Garrett ms. 1870"

Journal de Conchyliologie, 18(2): 224–225

3 syntypes SMF

Locality: Viti Levu, Fiji

MSD: 15.1 mm, 15.2 mm

C

Neritina dilatata Broderip, 1833

Proceedings of the Committee of Science and Correspondence of the Zoological Society of London for 1832, 2(25): 201 [13 March 1833]

2 syntypes SMF

Locality: Tahiti

MSD: 16.4–16.7 mm

Plate 61

Navicella cumingiana Récluz, 1843

Syntype
MSD: 15.2 mm

A

Neritina deltoidea Mousson, 1870

Syntype
MSD: 11.2 mm

B

Neritina dilatata Broderip, 1833

Syntype
MSD: 16.7 mm

C

Plate 62.

A

Neritina discors Martens, 1878

Die Gattung Neritina. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 160–161 (Pl.17, Figs.7,8)

Syntype SMF

Locality: Tuka, Flores, Indonesia

MSD: 7.1 mm

B

Navicella dispar Pease, "1868"

Ex. Pease, 1868?

7 "syntypes" SMF

Locality: Rarotonga, Cook Islands

MSD: 17.8–25.4 mm

C

Septaria elberti Haas, 1912

Annals and Magazine of Natural History 10: 419

Holotype SMF; 5 paratypes SMF

Locality: KaliSpell (Kali Spi), Flores, Indonesia

MSD: 24.3 mm (holotype), 12.6–22.0 mm (paratypes)

Plate 62

Neritina discors Martens, 1878

Syntype
MSD: 7.1 mm

Navicella dispar Pease, "1868"

"Syntype"
MSD: 25.4 mm

Septaria elberti Haas, 1912

Holotype
MSD: 24.3 mm

Plate 63.

A

Neritina globosa Broderip, 1833

Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832 (13 March 1833): 201 2 syntypes SMF

Locality: Chiriqui, Colombia

MSD: 22.9–26.7 mm

B

Neritina gravis Morelet, 1849

Testacea novissima insulae Cubanae et America Centralis Chez J.-B. Bailliére, Paris. Part1: 27

2 syntypes SMF

Locality: Belieze

MSD: 19.3–19.7 mm

C

Neritina (*Neritaea*) *hessei* Boettger, 1912

Annales de la Société royale malacologique de Belgique 47: 108 (Pl.2, Fig.4a,b)

Holotype SMF

Locality: Banana-Creek Brackish Water Flats, South Atlantic Ocean Democratic Republic of the Congo

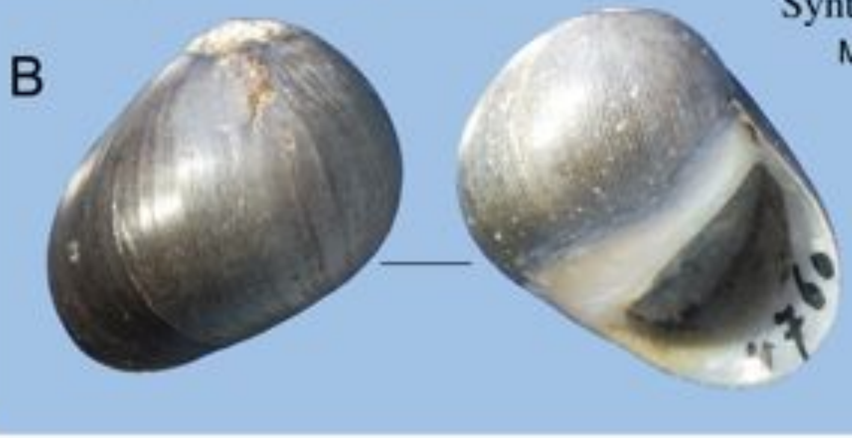
MSD: 20.7 mm

Plate 63

Neritina globosa Broderip, 1833

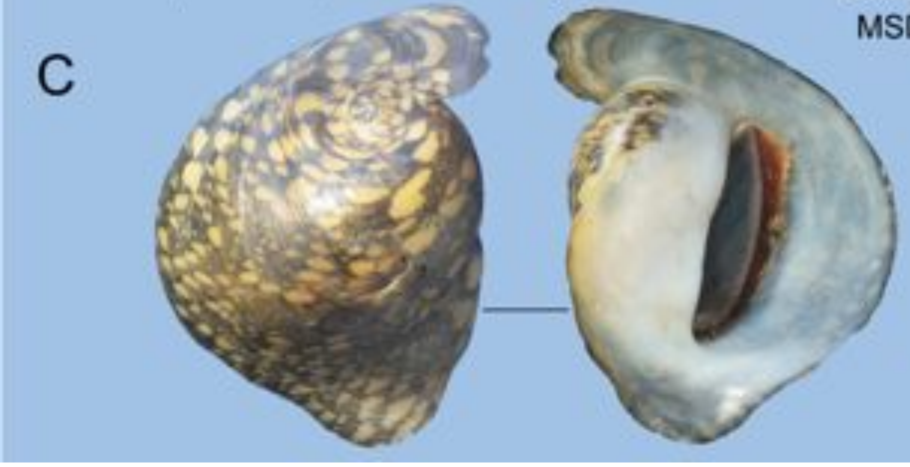
Syntype
MSD: 26.7 mm

Neritina gravis Morelet, 1849



Syntype
MSD: 19.7 mm

Neritina (Neritaea) hessei Boettger, 1912



Holotype
MSD: 20.7 mm

Plate 64.

A

Neritina intermedia Sowerby I, 1833

Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832 (13 March 1833): 201 (illustrated in Conchological Illustrations May 2, 1835: 87, fig. 7; Bay of Montijo)

2 syntypes SMF

Locality: Bay of Montijo, Panama "Mexico"

MSD: 19.0–19.7 mm

B

Neritina jamaicensis C.B. Adams, 1851

Contributions to Conchology 9: 174

Lectotype SMF

Locality: Jamaica

MSD: 9.0 mm

C

Neritina latissima Broderip, 1833

Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832 (13 March 1833): 200–201

2 syntypes SMF

Locality: Real Llejos, Mexico

MSD: 26.8–27.0 mm

Plate 64

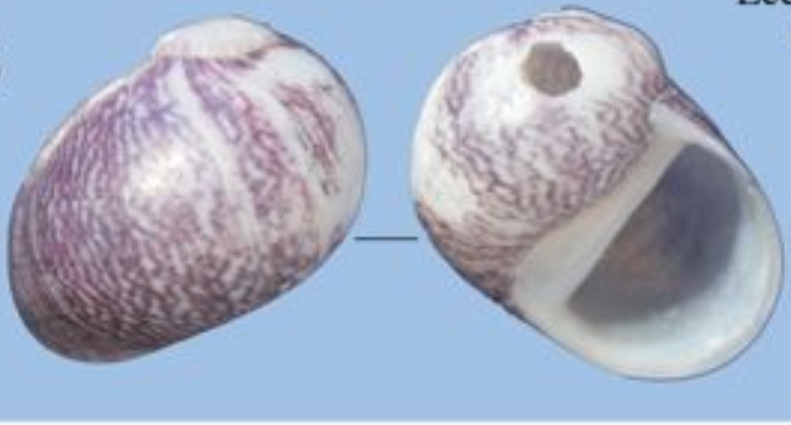
Neritina intermedia Sowerby I, 1833

A

Syntype
MSD: 19.7 mm

Neritina jamaicensis C.B. Adams, 1851

B



Lectotype
MSD: 9.0 mm

Neritina latissima Broderip, 1833

C

Syntype
MSD: 27.0 mm

Plate 65.

A

Neritina listeri Pfeiffer, 1840

Archiv für Naturgeschichte 6(1): 250-261

Syntype SMF

Locality: Cuba

MSD: 17.1 mm

B

Neritina mutica Sowerby, 1849

Thesaurus Conchyliorum or monographs of genera of shells: 523, Pl.109, Figs.1,2

2 syntypes SMF

Locality: Western Africa?

MSD: 15.1 mm

C

Neritina peguensis Blanfold, 1867

Journal of the Asiatic Society of Bengal 36: 58–59 (Pl.1, Fig.1–16)

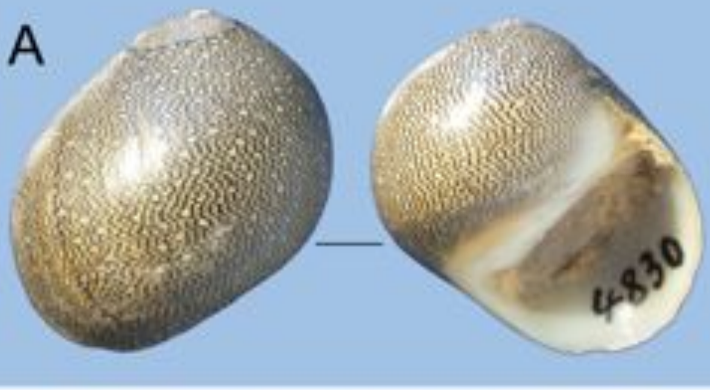
2 syntypes SMF

Locality: Port Dalhousie, Bago (Pegu), Myanmar

MSD: 5.1 mm, 5.2 mm

Plate 65

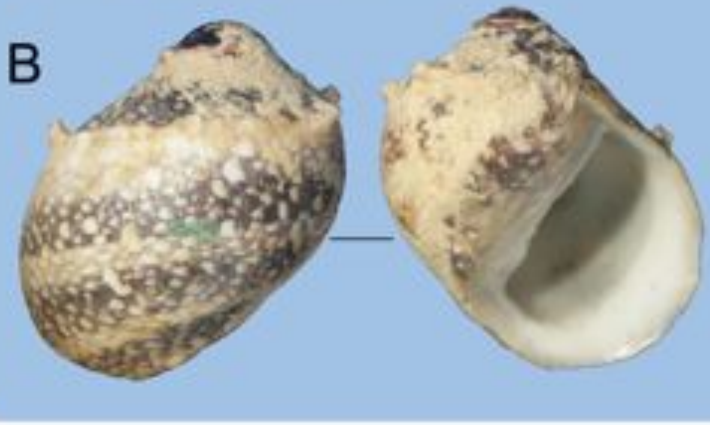
Neritina listeri Pfeiffer, 1840



Syntype
MSD: 17.1 mm

Neritina mutica Sowerby, 1849

Syntype
MSD: 15.1 mm



Neritina peguensis Blanfold, 1867

Syntype
MSD: 5.2 mm

Plate 66.

A

Neritina philippinarum Sowerby I, 1836

Conchological Illustrations: Pl.100, Fig.53 [June 30]

Syntype SMF

Locality: Manila

MSD: 21.4 mm

B

Neritina bensoni Récluz, 1850

Journal de Conchyliologie 1: 150

(A replacement name for Neritina reticulata Sowerby, 1833 non Neritina reticulata Cristofori & Jan, 1832)

Neritina reticulata Sowerby I, 1833

Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, Part II for 1832 (13 March 1833): 201 (illustrated in Conchological Illustrations September 29, 1835: 86, fig. 2; Lord Hood's Island)

2 syntypes SMF

Locality: Marutea Atoll (Lord Hood's Island), French Polynesia

MSD: 11.9 mm, 12.3 mm

C

Neritina (*Clithon*) *rhyssodes* Boettger, 1890

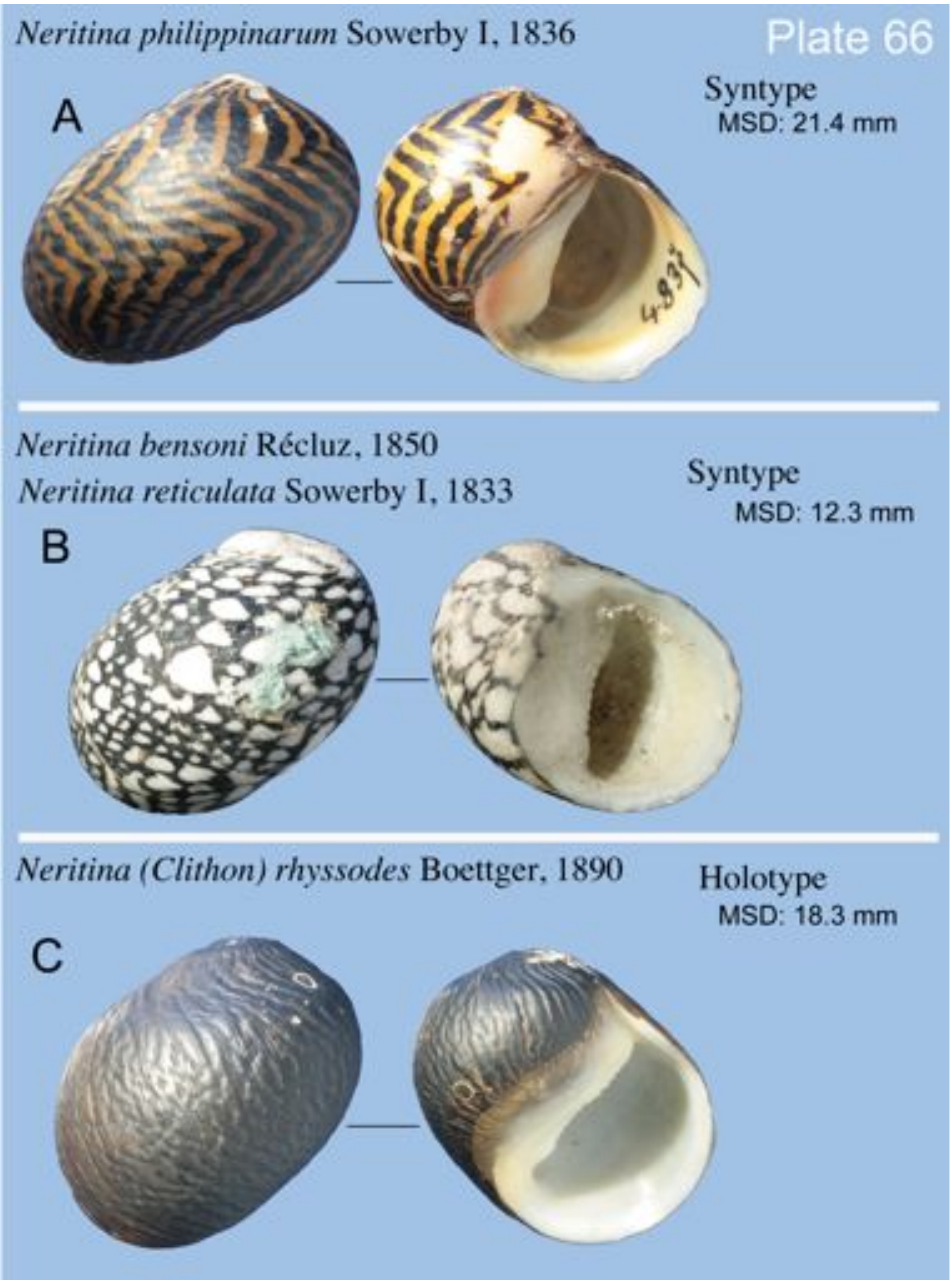
Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 3(4): 57–58

Holotype SMF

Locality: Lokobe, Nosy Be, Madagascar

MSD: 18.3 mm

Plate 66



Neritina philippinarum Sowerby I, 1836

Syntype
MSD: 21.4 mm

Neritina bensoni Récluz, 1850
Neritina reticulata Sowerby I, 1833

Syntype
MSD: 12.3 mm

Neritina (Clithon) rhyssodes Boettger, 1890

Holotype
MSD: 18.3 mm

Plate 67.

A

Neritina rhytidophora Tapparone-Canefri, 1883
Annali del Museo Civico di Storia Naturale di Genova 19: 72–73
2 syntypes SMF
Locality: Sorong, New Guinea, Indonesia
MSD: 16.6 mm, 18.6 mm

B

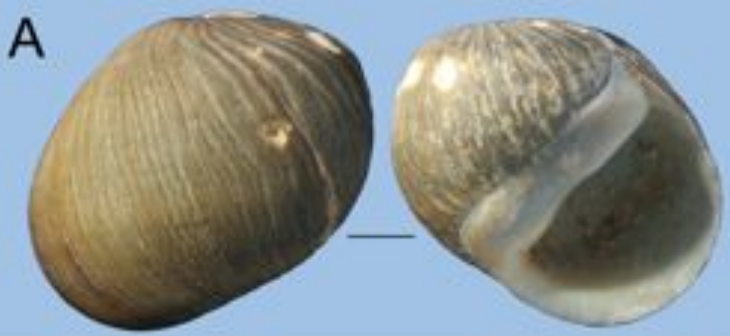
Neritina (*Clithon*) *soembawana* Haas, 1912
Annals and Magazine of Natural History 10: 418
Holotype SMF; 3 paratypes SMF; 10 paratypes SMF
Locality: Bima, Sumbawa (Soembawa), Indonesia
MSD: 21.4 mm (holotype), 13.1–19.0 mm (paratypes)

C

Neritina (*Neritaea*) *stumpffi* Boettger, 1890
Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 1(2): 99–101
Lectotype SMF; 3 paralectotypes SMF; 3 paralectotypes SMF; 3 paralectotypes SMF; 8 paralectotypes SMF; paralectotype SMF
Locality: Nosy-Komba, Nosy Be, Madagascar
MSD: 17.6–19.2 mm

Plate 67

Neritina rhytidophora Tapparone-Canefri, 1883



Syntype
MSD: 18.6 mm

Neritina (Clithon) soembawana Haas, 1912

Holotype
MSD: 21.4 mm

Neritina (Neritaea) stumpffi Boettger, 1890

Lectotype
MSD: 20.2 mm

Plate 68.

A

Neritina (*Neritaea*) *stumpffi leucostoma* Boettger, 1890
Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 1(2): 99–101
4 syntypes SMF
Locality: Nosy-Komba, Nosy Be, Madagascar
MSD: 17.6–19.2 mm

B

Neritina sumatrensis Sowerby I, 1836
Conchological Illustrations: Pl.100, Fig.54 [June 30]
Syntype SMF
Locality: ?
MSD: 21.4 mm

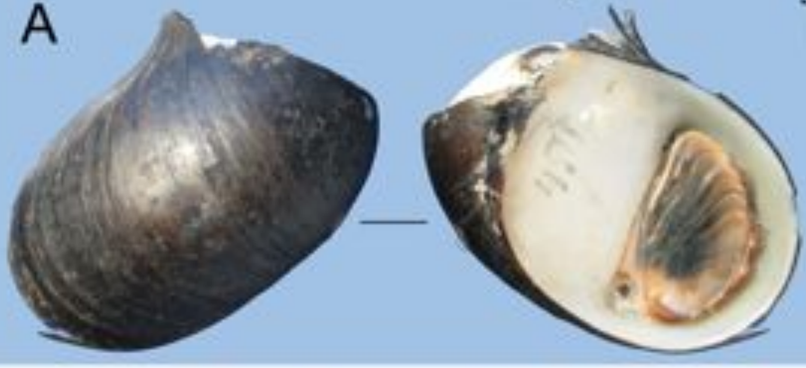
C

Navicella suborbicularis Sowerby I, 1825
A Catalogue of the shells contained in the collection of the late Earl of Tankerville arranged according to the Lamarckian Conchological System; together with an appendix, containing descriptions of many new species. Illustrated with several coloured plates. London. [February 1825]: 44, App.10
2 syntypes SMF; 2 syntypes SMF
Locality: Timor
MSD: 16.8–22.4 mm

Plate 68

Neritina (Neritaea) stumpffi leucostoma Boettger, 1890

A



Syntype
MSD: 19.2 mm

Neritina sumatrensis Sowerby I, 1836

B

Syntype
MSD: 16.0 mm

Navicella suborbicularis Sowerby I, 1825

C

Syntype
MSD: 16.8 mm

Plate 69.

A

Neritina tenebricosa C.B. Adams, 1851

Contributions to Conchology 9: 175

Syntype SMF

Locality: Black River, Jamaica

MSD: 9.8 mm

B

Neritina turbida Morelet, 1849

Testacea novissima insulae Cubanae et America Centralis Chez J.-B. Bailliére, Paris. Part1: 27

4 syntypes SMF

Locality: Machaquila, Guatemara

MSD: 7.8–8.1 mm

C

Neritina (*Neritina*) *wetarana* Haas, 1912

Annals and Magazine of Natural History 10: 419

Holotype SMF; 12 paratypes SMF

Locality: Ilwaki River, Wetar (Wetarana), Indonesia

MSD: 22.2 mm (holotype), 16.5–20.6 mm (paratypes)

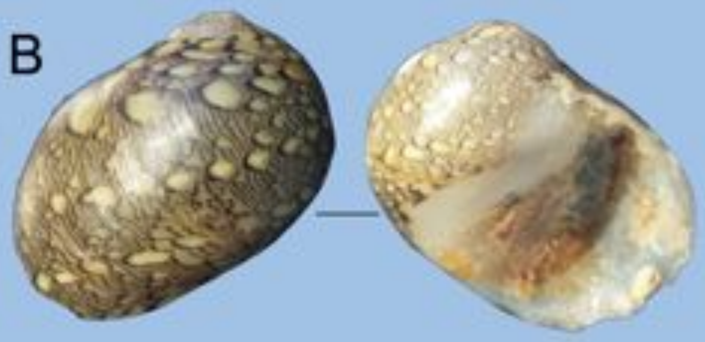
Plate 69

Neritina tenebricosa C.B. Adams, 1851

Syntype
MSD: 9.8 mm

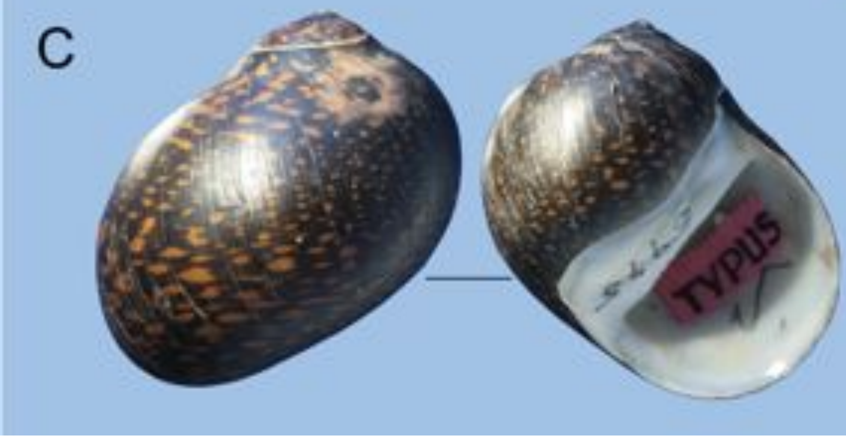
Neritina turbida Morelet, 1849

Syntype
MSD: 8.1 mm



Neritina (Neritina) wetarana Haas, 1912

Holotype
MSD: 16.8 mm



Type specimens, Berlin Museum

Plate 70.

A

Neritina bismarckiana Reich, 1935
Zoologischer Anzeiger 110: 240
Holotype or Syntype ZMB
Locality: Bismarck Archipelago, Papua New Guinea
MSD: 27.8 mm

B

Neritina (*Clithon*) *confluens* Martens, 1897
Süss- und Brackwasser Mollusken des Indischen Archipels (M. Weber, ed.), Zoologisch Ergebnisse einer Reise in Niederländish Ost-Indien, Leiden, 4(1): 81–82 (Pl.10, Fig.9)
Holo or Syntype ZMB
Locality: Adonara, Indonesia
MSD: 14.8 mm

C

Neritina conglobata Martens, 1875
Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 57 (Pl.8, Figs.7–9)
Holo or Syntype ZMB
Locality: Sulawesi (Celebes), Indonesia
MSD: 26.3 mm

Plate 70

Neritina bismarckiana Reich, 1935

Syntype
MSD: 27.8 mm

Neritina (*Clithon*) *confluens* Martens, 1897

Holo or Syntype
MSD: 14.8 mm

Neritina conglobata Martens, 1875

Holo or Syntype
MSD: 16.8 mm

Plate 71.

A

Neritina cryptospira Martens, 1875

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 61 (Pl.8, Figs.10–12)

2 syntypes ZMB

Locality: Borneo, Malaysia

MSD: 21.2 mm, 23.6 mm

B

Neritina discors Martens, 1878

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 160–161 (Pl.17, Figs.7,8)

28 syntypes ZMB

Locality: Tuka, Flores, Indonesia

MSD: 6.3–7.9 mm

C

Septaria elberti Haas, 1912

Annals and Magazine of Natural History 10: 419

Syntype? ZMB

Locality: KaliSpell (Kali Spi), Flores, Indonesia

MSD: 25.1 mm

Plate 71

Neritina cryptospira Martens, 1875

Syntype
MSD: 23.6 mm

Neritina discors Martens, 1878

Syntype
MSD: 7.9 mm

Septaria elberti Haas, 1912

Syntype?
MSD: 25.1 mm

Plate 72.

A

Neritina haemastoma Martens, 1878

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 167–168 (Pl.13, Figs.6,7)

Holo or Syntype ZMB

Locality: Philippines

MSD: 26.2 mm

B

Neritina hamuligera Troschel, 1837

Archiv für Naturgeschichte, Volume 3, Part 1: 177

11 syntypes ZMB

Locality: Ganges, India

MSD: 13.6–27.1 mm

C

Navicella junghuhni Martens, 1881 [ex. Herklots MS.]

Die Gattung *Navicella*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10-A): 23–24 (Pl.4, Figs.13–15)

Holo or Syntype ZMB

Locality: Java, Indonesia

MSD: 30.4 mm

Plate 72

Neritina haemastoma Martens, 1878

Holo or Syntype
MSD: 26.2 mm

Neritina hamuligera Troschel, 1837

Syntype
MSD: 27.1 mm

Navicella junghuhni Martens, 1881

Holo or Syntype
MSD: 30.4 mm

Plate 73.

A

Navicella lutea Martens, 1881
Die Gattung *Navicella*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10-A): 30 (Pl.6, Figs.1–4)
Holo or Syntype ZMB
Locality: Viti Levu, Fiji
MSD: 15.1 mm

B

Navicella luzonica adspersa Martens, 1881 “*Navicella luzonica* Souleyet var. *adspersa* Martens, 1881”
Die Gattung *Navicella*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10-A): 16–18 (Pl.2, Figs.9–11)
Holo or Syntype ZMB
Locality: Nicobar Is., India
MSD: 13.3 mm

C

Neiritona labiosa melanesica Reich, 1935
Zoologischer Anzeiger 110: 241–242
Holotype ZMB; 6 paratypes ZMB
Locality: New Britain, Bismarck Archipelago, Papua New Guinea
MSD: 46.2 mm (holotype), 37.4–52.1 mm (paratypes)

Plate 73

Navicella lutea Martens, 1881

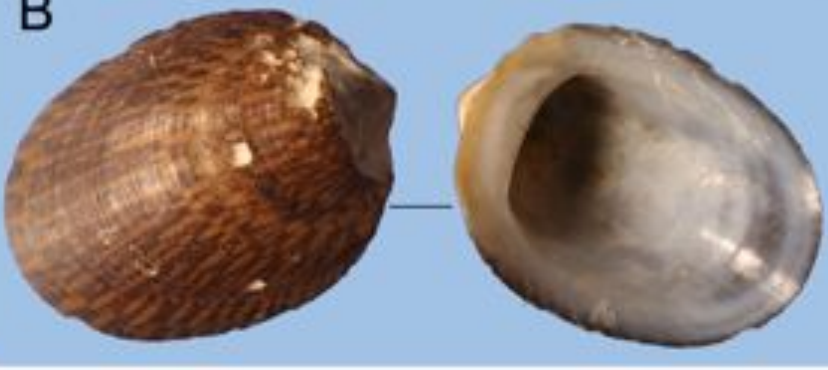
Holo or Syntype
MSD: 15.1 mm

A

Navicella luzonica adspersa Martens, 1881

Holo or Syntype
MSD: 13.3 mm

B



Neiritona labiosa melanesica Reich, 1935

Holotype
MSD: 46.2 mm

C

Plate 74.

A

Neritina melanostoma Troschel, 1837

Archiv für Naturgeschichte, Volume 3, Part 1: 179

8 syntypes ZMB; 7 syntypes ZMB

Locality: Ganges, India

MSD: 17.7–28.7 mm

B

Neritina nigrofusca Thiele, 1928

Thiele, J. Mollusken vom Bismarck-Archipel, von Neu-Guinea und Nachbar-Inseln. Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere 55: 119–120

2 syntypes ZMB

Locality: Bismarck Archipelago, Papua New Guinea

MSD: 9.4–10.8 mm

C

Neritodryas notabilis Riech, 1935

Zoologischer Anzeiger 110: 242–243

Holotype ZMB; 3 paratypes ZMB

Locality: New Britain, Bismarck Archipelago, Papua New Guinea

MSD: 50.2 mm (holotype), 39.9–47.0 mm (paratypes)

Plate 74

Neritina melanostoma Troschel, 1837

Syntype
MSD: 28.7 mm

Neritina nigrofusca Thiele, 1928

Syntype
MSD: 10.8 mm

Neritodryas notabilis Reich, 1935

Holotype
MSD: 50.2 mm

Plate 75.

A

Neritina nucleolus spinifera Martens, 1878 "*Neritina nucleolus* Morelet var. *spinifera* Martens, 1878"

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 177–179 (Pl.16, Figs.4–6)

Holo or Syntype ZMB

Locality: Philippines

MSD: 26.2 mm

16 syntypes ZMB

Locality: New Caledonia

MSD: 12.7–19.6 mm

B

Navicella pala Mousson, 1865

Journal de Conchyliologie 13(2): 206

2 syntypes ZMB

Locality: Viti Levu, Fiji

MSD: 22.4 mm

C

Neritina picta serta Martens, 1900 "*Neritina picta* Sowerby var. *serta* Martens, 1900"

Biologia Centrali-Americana (F.D. Godman and O. Salvin, eds.). R.H. Poter. London: 590 (Pl.28, Fig.13)

3 syntypes ZMB (Costa Rica)

Locality: N.W. Mexico; Panama; Equador; Costa Rica

MSD: 6.6–9.7 mm

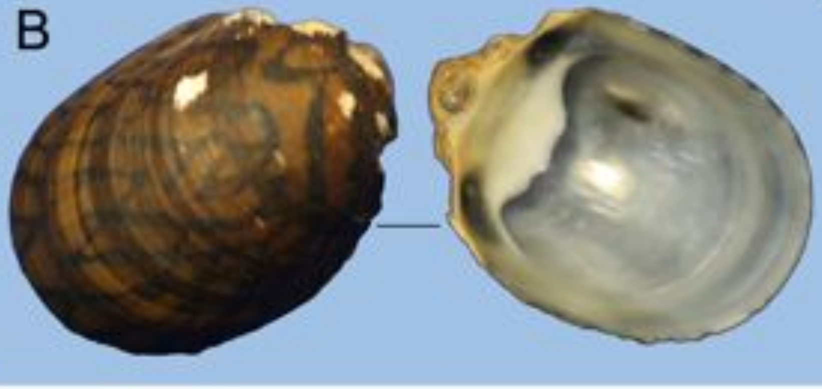
Plate 75

Neritina nucleolus spinifera Martens, 1878

Syntype
MSD: 19.6 mm

Navicella pala Mousson, 1865

Syntype
MSD: 22.4 mm



Neritina picta serta Martens, 1900

Syntype
MSD: 9.7 mm

Plate 76.

A

Neritina retropicta Martens, 1878

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 169–170 (Pl.17, Figs.18–20)

5 syntypes ZMB; 9 syntypes ZMB; 12 syntypes ZMB

Locality: Nagasaki, Kyushu, Japan

MSD: 7.1–18.1 mm

B

Neritina rubicunda Martens, 1875

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 32–33 (Pl.6, Figs.20–23)

3 syntypes ZMB

Locality: Borneo, Indonesia

MSD: 10.3–12.6 mm

C

Neripteron schneideri Riech, 1935

Zoologischer Anzeiger 110: 240–241

Holotype ZMB; 22 paratypes ZMB

Locality: New Britain, Bismarck Archipelago, Papua New Guinea

MSD: 10.3 mm (holotype), 8.8–10.2 mm (paratypes)

Plate 76

Neritina retropicta Martens, 1878

Syntype
MSD: 17.5 mm

Neritina rubicunda Martens, 1875

Syntype
MSD: 12.6 mm

Neripteron schneideri Riech, 1935

Holotype
MSD: 10.3 mm

Plate 77.

A

Navicella sculpta Martens, 1881

Die Gattung *Navicella*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10-A): 15–16 (Pl.2, Figs.5–8)

Holo or Syntype ZMB

Locality: Kepahiang, Sumatera, Indonesia

MSD: 13.0 mm

B

Neritina (*Clithon*) *soembawana* Haas, 1912

Annals and Magazine of Natural History 10: 418

2 syntypes ZMB

Locality: Bima, Sumbawa, Indonesia

MSD: 16.5 mm, 16.7 mm

C

Neritina sowerbiana lactiflua Martens, 1878 "*Neritina sowerbiana* Récluz var. *lactiflua* Martens, 1878"

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 172–174 (Pl.18, Fig.3)

2 syntypes ZMB

Locality: East Asia (Ostasien)

MSD: 11.6 mm, 11.7 mm

Plate 77

Navicella sculpta Martens, 1881

Holo or Syntype
MSD: 13.0 mm

A

Neritina (*Clithon*) *soembawana* Haas, 1912

Syntype
MSD: 16.7 mm

B

Neritina sowerbiana lactiflua Martens, 1878

Syntype
MSD: 11.7 mm

C

Plate 78.

A

Neritina sowerbiana maculofasciata Martens, 1878 "*Neritina sowerbiana* Récluz var. *maculofasciata* Martens, 1878"

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 172–174 (Pl.18, Figs.1–2)

Syntype ZMB; 2 syntypes ZMB

Locality: East Asia (Ostasien)

MSD: 10.7–15.1 mm

B

Neritina squarosa cruenta Martens, 1878 "*Neritina squarosa* Récluz var. *cruenta* Martens, 1878", "*Neritina squarosa* Récluz var. *minor* Martens, 1878"

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 162–163

Holo or Syntype ZMB

Locality: East Indian Archipelago (Indischer Archipel)

MSD: 9.9 mm

C

Neritina subpunctata glandiformis Martens, 1878 "*Neritina subpunctata* Récluz var. *glandiformis* Martens, 1878"

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 180–181 (Pl.18, Fig.22)

Syntypes ZMB

Locality: Adonara, Lesser Sunda Islands, Indonesia

MSD: 20.4–23.3 mm

Plate 78

Neritina sowerbiana maculofasciata Martens, 1878

Syntype
MSD: 15.7 mm

Neritina squarosa cruenta Martens, 1878

Holo or Syntype
MSD: 9.9 mm

Neritina subpunctata glandiformis Martens, 1878

Syntype
MSD: 23.3 mm

Plate 79.

A

Neritina sulculosa Martens, 1875

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 278 (Pl. 8, Fig.23–26)

9 syntypes ZMB

Locality: Larantuka, Flores Is., East Nusa Tenggara, Indonesia

MSD: 11.6–14.4 mm

B

Neritina tenebricosa parryi Martens "*Neritina tenebricosa* C.B. Adams var. parryi Martens"

Martens MS.

4 syntypes ZMB

Locality: Jamaica

MSD: 9.3–10.5 mm

C

Navicella tessellata compressa Martens, 1881 "*Navicella tessellata* Lamarck var. *compressa* Martens, 1881"

Die Gattung *Navicella*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10-A): 38–41 (Pl.8, Figs.4–9, 19–21)

Holo or Syntype ZMB

Locality: Timor, Indonesia; Borongan, Samar, Philippines; Viti-inseln, Vanua-Levu, Fiji

MSD: 17.4 mm

Plate 79

Neritina sulculosa Martens, 1875

Syntype
MSD: 14.4 mm

A

"Neritina tenebricosa parryi Martens MS"

MSD: 10.5 mm

B

Navicella tessellata compressa Martens, 1881

Holo or Syntype
MSD: 17.4 mm

C

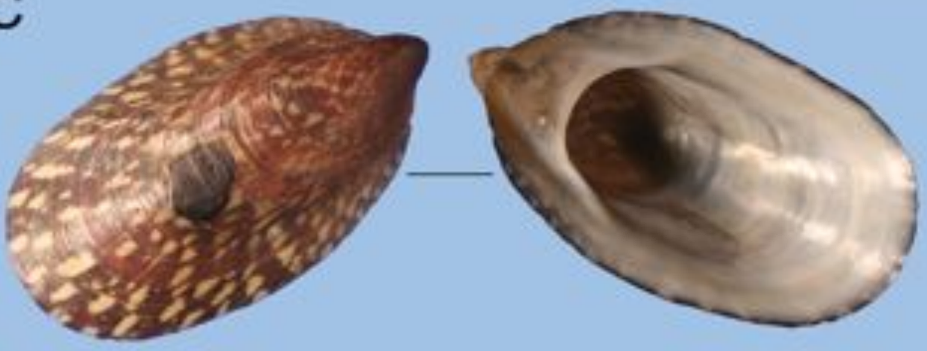


Plate 80.

A

Neritina (*Clithon*) *thermophila* Martens, 1877
Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin, 31 Mai 1877: 284–285 (Pl.1, Fig.12)
8 syntypes ZMB; 17 syntypes ZMB
Locality: New Britain, Bismarck Archipelago, Papua New Guinea
MSD: 9.3–10.5 mm

B

Neritina virginea oblonga Martens, 1865 “*Neritina virginea* Linnaeus var. *oblonga* Martens, 1865”
Malakozoologische Blätter 12: 62–63
5 syntypes ZMB
Locality: Cuba
MSD: 16.9–21.6 mm

C

Neritina virginea parvula Martens, 1865 “*Neritina virginea* Linnaeus var. *parvula* Martens, 1865”
Malakozoologische Blätter 12: 63–64
4 syntypes ZMB
Locality: Caba Cluz, Cuba; Puerto Rico
MSD: 7.5–7.6 mm

Plate 80

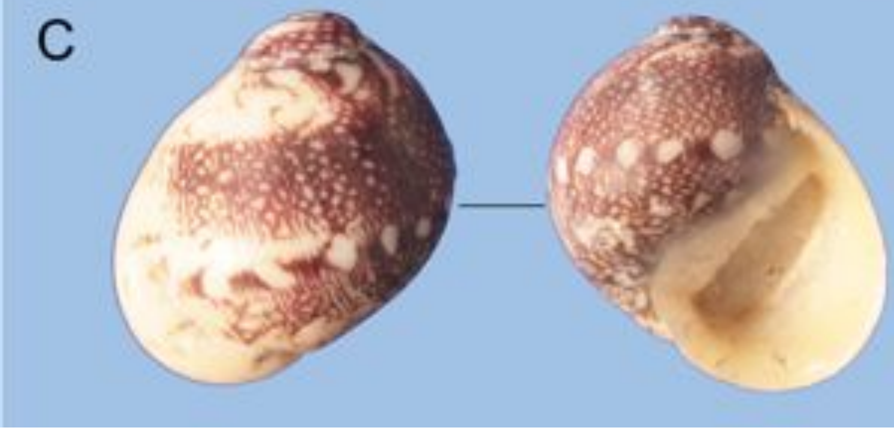
Neritina (*Clithon*) *thermophila* Martens, 1877

Syntype
MSD: 5.2 mm

Neritina virginea oblonga Martens, 1865

Syntype
MSD: 21.6 mm

Neritina virginea parvula Martens, 1865



Syntype
MSD: 7.6 mm

Plate 81.

A

Neritina vitiensis Mousson, 1865
Journal de Conchyliologie 13(2): 204
2 syntypes ZMB
Locality: Reva River, Viti Levu, Fiji
MSD: 18.8 mm, 19.8 mm

B

Neritina wetarana Haas, 1912
Annals and Magazine of Natural History 10: 419
3 syntypes ZMB
Locality: Ilwaki River, Ilmedo, Wetar, Maluku, Indonesia
MSD: 25.1 mm

C

Neritina iris wichmanni Martens, 1897 "*Neritina iris* Linnaeus var. *wichmanni* Martens, 1897"
Süss- und Brackwasser Mollusken des Indischen Archipels (M. Weber, ed.), Zoologisch Ergebnisse einer Reise in Niederländish Ost-Indien, Leiden, 4(1): 78 (Pl.10, Fig.10)
Holotype ZMB
Locality: Kuaniko, Timor, Nusa Tenggara, Indonesia
MSD: 25.1 mm

Plate 81

Neritina vitiensis Mousson, 1865

Syntype
MSD: 18.8 mm

Neritina wetarana Haas, 1912

Syntype
MSD: 21.0 mm

Neritina iris wichmanni Martens, 1897

Holotype
MSD: 25.1 mm

Plate 82.

A

Neritina zigzag glandiformis Martens "*Neritina ziczac* Lamarck var. *glandiformis* Martens"

Martens MS.

7 nontypes ZMB

Locality: Manila, Philippines

MSD: 20.2–24.0 mm

B, C

Neritina zigzag triangularis Martens, 1877 "*Neritina ziczac* Lamarck var. *triangularis* Martens, 1877"

Die Gattung *Neritina*. Systematisches Conchylien-Cabinet von Martini und Chemnitz [second edition] 2(10): 101–103 (Pl.10, Fig.24)

Syntype ZMB; 10 syntypes ZMB

Locality: East Indian Archipelago (Indischer Archipel)

MSD: 16.0–20.9 mm

Plate 82

“*Neritina zigzag glandiformis* Martens, MS”

MSD: 24.0 mm

Neritina zigzag triangularis Martens, 1877

Syntype
MSD: 21.0 mm

Syntype
MSD: 19.9 mm

Type specimens, Geneva museum Lamarck collection

Plate 83.

A

Neritina auriculata Lamarck, 1816
Encyclopédie méthodique. Tableau Encyclopédique et méthodique des trois règnes de la nature. Vingt-troisième partie. Mollusques et polypes divers. V. Agasse, Paris: 11 p (Pl.455, Fig.6)
3 syntypes MHNG
Locality: Australia (Nouvelle-Hollande) and the surrounding islands
MSD: 11.4–14.8 mm

B

Neritina brevispina Lamarck, 1822
Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l’auteur, au jardin du Roi: 185–186 p
4 syntypes MHNG
Locality: Timor Is.
MSD: 8.4–18.2 mm

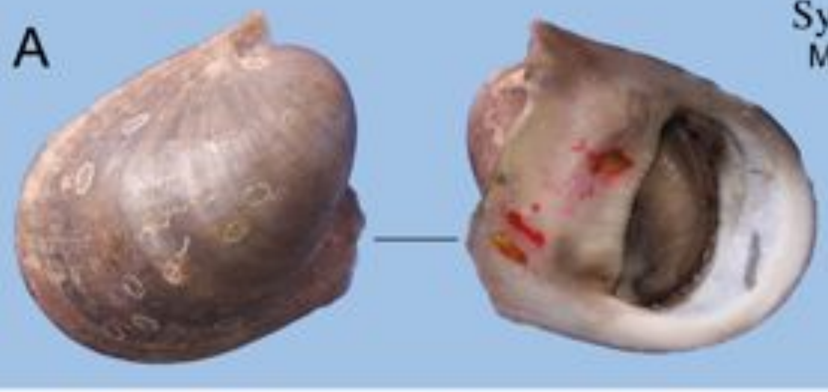
C

Neritina crepidularia Lamarck, 1822
Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l’auteur, au jardin du Roi: 186 p
2 syntypes MHNG
Locality: ?
MSD: 14.6 mm, 16.3 mm

Plate 83

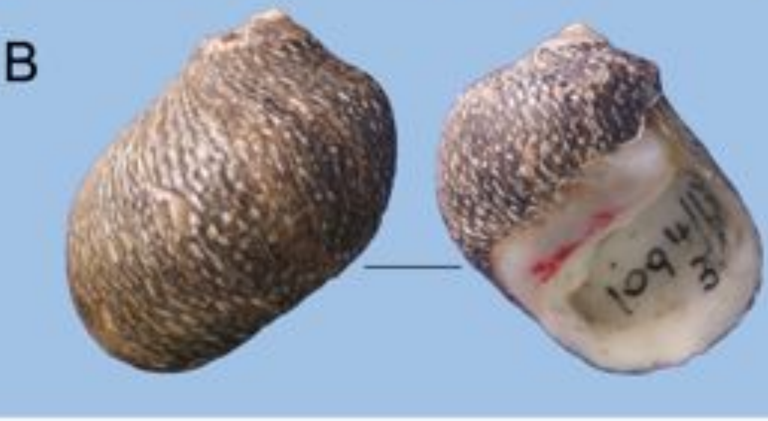
Neritina auriculata Lamarck, 1816

Syntype
MSD: 14.8 mm



Neritina brevispina Lamarck, 1822

Syntype
MSD: 18.2 mm



Neritina crepidularia Lamarck, 1822

Syntype
MSD: 16.3 mm

Plate 84.

A

Neritina domingensis Lamarck, 1822

Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l'auteur, au jardin du Roi: 186 p

2 syntypes MHNG

Locality: Sant Domingo (Saint-Domingue)

MSD: 16.0 mm, 16.5 mm

B

Navicella elliptica Lamarck, 1816

Encyclopédie méthodique. Tableau Encyclopédique et méthodique des trois règnes de la nature. Vingt-troisième partie. Mollusques et polypes divers. V. Agasse, Paris: 12 p (Pl.456, Fig.1)

7 syntypes MHNG

Locality: Maluku Is., Indonesia

MSD: 18.6–31.9 mm

C

Neritina fasciata Lamarck, 1816

Encyclopédie méthodique. Tableau Encyclopédique et méthodique des trois règnes de la nature. Vingt-troisième partie. Mollusques et polypes divers. V. Agasse, Paris: 11 p (Pl.455, Fig.5)

2 syntypes MHNG

Locality: ?

MSD: 19.6 mm, 20.3 mm

Plate 84

Neritina domingensis Lamarck, 1822

Syntype
MSD: 16.5 mm

A

Navicella elliptica Lamarck, 1816

Syntype
MSD: 31.9 mm

B

Neritina fasciata Lamarck, 1816

Syntype
MSD: 20.3 mm

C

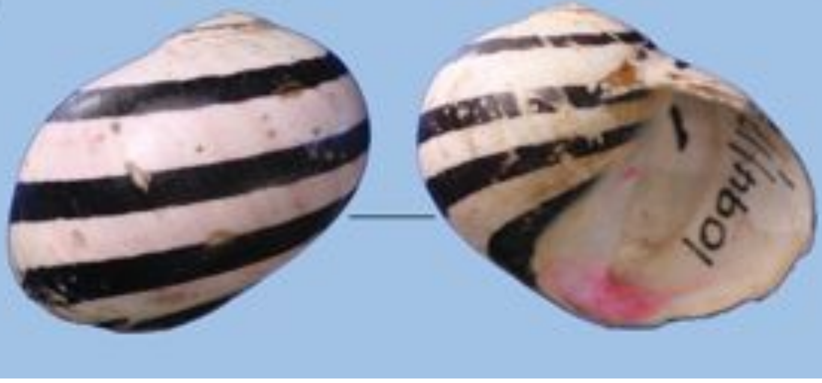


Plate 85.

A, B

Neritina gagates Lamarck, 1822

Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l'auteur, au jardin du Roi: 185 p

2 syntypes MHNG

Locality: ?

MSD: 20.5 mm, 24.6 mm

C

Navicella lineata Lamarck, 1816

Encyclopédie méthodique. Tableau Encyclopédique et méthodique des trois règnes de la nature. Vingt-troisième partie. Mollusques et polypes divers. V. Agasse, Paris: 12 p (Pl.456, Fig.2)

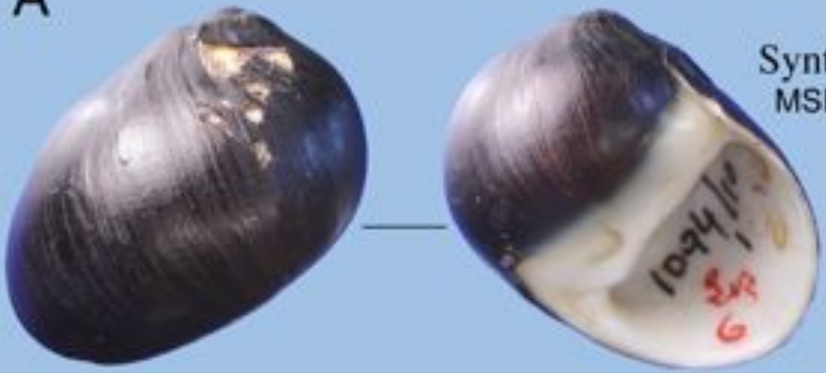
Possible holotype MHNG

Locality: India

MSD: 17.8 mm

Neritina gagates Lamarck, 1822

A



Syntype 1
MSD: 24.6 mm

B

Syntype 2
MSD: 20.5 mm

Navicella lineata Lamarck, 1816

Holo or Syntype
MSD: 17.8 mm

C

Plate 86.

A

Neritina lineolata Lamarck, 1822

Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l'auteur, au jardin du Roi: 186–187 p

2 syntypes MHNG

Locality: ?

MSD: 20.2 mm, 24.6 mm

B

Neritina lugubris Lamarck, 1822

Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l'auteur, au jardin du Roi: 185 p

2 syntypes MHNG

Locality: ?

MSD: 18.6 mm, 20.1 mm

C

Neritina meleagris Lamarck, 1822

Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l'auteur, au jardin du Roi: 187 p

5 syntypes MHNG

Locality: Sant Domingo (Saint-Domingue)

MSD: 11.6–17.0 mm

Plate 86

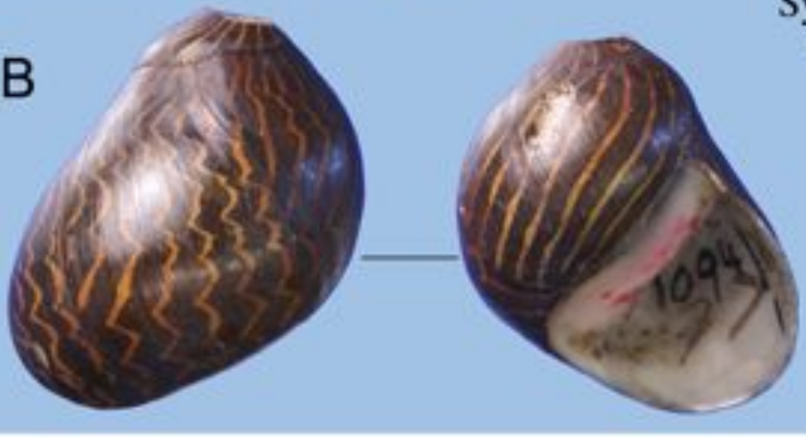
Neritina lineolata Lamarck, 1822

A

Syntype
MSD: 24.6 mm

Neritina lugubris Lamarck, 1822

B



Syntype
MSD: 20.1 mm

Neritina meleagris Lamarck, 1822

C

Syntype
MSD: 17.0 mm

Plate 87.

A

Neritina strigilata Lamarck, 1822

Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l'auteur, au jardin du Roi: 187 p

2 syntypes MHNG

Locality: "Antilles" India?

MSD: 26.6 mm, 31.2 mm

B

Navicella tessellata Lamarck, 1816

Encyclopédie méthodique. Tableau Encyclopédique et méthodique des trois règnes de la nature. Vingt-troisième partie. Mollusques et polypes divers. V. Agasse, Paris: 12 p (Pl.456, Fig.3, 4)

Possible holotype MHNG

Locality: India

MSD: 17.8 mm, 19.3 mm

C

Neritina zigzag Lamarck, 1822

Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux… Tome sixième. Deuxième partie. Chez l'auteur, au jardin du Roi: 185 p

3 syntypes MHNG

Locality: ?

MSD: 19.4–26.1 mm

Plate 87

Neritina strigilata Lamarck, 1822

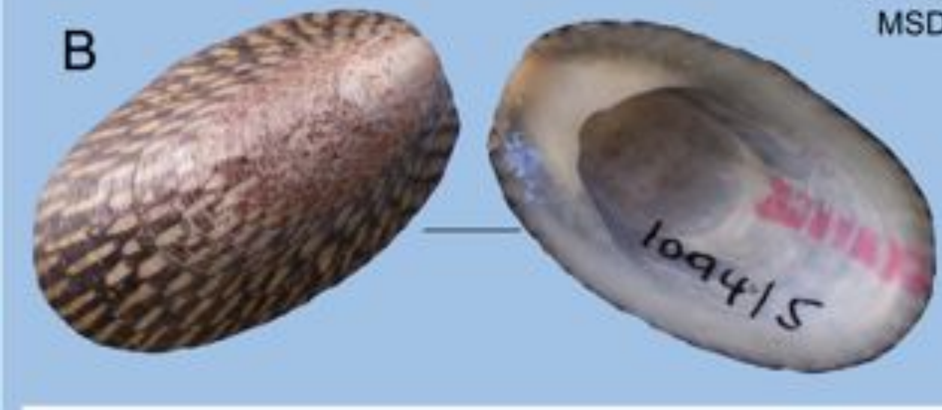
A

Syntype
MSD: 31.2 mm

Navicella tessellata Lamarck, 1816

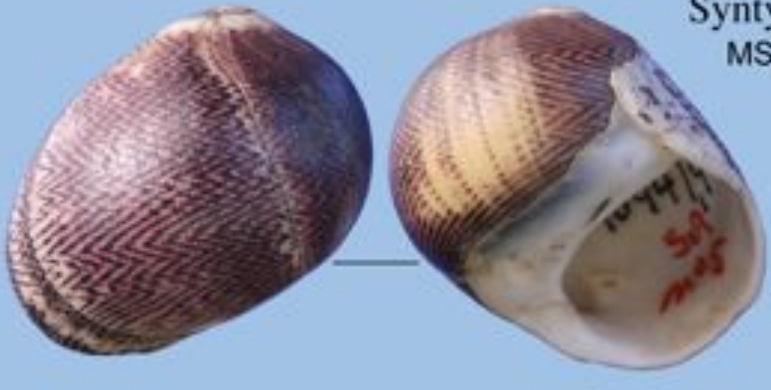
Syntype
MSD: 17.8 mm

B



Neritina zigzag Lamarck, 1822

C



Syntype
MSD: 26.1 mm

Type specimens, Geneva museum Récluz collection

Plate 88.

A

Nerita adansoniana Récluz, 1841
Revue Zoologique, par la Société Cuvierienne 4: 313–314
Lectotype MHNG; 22 paralectotypes MHNG
Locality: Senegal
MSD: 10.4 mm (lectotype), 10.2–10.7 mm (paralectotypes)

B

Navicella apiata Récluz, 1842
Revue Zoologique, par la Société Cuvierienne for 1841 [3 January], 4(12): 376
3 syntypes MHNG; 3 syntypes MHNG; 2 syntypes MHNG; syntype MHNG
Locality: Nouka Hiva, Fiji
MSD: 5.9–27.7 mm

C

Nerita (*Neritina*) *asperulata* Récluz, 1843
Proceedings of the Zoological Society of London for 1842, 10: 169–170
4 syntypes MHNG
Locality: Pasaguing, North Ilocos, Luzon Is., Philippines
MSD: 13.7–20.5 mm

Plate 88

Nerita adansoniana Récluz, 1841

Lectotype
MSD: 10.4 mm

Navicella apiata Récluz, 1842

Syntype
MSD: 27.7 mm

Nerita (*Neritina*) *asperulata* Récluz, 1843

Syntype
MSD: 20.5 mm

Plate 89.

A

Nerita (*Neritina*) *beckii* Récluz, 1841
Revue Zoologique, par la Société Cuvierienne 4: 275–276
2 syntypes MHNG
Locality: ?
MSD: 20.1 mm, 22.4 mm

B

Neritina braziliana Sowerby II, 1849 "*Neritina brasiliana* Récluz, 1850"
Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 533, pl. 116, Figs. 232–234, 236, 237 (A. Récluz 1850, Journal de Conchyliologie 1: 151)
5 "syntypes" MHNG ("*Neritina brasiliana*" Récluz, 1850); 4 "syntypes" MHNG ("*Neritina brasiliana*" Récluz, 1850); 3 "syntypes" MHNG ("*Neritina brasiliana*" Récluz, 1850)
Locality: ?
MSD: 10.8–24.0 mm

C

Nerita (*Neritina*) *bruguieri* Récluz, 1841
Revue Zoologique, par la Société Cuvierienne 4: 274–275
3 syntypes MHNG
Locality: Philippines?
MSD: 19.0–21.2 mm

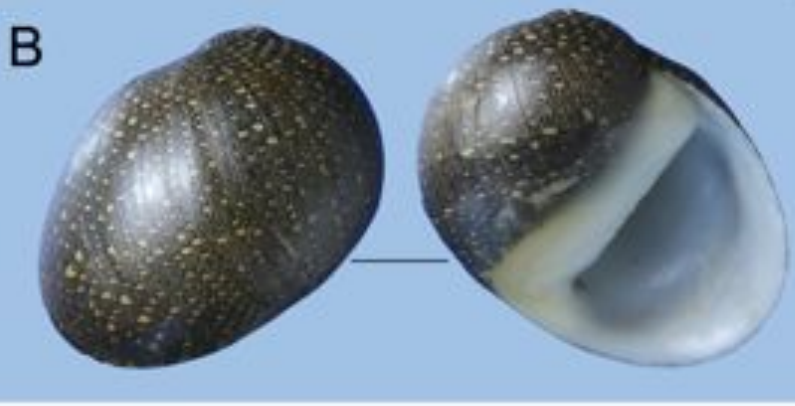
Plate 89

Nerita (*Neritina*) *beckii* Récluz, 1841

Syntype
MSD: 20.1 mm

Neritina braziliana Sowerby II, 1849

Syntype
MSD: 24.0 mm



Nerita (*Neritina*) *bruguieri* Récluz, 1843

Syntype
MSD: 12.2 mm

Plate 90.

A

Navicella caerulescens Sowerby II, 1850 [Récluz MS.]

Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 550, Pl. 118, Fig.29, 36–38

6 syntypes MHNG

Locality: Ganges, India

MSD: 14.5–17.8 mm

B

Neritina cochinsinae Récluz, 1850

Journal de Conchyliologie 1: 152

Holotype MHNG

Locality: Tourane, Viet Nam (Cochinchine)

MSD: 12.7 mm

C

Nerita (*Clithon*) *colombaria* Récluz, 1846

Proceedings of the Zoological Society of London 13: 121

Holotype MHNG

Locality: Colombo, Ceylon

MSD: 11.8 mm

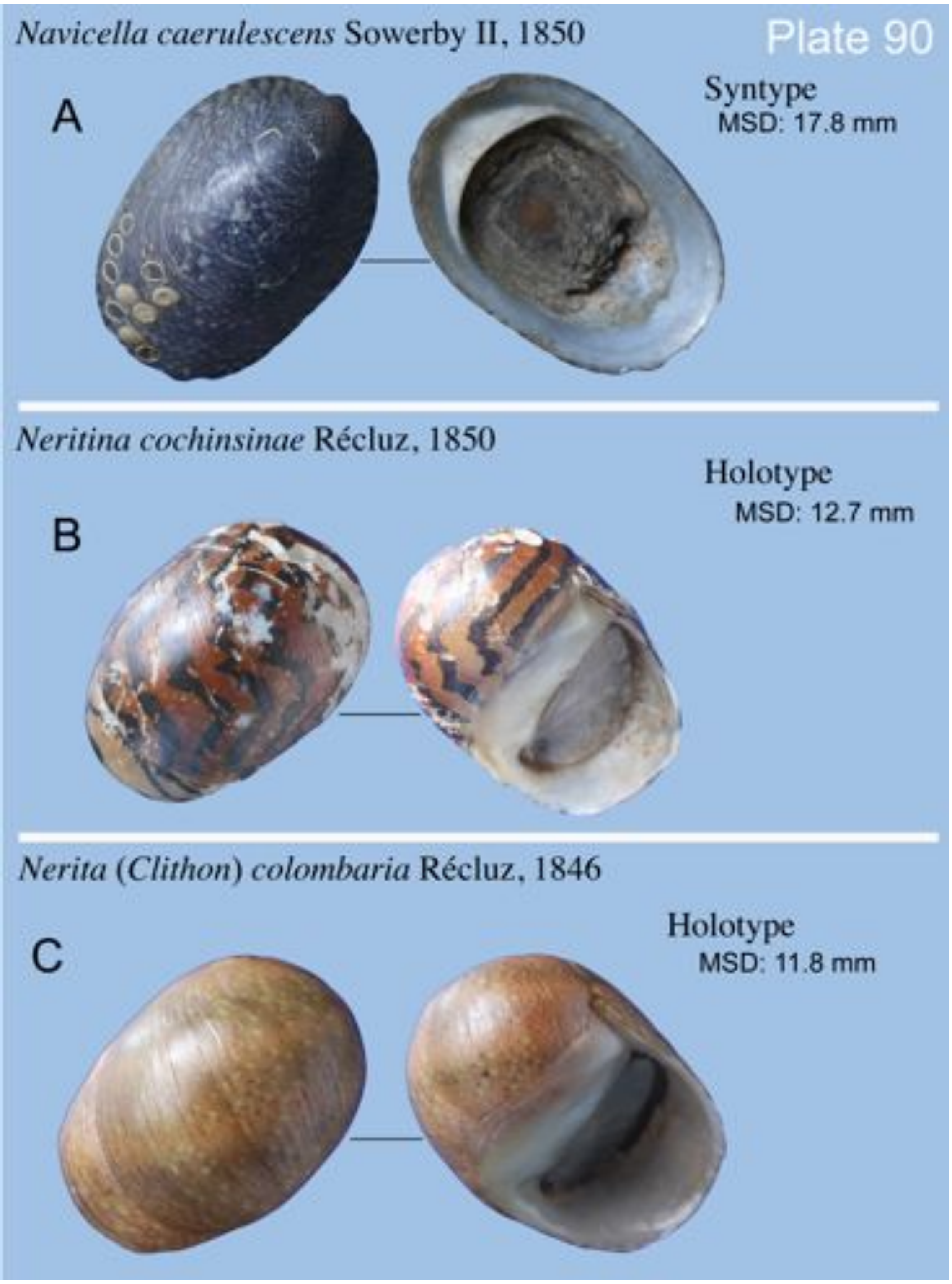


Plate 90
Navicella caerulescens Sowerby II, 1850
A
Syntype
MSD: 17.8 mm
Neritina cochinsinae Récluz, 1850
B
Holotype
MSD: 12.7 mm
Nerita (*Clithon*) *colombaria* Récluz, 1846
C
Holotype
MSD: 11.8 mm

Plate 91.

A

Neritina coromandeliana Sowerby I, 1836 "*Neritina coromandeliana* Récluz, 1849" "*Neritina coromandeliana* Sowerby II, 1849"
Conchological Illustrations: Pl.100, Fig.52 [June 30]
(G.B. Sowerby II. Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 540
4 "syntypes" MHNG (merely Récluz correction)
Locality: Coromandel (New Zealand?)
MSD: 16.2–20.7 mm

B

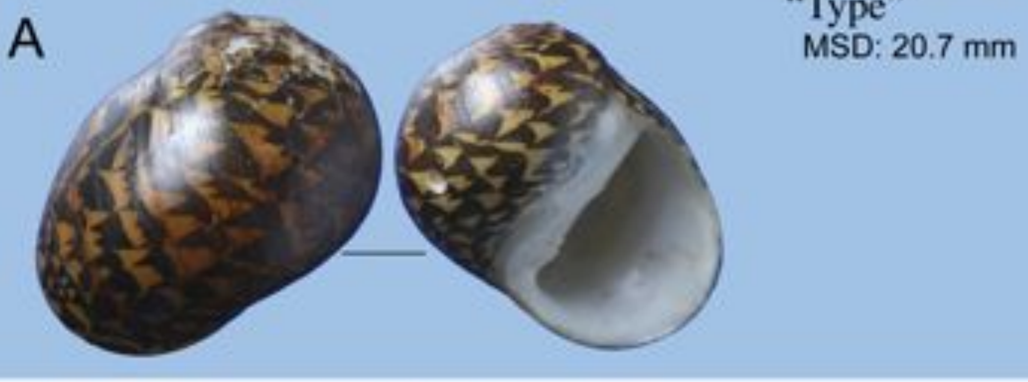
Nerita cuvieriana Récluz, 1841
Revue Zoologique, par la Société Cuvierienne 4: 338
3 syntypes MHNG
Locality: Guadeloupe?
MSD: 18.9 mm, 18.9 mm

C

Neritina delessertii Récluz, 1853
Journal de Conchyliologie 4: 260–261 (Pl.7, Fig.2)
Holotype MHNG
Locality: ?
MSD: 24.3 mm

Plate 91

Neritina coromandeliana Sowerby I, 1836



Nerita cuvieriana Récluz, 1841

Neritina delessertii Récluz, 1853

Plate 92.

A

Neritina delestennei Récluz, 1853
Journal de Conchyliologie 4: 259–260 (Pl.7, Fig.3)
Holotype MHNG; 2 paratypes MNHN
Locality: ?
MSD: 30.9 mm (holotype), 30.3 mm, 33.6 mm (paratypes)

B

Neritina desmoulinsiana Récluz, 1850
Journal de Conchyliologie 1: 153
3 syntypes MHNG; 10 syntypes MHNG
Locality: Noukahiva, French Polynesia
MSD: 11.2–16.7 mm

C

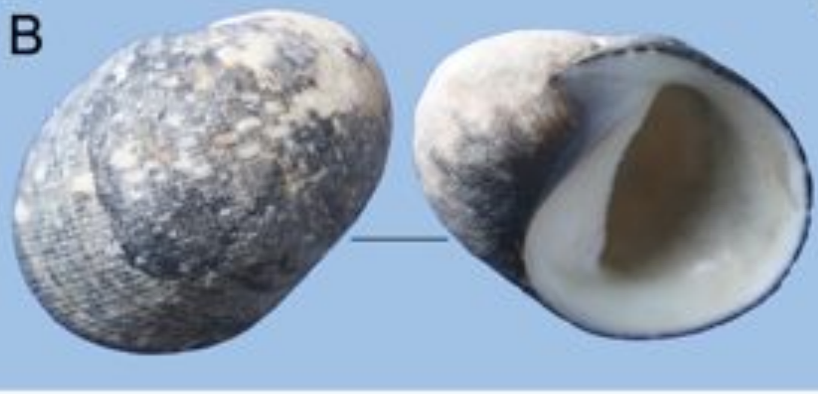
Neritina donovana Sowerby II, 1849 [Récluz MS.] (See Petit, 2009)
"*Nerita donovana* Récluz, 1843"
Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 526, pl. 110, Figs. 39,40 (= A. Récluz 1843, Proceedings of the Zoological Society of London 11: 73)
Nerita (*Clithon*) *donovani* Récluz, 1843
Proceedings of the Zoological Society of London for 1842, 10: 175
2 syntypes MHNG (Guimaras Is.); 4 syntypes MHNG (Negros Is.)
Locality: Guimaras Is., Philippines
MSD: 12.8–15.8 mm

Plate 92

Neritina delestennei Récluz, 1853

Holotype
MSD: 30.9 mm

Neritina desmoulinsiana Récluz, 1850



Syntype
MSD: 13.2 mm

Neritina donovana Sowerby II, 1849
Nerita (*Clithon*) *donovani* Récluz, 1843

Holotype
MSD: 24.3 mm

Plate 93.

A

Navicella durvillei Récluz, 1841
Revue Zoologique, par la Société Cuvierienne 4: 378
Lectotype MHNG; Paralectotype MHNG
Locality: Amboina, Indonesia
MSD: 28.6 mm (lectotype), 26.3 mm (paralectotype)

B

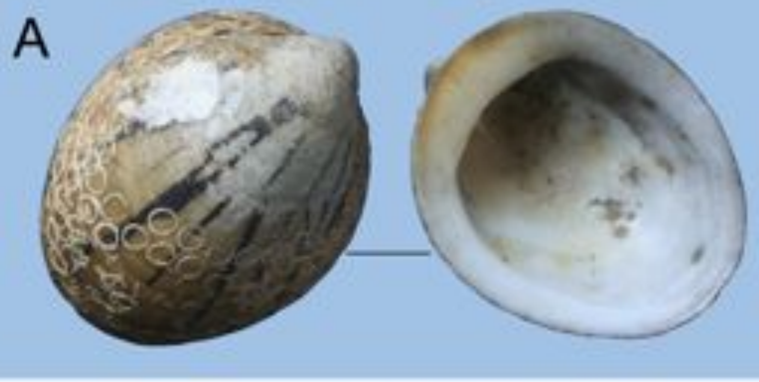
Navicella entrecastauxi Récluz, 1842
Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 380
2 syntypes MHNG
Locality: Australia (Nouvelle-Hollande)
MSD: 16.5 mm, 17.8 mm

C

Neritina exaltata Récluz, 1850
Journal de Conchyliologie 1: 65–66 (Pl.3, Fig.3)
3 syntypes MHNG
Locality: Philippines
MSD: 22.7–27.0 mm

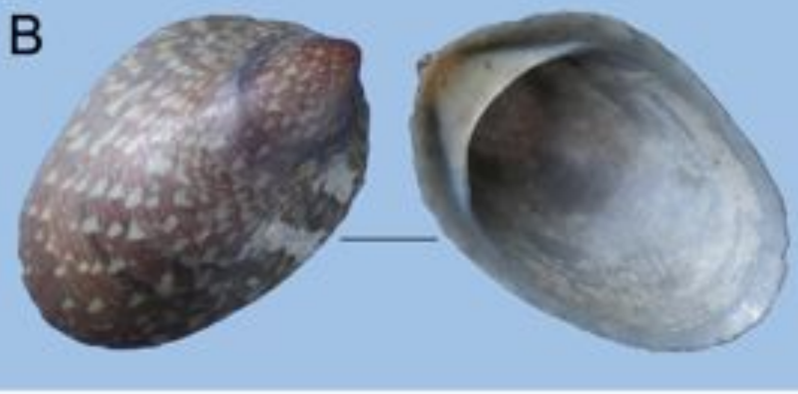
Plate 93

Navicella durvillei Récluz, 1841



Lectotype
MSD: 28.6 mm

Navicella entrecastauxi Récluz, 1842



Syntype
MSD: 16.5 mm

Neritina exaltata Récluz, 1850

Holotype
MSD: 27.0 mm

Plate 94.

A

Neritina florida Récluz, 1850

Journal de Conchyliologie 1: 145, 160–161 (Pl.7, Fig.6–7)

6 syntypes MHNG

Locality: Tahiti

MSD: 9.9–12.2 mm

B

Navicella freycineti Récluz, 1842

Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 375–376

Holotype MHNG

Locality: Makassar, Indonesia

MSD: 24.3 mm

C

Nerita guerini Récluz, 1841

Revue Zoologique, par la Société Cuvierienne 4(11): 314–315

Syntype MHNG; 3 syntypes MHNG

Locality: Sumatra, Indonesia

MSD: 7.5–12.2 mm

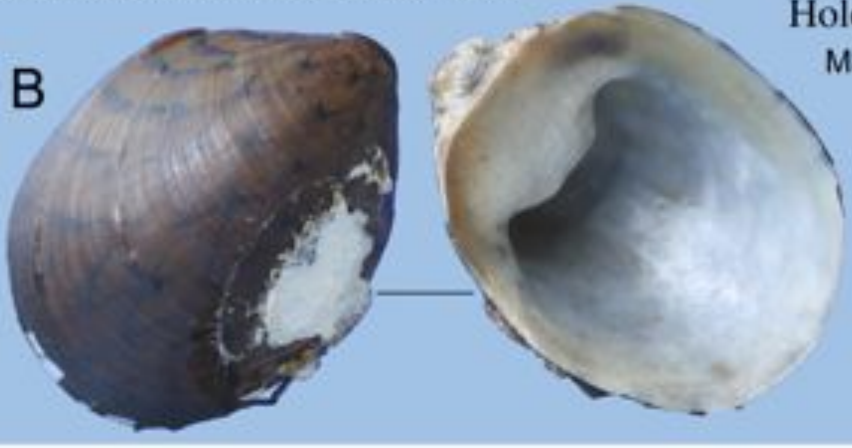
Plate 94

Neritina florida Récluz, 1850

Syntype
MSD: 12.2 mm

Navicella freycineti Récluz, 1842

Holotype
MSD: 24.3 mm



Nerita guerini Récluz, 1841

Syntype
MSD: 10.5 mm

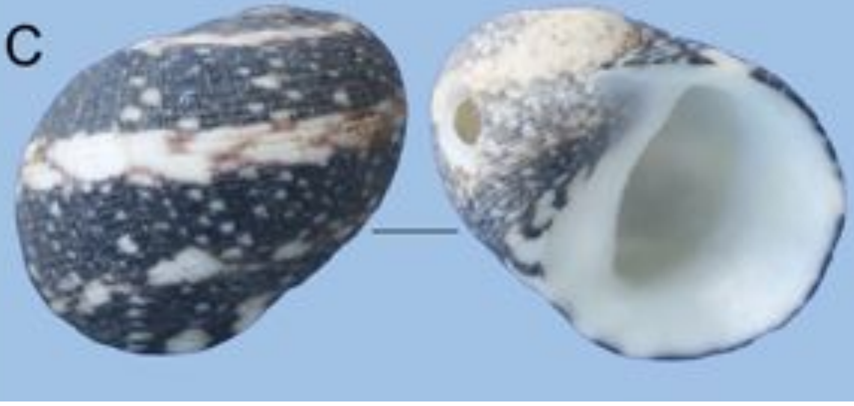


Plate 95.

A

Navicella laperousei Récluz, 1842

Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 378–380

Syntype MHNG; 2 syntypes MHNG; 2 syntypes MHNG; 3 syntypes MHNG

Locality: Guam; Fiji; Samoa

MSD: 17.6–31.4 mm

B

Nerita (*Clithon*) *leachii* Récluz, 1841

Revue Zoologique, par la Société Cuvierienne 4: 312

Holotype MHNG

Locality: Australia (Nouvellw-Hollande)

MSD: 12.8 mm

C

Navicella luzonica Récluz, 1842 "*Navicella luzonica* Soulayet, 1842"

Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 375

4 syntypes MHNG

Locality: Luzon Is., Philippines

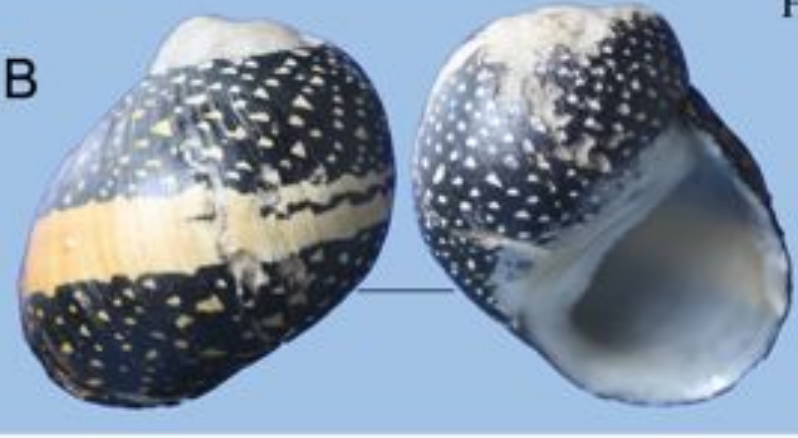
MSD: 11.7–17.2 mm

Plate 95

Navicella laperousei Récluz, 1842

Syntype
MSD: 31.4 mm

Nerita (*Clithon*) *leachii* Récluz, 1841



Holotype
MSD: 12.8 mm

Navicella luzonica Récluz, 1842

Syntype
MSD: 17.2 mm

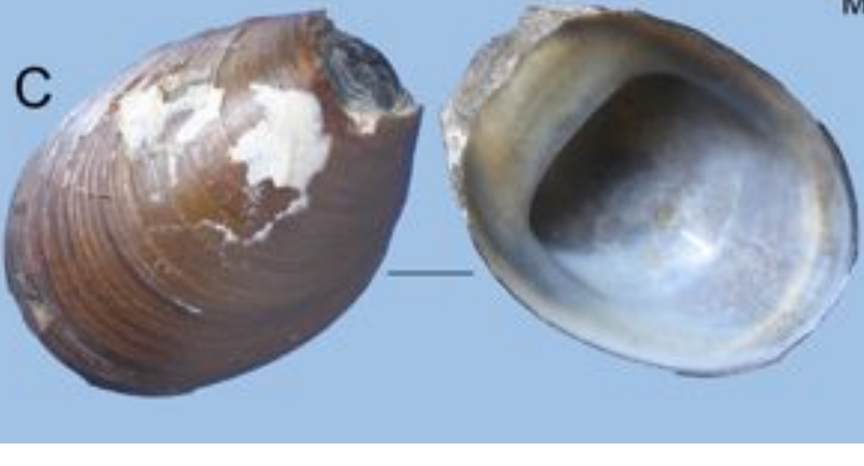


Plate 96.

A

Navicella macrocephala Récluz, 1842 "*Navicella macrocephala* Le Guillou, 1842"
Revue Zoologique, par la Société Cuvierienne for 1841, 4(12): 374
2 syntypes MHNG; 2 syntypes MHNG
Locality: Lebouka, Fiji
MSD: 17.4–31.9 mm

B

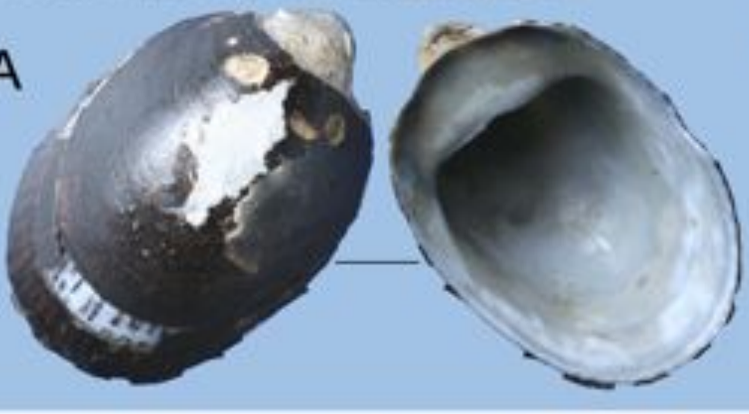
Neritina mauritii Sowerby II, 1849 [Récluz MS.]
Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 508
Published in synonymy of *Neritina sandwichensis* Deshayes, 1838
4 "syntypes" MHNG (Maurice Is.); 2 "syntypes" MHNG (Maurice Is.)
Locality: ?
MSD: 8.3–16.9 mm

C

Nerita (*Clithon*) *menkeana* Récluz, 1842
Revue Zoologique, par la Société Cuvierienne 5: 183–184
Holotype MHNG
Locality: Tahiti
MSD: 20.1 mm

Plate 96

Navicella macrocephala Récluz, 1842



Syntype
MSD: 31.9 mm

Neritina mauritii Sowerby II, 1849

Syntype
MSD: 16.9 mm

Nerita (*Clithon*) *menkeana* Récluz, 1842

Holotype
MSD: 20.1 mm

Plate 97.

A

Nerita michaudi Récluz, 1841

Revue Zoologique, par la Société Cuvierienne 4: 315

8 syntypes MHNG (Manila); 6 syntypes MHNG (Manila, “var. spinosa”)

Locality: ?

MSD: 6.6–12.3 mm

B

Neritina moquiniana Récluz, 1850

Journal de Conchyliologie 1: 152, 156–157 (Pl.7, Fig.9)

4 syntypes MHNG (Malaysia)

Locality: Islands of the South Sea

MSD: 8.2–10.9 mm

C

Nerita (*Clithon*) *obscurata* Récluz, 1842

Revue Zoologique, par la Société Cuvierienne 5: 183

2 syntypes MHNG (Tahiti); 3 syntypes MHNG (Philippines); 3 syntypes MHNG (Philippines); 3 syntypes MHNG (Cagayan, Mindanao, Philippines)

Locality: Tahiti

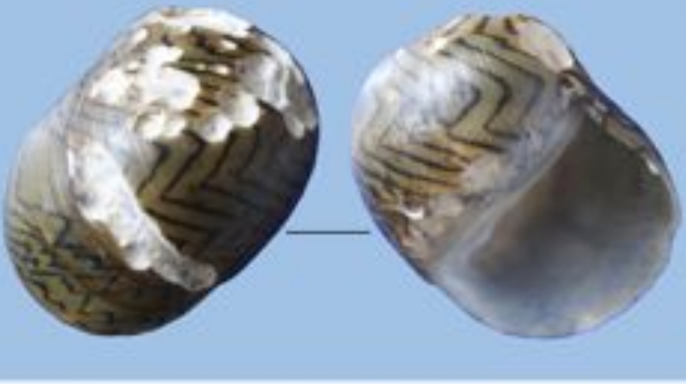
MSD: 16.4 mm, 19.6 mm (Tahiti); 19.6–23.5 mm (Philippines)

Plate 97

Nerita michaudi Récluz, 1841

Syntype
MSD: 12.3 mm

A



Neritina moquiniana Récluz, 1850

Syntype
MSD: 10.9 mm

B

Nerita (*Clithon*) *obscurata* Récluz, 1842

Syntype
MSD: 19.6 mm

C

Plate 98.

A

Nerita (*Neritina*) *panayana* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 170

3 syntypes MHNG

Locality: Dingle River, Ilo-Ilo, Panay, Negros Is., Philippines

MSD: 7.0–8.2 mm

B

Nerita (*Clithon*) *pulchella* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 175–176

12 syntypes MHNG

Locality: Saul, Pangasinan, Luzon Is., Philippines

MSD: 9.2–12.1 mm

C

Nerita royssyana Récluz, 1841

Revue Zoologique, par la Société Cuvierienne 4: 338–339

Nerita cuprina Récluz, 1843

Proceedings of the Zoological Society of London 11: 72

2 syntypes MHNG; 3 syntypes MHNG; 3 syntypes MHNG

Locality: ? (Wallis Is., Territory of the Wallis and Futuna Islands?)

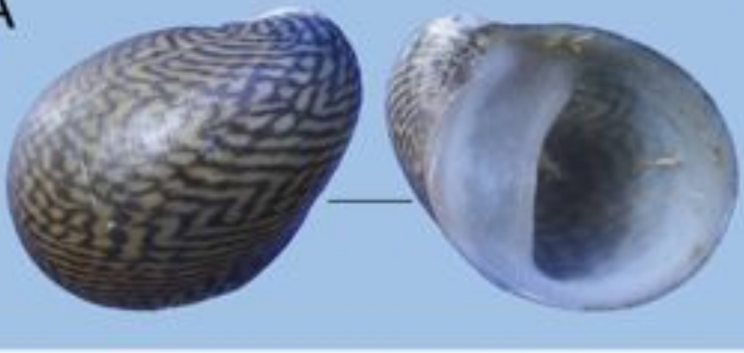
MSD: 13.2–19.9 mm

Plate 98

Nerita (*Neritina*) *panayana* Récluz, 1843

Syntype
MSD: 8.2 mm

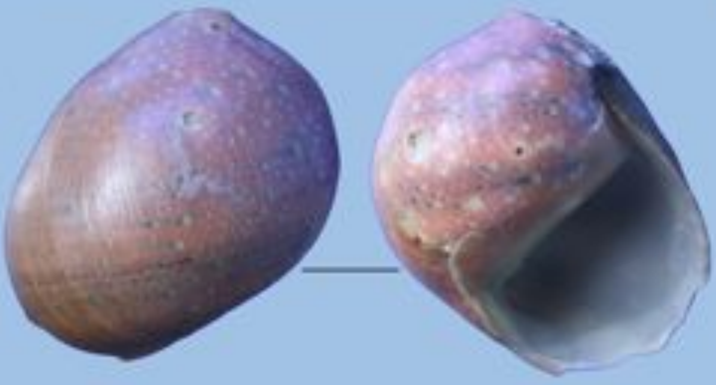
A



Nerita (*Clithon*) *pulchella* Récluz, 1843

Syntype
MSD: 12.1 mm

B



Nerita royssyana Récluz, 1841
Nerita cuprina Récluz, 1843

Syntype
MSD: 18.0 mm

C

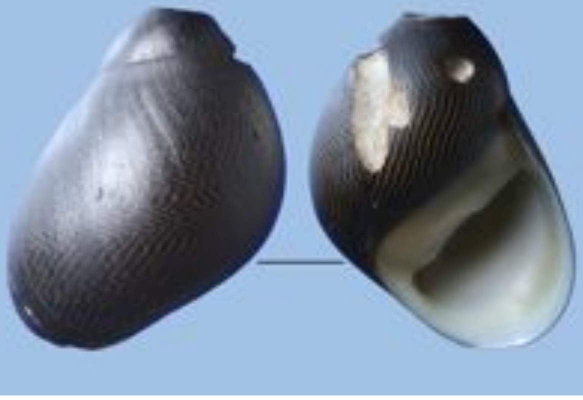


Plate 99.

A

Nerita rossmassleriana Récluz, 1846
Proceedings of the Zoological Society of London for 1845, 13: 119
Holotype MHNG
Locality: ?
MSD: 16.8 mm

B

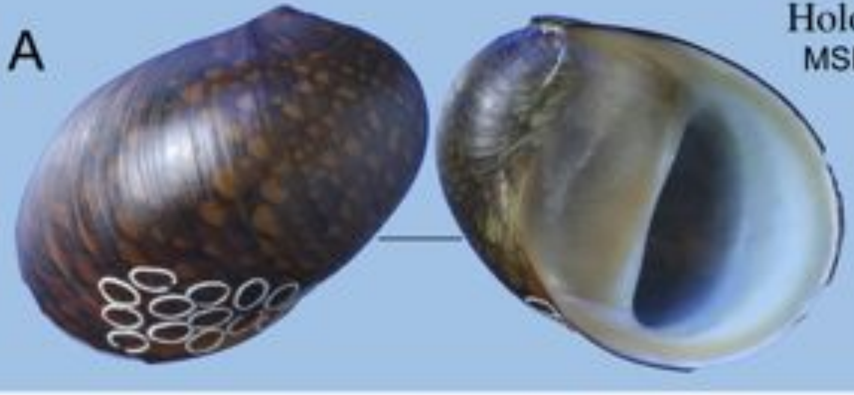
Nerita (*Clithon*) *ruginosa* Récluz, 1841
Revue Zoologique, par la Société Cuvierienne 4: 310–311
4 syntypes MHNG ("var. c"); Syntype MHNG ("var. f")
Locality: Hawaiian Islands?
MSD: 13.2–15.3 mm

C

Nerita sayana Récluz, 1844
Proceedings of the Zoological Society of London for 1843, 11: 199
4 syntypes MHNG
Locality: Guimaras Is., Philippines
MSD: 17.2–21.2 mm

Plate 99

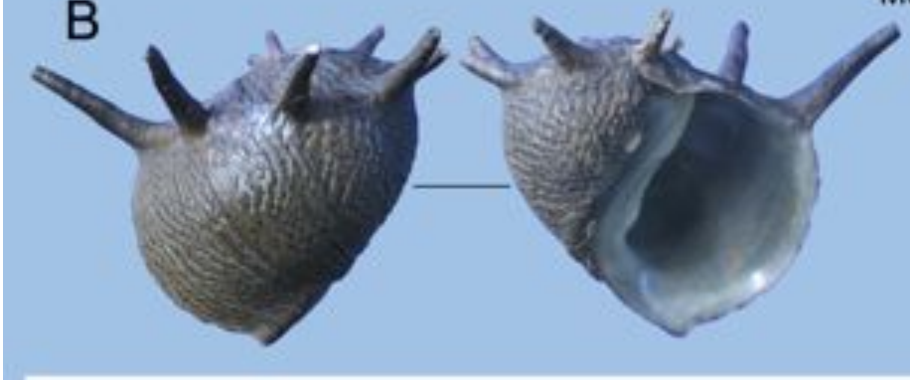
Nerita rossmassleriana Récluz, 1846



Holotype
MSD: 16.8 mm

Nerita (*Clithon*) *ruginosa* Récluz, 1841

Syntype
MSD: 15.3 mm



Nerita sayana Récluz, 1844

Syntype
MSD: 21.2 mm

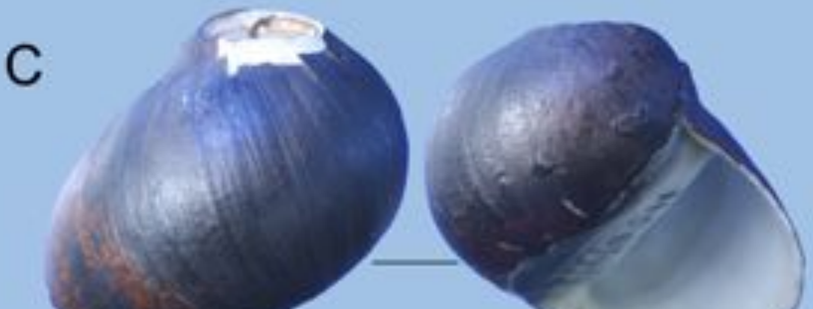


Plate 100.

A

Nerita (*Neritina*) *serrulata* Récluz, 1842

Revue Zoologique, par la Société Cuvierienne 5: 76–77

2 syntypes MHNG ("var. unicolor"); Syntype MHNG ("var. lineis arcuatis"); 3 syntypes MHNG ("var. maculata")

Locality: Sumatra, Indonesia

MSD: 17.6–19.8 mm

B

Nerita (*Clithon*) *souleyetana* Récluz, 1842

Revue Zoologique, par la Société Cuvierienne 5: 182–183

4 syntypes MHNG (Marquesas); 5 syntypes MHNG ("var. mutica", Noukahiva); 2 syntypes MHNG ("var. mutica", Noukahiva); 4 syntypes MHNG ("Taiti")

Locality: Tahiti?

MSD: 17.6–19.8 mm

C

Nerita (*Clithon*) *sowerbiana* Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 174

Neritina soverbiana Sowerby II, 1849 (?=*Nerita* (*Clithon*) *sowerbiana* Récluz, 1843, Proceedings of the Zoological Society of London for 1842, 10: 174) [Récluz MS.]

Monograph of the genus *Neritina*. Thesaurus Conchyliorum 2(10): 528, pl. 109, Figs. 5–8

5 syntypes MHNG

Locality: Sinaito, North Ylocos, Luzon, Philippines

MSD: 13.0–15.3 mm

Plate 100

Nerita (*Neritina*) *serrulata* Récluz, 1842

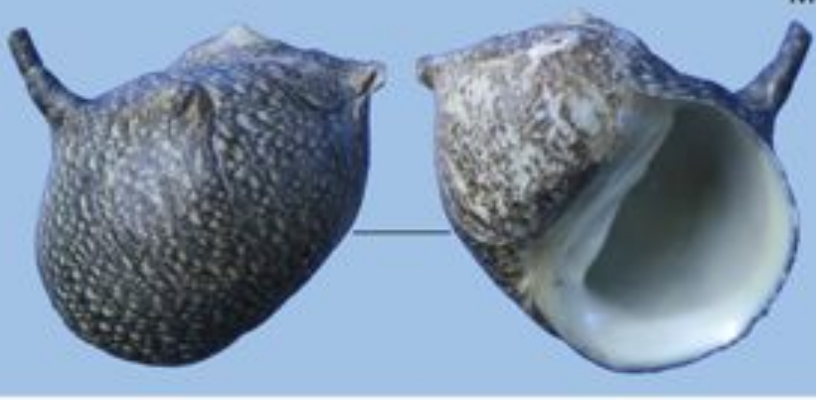
Holotype
MSD: 18.5 mm

A

Nerita (*Clithon*) *souleyetana* Récluz, 1842

Syntype
MSD: 16.2 mm

B



Nerita (*Clithon*) *sowerbiana* Récluz, 1843
Nerita soverbiana Sowerby II, 1849

Syntype
MSD: 15.3 mm

C

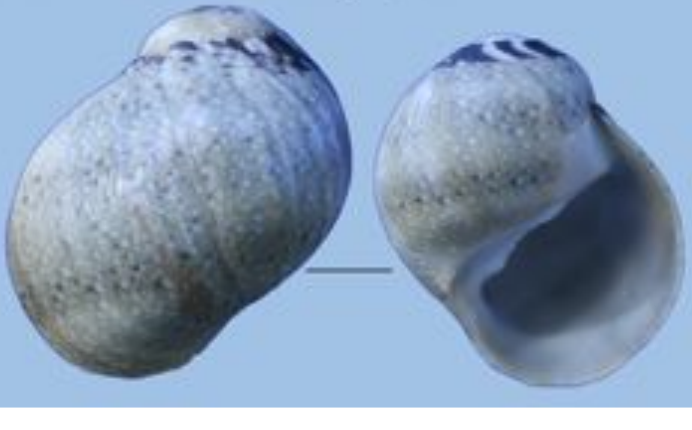


Plate 101.

A

Nerita (*Clithon*) *spinifera* Récluz, 1842
Revue Zoologique, par la Société Cuvierienne 5: 183
Holotype MHNG
Locality: Guam
MSD: 18.5 mm

B

Nerita striolata Récluz, 1841
Revue Zoologique, par la Société Cuvierienne 4: 337–338
4 syntypes MHNG
Locality: Antilles?
MSD: 14.8–16.6 mm

C

Nerita (*Clithon*) *subpunctata* Récluz, 1844
Proceedings of the Zoological Society of London for 1843, 11: 199–200
4 syntypes MHNG
Locality: Sinait, North Ilocos, Luzon, Philippines
MSD: 14.8–16.4 mm

Plate 101

Nerita (*Clithon*) *spinifera* Récluz, 1842

Holotype
MSD: 18.5 mm

A

Nerita striolata Récluz, 1841

Syntype
MSD: 16.6 mm

B

Nerita (*Clithon*) *subpunctata* Récluz, 1844

Syntype
MSD: 16.4 mm

C

Plate 102.

A

Navicella suffreni Récluz, 1842
Revue Zoologique, par la Société Cuvierienne for 1841 [3 January], 4(12): 374–375
Syntype MHNG ("var. A"); Syntype MHNG ("var. B"); Syntype MHNG ("var. C"); syntype MHNG
Locality: Lebouka, Fiji
MSD: 14.9–24.6 mm

B

Neritina (*Clithon*) *troschelii* Récluz, 1850
Journal de Conchyliologie 1: 147
11 syntypes MHNG
Locality: ?
MSD: 10.4–12.1 mm

C

Neritina (*Clithon*) *unidentata* Récluz, 1850
Journal de Conchyliologie 1: 147, 158–159
3 syntypes MHNG
Locality: Tahiti
MSD: 11.6–12.6 mm

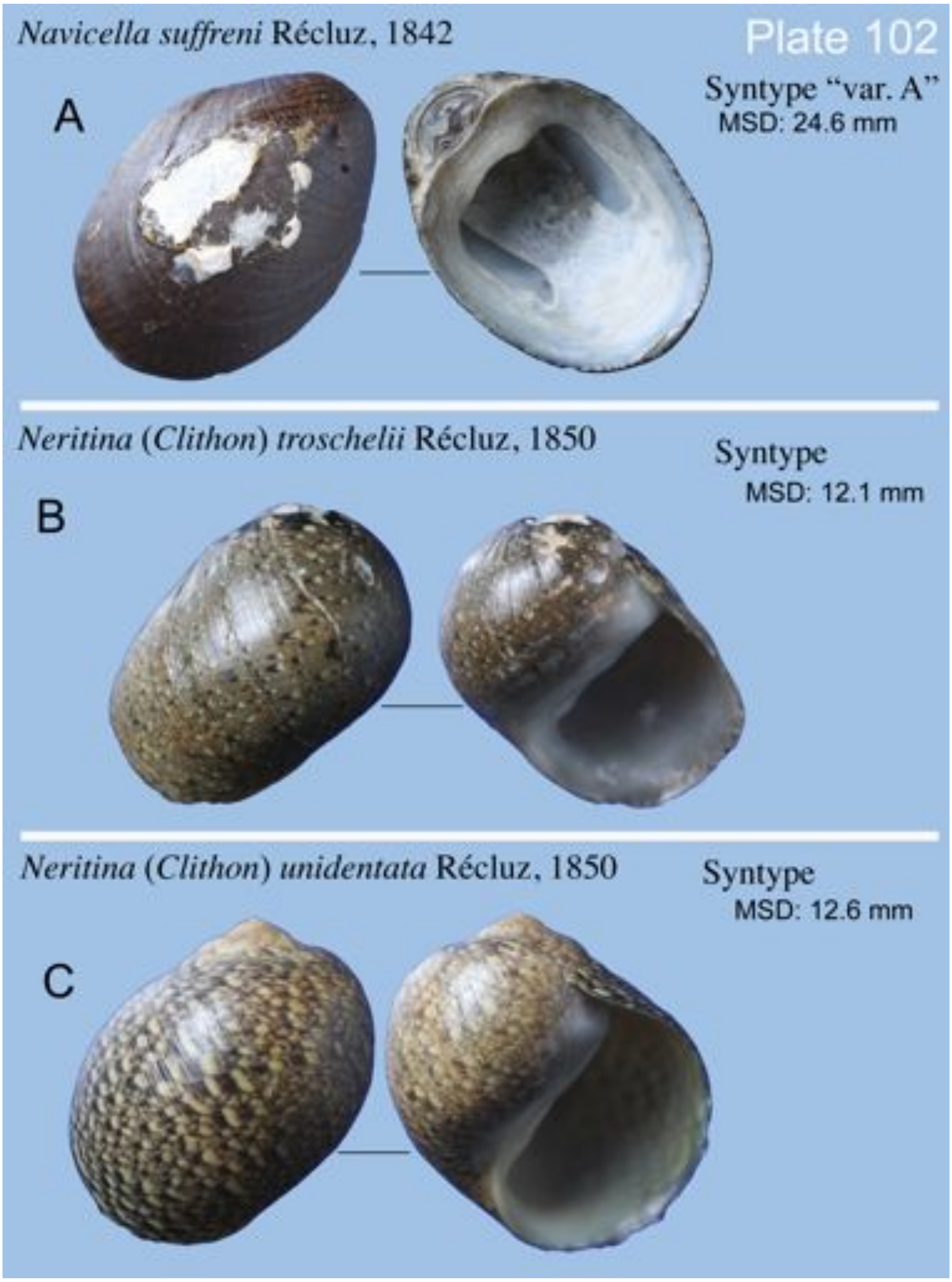


Plate 102

Navicella suffreni Récluz, 1842

Syntype "var. A"
MSD: 24.6 mm

Neritina (*Clithon*) *troschelii* Récluz, 1850

Syntype
MSD: 12.1 mm

Neritina (*Clithon*) *unidentata* Récluz, 1850

Syntype
MSD: 12.6 mm

Plate 103.

A

Navicella variabilis Récluz, 1843

Proceedings of the Zoological Society of London for 1842, 10: 155

3 syntypes MHNG

Locality: Cagayan, Misamis, Mindanao Is., Philippines

MSD: 25.7–31.0 mm

B

Nerita (*Neritina*) *webbei* Récluz, 1849

Revue et Magasin de Zoologie 2 (1)[February]: 70–71

6 syntypes MHNG; 14 syntypes MHNG; (16 syntypes MCZ;)

Grand-Bassam River, Ivory Coast, Senegal

MSD: 5.8–7.4 mm

Type specimens, Australian Museum Sydney

C

Neritina (*Neripteron*) *marmorata* Brazier, 1877

Proceedings of the Linnean Society of New South Wales for 1878, 2(1): 22 [January 1877]

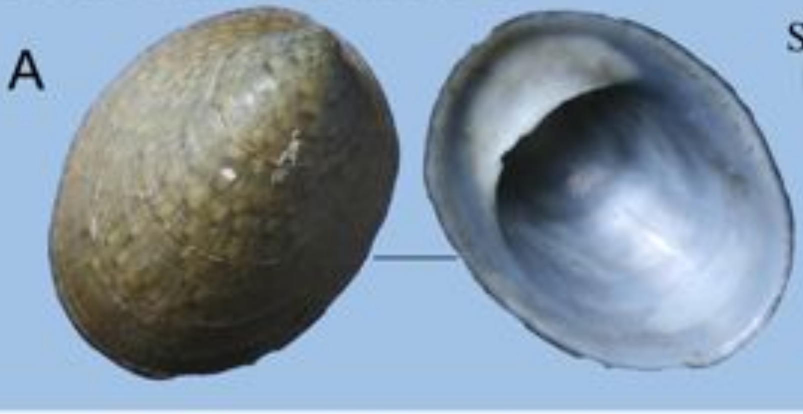
3 syntypes AMS

Locality: Katow River, New Guinea, Papua New Guinea

MSD: 15.0–17.4 mm

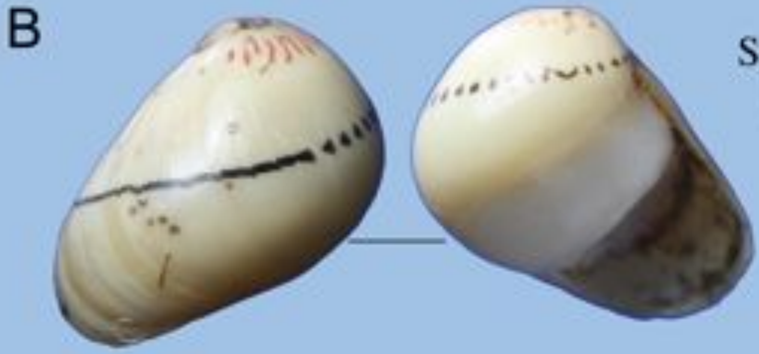
Plate 103

Navicella variabilis Récluz, 1843



Syntype
MSD: 31.0 mm

Nerita (*Neritina*) *webbei* Récluz, 1849



Syntype
MSD: 12.1 mm

Neritina (*Neripteron*) *marmorata* Brazier, 1877

Syntype
MSD: 17.4 mm

Synonym list of limnic neritids.

Species	Plate
Clithon castaneus (Hombron & Jaquinot, 1854)	
Neritina subrugata Baird in Brenchery, 1873	54C-F
Clithon chlorostoma (Sowerby I, 1833)	
Neritina chlorostoma Sowerby I, 1833	32C-E; 60B
Neritina dispar Pease, 1868	57C
Clithon corona (Linnaeus, 1758)	
Neritina brevispina Lamarck, 1822	83B
Neritina domingensis Lamarck, 1822	84A
Nerita (*Clithon*) *spinifera* Recluz, 1842	101A
Nerita angulosa Recluz, 1843	56A
Nerita (*Clithon*) *circumvoluta* Recluz, 1843	60C
Nerita (*Clithon*) *montacuti* Recluz, 1843	17A, B
Neritina fraseri Reeve, 1855	38D
Neritina spiniperda Morelet, 1858	53A-D
Neritina rhytidophora Tapparone-Canefri, 1883	67A
Neritina (*Clithon*) *rhyssodes* Boettger, 1890	66C
Clithon coronatus (Leach, 1815)	
Nerita (*Clithon*) *longispina* Recluz, 1841	15A (nontype)
Neritina mauritiana Morelet, 1867	16C; 44C
Clithon diadema (Recluz, 1841)	
Nerita cardinalis Le Guillou, 1841	4B
Nerita michaudi Recluz, 1841	97A
Nerita (*Clithon*) donovani Recluz, 1843	7A, B; 92C
Neritina donovana Sowerby II, 1849	92C
Neritina mutica Sowerby II, 1849	65B
Neritina cyanostoma Morelet, 1853	36A, B
Neritina pazi Gassies, 1858	48A, B
Neritina horrida Mabille, 1895	11C
Clithon exclamationis (Mabille, 1895)	
Neritina retusa Morelet, 1853	50C, D
Neritina (*Clithon*) *exclamationis* Mabille, 1895	8B-D
Neritina perfecta Mabille, 1895	19A-C
Clithon faba (Sowerby I, 1836)	
Neritina faba Sowerby I, 1836	38A, B
Nerita tritonensis Le Guillou, 1841	24A
Nerita (*Clithon*) *avellana* Recluz, 1842	56C
Nerita (*Clithon*) *pulchella* Recluz, 1843	98B
Nerita (*Clithon*) *colombaria* Recluz, 1846	90C

Neritina lentiginosa Reeve, 1856	42B
Neritina sowerbiana lactiflua Martens, 1878	77C
Neritina sowerbiana maculofasciata Martens, 1878	78A
Nerita deficiens Mabille, 1887	6A, B
Theodoxus eudeli Sowerby III, 1917	37A
Clithon nouletianus (Gassies, 1863)	
Neritina nouletiana Gassies, 1863	18A-C; 46C, D
Neritina comorensis Morelet, 1877	34A-C
Neritina flexuosa Gassies, 1878	38C
Clithon olivaceus (Recluz, 1843)	
Nerita (*Clithon*) *olivacea* Recluz, 1843	58B
Nerita (*Clithon*) *bicolor* Recluz, 1843	57B
Neritina subpunctata glandiformis Martens, 1878	78C
Neritina (*Clithon*) *francoisi* Mabille, 1895	10A, B
Neritina (*Clithon*) *soembawana* Haas, 1912	67B; 77B
Neritina bismarckiana Reich, 1935	70A
Clithon oualaniensis (Lesson, 1831)	
Neritina oualaniensis Lesson, 1831	18D, E
Nerita gaimardi Souleyet, 1842	11A
Neritina baconi Reeve, 1856	30C
Clithon pauluccianus (Gassies, 1870)	
Neritina paulucciana Gassies, 1870	47D, E
Neritina suavis Gassies, 1879	54A, B
Clithon rugatus (Recluz, 1842)	
Nerita (*Clithon*) *rugata* Recluz, 1842	58C
Nerita (*Clithon*) *squarrosa* Recluz, 1843	59B
Neritina squamosa Sowerby II, 1849	59B
Neritina squarrosa cruenta Martens, 1878	78B
Clithon siderea (Gould, 1847)	
Neritina siderea Gould, 1847	59C
Neritina morosa Gassies, 1870	45C, D
Neritina (*Clithon*) *thermophila* Martens, 1877	80A
Neritina discors Martens, 1878	62A; 71B
Clithon sowerbianus (Recluz, 1843)	
Nerita (*Clithon*) *sowerbiana* Recluz, 1843	21C; 100C
Nerita (*Clithon*) *dacostae* Recluz, 1844	5C
Nerita souverbiana Sowerby II, 1849	100C
Neritina (*Clithon*) *troschelii* Recluz, 1850	102B
Clithon spinosus (Sowerby I, 1825)	
Neritina spinosa Sowerby I, 1825	53E, F
Clithon undatus Lesson, 1831	24C, D

Clithon variabilis Lesson, 1831		
	Clithon variabilis Lesson, 1831	25B
	Nerita keraudrenii Le Guillou, 1841	13B
	Nerita recluziana Le Guillou, 1841	20A-C
	Nerita (*Clithon*) *ruginosa* Recluz, 1841	99B
	Nerita (*Clithon*) *menkeana* Recluz, 1842	96C
	Nerita (*Clithon*) *souleyetana* Recluz, 1842	21B; 100B
	Neritina aspersa Sowerby II, 1849	30A
	Neritina (*Clithon*) *unidentata* Recluz, 1850	25A; 102C
	Neritina deltoidea Mousson, 1870	61B
	Neritina subgranosa Mabille, 1895	23A, B
Dostia bicanaliculata (Recluz, 1843)		
	Nerita (*Neritina*) *bicanaliculata* Recluz, 1843	57A
	Neritina layardi Reeve, 1855	41D
	Neritina rostrata Reeve, 1856	50E, F
	Neritina rubicunda Martens, 1875	76B
Dostia cariosa (Gray, 1827)		
	Neritina cariosa Gray, 1827	32A, B
	Nerita cariosa Wood, 1828	32A, B
	Neritina solidissima Sowerby II, 1849	52E, F
Dostia florida (Récluz, 1850)		
	Neritina florida Recluz, 1850	9A, B; 94A
	Neritina christovalensis Reeve, 1856	33A
Dostia guamensis (Quoy & Gaimard, 1834)		
	Neritina reticulata Sowerby I, 1833	50A, B; 66B
	Nerita guamensis Quoy & Gaimard, 1834	11B
	Nerita guerini Recluz, 1841	94C
	Neritina bensoni Recluz, 1850	50A, B; 66B
	Neritina desmoulinsiana Recluz, 1850	92B
Dostia melanostoma (Troschel, 1837)		
	Neritina melanostoma Troschel, 1837	74A
	Nerita indica Souleyet, 1842	12C, D
Dostia siquijorensis (Recluz, 1843)		
	Nerita constellata Sowerby III, 1905	34D
Dostia subalata (Souleyet, 1842)		
	Nerita subalata Souleyet, 1842	22C
	Neritina montrouzieri Gassies, 1875	45A
Dostia violacea (Gmelin, 1791)		
	Nerita intermedia Deshayes, 1834	13A
	Neritina exaltata Recluz, 1850	8A; 93C
	Neritina pileolus Recluz, 1850	13A

Laodia cumingiana (Recluz, 1843)		
	Navicella cumingiana Recluz, 1843	5A; 35E, F; 61A
	Navicella junghuhni Martens, 1881	72C
	Septaria elberti Haas, 1912	62C; 71C
Laodia sanguisuga (Reeve, 1856)		
	Navicella sanguisuga Reeve, 1856	51C
	Navicella scarabaeus Reeve, 1856	52A, B
	Navicella sculpta Martens, 1881	77A
Neritina asperulata (Recluz, 1843)		
	Nerita (*Neritina*) *asperulata* Recluz, 1843	3A, B; 88C
	Nerita (*Neritina*) *panayana* Recluz, 1843	98A
Neritina canalis Sowerby I, 1825		
	Neritina californica Reeve, 1855	31C
Neritina iris Mousson, 1849		
	Neritina delessertii Recluz, 1853	91C
	Neritina cornata Reeve, 1855	34E
	Neritina cryptospira Martens, 1875	71A
	Neritina iris wichmanni Martens, 1897	81C
Neritina luzonica (Recluz, 1841)		
	Navicella luzonica Recluz, 1842	15B, C; 95C
	Navicella livida Reeve, 1856	43B
	Navicella magnifica Reeve, 1856	44B
Neritina petitii (Lesson, 1831)		
	Nerita (*Neritina*) petitii Lesson, 1831	19D, E
	Neritina lenormandi Gassies, 1870	42A
Neritina pulligera (Linnaeus, 1767)		
	Nerita (*Neritina*) *beckii* Recluz, 1841	89A
Neritodryas ampullaria (Lesson, 1831)		
	Neritina ampullaria Lesson, 1831	2A, B
	Neritina subsulcata Sowerby I, 1836	
Neritodryas cornea (Linnaeus, 1758)		
	Neritina amphibia Lesson, 1831	1C
	Neritina savesi Gassies, 1878	51D, E
Neritodryas dubia (Gmelin, 1791)		
	Neritina fasciata Lamarck, 1816	84C
	Neritina philippinarum Sowerby I, 1836	66A
	Nerita vestita Souleyet, 1842	26A, B
Septaria auriculata (Lamarck, 1816)		
	Neritina auriculata Lamarck, 1816	3C, D; 83A
	Neritina (*Neripteron*) *taitensis* Lesson, 1831	23C
	Neritina lamarckii Deshayes, 1838	13C

Neritina novocaledonica Reeve, 1855	47A, B
Neritina nigrofusca Thiele, 1928	74B
Septaria clypeolum (Recluz, 1843)	
Navicella clypeolum Recluz, 1843	33B-D
Navicella variabilis Recluz, 1843	55C-E; 103A
Navicella insignis Reeve, 1856	40C
Septaria lecontei (Recluz, 1853)	
Neritina lecontei Recluz, 1853	14C
Neritina lifuensis A. Adams & Angas, 1864	43A
Neritina (*Neripteron*) *marmorata* Brazier, 1877	103C
Neritina transversecostata Schepman, 1919	
Septaria porcellana (Linnaeus, 1758)	
Navicella suborbicularis Sowerby I, 1825	68C
Navicella depressa Lesson, 1831	6C
Navicella zebra Lesson, 1831	27C, D
Navicella durvillei Recluz, 1841	93A
Navicella laperousei Recluz, 1842	14A, B; 95A
Navicella bimaculata Reeve, 1856	31A
Navicella crepiduloides Reeve, 1856	35A-C
Navicella haustrum Reeve, 1856	40A
Navicella hupeiana Gassies, 1863	12A, B; 40B
Navicella moreletiana Gassies, 1866	45B
Navicella excelsa Gassies, 1870	37B
Navicella nana Montrouzier, 1879	46A
Navicella lutea Martens, 1881	73A
Navicella luzonica adspersa Martens, 1881	73B
Navicella splendens Mabille, 1895	22A, B
Septaria spiralis (Reeve, 1855)	
Neritina sulculosa Martens, 1875	79A
Septaria suffreni (Recluz, 1842)	
Navicella suffreni Recluz, 1842	102A
Navicella freycineti Recluz, 1842	94B
Navicella psittacea Reeve, 1856	49A
Septaria tessellata (Lamarck, 1816)	
Navicella tessellata Lamarck, 1816	87B
Navicella lineata Lamarck, 1816	85C
Navicella entrecastauxi Recluz, 1842	93B
Navicella caerulescens Sowerby II, 1850	90A
Navicella caerulescens Reeve, 1856	31B
Navicella eximia Reeve, 1856	37C
Navicella orientalis Reeve, 1856	47C

Navicella pulchella Reeve, 1856	49B
Navicella reticulata Reeve, 1856	49C, D
Navicella tessellata compressa Martens, 1881	79C
Navicella francoisi Mabille, 1895	9C
Vittina communis (Quoy & Gaimard, 1834)	
Nerita communis Quoy & Gaimard, 1834	4C
Nerita royssyana Recluz, 1841	98C
Nerita cuprina Recluz, 1843	98C
Neritina vitiensis Mousson, 1865	81A
Vittina cuvieriana (Recluz, 1841)	
Nerita cuvieriana Recluz, 1841	91B
Neritina adumbrata Reeve, 1855	29A
Vittina gagates (Lamarck, 1822)	
Neritina gagates Lamarck, 1822	10C; 85A, B
Neritina variegata Lesson, 1831	25C, D
Nerita reticulata Quoy & Gaimard, 1834	20D
Neritina sumatrensis Sowerby I, 1836	68B
Neritina moquiniana Recluz, 1850	17C, D; 97B
Neritina wallisiarum Recluz, 1850	27A, B
Neritina (*Neritina*) *wetarana* Haas, 1912	69C; 81B
Vittina lugubris (Lamarck, 1822)	
Neritina lugubris Lamarck, 1822	86B
Neritina coromandeliana Sowerby I, 1836	91A (nontype)
Nerita striolata Recluz, 1841	101B
Neritina cochinsinae Recluz, 1850	90B
Nerita (*Clithon*) *adspersa* Recluz, 1853	1A, B
Neritina zigzag triangularis Martens, 1877	82B, C
Vittina turrita (Gmellin, 1791)	
Neritina strigilata Lamarck, 1822	87A
Vittina zigzag (Lamarck, 1822)	
Neritina zigzag Lamarck, 1822	87C
Neritina atra Gray, 1831	30B
Nerita (*Clithon*) obscurata Recluz, 1842	97C
Neritina fulgetrum Reeve, 1855	39A
"*Neritina*" *bruguieri* (Recluz, 1841)	
Nerita (*Neritina*) *bruguieri* Recluz, 1843	89C
Nerita rossmassleriana Recluz, 1846	99A
Neritina sanguinea Sowerby II, 1849	50A, B
Neritina (*Neritaea*) *stumpffi* Boettger, 1890	67C
Neritina (*Neritaea*) *stumpffi leucostoma* Boettger, 1890	68A

Index for Appendix 2.

Genus	Species	Author	Year	Plate
Nerita	*adansoniana*	Recluz	1841	88A
Nerita (*Clithon*)	*adspersa*	Recluz	1853	1A, B
Neritina	*adumbrata*	Reeve	1855	29A
Neritina	*aequinoxiallis*	Morelet	1848	29B
Neritina	*africana*	Reeve	1856	29C
Neritina	*amphibia*	Lesson	1831	1C
Neritina	*ampullaria*	Lesson	1831	2A, B
Neritina	*andamanica*	Nevill	"1883"	60A
Nerita	*angulosa*	Recluz	1843	56A
Navicella	*apiata*	Recluz	1842	2C; 88B
Nerita	*apiata*	Recluz	1843	56B
Neritina	*aspersa*	Sowerby II	1849	30A
Nerita (*Neritina*)	*asperulata*	Recluz	1843	3A, B; 88C
Neritina	*atra*	Gray	1831	30B
Neritina	*auriculata*	Lamarck	1816	3C, D; 83A
Nerita (*Clithon*)	*avellana*	Recluz	1842	56C
Neritina	*baconi*	Reeve	1856	30C
Nerita	*bahiensis*	Recluz	1850	4A
Nerita (*Neritina*)	*beckii*	Recluz	1841	89A
Neritina	*bensoni*	Recluz	1850	50A, B; 66B
Nerita (*Neritina*)	*bicanaliculata*	Recluz	1843	57A
Nerita (*Clithon*)	*bicolor*	Recluz	1843	57B
Navicella	*bimaculata*	Reeve	1856	31A
Neritina	*bismarckiana*	Reich	1935	70A
Neritina	*braziliana*	Sowerby II	1849	89B
Neritina	*brevispina*	Lamarck	1822	83B
Nerita (*Neritina*)	*bruguieri*	Recluz	1843	89C
Navicella	*caerulescens*	Reeve	1856	31B
Navicella	*caerulescens*	Sowerby II	1850	90A
Neritina	*californica*	Reeve	1855	31C
Nerita	*cardinalis*	Le Guillou	1841	4B
Nerita	*cariosa*	Wood	1828	32A, B
Neritina	*cariosa*	Gray	1827	32A, B
Neritina	*chlorostoma*	Sowerby I	1833	32C-E; 60B
Neritina	*christovalensis*	Reeve	1856	33A
Nerita (*Clithon*)	*circumvoluta*	Recluz	1843	60C
Navicella	*clypeolum*	Recluz	1843	33B-D
Neritina	*cochinsinae*	Recluz	1850	90B
Nerita (*Clithon*)	*colombaria*	Recluz	1846	90C
Nerita	*communis*	Quoy & Gaimard	1834	4C
Neritina	*comorensis*	Morelet	1877	34A-C
Neritina (*Clithon*)	*confluens*	Martens	1897	70B
Neritina	*conglobata*	Martens	1875	70C
Nerita	*constellata*	Sowerby III	1905	34D
Neritina	*cornata*	Reeve	1855	34E
Neritina	*coromandeliana*	Sowerby I	1836	91A (nontype)
Neritina	*crepidularia*	Lamarck	1822	83C
Navicella	*crepiduloides*	Reeve	1856	35A-C

Neritina	*cristata*	Morelet	1864	35D
Neritina	*cryptospira*	Martens	1875	71A
Navicella	*cumingiana*	Recluz	1843	5A; 35E, F; 61A
Nerita (*Neritina*)	*cumingiana*	Recluz	1842	5B
Nerita	*cuprina*	Recluz	1843	98C
Nerita	*cuvieriana*	Recluz	1841	91B
Neritina	*cyanostoma*	Morelet	1853	36A, B
Nerita (*Clithon*)	*dacostae*	Recluz	1844	5C
Nerita	*deficiens*	Mabille	1887	6A, B
Neritina	*delessertii*	Recluz	1853	91C
Neritina	*delestennei*	Recluz	1853	92A
Neritina	*deltoidea*	Mousson	1870	61B
Navicella	*depressa*	Lesson	1831	6C
Neritina	*desmoulinsiana*	Recluz	1850	92B
Neritina	*dilatata*	Broderip	1833	36C, D; 61C
Neritina	*discors*	Martens	1878	62A; 71B
Navicella	*dispar*	Pease	"1868"	62B
Neritina	*dispar*	Pease	1868	57C ("cotypes")
Nerita	*doingii*	Recluz	1846	36E
Neritina	*domingensis*	Lamarck	1822	84A
Neritina	*donovana*	Sowerby II	1849	92C
Nerita (*Clithon*)	*donovani*	Recluz	1843	7A, B; 92C
Navicella	*durvillei*	Recluz	1841	93A
Septaria	*elberti*	Haas	1912	62C; 71C
Neritina	*elephas*	Mabille	1895	7C
Navicella	*elliptica*	Lamarck	1816	84B
Navicella	*entrecastauxi*	Recluz	1842	93B
Theodoxus	*eudeli*	Sowerby III	1917	37A
Neritina	*exaltata*	Recluz	1850	8A; 93C
Navicella	*excelsa*	Gassies	1870	37B
Neritina (*Clithon*)	*exclamationis*	Mabille	1895	8B-D
Navicella	*eximia*	Reeve	1856	37C
Neritina	*faba*	Sowerby I	1836	38A, B
Neritina	*fasciata*	Lamarck	1816	84C
Neritina	*flexuosa*	Gassies	1878	38C
Neritina	*florida*	Recluz	1850	9A, B; 94A
Navicella	*francoisi*	Mabille	1895	9C
Neritina (*Clithon*)	*francoisi*	Mabille	1895	10A, B
Neritina	*fraseri*	Reeve	1855	38D
Navicella	*freycineti*	Recluz	1842	94B
Neritina	*fulgetrum*	Reeve	1855	39A
Neritina	*gagates*	Lamarck	1822	10C; 85A, B
Nerita	*gaimardi*	Souleyet	1842	11A
Neritina	*globosa*	Broderip	1833	63A
Neritina	*granosa*	Sowerby I	1825	39B
Neritina	*gravis*	Morelet	1849	39C; 63B
Nerita	*guamensis*	Quoy & Gaimard	1834	11B
Nerita	*guerini*	Recluz	1841	94C
Neritina	*haemastoma*	Martens	1878	72A
Neritina	*hamuligera*	Troschel	1837	72B
Navicella	*haustrum*	Reeve	1856	40A
Neritina (*Neritaea*)	*hessei*	Boettger	1912	63C

Neritina	*horrida*	Mabille	1895	11C
Navicella	*hupeiana*	Gassies	1863	12A, B; 40B
Nerita	*indica*	Souleyet	1842	12C, D
Navicella	*insignis*	Reeve	1856	40C
Nerita	*intermedia*	Deshayes	1834	13A
Neritina	*intermedia*	Sowerby I	1833	41A; 64A
Nerita (*Clithon*)	*interrupta*	Recluz	1843	58A
Neritina	*iris wichmanni*	Martens	1897	81C
Neritina	*jamaicensis*	C. B. Adams	1851	64B
Navicella	*junghuhni*	Martens	1881	72C
Nerita	*keraudrenii*	Le Guillou	1841	13B
Neritona	*labiosa melanesica*	Reich	1935	73C
Neritina	*lamarckii*	Deshayes	1838	13C
Navicella	*laperousei*	Recluz	1842	14A, B; 95A
Neritina	*latissima*	Broderip	1833	41B, C; 64C
Neritina	*layardi*	Reeve	1855	41D
Nerita (*Clithon*)	*leachii*	Recluz	1841	95B
Neritina	*lecontei*	Recluz	1853	14C
Neritina	*lenormandi*	Gassies	1870	42A
Navicella	*lentiginosa*	Reeve	1855	42C
Neritina	*lentiginosa*	Reeve	1856	42B
Neritina	*lifuensis*	A. Adams & Angas	1864	43A
Navicella	*lineata*	Lamarck	1816	85C
Neritina	*lineolata*	Lamarck	1822	86A
Neritina	*listeri*	Pfeiffer	1840	65A
Navicella	*livida*	Reeve	1856	43B
Nerita (*Clithon*)	*longispina*	Recluz	1841	15A (nontype)
Neritina	*lugubris*	Lamarck	1822	86B
Navicella	*lutea*	Martens	1881	73A
Navicella	*luzonica*	Recluz	1842	15B, C; 95C
Navicella	*luzonica adspersa*	Martens	1881	73B
Neritina	*macgillivrayi*	Reeve	1855	43D
Navicella	*macrocephala*	Recluz	1842	16A, B; 96A
Neritina	*madecassina*	Morelet	1858	44A
Navicella	*magnifica*	Reeve	1856	44B
Neritina (*Neripteron*)	*marmorata*	Brazier	1877	103C
Neritina	*mauritiana*	Morelet	1867	16C; 44C
Neritina	*mauritii*	Sowerby II	1849	96B
Neritina	*melanostoma*	Troschel	1837	74A
Neritina	*meleagris*	Lamarck	1822	86C
Nerita (*Clithon*)	*menkeana*	Recluz	1842	96C
Nerita	*michaudi*	Recluz	1841	97A
Nerita (*Clithon*)	*montacuti*	Recluz	1843	17A, B
Neritina	*montrouzieri*	Gassies	1875	45A
Neritina	*moquiniana*	Recluz	1850	17C, D; 97B
Navicella	*moreletiana*	Gassies	1866	45B
Neritina	*morosa*	Gassies	1870	45C, D
Neritina	*mutica*	Sowerby II	1849	65B
Navicella	*nana*	Montrouzier	1879	46A
Neritina	*neglecta*	Pease	1860	46B
Neritina	*nigrofusca*	Thiele	1928	74B
Neritodryas	*notabilis*	Reich	1935	74C

Neritina	*nouletiana*	Gassies	1863	18A-C; 46C, D
Neritina	*novocaledonica*	Reeve	1855	47A, B
Neritina	*nucleolus spinifera*	Martens	1878	75A
Nerita (*Clithon*)	*obscurata*	Recluz	1842	97C
Nerita (*Clithon*)	*olivacea*	Recluz	1843	58B
Navicella	*orientalis*	Reeve	1856	47C
Neritina	*oualaniensis*	Lesson	1831	18D, E
Navicella	*pala*	Mousson	1865	75B
Nerita (*Neritina*)	*panayana*	Recluz	1843	98A
Neritina	*paulucciana*	Gassies	1870	47D, E
Neritina	*pazi*	Gassies	1858	48A, B
Neritina	*peguensis*	Blanfold	1867	65C
Neritina	*perfecta*	Mabille	1895	19A-C
Nerita (*Neritina*)	*petitii*	Lesson	1831	19D, E
Neritina	*philippinarum*	Sowerby I	1836	66A
Neritina	*picta*	Sowerby I	1833	48C, D
Neritina	*picta serta*	Martens	1900	75C
Neritina	*pileolus*	Recluz	1850	13A
Neritina	*pritchardi*	Dohrn	1861	48E
Navicella	*psittacea*	Reeve	1856	49A
Navicella	*pulchella*	Reeve	1856	49B
Nerita (*Clithon*)	*pulchella*	Recluz	1843	98B
Nerita	*recluziana*	Le Guillou	1841	20A-C
Navicella	*reticulata*	Reeve	1856	49C, D
Nerita	*reticulata*	Quoy & Gaimard	1834	20D
Neritina	*reticulata*	Sowerby I	1833	50A, B; 66B
Neritina	*retropicta*	Martens	1878	76A
Neritina	*retusa*	Morelet	1853	50C, D
Neritina (*Clithon*)	*rhyssodes*	Boettger	1890	66C
Neritina	*rhytidophora*	Tapparone-Canefri	1883	67A
Nerita	*rossmassleriana*	Recluz	1846	99A
Neritina	*rostrata*	Reeve	1856	50E, F
Nerita	*royssyana*	Recluz	1841	98C
Neritina	*rubicunda*	Martens	1875	76B
Nerita (*Clithon*)	*rugata*	Recluz	1842	58C
Nerita (*Clithon*)	*ruginosa*	Recluz	1841	99B
Neritina	*sandwichensis*	Deshayes	1838	21A
Neritina	*sanguinea*	Sowerby II	1849	50A, B
Navicella	*sanguisuga*	Reeve	1856	51C
Neritina	*savesi*	Gassies	1878	51D, E
Nerita	*sayana*	Recluz	1844	99C
Navicella	*scarabaeus*	Reeve	1856	52A, B
Neripteron	*schneideri*	Reich	1935	76C
Navicella	*sculpta*	Martens	1881	77A
Nerita (*Neritina*)	*serrulata*	Recluz	1842	100A
Neritina	*siderea*	Gould	1847	59C
Nerita	*smithii*	Wood	1828	52C, D
Neritina (*Clithon*)	*soembawana*	Haas	1912	67B; 77B
Neritina	*solidissima*	Sowerby II	1849	52E, F
Nerita (*Clithon*)	*souleyetana*	Recluz	1842	21B; 100B
Nerita	*souverbiana*	Sowerby II	1849	100C
Nerita (*Clithon*)	*sowerbiana*	Recluz	1843	21C; 100C

Neritina	*sowerbiana lactiflua*	Martens	1878	77C
Neritina	*sowerbiana maculofasciata*	Martens	1878	78A
Nerita (*Clithon*)	*spinifera*	Recluz	1842	101A
Neritina	*spiniperda*	Morelet	1858	53A-D
Neritina	*spinosa*	Sowerby I	1825	53E, F
Navicella	*splendens*	Mabille	1895	22A, B
Nerita (*Neritina*)	*squamaepicta*	Recluz	1843	59A
Neritina	*squamosa*	Sowerby II	1849	59B
Nerita (*Clithon*)	*squarrosa*	Recluz	1843	59B
Neritina	*squarrosa cruenta*	Martens	1878	78B
Neritina	*strigilata*	Lamarck	1822	87A
Nerita	*striolata*	Recluz	1841	101B
Neritina (*Neritaea*)	*stumpffi*	Boettger	1890	67C
Neritina (*Neritaea*)	*stumpffi leucostoma*	Boettger	1890	68A
Neritina	*suavis*	Gassies	1879	54A, B
Nerita	*subalata*	Souleyet	1842	22C
Neritina	*subgranosa*	Mabille	1895	23A, B
Navicella	*suborbicularis*	Sowerby I	1825	68C
Nerita (*Clithon*)	*subpunctata*	Recluz	1844	101C
Neritina	*subpunctata glandiformis*	Martens	1878	78C
Neritina	*subrugata*	Baird in Brenchery	1873	54C-F
Navicella	*suffreni*	Recluz	1842	102A
Neritina	*sulculosa*	Martens	1875	79A
Neritina	*sumatrensis*	Sowerby I	1836	68B
Neritina (*Neripteron*)	*taitensis*	Lesson	1831	23C
Neritina	*tenebricosa*	C. B. Adams	1851	69A
Neritina	*tenebricosa parryi*	Martens	MS	79B
Navicella	*tessellata*	Lamarck	1816	87B
Navicella	*tessellata compressa*	Martens	1881	79C
Neritina (*Clithon*)	*thermophila*	Martens	1877	80A
Nerita	*tritonensis*	Le Guillou	1841	24A
Neritina (*Clithon*)	*troschelii*	Recluz	1850	102B
Neritina	*turbida*	Morelet	1849	24B; 55A, B; 69B
Clithon	*undatus*	Lesson	1831	24C, D
Neritina (*Clithon*)	*unidentata*	Recluz	1850	25A; 102C
Clithon	*variabilis*	Lesson	1831	25B
Navicella	*variabilis*	Recluz	1843	55C-E; 103A
Neritina	*variegata*	Lesson	1831	25C, D
Nerita	*vestita*	Souleyet	1842	26A, B
Neritina	*virginea oblonga*	Martens	1865	80B
Neritina	*virginea parvula*	Martens	1865	80C
Neritina	*vitiensis*	Mousson	1865	81A
Neritina	*waigiensis*	Lesson	1831	26C, D
Neritina	*wallisiarum*	Recluz	1850	27A, B
Nerita (*Neritina*)	*webbei*	Recluz	1849	103B
Neritina (*Neritina*)	*wetarana*	Haas	1912	69C; 81B
Navicella	*zebra*	Lesson	1831	27C, D
Nerita	*zebra*	Bruguiere	1792	28A-C
Neritina	*zigzag*	Lamarck	1822	87C
Neritina	*zigzag glandiformis*	Martens	MS	82A
Neritina	*zigzag triangularis*	Martens	1877	82B, C