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Article

The neritid snails of Brunei Darussalam: their geographical, ecological and conservation significance

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Abstract
Neritid snails are diverse and conspicuous in tropical coastal environments. They can serve as indicators of environmental change and can provide conservation information. In the present review of the neritid species of Brunei Darussalam, we report sixteen species, including seven new records from estuarine, mangrove and rocky-shore habitats. These records update distributions across the Central Indo-Pacific realm, specifically the Palawan/North Borneo ecoregion. Under-sampling, species misidentifications and locally-rare species undermine the accuracy of records in previous studies for the region. Three of the rocky-shore and two of the mangrove species collected here are represented by single specimens; these rocky-shore species are possible colonizers from neighbouring regions and the scarcity of the mangrove species likely refers to under-sampling. We present novel shell characteristics that readily distinguish between *Neripteron violaceum* and *Nerip. cornucopia*. We describe the ecology and habitat use of the Brunei species and discuss conservation issues.

Key words: Borneo, *Nerita*, *Neripteron*, marine, freshwater, brackish, mangrove.

Introduction

Neritidae snails occur in marine, fresh and brackish water ecosystems across tropical and subtropical regions, and occupy intertidal rocky shores, sandy beaches, mudflats, estuaries and mangroves (Frey 2010a, 2010b). They are often conspicuous and abundant, and their habitat transitions have contributed towards ecological and evolutionary investigation (see Waters *et al.* 2005; Hurtado *et al.* 2007; Crandall *et al.* 2008; Frey & Vermeij 2008; Frey 2010b). Neritid snails have recently been used as models for climate change monitoring

(see Marshall *et al.* 2015, 2019). The diversity of these snails for Brunei Darussalam and north western Borneo is important as this represents the edge of the 'Coral Triangle' (Spalding *et al*. 2007; Frey & Vermeij 2008; Hoeksema & Lane 2014). Their local conservation and protection are under threat, requiring updated information and accurate species identifications.

Previous studies documenting the composition and abundance of local snail faunas are considered incomplete and outdated (Baharuddin & Marshall 2014; Marshall *et al.* 2017). The primary objective of the present study was thus to provide an updated, annotated list of the marine neritid species of Brunei Darussalam. This list includes information on abundance, habitat occupation, and local distribution (Fig. 1). In addition, we discuss the ecology and conservation of the species. The study updates the biogeographical distributions of the neritid snail species within the Western Coral Triangle province (Spalding *et al*. 2007).

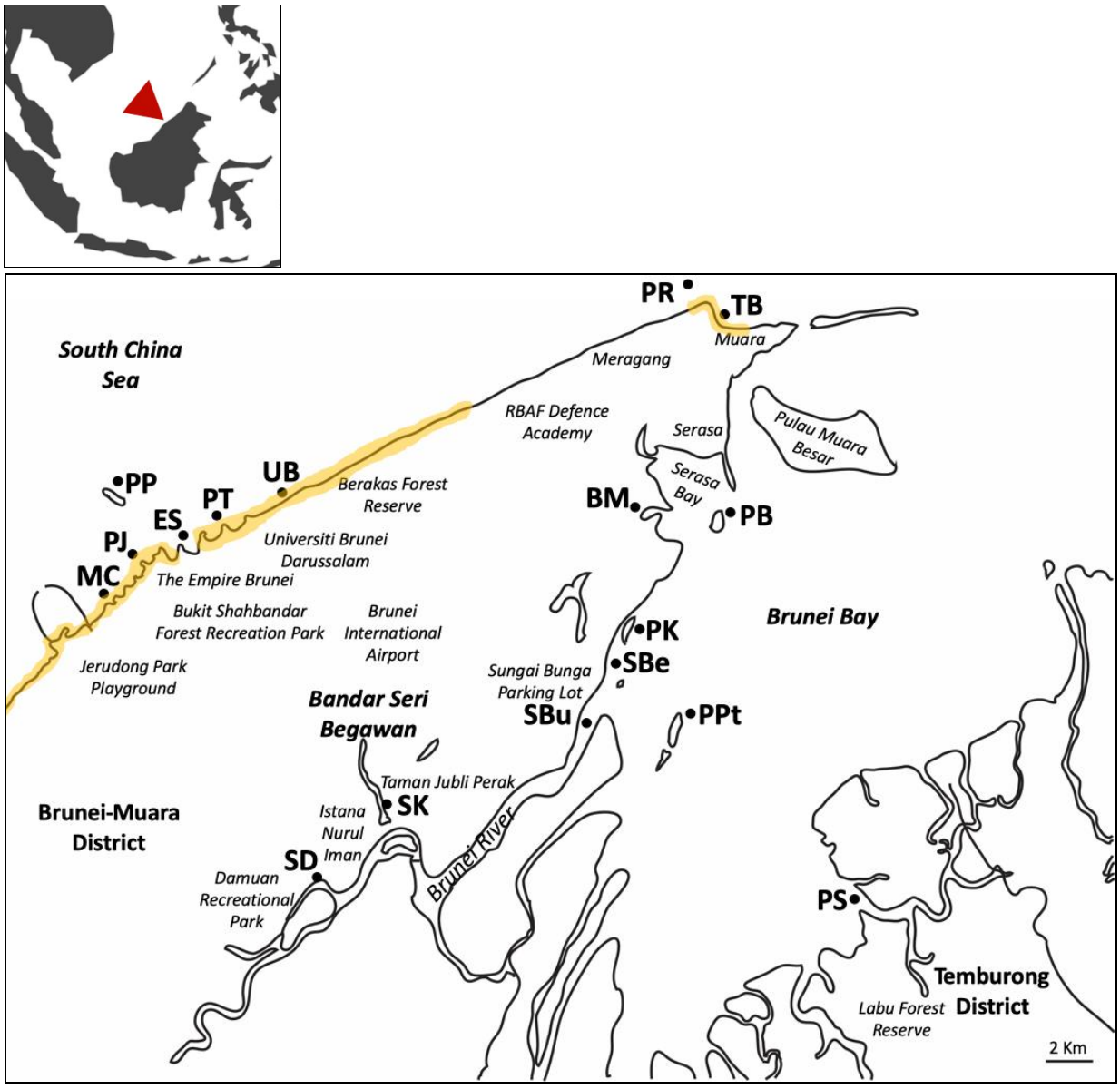

Figure 1. Brunei Darussalam is situated on the northwest coast of Borneo island in the Southeast Asia and is stretched along the South China Sea coastline. Bottom image shows the localities of Neritidae snails in Brunei. Abbreviations: **MC**. Jerudong Park Medical Centre (4.9486°N, 114.8283°E). **PJ**. Pantai Jerudong (4.9583°N, 114.8394°E). **ES**. Empire site (4.9694°N, 114.8551°E). **PP**. Pulau Punyit (4.9753°N, 114.8490°E). **PT**. Pantai Tungku (4.9703°N, 114.8667°E). **UB**. Universiti Brunei Darussalam (4.9853°N, 114.8994°E). **PR**. Pelong Rocks (5.0789°N, 115.0528°E). **TB**. Tanjung Batu (5.0388°N, 115.0617°E). **SK**. Sungai Kedayan (4.8981°N, 114.9341°E). **SBe**. Sungai Besar (4.9278°N, 115.0144°E). **SBu**. Sungai Bunga (4.9155°N, 115.0062°E). **SD**. Sungai Damuan (4.8689°N, 114.9117°E). **BM**. Batu Marang (4.9853°N, 115.0308°E). **PB**. Pulau Bedukang (4.9795°N, 115.0576°E). **PS**. Pulau Selirong (4.8765°N, 115.1296°E). **PPt**. Pulau Pepatan (4.9161°N, 115.0459°E). **PK**. Pulau Kaingaran (4.9474°N, 115.0277°E). Highlighted coastline indicates area with artificial seawalls.

Materials and Methods

Neritid snails were collected from rocky shore, mangrove and estuarine habitats in Brunei Darussalam (Fig. 1) between 2004 and 2019. Collection sites included natural rocky shores at Empire, Pulau Punyit, Tanjung Batu and Pelong Rocks as well as artificial rocky shores, together making an area of ~ 9 ha. Other collections were made in the Brunei Bay and estuarine system (Marshall *et al.* 2016), which is wide-ranging and fringed with pristine mangrove stands and mudflats (18,400 ha). Collection intensity varied at the sites, being most intensive at Empire, where multiple marine research projects are ongoing.

Samples were returned to the laboratory, preserved in 70% ethanol and later photographed using a digital camera (Canon PowerShot S110 or Panasonic Lumix DC-ZS200). Species identifications were based on shell attributes using Tan & Clements (2008), Eichhorst (2016a, 2016b) and Zvonareva & Kantor (2016). Names were checked and updated where necessary using WoRMS (Horton *et al.* 2019). Because detailed descriptions are already given in these papers, this information was not repeated here, but also full taxonomic information is available in WoRMS. Notably, there was little variation in the shell morphology between the Singapore (Tan & Clements 2008) and the Brunei specimens, with the exception of the *Neripteron* species. We therefore provide previously unreported information on the shell attributes of two of the local *Neripteron* species. All samples were ascribed accession numbers and deposited in the Universiti Brunei Darussalam (UBD) Museum (Polgar *et al.* 2018). Abundance was ranked according to the following procedure. A species was ranked as **abundant** if on any visit to a particular locality more than 10 snails were observed. If more than 1 but fewer than 10 snails were observed, abundance was ranked **intermediate**. Uncommon or **rare** referred to only 1 snail being observed at locality during numerous visits. Habitats were defined in terms of **low shore**, between 0.0 – 0.5 m Chart Datum (algal dominated zone), **mid shore**, between 0.5 – 1.3 m CD (barnacle zone) and **high-shore** (littorinid zone), above 1.3 m CD, within a tidal range of 2.2 m CD. Local abundance, habitat specialty, distribution and threat of habitat destruction or by other human activity (food resource) were considered when evaluating the local conservation status (low or high risk) of a species. Geographical distributions of the species were assessed from the literature (Table 1; with list of abbreviations meaning) and considered the geographical realm, province and ecoregion, focusing on the Palawan/North Borneo ecoregion and the Western Coral Triangle province (Spalding *et al*. 2007).

Species

A total of 16 neritid species, including 7 new records; *Nerita patula* Récluz, 1841, *N. insculpta* Récluz, 1841, *N. exuvia* Linnaeus, 1758, *N. histrio* Linnaeus, 1758, *Vittina coromandeliana* (G. B. Sowerby I, 1836), *Neripteron cornucopia* (Benson, 1836) and *Nerip. spirale* (Reeve, 1855) are reported, updating previous records (Baharuddin & Marshall 2014; Ng *et al*. 2015; Marshall *et al*. 2017).

Family Neritidae Rafinesque, 1815
Genus *Nerita* Linnaeus, 1758
Nerita albicilla Linnaeus, 1758

Figs. 2A–B and 4A

Nerita albicilla Linnaeus, 1758: 778.
Nerita albicilla – Tan & Clements, 2008: 483, figs. 2-1, 2-2; Zvonareva & Kantor, 2016: 407, figs. 3A, 3B.
Nerita (*Theliostyla*) *albicilla* – Eichhorst, 2016a: 441, pls. 105, 106.

Material. UBDM.7.00010. Sample was collected from PP.
Abundance. Very abundant.
Habitat. Rocky shore. Mid to low shore.
Local distribution. PJ, ES and PP.
Ecology and conservation. Populations are localised and common on natural rocky shores alongside another Neritidae species, *N. chamaeleon*. At ES and PP, this species gains protection through restricted access to the shore. Inhabiting the lower intertidal zone, *N. albicilla* is buffered against coastal edge deforestation causing increase in suspended sediment loads. This species is of low conservation concern in Brunei because they are highly abundant locally and currently resilient.
Biogeographical distribution. Associated with Western Coral Triangle at SB, PL, HI, BY, SR and BK and Sunda Shelf at TR, SW, AN, VN and SG. Generally distributed in Indo-West Pacific (Frey 2010b).

Nerita balteata Reeve, 1855

Figs. 2M–N and 4G

Nerita balteata Reeve, 1855: Species 28, plate vi, figs. 28a-28b.
Nerita articulata – Tan & Clements, 2008: 483, figs. 2-3, 2-4.
Nerita (*Cymostyla*) *balteata* – Eichhorst, 2016a: 455, pl. 113.

Material. UBDM.7.00020. Sample was collected from PB.
Abundance. Abundant.
Habitat. Arboreal species. On mangrove tree trunks, branches, roots and on muddy banks.
Local distribution. BM, PB, PK, PPt, SBe, and SBu.
Ecology and conservation. Despite being exploited, *N. balteata* remains abundant. They are renowned as a delicacy in the region (Somchai 1995; Hamli *et al.* 2013), and thus are heavily collected for food consumption. At BM, the population was seen to decline and not recover. Snail populations at SBe and PK have declined apparently in response to the nearby bridge construction (2014-2019) and the eradication of mangroves. Although mangrove stands in the Brunei Bay are extensive (18,400 ha) and these snails have vast area for colonisation, the apparently slow colonising potential and slow growth rates undermine population re-establishment. This species should benefit from monitoring, but is considered to be of low conservation importance in the face of the extensive mangrove stands in Brunei Bay.
Biogeographical distribution. Western Coral Triangle in SB and BY and Sunda Shelf at TR, JH, SW and SG. *N. balteata* is commonly distributed in Indo-West Pacific (Frey 2010b).

Nerita chamaeleon Linnaeus, 1758

Figs. 2C–D and 4E

Nerita chamaeleon Linnaeus, 1758: 779.
Nerita chamaeleon – Tan & Clements, 2008: 485, figs. 2-5, 2-6.
Nerita (*Argonerita*) *chamaeleon* – Eichhorst, 2016a: 458, pl. 114.

Material. UBDM.7.00030. Sample was collected from PP.
Abundance. Very abundant.
Habitat. Rocky shore. Low to high shore. Associated with breakwaters, seawalls and natural rocky shore.
Local distribution. MC, PJ, ES, PP, PT and UB.
Ecology and conservation. Common inhabitant of rocky shores for both natural rocks (ES and PP) and artificial seawalls (MC, PJ, PT and UB), though occurring in much greater numbers on the former (Marshall *et al.* 2017). Very likely to rapidly re-establish populations after degradation of local habitats. Compared to natural rocky shores, *N. chamaeleon* is heavily predated on in artificial rocky shores based on shell scars suspected of attacks from common shore crab. *N. chamaeleon* is of lowest conservation concern in Brunei because of its ability to rapidly colonise and establish large populations, and especially its tolerance to mud-inundated rock surfaces.
Biogeographical distribution. In Western Coral Triangle at SB, HI, BY, SR and BK and Sunda Shelf at TR, JH, SW and SG. Generally distributed in Indo-West Pacific (Frey 2010b).

**Nerita exuvia* Linnaeus, 1758

Figs. 2Q–R and 4P

Nerita exuvia Linnaeus, 1758: 779.
Nerita (*Theliostyla*) *exuvia* – Eichhorst, 2016a: 477, pl. 123.

Material. Unassigned. Sample was collected from ES.
Abundance. Rare (Only one specimen collected).
Habitat. Rocky shore. Low shore.
Local distribution. ES.
Ecology and conservation. Elsewhere, this species is noted to prefer open rocky shores that are exposed to strong wave action.
Biogeographical distribution. PL, HI and BY. Generally distributed in West Pacific (Eichhorst 2016a).

**Nerita histrio* Linnaeus, 1758

Figs. 2S–T and 4O

Nerita histrio Linnaeus, 1758: 778.
Nerita histrio – Tan & Clements, 2008: 486, figs. 2-11, 2-12.
Nerita squamulata – Zvonareva *et al*., 2015: 8.
Nerita (*Argonerita*) *histrio* – Eichhorst, 2016a: 498, pls. 135, 136.

Material. Unassigned. Sample was collected from ES.
Abundance. Rare (Only one specimen collected).
Habitat. Rocky shore. Low shore.
Local distribution. ES.
Ecology and conservation. This species seems to prefer slightly muddier habitats, and can often be found on muddy sand and rocks in estuaries, and occasionally in the edges of mangrove forests. It can also be found sympatrically with *N. chamaeleon*, with which they can be confused with, on rocky shores albeit less commonly.
Biogeographical distribution. BY, SR, JH, AN, VN and SG. Generally distributed in Indo-West Pacific (Eichhorst 2016a).

**Nerita insculpta* Récluz, 1841

Figs. 2G–H and 4C

Nerita insculpta Récluz, 1841: 152.
Amphinerita insculpta – Vermeij & Hoeft, 2018: 499.
Nerita (*Amphinerita*) *insculpta* – Eichhorst, 2016a: 505, pl. 139; Susintowati *et al*., 2018: 4.

Material. UBDM.7.00050. Sample collected from ES.
Abundance. Locally rare.
Habitat. Rocky shore. High-shore.
Local distribution. ES only.
Ecology and conservation. Inhabiting the upper intertidal zone, extending into the supratidal zone, high shore specialist *N. insculpta* is able to tolerate highly stressful environmental conditions (such as prolong exposure to extreme ambient air), with the littorinid snail *Echinolittorina malaccana* (e.g., Vermeij & Hoeft 2018; Brahim *et al.* 2019). Although several observations of this species have been made, it usually occurs in single numbers. High level of conservation concern because species is locally rare.
Biogeographical distribution. BY and SR of Western Coral Triangle. Generally distributed in Indo-West Pacific (Frey 2010b; Vermeij & Hoeft 2018).

Nerita litterata Gmelin, 1791

Figs. 2I–J and 4B

Nerita litterata Gmelin, 1791: 3685.
Nerita polita – Tan & Clements, 2008: 487, figs. 2-17, 2-18.
Nerita (*Linnerita*) *litterata* – Eichhorst, 2016a: 511, pls. 142–145.
Linnerita litterata – Vermeij & Hoeft, 2018: 499.

Material. UBDM.7.00070. Collected from PP.
Abundance. Locally rare (currently).
Habitat. Rocky shore. High-shore. Preference for rocky and sandy interface.
Local distribution. PP and ES.
Ecology and conservation. *N. litterata*, a habitat specialist, prefers the mixed rocks and sandy habitat of the upper intertidal zone. Sediment particle size is important as the species can be observed crawling with sand particles covering their shells but intolerant of muddy substratum. Once a significant population in ES (4 years ago) is now entirely lost following the destruction of fringing forest at ES, landslides and elevated suspended sediments loading (Marshall *et al.* 2019). Given its specialist habitat requirements, this species is vulnerable to local extinction. Colonisation potential remains unknown.

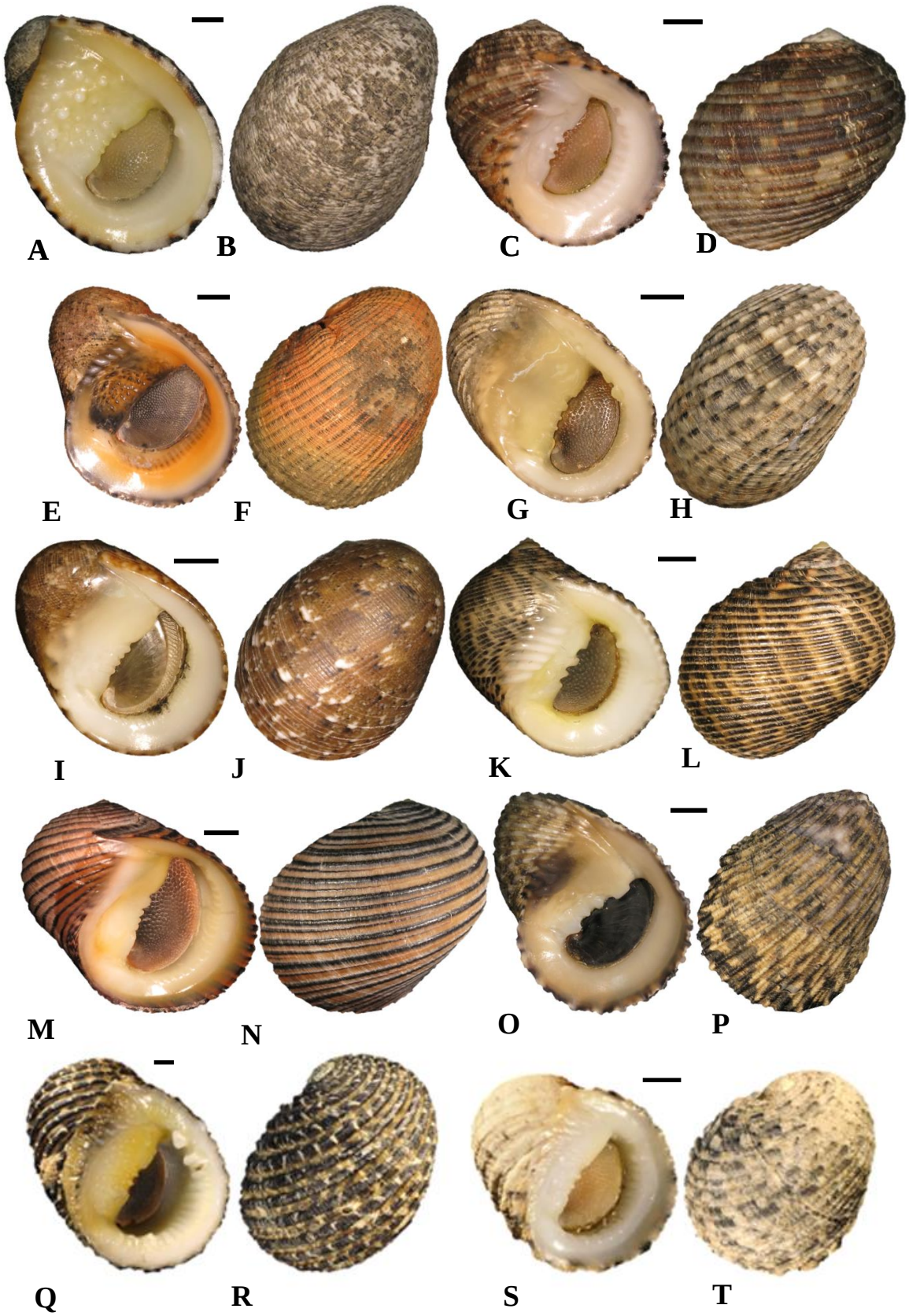

Figure 2. Neritidae species found associated with lower estuarine, mangroves and rocky shores of Brunei Darussalam, shown in apertural and abapertural view. **A–B.** *Nerita albicilla* Linnaeus, 1758. **C–D.** *Nerita chamaeleon* Linnaeus, 1758. **E–F.** **Nerita patula* Récluz, 1841. **G–H.** **Nerita insculpta* Récluz, 1841. **I–J.** *Nerita litterata* Gmelin, 1791. **K–L.** *Nerita undata* Linnaeus, 1758. **M–N.** *Nerita balteata* Reeve, 1855. **O–P.** *Nerita planospira* Anton, 1838. **Q–R.** **Nerita exuvia* Linnaeus, 1758. **S-T.** **Nerita histrio* Linnaeus, 1758. (*) indicates a new species record for Brunei Darussalam. Scale bar represents 3 mm.

Biogeographical distribution. SR of Western Coral Triangle. Generally, Indo-West Pacific (Frey & Vermeij 2008; Frey 2010b; Vermeij & Hoeft 2018).

**Nerita patula* Récluz, 1841

Figs. 2E–F and 4D

Nerita patula Récluz, 1841: 148.
Nerita (*Theliostyla*) *patula* – Eichhorst, 2016a: 458, pls. 161, 162.

Material. UBDM.7.00040. Collected from ES.
Abundance. Locally rare (only one specimen collected).
Habitat. Rocky shore. Mid-shore.
Local distribution. ES only.
Ecology and conservation. Co-habitant with the abundant *N. chamaeleon.* At the moment, the species is of high level of conservation importance in Brunei as it is very rare.
Biogeographical distribution. HI and SR of Western Coral Triangle. Generally distributed in Indo-West Pacific (Frey & Vermeij 2008; Frey 2010b; Vermeij & Hoeft 2018).

Nerita planospira Anton, 1838

Figs. 2O–P and 4H

Nerita planospira Anton, 1838: 30.
Nerita planospira – Tan & Clements, 2008: 486, figs. 2-13, 2-14; Zvonareva & Kantor, 2016: 408, figs. 3E, 3F.
Nerita (*Ilynerita*) *planospira* – Eichhorst, 2016a: 549, pl. 165.

Material. UBDM.7.00060. Sample was collected from PB.
Abundance. Abundant.
Habitat. Arboreal species. On mangrove tree trunks, branches, roots and on muddy banks.
Local distribution. PB, BM and PS.
Ecology and conservation. Co-habitant to *N. balteata*, *N. planospira* is suspected to exhibit similar intrinsic growth and reproductive attributes as *N. balteata* that could potentially constrain rapid population turnover in their habitats. In Brunei, *N. planospira* is placed under low conservation importance as it is widely distributed in local mangroves.
Biogeographical distribution. SB, BY and PN in Western Coral Triangle and JH, VN and SG in Sunda Shelf. In general, Indo-West Pacific (Frey 2010b).

Nerita undata Linnaeus, 1758

Figs. 2K–L and 4F

Nerita undata Linnaeus, 1758: 779.
Nerita undata – Tan & Clements, 2008: 487, figs. 3-21, 3-22; Zvonareva & Kantor, 2016: 408, figs. 3G, 3H.
Nerita (*Cymostyla*) *undata* – Eichhorst, 2016a: 583, pl. 184.

Material. UBDM.7.00080. Sample was collected from PP.
Abundance. Abundant.
Habitat. Rocky shore. Mid to high shore.
Local distribution. PP, MC and ES.
Ecology and conservation. The species has been found to rapidly repopulate areas, following habitat degradation. It occupies a similar niche to *N. chamaeleon* with which it seemingly competes, but usually extends higher on the shore. Unlike *N. chamaeleon*, *N. undata* appears less tolerant of high-suspended-sediment loads in water and sedimentation of the shoreline. Low conservation concern because of apparent high recolonization capability on local shores.
Biogeographical distribution. Distributed in HI, SR and BK of Western Coral Triangle and TR, JH, SW, AN, VN and SG of Sunda Shelf. Indo-West Pacific in general (Frey 2010b).

Genus *Neritodryas* von Martens, 1869
***Neritodryas dubia* (Gmelin, 1791)**
Figs. 3A–B and 4L

Nerita dubia Gmelin, 1791: 3678.
Neritodryas dubia – Eichhorst, 2016b: 757, pls. 222–224.

Material. UBDM.7.00110. Specimen collected from SK.
Abundance. Locally rare.
Habitat. Associated with estuaries and brackish water.
Local distribution. SK.
Ecology and conservation. Arboreal species found locally only on *Nipa* palm fronds. Not commonly seen and difficult to judge their conservation status, as they could occur in low abundance across the extensive mangrove stands in the region. Requires conservation monitoring.
Biogeographical distribution. TH of Sunda Shelf. Generally restricted to the Philippines and parts of Indonesia (Eichhorst 2016b).

Genus *Vittina* H. B. Baker, 1924
****Vittina coromandeliana* (G. B. Sowerby I, 1836)**
Figs. 3C–D and 4K

Neritina coromandeliana G. B. Sowerby I, 1836: part 100, species no. 53.
Neritina coromandeliana – Tan & Clements, 2008: 489, figs. 3-25, 3-26.
Vittina coromandeliana – Eichhorst, 2016b: 1084, pls. 331, 332.

Material. UBDM.7.00130. Sample was collected from SK.
Abundance. Rare (only one specimen collected).
Habitat. Estuaries, on rocks.
Local distribution. SK only.
Ecology and conservation. The species might be more common locally in typical freshwater habitats. *V. coromandeliana* was previously recorded by Martens & Thiele (1908) in 'Labuan-Brunei' but was not included in recent review of freshwater snails of Brunei (Ng *et al.* 2015). The species should be rated as high conservation concern to sustain local populations.
Biogeographical distribution. In Western Coral Triangle (SB, PL and PN) and Sunda Shelf at SG. Also, Hainan (Chen & Zhang 2018), and the Indo-West Pacific (Eichhorst 2016b).

Genus *Neripteron* Lesson, 1831
***Neripteron violaceum* (Gmelin, 1791)**
Figs. 3E–F and 4I

Nerita violacea Gmelin, 1791: 3686.
Neritina violacea – Tan & Clements, 2008: 490, figs. 3-33, 3-34.
Neripteron (*Dostia*) *violaceum* – Eichhorst, 2016a: 392, pl. 102.

Material. UBDM.7.00100. Sample was collected from SK.
Abundance. Abundant.
Habitat. Associated with brackish water. On muddy surfaces, rocks and mangroves in brackish water environments.
Local distribution. SK, SD and SBu.
Ecology and conservation. Widely distributed in the Sungai Brunei estuarine system. At some rocky localities, it is fairly abundant and closely cohabits with *Nerip. cornucopia*. *Neripteron violaceum* is exposed to highly acidic environmental condition and faces shell dissolution (Proum *et al.* 2018). Of low conservation importance.
Taxonomy. Descriptions in the literature often confuse the sister species, *Nerip. violaceum* and *Nerip. cornucopia.* This partly stems from the variable shell colours in either (Tudu *et al.* 2017). They can readily be differentiated as follows (see Figs. 4I–J). [1] in *Nerip. cornucopia* the shell lip is distinctly flared whereas in *Nerip. violaceum* the shell lip is not flared and; [2] in *Nerip. cornucopia* the apex (spire) is located

midway between the parietal edge (lip) and the upper surface of the shell, but in *Nerip. violaceum* the apex meets the anterior parietal edge (Fig. 4).

Biogeographical distribution. SB, PL, TH and SG. Generally distributed in Indo-West Pacific (Eichhorst 2016a).

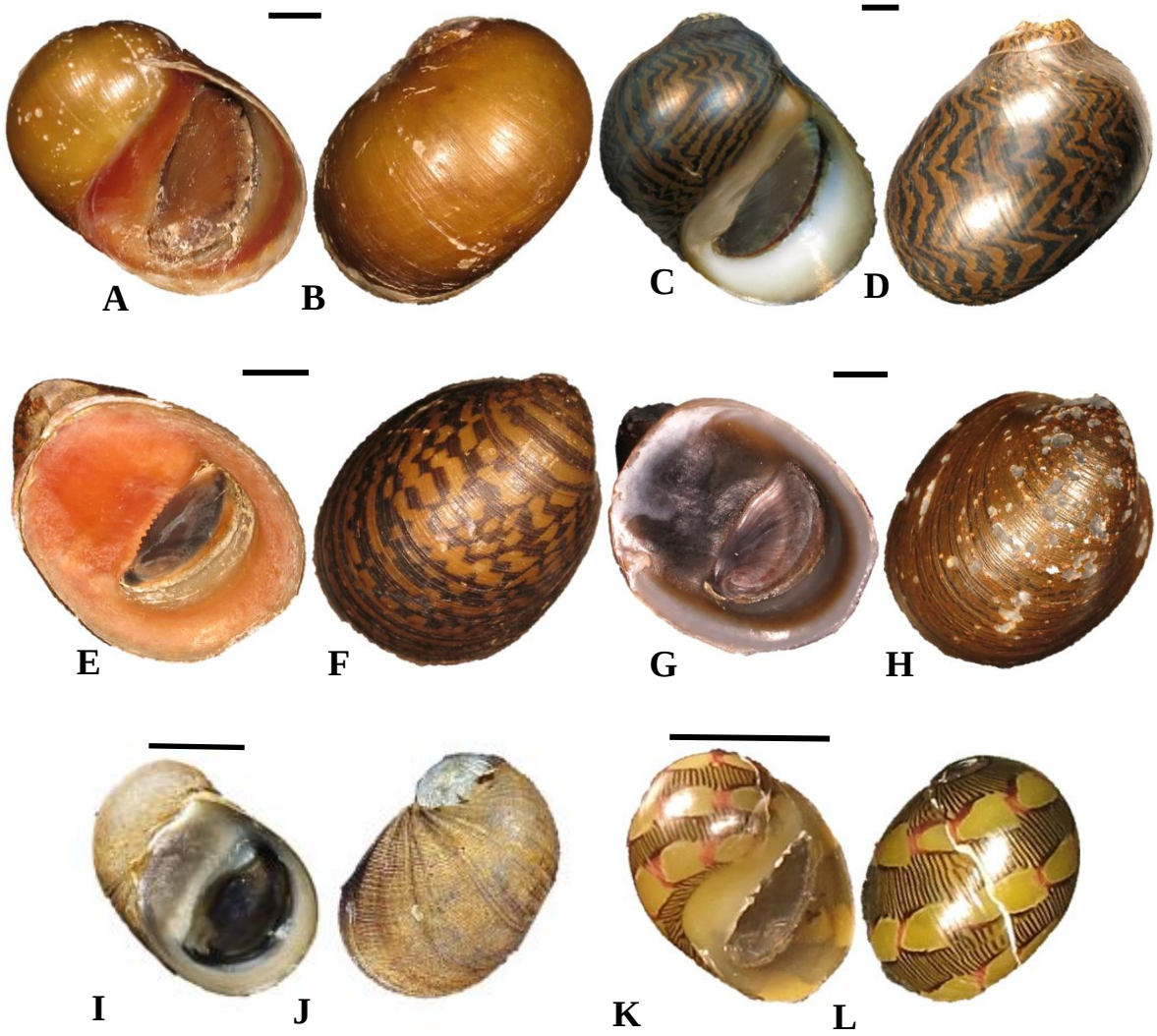

Figure 3. Neritidae species found associated with upper estuarine and brackish water habitats in Brunei Darussalam, shown in apertural and abapertural view. **A–B.** *Neritodryas dubia* (Gmelin, 1791). **C–D.** **Vittina coromandeliana* (G. B. Sowerby I, 1836). **E–F.** *Neripteron violaceum* (Gmelin, 1791). **G–H.** **Neripteron cornucopia* (Benson, 1836). **I-J.** **Neripteron spirale* (Reeve, 1855). **K–L.** *Clithon oualaniense* (Lesson, 1831). (*) indicates a new species record for Brunei Darussalam. Scale bar represents 3 mm.

***Neripteron cornucopia* (Benson, 1836)**

Figs. 3G–H and 4J

Neritina cornucopia Benson, 1836: 748.
Neritina cornucopia – Tan & Clements, 2008: 489, figs. 3-27, 3-28.
Neripteron (*Dostia*) *cornucopia* – Eichhorst, 2016a: 359, pl. 83.

Material. UBDM.7.00090. Sample was collected from SK.
Abundance. Intermediate.
Habitat. In the estuaries. Brackish water.
Local distribution. SK.
Ecology and conservation. The species can be found locally alongside *Nerip. violaceum* but is less common. *Nerip. cornucopia* is also exposed to highly acidic environmental condition and faces shell dissolution (Proum *et al.* 2018). Higher conservation concern than that of *Nerip. violaceum* because *Nerip. cornucopia* is distinctly less common.

Biogeographical distribution. SB in Western Coral Triangle and VN and SG in Sunda Shelf. Generally distributed from India to Japan and the Philippines (Eichhorst 2016a).

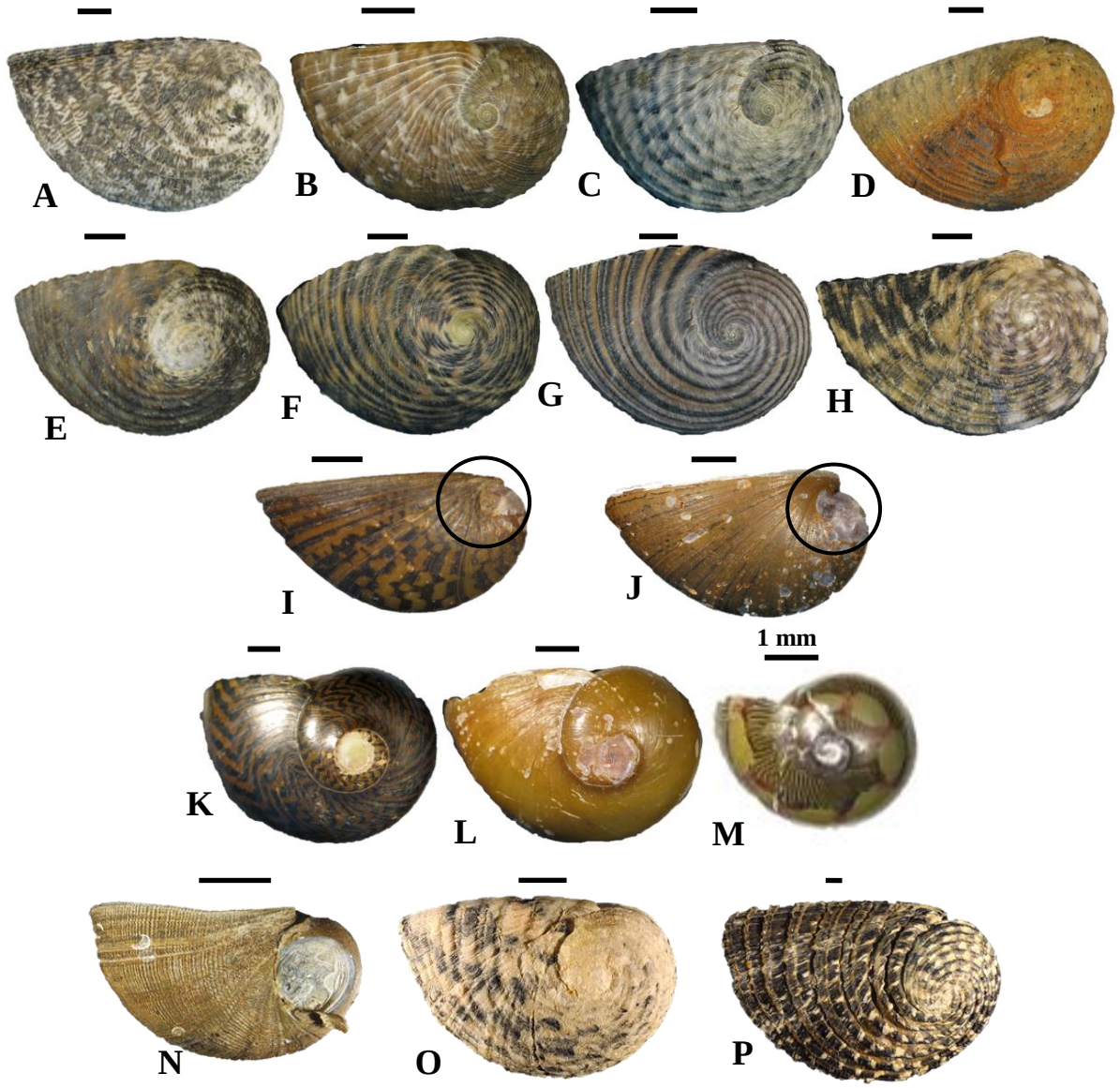

Figure 4. Side view showing off spire plasticity amongst *Nerita* species found in Brunei Darussalam. **A.** *Nerita albicilla* Linnaeus, 1758. **B.** *Nerita litterata* Gmelin, 1791. **C.** *Nerita insculpta* Récluz, 1841. **D.** *Nerita patula* Récluz, 1841. **E.** *Nerita chamaeleon* Linnaeus, 1758. **F.** *Nerita undata* Linnaeus, 1758. **G.** *Nerita balteata* Reeve, 1855. **H.** *Nerita planospira* Anton, 1838. **I.** *Neripteron violaceum* (Gmelin, 1791). **J**. *Neripteron cornucopia* (Benson, 1836). **K.** *Vittina coromandeliana* (G. B. Sowerby I, 1836). **L.** *Neritodryas dubia* (Gmelin, 1791). **M.** *Clithon oualaniense* (Lesson, 1831). **N.** *Neripteron spirale* (Reeve, 1855). **O.** *Nerita histrio* Linnaeus, 1758. **P.** *Nerita exuvia* Linnaeus, 1758. Markings on **I** and **J**: the spire hangs further midway in *N. cornucopia* compared to *N. violaceum.* Scale bar on top represents 3 mm, unless stated otherwise.

****Neripteron spirale* (Reeve, 1855)**

Figs. 3I–J and 4N

Neritina spiralis Reeve, 1855 (in 1855–1856): Species 99, plate xxiii, figs. 99a-99b.
Neritina sulculosa – Tan & Clements, 2008: 490, figs. 3-31, 3-32.
Neripteron (*Pseudonerita*) *spirale* – Eichhorst, 2016a: 382, pl. 97.

Material. Unassigned.

Abundance. Rare (one specimen collected).
Habitat. In the estuaries. Brackish water.
Local distribution. SK.
Ecology and conservation. This species appears to have a preference for flowing water in the upper reaches of canals and streams with lower salinity, thus it may more commonly occur in freshwater. It is small and can be easily overlooked or confused with juveniles of other congeners.
Biogeographical distribution. Generally distributed in Thailand and Malaysia, and possibly Indonesia (Eichhorst 2016a).

Genus *Clithon* Montfort, 1810
***Clithon oualaniense* (Lesson, 1831)**
Figs. 3K–L and 4M

Neritina oualaniensis Lesson, 1831: 379.
Clithon oualaniense – Tan & Clements, 2008: 491, figs. 3-37, 3-38; Eichhorst, 2016a: 208, pls. 34–38; Zvonareva & Kantor, 2016: 405, figs. 3M, 3N.

Material. UBDM.7.00120. Sample collected from PB.
Abundance. Very abundant.
Habitat. Mangroves. On muddy surfaces in mangrove stands.
Local distribution. PB.
Ecology and conservation. The species shows preference for seagrass turfs but occurs in lower density on muddy surfaces (see also Fong *et al.* 2018). Following the demise of locally dense seagrass turf, a vast population of relatively large *C. oualaniense* individuals is now lost from PB. This fast-growing species, suggested by their small size and thin shells, should rapidly recolonise when favourable habitat becomes available again. Although locally abundant, it is highly sensitive to habitat change, and can benefit from monitoring.
Biogeographical distribution. TR, AN, VN, TH and SG of Sunda Shelf. Generally distributed in Indo-West Pacific (Eichhorst 2016a).

Biogeographical comparisons

Our study adds eight new records of neritid snails to the Palawan/North Borneo (PNB) ecoregion (Spalding *et al*. 2007) as follows, *N. patula*, *N. insculpta*, *N. litterata*, *N. undata*, *N. histrio*, *Clithon oualaniense*, *Nerito. dubia* and *Nerip. spirale* (Table 1). Six of these species (*N. exuvia*, *N. insculpta*, *N. litterata*, *N. patula*, *Nerito. dubia* and *Nerip. spirale*) have been reported at 4 or fewer localities in the Western Coral Triangle and Sunda Shelf (Table 1). Despite uncertainty among the records, these species at least appear to be regionally rare. The absence in previous reporting of *N. patula*, *N. insculpta* and *Nerito. dubia* could relate to their being overlooked in local diversity studies. Species identification also presents a problem, especially when based only on shell characteristics (Carpenter & Niem 1998; Tan & Clements 2008; Zvonareva & Kantor 2016). *N. litterata*, for example was thought to be a form or polymorphic variation of *Nerita polita* (e.g., Tan & Clements 2008), so this might easily have been misidentified elsewhere.

Species numbers recorded in Brunei share similarity with other studies from the Western Coral Triangle (WCT): Sarangani (21 species) and Banyuwangi (16 species; Table 1). However, biogeographical comparisons between regions assume equality of sampling effort, which is rarely the case. Such discrepancies may arise from the range of local neritid habitats not being sampled in studies (Burghardt *et* al. 2006; Frey 2010a, 2010b; Dolorosa & Dangan-Galon 2014; Hombre *et al*. 2016; Ng *et al*. 2017; Baderan *et al*. 2019). More species (not listed here) are expected in regions centrally within the Coral Triangle, noting that Brunei is at the edge of this biogeographical region. However, an unusual complex interaction of ocean currents and gyres lies off the Brunei coast (SCS Southern Cyclonic Gyre, SCS Southern Anticyclonic Gyre, SE Vietnam Offshore Current, Gulf of Tonkin Surface Current), which should facilitate pelagic dispersal of species from widely across the South China Sea (Liu *et al.* 2016).

Table 1. Geographical distributions of neritid species in Brunei Darussalam and other Southeast Asian regions (1 = present, 0 = absent).

	Realm	**Central Indo-Pacific**															
	Province	**Western Coral Triangle**								**Sunda Shelf**							
	Ecoregion	**Palawan/North Borneo**			**Banda Sea**	**Lesser Sunda**	**Sulawesi Sea/Makassar Strait**		**Northeast Sulawesi**	**Sunda Shelf/Java Sea**				**Southern Vietnam**	**Gulf of Thailand**	**Malacca Strait**	
Species	**Location**	**BN**	**SB**	**PL**	**HI**	**BY**	**SR**	**BK**	**PN**	**TR**	**JH**	**SW**	**AN**	**VN**	**TH**	**SG**	**Records**
Nerita albicilla		1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	13
Nerita balteata		1	1	0	0	1	0	0	0	1	1	1	0	0	1	1	8
Nerita chamaeleon		1	1	0	1	1	1	1	0	1	1	1	0	0	1	1	11
Nerita exuvia		**1**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**4**
Nerita histrio		1	0	0	0	1	1	0	0	0	1	0	1	1	1	1	8
Nerita insculpta		**1**	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**4**
Nerita litterata		**1**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**4**
Nerita patula		**1**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**3**
Nerita planospira		1	1	0	0	1	0	0	1	0	1	0	0	1	1	1	8
Nerita undata		1	0	0	1	0	1	1	0	1	1	1	1	1	1	1	11
Neritodryas dubia		**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**2**
Vittina coromandeliana		1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	5
Neripteron violaceum		1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	5
Neripteron cornucopia		1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	5
Neripteron spirale		**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**2**
Clithon oualaniense		1	0	0	0	0	0	0	0	1	0	0	1	1	1	1	6
Other neritid species		0	4	3	5	9	14	6	1	4	0	7	3	6	15	7	
Total neritid species		**16**	**11**	**7**	**10**	**16**	**21**	**9**	**3**	**9**	**5**	**11**	**7**	**12**	**27**	**19**	

Abbreviations and references used are as follows: **BN**, Brunei Darussalam (present study); **SB**, Sabah, Malaysia (Manjaji-Matsumoto *et al.* 2017; Ng *et al.* 2017); **PL**, Palawan, Philippines (Dolorosa & Dangan-Galon 2014; Hombre *et al.* 2016); **HI**, Haruku Island, Eastern Indonesia (Haumahu & Uneputty 2018); **BY**, Banyuwangi, Indonesia (Susintowati *et al.* 2018); **SR**, Sarangani, Philippines (Manzo *et al.* 2014); **BK**, Bunaken National Park, Sulawesi (Burghardt *et al.* 2006); **PN**, Panango, South Bolaang Mongondow, North Sulawesi (Baderan *et al*. 2019); **TR**, Terengganu, Malaysia (Baharuddin *et al.* 2018, 2019); **JH**, Johor, Malaysia (Cob *et al.* 2012); **SW**, Sarawak, Malaysia (Hamli *et al.* 2013; Long *et al.* 2014); **AN**, Anambas and Natuna Island, Indonesia (Tan & Kastoro 2004); **VN**, Khanh Hoa, Vietnam (Zvonareva *et al.* 2015; Zvonareva & Kantor 2016); **TH**, Gulf of Thailand (Sri-aroon *et al.* 2005; Printrakoon *et al.* 2008; Wells *et al.* 2021); **SG**, Singapore (Tan & Clements 2008). Species recorded at less than five regions are marked in bold.

Ecology and Conservation

Consistent with a previous observation, the natural rocky shore supports a much greater neritid species diversity along the Brunei coastline (n = 8 species) than the more extensive seawalls (n = 3 species; see Marshall *et al.* 2017). The observation of single specimens of three species (*Nerita patula*, *N. exuvia* and *N. histrio*) on the spatially restricted natural rocky shore (ES) suggests 'seeding' from neighbouring north-west Bornean (Malaysian states, Labuan, Sabah and Sarawak), though notably, *N. patula* has not been reported from Palawan/North Borneo. Unlike Brunei, these regions comprise of extensive rocky shores which theoretically should support the species found in the present study, in addition to others. The inability of these scarce species to form significant populations relates to combinations of species interactions (competition) and life history features (growth, reproduction and dispersal capabilities), but ultimately this scarcity signals species likely to be at risk within the region. Two of the five single specimen records (*N. patula* and *Nerip. spirale*) are regionally rare (Table 1).

Nerita chamaeleon is by far the most abundant and widespread rocky-shore species on the Brunei coast and often prevails on artificial shores. It is a habitat generalist and has been found to persist under stress caused by sediment loading of the rocks. This species appears to outcompete *N. undata*, which takes a stronghold on shores devoid of *N. chamaeleon* and apparently tolerates conditions higher on the shore. *N. albicilla* is a low-shore generalist that forms significant populations below *N. chamaeleon. Nerita insculpta* occurs in the highest intertidal zone and is specialized to withstand high temperature and prolonged air exposure. *Nerita litterata* is habitat specialist at the interface of the rock and sandy beach, and has shown to be vulnerable to habitat change. Within the study period, a flourishing population became locally extinct following landscaping and deforestation of the fringe habitat at ES, causing excavation, erosion and change in the physical structure of the sandy interface.

Less clarity surrounds the local vulnerability of the mangrove/estuarine neritid snails, given the extent of the mangrove stands in Brunei Bay and our limited sampling of this. However, the Brunei Bay and estuarine system have been the subject of significant habitat modification over the last decade, derived from the construction of Brunei's landmark bridges (including SOAS Bridge). Notably, changes in populations have been observed for *N. balteata* and *C. oualaniense.* A very high *C. oualaniense* abundance at PB, declined in conjunction with declining seagrass cover at this site. Seagrass stabilises sediment, which benefits the snails aside from providing a preferred habitat/food source (Lee *et al.* 2001; Fong *et al.* 2018). The decline of *N. balteata* at BM matched collecting by researchers and harvesting of this larger species for food. Recruitment of these snails to these mangroves was found to be negligible over a five-year period, likely relating to their expected long lifespan and low reproductive potential (see Somchai 1995; Matsuura *et al.* 2000; Köhler *et al*. 2012; Hamli *et al.* 2013; Kano & Fukumori 2019). *Neripteron violaceum* and *Nerip. cornucopia* are widespread at the higher estuarine reaches, and local populations increase at more homogeneous substrates (rocky surfaces), with *Nerip. violaceum* always dominating numerically. The low abundances of the other higher estuarine, *Vittina coromandeliana, Nerip. spirale* and *Nerito. dubia*, could relate to undersampling or to the limit to their sometimes more freshwater distribution. *Neritodryas dubia* is clearly a *Nipa* palm specialist, and locally is always found associated with this tree.

Overall, most of our neritid snails can be categorised as having little conservation concern, implying that their populations should not experience undue risk of local extinction in the near future (*N. albicilla*, *N. balteata*, *N. chamaeleon*, *N. insculpta*, *N. planospira*, *N. undata*, *C. oualaniense*, *Nerip. violaceum* and *Nerip. cornucopia*). Those of greater conservation concern are *N. patula*, *N. histrio*, *N. exuvia* and *N. litterata.* Local extinction risk is inconclusive from this study for *V. coromandeliana*, *Nerito. dubia* and *Nerip. spirale.* It is likely that the small-sized *Nerip. spirale* is often overlooked in local habitats.

Summary

This study updates the neritid snails of Brunei, North Borneo and Palawan. We suggest that these snails are likely sensitive to habitat loss and human exploitation, causing local population declines and species losses. However, they are likely to be useful bioindicators of environmental change through local land use and/or anthropogenic climate change. Short-term studies can easily overlook the low abundance (scarce) species.

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