Ecologica Montenegrina
ISSN 2336-9744 (online) | ISSN 2337-0173 (print)

Ecologica Montenegrina 92: 123-153 (2025)
This journal is available online at: www.biotaxa.org/em
https://dx.doi.org/10.37828/em.2025.92.11

Article

The pteropod (Euthecosomata) and heteropod (Atlantidae) diversity of North West Borneo, based on inshore to oceanic sediment samples

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Received 3 November 2025 | Accepted by *V. Pešić*: 10 December 2025 | Published online 13 December 2025.

Abstract
Pelagic marine gastropods are functionally important to oceanic ecosystems, yet their species diversity is poorly known for the South China Sea (SCS). This paper describes the pteropod and heteropod diversity based on depositional sediment collections from 21 localities across North West Borneo (NWB), including intertidal (beached), continental shelf, continental slope and atoll biotopes. The paper briefly describes the species and assesses their local distributions spatially and with respect to environmental setting (sediment properties and seawater depth). The collections were found to contain 24 pteropod and 12 heteropod (atlantid) species. On the Brunei shelf, community structure is strongly influenced by the heteropod component, which increased in species richness along a depth gradient. It also shows that seabed sediment samples are seen as good indicators of the planktonic species in the above water column. Eleven pteropod species are newly recorded for NWB, and all of the atlantid species represent new records for this region and southern/central SCS. This study highlights the scarcity of information available for regional coastal pelagic gastropod diversities.

Key words Borneo, Brunei, Gastropoda, Malaysia, taxonomy, South China Sea.

Introduction

Pelagic marine gastropods are functionally important to oceanic ecosystems. They occur in large quantities, and essentially serve as a food resource for commercial fish, seabirds and whales (Bernard & Froneman, 2009). Where there is little influx of clastic sediments and there are no coral banks, their abundance is demonstrated by the sediment being largely made up by their skeletons and those of foraminifera. This provides valuable insight into their diversity in the water column (Kiran *et al*., 2025). Nevertheless, their distributions are poorly known for some geographical regions. The South China Sea (SCS) represents an important intersection of multiple biogeographical ecoregions (Spalding *et al*., 2007), forming part of the biogeographic realm with highest species diversity (Indo-Pacific seas & Indian Ocean; Costello *et al*., 2017). North West Borneo (NWB) comprises a rich and unique marine

faunal diversity. Together with the island of Palawan, the shelf areas of Sabah and Brunei (from which most of our samples stem) is recognised as a distinct marine ecoregion (129. Palawan / NW Borneo; Spalding *et al*. 2007), implying a unique combination of taxa that differs from those of the neighbouring South China Sea regions. The marine molluscs contribute significantly to regional species richness, but this fauna is incompletely explored, and published records are disparate (e.g. Raven, 2021; Raven & Recourt, 2018; Vermeij & Raven, 2009; Mustapha *et al*., 2021).

Previous comprehensive work on the pelagic gastropods, particularly the pteropods (O. Pteropoda), of NWB dates back to that by Rottman in the 1970s and 80s (1976, 1977, 1978, 1979, 1980). More recent studies on pteropods by Wang *et al.* (1997) refer to the northerly part of the SCS, whereas Jivaluk (1998) studied the composition of all zooplankton in NWB shelf waters. The heteropods (particularly F. Atlantidae; O. Littorinomorpha) form a second significant group of holoplanktonic gastropods. These are poorly investigated for the SCS, and there is no known record for this group from NW Borneo (e.g. Wall-Palmer *et al*., 2018).

The aim of this study was to improve understanding of the coastal pelagic gastropod diversity of the NWB. This paper reports the pteropod and heteropod species diversity based on sediment samples from NWB that span several decades. The specific objectives were, (1) to describe the pteropod and atlantid species in the NWB area, so as to update the taxonomic information with respect to new combinations and/or reinterpretations/reidentifications, and (2) to assess species diversites and distributions across environmental biotopes (sediment properties and depths), including providing a depth-related analysis of distributions for the Brunei Shelf. Because we studied the shell attributes only, our findings exclude the occurrence of the naked or gymnosomatous pteropods. Although the shells are light in weight, which suggests dead animals might be transported significant distances by currents before settling, they are also very fragile and prone to disintegration, suggesting that many of our sediment collections inform about the proximate distributions of the living individuals in the water column (see Rottman, 1980).

Materials & Methods

Sediment samples were collected on an *adhoc* basis between 1992 and 2020 (R). Additionally, sediments were made available to DM from the Brunei Shelf as part of a sub-contract with ERM. A Van Veen grab with a surface area of 0.1 m^2 was used to collect these sediments from a research vessel. Also, dredge samples from the HMS Dampier expedition (1963) were donated to R who subsequently donated them to Naturalis.

The below list summarises the samples taken at different localities and different environmental features (Table 1, Fig. 1). Abbreviations of locality names are given in parenthesis.

1. Temporary outcrops: samples were taken from Holocene shallow subtidal siliciclastic sediments at Sungai Liuk, Balingian (SL), and Sungai Baong and near Canada Hill, at Miri (M), Sarawak, Malaysia.
2. Beaches: samples were collected along clastic shorelines (Bako, Ba) and Bintulu (Bi) in Sarawak, Kuala Belait (KB) and Tutong (Tg) in Brunei, and Kampong Membakut (KM) and Tuaran (Tu) in Sabah. During quiet weather light material floating at the water surface and other light shells may accumulate locally on the beach along the high tide line. This typically includes pteropods, thin-shelled scaphopods, thin bivalves such as *Raeta pulchella* (A. Adams & Reeve, 1850). Due to this process the pteropods are predominantly undamaged. This material was carefully scraped off the sand surface.
3. Inner shelf coral banks: samples were collected by SCUBA diving (Siwa reefs, Mid reef, Tukau reef in northern Sarawak (MC), Hornet's and Sukun reefs in Brunei (BB). Samples of 0.5-7 litres of sediment were collected by hand. These coral banks are located on the inner shelf, up to 20 km from the coast, reaching to 15-30 m depth, the surrounding sandy seabed is slightly deeper. No specimens were found in shallow water fringing reefs and lagoons at Labuan island and Kota Kinabalu, Sabah. The most seaward coral bank sampled is Batu Mat, 60 km WSW of Miri, Sarawak (BM). The coral bank reaches to about 20 to 30 m below sea level, but the muddy seabed next to the coral bank is over 48 m deep. Due to its position away from the shore hardly any siliciclastics reach the area and

the detrital mollusc fauna comprises numerous species not recorded from the near coastal coral banks. Therefore this locality is counted as middle shelf.

4. Inner shelf siliciclastics: comprising Holocene to present-day material: these sediments occur along the coasts of northern Sarawak and Brunei. At two localities in Sarawak (Tyre Reef and Wreck No. 1 (MC)) material was sampled from the seabed at about 15 m by scuba diving. At other localities sand was dredged from similar depths and used for beach replenishment (Miri Marina (M), Penanjong (P), Jerudong beach and Tungku beach at Jerudong (Je)).
5. Shelf sediment grab sampling: These were collected by Integrated Envirotech from a research ship at 11 sites on the Brunei Shelf during marine ecological survey in 2013 (MES, see Fig. 1). Inner shelf (<50 m, MES1, 5, 8), middle shelf (50-100 m, MES15, 16, 17, 22, 25, 27) and outer shelf (>100-200 m) MES24, 29).
6. Shelf (silty) sand and continental slope planktonic ooze from dredge samples collected during the HMS Dampier cruise (1963, Haile *et al*., 1963; Pimm, 1964). These samples are a small part of the full samples collected present at NHMUK. Only a few of the larger samples were included in this study. They were donated by Simon Troelstra (Vrije Universiteit, Amsterdam). In addition to this C.D. Nuttall (NHMUK) donated a few larger specimens of pteropods from this expedition to S. van der Spoel for identification. These are now in Naturalis (ZMA collection numbers). Most of the latter are from the middle shelf to continental slope off southern Sarawak. As these are selected specimens only, the specimens are recorded, but the additional sample stations are not included on the overview map (Fig. 1). Note that identifications by Van der Spoel have been adjusted to reflect modern insights.

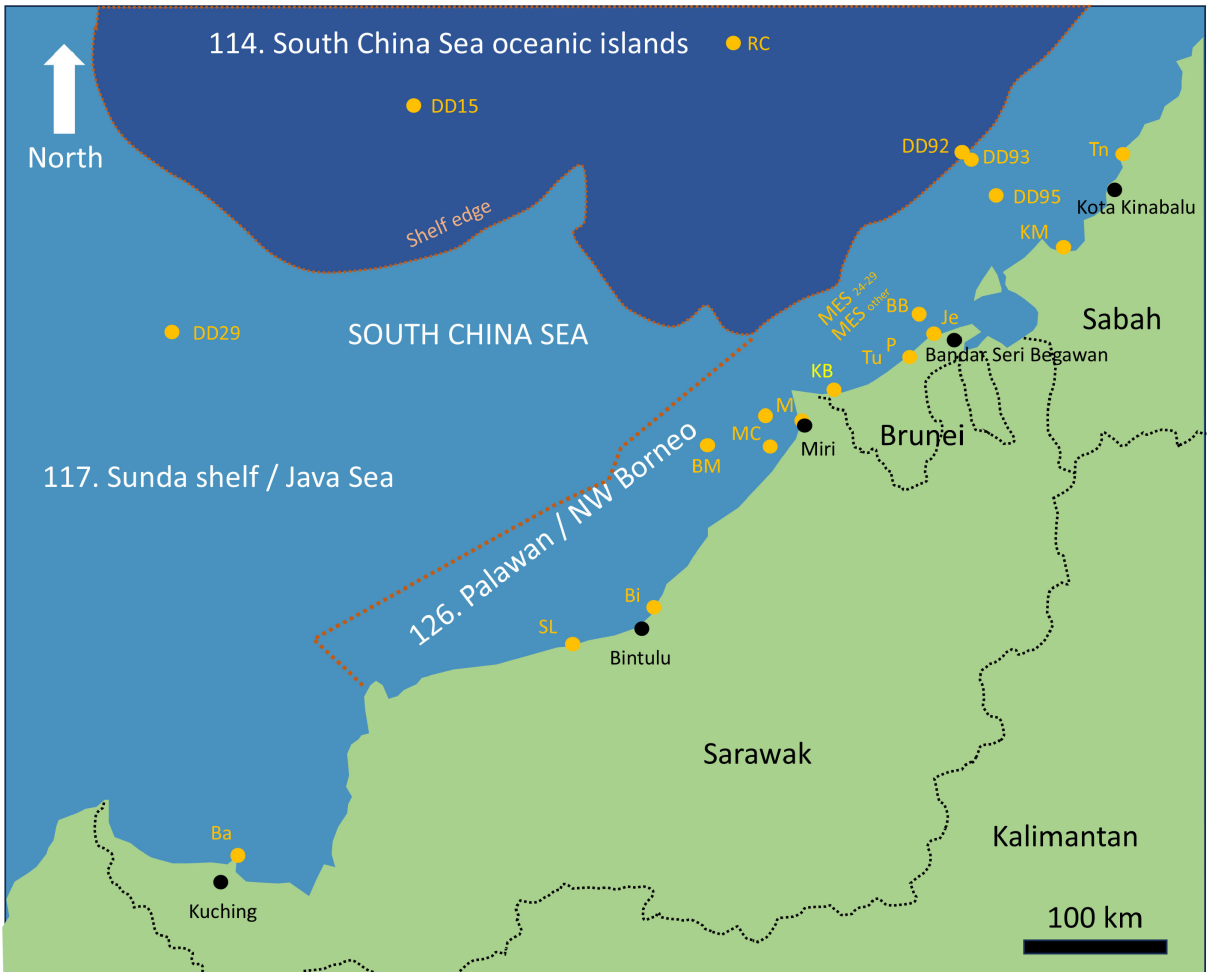

Figure 1. Map of the study area indicating sample points and biogeographical provinces (slightly modified after Spalding et al., 2007; white characters). Ba = Bako, SL = Sungai Liuk, Bi = Bintulu, BM = Batu Mat, MC = Miri coral banks, M = Miri, KB = Kuala Belait, Tu = Tutong, P = Penanjong, BB = Brunei coral banks, Je = Jerudong, KM = Kampong Membakut, Tn = Tuaran, RC = Royal Charlotte atoll, MES = Brunei offshore samples, DD = stations HMS Dampier expedition. The Brunei Shelf MES sites are shown in Appendix Figure 1.

7. Oceanic islands: 12 samples were taken by scuba diving and snorkelling at the Royal Charlotte atoll (Spratly islands, about 260 km from the coast, CR), which is in an oceanic setting. Sample size varies from 2-5 litres along the southern rim and centre to < 0.5 litres along the northern rim of the atoll. All samples comprised coral sand and rubble, the larger ones were collected taking handfuls of sediment along short tracks at selected localities from snorkelling depth (1-4 m) on the reef flat to about 36 m along the drop-off.

Table 1. Summary of the samples studied, indicating code used in Fig. 1, depositional environment, sediment samples and water depth. For the samples of Holocene material, assumed water depth of deposition. For coral banks between square brackets the water depth of the shelf on which the coral banks grow.

	locality	environment	sediment	depth	fossil?
	southern Sarawak				
Ba	Telok Pandan Besar, Bako (S03.24)	beach	sand	0	recent
SL	Sungai Liuk, Balingian (S18.05)	inner shelf	sand	5	Holocene
Bi	Bintulu (S92.09)	beach	sand	0	recent
DD29	HMS Dampier expedition	outer shelf	silty sand	126	recent
	northern Sarawak				
DD15	HMS Dampier expedition	continental slope	planktonic ooze	502-732	recent
MC	Siwa reefs, SW of Miri (S95.11; S97.15)	inner shelf	coral rubble	10-30 [30]	recent
MC	Mid reef, SW of Miri (S95.15)	inner shelf	coral rubble	24 [30]	recent
MC	Tukau reef, SW of Miri (S97.28)	inner shelf	coral rubble	20 [40]	recent
MC	Tyre reef, SW of Miri (S97.17)	inner shelf	sand	14	recent
MC	wreck No. 1, SW of Miri (S95.12)	inner shelf	sand	14	recent
BM	Batu Mat, SW of Miri (S96.26)	middle shelf	coral rubble	20 [48]	recent
BM	Batu Mat, SW of Miri (S96.25)	mid shelf	mud	48	recent
M	Kampong Ra'an, S of Miri (S92.04)	beach	sand	0	recent
M	Miri Marina (S05.19)	inner shelf	sand	15	recent
M	behind Canada Hill, Miri (F94.01)	inner shelf	sand	1	Holocene
M	Sungai Baong, Miri (F95.01)	inner shelf	sand	5	Holocene
M	Piasau beach, Miri (S92.01)	beach	sand	0	recent
	Brunei				
KB	Kuala Belait (S92.24)	beach	sand	0	recent
Tg	Tutong (S92.27)	beach	sand	0	recent
BB	Hornet's reef (S18.18)	inner shelf	coral rubble	7	recent
BB	Sukun reef (S18.19)	inner shelf	coral rubble	18	recent
P	Penanjong (S96.32)	inner shelf	sand	15	recent
Je	Jerudong (S93.27a)	inner shelf	sand	15	recent
MES	MES1, 5, 8	inner shelf	sand	14-34	recent
MES	MES15, 16, 17, 22, 25, 27	middle shelf	sand	68-93	recent
MES	MES24, 29	outer shelf	mud	144-190	recent
	Sabah				
KM	Kampong Membakut (S10.01)	beach	sand	0	recent
KK	Kota Kinabalu, SE of Pulau Gaya (S92.16)	inner shelf	coral rubble	10	recent
Tu	Tuaran (S97.18)	beach	sand	0	recent
DD92	west of Kota Kinabalu	outer shelf	silty sand	165-220	recent
DD93	west of Kota Kinabalu	outer shelf	sand	117	recent
DD95	west of Kota Kinabalu	middle shelf	sand	51	recent
	Spratly Islands				
RC	Royal Charlotte reef (S18.11-17; RC1-6)	oceanic atoll	coral rubble	1-36	recent

The samples were usually washed, sieved and picked. Those from the Brunei Shelf benthic grabs were preserved in 5% formalin and later transferred to 70% ethanol, prior to sieving and picking. Photographs were taken with a binocular microscope (Leica and Zeiss using stacking at Naturalis; Olympus at UBD). Side views were taken to observe important features for the identification of *Cavolinia* or *Diacavolinia* (Burridge *et al.*, 2019).

For each species, a short description and photographs are provided. The descriptions are partially based on the literature, and standard terminology is used. Although Van der Spoel uses protoconch I and II, later authors (e.g. Janssen *et al*., 2019) use the protoconch and larval shell, an approach followed here. Similarly, for Atlantidae, spire and adult shell are frequently used (Wall-Palmer, 2017), and we use the generic terminology protoconch and teleoconch. The protoconch whorls are counted as in Raven (2025).

For species recorded from the study area under other names, those names are listed but the provision of full chresonymies is beyond the scope of this paper. Although multiple forms or subspecies have been described in some cases, for simplicity only the "nominal species" names are referred to herein.

In some cases abundances were roughly estimated, but these were not calibrated to sample size and generally only complete shells were picked. However, as it was noted that at Royal Charlotte atoll, the majority of shells (including planktonic molluscs) were broken, so recognisable fragments were collected. For these samples, both the numbers of complete and fragmented specimens are given (Table 2). The latter was estimated by counting only fragments comprising (part of) the aperture (2 such fragments represent one specimen). Number of specimens indicated: 1; "few" = 2-3; "several" = 4-10; "many" = 11-100; "abundant" = >100. Regarding the preservation of the material, the following categories have been used: "alive"; "fresh"; "quite fresh"; "old"; "fossil".

All material collected by R is held in the collection of the author and will be deposited in Naturalis. Reference material of the specimens collected by DM is deposited in UBD museum (UBDM).

Abbreviations are as follows: fr., fragment(s); juv., juvenile(s); sp., specimen(s), and samples and legit are: DM, David Marshall (UBD); Naturalis, Naturalis Biodiversity Center (Leiden, The Netherlands); R, Han Raven (The Hague, The Netherlands); RMNH, Rijksmuseum voor Natuurlijke Historie, collection in Naturalis; UBD, Universiti Brunei Darussalam, Brunei Darussalam; UBDM, UBD Museum, Environmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam; ZMA, Zoologisch Museum Amsterdam, collection in Naturalis.

Results & Discussion

Twenty-one species of pteropod and 12 species of heteropod were retrieved from sediment samples collected from North West Borneo (Table 1). The Atlantidae were only found from middle shelf to oceanic settings, whereas the pteropods were collected from a wider range of environments, including inner shelf and beached samples. Brief descriptions of the species and simple faunistic analyses are given below.

Taxonomy and species descriptions

Order Littorinimorpha Golikov & Starobogatov, 1975

Family Atlantidae Rang, 1829 (Figs 2-3)

Genus *Atlanta* Lesueur, 1817

Remarks. – In many shells of this genus the protoconch is missing or damaged. Generally this renders the specimens unidentifiable.

***Atlanta brunnea* J.E. Gray, 1850** (Figs 2A-D)

Description. – Protoconch high, triangular, ornamented with zigzag spiral lines, ~4 whorls, brown. Single teleoconch whorl (W 1.4 mm), smooth, white or brown, with white wide keel.

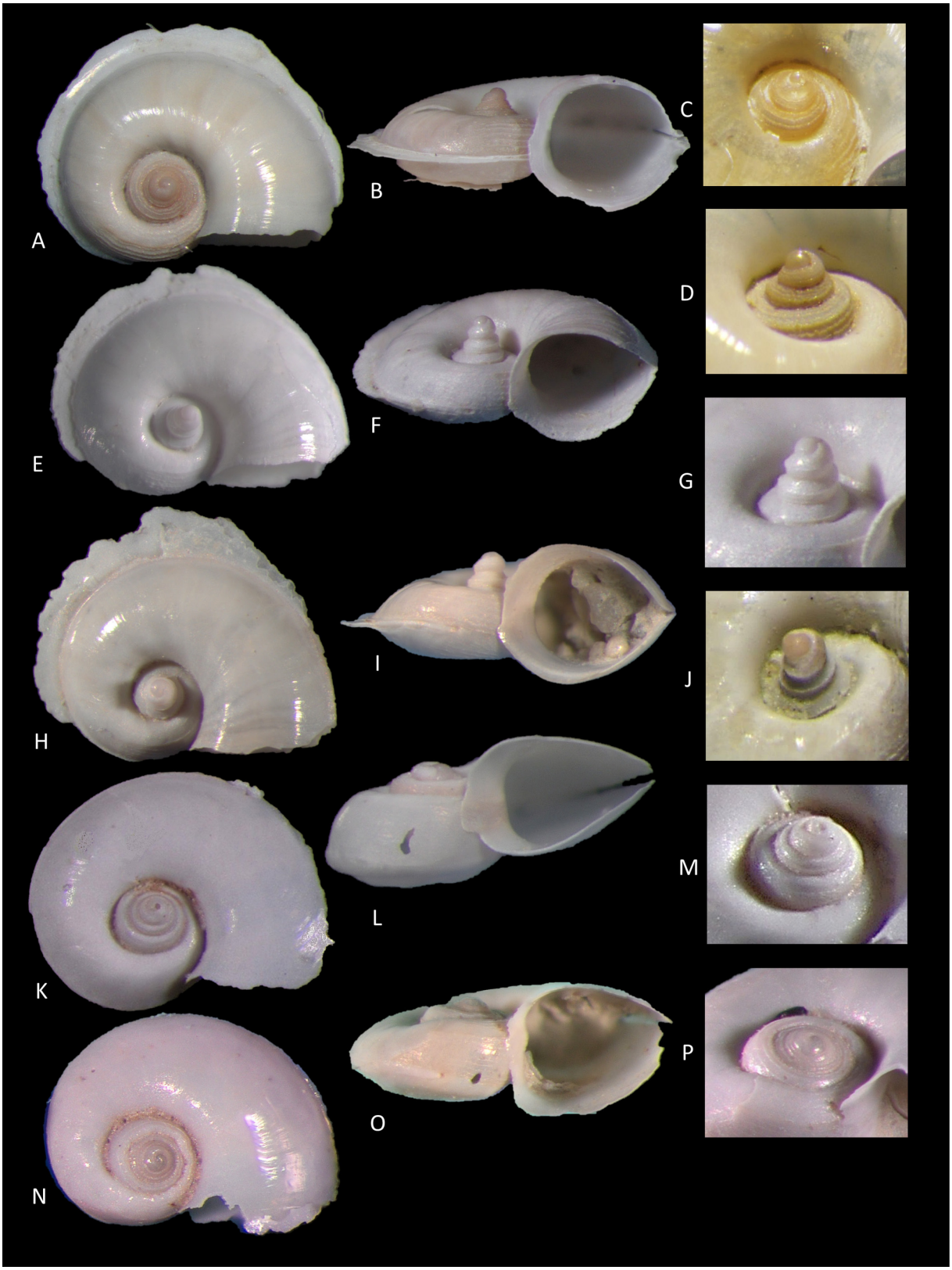

Figure 2. Atlantidae. (A-D) *Atlanta brunnea,* Brunei MES25, L 1.4, W 1.7 mm (DM UBDM.7.00153). (D) atypical form with stepped spire whorls. (E-G) *Atlanta vanderspoeli*, Brunei MES25, L 1.1, W 1.4 mm (DM UBDM.7.00155). (H-J) *Atlanta turriculata*, Brunei MES24, L 1.1, W 1.5 mm (DM UBDM.7.00154). (K-M) *Atlanta echinogyra,* Brunei MES24, (DM UBDM.7.00166). (N-P) *Atlanta helicinoidea*, Brunei MES25 L 1.2, W 0.95 mm (DM UBDM. DM UBDM.7.00156).

Remarks. – The species is easily recognised based on the brown protoconch which is not as high as in *A. turriculata*, and the teleoconch whorls are more globose, rising above the protoconch. The protoconch is heavily ornamented, but the spiral lines are only visible at high magnification. Some specimens have a more stepped protoconch. Generally, the teleoconch is whitish, occasionally brown, except for the white keel. Wall-Palmer *et al*. (2019) recognised Atlantic and Pacific forms for this species.

Distribution. – This species has been found on the Brunei middle to outer shelf (MES17, 24, 25), Sarawak outer shelf (DD29), Sabah outer shelf (DD93) and at Royal Charlotte atoll in oceanic setting.

***Atlanta echinogyra* Richter, 1972** (Figs 2K-M)

Description. – Protoconch medium high, broad, slightly tilted, heavily ornamented with spiral ridges and some finer ornamentation, ~4 whorls, red-brown. Teleoconch colourless, last part of the whorl rises markedly. Aperture pointed towards the keel.

Remarks. – The medium high heavily ornamented spire of the protoconch characterises this species.

Distribution. – This species has only been found on the Sarawak outer shelf (DD29), Brunei middle to outer shelf (MES24, 25) and protoconchs on Sabah middle shelf (DD95)

***Atlanta gaudichaudi* J.E. Gray, 1850 (**Fig. 3I)

Description. – Protoconch globose, medium high, with ~2 smooth whorls, deep suture, two teleoconch whorls, keel base yellow.

Remarks. – The medium high spired protoconch without ornamentation and with few whorls, and small teleoconch characterise this species. Compared to *A. plana* the whorls are more inflated and the aperture more rounded and the early teleoconch whorls are much narrower. The protoconch is smooth, compared to that of *A. plana* having two spiral ridges.

Distribution. – This species is widely distributed on the Brunei shelf, from inner (MES5, 8) middle (MES15, 16, 17, 22, 25, 27) to outer shelf (MES24, 29). It has also been found in Sarawak at the Batu Mat coral bank and at the Royal Charlotte atoll.

***Atlanta helicinoidea* J.E. Gray, 1850** (Figs 2N-P)

Description. – Low spired protoconch of ~4.5 whorls with marked spiral ridges, generally cream coloured. Teleoconch wide (W to 2 mm), single relatively inflated whorl, smooth, translucent.

Remarks. – This species has a remarkably large protoconch (>0.25 of shell diameter) of closely positioned whorls. The teleoconch is just under a whorl thus revealing the protoconch sculpture near the aperture. Both characteristics differentiate it from the similar *Atlanta inflata* J.E. Gray, 1850.

Distribution. – Only few shells of this species were found at Batu Mat coral bank, Sarawak, and in the shelf mud surrounding it, one at Royal Charlotte atoll and the Brunei middle shelf (MES 25).

***Atlanta inflata* J.E. Gray, 1850** (Fig. 3J)

Description. – Small shell (W 1.5 mm). Protoconch 4¼ to 4½ whorls, low, with numerous spiral ridges. Teleoconch 1¼-1.5 high, inflated whorls.

Remarks. – The small shell and ornamented protoconch make identification of this species straightforward.

Distribution. – This species was found on the Tukau coral bank, in middle shelf mud next to Batu Mat coral bank, both in Sarawak and at the Royal Charlotte atoll.

***Atlanta peronii* Lesueur, 1817** (Figs 3A-B)

Description. – Largest species of the genus, W to 12 mm, but in NW Borneo much smaller. Protoconch ~3.5 whorls, smooth, deep suture, white. Teleoconch rather flat, but last whorl inflated, raising well above protoconch. Keel with brown base, generally partially preserved.

Remarks. – In very large specimens the keel inserts between the final and penultimate whorls (Wall-Palmer, 2017) but the studied specimens are generally much smaller and this character has only been seen in few specimens. The largest *Atlanta* shells in a sample generally belong to this species.

Figure 3. Atlantidae. (A-B) *Atlanta peronii*, Brunei MES15, L 1.5, W 1.2 mm (DM UBDM.7.00158). (C-E) *Protatlanta souleyeti*, Dampier expedition stn DD15, offshore Sarawak, Malaysia, -502-732 m, L 0.8, W 1.7 mm (R T10961). (F-G) *Atlanta plana,* S97.25 NE of Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -20 m, leg. R, L 0.5, W 1.6 mm (R T08704). (H) *Atlanta tokiokai* Brunei MES 24 (specimen unavailable). (I) *Atlanta gaudichaudi,* Brunei MES15, L 2.2, W 1.7 mm (DM UBDM.7.00157). (J) *Atlanta inflata,* S18.17 Royal Charlotte atoll, Spratly Islands, -10 to -26 m, leg. R, W (protoconch only) 0.3 mm (R T10822). (K-L*) Oxygyrus inflatus*, S97.25 NE of Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -48 m, leg. R, L 0.8, W 1.1 mm (R T10768).

Distribution. – This is a widespread species, found beached, on inner shelf coral banks, on middle (Batu Mat) and outher (DD29) Sarawak shelf, on middle (MES5, 15) and outer (MES24) Brunei shelf, Sabah outer shelf (DD93), on the continental slope of Sarawak (DD15)and at Royal Charlotte atoll. Three specimens were found in the Sungai Baong temporary outcrop of Holocene sediments in Miri, Sarawak.

***Atlanta plana* Richter, 1972** (Figs 3F-G)

Description. – Protoconch 3.5 whorls, rather high, deep suture, pink, especially in the suture. Including teleoconch the shell has 4.7 whorls, W 1.3 mm. Flat last whorl, low enough for protoconch to reach similar level or raise above it. Keel very fragile and typically largely absent, base brown. No keel between penultimate and last whorl.

Remarks. – This species is easily identified based on its pink protoconch and flat shape. It differs from the very similar *Atlanta gaudichaudi* J.E. Gray, 1850 in the colour of the protoconch and the presence of spiral ridges on the protoconch (which are only visible at very high magnification, SEM).

Distribution. – This species is most abundant at Tukau and Batu Mat coral banks in Sarawak, and in the shelf mud next to Batu Mat, but also in middle (DD95) to outer shelf (DD93) of Sabah. Only two specimens were found at Royal Charlotte atoll and a few in the sand dredged near Jerudong, Brunei.

***Atlanta tokiokai* Van der Spoel & Troost, 1972** (Fig. 3H)

Description. – Protoconch large, globose, transparent, with 5.5 whorls (specimen unavailable) that is markedly tilted relative to the plane of coiling and has some rows of tubercles. Teleoconch wide, up to 7 mm (Borneo specimens), keel wide, base orange-brown, inserts between penultimate and ultimate whorl.

Remarks. – The protoconch has an ornamentation of scattered rows of small tubercles, only visible with very high magnification. *Atlanta inclinata* has a protoconch with 5 whorls. The specimen from DD93 has the last half whorl attached to the carina of the preceding whorl, making it semi-detached. Even if much of the protoconch is missing the shells of *Atlanta tokiokai* are still identifiable by the characteristic inclined outer protoconch whorl.

Distribution. – Found at Royal Charlotte atoll, the outer shelves off Sabah (DD93) and Sarawak (DD15) and on the Brunei shelf (MES24).

***Atlanta turriculata* d'Orbigny, 1836** (Figs 2H-J)

Description. – Small shell, W to 1.8 mm. Protoconch high and narrow, 4¼ whorls, purple colour, with thin, wavy spiral ribs on the last whorl. Teleoconch (slightly less than 1 whorl) smooth, with well-developed keel, high whorls resulting in large aperture, surface with purplish colour. Keel wide and generally largely preserved.

Remarks. – The narrow protoconch is higher elevated than in other species of the genus, making this species easily recognisable.

Distribution. – This species has been found at Tukau coral bank on the inner shelf, Sarawak outer shelf (DD29) and continental slope (DD15), and the Brunei middle to outer shelf (MES24, 25), Sabah outer shelf (DD93) and the Royal Charlotte atoll, clearly preferring water depths > 40 m.

***Atlanta vanderspoeli* Wall-Palmer, Hegmann & Peijnenburg, 2019** (Figs 2E-G)

Description. – Small shell, W to 1.8 mm. Protoconch moderately high and narrow, 3-4 whorls, purple colour, with thin spiral ribs on the last whorl, which are wavy below the carina. Teleoconch (slightly less than 1 whorl) smooth, with well-developed keel, high whorls resulting in large aperture, surface with purplish colour. Keel wide and generally largely preserved.

Remarks. – The narrow protoconchs of this species and *Atlanta turriculata* are higher elevated than in other species of the genus. The protoconch of *A. vanderspoeli* is slightly broader and less high than that of *A. turriculata* (Wall-Palmer, 2017).

Distribution. – This species has been found at Batu Mat and on the Brunei (MES24) outer shelf.

Genus *Oxygyrus* W.H. Benson, 1835

***Oxygyrus inflatus* W.H. Benson, 1835 (**Figs 3K-L)
Description. –Very small (W 1.1 mm), planorbid shell with very inflated whorls that largely envelop anterior whorls.

Remarks. – Based on their planorbid shape the shells of this species are instantly recognised. In addition, in the middle of the whorl there is a marked sinus.

Distribution. – Few specimens were found: in the middle shelf mud near the Batu Mat coral bank, outer shelf (DD29) and continental slope (DD15) off Sarawak and on the Brunei middle to outer shelf (MES24, 25, 27).

Genus *Protatlanta* Tesch, 1908

***Protatlanta souleyeti* (E.A. Smith, 1888)** (Figs 3C-E)

Description – Very small (W to 1.7 mm). Protoconch medium high, broad, 3.5 whorls, brown. Teleoconch single, rounded whorl, rapidly increasing in size, upper part higher, colourless.

Remarks. – The shells of this genus have a calcareous shells with a keel of conchiolin which is missing in all specimens seen. In outline the shell is similar to that of *Atlanta echinogyra*, but the protoconch is lower, laterally the shell is more rounded and the last part of the teleoconch whorl rises less.

Distribution. – The species was found on the Sarawak continental slope (DD15), Brunei MES 25 and Sabah outer shelf (DD92).

Order Pteropoda Cuvier, 1804 (Figs 4-6)

Superfamily Cavolinioidea J.E. Gray, 1850 (1815)

Family Cavoliniidae J.E. Gray, 1850 (1815)

Genus *Cavolinia* Abildgaard, 1791
Remarks. – The shells of this genus keep the larval shell in adult stage. Several larval shells were found (Figs 5K-L, 5N-Q), as well as caudal spines from broken adult shells. These were found to differ per species.

***Cavolinia gibbosa* (d'Orbigny, 1835**) (Figs 4A-B)
Description. – A large *Cavolinia* (L 9.5 mm) with markedly protruding dorsal lip, straight ventral lip base, and marked caudal spine. The dorsal shell has very weak longitudinal ribs, otherwise smooth. Ventral part of the shell globose with weak transverse riblets. The lateral spines point slightly in caudal direction. Translucent with narrow brown line along ventral lip.

Remarks. – This large species is easily recognised based on the markedly protruding dorsal lip.

Distribution. – Very few specimens of this large species have been found on the middle shelf Batu Mat coral bank and at the Royal Charlotte atoll (both at 20 m depth).

***Cavolinia globulosa* (Gray, 1850)** (Figs 4C-H)
Description. – A medium large *Cavolinia* (L 5 mm) with rounded dorsal lip, ventral lip with median depression, and short caudal spine. The dorsal shell has five vaguely indicated broad longitudinal ribs, weaker towards the caudal spine mark, otherwise smooth. Ventral part of the shell globose with marked transverse riblets. The lateral spines point slightly in caudal direction. White with brown near the ventral lip.

Remarks. – Differs from *Cavolinia gibbosa* in being smaller, much more globose, having a rounded dorsal lip, a more rounded ventral lip base and shorter caudal spine.

Distribution. – A single specimen in the middle shelf mud near Batu Mat, Sarawak; several specimens on the continental slope off Sarawak (DD15, DD53, DD54) and a few on the outer shelf of Sabah (DD92); abundant in Brunei middle shelf (MES15, 25) and small numbers in Brunei outer shelf (MES24).

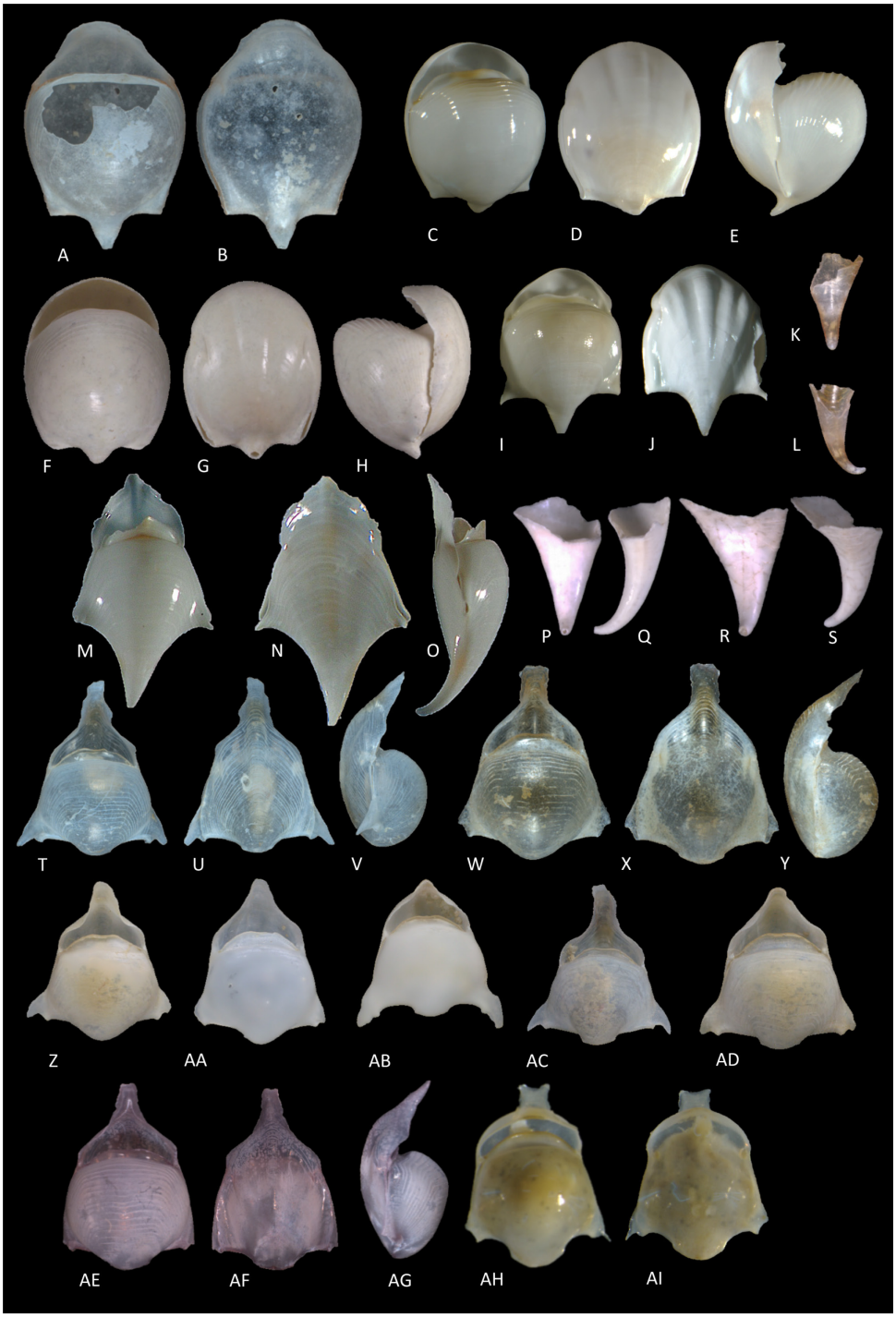

Figure 4. Cavoliniidae. (A-B) *Cavolinia gibbosa,* S97.26 Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -20 m, leg. R, L 9.5 mm (R T07463). (C-H) *Cavolinia globulosa*. (C-E) Brunei MES15, L 4.8, W 3.9 mm (DM UBDM.7.00159). (F-H) Dampier expedition stn DD54, Sarawak, Malaysia, -370 m, L 5 mm (ZMA.MOLL.18015). (I-L) *Cavolinia uncinata*. (I-J). Brunei MES24, L 6.6, W 5.2 mm (DM UBDM.7.00160). (K-L) Larval shell / caudal spine, S18.14 Royal Charlotte atoll, Spratly Islands, -20 m, leg. R, L 1.8 mm (R T10294). (M-Q) *Cavolinia inflexa.* (M-O) Brunei MES25 (DM UBDM.7.00161). (P-Q) Larval shell / caudal spine, Dampier expedition stn DD15, offshore Sarawak, Malaysia, -502-732 m, L 2.0 mm (R T10974). (R-S) *Cavolinia uncinata,* larval shell / caudal spine, Dampier expedition stn DD93, outer shelf W of Kota Kinabalu, Sabah, Malaysia, -117 m, L 1.9 mm (R T11018). (T-AD). *Diacavolinia longirostris*. (T-Y) S97.28 Tukau reef, 26.4 km W of Miri, Sarawak, Malaysia, -20 m, leg. R (R T07458). (T-V) L 4.9 mm. (W-Y) L 3.8 mm. (Z-AD S18.19 Sukun reef near Champion oil field, Brunei, -18 m, leg. Laszló Kocsis (R T09356). (Z) L 3.8 mm. (AA) L 4.8 mm. (AB) L 3.8 mm. (AC) L 4.1 mm. (AD) L 4.0 mm. (AE-AG) *Diacavolinia* spec. A, S18.14a Royal Charlotte atoll, Spratly Islands, -36 m, leg. R, L 4.7 mm (R T10298). (AH-AI) *Diacavolinia angulata,* Brunei MES25, L 2.9, W 2.3 mm (DM UBDM.7.00163).

***Cavolinia inflexa* (Lesueur, 1813)** (Figs 4M-Q)

Description. – Shell (L to 4.5 mm) elongate, with flat side, two broad and short, slightly abapically pointed lateral spines located above the middle, and a broad, markedly dorsally curved central spine formed by the larval shell hat is typically retained on the adult shell. The aperture is rather narrow, but the dorsal (upper) lip is markedly broad extending well beyond the ventral (lower) lip. The shell is translucent to white in colour with some elongate brown median line or spot on the dorsal side.

Remarks. – This species is poorly represented in the area, but various broken adults and larval shells / caudal spines were found. The adults have a very characteristic outline. The larval shells / caudal spines (Pl. 3 Fig. 2) are slender and have a marked carina on both sides. In those samples where only the larval shells / caudal spines are found it is not always possible to determine whether those are of *C. inflexa* or *C. uncinata*. See also under *C. uncinata*.

Distribution. – Found in continental slope sediments off Sarawak (DD15, DD53, DD54) and Brunei (MES25) and middle (DD95) to outer shelf of Sabah (DD92).

***Cavolinia uncinata* (d'Orbigny, 1835)** (Figs 4I-L, 4R-S)

Description. – A medium large *Cavolinia* (L 7.5 mm) with rounded dorsal lip, ventral lip with median depression, and long caudal spine. Relatively straight sides. The dorsal shell has five longitudinal ribs, a marked central rib and narrower lateral and lock ribs, all weaker towards the caudal spine, otherwise smooth with flattened edge. Ventral part of the shell globose and smooth. The lateral spines are medium long and point outward in caudal direction. Shell white to brownish.

Remarks. – Differs from *Cavolinia globulosa* in relatively straight parallel sides, having narrower and more marked longitudinal ribs, lack of transverse riblets, longer caudal spine and longer lateral spines that point outward.

The larval shells / caudal spines (Figs 4K-L, 4R-S) are wider than those of *C. inflexa* (Figs 4M-Q), and lack the lateral carinae, but have narrow flattened sides with short lateral ridges.

Distribution. – Four specimens found on the Brunei middle to outer shelf (MES15, 24, 25); 16 on the outer shelf off Sarawak (DD29, DD36), some specimens, fragments and larval shells / caudal spines on the continental slope off Sarawak (DD15) and the outer shelf of Sabah (DD92, DD93); and a larval shell / caudal spine at Royal Charlotte atoll.

Genus *Diacavolinia* Van der Spoel, 1987

Description. – Shell dorsoventrally depressed, with lateral spines. In adults the protoconch and larval shell are thrown off and the resulting opening closed. Shell aperture with closing structure linking dorsal and ventral sides (abbreviated from Van der Spoel, 1987).

Remarks. – Van der Spoel (1987) introduced the genus based on a single species, *D. longirostris*. Later, Van der Spoel *et al.* (1993) recognised 24 species. Based on molecular studies, later authors (e.g., Maas *et al.*, 2013; Burridge *et al.*, 2019) realised that large morphological variation may occur within a single species and proposed different groupings, but further work is needed. In the NW Borneo material three to four different morphospecies are recognised, but allocation to the right species name is problematic as long as the overall revision of the genus is not completed. Therefore the names used here should be considered as preliminary assignment.

***Diacavolinia angulata* (Souleyet, 1852)** (Figs 4AH-AI)

Diacavolinia elegans Van der Spoel, Bleeker & Kobayasi, 1993

Description. – Medium size *Diacavolinia* (L 2.9 mm, W 2.3 mm). Triangular shell with uninterrupted parallel ventral and dorsal lips, the latter with a marked short, bifid rostrum. Dorsal side rounded, with weak central rib. Ventral side globose, smooth. Lateral spines short and only slightly bent. Hyaline shell with brown colour especially the central part of the ventral side and the edges of the lips.

Remarks. – In the study area this species is easily recognised based on the uninterrupted dorsal lip with bifid rostrum. Through its range it is variable, both in angle and shape of the dorsal lip, based on which initially *D. elegans* Van der Spoel, Bleeker & Kobayasi, 1993 was interpreted as representing a separate species. DNA barcoding analysis of numerous specimens (Maas *et al.*, 2013) demonstrated this to be intraspecific variation.

Distribution. – Ten shells were picked from the outer shelf sample DD92 off Sabah, four in Brunei (MES25) a single fragment on the outer shelf off Sarawak (DD29).

***Diacavolinia* cf. *longirostris* (Blainville, 1821)** (Figs 4T-AD)

Description. – Medium size *Diacavolinia* (L 5-7 mm, W 5-7 mm). Triangular shell with long dorsal lip that may have varied shape, but lacks constrictions, ventral lip with median depression. Dorsal side with well-developed central rib and weaker lateral ribs and lock ribs. Ventral side globose and smooth. Lateral spines sharp, slightly bent and hooked, but damaged in many specimens. Most specimens have clear growth lines, especially on the ventral side. Translucent, white to yellowish or brownish.

Remarks. – The late A.W. Janssen originally identified these specimens as *Diacavolinia elegans* Van der Spoel, Bleeker & Kobayasi, 1993, then changed this to *D. longirostris.* As *D. longirostris* is now interpreted to be restricted to the Atlantic (Burridge *et al.*, 2019) it is unclear to what species these specimens represent. They have a constant lateral profile, but the lateral spines vary from short to relatively long. It is well possible that this morphotype comprises various species, e.g. *Diacavolinia triangulata* Van der Spoel, Bleeker & Kobayasi, 1993 (Figs 4T-V 4Z, 4AB-AD).

Distribution. – This is a very common and widely distributed species that occurs in large quantities throughout the North Sarawak-Brunei area and Royal Charlotte atoll, in shelf to continental slope mud, subtidal coral banks, coral reefs, subtidal sandy areas and frequently washes up on beaches.

***Diacavolinia* spec. A** (Figs 4AE-AG)

Description. – Small size *Diacavolinia* (L 4.7 mm, W 3.5 mm). Rectangular shell with long and narrow dorsal lip, ventral lip with median depression. Dorsal side with well-developed central rib and weaker lateral ribs and lock ribs. Ventral side globose and smooth. Lateral spines very short, caudal joint wide. Most specimens have clear growth lines, especially on the ventral side. Translucent, purple.

Remarks. – This species is easily identified based on its purplish colour, but also differs from *D.* cf. *longirostris* in having extremely short lateral spines. The ventral side is much flatter, resulting in a more pointed anterior. The shell is also smaller and narrower. According to Van der Spoel *et al*., 1993) the only species with a shell of this colour is *Diacavolinia limbata* (d'Orbigny, 1836), a species only known from the Atlantic. Note that after several years the purple colour has faded.

Distribution. – *Diacavolinia spec.* A has only been found on the Royal Charlotte reef (Spratly Islands) in fully oceanic setting in the central part of the South China Sea, where it occurs in small numbers, besides large numbers of *D.* cf. *longirostris.*

Genus *Diacria* Gray, 1840

***Diacria major* (Boas, 1886)** (Figs 5A-B)

Description. – A large species (L to 13 mm without caudal spine, W to 11 mm), with a strongly dorso-ventrally compressed shell and wide that has the lateral spines pointing in a caudal direction. Ventral side with three longitudinal ribs, dorsal side five. The long slit-like aperture is continuous. The rim of the aperture and other thick parts of the shell are brownish coloured.

Remarks. – Van der Spoel (1967) considered this species a form of *Diacria trispinosa* (Blainville, 1821) but already mentioned that both 'forms' often occurred within a single sample and therefore could constitute a higher rank. *Diacria trispinosa* has the lateral spines perpendicular to the shell axis and is smaller. The caudal spine is usually thrown off and a septum formed (Van der Spoel, 1967: 85). A single larval shell was found, which is relatively long (2.9 mm), slightly curved and ellipsoid in outline. As the shape perfectly matches the growth lines it is interpreted as larval shell, rather than a thrown off caudal spine.

Distribution. – Few specimens have been found: offshore Sarawak, in outer shelf silty sand to continental slope planktonic ooze (DD20, DD29, DD15), an adult specimen at Royal Charlotte atoll, a few specimens on the Brunei middle to outer shelf (MES24, 25) and fragments in outer shelf muds in Sabah (DD93). Larval shells / caudal spines are very narrow and have a characteristic corneous colour.

Genus *Telodiacria* Rampal, 2019

The identification of species within this group was complicated by the absence of a clear enumeration of key differences. Therefore initially only *Telodiacria costata* and *T. danae* were recognised, the former being very abundant and the latter being scarce. On the other hand, Rottman (1976, 1980) recorded only *T. quadridentata* (Blainville, 1821). Based on the paper by Van der Leyen & Van der Spoel (1982), it

Figure 5. (A-R) Cavoliniidae (A-B) *Diacria major*. Brunei MES25, L 7.1, W 7.7 mm (DM UBDM.7.00164). (C-E) *Telodiacria costata,* S97.28 Tukau reef, 26.4 km W of Miri, Sarawak, Malaysia, -20 m, leg. R, L 2.4, W 2.1 mm (R T07459). (F-H) *Telodiacria quadridentata*, S93.27 Jerudong beach, Muara, Brunei, leg. R, L 2.7, W 2.3 mm (R T08335). (I-K) *Telodiacria* spec. A, -20 m, S97.28 Tukau reef, 26.4 km W of Miri, Sarawak, Malaysia, leg. R, L 2.6, W 2.0 mm (R T10818). (L-N) *Telodiacria danae*, S18.17 Royal Charlotte atoll, Spratly Islands, -10 to -26 m, leg. R, L 1.6, W 1.3 mm (R T10468). (O-Q) *Telodiacria costata,* larval shells (O-P) S97.28 Tukau reef, 26.4 km W of Miri, Sarawak, Malaysia, -20 m, leg. R, L 1.8 mm (R T07459). (Q) Dampier expedition stn DD93, outer shelf W of Kota Kinabalu, Sabah, Malaysia, -117 m, L 2.0, W 0.9 mm (R T11030). (R) *Telodiacria* spec., larval shell, Dampier expedition stn DD93, outer shelf W of Kota Kinabalu, Sabah, Malaysia, -117 m, L 2.4 mm (R T11054). (S-T) Cliidae, *Clio pyramidata.* (S) Brunei MES25, L 9 mm (DM UBDM.7.00165). (T) S97.26 Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -20 m, leg. R, L 4.4 mm (R T08330).

became clear that the key differences are (1) size, with *T. quadridentata* (Blainville, 1821) being the largest and relatively broad, *T. costata* medium and *T. danae* the smallest, and, (2) transversal sculpture on the dorsal side near the aperture, with *T. costata* having five pronounced imbricate ribs, *T. danae* having three imbricate striae, and *T. quadridentata* having 7 or more cosely placed narrow ribs or striae.

Based on this we identified small numbers of *T. quadridentata* in some samples from the study area. Rottman's (1976: figs 2b-d) images of *T. quadridentata* clearly represent *T. costata*. Rottman's material warrants a reidentification.

***Telodiacria costata* (Pfeffer, 1879)** (Figs 5C-E, 5O-Q)

Description. – Shell rounded in outline (L 1.8-2.7 mm), dorsal shell part with five well-developed longitudinal ribs, with weak to marked growth lines in between, and five pronounced imbricate transversal striae adjoining the aperture. The lateral spines point outward. Ventral part of the shell globose and smooth, with well-developed transverse imbricate striae. In fresh specimens the thickened apertural margins are brown to orange coloured.

Remarks. – Initially identified as *T. quadridentata* (Blainville, 1821), Rottman (1976, 1980) also recorded the species as *T. quadridentata* and did not mention *costata.* This is because only later Van Leyen & Van der Spoel (1982) revised the *Teleodiacria quadridentata* group and distinguished *T. costata* and *T. danae* on shell morphology. Comparison with material in Naturalis and Van Leyen & Van der Spoel (1982) clarified that most specimens are *T. costata*, which is smaller and has 5 transverse striae on the dorsal side (about 7 in *quadridentata*).

Larval shells (Figs 5O-Q) occur in small numbers. They are elongated triangular (L 2.0, W 0.87 mm), flattened, with a small protoconch (W ~150 µm). In the outer shelf deposits off Sabah (DD93) a few larger and less elongate shells occur (L 2.4, W 1.3 mm) with a wider protoconch (~250 µm). It is unclear to which species these belong, they may not even be *Telodiacria*.

Distribution. – In the study area this is the most abundant *Telediacria* species. Large numbers of specimens occur in the calcareous sediments of inner shelf coral banks, and mid shelf to continental slope sand and planktonic ooze in Sarawak and Sabah, the Royal Charlotte atoll, all samples of inner to outer shelf (Brunei MES1-29) and even on beaches. It was also abundant in the Sungai Baong temporary outcrop of Holocene sediments in Miri, Sarawak.

***Telodiacria danae* (Van Leyen & Van der Spoel, 1982)** (Figs 5L-N)

Description. – Shell slightly elongate in outline, relatively wide (L 1.2-1.8 mm, W 1.0-1.4 mm), dorsal shell part with five vaguely indicated longitudinal ribs, weaker towards the caudal spine mark, with marked growth lines in between and about three imbricate transversal striae adjoining the aperture. The lateral spines point slightly in a caudal direction. Ventral part of the shell globose and smooth with about four transverse imbricate stria. In fresh specimens the thickened apertural margins are brown.

Remarks. – Easily identifiable as smallest of the *Telodiacria* species with a virtually smooth shell.

Distribution. – Few specimens have been found on the Sarawak inner to mid shelf coral banks (only Tukau and Batu Mat which are further from the shore) and in middle (DD95) to outer (DD92-93) shelf sand in Sabah, but the species is more abundant in outer shelf sediments (DD29) and in continental slope planktonic ooze (DD15) in Sarawak and on the Royal Charlotte atoll, Spratly Islands. It is always accompanied by the more numerous *T. costata.*

***Telodiacria quadridentata* (Blainville, 1822)** (Figs 5F-H)

Description. – Shell only slightly longer than wide (L 2.7, W 2.3 mm), dorsal shell part with five clear longitudinal ribs, weaker towards the caudal spine mark, with marked growth lines in between and about 7 imbricate transversal striae adjoining the aperture. The lateral spines point outward. Ventral part of the shell globose and smooth. In fresh specimens the thickened apertural margins are orange-brown coloured.

Remarks. – The shells are larger and wider than those of *T. costata*, but for firm identification the number of transverse striae on the dorsal side are key: 5 or more in *T. quadridentata*.

Distribution. – The species is occurs in small numbers on the inner to mid shelf sands and coral banks in Sarawak and Brunei, outer shelf (silty) sand in Sarawak (DD29) and Sabah (DD92-93), but is more abundant on the Royal Charlotte atoll, Spratly Islands. One specimen was found in the Holocene shoreface deposits of Sungai Baong, Miri, It always occurs together with *T. costata.*

***Telodiacria* spec. A** (Figs 5I-K)

Description. – Shell rounded in outline (L 2.6, W 2.0 mm), dorsal shell part with five well-developed longitudinal ribs, with weak to marked growth lines in between, and three pronounced imbricate transversal striae adjoining the aperture. The lateral spines point outward. Ventral part of the shell globose and smooth, with well-developed transverse imbricate striae. Shell purple; the thickened apertural margins are brown coloured.

Remarks. – Amongst *Telodiacria costata* from the Tukau coral bank, Sarawak, where the species is particularly abundant (>1000 specimens) one specimen and a fragment were found with a clear purple colour. Key differences are the three broader transversal striae, the slightly more elongate shell with less inflated sides. Probably this is intraspecific variation.

Distribution. – Only known from Tukau coral bank, Sarawak.

Family Cliidae Jeffreys, 1869

Genus *Clio* Linnaeus, 1767

Remarks. – *Clio recurva* (Children, 1823) was recorded by Rottmann (1976) from the Gulf of Thailand / South China Sea north of the study area, whereas *Clio convexa* (Boas, 1886) and *Clio cuspidata* (Bosc, 1802) were recorded in Rottman (1980). These species have not been found during the present study.

***Clio pyramidata* Linnaeus, 1767** (Figs 5S-T)

Description. – Pyramidally shaped shell (L to 20 mm, W to 10 mm) with greatest width above the middle of the shell. Two lateral ribs that are thickened and only slightly diverging. Distinct transverse striation and growth lines. Cross-section triangular except in the most posterior part. Longitudinal rib over the ventral side. Embryonic shell droplet-shaped with small cusp.

Remarks. – This characteristic shell is easily identified, but generally the shells are broken. The larval shells or apical parts can be recognised based on their triangular outline with quickly widening shell. In apertural view the larval shell is initially mostly round, but gradually becomes boat shaped with round ventral (lower) side, two quickly expanding, marked carinas that are open on the inside, and a convex dorsal (upper) side (Raven & Alonso, 2023: figs 13b, 14b, 15a-b).

Distribution. – A single specimen was found at Batu Mat coral bank and several in outer shelf sand (DD29) to continental slope planktonic ooze (DD15) off Sarawak, several more at Royal Charlotte atoll, small numbers in middle to outer shelf of Brunei (MES15-29) and outer shelf sand in Sabah (DD92-93).

Family Creseidae Rampal, 1973

Genus *Boasia* Dall, 1889

***Boasia chierchiae* (Boas, 1886)** (Fig. 6A)

Creseis virgula constricta C. Chen & Bé, 1964 – Rottman, 1976: pl. 4 figs 2a-b
Creseis chierchiae Boas, 1886 – Rottman, 1976: pl. 4 figs 4a-b
Creseis bulgia Sakthivel, 1974 – Rottman, 1976: pl. 4 fig. 5

Description. – Conical shell (L to 3.6 mm), straight (some bent), with apical angle to about 15°. Protoconch inflated, clearly separated from teleoconch, including larval shell about 0.5 mm long. Shell colourless, larval shell shiny, teleoconch matt.

Remarks. – Until intraspecific variation was properly understood (Rampal, 1985; Gasca & Janssen, 2013), the classification of the species in the Creseidae has varied considerably. The taxa which Rottman (1976) considered subspecies of *Creseis virgula* (Rang, 1828) are now considered valid species. On the other hand, Rottman (1976, 1980) distinguished *Creseis chierchiae, Creseis bulgia* Sakthivel, 1974, and *Creseis virgula constricta* C. Chen & Bé, 1964, but these names have all been synonymised. *Boasia chierchiae* generally has a teleoconch completely or partly covered with annulations (Gasca & Janssen, 2013), but the specimens from NW Borneo are all smooth, constituting the forma *constricta* Chen & Bé, 1964.

Distribution. – Small numbers were found in middle shelf mud near Batu Mat, Sarawak and on the Brunei shelf (MES8, 15).

Figure 6. (A-H) Creseidae. (A) *Boasia chierchiae*, S97.25 NE of Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -48 m, leg. R, L 2.3 mm (R T10800). (B) *Creseis acicula*, S97.28 Tukau reef, 26.4 km W of Miri, Sarawak, Malaysia, -20 m, leg. R, L 4.3 mm (R T07460). (C-D) *Creseis conica.* (C) S97.25 NE of Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -48 m, leg. R, L3.6 mm (R T10772). (D) S97.26 Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -20 m, leg. R, L 3.4 mm (R T08334). (E-F) *Creseis virgula*, S97.25 NE of Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -48 m, leg. R, (R T10773). (E) L 3.1 mm. (F) L 1.1 mm. (G-H) *Styliola subula*, Brunei MES22, L 6.5 mm (photographed specimen lost). (I-L) Cuvierinidae, (I) *Cuvierina urceolaris,* S97.26 Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -20 m, leg. R, L 6.1mm (R T08329). (J-L) *Cuvierina urceolaris* (uncertain), larval shell lacking protoconch, S97.18 Dalit beach, Tuaran, Sabah, Malaysia, leg. R, L 2.9 mm (R T07699). (M) Hyalocylidae, *Hyalocylis striata*, Brunei MES24, L 8 mm (specimen unavailable). (N-O) Heliconoididae, *Heliconoides inflatus*, -S18.11 Royal Charlotte atoll, Spratly Islands, 24 m, leg. R, L 1.2 mm (R T08989). (P-S) Limacinidae. (P) *Limacina* spec. A, S18.14a Royal Charlotte atoll, Spratly Islands, -36 m, leg. R, L 1.1, W 0.6 mm (R T10650). (Q-R) *Limacina lesueurii* -Dampier expedition stn DD15, offshore Sarawak, Malaysia, -502-732 m, leg. R, L 0.9, W 1.1 mm (R T10962). (S) *Limacina trochiformis*, S97.26 Batu Mat coral bank, 60 km WSW of Miri, Sarawak, Malaysia, -20 m, leg. R, L 1.6,W 1.4 mm (R T08331).

Genus *Creseis* Rang, 1828

***Creseis acicula* (Rang, 1828)** (Fig. 6B)
Creseis acicula (Rang, 1828) – Rottman 1976: pl. 4 fig. 3
Description. – Very slender, needle-shaped shell (L to 25 mm, W 1.5 mm). Basal part of the larval shell not substantially inflated. Shell translucent and colourless.

Remarks. – Based on their needle-like shape the shells of this species are easily recognised. Often the shells are not perfectly straight, but have slight kinks due to growth irregularities. Rang (1828) described both *Creseis acicula* and *Creseis clava*, which turned out to be synonyms. For some time A.W. Janssen (e.g. 2007: 69-71) considered *Creseis clava* (Rang, 1828) the senior synonym, but consensus is that *Creseis acicula* is the correct name.

Distribution. – One of the most widespread pteropods, both at localities with corals as siliciclastic sediment. Locally very abundant, especially near the coast, as a result of which it is often found beached in large numbers. In Brunei found in middle to outer shelf settings (MES15-29) but also in continental slope planktonic ooze off Sarawak (DD15). It was also abundant in the Sungai Baong temporary outcrop of Holocene sediments in Miri, Sarawak. On the other hand, only few specimens were found around the Royal Charlotte atoll in oceanic setting.

***Creseis conica* Eschscholtz, 1829** (Figs 6C-D)
Creseis virgula conica (Eschscholtz, 1829) – Rottman, 1976: pl. 4 figs 2c,d and other papers by her.
Description. – Slender, but quickly and regularly expanding extended conical shell (L to 6 mm, W 1 mm), apical angle to 11º. Protoconch not substantially inflated. Shell colourless.

Remarks. – In side view similar to *Styliola subula*, but In apertural view the shell is round, whereas that of the latter is boat shaped with round ventral (lower) side and a convex dorsal (upper) side. Similar to *Boasia chierchiae*, but the protoconch is not swollen, and the apical angle is smaller.

Distribution. – A species that is much less abundant than *Creseis acicula*. Not found at localities with siliciclastic sediment, in small numbers at inner shelf coral banks, most abundant at the middle shelf Batu Mat, both on the coral bank and in the shelf mud next to it, and in small numbers at Royal Charlotte atoll in oceanic setting. In Brunei found on mid to outer shelf (MES 15-27).

***Creseis virgula* (Rang, 1828)** (Figs 6E-F)
Description. – Broad conical shell (L to 6 mm, W 2 mm) with marked kink in the final part of the larval shell. Protoconch slightly inflated. Shell translucent and colourless.

Remarks. – The marked kink makes the shells of this species instantly recognisable. The other species in the genus may also be slightly bent, but that is at a modest angle of <10º.

Distribution. – The species has been found in a wide range of settings, from inner shelf to continental slope, but only in small numbers, except for the Tukau coral bank off Sarawak where it is abundant. In Brunei found on inner to outer shelf (MES5, 17, 24, 25, 27).

Genus *Styliola* Gray, 1847

***Styliola subula* (Quoy & Gaimard, 1827)** (Figs 6G-H)
Styliola subula (Quoy & Gaimard, 1827) – Rottman (1976: pl. 5 figs 1a-b)
Description. – Elongated, bullet shaped protoconch narrowing towards the teleoconch, shiny ring hinting at presence of a septum between protoconch and teleoconch. Teleoconch conical, transparent, with marked growth lines (L to 6.5 mm). The upper half expands more rapidly, resulting in concave sides, and is white coloured. In apertural view the shell is initially mostly round, but gradually becomes boat shaped with round ventral (lower) side and a convex dorsal (upper) side. Remarks. – The protoconch and the groove on the dorsal side set this species apart from *Creseis*. The groove is not straight, but slightly twisted. Raven & Alonso (2023) recorded the species from Asturias (Spain) but based on the material from NW Borneo it now realised this concerns juveniles of *Clio pyramidata* as is best seen from the apertural views (their figs 13b, 14b). In apertural view the shell of *Styliola subula* is round with a small indent for the longitudinal groove.

Distribution. – Found in deeper water samples from outer shelf (DD29) to continental slope (DD15) in Sarawak (abundant in the latter), on the shelf in Brunei (MES22) and middle (DD95) to outer (DD92-93) shelf sand in Sabah where it is abundant.

Cuvierinidae Van der Spoel, 1967

Genus *Cuvierina* Boas, 1886

Description. – As adults, all species of this genus have a bottle shaped shell. The juvenile shells are shed once the specimens reach maturity.

***Cuvierina urceolaris* (Mörch, 1850)** (Figs 6I-L)

Cuvierina columnella (Rang, 1827) - Rottman, 1976: pl. 2 figs 3a,b

Description. – Adult shell about 6 mm long, bottle shaped, apex formed by convex septum. Posterior psrt of the shell swollen with widest point at 1/3rd from the apex, constricted towards the aperture which is rather narrow (ventral-dorsal about 1 mm).

Remarks. - Rottman (1976, 1978, 1980) recorded *Cuvierina columnella* (Rang, 1827) from the Gulf of Thailand and South China Sea. However, in the reviews of *Cuvierina* by Janssen (2005: fig. 35) and Burridge *et al.* (2017: fig. 5) only *Cuvierina urceolaris* was recorded from that area. The specimens illustrated by Rottman (1976: pl. 2 figs 2a-2b) clearly represent *C. urceolaris*. *Cuvierina columnella* is substantially larger (about 6 mm long), has almost parallel sides and has a much wider aperture (about 1.3 mm) (based on Burridge *et al.* (2015: fig. 2). Occasionally the juvenile shell remains attached to the adult shell (Rottman, 1976: pl. 2 fig. 3b). The larval shells of this species can be distinguished from *Creseis constricta* by their larger size, straighter sides and greater diameter for a given length (Rottman, 1976). A larval shell (Figs 6J-L) found beached at Tuaran (Sabah) likely belongs to this species – it is laterally slightly flattened and has the characteristic colour, but lacks the protoconch.

Distribution. Only small numbers of this species were found to occur from the Tukau and Batu Mat coral banks, and from outer shelf silty sand (DD29, DD30, DD48) to continental slope planktonic ooze (DD15) in Sarawak, and Brunei middle to outer shelf (MES15, 24, 25), all somewhat further from the coast.

Family Hyalocylidae A.W. Janssen, 2020

***Hyalocylis* Fol, 1875**

***Hyalocylis striata* (Rang, 1828)** (Fig. 6M)

Hyalocylis striata (Rang, 1828) – Rottman, 1976: pl. 4 figs 1a-b

Description. – Conical shell (L to 8 mm), gradually widening towards the aperture in frontal view. In lateral view with parallel sides in final half, but tapering towards the apex, curved dorsally. Entire surface covered by regularly placed rather broad transverse ribs. Aperture with oval shape in fully grown specimens, oval in younger ones. Embryonic shell thrown off in adults, closing membrane formed. Shell translucent and colourless.

Remarks. – This species has very fragile shells which generally will break during processing of sediment samples. Therefore it may be underreported, although the fragments are very characteristic and thus easily identified.

Distribution. – Found in small numbers at Tukau coral bank in Sarawak, in Brunei inner to outer shelf (MES5, 16, 24, 25, 27, 29), outer shelf of Sabah (DD92) and at the Royal Charlotte atoll. Several specimens were found in middle shelf mud at -48 m near Batu Mat in Sarawak. Various specimens were found on the beach at Mukah and between Bako and Buntal, Sarawak, Malaysia (Marzuki, 2021).

Superfamily Limacinoidea Gray, 1840

Family Heliconoididae Rampal, 2019

Genus *Heliconoides* d'Orbigny, 1836

***Heliconoides inflatus* (d'Orbigny, 1835)** (Figs 6N-O)

Limacina inflata (d'Orbigny, 1836) – Rottman 1976: pl. 3 figs 1a-c

Description. – Sinistral shell (W to 2.4 mm), planispiral planorboid, with flat upper side, slightly sunken near apex. Three whorls, inflated with wide umbilicus at base. Last whorl has apertural margin strengthened internally by a subperipheral belt, allowing (in view from below) the outer part to protrude substantially, whereas the growth lines are clearly concave. Translucent.

Remarks. – Two forms can be distinguished (Janssen 2005: 109) with a subperipheral belt starting on earlier whorls, continuing to apertural margin, or a subperipheral belt only present in second half of last adult whorl and whorl from there on more or less swollen. It is unknown if these two morphological forms represent two taxa, as transitional forms also occur. It is possible that the forms have different geographical distributions.

Distribution. – The species occurs in small numbers at Tukau and Batu Mat coral banks, and is abundant in outer shelf silty sand (DD29) to continental slope planktonic ooze (DD15) in Sarawak and at Royal Charlotte atoll. In Brunei is was found in small numbers on the inner shelf (MES5) and larger numbers in middle to outer shelf setting (MES24-29). It is also abundant in outer shelf deposits sand in Sabah (DD92-93). Clearly it prefers an outer shelf to oceanic setting.

Family Limacinidae Gray, 1840

Genus *Limacina* Bosc, 1817
Species within this genus have sinistral shells.

***Limacina lesueurii* (d'Orbigny, 1836)** (Figs 6Q-R)
Description. – Sinistral shell, very low spire (wider than high; L 0.9 mm, W 1.1 mm), about 4 globose whorls, smooth with marked suture. Aperture wide, .columellar part straight Marked but narrow umbilicus. Translucent.

Remarks. –The shell is easily recognised based on its width and very low spire. The shell has a similar shape as juveniles of *L. limacina* (Phipps, 1774), but that species has a shell with wider umbilicus and marked axial riblets.

This species has not been recorded by Rottman (1980), but Rottmann (1976) recorded it from the Gulf of Thailand / South China Sea north of the study area.

Distribution. – This species has only been found in continental slope planktonic ooze offshore Sarawak (DD15). It has not been seen anywhere on the shelf.

***Limacina trochiformis* (d'Orbigny, 1835)** (Fig. 6P)
Limacina trochiformis (d'Orbigny, 1836) – Rottman (1976: pl. 3 fig. 2)
Description. – Sinistral shell, low spire (slightly higher than wide; L 1.6 mm, W 1.4 mm), whorls globose. Aperture wide and round. Marked umbilicus. Translucent, with pale brown at the base of the rostrum.

Remarks. – The sinistral shell that is equally wide as high sets this species apart.

Distribution. – This species has been found on inner and middle shelf coral banks, and in middle shelf mud near the Batu Mat coral bank, everywhere in small numbers. A single specimen was found on the Kuala Belait beach (Brunei). A few specimens were found in outer shelf sands offshore Sabah (DD92-93).

***Limacina* spec. A** (Fig. 6S)
Limacina bulimoides (d'Orbigny, 1836) – Rottman (1976: pl. 3 fig. 3)
Description. – Sinistral shell, high spire (about twice as high as wide; L 1.1 mm, W 0.6 mm), whorls slightly globose. Straight columella, resulting in pointed aperture. No umbilicus. Translucent, with brown suture, columella and rostrum.

Remarks. – The sinistral shell, narrow, with high spire is easily recognised. Also the narrow aperture with pointed base sets it apart from *Limacina trochiformis*.
Thus far this species has been identified as *Limacina bulimoides* (d'Orbigny, 1835). Based on molecular and morphometric analysis Choo *et al*. (2023) found different lineages for *Limacina bulimoides* in the Atlantic, Indo-West Pacific and SE Pacific. As d'Orbigny (1835) based his species on material from the Atlantic and SE Pacific, the taxon from the South China Sea is thus far undescribed.

Distribution. – In the study area the taxon has been found in low numbers at the Batu Mat coral bank, outer shelf sand (DD29) and continental slope planktonic ooze (DD15) off Sarawak, on the Royal Charlotte atoll, Brunei middle to outer shelf (MES24, 25) and Sabah middle (DD95) to outer shelf (DD92-93).

Species richness and geographical distribution patterns

Planktonic gastropods are fundamental components to oceanic pelagic ecosystems. They contribute to our understanding of ecosystem functioning and more recently are used as indicators of oceanic acidification (e.g. Bednaršek *et al.*, 2023). Although regularly sampled during research cruises, their distributions across the economically and ecologically important South China Sea (SCS) are incompletely recorded. The most comprehensive records of pteropods for the North West Bornean (NWB) coast date back decades, and there are no published data for the heteropods (atlantids) of the southern SCS (see Rottman, 1980; Wall-Palmer, 2016). The present study reports the occurrence of 12 species of heteropods and 24 of pteropods along the NWB coast (Table 2). With respect to the heteropods and based on a recent review by Wall-Palmer *et al*. (2016), our records indicate that more than half of the known global extant species occur in NWB. Previously, only *A. brunnea*, *A. gaudichaudi*, *A. lesueurii*, *A. peronii* and *A. turriculata* were known from the northern SCS (northern Vietnam; Wall-Palmer *et al*., 2016). Thus, *A. echinogyra*, *A. helicinoidea*, *A. inflata*, *A. plana*, *A. tokiokai*, *A. vanderspoeli*, *Oxygyrus inflatus* and *Protoatlanta souleyeti* formally represent new species records for

Table 2. Overview of heteropods and pteropods found during the present study. Shaded boxes indicate presence of each species. The darker shaded boxes indicate settings in which species were found to be more abundant. For the siliciclastic environments the arrows indicate increasing water depth; for the carbonate environments (coral banks and reefs) increasing distance from the coast is indicated as the coral build ups are generally well above the surrounding sea floor. Inner shelf, 0-50m; Mid shelf, 50-100m; Outer shelf > 100m; Continental slope > 200m.

Family	Species	Distribution								Setting								
		Holocene	Present-day	A. South Sarawak	B1. North Sarawak	B2. Brunei	C. West Sabah	Spratly*	Beach	Inner shelf siliciclastic	Mid shelf siliciclastic	Outer shelf siliciclastic	Continental slope	Coral reef	Coral bank <50 km	Coral bank >50 km	Oceanic / Atoll
Littorinimorpha - Atlantidae																		
Atlantidae	*Atlanta brunnea* J.E. Gray, 1850																	
Atlantidae	*Atlanta echinogyra* Richter, 1972																	
Atlantidae	*Atlanta gaudichaudi* J.E. Gray, 1850																	
Atlantidae	*Atlanta helicinoides* J.E. Gray, 1850																	
Atlantidae	*Atlanta inflata* J.E. Gray, 1849																	
Atlantidae	*Atlanta peronii* Lesueur, 1817																	
Atlantidae	*Atlanta plana* Richter, 1972																	
Atlantidae	*Atlanta tokiokai* Van der Spoel & Troost, 1972																	
Atlantidae	*Atlanta turriculata d'Orbigny, 1836*																	
Atlantidae	*Atlanta vanderspoeli* Wall-Palmer et al.,2019																	
Atlantidae	*Oxygyrus inflatus* W.H. Benson., 1835																	
Atlantidae	*Protoatlanta souleyeti* (E.A. Smith, 1888)																	
Pteropoda - Cavolinioidea																		
Cavoliniidae	*Cavolinia gibbosa* (d'Orbigny, 1835)																	
Cavoliniidae	*Cavolinia globulosa* (Gray, 1850)																	
Cavoliniidae	*Cavolinia inflexa* (Lesueur, 1852)																	
Cavoliniidae	*Cavolinia uncinata* (d'Orbigny, 1835)																	
Cavoliniidae	*Diacavolinia angulata* (Souleyet, 1852)																	
Cavoliniidae	*Diacavolinia* cf. *longirostris* (Blainville, 1821)																	
Cavoliniidae	*Diacavolinia* spec. A																	
Cavoliniidae	*Diacria major* (Boas, 1886)																	
Cavoliniidae	*Telodiacria costata* (Pfeffer, 1879)																	
Cavoliniidae	*Telodiacria danae* (Van Leyen & Van der Spoel, 1982)																	
Cavoliniidae	*Telodiacria quadridentata* (Blainville, 1822)																	
Cavoliniidae	*Telodiacria* spec. A																	
Cliidae	*Clio pyramidata* Linnaeus, 1767																	
Creseidae	*Boasia chierchiae* (Boas, 1886)																	
Creseidae	*Creseis acicula* (Rang, 1828)																	
Creseidae	*Creseis conica* Eschscholtz, 1829																	
Creseidae	*Creseis virgula* (Rang, 1828)																	
Creseidae	*Styliola subula* (Quoy & Gaimard, 1827)																	
Cuvierinidae	*Cuvierina urceolaris* (Mörch, 1850)																	
Hyalocylidae	*Hyalocylis striata* (Rang, 1828)																	
Pteropoda - Limacinoidea																		
Heliconoididae	*Heliconoides inflatus* (d'Orbigny, 1835)																	
Limacinidae	*Limacina lesueurii* (d'Orbigny, 1836)																	
Limacinidae	*Limacina trochiformis* (d'Orbigny, 1835)																	
Limacinidae	*Limacina* spec. A																	

the SCS. Regionally, all 12 atlantid species collected in this study were previously unknown from southern Vietnam, the Gulf of Thailand and the Sunda Shelf (Wall-Palmer *et al*., 2016).

In comparison with the studies by Rottman (1980), the 24 reported species for NWB are reflected in that document (see note 1). Also, some species were indicated by Rottman (1980) with different names, resulting from new interpretations and a misidentification. However, several species recorded by Rottman (1976, 1980) were not found in our study: *Clio convexa, C. cuspidata, C. recurva*, whereas we uniquely recorded the species: *Cavolinia gibbosa, C. globulosa, C. inflexa, C. uncinata, Diacavolinia strangulata, D.* spec. A, *Diacria major, Telodiacria costata, T. danae, T.* spec. A and *Limacina trochiformis*. Although this may be partly due to different areas sampled and different methodologies used, it suggests that different surveys capture different elements of the biodiversity of an area.

Table 3. Overview of all pteropods reported from the southern part of the South China Sea (Rottman, 1980) or specifically from NW Borneo. Records from the present study are indicated with shading, records from net tows (Rottman, 1980) with a solid dot, records from sediment samples (Rottman, 1980) with open circles. Rottman recorded the species marked with * as (1) *Telodiacria quadridentata* (Blainville, 1821), (2) under 3 names, (3) as *Creseis virgula conica* (Eschscholtz, 1829), (4) as *Cuvierina columnella* (Rang, 1827), (5) as *Limacina inflata* (d'Orbigny, 1836), (6) as *Limacina bulimoides* (d'Orbigny, 1835).

Family	Species	Distribution				
		A. South Sarawak	B1. North Sarawak	B2. Brunei	C. West Sabah	Spratly*
Pteropoda - Cavolinioidea						
Cavoliniidae	*Cavolinia gibbosa* (d'Orbigny, 1835)					
Cavoliniidae	*Cavolinia globulosa* Gray, 1850)					
Cavoliniidae	*Cavolinia inflexa* (Lesueur, 1852)					
Cavoliniidae	*Cavolinia uncinata* (d'Orbigny, 1835)					
Cavoliniidae	*Diacavolinia angulata* (Souleyet, 1852)					
Cavoliniidae	*Diacavolinia* cf. *longirostris* (Blainville, 1821)	●○	○		○	
Cavoliniidae	*Diacavolinia* spec. A					
Cavoliniidae	*Diacria major* (Boas, 1886)					
Cavoliniidae	*Telodiacria costata* (Pfeffer, 1879) *1	●○	●○		●○	
Cavoliniidae	*Telodiacria danae* (Van Leyen & Van der Spoel, 1982)					
Cavoliniidae	*Telodiacria quadridentata* (Blainville, 1822)					
Cavoliniidae	*Telodiacria* spec. A					
Cliidae	*Clio convexa* (Boas, 1886)	●	●		●	
Cliidae	*Clio cuspidata* (Bosc, 1802)				●	
Cliidae	*Clio pyramidata* Linnaeus, 1767				●○	
Creseidae	*Boasia chierchiae* (Boas, 1886) *2	●	●○		●○	
Creseidae	*Creseis acicula* (Rang, 1828)	●○	●○		●○	
Creseidae	*Creseis conica* Eschscholtz, 1829 *3	●○	●○		●○	
Creseidae	*Creseis virgula* (Rang, 1828)	●	●			
Creseidae	*Styliola subula* (Quoy & Gaimard, 1827)		●		●	
Cuvierinidae	*Cuvierina urceolaris* (Mörch, 1850) *4					
Hyalocylidae	*Hyalocylis striata* (Rang, 1828)	●○	●		●	
Pteropoda - Limacinoidea						
Heliconoididae	*Heliconoides inflatus* (d'Orbigny, 1835) *5	○	○		●	
Limacinidae	*Limacina lesueurii* (d'Orbigny, 1836)					
Limacinidae	*Limacina trochiformis* (d'Orbigny, 1835)					
Limacinidae	*Limacina* spec. A *6	●	●		●	

Although many planktonic gastropod species are cosmopolitan and comparative cases with the SCS are rare, the large number of species and several novel records reported here suggest that NWB could represent a region of enhanced faunistic diversity. This would seem likely in terms of its regional placement and contiguity with three oceanic seas. Spalding *et al*. (2007) grouped a large part of NWB with the coastline of Palawan, in the so-called ecoregion 126. Palawan-North Borneo, which implies oceanic and faunistic associations among the southern South China, Sulu and Celebes seas. Along the

coast of Sabah and Brunei, this is represented by a markedly narrow shelf (about 70 km wide) with a relatively steep depth gradient. Based on the study of nearshore molluscs, a real break in fauna more likely occurs further SW, at the position of the Rajang river delta (as first mentioned in Raven & Recourt, 2018 and reflected in Fig. 1). In the south west the Palawan / NW Borneo ecoregion connects with the wide Sunda Shelf (ecoregion 117; Fig. 1) which connects with the Gulf of Thailand and Southern Vietnam (see Spalding *et al.* 2007: ecoregions 115 and 116). The deepest part of the South China Sea, including the Spratly Islands, forms the last ecoregion for this sea (114. South China Sea oceanic islands; Fig. 1) providing an oceanic thoroughfare for planktonic organisms between all ecoregions surrounding it. Prominent current systems along the basin edge (Sunda Shelf) likely facilitate pelagic gastropod dispersal between the northerly ecoregions and NWB.

Because of the isolation of the South China Sea from the global oceans one might expect morphological/species differences. The few specimens found of *Diacavolinia* spec. A (Pl. 2 Fig. 13) and *Telodiacria* spec. A (both having a purple shell) could be undescribed and endemic to the South China Sea, but alternatively could fall within the variability of known species. Further taxonomic studies are needed to redefine the species of *Diacavolinia* (Burridge *et al.*, 2019) and investigate the species recorded in open nomenclature: *Diacavolinia* spec. A, *Telodiacria* spec. A and *Limacina* spec. A.

Sampling vs. depositional environments

Studies of planktonic organisms are based on material from net tows or from sediment samples. Rottman (1980) made a comparison between both methods and found that different collection methods reflected similar distributions, with few exceptions; *Telodiacria "quadridentata"* extended further into shallow water sediments than predicted from net tows. The presence of several oceanic pteropod species in shallow-water sediments south of Singapore (to the west of our study area) suggests their sediment transportation after settling (Rottman, 1980).

Net tows are impacted by seasonal and longer term variations in presence/absence of populations (see seasonal migrations documented by Jivaluk, 1998). Sediments are not impacted by such effects as they accumulate over long periods, but sediment samples are taken over relatively very small surface areas, which increases the likelihood of missing species that occur in a region. Rate of deposition can vary greatly between depositional environments: shallow siliciclastic sediments accumulate rapidly and dilute the presence of planktonic organisms, whereas further offshore these organisms should become more concentrated.

Considering that all the sediment samples studied here were collected from the seabed, they mostly represent present-day (recent) material, at most a few hundred years old. Fresh pteropod shells are generally completely transparent, but in the sediment they quickly become less transparent and have a whitish colour. Some species have coloured parts, such as reddish apertural margins in *Telodiacria*, whilst some *Cavolinia, Diacavolinia*, and *Telodiacria* species have yellowish or purple coloured shells. On the Batu Mat coral bank, 60 km offshore Sarawak, some of the pteropod shells, Atlantidae, and some other molluscs, are filled with solidified sediment. It is possible that limited fossilisation has occurred during the last glacial lowstand, when the coral bank and surrounding shelf were subaerially exposed for longer. That such fossils are still found at the sediment surface suggests sedimentation is slow. These fossils were excluded from the listings.

The shells of planktonic molluscs can occur in very large numbers (hundreds per litre of sediment), but their density varies massively between depositional environments and even within each environment. In Brunei, the samples taken from shelf mud were rich in pteropods and Atlantidae. In Sarawak, most samples were taken from subtidal coral banks, in which the pteropods were generally present in large numbers and identifiable, but the Atlantidae were less numerous, with many having damaged protoconchs, making identification impossible. Therefore, the Atlantidae in Sarawak are underrepresented in this study. An overview of species found and their presence at stations on different parts of the NWB area and depositional environments are summarised in Table 2. Most of the collected species have a wide distributional area. The most abundant and widely distributed species are *Diacavolinia* cf. *longirostris, Telodiacria costata* and *Creseis acicula.*

Small numbers of planktonic molluscs occur in Holocene inner shelf sands - which is explained by the high rate of sedimentation. Present-day *Creseis acicula* and *Diacavolinia* cf. *longirostris* are abundant in current inner shelf environments and as result are the species most frequently found beached. Densities of these shells can be very high along the high tide mark, but this only occurs locally during

special weather conditions: calm weather with onshore wind concentrating floating objects. They then typically occur in fine floating material with small/light gastropods, bivalves and scaphopods. Shells of various other species were found in small numbers: *Telodiacria costata, Hyalocylis striatula* and *Limacina trochiformis* (Table 2). This floating at the water surface may explain the discrepancy noted by Rottman (1980) between specimens of *Telodiacria "quadridentata"* (i.e. *T. costata, T. danae* and *T. quadridentata*) and *Creseis virgula* recovered from net tows to those collected from bottom sediments: these species do not live close to the coast but their shells may reach shallower environments floating at the surface, especially during persisting onshore winds.

Table 4. Comparison of planktonic mollusc shells found in coral sand at Batu Mat coral bank (-20 m, 7 litre sample) and in the shelf mud NE of this bank (-48 m, handful of mud).

Family	Species	Coral bank	Shelf mud
Littorinimorpha - Atlantidae			
Atlantidae	*Atlanta brunnea* J.E. Gray, 1850		
Atlantidae	*Atlanta gaudichaudi* J.E. Gray, 1850		•
Atlantidae	*Atlanta helicinoidea* J.E. Gray, 1850		
Atlantidae	*Atlanta inclinata* J.E. Gray, 1850		
Atlantidae	*Atlanta inflata* J.E. Gray, 1849		○
Atlantidae	*Atlanta lesueurii* J.E. Gray, 1850		
Atlantidae	*Atlanta peronii* Lesueur, 1817		
Atlantidae	*Atlanta plana* Richter, 1972		
Atlantidae	*Atlanta turriculata d'* Orbigny, 1836	•	
Atlantidae	*Oxygyrus inflatus* W.H. Benson., 1835		
Pteropoda - Cavolinioidea			
Cavoliniidae	*Cavolinia gibbosa* (d'Orbigny, 1835)		
Cavoliniidae	*Cavolinia globulosa* Gray, 1850)		
Cavoliniidae	*Cavolinia inflexa* (Lesueur, 1813)		
Cavoliniidae	*Cavolinia uncinata* (d'Orbigny, 1835)		
Cavoliniidae	*Diacavolinia angulata* (Souleyet, 1852)		
Cavoliniidae	*Diacavolinia* cf. *longirostris* (Blainville, 1821)		
Cavoliniidae	*Diacavolinia* spec. (purple)		
Cavoliniidae	*Diacria major* (Boas, 1886)		
Cavoliniidae	*Telodiacria costata* (Pfeffer, 1879)		
Cavoliniidae	*Telodiacria danae* (Van Leyen & Van der Spoel, 1982)		
Cavoliniidae	*Telodiacria quadridentata* (Blainville, 1822)		○
Cliidae	*Clio convexa* (Boas, 1886)		
Cliidae	*Clio cuspidata* (Bosc, 1802)		
Cliidae	*Clio pyramidata* Linnaeus, 1767		
Creseidae	*Boasia chierchiae* (Boas, 1886)		○
Creseidae	*Creseis acicula* (Rang, 1828)		
Creseidae	*Creseis conica* Eschscholtz, 1829	•	•
Creseidae	*Creseis virgula* (Rang, 1828)		○
Creseidae	*Styliola subula* (Quoy & Gaimard, 1827)		
Cuvierinidae	*Cuvierina urceolaris* (Mörch, 1850)		
Hyalocylidae	*Hyalocylis striata* (Rang, 1828)		○
Pteropoda - Limacinoidea			
Heliconoididae	*Heliconoides inflatus* (d'Orbigny, 1835)		
Limacinidae	*Limacina helicina* (Phipps, 1774)		
Limacinidae	*Limacina trochiformis* (d'Orbigny, 1835)	•	•
Limacinidae	*Limacina* spec. A		

○ >3-10
• >10-30
up to 3
>30-100
>100

As expected, there is a marked difference in benthic mollusc species (Table 4) between the middle shelf Batu Mat coral bank (-20 m, coral sand, sample size 7 litres) and the nearby seabed (-48 m, fine mud, sample size a handful collected from the anchor chain) (pers. obs. R). It was expected that planktonic molluscs would be similar at both localities. Logically, the concentration of specimens is much higher in the shelf mud, where sedimentation is very slow, resulting in comparable numbers of the commonest species, despite a large difference in sample size (Table 4). Many of the species of which less than 11 specimens have been found were present at only one of the localities, but generally larger

samples would be needed to know the significance of the species abundance variation. *Boasia cheirchiae* was only found in middle shelf mud near Batu Mat, suggesting this species avoids coral banks. Blatterer (2019: figs 7g-i) illustrated how in the Red Sea numerous *Creseis acicula* are captured and eaten by corals, which may explain this behaviour. Two species with >10-30 specimens occur only at one of the localities: *Atlanta gaudichaudi* in the shelf mud and *A. turriculata* in the coral bank sediment. This could be related to the difference in length of the water column, allowing more vertical migration on the deeper shelf, thus exposing them to different food sources. Also, on the coral bank there is a larger concentration of predators. As mentioned above, besides obvious candidates such as fish and crustaceans that are concentrated around coral banks, the corals themselves prey on planktonic molluscs.

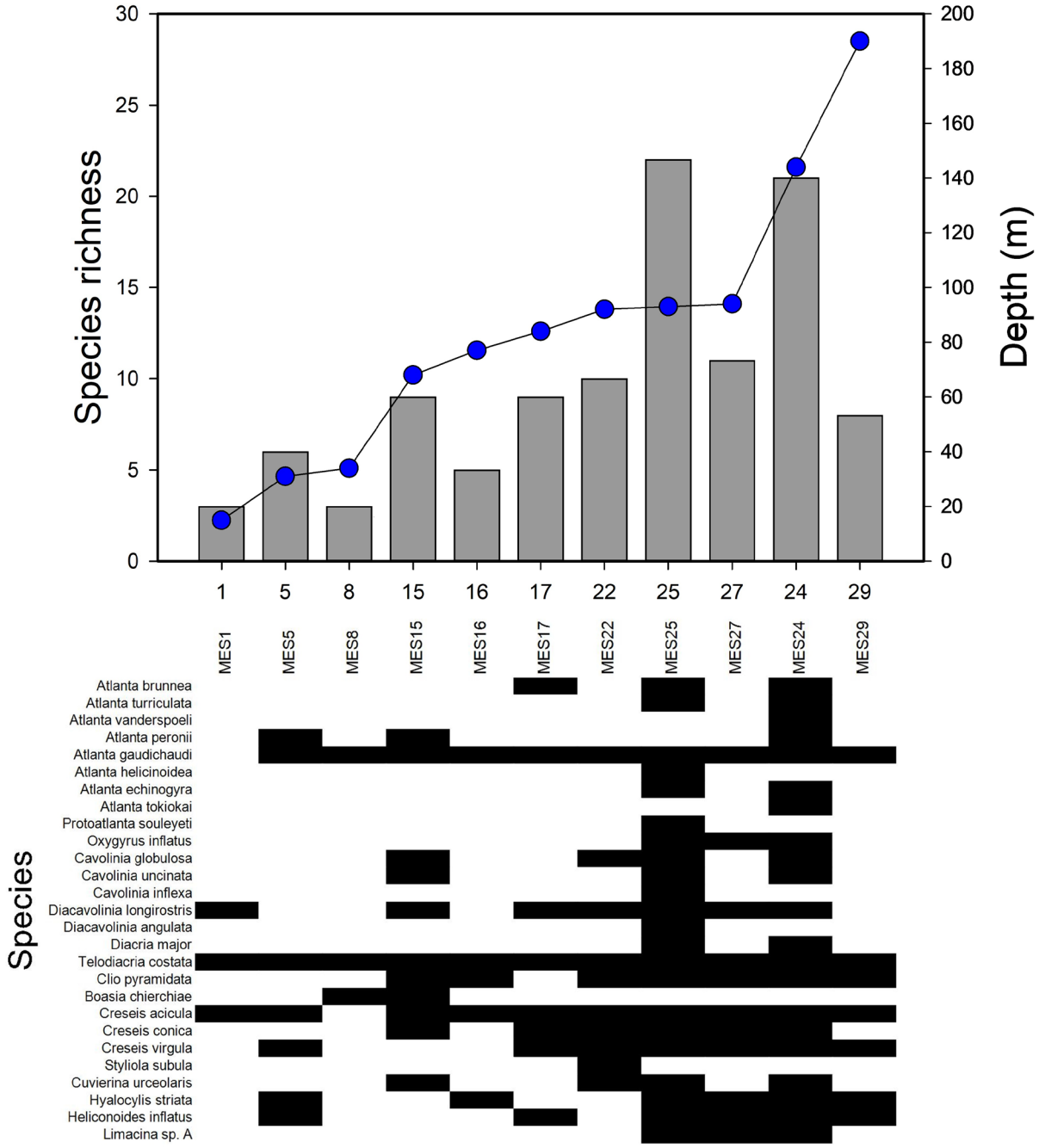

Figure 7. Species richness (bars) and diversity (lower panel) on the Brunei Shelf (MES samples) in relation to depth (blue symbols).

Species-depth relationships

Standardized sampling on the narrow Brunei Shelf along a depth gradient of between 15 and 190 m, allowed determination of faunistic and assemblage patterns of the pelagic gastropods relative to depth (Fig. 7). The Brunei Shelf was found to support 27 species of the total of 35 species recorded for NWB. Species richness was greater in the deeper water, towards the edge of the shelf (84-144 m), but fell markedly at the deepest sample site (MES 29, 190 m; Fig. 7). Specifically, sites MES 24 and 25 were most species rich, respectively containing 21 and 22 species (Fig. 7). Species richness at the relatively shallow sites closer to the shore (MES 1, MES5, and MES 8; depth 15-34 m) varied between 3 and 6 (Fig. 7). Eighteen species occurred exclusively in the deeper water sediments (Fig. 7). All of the heteropod (atlantid) species, except *A. gaudichaudi* and *A. peronii* occurred in the deeper water sediments (Fig. 7; > 80 m). Together with *Creseis acicula* and *Telodiacria costata, A. gaudichaudi* was one of the most common species, occurring at less than ten of the eleven sites (Fig. 7). Sample DD15 (a foraminiferal ooze with numerous heteropods and pteropods present) from the continental slope off Sarawak (502 – 732 m depth, the deepest station in this study) shows a continuation of species richness continues, with 21 species in this small sample. Additionally, the numerous samples from coral rubble at the Royal Charlotte atoll in an oceanic setting shows the relatively high richness of 23 species (Table 2).

Throughout the area the following species are restricted to outer shelf / continental slope: *Atlanta vanderspoeli, Protatlanta souyeleti, Diacavolinia angulata, Limacina lesueurii* and *L. trochiformis.* If middle shelf environments are also included the number of species increases with *Atlanta echinogyra, Oxygyrus inflatus, Cavolinia gibbosa, C. globulosa, Cavolinia inflexa, C. uncinata, Diacria major, Clio pyramidata, Boasia chierchiae, Styliola subula,* and *Limacina* spec. A.

Possibly most heteropods and pteropod species avoid neritic to inner shelf environments as sediment in suspension creates cloudy waters. Many species practice diurnal migration, living near the surface at night to feed and in deeper water during the day (Wall-Palmer *et al.,* 2018). All heteropod species studied by Wall-Palmer *et al*. (2018) depended on aragonite supersaturated water in the upper <150 m of the ocean to produce their shells. In contrast to findings at other localities (Rottman, 1980), we found that the shells of heteropods and pteropods living in deeper water are deposited far offshore, with no indication of currents transport of such shells to the shallower environments. This observation is consistent with that for benthic foraminifera collected from the same MES sites (Goeting *et al.,* 2023). Seabed sediment samples in some cases can be good indicators of the planktonic species in the above water column.

Other observations

Several groups of pteropods (Cavoliniidae, Cliidae) shed their larval shell as they grow (Van der Spoel, 1967; Van der Spoel & Newman, 1990: fig. 6 and table 1). On beaches of the Cantabrian Sea (NW Spain) multiple larval shells of several species were found, but no adult shells (Raven & Alonso Suárez, 2023). On the other hand, in NW Borneo thousands of adult shells were recovered from a variety of depositional environments, but only two (shedded) larval shells of *Diacria* spec. on the beach of Kuala Belait (Brunei) and 35 of *Telodiacria costata*, one *Cavolinia* spec. and one *Clio pyramidata* at the Batu Mat coral bank, 60 km offshore Sarawak, whereas more (shedded) larval shells of *Telodiacria costata*, some *Diacavolinia* spec. and one *Cavolinia* spec. were collected from mid-shelf mud next to the Batu Mat coral bank). Apparently, there is a difference between areas where pteropods hatch and where they live as adults and die.

The relative share of broken shells is much higher than on coral banks on the shelf. Whereas other shells appear to have been broken mainly by crabs, the pteropods must have been broken by other predators, maybe fish. As sample size varied greatly the specimen counts are only indicative of abundance.

On the Batu Mat coral bank, 60 km offshore Sarawak, some of the pteropod shells, Atlantidae, and some other molluscs, are filled with solidified sediment. It is well possible that this fossilisation occurred during the glacial lowstand, when the coral bank and surrounding shelf were subaerially exposed for a long period. That such fossils are still found at the sediment surface suggests sedimentation is slow.

No planktonic molluscs have been in recorded from Miocene shelf mud (Sibuti, Miri, Belait and Seria formations in Sarawak and Brunei), despite extensive sampling (pers. obs. R). Note that collecting depended on visual inspection as from most outcrops the sediment could not be sieved.

Concluding remarks

This study provides an update of the pteropod (Euthecosomata) and heteropod (Atlantidae) diversity of North West Borneo. Previous understanding of this diversity dates back many decades when the taxonomy was also less well resolved. A notable finding was depositional material and seawater depth influenced the assemblage of settled shells. Clear assemblage structuring with depth suggests limited mixing of the benthos spatially across coastal shelves in the region, and that settled shells are likely good indicators of the distributions of living pelagic assemblages. Our findings contribute to the typically poorly known pelagic invertebrate diversity of the Palawan / NW Borneo ecoregion (Spalding *et al*. 2007), which is important in terms of its regional membership within the SCS.

Acknowledgements

The late Arie Janssen (Naturalis) identified many of the specimens in the first author's collection. Deborah Wall-Palmer (Naturalis) checked the identification of most of the Atlantidae. She and Katja Peijnenburg (Naturalis) inspired with their presentations. Laszlo Kocsis (UBD) organised the sampling trip to Royal Charlotte atoll, collected material from coral banks in Brunei and made the Geological Laboratory at UBD available for processing the samples. He and Bernie Landau also helped with the sampling at Royal Charlotte reef. Frank Wesselingh (Naturalis) provided access to the stereomicroscopes at Naturalis (Leiden, The Netherlands) with which many of the photos were made. Simon Troelstra (Vrije Universiteit, Amsterdam) donated samples from the HMS Dampier expedition (1963) which substantially expanded the area and depth range of sediment samples covered in this study. David JW Lane worked with DM to sort and organise the original MES collections. Kiran Shah reviewed the manuscript and made some constructive comments. DM was supported by a Universiti Brunei Darussalam research grant (number UBD/RSCH/1.4/FICBF(b)/2021/033).

Statement
All sampling was performed in accordance with relevant laws and institutional guidelines.

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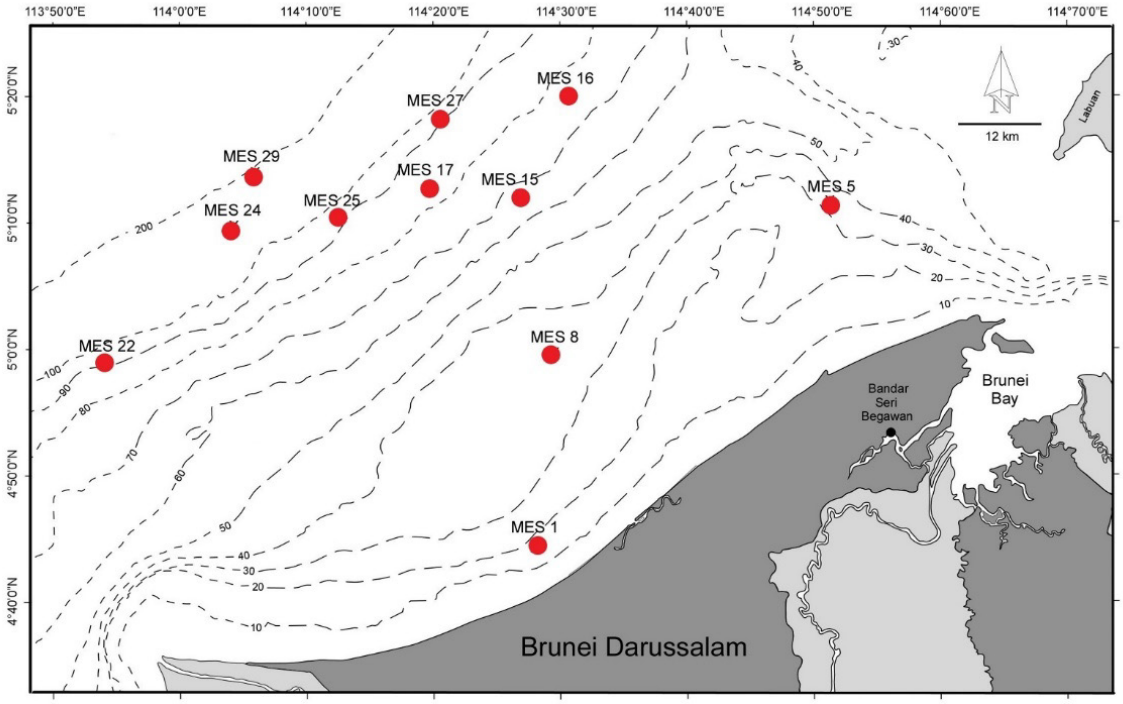
Appendix



Appendix Figure 1. Map showing the collections sites of the MES samples on the Brunei Shelf.