The deep-sea chiton *Nierstraszella* (Mollusca: Polyplacophora: Lepidopleurida) in the Indo-West Pacific: taxonomy, morphology and a bizarre ectosymbiont

Julia D. Sigwart

*Natural History Division, National Museum of Ireland, Dublin, Ireland, and School of Biological Sciences, Queen’s University Belfast, Belfast, UK*

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This study investigated the taxonomy and distribution of the deep-sea polyplacophoran mollusc *Nierstraszella* Sirenko, 1992 in the Indo-West Pacific, based on a collection of 516 specimens collected in the Philippines and Solomon Islands. Although seven species names have historically been proposed in this group of chitons, all have been considered as synonyms of the monotypic *N. lineata* (Nierstrasz, 1905). Morphological examination of this new material reveals the presence of two species. *N. lineata* is distinct from *N. andamanica* (Smith, 1906), based on morphological characters given in the original species description and very distinctly different morphology of aesthete pores in the shell surface. Furthermore, populations of *N. andamanica* in the Philippines and Solomon Islands are locally colonized with the epibiotic (ectoparasitic) bryozoan *Pseudobathyhalozoon profundum* d'Hondt, 2006. These bryozoans attach ventrally to the girdle of the host chiton and the erect zooids feed within the pallial cavity, among the chiton’s gills.

**Keywords:** Lepidopleurida; Nierstraszellidae; deep-sea chitons; epibiont

**Introduction**

Polyplacophoran molluscs (chitons) are known from the intertidal zone to the deep sea. Chitons in the earliest-diverging lineage of living chitons, order Lepidopleurida, are typically small, plain in appearance and found in the deep sea, with the majority of species living below 500 m and many found at abyssal depths to 6000 m (e.g. Saito 2006). Although the majority of lepidopleuran chitons are classified in the large genus *Leptochiton*, several forms with distinctive morphologies have been classified as separate genera or families (Sirenko 2006). The family Nierstraszellidae Sirenko, 1992, erected to contain the monotypic genus *Nierstraszella lineata* (Nierstrasz, 1905), is widely distributed through the tropical Pacific and is endemic to sunken wood. *Nierstraszella* is primarily distinguished from other lepidopleuran chitons by having a thick, proteinaceous periostracum covering its shell valves, which forms large raised pustules (Sirenko 1992). By contrast, most species of *Leptochiton* have shells sculptured with raised granules intrinsic to the shell structure. This distinction of fleshy pustules, rather than solid granules, lends *Nierstraszella* a plastic shell surface morphology which was previously taken as evidence for the unity of a single diverse species, *N. lineata.*
Cryptic species from the deep sea are often distinguished by microscopic features, but can also be separated by aspects of their biology and ecology. Although relatively few parasites or epibionts are known to colonize chitons (Sigwart forthcoming), the evidence reported here includes an epibiotic bryozoan found on three species of chitons.

Ctenostome bryozoans commonly adopt epibiotic lifestyles and are known primarily from modern shallow seas as well as several instances of exceptionally preserved fossils (e.g. Bordeaux and Brett 1990; Todd and Hagdorn 1993; Evans and Todd 1997; Jakobsen et al. 2004). There are no known records of fossil ctenostome bryozoans colonizing molluscs, although they are found on living shallow-water gastropods and bivalves, particularly in the ctenostome genus *Alyconium* (e.g. Ryland and Porter 2006). They were also reported for the shallow-water Mediterranean species *Chiton olivaceus* Spengler, 1797 (Dell’Angelo and Laghi 1980). Epibiotic bryozoans can occur in dense mats, but do not penetrate to feed parasitically on the host tissue and do not appear to have any detrimental effect on the host (e.g. Gordon and Wear 1999).

*Pseudobathyvalozoon profundum* d’Hondt, 2006 is the first bryozoan reported to infest a deep-sea chiton. The mode of life is also unusual, as the bryozoan lives on the ventral girdle surface and zooids feed in the pallial cavity of the chiton. This same mode of epibiosis was reported by Helpman (1968) in the common shallow-water chiton *Lepidozona mertensii* (Middendorff, 1847) in the Eastern Pacific. The deep-sea *Pseudobathyvalozoon* animal was discovered by the author (J.D.S.) in 2006 and described as a new genus and species by d’Hondt (2006) from material from the Philippines. More bryozoan material has subsequently been found colonizing specimens from the Solomon Islands and is reported herein. Ctenostome bryozoans living on the ventral side of the chiton girdle, as in *Pseudobathyvalozoon* here and *Farella elongata* (van Beneden, 1845) as reported in Helpman (1968), are presumed to grow by extending their stolons between the ventral girdle scales of the host and budding new zooids in a chain (Helpman 1969; d’Hondt 2006). Other epibiotic bryozoans are known in four other ctenostome genera; however, other ctenostome species are typically known from shallow waters. The depth of the infested chitons (200–1775 m) makes this by far the deepest bryozoan with a similar lifestyle and morphology (d’Hondt, personal communication, 2006).

A large dataset based on the “Panglao 2005” and “Salomon 2” expedition collections provides new insights into the distribution of *Nierstraszella* and their bryozoan associates. This material provided an opportunity to observe all growth stages of the host chitons, providing insights into the distribution of the bryozoan as well as the effects on the growth of the host animals.

**Material and methods**

The material used in the present study is drawn from three separate collecting expeditions led by the Museum National d’Histoire Naturelle (MNHN, Paris), on the R/V *Alis*. Most specimens were collected by the expeditions “Panglao 2005” (Philippines, May 2005), and “Salomon 2” (Solomon Islands, October–November 2004). A small amount of additional material was also examined from the “Salomon 1” expedition (Solomon Islands, September–October 2001). The expeditions “Salomon 1” and “Salomon 2” were named for the French spelling of the Solomon Islands (îles Salomon). The French spelling is used here for station numbers to maintain consistency with museum specimen records, although the English spelling of the geographic region is used to describe the distribution and locality data.
All specimens were initially preserved in ethanol (typically 90–100%) and permanently stored in 70% ethanol. A small number of specimens were accidentally or deliberately dehydrated and preserved as shell specimens with the complete body intact. As all specimens were collected as part of bulk samples and preserved en masse in the field, they are frequently tightly curled and have sometimes suffered some minor post-mortem abrasion from overcrowding in the sample jars. Because animal length is difficult to measure accurately in specimens that are tightly curled, width is used as a proxy for chiton size.

In the course of this research, all chiton specimens were examined, sorted and identified by the author through comparison with original species descriptions and name-bearing type material held in the MNHN (Paris), as well as types and additional historical comparative material in the Museum für Naturkunde of the Humboldt-Universität Berlin (ZMB), The Natural History Museum, London (BMNH), Zoological Museum, Amsterdam (ITZ), Royal Belgian Institute of Natural Sciences (RBINS), and in the former private collection of Piet Kaas, National Museum of Natural History, Naturalis, Leiden (RMNH).

All specimens of *N. andamanica* from Panglao 2005 were examined for the presence or absence of epibiotic bryozoans. Further to that, all specimens of *N. andamanica* and *N. lineata* from the Solomon Islands (“Salomon 2”, “Salomon 1” partim) were additionally measured for gross dimensions (width, elevation and length where possible) to the nearest 0.1 mm and examined for the presence of epibiotic bryozoans. For statistical analysis, all chitons were divided into five size classes each of one standard deviation in range.

For examination of aesthete arrangement, valve II was removed from specimens and each valve was cut in half along the dorsal midline. One half of each valve was soaked in bleach (5% aqueous solution of sodium hypochlorite, NaOCl) to remove tissue from the surface and aesthete channels, gently brushed with a fine synthetic paintbrush to dislodge tissue material from surface, then rinsed in ethanol (80%) to remove hypochlorite, and air dried. The other (untreated) half of the valve was dehydrated in a graded ethanol series (70%, 80%, 95%) then air dried. Radulae were dissected and briefly soaked in bleach to remove muscle tissue and radular sheath, rinsed in ethanol, then air dried. Girdle elements were removed with a section of muscle tissue from the right side of the animal under valve II, the tissue block was briefly soaked in bleach (30 seconds) to dissolve tissue, then the tissue block was moved to ethanol (80%) and the spicular epithelium was manually removed in a single piece (including dorsal and ventral spicules). All prepared anatomical elements were transferred to scanning electron microscope (SEM) stubs with self-adhesive carbon stickers. Examinations were conducted using a JEOL JSM 6480 SEM (Naturalis) at 7–15 kV.

**Results**

**Class** POLYPLACOPHORA Gray, 1821  
**Order** LEPIDOPLEURIDA Thiele, 1909  
**Family** NIERSTRASZELLIDAE Sirenko, 1992  
**Genus** Nierstraszella Sirenko, 1992

*Type species*  
*Lepidopleurus lineatus* Nierstrasz, 1905 by original designation (Sirenko 1992, p. 84).
Diagnosis
Animal of medium size, up to 27 mm long, elongate oval, rather elevated (dorsal elevation 0.40 on valve II), subcarinate, side slopes convex. Head valve semicircular, posterior margin widely V-shaped. Valves smooth, not sculptured, valve surface rough, but covered with thick periostracum which may form raised pustules. Tail valve with central mucro, not prominent. Outer appearance of valves (periostracum) golden yellow to orange, sometimes covered in black mineral deposit. Girdle variable, covered in small, blunt to club-shaped spicules. Gills variable in size, up to 20 per side. Radula major lateral teeth tricuspid in juvenile specimens and bicuspid in adults.

Remarks
The genus *Nierstraszella* (the sole genus in the family Nierstraszellidae) has a distinctive thick periostracum layer, which in *N. lineata* grows into complex patterns of raised pustules (Figure 1). The radula of *Nierstraszella* varies ontogenetically, the major lateral tooth is tricuspid in juvenile specimens and bicuspid in older (larger) individuals (Sirenko 1992). The girdle is dorsally and ventrally covered in short, blunt spicules and dorsally with scattered longer spines.

There are seven taxon names proposed for species in *Nierstraszella*, placed either in *Leptochiton* Gray, 1847 or historically as *Lepidopleurus* Risso, 1826. Sirenko (1992) considered all of these to be junior synonyms of *N. lineata*. He proposed that

![Figure 1. Two species of Nierstraszella; N. andamanica comb. nov., nom. rev. (top) and N. lineata (bottom). Note the raised texture created by periostracum pustules on N. lineata, and the abraded patches (white) where periostracum as rubbed away on N. andamanica. Scale bar applies to both images. Specimens are from the Solomon Islands, “Salomon 2” sta. CP2264 (N. andamanica) and sta. CP2226 (N. lineata).](image-url)
all conchological variation reported in these taxa was the result of plasticity in the overlying thick periostracum, which grows into quite complex zigzag patterns of raised pustules on *N. lineata*. Removing the periostracum layer with bleach or KOH, reveals the aesthete openings, which Sirenko (1992) argued were identical in all involved taxa. The radular morphology also presents little difference between proposed taxa.

Sirenko (1992) further proposed that Nierstraszellidae represented a phylogenetically intermediate group between Lepidopleurida and Chitonida. This was before his work on Ferreiraeellidae (another group restricted to sunken wood; Sirenko 1997).

*Nierstraszella lineata* (Nierstrasz, 1905)

Chresonymy and synonymy revised from Saito (1997), Sirenko (1992) and Schwabe et al. (2008).

*Lepidopleurus lineatus* Nierstrasz, 1905, p. 8, figures 4, 48–51; Nierstrasz 1906, p. 146, 157; Ferreira 1979, p. 163, figures 23, 24; Dell’Angelo and Palazzi 1989, p. 80; Higo et al. 1999, p. 23.

*Lepidopleurus niasicus* Thiele, 1906, p. 13, pl. 29, figures 1–5 (Lectotype in ZMB Moll 59912a [designated by Schwabe et al. 2008], two paralectotypes ZMB Moll 59912b, type locality: Indonesia, northwest off Nias Island, 01°47.1’ N 96°58.7’ E, Valdivia St. 203, 660 m); Kilias 1995, p. 166.


*Lepidopleurus diomedeae* [sic]: Taki 1938, p. 412; Sirenko 1973, p. 59 (English version).

*Lepidopleurus (Deshaysiella) diomedeae*: Taki and Taki 1929, p. 162; Taki 1961, p. 3; Taki 1962, p. 32.

*Lepidopleurus (Deshaysiella) [sic] diomedeae*: Itoigawa et al. 1977, p. 57; Ogasawara 2003, p. 277.


*Lepidopleurus belknapioides* Leloup, 1981, p. 317, figure 1, pl. 1, figure 1–3 (holotype MNHN 5862, one paratype RBINS, type locality: Philippines, 13°46.9’ N 120°29.5’ E, Campagne MUSORSTOM 1: stn CP44, 592–610 m); Kaas and Van Belle 1985, p. 113; Kaas and Van Belle 1998, p. 29; Sliker 2000, p. 139.

*Nierstraszella lineata*: Sirenko 1992, p. 84, figures 3–7, 8A–D, 9; Saito 1997, p. 46, pl. 2, figure 2; Sirenko 1998, p. 1; Sirenko 2001, p. 61, figures 196–197; Sirenko 2004, p. 112; Saito 2001, p. 9, pl. 4, figure 18; Saito 2004, p. 84, figure 2B; Saito 2005, p. 104; Schwabe 2005, p. 52, pl. 1, figure 1; Saito 2006, p. 210, 220; Schwabe 2006a, p. 108; Schwabe 2006b, p. 20. (Where figures are not provided these records are assumed to refer to *N. lineata* s.s.)

*Leptochiton diomedeae* [sic]: Higo et al. 1999, p. 23.
Leptochiton diomedeae: Slieker 2000, p. 96, pl. 36, figure 1.

Type material
Lectotype (ITZ Moll. 3.05.011) designated by Ferreira (1979, p. 163).

Type locality
Savu Sea, “Siboga” sta. 297, 10°39' S 123°40' E, 520 m.

Material examined
Lepidopleurus lineatus lectotype (ITZ); Lepidopleurus belknapioides holotype (MNHN 5862); L. belknapioides paratype (RBINS); Lepidopleurus diomedeae holotype pro parte RMNH MOL.K.4897; RMNH MOL.HLS.1746; RMNH MOL.HLS.2010; RMNH MOL.K.4967; for new expedition material from the West Pacific please see Appendix 1.

Diagnosis
As for genus. Valves covered in thick periostracum in raised pustules forming zigzag lines. Megalaesthetes surrounded by many irregularly distributed micraesthetes forming a lattice-like pattern over the whole valves. Girdle covered in small club-shaped spicules. Gills increasing in number with the size of the animal, from six in juvenile specimens (1.2–1.4 mm wide) to 12–18 per side in adult specimens.

Description
The morphology of this species has been thoroughly and accurately described, particularly by Kaas and Van Belle (1985) and Sirenko (1992).

Distribution
Widely distributed in the Western Pacific, in Japan, Philippines, Solomon Islands, Indonesia, Vanuatu; 200–1750 m (e.g. Sirenko, 1992, 2001; Saito 2005; Schwabe et al. 2008). Material studied here represents the deepest record for the species (“Panglao 2005” sta. CP2353, CP2356). Locally abundant species and common on sunken wood.

Remarks
Kaas and Van Belle (1985, p. 113) correctly included L. belknapioides in synonymy with L. lineatus. The descriptions provided for Lepidopleurus lineatus (Kaas and Van Belle 1985, p. 113–114, figure 49; Sirenko 1992), Lepidopleurus diomedeae (Kaas and Van Belle 1985, p. 101–103, figure 44), Lepidopleurus niasicus (Kaas and Van Belle 1985, p. 116–118, figure 51) are all applicable to Nierstrazella lineata. Conchological features in this species are plastic and show a range of morphologies as noted by Sirenko (1992). The figures included in earlier descriptive works, as well as all others included in the chresonymy above are clearly illustrations of N. lineata. The species is easily identifiable from the distinctive raised periostracum which creates pustules
arranged in diagonal or zig-zag arrangement. Published SEM images of valve surfaces in Sirenko (1992) and Saito (2001) show the clusters of raised pustules as well as distinctive aesthete arrangement in this species (Figures 2,3). The differences that separate *Lepidopleurus diomedeae*, *Lepidopleurus niasicus* and *L. belknapiodes* in earlier descriptions are minor and are thoroughly discussed in Sirenko’s revision of the genus (Sirenko 1992).

*Nierstraszella andamanica* (Smith, 1906) comb. nov., nom. rev.

Chresonymy and synonymy revised from Saito (1997), Sirenko (1992), and Schwabe et al. (2008).

*Lepidopleurus andamanicus* Smith, 1906, p. 251 [lectotype BMNH 1906.10.12.86 (designated by Kaas and Van Belle 1985: 118), three paralectotypes BMNH 1906.10.12.87–89, paralectotype pro parte (girdle preparation) RMNH MOL.K.5024; type locality: India, Andaman Island off North Sentinel Island (11°33’ N 92°15’ E), 240 fathoms (439 m)]; Annandale and Stewart 1909, figures 4, 4a; Winckworth, 1940, p. 19; Rajagopal and Subba Rao 1974, p. 400; Schwabe 2006b, p. 20.

*Lepidopleurus porosus* Leloup, 1981, p. 322, figures 5–6, pl. 2, figures 4–6 (holotype MNHN 6012, type locality: Philippines, 13°40.7’ N 120°30’ E, Campagne

![Figure 2. Scanning electron micrograph of aesthete cluster morphology in Nierstraszella, where valve periostracum has been removed by bleach; *N. andamanica* comb. nov., nom. rev. (top) and *N. lineata* (bottom). Specimens of *N. lineata* are from Solomon Islands, “Salomon 2” sta. CP2226 (top left) and from Japan (identified as *Leptochiton diomedeae*), RMNH MOL.HLS.2010 (top right). Specimens of *N. andamanica* are from Solomon Islands, “Salomon 2” sta. CP2264 (bottom left) and sta. CP2280 (bottom right).]
Figure 3. *Nierstraszella lineata*. (A) Valves I, II and VIII (with periostracum intact), white lines indicate original shape of apophyses broken on specimen during preparation, scale bar is 1 mm, specimen RMNH MOL.K.4966 (Philippines, 13°03′ S 122°37′ E, 1030–1190 m); (B) close up of texture on valve I shown in (A); (C) close up of texture on valve II shown in (A); (D) dorsal girdle

*Lepidopleurus philippinus* Leloup, 1981, p. 322, figure 4, pl. 2, figures 1–3 (holotype MNHN 5981, paratypes MNHN 5979, 5980, 5988, type locality: Philippines, 13°50.5’ N 120°28’ E, Campagne MUSORSTOM 1: stn CP43, 448–484 m); Sirenko 1992, p. 84.


*Nierstraszella lineata* e.p.: Sirenko 1992, p. 84.


**Type material**

BMNH 1906.10.12.86 (lectotype, designated by Kaas and Van Belle 1985); 1906.10.12.87-89 (three paralectotypes); RMNH MOL.K.5024 (paralectotype *pro parte*, girdle preparation).

**Type locality**

Bay of Bengal, off North Sentinel Island, Andaman Islands group, 432 m.

**Material examined**

*Lepidopleurus andamanicus* lectotype BMNH 1906.10.12.86; *L. andamanicus* paralectotypes BMNH 1906.10.12.87-89; *L. andamanicus* paralectotype *pro parte* RMNH MOL.K.5024; *Lepidopleurus philippinus* holotype (MNHN 5981) and paratypes (MNHN); *Lepidopleurus niasicus* holotype (ZMB); *Lepidopleurus porosus* holotype (MNHN 6012); RMNH MOL.HLS.1748; RMNH MOL.K.4966; for new expedition material from the West Pacific please see Appendix 1.

**Diagnosis**

As for genus. Periostracum without pustules, sometimes abraded on older area of valve. Aesthete caps visible or abraded, forming impression of regularly spaced pores. Each megalaesthete with two rows of micraesthetes, six or seven each side. Girdle covered in small blunt-pointed spicules. Gills increasing in number with the size of the animal, eight per side in juvenile specimens (1.7 mm wide) to 15–20 per side in adults.

**Description**

Animal up to 27 × 13 mm long (“Salomon 2” CP2228). Valves carinated, moderately elevated (dorsal elevation ratio approx. 0.5 on valve II), valves distinctly beaked.
Head valve semicircular, slightly narrower than tail valve. Intermediate valves rectangular, lateral areas distinct but little inflated, and not depressed near apices. Anterior margin slightly convex, and posterior margin concave around projecting apex, side margins straight.

Tegmentum smooth, without sculpture, covered in thick periostracum. Aesthete caps clearly visible, protruding from aesthete openings. Aesthete pores arranged quincunxually, sometimes giving an appearance of sculpture. Periostracum sometimes abraded; where thin, aesthete openings are visible as pores or slightly discoloured points. Colour of tegmentum white, older parts of valves (near apex) covered with black mineral deposits, sometimes extending to cover dorsal surface of entire animal.

Aesthete pores arranged in quincunx, with one megalaeasthete with micraesthetes in rows on either side, approximately six per side. Megalaesthete 5 μm in diameter.

Articulamentum well developed; apophyses short and broad, widely separated, bluntly triangular in valves II–VII, round to trapezoidal in tail valve. Articulamentum forming flat thickened ridge along outer margins of end valves.

Girdle narrow, dorsally densely covered in elongate, bluntly pointed spicules (120 × 16 μm), with approximately five ribs covering entire length of spicule. Intersegmental areas with larger scales. Marginal fringe absent. Ventrally, girdle covered with elongate, flat, narrow scales with approximately five ribs as in dorsal scales (64 × 16 μm).

Radula major lateral teeth with bicuspid head; interior denticle shortest. In juvenile specimens, major lateral teeth are tricuspid (juvenile specimen examined 2.3 mm wide, approximately 4.1 mm long; smallest adult specimen with bicuspid major lateral cusps 6.5 mm wide, approximately 11.7 mm long).

In smallest juvenile specimens, there are eight gills per side (animal width 1.7 mm, eight gills, “Salomon 2” CP2263). Number of gills increases with size of animal, up to 20 per side (animal width 10.4 mm, “Salomon 2” CP2219), usually 16 gills per side in animals of width 5 mm or more.

Distribution
Widely distributed in the South Pacific, in the Philippines, Andaman Islands, Indonesia, Solomon Islands, and Vanuatu; from 177 to 1760 m.

Remarks
The name Lepidopleurus andamanicus Smith, 1906 has been selected as the earliest available name for this species. Lepidopleurus porosus Leloup, 1981 and Lepidopleurus philippinus Leloup, 1981 are junior synonyms, and have previously been recognized as having strong affinities with L. andamanicus. Kaas and Van Belle (1985, p. 128) noted that “L. philippinus bears a close resemblance with L. andamanicus (Smith). In fact the two are so similar that we first were apt to believe them to be conspecific.” In their redescription of Lepidopleurus philippinus Kaas and Van Belle (1985, p. 128) also noted “The unique type of L. porosus…is in all respects identical with philippinus.”

Examination of the morphology, and particularly of the aesthetes of the present material, shows that there are in fact two distinct species of Nierstraszella, which correspond to Lepidopleurus lineatus and L. andamanicus (Figures 1, 4). Before this
study few specimens of *L. andamanicus* had been collected, whereas *L. lineatus* is locally abundant in many sites throughout the Indo-West Pacific (e.g. Saito 2001). Previous descriptions of “Nierstraszella” sp. therefore correspond to accurate reports of *L. lineatus*.

*Lepidopleurus andamanicus* does not have raised pustules and the aesthetes are arranged in discrete groups with a single megalaeathete, approximately 5μm wide, surrounded by approximately 12 microaesthetes arranged in two rows, on either side of the central megalaeathete. *Lepidopleurus lineatus*, by contrast, has a distinctive pattern of randomly dispersed, very large megalaeathetes (approximately 10μm wide), with scattered microaesthetes over the whole valve surface underneath large pustules (Figures 2, 3F). During the course of this study it was not possible to examine name-bearing type material by SEM imaging, which would be required to see the pattern of aesthete arrangement in the two species. However, *L. andamanicus* is distinguished by several macroscopic features which clearly separate this species from *L. lineatus* and which have been compared on the type specimens examined.

*Nierstraszella andamanica* can be distinguished by its valves having higher elevation, more pronounced apex, and lacking the large raised pustules distinctive of *L. lineatus*. The periostracum in *L. andamanicus* usually does not form “sculpture” but in some cases where the periostracum is very thin small pustules are formed over aesthete caps, arranged in widespread quincunx (Figure 4A); the periostracum and any appearance of sculpture always rub off easily with scraping (Figure 4F). The shape of valve VIII is closer to semicircular in *L. andamanicus*, and the mucro is slightly anterior; in *L. lineatus* the tail valve appears larger and the mucro is medial. The girdle typically appears narrower in *L. andamanicus* and quite wide in *L. lineatus*.

**Epibiotic bryozoans**

The bryozoan *Pseudobathyalozoon profundum* colonizes the ventral girdle of the chitons, with the zooids invading the pallial cavity of the host (Figure 5). *Pseudobathyalozoon* preferentially colonizes *N. andamanica* and is less frequently found associated with the congener *N. lineata*. In material from the Philippines, *N. andamanica* was the only host organism colonized with the bryozoan. However, in the Solomon Islands, the bryozoan has been found on a small number of specimens of *N. lineata* (three specimens in two stations; “Salomon 2” CP2280, CP2273) and on one specimen of the chiton *Ferreiraella plana* (Nierstrasz, 1905) (“Salomon 2” CP2289). In two stations (CP2280, CP2289), the bryozoan *Pseudobathyalozoon* was found on these additional host species where *N. andamanica* was abundant and the majority of chiton specimens collected in a sample were colonized; in the third station (CP2273) the single specimen of *N. lineata* was one of three individual chitons collected.

In total, 307 specimens of *N. andamanica* were examined from the Philippines and Solomon Islands. Of those, 35% (n=107) hosted epibiotic bryozoans. However, colonization was not present in all collecting stations, and was limited to localized areas in both the Philippines (Figure 6) and the Solomon Islands (Figure 7). In the Solomon Islands, areas where the epibiotic bryozoan is present show that 84% of specimens of *N. andamanica* are colonized; in the Philippines, however, only 59% of chitons in colonized areas carry the bryozoans (Table 1).
Figure 4. *Nierstraszella andamanica* comb. nov., nom. rev. (A) Valves I, II, and VIII (with periostracum intact), white lines indicate original shape of apophyses broken on specimen during preparation, scale bar is 1 mm, specimen RMNH MOL.HLS.2010 (Japan, Suruga Bay); (B) close up of texture on valve I shown in (A); (C) close up of texture on valve II shown
In the Solomon Islands, animals ranged from 0.5 to 12.9 mm in width, with the smallest individual colonized at 2.3 mm wide. Within collecting stations where the colonizing bryozoan was present, the largest individual in the station was always colonized, with the rate of colonization increasing in larger size classes (Table 2). For specimens of *N. andamanica* collected in these stations where *Pseudobathyalozoon* was present, there was a significant relationship between size of host and the presence of *Pseudobathyalozoon* zooids ($\chi^2 = 31.9; \text{df}=4; p<0.001$). The largest individual chitons overall occurred in stations where there was no colonization, but the difference in size was not great (12.9 mm wide, compared with 11.9 mm for colonized chitons; both approximately 23 mm long).

The two populations of the epibiotic bryozoan have very different depth profiles and occur much deeper in the Philippines than in the Solomon Islands (Table 1).

The bryozoans are attached all along the pallial cavity, on the ventral side of the girdle. Although quantitative data are not available for the distribution of the bryozoans on the host chitons, a number of points are readily apparent. Most

in (A); (D) dorsal girdle armature, specimen from Solomon Islands, “Salomon 2” sta. CP2243; (E) ventral girdle armature, specimen from “Salomon 2” sta. CP2243; (F) intermediate valve dorsal surface showing aesthete caps on individual aesthete clusters, specimen from “Salomon 2” sta. CP2226; (G) ventral view of preserved animal, anterior at left, specimen from “Salomon 2” sta. CP2243; (H) radula, showing half of central area of radular row, specimen RMNH MOL.HLS.2010. (A–F) Anterior is at top; (B–F,H) scale bars 100\,\mu m.
bryozoan specimens were attached at the posterior half of the host, invading the space occupied by the host’s gills (Figure 5). A number were also found around the host’s head. Relatively few bryozoans attached along the intermediate part of the host body, along the anterior half of the foot, although bryozoans were occasionally present at all points on the pallial cavity. Bryozoans always attach basally to the ventral girdle and never to the pallial groove. There is no apparent preference for left or right side of the host overall, although bryozoans on an individual host may be either restricted to a small area or distributed along the entire length of the pallial groove.

Table 1. Number and depth coverage of collecting stations that recovered specimens of Nierstraszella andamanica over the total collecting effort in the Solomon Islands and the Philippines, and colonization rate in the subset of stations where the epibiotic bryozoan Pseudobathyloozoon was present. The total number of specimens examined is indicated, with the number colonized in parentheses.

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<td><strong>Solomon Islands</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without bryozoans</td>
<td>21</td>
<td>127</td>
<td>362–1060 m</td>
</tr>
<tr>
<td>Colonization</td>
<td>5</td>
<td>95 (80)</td>
<td>195–627 m</td>
</tr>
<tr>
<td><strong>Philippines</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without bryozoans</td>
<td>6</td>
<td>12</td>
<td>255–1260 m</td>
</tr>
<tr>
<td>Colonization</td>
<td>7</td>
<td>73 (27)</td>
<td>569–1775 m</td>
</tr>
</tbody>
</table>

Figure 6. Distribution of Nierstraszella andamanica comb. nov., nom. rev. (grey dots) and N. lineata (black circles) in the Philippines, collected by the Panglao 2005 expedition. Grey dots with black outlines indicate co-occurrence of the two species. Pie charts for each collecting station indicate the fraction (in black) of N. andamanica specimens colonized with the epibiotic bryozoan Pseudobathyloozoon. Inset shows the map area relative to the island of New Guinea and surrounding islands.
Discussion

Both species of *Nierstraszella* are abundant and widespread, and, as noted by Sirenko (1992), they are morphologically diverse. The valve elevation, extent of the posterior apex on intermediate valves, and body size are all variable. In some specimens of *N. andamanica*, the periostracum is very thin or appears to be absent.

Table 2. Colonisation of *Nierstraszella andamanica* with the epibiotic bryozoan *Pseudobathyolozoon* in cruise samples from the Solomon Islands (“Salomon 2”) where the bryozoan was present.

<table>
<thead>
<tr>
<th>Size range (mm width)</th>
<th>0.0–3.9</th>
<th>4.0–5.9</th>
<th>6.0–7.9</th>
<th>8.0–9.9</th>
<th>10.0–11.9</th>
<th>Total recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of specimens</td>
<td>7</td>
<td>6</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td>without bryozoans</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number with epibionts</td>
<td>3</td>
<td>18</td>
<td>17</td>
<td>27</td>
<td>15</td>
<td>80</td>
</tr>
<tr>
<td>% colonized</td>
<td>30%</td>
<td>75%</td>
<td>89%</td>
<td>100%</td>
<td>100%</td>
<td>84%</td>
</tr>
</tbody>
</table>
This particularly led to historical confusion about the differences in “sculpture” that were used to diagnose *N. philippina* and *N. porosa*, which are both junior synonyms of *N. andamanica*. Comparison of the type specimens of these three shows that there is no substantial difference to separate the two; the only morphological difference is more prominent growth lines on the valves of *N. philippina*. As noted above, *N. andamanica* is the first name to be assigned to this species, and therefore has priority.

The two species of *Nierstraszella* are the most abundant chiton species collected in the three expeditions considered here (Table 3; Sigwart 2008). *Nierstraszella lineata* is the single most abundant species overall, but *N. andamanica* is also extremely abundant, and is more numerous in the Solomon Islands (“Salomon 2”) than its congener. Differentiating these two species is clearly important to understanding the ecology and biology of the chiton fauna found with sunken wood.

Although the two species are superficially similar in their morphology, there are clear biological differences between them. Although the function of aesthetes is poorly understood, they are clearly sensory organs (e.g. Reindl et al. 1997). Structural differences in sensory systems (even in acephalic animals such as chitons, which lack cephalized sensory systems) are usually correlated with profound differences in biology and lifestyle. It is difficult to imagine the adaptive significance of aesthete pore size and arrangement, particularly in animals that have such a conserved mode of life as deep-sea chitons.

Further to the morphological differences between these co-occurring and closely related chitons, biological differences also underpin the preference of the epibiotic bryozoan *Pseudobathyalozoon* for *N. andamanica* as its host.

The position of the bryozoans indicates that they are feeding on particulate material in the respiratory currents of the host chiton. All chitons inhale under the anterior end of the girdle, generating a water current that passes over the pallial cavity on both sides and then exits under the girdle at the posterior.

Because the zooids of *Pseudobathyalozoon* occupy the area within the pallial cavity of the host chiton, it could potentially be considered to be an endosymbiont. Although the gills are external in chitons, they create an effectively interior enclosed space in the ventral pallial cavity. However, the attachment of the bryozoan is on the girdle, and the stolon is assumed to be embedded between the scales covering the girdle epithelium, and not penetrating into the flesh of the girdle. The attachment is therefore entirely external, and *Pseudobathyalozoon* can be considered ectosymbiotic.

Table 3. Number of specimens recovered in the three expeditions examined in this study, in the Philippines (Panglao 2005) and Solomon Islands (“Salomon 1” and “Salomon 2”). The two species of *Nierstraszella* are the most abundant chiton species collected, exceeding the number of specimens collected in all other species of chitons combined (data from Sigwart 2008). The number of species recovered includes all chitons (*Nierstraszella* spp. and other genera).

<table>
<thead>
<tr>
<th></th>
<th>Philippines</th>
<th>Solomon Islands</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>N. andamanica</em></td>
<td>85</td>
<td>200</td>
</tr>
<tr>
<td><em>N. lineata</em></td>
<td>128</td>
<td>103</td>
</tr>
<tr>
<td>Other species</td>
<td>102</td>
<td>228</td>
</tr>
<tr>
<td>Number of species recovered</td>
<td>9</td>
<td>18</td>
</tr>
</tbody>
</table>
Pseudobathyalozen is only known from preserved specimens in ethanol (not fixed in formalin), therefore some aspects of the morphology have not been observed, particularly the tentacular region and digestive morphology of the zooids. The bryozoans occur in what appear to be relatively restricted areas (Figures 6, 7), and future material collected from these regions should be preserved in fixatives that will allow for proper anatomical examination. d’Hondt (2006) noted that there were possible associations with four ctenostome families: Mimosellidae, Farrellellidae, Bathyalozoontidae and Triticellidae. The epibiotic lifestyle is most closely aligned with the shallow-water Triticellidae; however, triticellids grow zooids in small clusters at intervals on the connecting stolon (unlike the individual and sparsely connected zooids in Pseudobathyalozen). The bryozoan Farella elongata (Farellidae) has been found living in a similar epibiotic mode on the ventral girdle of Lepidozona mertensis (Helpman 1968; Dell’Angelo and Laghi 1980). Helpman (1968) was apparently able to observe the Farella/Lepidozona association in living animals and confirmed that the zooids feed by extending their tentacular region into the chiton’s pallial cavity. The inferred morphology of the zooid growth on the connecting stolon is most similar to Bathyalozoontidae, but this may be subject to further revision when the morphology is studied in more detail.

In decapod crustaceans, epibiotic bryozoans settle in several events during the life of the host, and may time reproductive activity to coincide with moulting or social behaviour of the host (Gordon and Wear 1999). Epibionts and other fauna that are limited to specific substrates may have high rates of growth and reproduction, to take advantage of what suitable substrate becomes available (Jackson 1977). It is not known whether the colonization of Pseudobathyalozen represents a single colony of bryozoans in a long string of zooids around the pedal margin of the girdle, or multiple unrelated colony-individuals that have settled on the same chiton. However, as larger individuals are more frequently colonized, it appears that the chitons accumulate bryozoans throughout their life and that an individual chiton hosts multiple colonies of Pseudobathyalozen.

Triticella capsularis Gordon and Wear, 1999 has a clear settlement preference for the ventral anterior area of the host crab, to take advantage of “messy and voracious feeding” (Gordon and Wear 1999). In that association, the bryozoan can form dense and visually obvious mats of growth on the crab carapace; however, there is no apparent detrimental effect on the host species (Gordon and Wear 1999).

Whether or not the Pseudobathyalozen is negatively affecting the host chitons is unclear. The colonization of the pallial cavity could hinder effective respiration across the gills. However, bryozoan zooids may also not be in direct competition with the gills because they are utilizing different resources in the respiratory current (edible particulates for bryozoans, oxygenated water for gill membranes). If bryozoans clean the current of particulates they may even prevent fouling of the gills, to the advantage of the chiton. Without measurable evidence of negative or positive impact of the bryozoan on the host chiton, a neutral symbiosis or commensalism is the most parsimonious assumption.

Bryozoan epibionts on N. andamanica are presumed to take advantage of particulate nutrients within the pallial cavity. A minority of bryozoans observed here have zooids around the host’s head, where they could feed on particulates disturbed by chiton grazing. The majority must find it more advantageous to feed on
particulates carried to the posterior with the respiratory current, as well as nitrogenous waste and potentially particulates from faecal material.

The two nierstraszellid species, *N. andamanica* and *N. lineata*, are morphologically distinct. These species show a range of morphological variation, particularly in the external form of raised pustules formed by the periostracum on the shell valves, which has previously confounded taxonomists. Both are abundant and co-occur in the Indo-West Pacific over a broad distribution and at a wide range of depths. The preference demonstrated by the epibiotic bryozoan *Pseudobathyalozoon* for one species hints at significant biological differences between these two sympatric congeners.

Acknowledgements

I thank Philippe Bouchet (MNHN) who organized the expeditions that produced the material described here. B. Sirenko and two anonymous reviewers provided helpful and constructive comments that improved this manuscript. Funding support for this work was provided by the European Commission SYNTHESYS programme (awards FR-TAF-1157, NL-TAF-437, NL-TAF-5088, DE-TAF-407 and GB-TAF-436). R. Moolenbeek (ITZ), J. Goud (RMNH), M. Glaubrecht (ZMB), K. Way (BMNH) and V. Héros (MNHN) kindly provided access to collections. J. Goud (RMNH) and P. Maestrati (MNHN) also provided assistance with SEM imaging.

References


Sirenko BI. 1998. One more deep-water chiton living and feeding on sunken wood: Leptochiton vietnamensis sp. nov. from the South China Sea (Mollusca, Polyplacophora). Ruthenica. 8:1–6.
Appendix 1

Station list for specimens of *Nierstraszella* spp., including material from three separate collecting expeditions led by the Museum National d'Histoire Naturelle (MNHN, Paris): Panglao 2005 (Philippines, May 2005), Salomon 2 (Solomon Islands, October–November 2004) and Salomon 1 (Solomon Islands, September–October 2001). This refers only to collection of species in the genus *Nierstraszella*, although other polyplacophoran species occurred at most stations (see Sigwart 2008).

<table>
<thead>
<tr>
<th>Nierstraszella andamanica</th>
<th>Nierstraszella lineata</th>
<th>both species co-occurring</th>
</tr>
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<tbody>
<tr>
<td>“Panglao 2005”</td>
<td>“Panglao 2005”</td>
<td>“Panglao 2005”</td>
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<tr>
<td>sta. CP2335, 9.57° N 123.63° E, 729–733 m</td>
<td>sta. CP2331, 9.65° N 123.79° E, 255–268 m</td>
<td>sta. CP2336, 9.54° N 123.65° E, 757–760 m</td>
</tr>
<tr>
<td>sta. CP2352, 9.46° N 124.05° E, 923–1260 m</td>
<td>sta. CP2333, 9.64° N 123.72° E, 584–596 m</td>
<td>sta. CP2353, 9.43° N 124.03° E, 1750–1767 m</td>
</tr>
<tr>
<td>sta. CP2354, 9.43° N 124.1° E, 1769–1773 m</td>
<td>sta. CP2340, 9.49° N 123.74° E, 271–318 m</td>
<td>sta. CP2356, 9.35° N 124.14° E, 1764 m</td>
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<td>sta. CP2355, 9.41° N 124.17° E, 1764–1775 m</td>
<td>sta. CP2343, 9.46° N 123.82° E, 273–356 m</td>
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<td>sta. CP2357, 9.34° N 124.05° E, 1760–1762 m</td>
<td>sta. CP2359, 8.83° N 123.58° E, 437–476 m</td>
<td>sta. CP2372, 8.64° N 123.26° E, 255–301 m</td>
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<td>sta. CP2388, 9.45° N 123.57° E, 762–786 m</td>
<td>sta. CP2360, 8.82° N 123.62° E, 357–372 m</td>
<td>sta. CP2383, 8.75° N 123.3° E, 338–351 m</td>
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<td>sta. CP2385, 8.85° N 123.16° E, 982–989 m</td>
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<td>sta. CP2373, 8.7° N 123.22° E, 165–237 m</td>
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<tr>
<td>CP1804</td>
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<td>S 157.64</td>
</tr>
</tbody>
</table>

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**Salomon 1**

sta. CP2195, 8.96 S 159.12 E, 1001–1012 m.

sta. CP2211, 7.80 S 157.71 E, 313–387 m.

sta. CP2186, 7.65 S 156.98 E, 495–540 m.

sta. CP2218, 7.49 S 157.57 E, 802–864 m.

sta. CP2273, 8.53 S 157.72 E, 720–739 m.

sta. CP2221, 8.63 S 157.74 E, 408–470 m.

sta. CP2227, 8.62 S 156.21 E, 508–520 m.

sta. CP2228, 8.61 S 156.23 E, 504–522 m.

sta. CP2230, 8.61 S 156.25 E, 403–480 m.

sta. CP2231, 8.63 S 156.27 E, 659–677 m.

sta. CP2232, 8.64 S 156.30 E, 402–480 m.

sta. CP2234, 8.40 S 156.33 E, 320–342 m.

sta. CP2195, 8.40 S 156.35 E, 308–337 m.

sta. CP2196, 8.37 S 156.36 E, 200–208 m.