

***Pedicularia vanderlandi* spec. nov., a symbiotic snail (Caenogastropoda: Ovulidae) on the hydrocoral *Distichopora vervoorti* Cairns & Hoeksema, 1998 (Hydrozoa: Stylasteridae), from Bali, Indonesia**

J. Goud & B.W. Hoeksema

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Jeroen Goud & Bert W. Hoeksema, National Museum of Natural History, P.O. Box 9517, 2300 RA Leiden, The Netherlands.

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A new species of ovulid gastropod is described from Bali as *Pedicularia vanderlandi* spec. nov. It was predominantly found in shallow water on the stylasterid hydrocoral *Distichopora vervoorti* Cairns & Hoeksema, 1998. The snails are compared with type specimens of congeneric taxa and with material of *Pedicularia pacifica* Pease, 1865, which was found in shallow water on an unidentified *Stylaster*. Various notes on Indo Pacific *Pedicularia* species are given in an annotated, preliminary check-list. Finally, the host relationships of *Pedicularia* are discussed in general.

Introduction

When the type material of *Distichopora vervoorti* Cairns & Hoeksema, 1998 (Hydrozoa: Stylasteridae) was collected at Nusa Lembongan off Bali, several small violet snails, tentatively classified as *Pedicularia* spec. (Caenogastropoda: Ovulidae), were discovered, living attached to the coral branches. The animals occurred on a shallow reef slope (15-35 m deep) in strong currents of cold, up-welled water. No *Pedicularia* spec. associated with *Distichopora* spec. had been reported before from such an aberrant Indo-Pacific reef environment. Because the gastropod shells are unlike those of geographically close *Pedicularia* species (Schilder, 1931; Neubert, 1998), we could not identify these molluscs. Therefore, we decided to study type material of the Indo-Pacific *Pedicularia* species most likely resembling our specimens. In a comparative study, we included many specimens of a *Pedicularia* from an unidentified, shallow water *Stylaster* spec. (Hydrozoa: Stylasteridae) from Lembeh Strait, North Sulawesi, Indonesia and from the type locality of *Distichopora vervoorti*.

Material and methods

Apart from a few collection samples and type specimens, most of the studied material was collected during fieldwork off Bali, Indonesia. The material was collected by scuba diving down to 35 meters in an area with upwelling and strong currents. The fragile *Stylaster* spec., host of *Pedicularia pacifica*, was collected by hand by bringing the whole colony in a plastic bag and then loosening it from the substrate. Specimens

mens of the much stronger attached *Distichopora* species, hosts of *Pedicularia vanderlandi* spec. nov., had to be loosened before transferring them into a plastic bag. In this way many of the mobile male specimens may have been lost. In total 154 specimens (88 females and 66 males) of *P. pacifica* and 231 specimens (166 females and 65 males) of *P. vanderlandi* were collected. Also a few dozen of juveniles of both species were collected, which were morphologically distinct from the adults. The sizes of these juveniles were not used for comparison between the two species, whereas the measurements of the females resp. the males were statistically used for comparing the species morphology. Measurements were carried out by a gauged measuring ocular on a microscope.

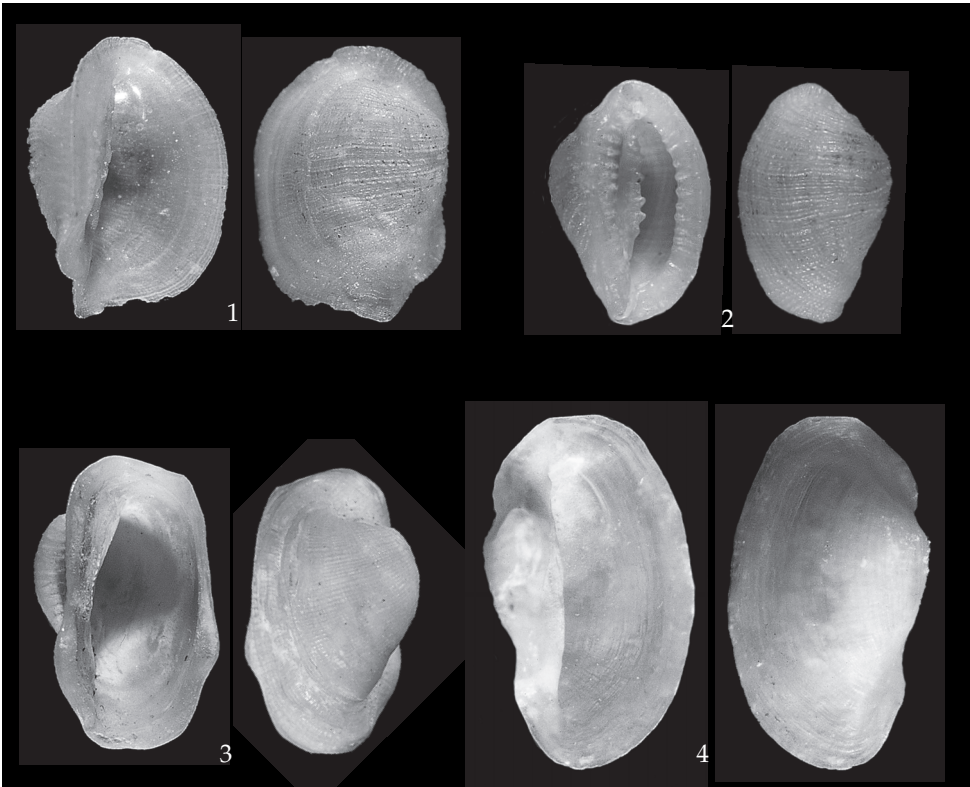
Type specimens of all Indo Pacific nominal taxa, except for *Pedicularia elegantissima*, were studied. This material was received in loan from the following institutes (with abbreviations used in the text): Australian Museum, Sydney (AMS); Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ), Paleontological Research Institute, Ithaca, New York (PRI) and Zoologisches Museum, Berlin (ZMB). Other institutes mentioned are: The Natural History Museum, London (BMNH), Nationaal Natuurhistorisch Museum, Leiden (RMNH) and National Museum of Natural History, Smithsonian Institution, Washington (USNM). Most of these type specimens proved to be in a rather poor condition. Apart from that, since they are either male or female, the sexual dimorphism makes comparisons difficult.

Taxonomy

According to Schilder (1931: 165-166) there are at least two genera in the Pediculariinae: "*Pediculariella* has a radula very similar to living Cypraediinae, while in *Pedicularia* there is a small accessory third lateral plait, which has never been observed in any other group of Cypraeacea. If Macdonald's drawing of the radula of *Pedicularia stylasteris* is correct, a third recent genus should be erected for the Indopacific species, in which the first lateral plait is not flabellate, but simply cusp-like as it is in Eratoidea (= Triviidae)"

The differentiation between *Pediculariella* and *Pedicularia* can additionally be based, rather vaguely, on very few shell characters. In *Pediculariella* the columella is distinctly excavate and its inner margin is carinate, whereas the columellar sulcus is obsolete or nearly so in *Pedicularia*.

Schilder (1931: 1965-169) revised the subfamily Pediculariinae and listed ten living species, four of these assigned to *Pediculariella* and six to *Pedicularia*. Later on, Schilder & Schilder (1971) placed only *Pedicularia californica* Newcomb, 1864, the type species, in *Pediculariella*, whereas the three other species were listed as *Pedicularia*. In recent literature *P. californica* is usually placed in *Pedicularia* (Schmieder, 1980: 382; Schmieder, 1982: 272; Liltved, 1987: 13; Lindahl, 1991: 79; Catarius, 1991: 83). Schilder also changed his opinion about the differentiation within *Pedicularia* and *Pediculariella*. The status of several taxa that were originally described as species was lowered to subspecies level and one nominal taxon is considered a synonym. All this resulted in only six species in *Pedicularia* s.s.: *P. sicula* Swainson, 1840, (with subspecies *decurvata* Locard, 1897) from the NE. Atlantic Ocean; *P. elegantissima* Deshayes, 1863, from the SW. Indian Ocean; *P. pacifica* Pease, 1865, (with subspecies *stylasteris* Hedley, 1903



Figs 1-4. Type specimens of *Pedicularia* species. 1, *Pedicularia pacifica* Pease, 1865, 3.8 × 2.75 mm, paralectotype MCZ 297958; 2, *Dentiora rubida* Pease, 1862, 3.4 × 2.2 mm, holotype MCZ 297951; 3, *Pedicularia stylasteris* Hedley, 1903, 6.5 × 3.8 mm, holotype AMS C.016265; 4, *Pedicularia subtilis* Schilder, 1931, 3.7 × 2.4 mm, lectotype ZMB 484.

and *maoria* Powell, 1937) from the Pacific Ocean and the Philippines; *P. japonica* Dall, 1871, from Japan; *P. decussata* (Gould, 1855) from the W. Atlantic and *P. dautzenbergi* Schilder, 1931, from Sulawesi. *P. maoria* Powell, 1937, was synonymized by Powell (1979: 116) with *P. pacifica* and according to Habe (1978: 98) *P. japonica* Dall, 1871, is a synonym of *P. pacifica*. Most recently a new species has been described from the Red Sea, viz. *P. granulata* Neubert, 1998.

Results

A detailed study of the taxonomy of *Pedicularia* is complicated, if not impossible, if only shell characters are considered. First of all, *Pedicularia* species are of separate sexes, showing conspicuous sexual dimorphism. Females are twice as large as males and have a widely open aperture, which matches in shape the spot on the branches of the hydrocorals on which they live and were the hydrocoral forms a so-called scar. Males have an ovulid-like shell (called *Trivia*-stage by Bouchet & Warén, 1993: 752) (fig. 17) and are much more mobile than the females. Bouchet & Warén (1993: 752) suppose that *Pedicularia sicula* is a protandric hermaphrodite: 'Some specimens would

then change sex and become females.' However, in populations of two other species, viz. *Pedicularia pacifica* and *Pedicularia vanderlandi* spec. nov., we found juveniles, males and females but no individuals with intermediate characters. In case of a change in sex one would expect at least some shells, halfway the resorption process, with at least part of the male characters, such as the heavy dentition on the columella and the aperture, still visible. All larger individuals are females, but without any remains or scars indicative of an earlier male stage. On the other hand, Schmieder (1980: 383, fig. 2) reported and illustrated intermediate forms between *Pedicularia ovuliformis* (with dentition and 'ovulid' characters) and *Pedicularia californica*, which lead him to the conclusion that these two forms are representatives of the same species. The former form could represent the male snails then and the latter form the female ones, with intermediate forms indicative of a change in sex. Without any data on the anatomy of these forms, we cannot accept this interpretation of the so-called intermediate specimens, which might also be considered extreme specimens of one of the forms. Liltved (1989: 35, fig.18) reported the presence of a short, vestigial penis among fully developed female structures in *Pedicularia elegantissima* from deep water off the eastern Cape Province of South Africa. Nevertheless, in our view, there are still no really convincing arguments against the hypothesis that in *Pedicularia* the separate sexes develop independently.

As soon as additional material of more populations of other *Pedicularia* taxa becomes available, a more thorough study of the anatomy and a molecular analysis of some DNA markers can possibly aid substantially in resolving the taxonomy and phylogeny of this group. For the time being we have to restrict ourselves to the description of a new species of *Pedicularia*, summarising data on the congeneric nominal taxa and their type specimens in an annotated check-list.

The Indo-West Pacific species

Gastropoda Cuvier, 1797

Caenogastropoda Cox, 1959

Cypraeoidea Rafinesque, 1815

Ovulidae Fleming, 1822

Pediculariinae H. & A. Adams, 1854

Pedicularia Swainson, 1840

Pedicularia Swainson, 1840: 242, 244, 357, fig. 44. Type species (by monotypy): *Pedicularia sicula* Swainson, 1840; type locality: Sicily, Italy.

Thyreus Philippi, 1844: 92. Type species (by monotypy): *Thyreus paradoxus* Philippi, 1844; type locality: Sicily, Italy.

?*Dentiora* Pease, 1862: 240. Type species (by monotypy): *Dentiora rubida* Pease, 1862; type locality: 'Sandwich Islands' [Hawaiian Islands]

Pediculariona Iredale, 1935: 101. Type species (by monotypy): *Pedicularia stylasteris* Hedley, 1903; type locality: off Wollongong, New South Wales, Australia.

Notes.— The type species, *Pedicularia sicula* Swainson, has been reviewed first by Settepassi (1977), mainly based on the literature and more recently, based on a fair

amount of specimens, by Bouchet & Warén (1993). According to the latter authors, all nominal taxa described from the north-eastern Atlantic Ocean fall within the range of variation of *Pedicularia sicula*. They refrain from synonymising the western Atlantic nominal species *Pedicularia decussata* with the European species mainly because of sculptural differences in the teleoconches.

Although no type material is known of *Thyreus paradoxus*, Settepassi (1977) synonymised this name with *Pedicularia sicula*. The description and the figure published by Philippi (1844: 92, pl. 18 fig. 1) clearly represent *Pedicularia sicula*.

The holotype of *Dentiora rubida* (Pease, 1862: 240; type locality: 'Sandwich Islands' [= Hawaii]; in MCZ, reg. no. 297951) here figured (fig. 2) is a male stage specimen of a *Pedicularia* species. Its sculpture and color, shows much resemblance with the paralectotype of *Pedicularia pacifica* (Pease, 1865: 516, 'Islands of Central Pacific', type in MCZ reg. no. 297958) which is a not fully grown specimen of the female stage (fig. 1). The different sex stages of these two types and the worn condition of the type of *D. rubida* make it impossible for us to conclude that *Pedicularia pacifica* and *D. rubida* are conspecific.

Iredale created the genus *Pediculariona* for *Pedicularia stylasteris* Hedley, which is regarded nowadays as a synonym of *Pedicularia pacifica*.

Pedicularia pacifica Pease, 1865

Pedicularia sp. MacDonald, 1856: 241, pl. 42, figs 7, 8 (New South Wales, Elizabeth Reef, Kingsmill and Marshall Islands)

?*Dentiora rubida* Pease, 1862: 240; type locality: 'Sandwich Islands' [= Hawaii]; holotype in MCZ, reg. no. 297951.

Pedicularia pacifica Pease, 1865: 516, 'Islands of Central Pacific', paralectotype in MCZ reg. no. 297958.

Pedicularia pacifica; Pease, 1868: 96, pl. 11, figs 17, 18; type locality: 'Insl. Apaian' [Apaian Island = Charlotte Isl.; = part of Gilbert Islands, Micronesia].

Pedicularia japonica Dall, 1871: 121, pl. 16 fig. 12; type locality: 'Nippon, Japan, 60 fms on *Gorogonia*, R. Pumpelly'. The type specimen (located at the USNM) has been figured by Habe (1978: 98, figs 1, 2.) He wrote: 'This is an extremely large specimen of *Pedicularia pacifica* Pease which rather commonly attaches to stylasterid corals of 20 to 100 m deep in the Japanese waters.'

Pedicularia stylasteris Hedley, 1903: 342, figs 69, 70; type locality: 'Sta. 44, off Wollongong, depth 55-66 fathoms, New South Wales, Australia, on *Stylaster sanguineus* Val. [= *incompletus* Tenison-Woods], holotype in AMS reg. no. C.016265.

Pediculariella pacifica (Pease, 1865); Thiele, 1925: 88.

Pediculariella pacifica (Pease, 1865); Schilder, 1931: 167; pl. vi, fig. 1 (Savage Island, New Caledonia, Marshall Islands).

Pedicularia pacifica; Dautzenberg & Bouge, 1933: 265 (Tuafutu [= Tuamotus]).

Pedicularia stylasteris; Schilder, 1933: 296, 301, figs 11, 12 (Bismarck Archipelago).

Pediculariona stylasteris; Iredale, 1935: 101.

Pedicularia pacifica; Viader, 1937: 36 (Mauritius).

Pedicularia maoria Powell, 1937: 162, 208, pl. LIV, figs 13, 14; type locality: 'Sta. 933, off Three Kings Islands, 260 m' [New Zealand], holotype in Auckland Museum.

Pedicularia pacifica; Schilder, 1945: 29-31 (Gilbert Islands).

Pedicularia pacifica; Habe, 1964: 63, pl. 19, fig. 1 (Sagami Bay, Honshû to Kyûshû).

Pedicularia pacifica; Kay, 1965: 84, pl. 14, figs 13, 14, lectotype designated: BMNH reg. no. 1964321 (female stage).

Pedicularia pacifica; Cernohorsky, 1968: 366, fig. 4 (Fiji).

Pedicularia (Pediculariona) pacifica; Kuroda, Habe & Oyama, 1971: 157, 103, pl. 108, figs 24, 25 (Sagami Bay, Japan).

Pedicularia pacifica; Cernohorsky, 1971: 116.

Pedicularia pacifica; Powell, 1979: 152, pl. 32, fig. 5.

Material studied.— Paralectotype (female) of *Pedicularia pacifica* Pease, Apaiian(g) Island [Gilbert Islands], MCZ: no. 297958, Ex. Pease coll. Holotype (female) of *Pedicularia stylasteris* Hedley, AMS: no. C.016265, 7-8 mile off Wollongong, 34°26'S 151°05'E, 100-102 m, 18.iii.1898, on *Stylaster spec.*; Japan, Wakayama Pref., Nada, 10-30 fms, ex. coll Hemmen on *Stylaster spec.*, 4 females; Tethyana Expedition to the Togian Islands, Sta. 3, Indonesia, NE Sulawesi, Bitung, Selat Lembeh, 18 m, B.W. Hoeksema, c., 16.ix.1999, 3 males, 3 females, 5 juveniles on *Stylaster spec.*; Bali-Lombok Strait Expedition, 2001, Sta. 22, Indonesia, Bali, SE-end Tulamben beach, 08°16'40''S 115°35'45''E, reef flat with drop-off and slope, sandy base, 30 m, J. Goud, c., 14.iv.2001, 6 males, 5 females, 1 juvenile on *Stylaster spec.*; Bali-Lombok Strait Expedition, 2001, Sta. 26, Indonesia, Bali, N side Nusa Penida, off Desa Ped, 08°40'28''S 115°30'50''E, deep reef slope with dense coral cover and patches of sand, 25 m, J. Goud c., 17, 19.iv.2001, 26 males, 29 females, 11 juveniles on *Stylaster spec.*; Bali-Lombok Strait Expedition, 2001, Sta. 27, Indonesia, Bali, NE side of Nusa Lembongan, Tanjung Jangka, 08°39'46''S 115°28'06''E, deep reef slope, rocky with patches of sand, strong currents, 18 m, B.W. Hoeksema c., 18.iv.2001, 26 males, 44 females, 13 juveniles on *Stylaster spec.*; Bali-Lombok Strait Expedition, 2001, Sta. 30, Indonesia, Bali, N side of Nusa Lembongan, Tanjung Taal, 08°39'33''S 115°26'37''E, well developed reef slope with overhanging ridges, rocky, strong currents, to 28 m depth, B.W. Hoeksema c., 19.iv.2001, 2 males, 7 females on *Stylaster spec.*

Notes.— After its original description, this species has never been properly figured or described. The lectotype (female stage) was designated and figured by Kay (1965: 84). We have studied a paralectotype (fig. 1), the holotype of *Dentiora rubida* (fig. 2) and the holotype of *Pedicularia stylasteris* (fig. 3). The paralectotype of *Pedicularia pacifica* is a rather flat and broad shell. The surface of the outside shows a pattern of alternating, finer and rougher, nodulous spiral cords, similar to the pattern on the holotype of *Dentiora rubida*, which represents a male stage; both have a reddish colour. The inside of the paralectotype of *Pedicularia pacifica* has a rather deep groove along the columella. The overall shape of this shell (flat and broad) as well as the columellar groove could very well be the result of adaptation to the shape of the branches of its stylasterid host. It is unclear whether the structure of the shell surface is diagnostic since Bouchet & Warén (1993: 746-752) illustrated much variation in this character in large numbers of shells of *Pedicularia sicula*. The holotype of *Pedicularia stylasteris* is almost twice as big and much more globular than the paralectotype of *Pedicularia pacifica*. It is a shell of a much more mature (full-grown) stage. Its colour is white-yellowish with some very light pink.

In the samples of the Bali-Lombok Strait Expedition, which could be studied provisionally, all males are smaller than the females. Females are recognisable as such as soon as the outer margin is undulate; most of the specimens have already a brood-pouch with embryos at that stage. Male specimens have an inflected outer lip with many lirate denticles, large teeth on the inner ridge of the columella and smaller denticles on the outer ridge of the columella. Two specimens collected from North Sulawesi (near Bitung) are figured here for comparison (figs 7, 8 & 10). Shells of males of *Pedicularia pacifica* are slightly smaller and more slender and have a straighter columella than those of the males of *P. vanderlandi* spec. nov. The shells of females of *P. pacifica* are considerably smaller and more elongate than those of *P. vanderlandi*, and

have an undulated outer margin. The number of spiral riblets on the middle of the back is ca. 12 per mm. All shells are whitish to pink, with only a darker protoconch. All specimens were collected alive on *Stylaster* spec.

Measurements, extremes with average size.— Shell height in females (N = 88), 2.95-4.0-5.0 mm; shell width 1.8-2.3-3.0 mm; mean H/W, 1.71. Shell height in males (N = 66), 2.0-2.7-3.40 mm; shell width 1.3-1.7-2.1 mm; mean H/W, 1.56. (table 1).

Pedicularia vanderlandi spec. nov.

Type material.— holotype RMNH 82354: female specimen 6.1 × 3.9 mm (H × B), paratypes RMNH 82355: 138 female, 48 male and 18 juvenile specimens: Bali-Lombok Strait Expedition, 2001, Sta. 30, Indonesia, Bali, N side of Nusa Lembongan, Tanjung Taal (= Tanjung Ental = 'Blue Corner'); 08°39'33''S 115°26'37''E; well developed reef slope with overhanging ridges, rocky, strong currents; scuba-diving to 35 m depth; J. Goud & B.W. Hoeksema, c.; 24-29.v.1998 and 19, 21.iv.2001; on the hydrocoral *Distichopora vervoorti* Cairns & Hoeksema, 1998.

Additional material.— Bali-Lombok Strait Expedition, 2001, Sta. 02, Indonesia, Bali, Sanur, off Kesumasari Beach, Palung Semawang, N of tidal channel; 08°42'35''S 115°16'13''E; slowly declining reef slope, sandy base; scuba-diving to 19 m depth; B.W. Hoeksema, c.; 31.iii.2001; 3 females, 2 males, 2 juveniles on the hydrocoral *Distichopora violacea* Lamarck (Pallas, 1766).

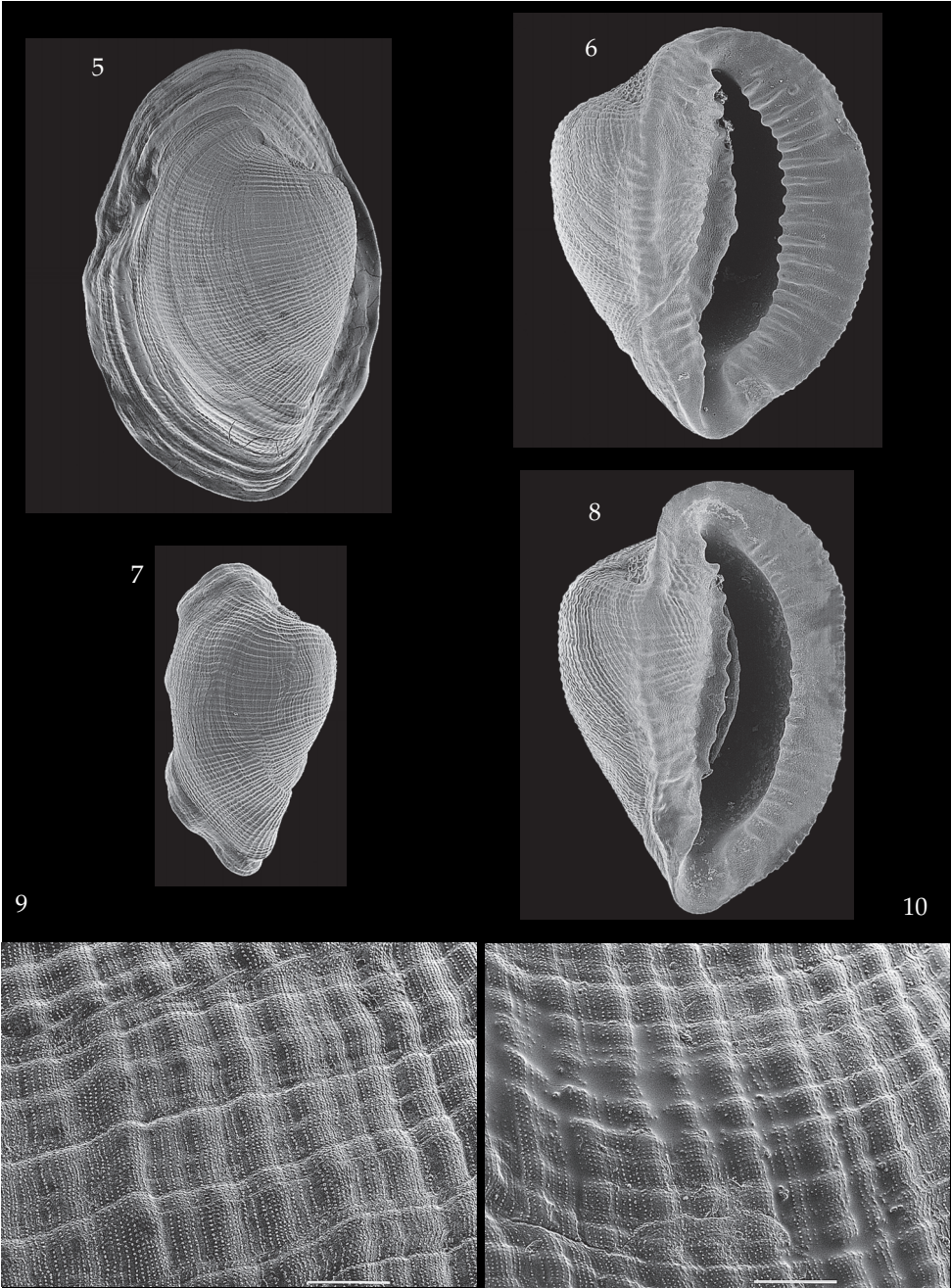
Bali-Lombok Strait Expedition, 2001, Sta. 23, Indonesia, Bali, Tulamben area, bay S of 'Emerald Hotel'; 08°17'05''S 115°36'11''E; deep reef slope with dense coral cover; scuba-diving to 30 m depth; J. Goud, c.; 12-15.iv.2001; 1 female, 1 male, 3 juveniles on the hydrocoral *Distichopora violacea* Lamarck (Pallas, 1766).

Bali-Lombok Strait Expedition, 2001, Sta. 29, Indonesia, Bali, NW side of Nusa Penida, Toyapakeh; 08°40'56''S 115°28'56''E; deep reef slope, rocky with dense coral cover, strong currents; scuba-diving to 30 m depth; B.W. Hoeksema, c.; 19, 20.iv.2001; 6 females, 4 males, 3 juveniles on the hydrocoral *Distichopora vervoorti* Cairns & Hoeksema, 1998.

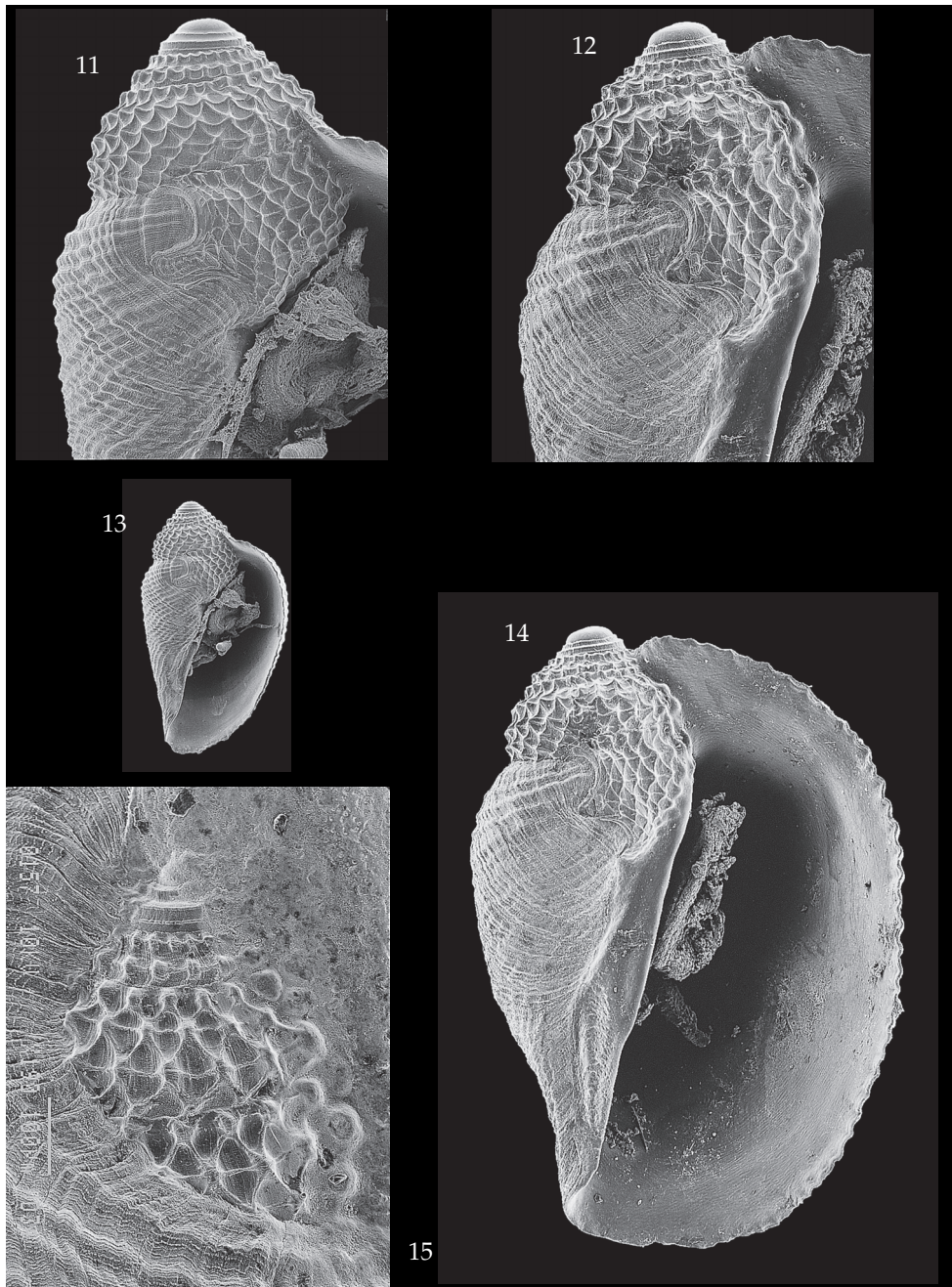
Bali-Lombok Strait Expedition, 2001, Sta. 31, Indonesia, Bali, N side of Nusa Penida, Tanjung Biasmuntig; 08°40'23''S 115°29'13''E; deep reef slope with patches of dense coral cover and sand; scuba-diving to 30 m depth; J. Goud, c.; 20.iv.2001; 15 females, 9 males, 3 juveniles on the hydrocoral *Distichopora vervoorti* Cairns & Hoeksema, 1998.

Diagnosis.— This large *Pedicularia* species is usually of a dark purple to violet colour with an oblique pattern of dots and stripes. The peristome in females undulates and protrudes not much but curves outward substantially, giving the shell a broad appearance. The males are very convex below the shoulder giving them a globular appearance and the thickened callus in the aperture bends outward, both more than in other *Pedicularia* species.

Description.— The female shell is elongated oval. The protoconch and approximately a half whorl of the adult shell are completely or nearly so concealed by the last whorl. The protoconch consists of 4.5 whorls, the teleoconch has 1.5 to 2 whorls. The initial two whorls of the protoconch (PI) are usually brownish, sometimes purple to violet. The upper half of the next 2.5 whorls (PII) has the base colour of the adult shell. The lower half of the PII whorls is usually brownish. The first whorl of PI is smooth, the second one has a simple carina with one or two spiral lines below it. The PII whorls are sculptured with oblique rhombs, pointing out at the corners and connected by spiral lines. The aperture of the larval shell shows two arc-shaped notches with a spoon-shaped lip in between (fig. 11).



Figs 5-10. SEM figures of *Pedicularia vanderlandi* spec. nov., type locality, (5, 6, 9) and *Pedicularia pacifica* Pease, 1865, Selat Lembeh, North Sulawesi, (7, 8, 10). 5, female specimen, 6.1 × 3.9 mm, holotype RMNH 82354; 6, male specimen, 3.0 × 2.2 mm, paratype RMNH 82355; 7, female specimen, 4.0 × 2.2 mm; 8, male specimen, 2.8 × 1.9 mm; 9, 10, structure of bodywhorl, scale bar = 0.1 mm.



Figs 11-15. SEM figures of details of juveniles of *Pedicularia vanderlandi* spec. nov. (11, 13, 15) and *P. pacifica* (12, 14). 11, protoconch (H = 0.75 mm); 12, protoconch (H = 0.82 mm); 13, juvenile (1.8 × 1.1. mm); 14, juvenile (2.05 × 1.35 mm); 15, detail of protoconch visible at the lateral side of a male specimen, scale bar = 01. mm.

The teleoconch, of which only the last whorl is completely visible, has a sculpture of more or less regular, spiral riblets (15-20 per mm on the middle of the back), crossed by irregular growth lines. The spiral ribs and the interstices are covered by very fine, dotted spiral lines, which are usually less dense in the interstices. The spiral ridges are more prominent towards the peristome. The widely open aperture reaches to 25% of the shell length above the top of the spire. The aperture is ovaly elongate, always wider than the body whorl and usually has some undulations due to the adaptation to the surface of the host coral. Along the lower part of the columella a shallow sinus bends outward. Between the body whorl and the somewhat protruding columellar side of the peristome, spiral ridges are connecting those of the body whorl with the edge of the peristome. Often there are rays of irregularities on the outside of the shell, which probably develop where the shell edge crosses large pores in the host coral.

The male stage has a shell which is usually smaller than the female stage, although the largest males in the material are bigger (up to 4.35 mm high) than the smallest females (minimal height 3.40 mm). The general shape is ovulid-like, with a shoulder in the upper part. Below the shoulder the body whorl is convex and somewhat concave above. The protoconch is identical to that of the females, as are the sculpture and the colour of the shell. Part of the protoconch is always visible, sometimes only one whorl, usually more (up to 4.5). The aperture shows a very characteristic outer lip; in full-grown specimens it is even wider than the remaining opening of the aperture. This lip has c. 20 elongated teeth, running clearly and sharp over the inner rim of the lip and fading away towards the outer side. On the outer edge of the lip small denticles occur, corresponding with the spiral ridges of the sculpture on the outside. On the columella there is an inner ridge with some irregular bigger teeth. In front of this columellar ridge, on the callus along the body whorl, there is a row of spiral ridges, forming a second ridge. The upper two or three spiral ridges are more prominent, showing as teeth in the upper, inner part of the aperture. The columellar side has a heavy callus, which forms a thickened, curved ridge on the inner side of the aperture, with spiral ridges almost as prominent as the teeth on the outer lip. Apically the lip has a clear, curved sinus; apically a much shallower sinus is usually present.

The colour of both males and females is usually purple to violet (more than 90% of the material studied) but occasionally it is reddish, orange or yellowish; sometimes there are colour rays towards the peristome. Most of the specimens show a characteristic, oblique pattern of white dots and stripes. In general, the colour matches that of the host coral *Distichopora vervoorti*, although animals with purple shells were occasionally found on yellow corals and the other way around.

Measurements (extremes with average size).— Shell height in females (N = 160), 3.40-5.55-8.85 mm; shell width 2.5-3.79-5.25 mm; mean H/W, 1.45. Shell height in males (N = 61), 2.5-3.36-4.35 mm; shell width 1.6-2.3-2.9 mm; mean H/W, 1.46. (table 2).

Animals.— Most of the animals are white to cream-coloured, only a few had a purplish glaze over the head, body and mantle. The head has a slender proboscis and two very long tentacles, both with a black eye at the base. The foot, with two lobes in front, is almost as long as the shell. Most females have a broodpouch filled with either



Figs 16-19. *Pedicularia vanderlandi* spec. nov. 16, juvenile; 17, male; 18, female; 19, female with brood pouch.

white eggs or brown, shelled embryos on the right side of the body, practically as long as the foot. Some female individuals had broodpouches so big, that they filled almost 50% of the aperture. One of these contained over thousand shelled embryos. The shells are transparent, brown, and c. 150 μm wide.

Etymology.— The species is named in honour of the Dutch marine biologist Dr J. van der Land.

Host coral.— The species was found mainly on *Distichopora vervoorti* Cairns & Hoeksema, 1998. The females live attached to the branches of this stylasterid coral. The males are free living on the coral; usually they are found hidden at the base of the branches, sometimes they can be found on the edge of a female. Two small populations were found on small specimens of *Distichopora violacea* Lamarck (Pallas, 1766).

Pedicularia elegantissima Deshayes, 1863

Pedicularia elegantissima Deshayes, 1863: 50, pl. 6, figs 23-26; type locality Reunion; type not located (not in MNHN, pers. com. V. Heros).

Pedicularia elegantissima; Reeve, 1875: species 3, figs 3a, b.

Pedicularia elegantissima; Von Martens, 1880: 275 (Réunion, Mauritius).

Pedicularia lienardi Robillard, 1871: 5 (Mauritius). According to Schilder & Schilder, 1971: 23, 128.

Pedicularia sicula; Sowerby, 1903 non Swainson: 230 (94 miles off Cape St. Blaize, 116 fathoms, South Africa).

Pedicularia sicula; Smith, 1906 non Swainson: 42.

Pedicularia elegantissima; Schilder, 1931: 168.

Pedicularia elegantissima; Viader, 1937: 36 (Mauritius).

Pedicularia elegantissima; Barnard, 1963: 53 (South Africa).

Pedicularis elegantissima; Schilder & Schilder, 1971: 22.

Pedicularia elegantissima; Liltved, 1989: 148, figs 18, 19, 26G-H, 224-227 (eastern Cape Province and Transkei, South Africa).

Notes.— *Pedicularia elegantissima* has been figured very well by Liltved, 1989: 22 (anatomy and embryo shell), 27 (radula), 148 (female and juvenile shells), 149 (scar on its host *Stylaster* spec.).

Since no type of *Pedicularia elegantissima* is available for study, we assume for the moment that the *Pedicularia* populations of the SW Indian Ocean are conspecific with the type, which was also done by Barnard (1963) and Liltved (1989).

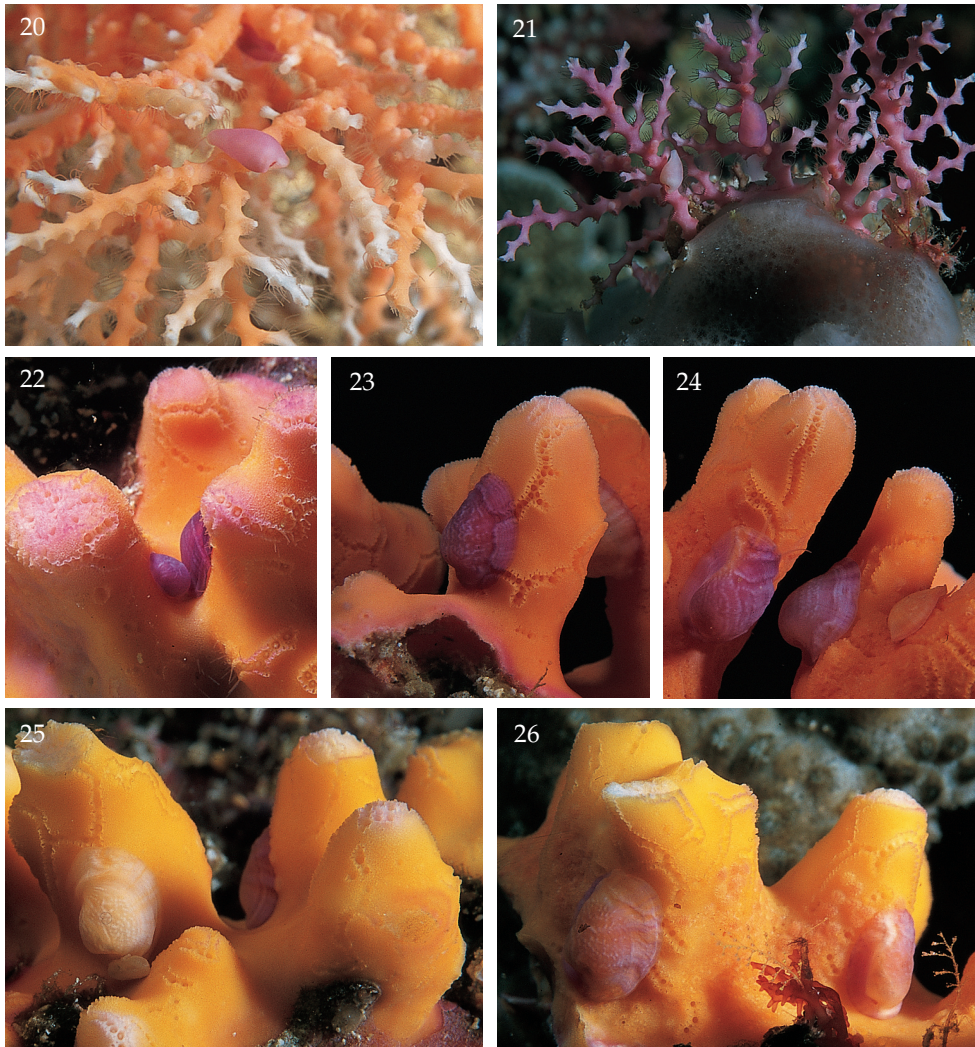
In the original description no particular discriminating characters were given that would not be applicable to any of the other *Pedicularia* species. The given sizes (6 x 3.5 mm) for this particular specimen shows a H/W ratio of ca. 1.71, which is the same as the mean ratio we found for the females of *Pedicularia pacifica*. The figure of Deshayes shows a regular, oval shell, not so much constricted and undulate as the specimens figured by Liltved. Barnard (1963) indicates 10 for the number of spiral riblets per mm on the back of *P. elegantissima* (sensu Barnard). In *P. pacifica* we counted ca. 12 spiral riblets per mm and for *P. vanderlandi* spec. nov. 15-20.

Pedicularia dautzenbergi (Schilder, 1931)

Pediculariella dautzenbergi Schilder, 1931: 166, 167, pl. VI, fig. 3 a, b; type locality: 'Celebes' [= Sulawesi]; type specimens originally in the collection Dautzenberg, now 1 'paratype' and 1 specimen in the collection Schilder in MNHU-B, no. 3599. No holo- or paratypes were found in the Dautzenberg collection (KBIN, personal communication J. Van Goethem).

Notes.— Original description, after Schilder (1931: 166, table): length 2.5-3.0 mm; subconical in general outline (dorsum subcarinate); spire discernible also in adult shells; colour usually yellowish to pinkish; radial dorsal ribs fine, not decussate; columellar sulcus deeply excavate, inner margin crenulate.

There is a shell labelled 'paratype' in the Schilder collection (no. 3599). This shell is definitely not a *Pedicularia*, but more likely a *Primovula* spec. While comparing Schilder's (1931) original description and his illustration, it turns out that this cannot be a paratype. China is indicated as provenance for the alleged paratype in the Schilder collection, whereas according to the original description the type locality of



Figs 20-26. In situ figures of *Pedicularia pacifica* (20-21) on *Stylaster* spec. and *P. vanderlandi* spec. nov. (22-26) on *Distichopora vervoorti* Cairns & Hoeksema, 1998; 20, Selat Lembeh, North Sulawesi, 16.ix.1999, male; 21, N side of Nusa Lembongan, Bali, 19.iv.2001, male (left) and female; 22-26, N side of Nusa Penida, 19/22.iv.2001, yellow and violet females on yellow and orange hydrocoral *D. vervoorti*.

Pedicularia dautzenbergi is Sulawesi. As a consequence of all this, the taxonomic status of *Pedicularia dautzenbergi* cannot be clarified.

Pedicularia subtilis Schilder, 1931 (fig. 4)

Pedicularia subtilis Schilder, 1931: 166, 167, 168, pl. VI, fig. 4 a, b; type locality: Reunion; 2 syntypes originally in coll. Schilder no's 484 and 485, now in MNHU-B. Schilder's figures 4a and b are very similar to syntype no. 484, which is now labeled 'holotype'. Therefore, we here select this specimen (no. 484) as the lectotype.

Notes.— Original description, after Schilder (1931: 166, table): length 3.5-4.0 mm; semi-circular in general outline; spire concealed in adult shells; white to flesh-colour; radial dorsal ribs obsolete, only concentric striae distinct; columellar sulcus indistinct.

In his note 6, Schilder shortly described both specimens: "Two specimens from 'Bourbon' in the writer's coll. (No. 484/485, bought from H.C. Fulton who possessed many quite similar shells); (a) 3.4 x 2.4 mm, extremely thin, pellucid, white; (b) 4.2 x 2.6 mm, pellucid, dorsum pale pinkish flesh colour, margins white; in both specimens the extremely fine and numerous radial ribs are practically obsolete, so that the close, concentric lines form the only visible structure." Both specimens have extremely big columellar sulci, which are difficult to see in our figure. We do not know this species from any other material.

Pedicularia granulata Neubert, 1998

Pedicularia granulata Neubert, 1998: 466-468, figs 8-15.

Notes.— This recently described species is most similar to *Pedicularia elegantissima* (sensu Liltved). In fully-grown females (e.g. the holotype) we noticed some undulations of the peristome, directly on the columella, just as in *Pedicularia elegantissima* (Liltved, 1989: fig. 224). In *Pedicularia pacifica* the peristome is distinct and in adult, female specimens protruding substantially

Host relationships of *Pedicularia*

Because *Distichopora* is a relatively unknown host for *Pedicularia*, we wondered whether host specificity is also a distinctive character of the new species. A comparison of *Pedicularia* hosts has been made based on published and present data (Table 3). The association of *Pedicularia* species with specific stylasterid hosts can almost only be established when the hosts are found with the living pediculariid snails still attached (figs. 20-26 and also Hedley, 1903: fig. 70; Boschma, 1956: fig. 2; Schmierer 1982: fig. 1; Liltved, 1989: fig. 227; Lindahl, 1991: fig. 1). However, many records of *Pedicularia* concern empty shells or dead specimens in mixed debris without clear connection with the original hosts. Only a few specific papers on stylasterid hydrocorals appear to mention the occurrence of the symbiotic snail (Boschma, 1956; Cairns, 1991; Zibrowius & Cairns, 1992). When only *Pedicularia* scars are found on stylasterids, no identity can be given for sure (Cairns, 1991; Zibrowius & Cairns, 1992).

Most information in table 3 has been derived from malacological publications. Although malacologists and marine biologists may be aware that pediculariids live on stylasterids (Cernohorsky, 1968: 365; Barrier et al., 1991: 7; Bouchet & Warén, 1993: 746; Neubert, 1998: 468), various others have erroneously referred to substrates such as scleractinians and octocorals (Kobelt, 1908: 31-32; Kay, 1965: 84; Ladd, 1982: 17). The *Pedicularia* specimens concerned were probably not found attached or the hosts were simply misidentified. Identification of the snail may also appear difficult in order to establish host specificity because of the variable shell shape, which depends on the branch morphology of the host (Arnaud & Zibrowius,

Table 1: Seizes (in mm +/- 0.05) of female and male specimens of *Pedicularia pacifica* from different populations. See under 'Material studied' for the localities. H/W = height/width ratio; SD = standard deviation.

Locality	Height			Width			H/W ratio mean	SD	n
	mean	minimum	maximum	mean	minimum	maximum			
FEMALES									
Bitung	3.93	3.60	4.10	2.30	2.20	2.45	1.71		3
BAL.22	3.49	2.95	4.25	2.04	1.80	2.45	1.71		5
BAL.26	3.87	3.20	4.80	2.28	1.90	2.95	1.70		30
BAL.27	4.12	3.30	5.00	2.40	2.00	2.95	1.72		44
BAL.30	3.99	3.50	3.80	2.28	1.95	3.00	1.75		6
TOTAL	3.98	2.95	5.00	2.33	1.80	3.00	1.71	0.01	88
MALES									
Bitung	2.91	2.70	3.15	1.94	1.90	2.00	1.50		3
BAL.22	2.97	2.80	3.10	1.81	1.75	1.90	1.64		6
BAL.26	2.50	2.00	3.05	1.60	1.30	1.85	1.56		26
BAL.27	2.82	2.30	3.40	1.81	1.50	2.10	1.56		29
BAL.30	2.50	2.75	2.75	1.63	1.55	1.70	1.53		2
TOTAL	2.70	2.00	3.40	1.73	1.30	2.10	1.56	0.03	66

Table 2: Seizes (in mm +/- 0.05) of female and male specimens of *Pedicularia vanderlandi* spec. nov. from different populations. See under 'Material studied' for the localities. H/W = height/width ratio; SD = standard deviation.

Locality	Height			Width			H/W ratio mean	SD	n
	mean	minimum	maximum	mean	minimum	maximum			
FEMALES									
BAL.29	4.88	3.65	5.70	3.42	2.40	4.10	1.43		6
BAL.30	5.55	3.40	8.85	3.83	2.50	5.25	1.45		139
BAL.31	5.21	3.70	7.05	3.59	2.40	5.25	1.45		15
TOTAL	5.50	3.40	8.85	3.79	2.50	5.25	1.45	0.02	160
MALES									
BAL.29	3.35	2.90	3.60	2.31	1.9	2.55	1.45		4
BAL.30	3.42	2.50	4.35	2.35	1.6	2.90	1.46		48
BAL.31	3.09	2.50	3.95	2.06	1.65	2.85	1.50		9
TOTAL	3.36	2.50	4.35	2.30	1.6	2.90	1.46	0.02	61

1979; Schmieder, 1982; Liltved, 1989; Bouchet & Warén, 1993).

Bouchet & Warén (1993: 749) conclude that *Pedicularia sicula* in particular, can inhabit more than one stylasterid species. The records of other *Pedicularia* species and their stylasterid hosts (Table 3) also indicate the availability of multiple hosts per species. However, not all of the records are reliable due to the absence of illustrations or descriptions. Habe (1976), for example, mentions four host species for *Pedicularia pacifica* Pease, 1865, but only presents one illustrated specimen.

Table 3. *Pedicularia* species and their stylasterid hosts (current nomenclature of stylasterids in Cairns et al., 1999). ¹ Host identity probably mistaken. ² Identity of *Pedicularia sicula* (and its synonymy) is given or confirmed by Bouchet & Warén, 1993.

<i>Pedicularia</i> species	Host	Locality	Depth range (m)	References
scars only	<i>Stylaster complanatus</i> Pourtalès, 1867	W Atlantic	-	Zibrowius & Cairns, 1992
scars only	<i>Stylaster erubescens</i> Pourtalès, 1868	W Atlantic	505	Zibrowius & Cairns, 1992
scars only	<i>Conopora</i> sp.	W Atlantic	-	Zibrowius & Cairns, 1992
scars only	<i>Crypthelia peircei</i> Pourtalès, 1867	W Atlantic	-	Zibrowius & Cairns, 1992
one specimen + scars	<i>Errina atlantica</i> Hickson, 1912	Azores	810-983	Zibrowius & Cairns, 1992
scars only	<i>Lepidopora eburnea</i> (Calvet, 1903)	Azores	480-895	Zibrowius & Cairns, 1992
scars only	<i>Errina dabneyi</i> (Portalès, 1871)	Azores	215-560	Zibrowius & Cairns, 1992
scars only	<i>Stenohelia maderensis</i> (Johnson, 1862)	Madeira	300-340	Zibrowius & Cairns, 1992
<i>P. sicula</i> Swainson, 1840	<i>Errina aspera</i> (Linnaeus, 1767)	Mediterranean Sea	about 100	Arnaud & Zibrowius, 1979
<i>P. sicula</i> Swainson, 1840	<i>Errina aspera</i> (Linnaeus, 1767)	Mediterranean Sea	181-236	Natale & Mangano, 1985
<i>P. sicula</i> Swainson, 1840	<i>Errina aspera</i> (Linnaeus, 1767)	Mediterranean Sea	100-300+	Giudice, 1990
<i>P. sicula</i> Swainson, 1840 ²	<i>Errina aspera</i> (Linnaeus, 1767)	Mediterranean	220-633	Zibrowius & Cairns, 1992
<i>P. sicula</i> Swainson, 1840 ²	<i>Stylaster ibericus</i> Zibrowius & Cairns, 1992	Bay of Biscay	500-515	Zibrowius & Cairns, 1992
scars only	<i>Stylaster erubescens</i> Pourtalès, 1868	Bay of Biscay	1080	Zibrowius & Cairns, 1992
scars only	<i>Pliobothrus symmetricus</i> Pourtalès, 1868	Bay of Biscay	380-1050	Zibrowius & Cairns, 1992
<i>P. granulata</i> Neubert, 1998	"hydrocoral species"	Gulf of Aden	45-296	Neubert, 1998
<i>P. elegantissima</i> Deshayes, 1863	<i>Errina capensis</i> Hickson, 1912	South Africa	90-500	Liltved, 1989
<i>P. elegantissima</i> Deshayes, 1863	<i>Errina</i> sp.	South Africa	90-500	Liltved, 1989
<i>P. elegantissima</i> Deshayes, 1863	<i>Stylaster</i> sp.	South Africa	250	Liltved, 1989
<i>P. stylasteris</i> Hedley, 1903	<i>Stylaster incompletus</i> (Tenison-Woods, 1883)	NSW Australia	100-120	Hedley, 1903; Boschma, 1956
scars only	<i>Adelopora moseleyi</i> Cairns, 1991	off New Zealand	285-290	Cairns, 1991
scars only	? <i>Stylaster gracilis</i> M.E. & H., 1850	off New Zealand	406-951	Cairns, 1991
<i>P. japonica</i> Dall, 1865	" <i>Gorgonia</i> " ¹	Japan	108	Dall, 1865; Habe 1978
= <i>P. pacifica</i> (synonymy Habe, 1978)				

<i>P. pacifica</i> Pease, 1865	<i>Distichopora</i> spp.	Fiji, Marshall Is, Hawaii -	Schmeltz, 1874
? <i>P. elegantissima</i> Deshayes, 1863	<i>Distichopora</i> spp.	Fiji, Marshall Is, Hawaii -	Schmeltz, 1874
<i>P. pacifica</i> Pease, 1865	<i>Distichopora coccinea</i> Gray, 1860	Nieu - Central Pacific -	Hedley, 1903
<i>P. pacifica</i> Pease, 1865	<i>Stylaster profundiporus</i> Broch, 1936	Japan?	Habe, 1976
<i>P. pacifica</i> Pease, 1865	<i>Stylaster dentatus</i> Broch, 1936	Japan?	Habe, 1976
<i>P. pacifica</i> Pease, 1865	<i>Distichopora borealis</i> Fischer, 1936	Japan?	Habe, 1976
<i>P. pacifica</i> Pease, 1865	<i>Stenohelia echinata</i> Eguchi, 1968	Japan?	Habe, 1976
<i>P. pacifica</i> Pease, 1865	stylasterid corals	Japan	Kuroda et al., 1971; Habe, 1978
<i>P. pacifica</i> Pease, 1865	<i>Stylaster</i> sp.	N Sulawesi, Indonesia	present study
<i>P. pacifica</i> Pease, 1865	<i>Stylaster</i> sp.	Bali, Indonesia	present study
<i>P. vanderlandi</i> spec. nov	<i>Distichopora vervoorti</i> Cairns & Hoeksema, 1998	Bali, Indonesia	present study
<i>P. vanderlandi</i> spec. nov	<i>Distichopora violacea</i> (Pallas, 1766)	Bali, Indonesia	present study
<i>P. californica</i> Newcomb, 1864	<i>Stylaster venustus</i> (Verrill, 1870)	California	Berry, 1946
<i>P. californica</i> Newcomb, 1864	<i>Stylantheca porphyra</i> Fischer, 1931	California	Schmieder, 1980, 1982
<i>P. californica</i> Newcomb, 1864	<i>Stylaster californicus</i> (Verrill, 1866)	California	Liltved, 1987
<i>P. californica</i> Newcomb, 1864	<i>Stylaster californicus</i> (Verrill, 1866)	California	Lindahl, 1991
<i>P. californica</i> Newcomb, 1864	<i>Stylaster californicus</i> (Verrill, 1866)	California	Catarius, 1991

Many of these hosts are from deep-water. Stylasterids, which are azooxanthellate, do not need sunlight and are generally restricted to insular areas (Cairns, 1992). Apart from *Distichopora verwoorti*, *D. violacea* Lamarck (Pallas, 1766), and the shallow unidentified *Stylaster* species, no other shallow-living stylasterids are known from Indonesia. *D. violacea* was observed (by BWH) at *D. verwoorti*'s type locality as small, rudimentary corals without *Pedicularia*. At other Indonesian localities (for example Ambon) where *D. violacea* has been observed in large quantities of full-grown specimens in various colours, also no *Pedicularia* was found. In the present publication specimens of *P. vanderlandi* spec. nov. are recorded from small colonies of *Distichopora violacea* at Bali, although not from the type locality of *D. verwoorti*. Apart from the records of *P. pacifica* from unknown depths (Table 3), all other Indo-West Pacific hosts of *P. elegantissima*, *P. granulata*, *P. japonica* (synonym of *P. pacifica* according to Habe, 1978), and *P. stylasteris* appear to come from depths greater than 45 m. The latter of these (also a synonym of *P. pacifica* according to Habe, 1978) does not show a tropical distribution. *P. pacifica* is probably the most common species in the Indo-West Pacific and may be able to dwell in shallow water.

The present records from Indonesia are all from shallow water (15-35 m), but from different host genera, *Distichopora* Lamarck, 1816, and *Stylaster* Gray, 1831. We consider the two pediculariid populations to represent two species because they differ in colour and teleoconch shape. Their hosts live at similar depth ranges but otherwise in different habitats. The *Stylaster* species at north Sulawesi lives in sheltered, warm water (c. 27-30 °C) underneath cave ceilings or protruding ridges on vertical substrata. This species is common in Indonesia and the Philippines but pending a taxonomic revision of tropical shallow-water stylasterids we cannot identify it (Cairns pers. comm.). *D. verwoorti*, on the other hand, was mostly found exposed on a slope with strong currents of cold, up-welled water (c. 17-20 °C). Hence, the difference in environment for the hosts may also be important for the two *Pedicularia* species. Since most *Pedicularia* species and their hosts appear to live in deep, cold water, the one from north Sulawesi, *P. pacifica*, living on the warm-water *Stylaster* sp., may be typical for warm water and therefore exceptional in relation to other *Pedicularia* species.

It has been assumed that *Pedicularia* specimens obtain their colour from their host (Hedley, 1903: 343). The observations on the present specimens contradict this finding. The colour of the *Distichopora* specimens from Bali vary from orange yellow to pink, ruby and mauve (Cairns & Hoeksema, 1998), while the *Pedicularia* shells varied in several gradations of violet with occasionally some orange or yellowish specimens. The shells from *P. pacifica* are dark pink or rose, whereas their hosts were light orange or pink. Hence, with regard to coloration, there is no clear link between the mollusc and its host. If the symbiont would derive its colour from its host, one would assume that it could obtain this colour from eating the host's colourful coral tissue. What the snail is eating in its predominantly sedentary adult stage is not exactly clear, but it has been suggested that it most likely eats the mucus off the coral's surface with its comb-like radular teeth (Liltved, 1989: 149; Giudice, 1990: 102). Anyway, it appears that the violet colour of *P. vanderlandi* is a distinctive character which is not host-dependent. The bright orange colour, occasionally found, is not found in any other *Pedicularia* species.

We can conclude that although one *Pedicularia* species may inhabit more than one

stylasterid host, in the case of *P. vanderlandi*, living in shallow water, only two *Distichopora* species are known. Because it lives in cold water, possible alternative hosts may be deep-water species. Not many of those are known from Indonesia (Boschma, 1953, 1959; Cairns 1992). Hence, so far we may assume that *P. vanderlandi* is restricted to *Distichopora vervoorti* and *D. violacea* as host species.

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