

The association between a deep-sea gastropod *Pedicularia sicula* (Caenogastropoda: Pediculariidae) and its coral host *Errina dabneyi* (Hydrozoa: Stylasteridae) in the Azores

Andreia Braga-Henriques^{1*}, Marina Carreiro-Silva¹, Filipe M. Porteiro¹, Valentina de Matos¹, Íris Sampaio¹, Oscar Ocaña², and Sérgio P. Ávila³

¹IMAR/DOP-UAz, Department of Oceanography and Fisheries, University of the Azores, 9901-862 Horta, Portugal

²Departamento de Biología Marina, Fundación Museo del Mar, Autoridad Portuaria de Ceuta, Muelle Cañonero Dato S/N 51001, North Africa

³Department of Biology and CIBIO, University of the Azores, Rua da Mãe de Deus, Apartado 1422, 9501-801 Ponta Delgada, Portugal

*Corresponding Author: tel: +351 292 207800; fax: +351 292 207811; e-mail: andreiahenriques@uac.pt.

Braga-Henriques, A., Carreiro-Silva, M., Porteiro, F. M., de Matos, V., Sampaio, Í., Ocaña, O., and Ávila, S., P. 2011. The association between a deep-sea gastropod *Pedicularia sicula* (Caenogastropoda: Pediculariidae) and its coral host *Errina dabneyi* (Hydrozoa: Stylasteridae) in the Azores. – ICES Journal of Marine Science, 68: 399–407.

Received 31 August 2009; accepted 8 April 2010; advance access publication 30 June 2010.

The Azores region harbours the richest communities of stylasterid corals in the Northeast Atlantic area. Of the nine deep-water species found there, *Errina dabneyi* seems to be the most abundant species; it is commonly collected as bycatch from longline fishing. *E. dabneyi* host *Pedicularia* gastropods on their branches, and a detailed study of shell shape and morphometry at different growth stages, complemented by shell characterization through scanning electron microscopy, allows the individuals to be identified as *Pedicularia sicula*. The incidence of this species on *E. dabneyi* was high (69.8%), with abundances ranging between 1 and 223 individuals per colony. The pediculariids exhibited a high degree of plasticity and produced evident traces on the stylasterid skeletons at their fixation points, suggesting that they are ectoparasites and not predators of *E. dabneyi*. The stylasterid colonies also hosted a rich associated fauna dominated by suspension-feeders using the coral as substratum and for protection.

Keywords: Azores, cold-water corals, parasitism, *Pedicularia*, Pediculariidae, Stylasteridae, symbiont.

Introduction

The genus *Pedicularia* Swainson, 1840 (Caenogastropoda: Pediculariidae) encompasses 10 gastropod species (Simone, 2005; Lorenz and Fehse, 2009), commonly reported as symbionts of stylasterid corals (Zibrowius and Cairns, 1992; Bouchet and Warén, 1993; Goud and Hoeksema, 2001). Many gastropods living in association with corals are described in the literature as parasites (Goh *et al.*, 1999) or predators (Théodor, 1967; Robertson, 1970; Cate, 1973; Morton, 1988; Wu *et al.*, 1990; Goh and Chou, 1994; Oliverio *et al.*, 1995; Schiaparelli *et al.*, 2005). It is sometimes difficult to distinguish between parasitism and predation, so their functional classification remains uncertain (Buhl-Mortensen and Mortensen, 2004).

The association between pediculariids and stylasterids has been reported in 12 host species and one subspecies from several locations in the Atlantic and the Mediterranean (Table 1), with western Atlantic records rarer than those from the Northeast Atlantic and Mediterranean (Zibrowius and Cairns, 1992). Records for the Azores were mostly based on traces and identification to species level was never achieved (Cairns, 1991; Zibrowius and Cairns, 1992), except a few observations made by Wisshak *et al.* (2009); however, no method of identification was provided.

Of the nine stylasterid species recorded for the Azores (reviewed by Zibrowius and Cairns, 1992), *Errina dabneyi* (Pourtales, 1871) is by far the most common. Unlike most

stylasterids, which appear widely distributed throughout insular areas (Cairns, 1992), this species is known to occur only in the Azores and the Mid-Atlantic Ridge southwest of the Azores, mainly at upper bathyal depths (Zibrowius and Cairns, 1992). It possesses a uniplanar fan-shaped calcified skeleton up to 40 cm high and wide with a reticulate-granular texture, which is covered by a thin layer of tissue (Zibrowius and Cairns, 1992).

Many specimens of *E. dabneyi* hosting *Pedicularia* on their branches have been collected in the Azores. The main goal of this study was to contribute to our knowledge of the association between pediculariids and stylasterids, because most of the available records of *Pedicularia* consist of empty shells or dead animals in mixed debris (Goud and Hoeksema, 2001), lacking any reference to the host species. Specific aims were: (i) to identify the *Pedicularia* individuals present in *E. dabneyi* colonies, and describe shell morphology at various growth stages; (ii) to characterize the *Pedicularia* traces found on the host; and (iii) to provide new insights on the nature of this symbiotic relationship. The epifauna present on *E. dabneyi* is also briefly described.

Material and methods

Collection and examination of specimens

In situ observations of *E. dabneyi* hosting *Pedicularia* were made with the manned submersible “Lula” from the Rebicoff-Niggeler Foundation. The dive was carried out on the southern slope

Table 1. *Pedicularia* and their stylasterid hosts known for the Atlantic and the Mediterranean.

Symbiont	Host	Locality	Depth range (m)	Reference
One specimen + traces	<i>Errina atlantica</i> Hickson, 1912	Azores	810–983	Zibrowius and Cairns (1992)
One specimen + traces	<i>Errina dabneyi</i> Pourtalès, 1871	Azores	215–560	Zibrowius and Cairns (1992)
Traces only	<i>Lepidopora eburnea</i> Calvet, 1903	Azores	480–895	Zibrowius and Cairns (1992)
<i>P. sicula</i> Swainson, 1840	<i>Errina dabneyi</i> Pourtalès, 1871	Southern Faial Channel, Azores	475; 490	Wisshak et al. (2009)
<i>P. splendida</i> Lorenz, 2008	<i>Errina atlantica</i> Hickson, 1912	Hyères and Atlantis Seamounts	845–1520	Lorenz (2008)
Traces only	<i>Stenohelia maderensis</i> Johnson, 1862	Madeira	300–340	Zibrowius and Cairns (1992)
Traces only	<i>Stylaster erubescens</i> Pourtalès, 1868	Blake Plateau, W Atlantic	505	Zibrowius and Cairns (1992)
Traces only	<i>Stylaster complanatus</i> Pourtalès, 1867	Cuba, W Atlantic	–	Zibrowius and Cairns (1992)
Traces only	<i>Crypthelia peircei</i> Pourtalès, 1867	Guadaloupe and St Vincent, W Atlantic	–	Zibrowius and Cairns (1992)
Traces only	<i>Conopora</i> sp.	NW Brazil, W Atlantic	–	Zibrowius and Cairns (1992)
<i>P. tibia</i> Simone, 2005	<i>Stylaster</i> sp.	Canopus Bank, Brazil, W Atlantic	60	Simone (2005)
<i>P. bonfigliolii</i> Cossignani, 2006 ^a	<i>Stylaster</i> sp.	Canopus Bank, Brazil, W Atlantic	60	Cossignani (2006)
<i>P. sicula</i> Swainson, 1840 ^b	<i>Stylaster ibericus</i> Zibrowius and Cairns, 1992	Bay of Biscay	500; 515	Zibrowius and Cairns (1992)
Traces only	<i>Pliobothrus symmetricus</i> Pourtalès, 1868	Celtic Sea	380; 1050	Zibrowius and Cairns (1992)
Traces only	<i>Stylaster erubescens britannicus</i> Zibrowius and Cairns, 1992	Celtic Sea	1080	Zibrowius and Cairns (1992)
<i>P. sicula</i> Swainson, 1840	<i>Errina aspera</i> Linnaeus, 1767	Strait of Gibraltar	61–443	Álvarez-Pérez et al. (2005)
<i>P. sicula</i> Swainson, 1840	<i>Errina aspera</i> Linnaeus, 1767	Mediterranean Sea	about 100	Arnaud and Zibrowius (1979)
<i>P. sicula</i> Swainson, 1840	<i>Errina aspera</i> Linnaeus, 1767	Mediterranean Sea	181–236	di Natale and Mangano (1985)
<i>P. sicula</i> Swainson, 1840 ^b	<i>Errina aspera</i> Linnaeus, 1767	Mediterranean Sea	220–633	Zibrowius and Cairns (1992)
<i>P. sicula</i> Swainson, 1840	<i>Errina aspera</i> Linnaeus, 1767	Strait of Messina, Sicily	100–300 +	Giudice (1990)

^a*Pedicularia bonfigliolii* was recently synonymized with the western Atlantic species *Pedicularia decussata* (Gould, 1855; see Lorenz and Fehse, 2009).

^bIdentity of *Pedicularia sicula* (and its synonymy) is given or confirmed by Bouchet and Warén (1993).

of the Faial-Pico Channel (start position 38°29'260''N 28°37'310''W; end position 38°29'400''N 28°37'260''W) between depths of 330 and 480 m, on 4 September 2008. Specimens used for detailed examination and measurement were obtained as bycatch from longline fishing cruises with RV “Arquipélago” (ARQDAÇO-03-P95; ARQDAÇO-29-P08) and from the local longline fleet. A total of 43 living colonies of *E. dabneyi* have been collected over the past 14 years within the Azores EEZ, from depths between 201 and 1097 m (Figure 1). The material is deposited in the collection of the Department of Oceanography and Fisheries of the University of the Azores (DOP-UAz).

Each colony was carefully examined for the presence of *Pedicularia* or their traces with the aid of a stereomicroscope. The number of *Pedicularia* individuals per colony was counted and a few individuals with intact shell aperture were preserved in 70% ethanol for later identification to species level ($n = 107$). These specimens were identified by comparison with related Atlantic species [*Pedicularia sicula* Swainson, 1840, *Pedicularia decussata* (Gould, 1855), *Pedicularia splendida* Lorenz, 2009, and

Pedicularia tibia Simone, 2005]. The species *P. tibia* and *Pedicularia bonfigliolii* Cossignani, 2006, both described from the same type of locality (Canopus Bank, Brazil), were treated by Lorenz and Fehse (2009) as synonyms of *P. decussata*. This classification is accepted for *P. bonfigliolii*, but is still controversial for *P. tibia* (L. Simone, pers. comm.). Therefore, the latter species was considered as a valid species.

Some of the preserved specimens were soaked in distilled water for 48 h without their shells for observation of anatomical characters. Finally, 10 squashes of *Pedicularia* stomachs were examined under a light microscope to look for the presence of nematocysts (i.e. proteinaceous capsules found in all cnidarians).

Morphometric characterization

The width and height of 63 *Pedicularia* individuals were measured to the nearest millimetre using a Leica MZ 16FA stereomicroscope and the software Leica Application Suite version 2.8.1. Given that juveniles have distinct shell characters, only size data of sedentary adults ($n = 54$) were used for the morphometric analysis within

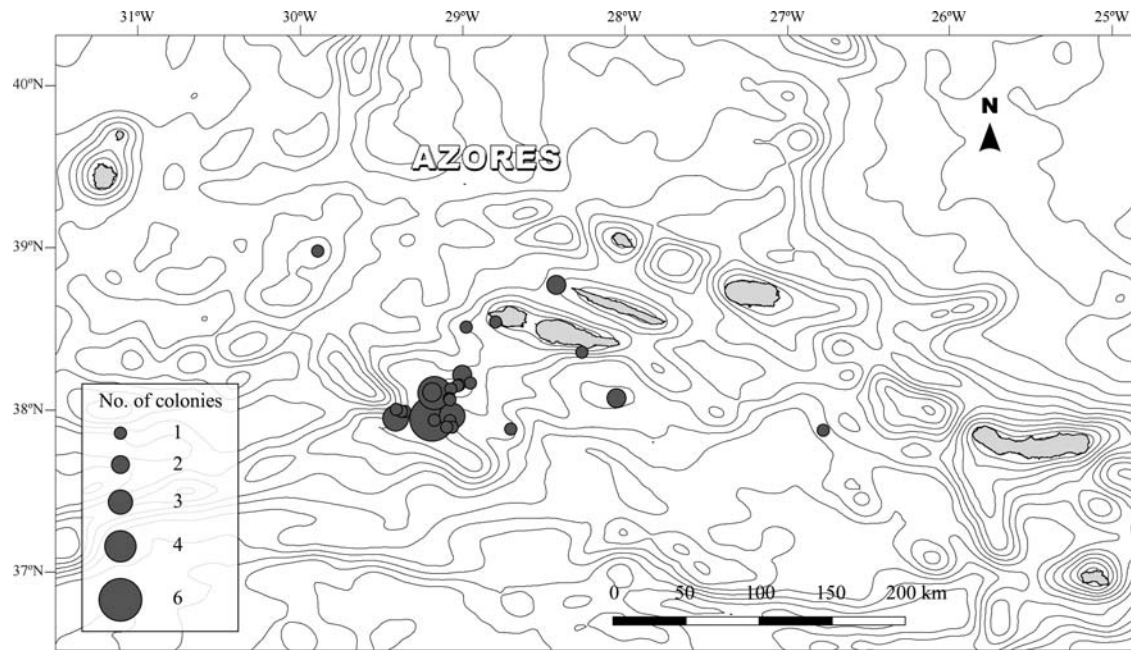


Figure 1. Distribution of the localities within the Azores Archipelago where *Errina dabneyi* was collected. The size of grey circles is proportional to the number of colonies obtained at each locality. Spacing of contour lines is 300 m.

localities. The shell morphology of distinct morphotypes of adult *Pedicularia* was characterized through high-magnification images by scanning electron microscopy (SEM), obtained with a JEOL JFM-5410 at the Department of Biology of the University of the Azores (DBUA). The samples were covered with gold/palladium 40/60 in a vacuum evaporator JEOL JEE 400 before scanning. Particular attention was paid to the protoconch and to the microsculpture of the shell. This material is deposited in the DBUA reference collection.

Results

In the present study we have identified the pediculariids associated with the stylasterid *E. dabneyi* in the Azores Archipelago as belonging to the species *P. sicula*. The presence of *P. sicula* was recorded in colonies collected between depths of 201 and 548 m. Details of the material examined in this study are available in the Supplementary data online.

Taxonomic description

Gastropoda Cuvier, 1797

Caenogastropoda Cox, 1959

Cypraeoidea Rafinesque, 1815

Pediculariidae H. and A. Adams, 1855

Pedicularia sicula Swainson, 1840: 357, Fig. 44.

Synonyms: *Calyptrea polymorpha* Calcara, 1842: 17; *Thyreus paradoxus* Philippi, 1844: 92, p1. 18 Fig. 1; *Pedicularia decurvata* Locard, 1897: 96–99, p1. 3 Fig. 12–15; *Pedicularia sicula* var. *sublaevigata* Locard, 1897: 99; *Mioseguenzia cimbrica recens* Nordsieck, 1973; *Mioseguenzia conica* Nordsieck, 1973; *Pedicularia sicula* Swainson, 1840: Bouchet and Warén 1993: 746–752, Figs 1772–1787.

Description

The embryonic shell (protoconch I) consists of about one whorl of 156–197 μm width, 90 μm height, and shows the typical finely pitted sculpture of *P. sicula* (Figure 2a and b). Protoconch II consists of about four whorls with a diagonally reticulated surface (Figure 2a–d). The transition between protoconch I and II is smooth. The first whorl of protoconch II shows, in apical view, two distinct horizontal rows that disappear at the beginning of the second whorl (Figure 2b). Protoconch II has a width of about 662 μm (Figure 2c) and a height of 652 μm (Figure 2d). These planktonic veliger larvae are ovate in shape and possess a distinct beak on the aperture of the larval shell (Figure 2d) that is still visible after the first whorl of the teleoconch has grown. The axis of the protoconch is not tilted against the axis of the teleoconch.

The growth of the teleoconch progressively covers the protoconch during the male phase of the shell (up to around 4 mm height; Figure 2d and e). The male shell (~3.2 mm height, 2.2 mm width) was called the “Trivia” stage by Bouchet and Warén (1993: 752) and it has a very consistent shape (Figure 2e). The labrum forms a rounded anterior and posterior extremity and the columella has a parietal shield. In more calloused shells, the columellar ridge and the labral edge are more developed and fine transverse ridges are visible all around the aperture; in this phase, the outer lip is usually crenulated (Figure 2f).

Average shell height of adult *P. sicula* was 5.99 mm (3.45–9.88), average shell width was 2.75 mm (1.41–4.09), and the height/width ratio ranged from 1.51 to 3.08 mm (Table 2). Most adult specimens were females presenting a reddish colouration, with a few individuals cream-coloured. Usually, shells >4 mm in height are females. The largest females observed were collected at Açor Bank3 (38°04'48"N 28°02'24"W; 402 m depth) and measured 9.88 × 3.25 mm. In ventral view, females show the brood-pouch, a cavity which extends along the foot and where

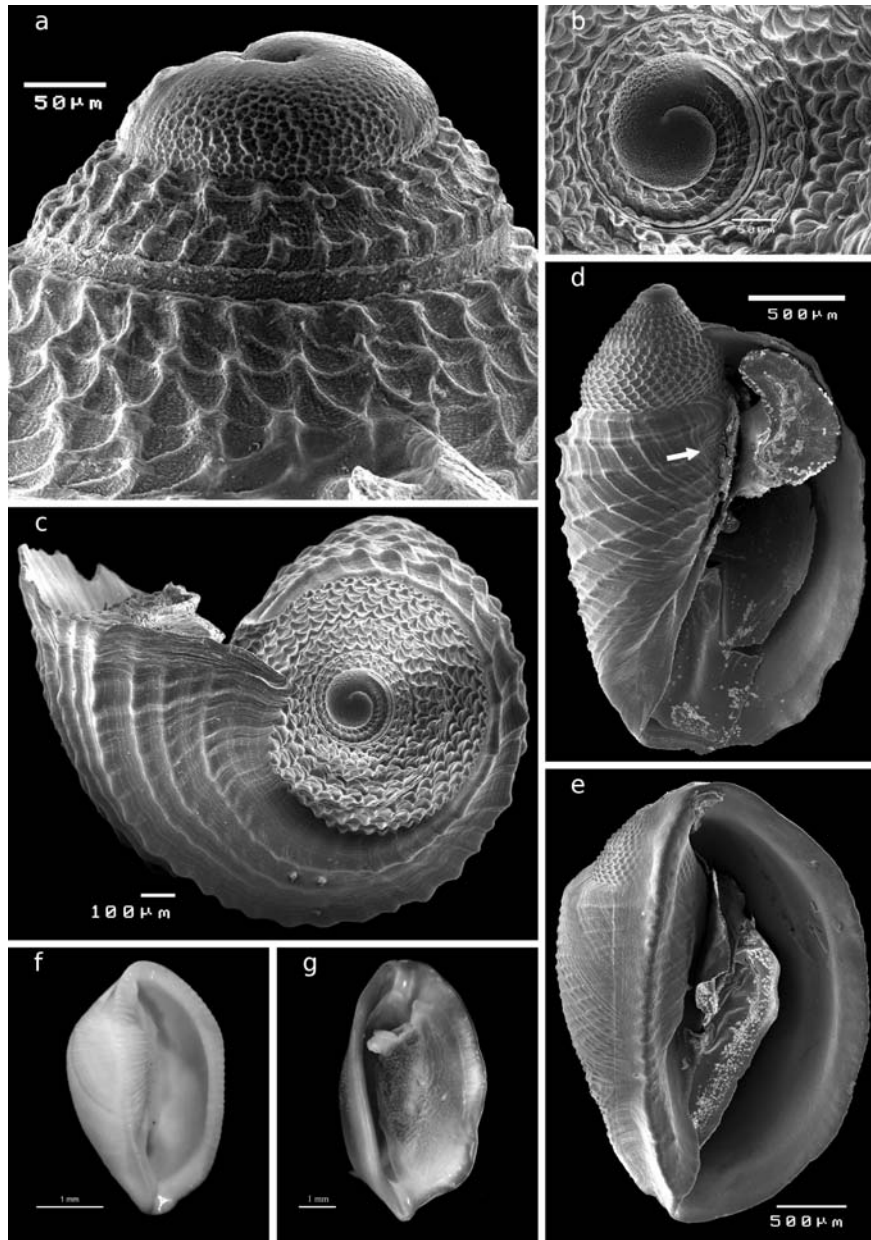


Figure 2. *Pedicularia sicula* (a) lateral view showing protoconch I and the first two whorls of protoconch II, DBUA Suppl 191–3; (b) frontal view of the protoconch I, DBUA Suppl 191–3; (c) apical view of the shell (male phase), DBUA Suppl 191–3; (d) male phase of the shell, DBUA Suppl 191–3. The white arrow shows the beak on the aperture of the larval shell; (e) male phase of the shell (“Trivia” stage *sensu* Bouchet and Warén, 1993), DBUA Suppl 191–4; (f) male phase of the shell, with crenulated outer lip (3.82 × 2.36 mm), DOP-1107; (g) ventral view of female with brood pouch, DOP-1457.

the embryos are brooded (Figure 2g). The shells were irregular and sub-patelliform, with a very long aperture channelled at both ends, and exhibited a high level of plasticity (Figure 3). The surfaces of the female shells have irregular girdles with fine transverse vertical ribs (Figure 3a); sometimes, these are almost smooth and porcelainous. The top surface of the shell is sculptured by about 16–20 vertical, narrow, uniformly distributed spiral lines that form tubercles with the additional perpendicular growth lines; the space between the lines is about twice the width of the lines (Figure 3b), with alternating strong and fine ridges. Younger regions of the shell expand widely, the transverse ridges are absent, and growth lines are present (Figure 3c and d).

The head of *P. sicula* has two tentacles, both with a black eye at the base. The foot is slightly shorter than the shell and has two lobes in front. Juveniles were morphologically distinct from the adult specimens.

Diagnosis

All the specimens examined were identified as *P. sicula*, according to the distinguishing characters summarized in Table 3. *P. sicula* differs from *P. tibia* by possessing five whorls in the protoconch against four in *P. tibia*, by the lower number of teleoconch vertical spiral lines (ribs)—16–20 for *P. sicula*, 35–40 for *P. tibia*—and by the differences detected in the width of the spaces between the

Table 2. Body size measurements of sedentary adults of *Pedicularia sicula* from different localities.

Locality	n	Height (mm)	Width (mm)	H/W ratio
Açor Bank2	2	7.20 (6.85–7.55)	3.35 (2.60–4.07)	2.23 (1.86–2.60)
Açor Bank3	14	6.16 (4.31–9.88)	2.66 (1.90–3.74)	2.35 (1.70–3.08)
Açor Bank4	6	5.79 (4.95–7.20)	2.68 (2.19–3.57)	2.19 (1.87–2.69)
Açor Bank5	4	6.61 (5.45–7.39)	3.21 (2.76–3.64)	2.07 (1.83–2.48)
Açor Bank6	11	6.09 (5.23–7.17)	2.78 (2.15–4.09)	2.23 (1.60–2.70)
Açor Bank7 (35 miles)	1	7.64	2.74	2.79
Gigante Seamount	1	5.33	2.82	1.89
Princesse Alice Bank3	6	5.84 (4.90–6.37)	2.57 (2.37–3.11)	2.29 (2.01–2.57)
Princesse Alice Bank4	3	6.12 (6.09–6.13)	3.31 (3.04–3.53)	1.86 (1.72–2.02)
Princesse Alice Bank5	3	5.07 (4.29–6.47)	2.16 (1.41–2.55)	2.45 (1.76–3.04)
Rosais, São Jorge Island	3	4.32 (3.45–5.02)	2.57 (2.29–2.73)	1.67 (1.51–1.84)

Height value = mean (min–max); width value = mean (min–max); H/W value (height/width ratio) = mean (min–max).

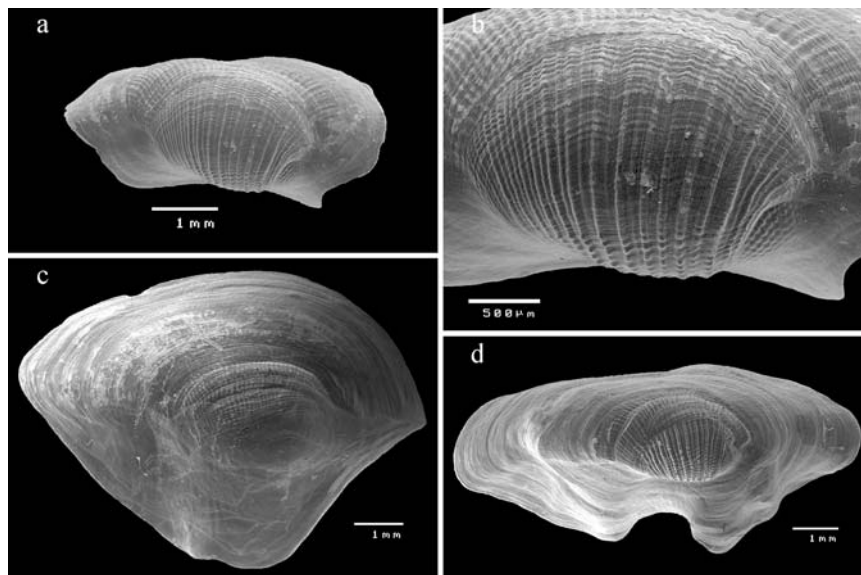


Figure 3. SEM images of adult sedentary specimens of *Pedicularia sicula* showing variation of sculpture and shape. (a) Frontal view, DOP-1378, DBUA Suppl 224–2; (b) detail of the teleoconch, DOP-1378, DBUA Suppl 224–2; (c) frontal view, DOP-1114 DBUA Suppl 223–1; (d) frontal view, DOP 1114, DBUA Suppl 222–1.

Table 3. Main distinguishing characters of Atlantic species of *Pedicularia*.

Diagnostic characters	<i>P. sicula</i> Swainson, 1840	<i>P. splendida</i> Lorenz, 2009	<i>P. tibia</i> Simone, 2005
Number of protoconch whorls	5	5	4
Axis protoconch/teleoconch tilted	No	Yes (8–10°)	No
Teleoconch spiral lines	16–20	Fine; teleoconch smooth-like	35–40
Space between teleoconch spiral lines	Twice the width of the lines	Indistinct	Same width as the lines

teleoconch spiral lines, which are about the same width as the lines for *P. tibia*, and about twice the width of the lines for *P. sicula*.

Pedicularia sicula differs from *P. splendida* in the axis between protoconch and teleoconch, which is tilted (8–10°) in *P. splendida* and not tilted in *P. sicula*; also *P. splendida* lacks a dorsal sculpture in the adult shell, in contrast to both *P. sicula* and *P. tibia*.

Neither *P. decurvata* nor the western Atlantic species *P. decussata*, both considered as valid species by Lorenz (2008) and Lorenz and Fehse (2009), were observed. The specimens examined differ from these two species by having a stronger dorsal sculpture, while *P. decurvata* has obscured dorsal ribs and *P. decussata* has rather fine and decussate dorsal striae.

Distribution

Pedicularia sicula is distributed from the northern part of the Bay of Biscay southwards along the continental slope to the Iberian Peninsula and Gulf of Morocco. It also occurs in the Mediterranean, as far east as the Strait of Messina and the sill of the Sicilian Channel. In the Atlantic Ocean, *P. sicula* is a bathyal species, while in the Strait of Messina it occurs as shallow as 100 m.

Description of the association

In situ footage from the southern slope of the Faial-Pico Channel revealed that most living *E. dabneyi* colonies had *P. sicula* on their surface (Figure 4). A total of 30 of the 43 colonies obtained as

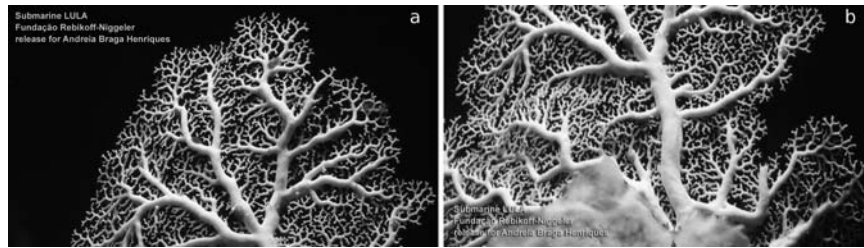


Figure 4. *In situ* observations of *Pedicularia sicula* on *Errina dabneyi* captured with LULA submersible on the southern slope of the Faial-Pico Channel, Azores Archipelago, (38°29'N 28°37'W) at 450 m.

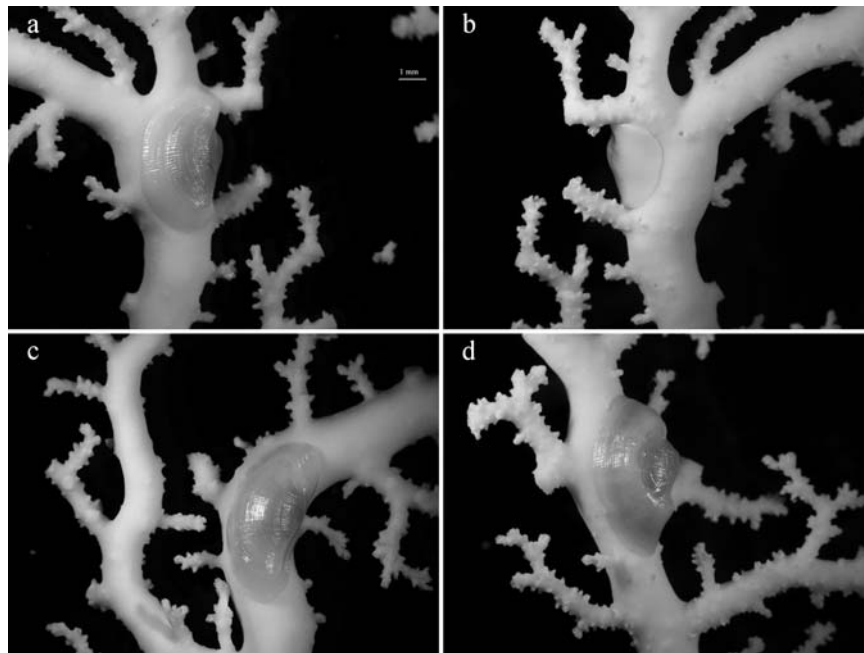


Figure 5. *Pedicularia sicula* on *Errina dabneyi* at several fixation points. (a) and (b) Front and back side view of one of the colony branches; (c) and (d) pediculariid fully adjusted to the morphology of the host; scale bar = 1 mm.

bycatch (69.8%) also carried *P. sicula* on their main and secondary branches (Figure 5). Abundances ranged between 1 and 223 individuals per colony (30.6 ± 46.2 ; mean \pm s.d.), with higher densities on the concave side of the stylasterid. Colour matching between the pediculariid and the host (pure white) was never observed.

The traces produced by *P. sicula* were often not clearly visible to the naked eye, only becoming evident under the stereomicroscope. They consisted of a depression on the stylasterid exoskeleton with the size and shape of the shell margin, delimited by a thick and prominent border. Whereas *P. sicula* traces on distal and tip branches were elongated, when the pediculariid adhered to the branch axis an ovulated trace was created. Several traces were also found in some colonies lacking *P. sicula* individuals. Skeleton injuries at the fixation point of the pediculariid were observed in all *E. dabneyi* (Figure 6). Many of these consisted of prominent calcareous crests. Moreover, occasional branch anastomosis (i.e. branch fusion) with a pediculariid or a scar between the two branches was found in some colonies (Figure 7).

The analysis of stomach contents did not reveal the presence of nematocysts.

Other epibionts

Several invertebrate species belonging to different taxonomic groups, such as sponges, hydroids, anthozoans, bryozoans, polychaetes, and decapods, were found attached to both dead and living sections of *E. dabneyi* skeletons. Among the anthozoans, many solitary scleractinians were recorded, of which *Caryophyllia cyathus* was the most common species (dead and alive). A few live specimens of *Javania cailleti* were observed on the thicker branches of an *E. dabneyi* colony collected at the Açor seamount at 201 m. The latter also had one *C. cyathus* specimen adhered to the base of the corallum. Moreover, soft corals (order Corallimorpharia) were found on the branch surface of some colonies. A few *E. dabneyi* hosted many barnacles of an unidentified species on the surface of the main branches and growing tips. Other colonies were infested by tube worms, with the stylasterid growing over them and leaving only the opening at the top exposed. Two squat lobsters were also recorded inhabiting one *E. dabneyi* from Princesse Alice Bank at 201 m.

Some *E. dabneyi* were growing over dead exoskeletons of *Errina atlantica*, sharing the available surface with other epibionts (e.g. sponges, bryozoans, polychaetes, and young colonies of the primnoid octocoral *Candidella imbricata*).

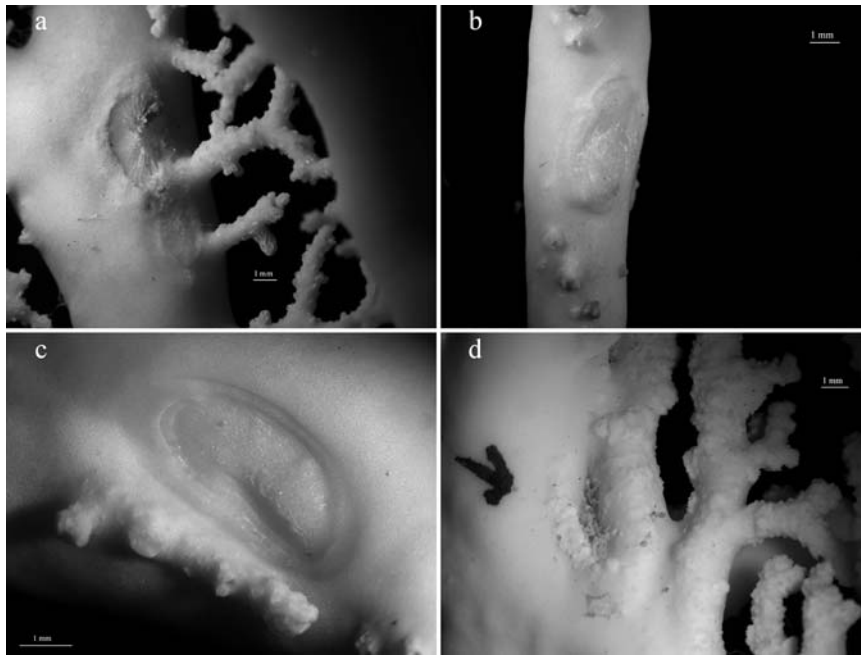


Figure 6. Skeleton injuries caused by *Pedicularia sicula*. Each letter corresponds to an *Errina dabneyi* colony.

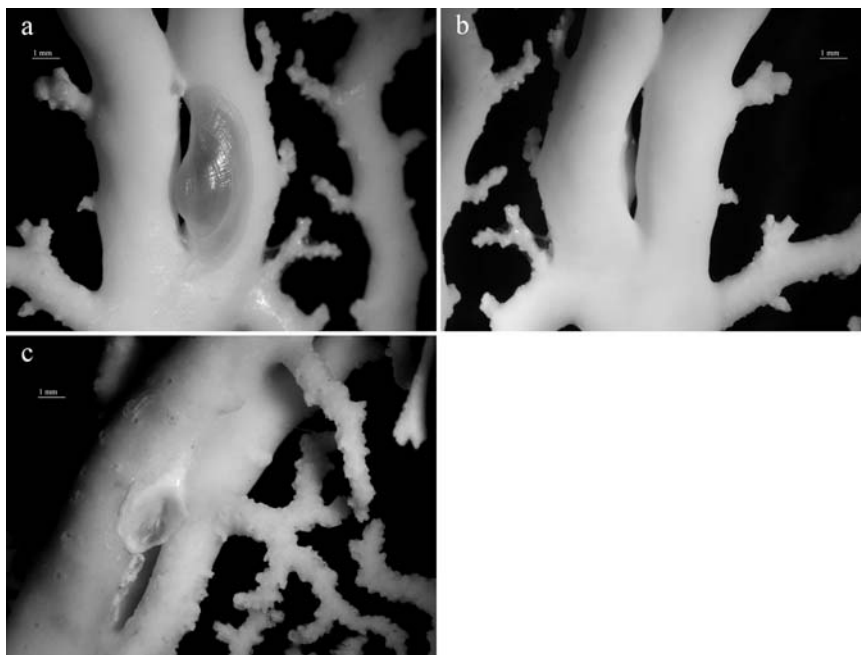


Figure 7. Branch anastomosis in *Errina dabneyi*. (a) and (b) *Pedicularia sicula*, front and back side view, DOP-2107; (c) *Pedicularia* trace, DOP-422.

Discussion

We have documented here the association between two species in the Azores, a pediculariid gastropod and its cnidarian host. The pediculariid found on the *E. dabneyi* has been identified as *P. sicula*, which agrees with the known geographical distribution for this species, the Northeast Atlantic and the Mediterranean (Bouchet and Warén, 1993). In addition to *Errina aspera* and *Stylaster ibericus* (see Table 1), *E. dabneyi* is now also confirmed

as a host of *P. sicula*, reinforcing the evidence that *P. sicula* can inhabit multiple hosts.

Species description

Specimens of *P. sicula* were well adjusted to the morphology of their host, displaying a high degree of plasticity even within the same host. The infested *E. dabneyi* hosted pediculariids of different size and shell shape, depending on the corallum fixation point.

Shape irregularity was also reported by Schmieder (1982) for *Pedicularia californica* Newcomb, 1864, living on *Stylantheca*. In the review by Bouchet and Warén (1993), it is stated that the shell shape of *Pedicularia* depends on the branch morphology of the stylasterid host. In fact, the identification of *Pedicularia* has been troublesome because of the variable shell shape, making taxonomic studies difficult (Schmieder, 1980; Bouchet and Warén, 1993). Several authors have argued that *P. decussata*, which occurs in the West Atlantic, should be considered as being *P. sicula* (Scheltema, 1971; Settepassi, 1971; Bouchet and Warén, 1993). However, because of the differences found in the teleoconch sculpture, *P. decussata* was never synonymized with the European species (Settepassi, 1971; Bouchet and Warén, 1993). Furthermore, Schmieder (1980) argues that *Pedicularia* species can exhibit an intermediate growth form which could be misidentified as another species, as for *Pedicularia ovuliformis* Berry, 1946, shown to be a growth phase of *P. californica*.

Hedley (1903) suggested that the colouration displayed by *Pedicularia* individuals is given by their hosts. Although that may be true for some species, such as *P. californica* associated with *Allopora californica* (Ostarello, 1973), this has not been observed in the present study. A wide variety of colours has been reported for *Pedicularia vanderlandi* (Goud and Hoeksema, 2001), which lives on the shallow-water stylasterid *Distichopora vervoorti*, as well as for *Pedicularia japonica* Dall, 1871, living on *Stylaster*, providing further evidence of no clear connection between the colour of the pediculariid and its host (Goud and Hoeksema, 2001).

Description of the association

Some authors suggested that the exoskeleton of the host is prevented from growing at the fixation point of *Pedicularia* by the deposition of a lime layer by the snail to optimize the foot's fixation (Zibrowius and Cairns, 1992; Bouchet and Warén, 1993). All traces observed in this study consisted of depressions on the corallum limited by a thick border, indicating that only the surrounding areas of the skeleton were able to grow after attachment of the pediculariid. Prominent crests within traces were observed, and although Zibrowius and Cairns (1992) argued that they are a result of the lime layer deposition, some of these injuries could also be radular marks. Some authors mention that *Pedicularia* feeds on stylasterids, among them *Errina* (Habe, 1955; Robertson, 1970). For instance, Giudice (1990) suggests that *P. sicula* feeds on the humours of the polyps of *E. aspera*. No direct observations were made to support these assumptions, and what the snail feeds on is not clearly known. The radular marks could indicate that *P. sicula* feeds by scraping off the mucus from the coral surface with its radular teeth, as suggested by Liltved (1989) for *Pedicularia elegantissima* Deshayes, 1863. Furthermore, the analysis of stomach contents did not reveal the presence of nematocysts, which would be expected if *P. sicula* feeds on coenenchyme tissues.

The high density of *P. sicula* per colony as well as the presence of many skeleton injuries suggests that *P. sicula* is best characterized as an ectoparasite rather than a predator. The anastomosis on branches with pediculariids or traces may indicate a defence mechanism developed by the coral, which is trying to expel the snails from its skeleton. Therefore, like other gastropod species living on corals (Goh et al., 1999), *P. sicula* seems to benefit from this close association whereas the host is being harmed, which can be

defined as parasitism (Goh et al., 1999; Buhl-Mortensen and Mortensen, 2004).

E. dabneyi epibionts

The abundant and diverse epibiontic fauna found attached to *E. dabneyi* confirms that this species is an important habitat provider for sessile invertebrates in the deep sea, where hard substratum can be a limiting resource (Buhl-Mortensen and Mortensen, 2004). Those epibionts probably also receive protection from harsh environmental conditions and predators (Metaxas and Davies, 2005). Moreover, access to food may be increased, given the fan-shaped morphology of *E. dabneyi* (Wainwright and Dillon, 1969; Wainwright and Koehl, 1976). Filter-feeding organisms can also feed on detritus or microorganisms trapped in the mucus secreted by gorgonians (Patton, 1972). Mobile epifauna, like the two squat lobsters found, probably not only have access to the food trapped on the skeleton of *E. dabneyi*, but also receive protection from predators.

Stylasterids are an important structural component of coral gardens (Roberts et al., 2006), and are highly susceptible to disturbance by fishing activities. All the material examined was coral bycatch, which means that although bottom trawling is forbidden in the Azores, *E. dabneyi* and its associated fauna are still vulnerable to the local fishery. Buhl-Mortensen and Mortensen (2004) argue that because the number of obligate symbionts is lower than that of their hosts, when the abundance of corals in a given habitat decreases, the successful reproduction of their symbionts could be compromised. For that reason detailed information on the species living in association with *E. dabneyi* as well as on the nature of their relationships is needed.

Supplementary material

Supplementary material is available at ICESJMS online.

Acknowledgements

We thank the captain (Fernando Serpa), chief scientists (O. Melo, D. Catarino, G. Menezes) and crew of RV "Arquipélago" for collecting the specimens, Kirsten Jakobsen and Joachim Jakobsen (Fundação Rebikoff-Niggeler) for their cooperation and imaging data, and Jorge Medeiros (CIRN/UAç) for the SEM photos. We are also grateful to R. Rosa and local fishers, in particular J. Gonçalves, for collection of specimens. This study was supported by the following projects: (1) BANCOMAC (funded by INTERREG IIIB programme); (2) "Taxonomy of cold-water corals of the Azores' seamounts" (funded by CenSeam mini-grant/2008); (3) CORAZON (funded by Fundação para a Ciência e a Tecnologia, FCT/PTDC/MAR/72169/2006); and (4) CoralFISH (funded by the EC-FP7 Programme under the priority "Sustainable Management of Resources", grant agreement no. 213144). AB-H is funded by an FRCT Doctoral grant (ref. M3.1.2/F/016/2008) and MC-S by a post-doctoral grant (SFRH/BPD/34634/2007).

References

- Álvarez-Pérez, G., Busquets, P., De Mol, B., Sandoval, N. G., Canals, M., and Casamor, J. L. 2005. Deep-water coral occurrences in the Strait of Gibraltar. In *Cold-water Corals and Ecosystems*, pp. 207–221. Ed. by A. Freiwald, and J. M. Roberts. Springer, Berlin. 1243 pp.
- Arnaud, P. M., and Zibrowius, H. 1979. L'association *Pedicularia sicula*–*Errina aspera* en Méditerranée (Gastropoda

- Prosobranchia et Hydrocorallia Stylasterina). Rapport de la Commission Internationale de la Mer Méditerranée, 25/26(4): 123–124.
- Bouchet, P., and Warén, A. 1993. Revision of the northeast Atlantic bathyal and abyssal Mesogastropoda. *Bollettino Malacologica*, 4: 746–752.
- Buhl-Mortensen, L., and Mortensen, P. B. 2004. Symbiosis in deep-water corals. *Symbiosis*, 37: 33–61.
- Cairns, S. D. 1991. A generic revision of the Stylasteridae (Coelenterata: Hydrozoa). Part 3. Keys to the genera. *Bulletin of Marine Science*, 49: 538–545.
- Cairns, S. D. 1992. Worldwide distribution of the Stylasteridae (Cnidaria: Hydrozoa). *Scientia Marina*, 56: 125–130.
- Cate, C. N. 1973. A systematic revision of the recent cypraeid family Ovulidae. *The Veliger*, 15: 1–116.
- Cossignani, T. 2006. Una nuova *Pedicularia* dal Brasile (Gastropoda: Hypsogastropoda, Ovulidae, Pediculariidae). *Malacologia Mostra Mondiale*, 51: 12–13.
- di Natale, A., and Mangano, A. 1985. *Pedicularia sicula* Swainson, 1840 in the Strait of Messina: a preliminary report. Rapport de la Commission Internationale de la Mer Méditerranée, 29: 343–344.
- Giudice, A. 1990. La famiglia Ovulidae Fleming, 1822 nel mar Mediterraneo. *Argonauta*, 6: 100–103.
- Goh, N. K. C., and Chou, L. M. 1994. The associates of Singapore gorgonians: Crustacea, Mollusca, Echinodermata and Chordata. In *Proceedings of the 3rd ASEAN – Australia Symposium on Living Coastal Resources*, Research Papers, vol. 2, pp. 215–218. Ed. by S. Sudara, C. R. Wilkinson, and L. M. Chou. Chulalongkorn University, Bangkok, Thailand.
- Goh, N. K. C., Ng, P. K. L., and Chou, L. M. 1999. Notes on the shallow water gorgonian-associated fauna on coral reefs in Singapore. *Bulletin of Marine Science*, 65: 259–282.
- Goud, J., and Hoeksema, B. W. 2001. *Pedicularia vanderlandi* spec. nov., a symbiotic snail (Caenogastropoda: Ovulidae) on the hydrocoral *Distichopora vervoorti* Cairns and Hoeksema, 1998 (Hydrozoa: Stylasteridae), from Bali, Indonesia. *Zoologische Verhandelingen (Leiden)*, 334: 77–97.
- Habe, T. 1955. Notes on *Pedicularia (Pediculariona) stylasteris* Hedley var. *Venus*, 18: 157–160.
- Hedley, C. 1903. Scientific results of the trawling expedition of H.M.C.S. “Thetis”. Mollusca (Part 2). Scaphopoda and Gastropoda. *Memoirs of the Australian Museum*, 4: 325–402.
- Liltved, W. R. 1989. Cowries and their Relatives of Southern Africa. Seacomber Publications, South Africa. 208 pp.
- Lorenz, F. 2008. Two new Pediculariidae from Hyères Seamount, eastern central Atlantic (Gastropoda: Cypraeoidea). *Acta Conchyliorum*, 10: 1–5.
- Lorenz, F., and Fehse, D. 2009. The Living Ovulidae. A Manual of the Families Ovulidae, Pediculariidae and Eocypraeidae. *ConchBooks*, Hackenheim. 650 pp.
- Metaxas, A., and Davies, J. 2005. Megafauna associated with assemblages of deep-water gorgonian corals in Northeast Channel, off Nova Scotia, Canada. *Journal of the Marine Biological Association of the UK*, 85: 1381–1390.
- Morton, B. 1988. Partnerships in the Sea: Hong Kong’s Marine Symbioses. Hong Kong University Press, Hong Kong.
- Oliverio, M., Chemello, M., and Taviani, M. 1995. Host association and external morphology of *Dentiovula dorsuosa* from the Red Sea (Prosobranchia, Caenogastropoda, Ovulidae). *Argonauta*, 9: 23–30.
- Ostarello, G. L. 1973. Natural history of the hydrocoral *Allopora californica* Verrill (1866). *Biological Bulletin*, 145: 548–564.
- Patton, W. K. 1972. Studies on the animal symbionts of the gorgonian coral *Leptogorgia virgulata* (Lamarck). *Bulletin of Marine Science*, 22: 419–431.
- Roberts, J., Wheeler, A., and Freiwald, A. 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science*, 312: 543–547.
- Robertson, R. 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. *Pacific Science*, 24: 43–54.
- Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow water benthic marine gastropods. *Biological Bulletin*, 140: 284–322.
- Schiaparelli, S., Canapa, A., Barucca, M., and Boyer, M. 2005. Phylogenetic relationships within the Ovulidae (Gastropoda: Cypraeoidea) based on 16S rRNA gene. *Marine Biology*, 147: 411–420.
- Schmieder, R. W. 1980. Intermediate forms and range extension of *Pedicularia californica* and *Pedicularia ovuliformis*. *The Veliger*, 22: 382–384.
- Schmieder, R. W. 1982. Shape irregularity in *Pedicularia californica*. *The Veliger*, 24: 272.
- Settepassi, F. 1971. Molluschi marini viventi nel Mediterraneo. *Familia Amphiperatidae*. *Atlante Malacologico*, 2: 1–3.
- Simone, L. R. L. 2005. Two new limpet-like gastropods from Canopus Bank, N.E. Brazil (Caenogastropoda, Hipponicidae and Pediculariidae). *Strombus*, 12: 5–11.
- Théodor, J. 1967. Contribution l’étude des gorgones (VI): la dénudation des branches des gorgones par des mollusques prédateurs. *Vie et Milieu*, 18: 73–78.
- Wainwright, S. A., and Dillon, J. R. 1969. On the orientation of sea fans (genus *Gorgonia*). *Biological Bulletin*, 136: 130–139.
- Wainwright, S. A., and Koehl, M. A. R. 1976. The nature of flow and the reaction of benthic Cnidaria to it. In *Coelenterate Ecology and Behavior*, pp. 5–21. Ed. by G. O. Mackie. Plenum Press, New York.
- Wisshak, M., López Correa, M., Zibrowius, H., Jakobsen, J., and Freiwald, A. 2009. Skeletal reorganisation affects geochemical signals, exemplified in the stylasterid hydrocoral *Errina dabneyi* (Azores Archipelago). *Marine Ecology Progress Series*, 397: 197–208.
- Wu, S. K., Chen, C. C., and Chang, K. H. 1990. Three ovulids (Gastropoda: Ovulidae) from southern Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica (Taipei)*, 29: 273–282.
- Zibrowius, H., and Cairns, S. D. 1992. Revision of the northeast Atlantic and Mediterranean Stylasteridae (Cnidaria: Hydrozoa). *Mémoires du Muséum National d’Histoire Naturelle (Serie A, Zoologie)*, 153. 136 pp.