

# Piggybacking pycnogonids and parasitic narcomedusae on *Pandea rubra* (Anthomedusae, Pandeidae)

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**Abstract:** Associations between pycnogonids and the mesopelagic anthomedusan *Pandea rubra* are reported from two *in situ* video footage records off the Pacific coast of northern Japan, and from a plankton sample collected in the Weddell Sea (one juvenile of the pycnogonid *Pallenopsis* (*Bathypallenopsis*) *tritonis*). This is the first pelagic record of a pycnogonid in the Southern Ocean and the first record of an association between pycnogonids and a hydroidomedusa at mesopelagic depths. Taxonomic descriptions of both host and associate are given. Two early stages of a parasitic narcomedusa adhered to the medusan subumbrella are also reported. Possible origins for the pycnogonid-medusa association are postulated.

**Key words:** Antarctica, anthomedusa, association, Japan, mesopelagic, pycnogonid

## Introduction

Pycnogonids are marine arthropods that are usually benthic in habitat. However, occasionally they are observed swimming in coastal surface waters (Clark & Carpenter 1977) or are found in plankton samples collected in upper waters (Lebour 1916, Ohshima 1933, Franc 1951). Records of pycnogonids in deep-water plankton samples are unusual. Hedgpeth (1962) summarized only six records of bathypelagic pycnogonids, almost all concerning the occurrence of *Pallenopsis* (*Bathypallenopsis*) *calcarena* Stephensen in Atlantic and Pacific waters. Stock (1964) described *P. juttingae* from a plankton sample collected in the Bay of Biscay. Mauchline (1984) found *P. calcarena*, *P. scoparia* Fage and *P. tritonis* Hoek in bathypelagic samples from the northeastern Atlantic Ocean. Recently, the occurrence of *P. tritonis*, *P. calcarena*, *P. juttingae*, *P. mollissima* (Hoek), *P. scoparia* and perhaps *P. tydemani* Loman has been reported from mesopelagic depths in the North Atlantic (Bamber 2002a, 2000b). Our discovery of a young male of *P. tritonis* in a plankton sample collected at mesopelagic depths in the Weddell Sea is therefore notable as it is the first pelagic record of a pycnogonid from the Southern Ocean.

Hedgpeth (1962) suggested that bathypelagic pycnogonids are parasites or commensals upon larger organisms, possibly medusae, as previous observations had shown that the larval stages of pycnogonids can be parasitic on hydroidomedusae in coastal waters (Lebour 1916, Ohshima 1933, Okuda 1940). Later, Child and Harbison (1986) demonstrated, from *in situ* observations and material collected at mesopelagic depths by a manned submersible, that *P. calcarena* parasitizes the scyphomedusan *Periphylla periphylla* (Péron and Lesueur). They considered it probable that other *Pallenopsis* species would be found living in the water column and that the long, pointed distal extremities of the legs in this subgenus suggested parasitism on planktonic cnidarians. The two observations of pycnogonids resting on the exumbrella of the anthomedusan *Pandea rubra* at mesopelagic depths in Japanese waters and their simultaneous videotaping by a remotely-operated vehicle (ROV) allow us to infer with confidence that the juvenile specimen of *P. tritonis* collected in the same plankton sample as *P. rubra* in the Weddell Sea, was originally associated with this medusan substratum. *Pandea rubra* is known to occur throughout the world's oceans, with the exception of the Arctic, usually in deep waters.

To report this co-occurrence, we describe the immature specimen of *Pallenopsis tritonis* and the *Pandea rubra* specimen, and propose possible origins of this pycnogonid-

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anthomedusan association. Likewise, two vesicle-shape structures adhered to the medusan subumbrella and identified as parasitic narcomedusan larvae are described.

## Materials and Methods

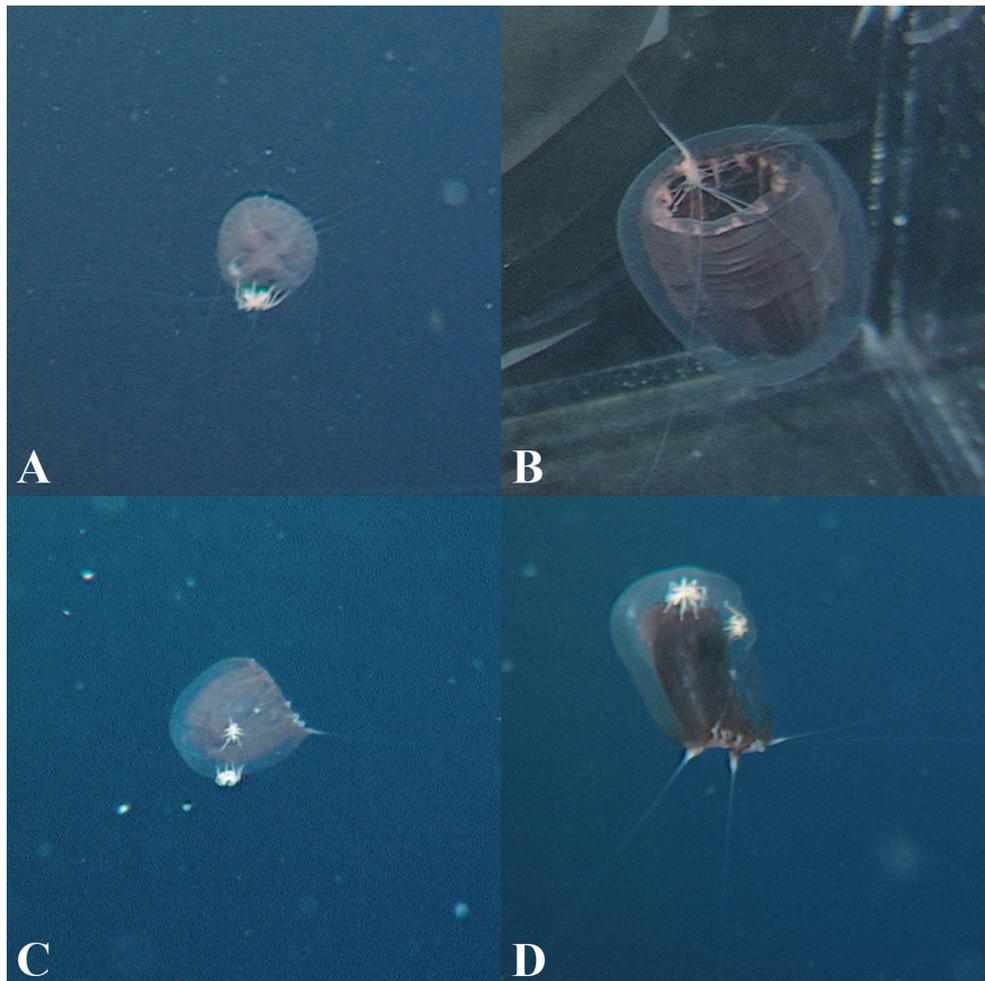
### Antarctic specimens

One immature specimen of the pycnogonid *Pallenopsis tritonis* and one specimen of the anthomedusan *Pandea rubra* were collected by a Multinet (0.25 m<sup>2</sup> open mouth, 100 µm mesh size) in the Weddell Sea on 15 January 1993 during the *Polarstern* cruise Antarktis X/7. The haul depth range was 1,000–500 m and bottom depth was 1,434 m. The geographic position was 68°38.7'S 55°27.67'W, off the Larsen Ice Shelf. Water temperature ranged from –0.4 to 0.4°C, and salinity from 34.60 to 34.64 (Boehme et al. 1995). Both specimens were preserved in 4% formalin.

### Japanese specimens

*In situ* high definition video footage of two pycnogonids perched on the exumbrella of a specimen of *P. rubra* (Fig. 1A) was taken south of Hokkaido Island, Japan (41°00.37'N, 144°41.27'E), below Oyashio Current-derived waters at 14:22 by the ROV HyperDolphin (JAMSTEC) at 792 m depth on Dive 98 (22 April 2002). Sampling was attempted but was unsuccessful. Physico-chemical parameters of the environment were as follows: temperature 2.96°C, salinity 34.25, dissolved oxygen 3.67 ml L<sup>-1</sup>, sigma-t 27.29 kg m<sup>-3</sup>. A second individual of this anthomedusan species (Fig. 1B) was observed and sampled at 15:18 at 868 m depth (temperature 2.86°C, salinity 34.29, dissolved oxygen 3.54 ml L<sup>-1</sup>, sigma-t 27.33 kg m<sup>-3</sup>) during the same dive and the *in situ* identification of the medusan was confirmed on board the vessel.

A second observation of two pycnogonids piggybacking on *P. rubra* (Fig. 1C, D) was made off the east coast of



**Fig. 1.** *In situ* images of the mesopelagic anthomedusa *Pandea rubra* Bigelow, 1913; A, aboral view taken at 792 m depth during ROV HyperDolphin Dive 98 with one adult and one juvenile (?) pycnogonid attached; B, at 868 m depth within a gate sampler (Lindsay 2003) during ROV HyperDolphin Dive 98; C, at 913 m depth during ROV HyperDolphin Dive 105 with one adult and one juvenile (?) pycnogonid attached; D, another frame grab of the same individuals as in C.

northern Honshuu (39°51.97'N, 144°21.77'E), below a warm core eddy of the Kuroshio Current, between 16:11 and 16:19 by the ROV HyperDolphin (JAMSTEC) at 913 m depth on Dive 105 (01 May 2002). An egg-bearing male and a smaller pycnogonid of just under half the size of the male were observed attached to the aboral end of the exumbrella at the level to which the subumbrella extends. Sampling was attempted but was unsuccessful. Physico-chemical parameters of the environment were as follows: temperature 3.34°C, salinity 34.34, dissolved oxygen 0.81 ml L<sup>-1</sup>,

sigma-t 27.32 kg m<sup>-3</sup>.

## Results

### Systematic account

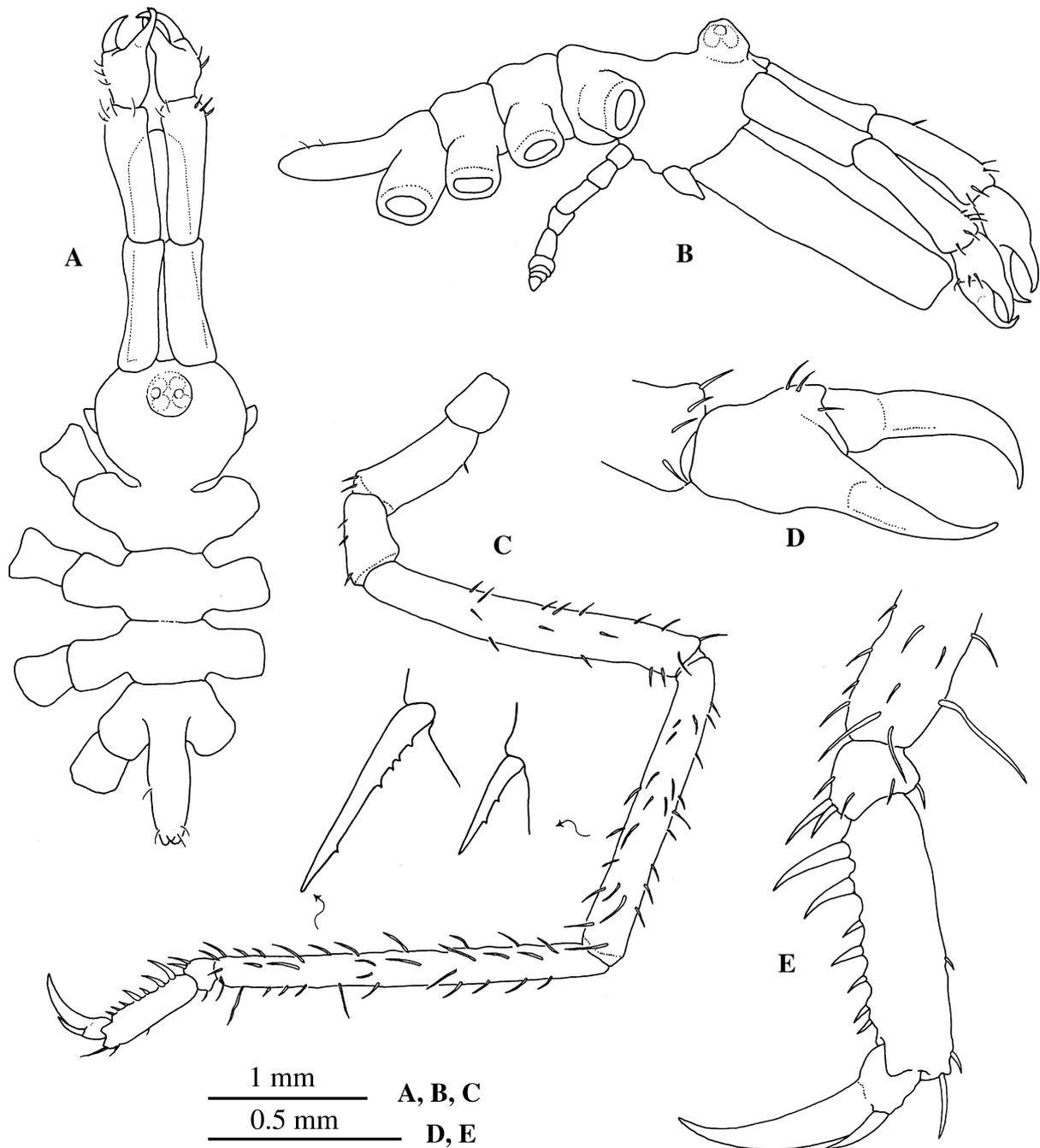
Phylum Arthropoda von Siebold, 1845

Class Pycnogonida Latreille, 1810

Family Pallenopsidae Fry, 1978

Genus *Pallenopsis* Wilson, 1881

Subgenus *Bathypallenopsis* Stock, 1975



**Fig. 2.** *Pallenopsis* (*Bathypallenopsis*) *tritonis*; A, trunk in dorsal view; B, trunk in lateral view; C, third leg with tibial spines shown at higher magnification; D, chela; E, distal leg segments.

*Pallenopsis (Bathypallenopsis) tritonis* Hoek, 1883

### Description of the Antarctic specimen

Immature. Trunk segmented, smooth (Fig. 2A). Lateral processes slightly longer than their diameters, without tubercles or spines, and separated by more than half their diameters (Fig. 2B). Neck rounded. Ocular tubercle at the anterior extreme of segment, bearing four eyes and two latero-distal papillae. Proboscis two thirds of trunk length, wider proximally and slightly oriented downwards (Fig. 2B). Abdomen almost horizontal, with few, small setae extending beyond distal rim of first coxa of fourth leg.

Chelifores long, scape consisting of 2 well-articulated segments, second segment slightly longer than the first, with some small distal setae (Fig. 2B). Chela palm with few setae near the movable finger (Fig. 2D). Fingers well curved, longer than the palm, tips overlapping. Lateral palp buds short. Oviger not fully developed, 9-segmented, without setae.

Second coxa of the third leg longer than both first and third coxa together (Fig. 2C). Femur with some small spines that increase in length and number towards the second tibia, the latter being the longest segment. Tibial spines with distal denticulation. Tarsus very short with a long ventral spine and a few short setae (Fig. 2E). Propodus straight, with two strong proximal spines on the heel and five small spines on the sole. Claw large, longer than three-fourths of the propodal length; auxiliaries about one third of main claw (Fig. 2E).

### Measurements (in mm)

Trunk length (from chelifore insertion to the tip of fourth lateral process): 2.67; trunk width (across second lateral processes): 1.42; proboscis length: 1.97; chelifore scape 1: 0.75; chelifore scape 2: 0.8; abdomen length: 0.77; third leg, coxa 1: 0.35; coxa 2: 0.95; coxa 3: 0.5; femur: 2.22; tibia 1: 2.07; tibia 2: 2.45; tarsus: 0.12; propodus: 0.72; main claw: 0.6; auxiliary claw 0.2.

### Remarks

This specimen belongs to the subgenus *Bathypallenopsis* according to the shape of the chela, the articulation of the scape and the reduced auxiliary claws. Within this subgenus, it may be assigned to the *tydemani*-group (*sensu* Stock 1975) by its styliform proboscis. Two species of *Pallenopsis (Bathypallenopsis)* have been recorded from Antarctic waters, namely *P. longiseta* Turpaeva and *P. meridionalis* Hodgson (Child 1995); both belong to the *mollissima*-group (Stock 1975). Our specimen does not fit with the description of either of these species but the morphological features agree with those of *P. tritonis* within the range of variation observed by Bamber (2002a), except for the ratios scape 1: scape 2 and the abdomen length:abdomen width that are slightly lower (0.93 compared with

0.95–1.23 and 3 compared with 3.31–6.55, respectively). However, the tibial spines are denticulated distally as observed in specimens of *P. tritonis* from the northern hemisphere and the above mentioned differences may be due to the early stage of development. It is also similar to *P. calcanea*, but this last species does not have auxiliary claws.

Phylum Cnidaria Verrill, 1865

Class Hydroidomedusae Claus, 1877

Sub-class Anthomedusae Haeckel, 1879

Order Filifera Kühn, 1913

Family Pandeidae Haeckel, 1879

*Pandea rubra* Bigelow, 1913

### Description of the Antarctic specimen

Umbrella dome-shaped, 15 mm in height, 14 mm wide (Fig. 3A). Mesogloea thin but consistent. Exumbrella transparent, smooth, without cnidocyst tracks. Stomach brownish in preserved specimen, cruciform, with wide base, hanging down to one fourth of the subumbrellar cavity. Mouth with four lips very crenulated. Mesenteries short. Radial canals four, wide, jagged. Gonads not discernible. Fourteen tentacles, all equal, with wide triangular basal bulbs and abaxial spurs. Velum medium.

### Remarks

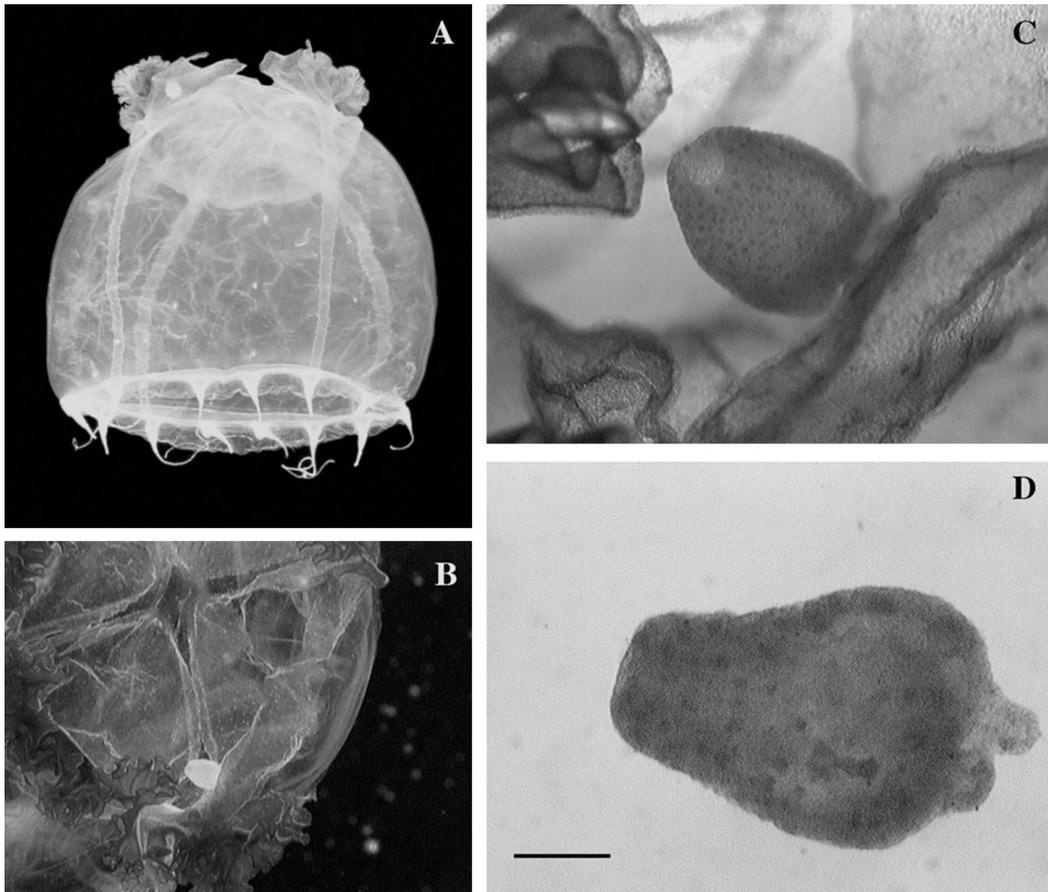
The specimen fits the description for juveniles of *Pandea rubra* given by Russell (1953). In looking for signs of predation by the pycnogonid, two vesicle-shape structures settled side by side in the outer wall of the stomach and identified as parasitic narcomedusae were discovered (Figs. 3A–D). The smallest one (Fig. 3D) detached itself after a short time while the other one (Fig. 3B) was detached later for better microscopic examination (Fig. 3C). The descriptions of both early stages are as follows:

Sacculiform larval narcomedusan (Fig. 3C): 0.87 mm in length, 0.73 mm maximum diameter. The distal circular opening is 0.35 mm in diameter. There are six proximal points of attachment, about 0.15 mm in length each.

Pyriform larval narcomedusan (Fig. 3D): 0.75 mm in length, 0.45 mm maximum diameter. The distal circular opening is 0.25 mm in diameter. There is one proximal point of attachment, about 0.1 mm in length.

### Description of the Japanese specimens

Sampled specimen description as for the Antarctic specimen except for size (30 mm height, 38 mm wide in partially contracted state), tentacle number (16), and that the stomach colour was red in the live animal, brown when preserved. Unsampled individuals had 24 (Fig. 1A) and 18 (Fig. 1C, D) tentacles respectively but size was unable to be estimated.



**Fig. 3.** *Pandea rubra*; A, view of the specimen with the subumbrella everted. Note the whitish spot that is the larger and sacculiform parasitic narcomedusan. B, location of the sacculiform parasitic narcomedusan attached to the stomach. C, view of the sacculiform parasitic narcomedusan after detachment. D, view of the pyriform parasitic narcomedusan after detachment, scale=0.15 mm.

### Discussion

The co-occurrence of the pycnogonid and the anthomedusan in the same plankton sample from the Weddell Sea suggested that *Pandea rubra* was the pelagic substratum to which *Pallenopsis tritonis* was attached. Both specimens were the largest organisms by far in the mesozooplankton sample, which was numerically dominated by small copepods. The volume of water filtered was relatively small ( $125\text{ m}^3$ ) and, because of the rarity of both of these species in plankton samples, the probability that these two large, rare animals were collected independently by chance in the same net tow was considered extremely low. This assumption was further validated by the two *in situ* observations of pycnogonids in association with *P. rubra* at mesopelagic depths in Japanese waters. To date, nine pycnogonid species had been found attached to ten medusae species (Table 1) but the possibility that any of these interspecific associations are exclusive has not yet been addressed.

*Pallenopsis tritonis* is widespread in the north Atlantic and the north Pacific, at depths ranging from 344 to 7,280 m, and it is associated with gelatinous plankton (Bamber

2002a). The present record is the first for the southern hemisphere. *P. rubra* can attain 10 cm in height (Pagès unpublished data) and it lives mainly in mesopelagic waters of all oceans except the Arctic (Kramp 1961). In waters off Japan it has previously been reported, as *Hydroidomedusae* sp. A, from 703 m depth in Sagami Bay ( $35^{\circ}00.07'N$ ,  $139^{\circ}14.07'E$ ; temperature  $4.8^{\circ}C$ , salinity 34.25, dissolved oxygen  $1.6\text{ ml L}^{-1}$ ) (Hunt & Lindsay 1999) and more recently as *P. rubra* (Lindsay & Hunt 2005, Lindsay 2006). In the Weddell Sea, it has been collected mostly in the 500–1,000 m depth range and once in the 1,000–2,000 m depth range (Pagès et al. 1994), always in very low densities (up to  $0.66\text{ specimens }10^4\text{ m}^{-3}$ ). In the same waters, a more discrete vertical sampling collected specimens in three consecutive 100-m range hauls between 700 and 1,000 m depth (up to  $0.30\text{ specimens }10^4\text{ m}^{-3}$  respectively) (Pugh et al. 1997). In the Antarctic Polar Frontal Zone it has been collected in the 600–800 and 800–1,000 m depth ranges, respectively (up to  $0.12\text{ specimens }10^4\text{ m}^{-3}$ ) (Pagès et al. 1996).

Child & Harbison (1986) concluded that *P. scoparia* parasitized *Periphylla periphylla* because most of the jellyfish

**Table 1.** Records of pycnogonid species associated with planktonic medusae.

Pycnogonid	Medusae	Reference
<i>Ammothea</i> sp.	<i>Polyorchis karafutoensis</i>	Uchida 1927
<i>Ammothea alaskensis</i>	<i>Polyorchis karafutoensis</i>	Okuda 1940
<i>Anoplodactylus petiolatus</i>	<i>Clytia hemisphaerica</i> <i>Amphinema dinema</i>	Franc 1951
<i>Anoplodactylus petiolatus</i>	<i>Obelia</i> sp.	Dogiel 1913, Lebour 1945
<i>Anoplodactylus petiolatus</i>	<i>Obelia</i> sp., <i>Cosmetira pilosella</i> , <i>Leuckartiara octona</i> , <i>Clytia hemisphaerica</i>	Lebour 1916
<i>Anoplodactylus virescens</i>	<i>Sarsia eximia</i>	Dogiel 1913, Lebour 1945
<i>Endeis spinosa</i>	<i>Obelia</i> sp.	Lebour 1916
<i>Pallenopsis calcanea</i>	?	Hedgpeth 1962
<i>Pallenopsis scoparia</i>	<i>Periphylla periphylla</i>	Child & Harbison 1986
<i>Pallenopsis tritonis</i>	<i>Pandea rubra</i>	This study
<i>Phloxichilidium femoratum</i>	<i>Sarsia eximia</i>	Dogiel 1913, Lebour 1945
Unidentified juvenile	<i>Periphylla periphylla</i>	Mauchline 1984
Unidentified species	<i>Voragonema (Benthocodon) pedunculata</i> <i>Aeginura grimaldii</i>	Larson et al. 1991

tentacles had been eaten and the gut diverticulae of the pycnogonid were filled with cnidocysts. Was *P. tritonis* parasitizing *P. rubra*? The tentacles of the Antarctic anthomedusan were contracted and no signs of predation could be discerned on them, or on any other parts of the body, apparently indicating that the association was not parasitic. No obvious signs of predation were seen on the medusae from the *in situ* observation either. However, this is not conclusive evidence as the gut diverticulae of *P. tritonis* were not examined due to the tiny size of the specimen, and the specimens observed by the ROV were unable to be sampled.

Staples & Watson (1987), in reviewing the associations between hydroids and pycnogonids, referred to the occurrence of pycnogonid larvae (protonymphs) encapsulated in highly modified polyps named “fusiform bodies”, “pyriform sacs” “pyriform vesicles” and “galls”. The life cycle of *Pallenopsis* is poorly known, particularly whether *Pallenopsis* develops through larval encystment. Adult pycnogonids mate and their eggs are then carried by the male until they hatch as typical protonymphon larvae (Bain 2003). It is assumed that both the adults and larvae of pycnogonids feed on the medusae but the only evidence is that demonstrated by Child & Harbison (1986).

How do the pycnogonids reach the anthomedusan? Child & Harbison (1986) suggested two mechanisms of host location, namely generation of benthic polyps or resting of the medusae on the bottom (as they had previously observed such an event). The first explanation is not plausible for *Periphylla periphylla* as Jarms et al. (1999) have demonstrated that this species is holoplanktonic.

The medusa stage of *P. rubra* has neither been observed staying on the sea bottom nor has it been reported from benthic-pelagic samples. The polyp stage is believed to be *Campaniclava clionis* Vanhöffen (Rees 1967), and is an epizoic associate of the euthecosome pteropod *Clio recurva* (Childern) (see Lalli & Gilmer 1989, p. 127), which is

found throughout the world’s temperate and tropical oceans. Also attached to the shell of another pteropod, *Clio cuspidata* (Bosc), lives the polyp stage of *P. conica*, the only congeneric medusa species (Picard 1956), if *Pandea cybeles* Alvarino 1988 is an invalid species as suspected (Pagès, unpublished information). Likewise four little-known polyp species, two of them also pandeids, have been identified attached to four different euthecosome pteropod species (Lalli & Gilmer 1989, p. 128). A hypothesis arises from these coincidences. Like many epibenthic pycnogonids that live on benthic hydroids (e.g. Staples & Watson 1987), the larval stages (protonymphs) of *P. tritonis* could develop and grow on hydroids epizoic on pteropods. Then, protonymphs could ride piggyback on medusae buds before these are released from the hydrorhiza, the hydroid stolon. The key question is if *Pallenopsis* eggs or protonymphs could become encysted in the hydroids that are epizoic on *Clio*. The present two *in situ* observations suggest that the pycnogonids at least reach adulthood on their host, but whether the protonymphs are transferred directly to adult medusae by the egg-bearing male pycnogonid after hatching or somehow find their way to polyp colonies growing on euthecosome pteropods remains to be verified. A report (Larson et al. 1991) of pycnogonids attached to *Voragonema pedunculata*, a trachymedusa without a polyp stage in its life cycle, in combination with the report concerning parasitism of the scyphomedusa *P. periphylla* (Child & Harbison 1986), also holoplanktonic, suggests that the former hypothesis, not involving an intermediate polyp host, is more likely. Perhaps the protonymphon larvae have larval legs with greatly elongated distal spines, as has been reported for *Phoxichilidium femoratum*, which is also a member of the family Phoxichilidiidae to which *Pallenopsis* has been proposed to belong by some authors (Stock 1978, Arnaud & Bamber 1987). They may also have cement glands on the chelifores that can secrete elongate filaments, also reported for *P. femoratum*, and either of

these could aid in passive distribution of the larvae similar to the strategy used by baby spiders or lamellibranch postveligers until they are “captured” by their new hosts. Alternatively the larvae-bearing male pycnogonid may “jump ship” when a possible new host for its young comes near, as short bouts of swimming have been reported for some species.

The parasitic narcomedusan larvae (Fig. 3, C–D) could not be identified to species level owing to their early stage of development. Similar larvae parasitizing medusae had been described and drawn (e.g. Uchida 1928, Bouillon 1987) but we provide the first photographs. This is also the first record involving a medusa species of the highly diverse family Pandeidae.

Hopefully, future *in situ* observations on midwater medusae with piggybacking *Pallenopsis*, and intensive searches of polyp colonies on euthecosome pteropods for protonymphon larvae will shed more light on this biological association and the life cycle of these intriguing arthropods.

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