

# A ten-legged sea spider (Arthropoda: Pycnogonida) from the Lower Devonian Hunsrück Slate (Germany)

GABRIELE KÜHL\*†, MARKUS POSCHMANN‡ & JES RUST\*

\*Steinmann Institute for Geology, Mineralogy and Palaeontology, Division of Palaeontology,  
Nussallee 8, 53115 Bonn, Germany

‡Generaldirektion Kulturelles Erbe RLP, Direktion Landesarchäologie, Referat Erdgeschichte,  
Große Langgasse 29, 55116 Mainz, Germany

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**Abstract** – A new sea spider (Arthropoda: Pycnogonida) from the Lower Devonian Hunsrück Slate (Germany) is described as *Pentapantopus vogteli* gen. et sp. nov. This is the fifth pycnogonid species known from this exceptional fossil Lagerstätte. The most conspicuous character of the new species is the presence of five pairs of walking legs. This character, in concert with a reduced abdomen, indicates a phylogenetic position of *P. vogteli* among the crown group pycnogonids. *P. vogteli* extends the knowledge of fossil pycnogonid body plans and underlines the significance of the Hunsrück Slate, as this locality shows the highest diversity of sea spiders for the entire fossil record so far.

Keywords: Arthropoda, sea spider, Pycnogonid, Hunsrück Slate, Lower Devonian, *Pentapantopus*.

## 1. Introduction

Pycnogonids or sea spiders are arthropods with a quite unusual morphology. They seem to consist only of legs and indeed, in some pycnogonids, organs extend into the legs, because of lack of space in the reduced trunk region. More than 1300 species of extant pycnogonids have been described, showing a worldwide distribution from marine abyssal depths to the intertidal zone (Arango & Wheeler, 2007). The morphology of sea spiders is quite well known, in contrast to their lifestyles. An overview of the most relevant facts in pycnogonid biology is given in Arnaud & Bamber (1987).

Though today quite common, there is only a sparse fossil record for sea spiders. The earliest record is a larval specimen that is found in Upper Cambrian deposits (Waloszek & Dunlop, 2002). Doubts concerning the pycnogonid nature of these fossils (Bamber, 2007) were partly unsubstantiated (Edgecombe, 2010). An Upper Ordovician sea spider has been recorded from a Lagerstätte deposit in central Manitoba, Canada (Rudkin *et al.* 2009), but no detailed information on this discovery has been published yet. A remarkably well-preserved fossil of an adult sea spider is *Haliestes dasos* Siveter, Sutton, Briggs & Siveter, 2004 from the Silurian Herefordshire Lagerstätte (Siveter *et al.* 2004). The Lower Devonian Hunsrück Slate is another Lagerstätte yielding fossil pycnogonids. Four species in the same number of genera have previously been described (Bergström, Stürmer & Winter, 1980; Poschmann & Dunlop, 2006) and here we add a further new taxon. After the Lower Devonian there is a gap in the fossil record of pycnogonids, which extends to the Middle Jurassic with three species known from the La

Voulte-sur-Rhône Lagerstätte in France (Charbonnier, Vannier & Riou, 2007).

The Lower Devonian Hunsrück Slate is exceptional in providing us with a glimpse of Palaeozoic pycnogonid diversity, yielding by far the highest number of fossil specimens. *Palaeoisopus problematicus* Broili, 1928 is most common with more than 60 specimens. *Palaeopantopus maucheri* Broili, 1929 is known from four specimens and *Palaeothea devonica* Bergström, Stürmer & Winter, 1980 and *Flagellopantopus blocki* Poschmann & Dunlop, 2006 are each known from single finds. Some of the Hunsrück Slate species (excluding *P. devonica* and the species described herein) differ from all other extant and extinct pycnogonids in having an abdomen (including the telson) with three (*P. maucheri* and *F. blocki*) or even five (*P. problematicus*) segments. This might be phylogenetically relevant as it is interpreted as a plesiomorphic condition in pycnogonids (Hedgpeth, 1955; Waloszek & Dunlop, 2002; Siveter *et al.* 2004; Poschmann & Dunlop, 2006). This view has recently been challenged by combined analysis of molecular and morphological data (Arango & Wheeler, 2007). Here the fossil pycnogonids *P. devonica*, *P. maucheri*, *H. dasos* and *P. problematicus* grouped within the paraphyletic grown group Ammotheidae.

## 2. Geological setting

The fossil association described here originates from the Obereschenbach Quarry, an open-cast mine southwest of Bundenbach, and was found between 1996 and 1997 (Peter Hohenstein, pers. comm. 2011) not long before roof slate production ceased in 1999. The precise stratigraphic horizon is given as the Wingertshell member (*sensu* Schindler *et al.* 2002). The sequence of roof slates exposed in the Eschenbach-Bocksberg

†Author for correspondence: gkuehl@uni-bonn.de

and the adjacent Obereschenbach quarries is about 140 m thick and thus represents only a part of the entire Hunsrück Slate sediment sequence (Schindler *et al.* 2002; Sutcliffe, Tibbs & Briggs, 2002). This unit has been assigned to the middle Kaub Formation of Early Emsian age, as evidenced by biostratigraphic data (e.g. Mittmeyer, 1980; Schindler *et al.* 2002; De Baets *et al.* in press). It is famous for the occurrence of a well-preserved, pyritized and highly diverse fauna comprising more than 270 taxa (see Bartels, Briggs & Brassel, 1998 and Köhl *et al.* 2011 for overviews). The dark grey clay to silt-sized sediments containing these exceptionally preserved fossils were interpreted as having been deposited within the intrashelf central Hunsrück Basin (e.g. Dittmar, 1996) at the distal edge of a submarine fan by low-density turbidity currents, at or just below storm-wave base (Sutcliffe, Briggs & Bartels, 1999; Sutcliffe, Tibbs & Briggs, 2002). Although anoxia within the sediment favoured pyritization, the water column was well oxygenated and allowed a diverse epifauna to be established (Briggs *et al.* 1996; Bartels *et al.* 2002; Sutcliffe, Tibbs & Briggs, 2002). Ostracod events periodically overwhelmed parts of this fauna and led to their autochthonous to parautochthonous burial (e.g. Bartels, Briggs & Brassel, 1998; Sutcliffe, Briggs & Bartels, 1999; Sutcliffe, Tibbs & Briggs, 2002; Bartels & Poschmann, 2002).

### 3. Material and methods

This investigation is based on two incomplete specimens, associated with a crinoid and two further undeterminable pycnogonid specimens. The fossil bearing slab with the collection number MNHM PWL 2010/5-LS is stored in the Natural History Museum Mainz; State Collection of Natural History, Rhineland-Palatinate. It was prepared by Peter Hohenstein, Lautertal.

The specimens were photographed using a D100 and a JVC Camera KY-F70B through a Leica MZ16 microscope. Radiographs were obtained with a Phoenix v|tome|x s Micro Tomograph using 120 kV and 130  $\mu$ A, but yielded no additional information. Drawings were either made using a Leica MZ75 stereomicroscope with a *camera lucida* attachment or using Adobe Illustrator<sup>®</sup> CS3. Adobe Photoshop<sup>®</sup> CS3 and Adobe Illustrator<sup>®</sup> CS3 were used for editing pictures. ImageJ was used for measurements.

### 4. Preservation

Four pycnogonid specimens and one crinoid *Parisangu-locrinus zaeformis* (Follmann, 1887) are associated on one slab of Hunsrück Slate. One very small pycnogonid specimen (Fig. 1a) is attached to the arms of the crinoid on the left hand side of the slab. Only the remains of one chelifore, lateral parts of the trunk and parts of three legs are preserved. A second small pycnogonid specimen (Fig. 1b) is visible near the distal part of the crinoid anal tube. Again only the remains of one

chelifore, lateral parts of the trunk and parts of three legs are preserved. On the right side of the crinoid two additional specimens are preserved (Fig. 1c, d). In the following, the terms left and right refer to the left and right side of a living animal seen from the dorsal surface. The most completely preserved specimen (Fig. 1c) is situated beneath the distal part of one crinoid arm. It is ventrally exposed, but lacks most parts of the right half of the body. Only the remains of the proximal two podomeres of the left chelifore are preserved. The right chelifore lacks the chela. Ovigerae are either not preserved or were not developed. The left palp lacks the distal part and the right palp is not preserved. The body is largely covered by crinoid arms (or brachia) and the four anterior walking legs on the right side are not preserved. The next pycnogonid specimen (Fig. 1d) is laterally embedded adjacent to the last mentioned pycnogonid specimen. It is not in contact with the crinoid. This specimen lacks parts of both chelifores, including most parts of the chelae, the distal parts of the palps, the distal parts of the first four walking legs on the left side and most distal parts of the right walking legs. From the fifth pair of walking legs no remains are preserved.

### 5. Systematic palaeontology

Class PYCNOGONIDA Latreille, 1810

Genus *Pentapantopus* gen. nov.

*Etymology.* From penta (five) and the name Pantopoda.

*Type species.* *Pentapantopus vogteli* sp. nov., by monotypy.

*Diagnosis.* Pycnogonid with elongate body and five pairs of walking legs consisting of eight podomeres plus a flattened main claw; distal leg podomeres (femur to propodus) flattened and setose; chelifores large; palps present; abdomen short.

*Pentapantopus vogteli* sp. nov.

*Etymology.* From Hans Vogtel (Rhaunen), a former slate worker, recognizing his detection of many important fossils during the process of roof-slate production.

*Diagnosis.* As for the genus.

*Holotype.* Slab MNHM PWL2010/5-LS; Figs 1c, 2 (specimen 1).

*Paratype.* Slab MNHM PWL2010/5-LS; Figs 1d, 2 (specimen 2).

*Description.* The cephalosoma of *Pentapantopus vogteli* gen. et sp. nov. bears a pair of large chelifores consisting of a long proximal segment, a second segment that is only half the length of the first one, and the terminal chela (Fig. 2a–c). The proboscis is long, probably reaching the third pair of walking legs when tucked underneath the body and directed backwards. The terminal part of it has a roundish shape and the mouth opening is triangular (Fig. 2a, b, d). The position of the proboscis in specimen 2 (Fig. 2d) indicates that it was ventrally directed in the living pycnogonid. The second pair of prosomal appendages are palps, which insert at the lateral margin of the cephalosoma posterior to the chelifores. The number of palp segments is unknown (Fig. 2a–d). The next pair of prosomal appendages is the first pair of walking legs. It is morphologically similar to the following four pairs



Figure 1. MNHM PWL2010/5-LS. Hunsrück Slate slab with crown of the crinoid *Parisangulocrinus zaeiformis* and four pycnogonid specimens. (a, b) Two specimens of undetermined pycnogonids; (c, d) two specimens of *Pentapantopus vogteli* gen. et sp. nov. Scale bar represents 3 mm.

of trunk appendages. All leg pairs are inserted at a lateral process of the body wall. This process is ornamented with up to four rings. The legs consist of eight podomeres, which can be divided into coxae I to III, femur, tibia I and II, tarsus and propodus, plus a terminal main claw (Fig. 2a, b). At least the distal podomeres (femur to propodus) were slightly flattened. Short marginal setae are situated on the dorsal margin of tibia I and II and the proximal part of the tarsus. The abdomen may be partly preserved in specimen 1 (Fig. 2a, b, e). It is a short remnant located on the expected position of an abdomen. Judging from the available evidence, it is concluded that the abdomen of *P. vogteli* gen. et sp. nov. is short and unsegmented.

**Measurements.** In comparison to other Hunsrück Slate pycnogonids, *Pentapantopus vogteli* gen. et sp. nov. is small, with a total length (chelifore to abdomen) of approximately 12 mm. In the chelifores the most proximal segment is 1.6 mm in specimen 1 and 2.1 mm in specimen 2, and it is at least twice as long as the following segment.

Referring to the walking legs of specimen 1 (specimen 2 is too incomplete) coxa 1 seems to be the shortest leg podomere and is about 0.6 mm in length. Coxa 2 is the longest podomere with 3.9 mm length in the first walking leg and 5.2 to 5.6 mm length for the walking legs II to IV. The length of coxa 2 for walking leg V is unknown. Coxa 3, which seems to function as the knee bend is again only between 0.7 and 0.8 mm in length. Tibia 1, tibia 2, and the propodus are comparable in their lengths; they vary between 1.8 and 2.5 mm. Leg I seems to be the shortest walking leg, based on the relatively short coxa 2. However, legs II to V are more or less of the same length (Table 1).

## 6. Phylogeny

Only a few attempts to resolve the internal phylogenetic relationships of the Pycnogonida including fossil

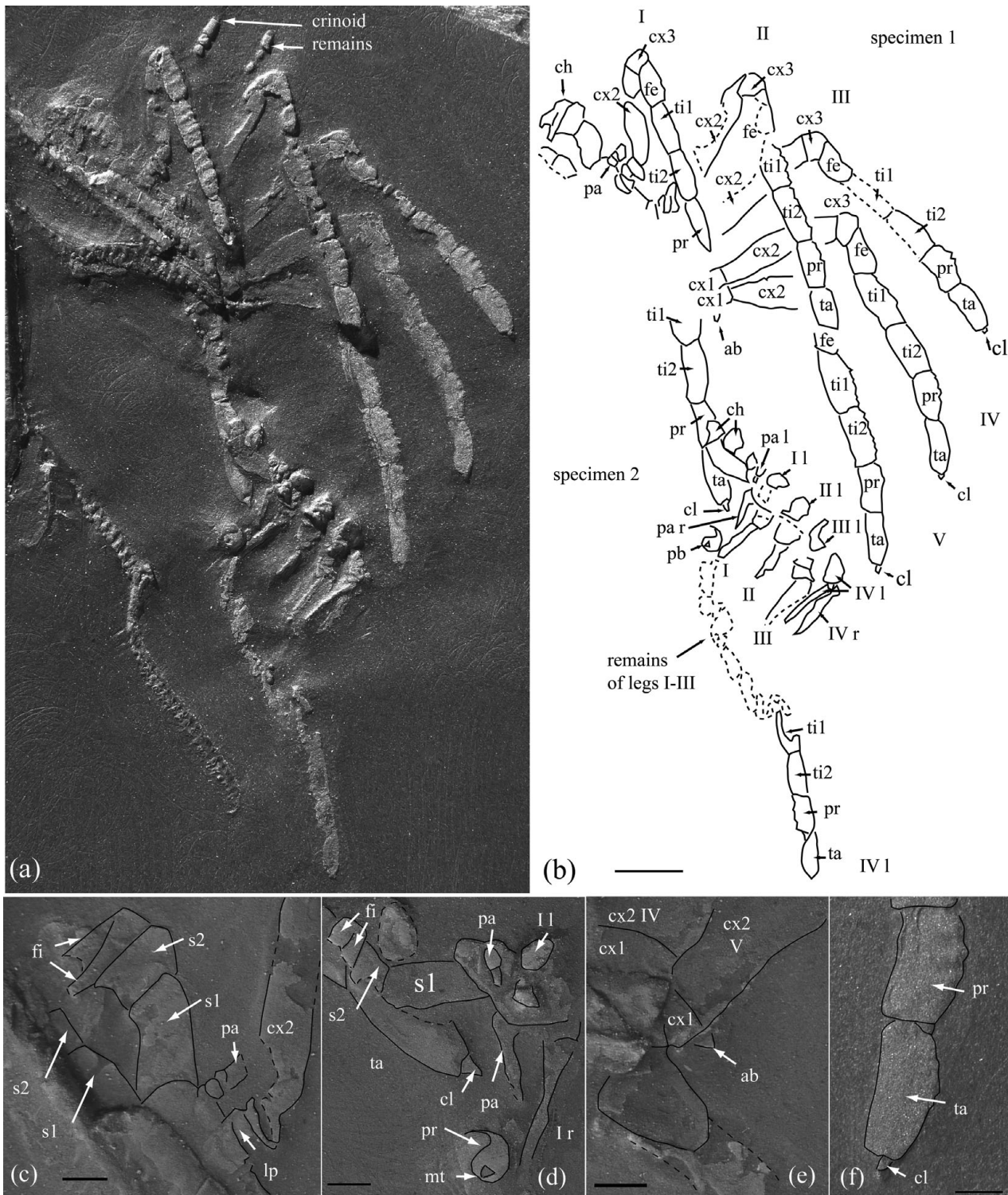


Figure 2. MNHM PWL2010/5-LS. Specimens 1 and 2 of *Pentapantopus vogteli* gen. et sp. nov. (a) Photograph; (b) interpretative drawing; (c) detail of the anterior region of specimen 1 showing the chelifore and the palp; (d) detail of the anterior region of specimen 2 showing the chelifore, palps and remains of the proboscis; (e) remains of the abdomen in specimen 1; (f) propodus, tarsus and terminal claw of the third walking leg of specimen 1. Scale bar represents 3 mm (a, b); 1 mm (c–f). Note that in (c–f) our interpretation (drawing) is superimposed on the photograph. Abbreviations: ab – abdomen; ch – chelifore; cl – claw; cx – coxa; fe – femur; fi – finger; l – left; mt – mouth; pa – palp; pb – proboscis; lp – lateral process; pr – propodus; r – right; s – segment; ta – tarsus; ti – tibia.

species are available (for a review see Dunlop & Arango, 2005) and the results are quite contradictory (for criticism see Bamber 2007). Morphology-based investigations carried out by Waloszek & Dunlop

(2002), Siveter *et al.* (2004), and Poschmann & Dunlop (2006) favour a concept with *Palaeoisopus problematicus* as a stem lineage representative of the Pycnogonida, and *Palaeopantopus maucheri* as sister

Table 1. Measurements of the appendages of *Pentapantopus vogteli* gen. et sp. nov.

	Sp 1 right	Sp 1 left	Sp 2 right	Sp 2 left	Sp 1 right	Sp 1 right	Sp 1 left	Sp 1 right	Sp 2 left	Sp 1 right
Chelifores										
S1 (proximal)	1.6	1.2	2.1							
S2	0.8		0.8							
S3 + S4 (chela)	0.6		0.8							
Legs	I				II	III		IV		V
CX1								0.6		0.6
CX2	3.9				5.2	5.6		5.4		
CX3	0.7				0.8	0.7		0.8		
Fe	1.8				1.8	1.7		1.8		
Ti1	2.2				2.4	2.4		2.5		2.5
Ti2	2.2				2.5	2.4	2.5	2.4	2.0	2.5
Pr	2.4				2.1	1.9	2.0	2.1	1.7	2.1
Ta					1.8	2.2	2.6	2.3	2.0	2.3
Abdomen*	0.3									
Proboscis†				4.1						

All measurements are length specifications and are given in mm

Sp – specimen; S – segment; CX – coxa; Fe – femur; Ti – tibia; Pr – propodus; Ta – tarsus

\* abdomen may be incomplete

† length of proboscis is interpolated as the middle part is not preserved

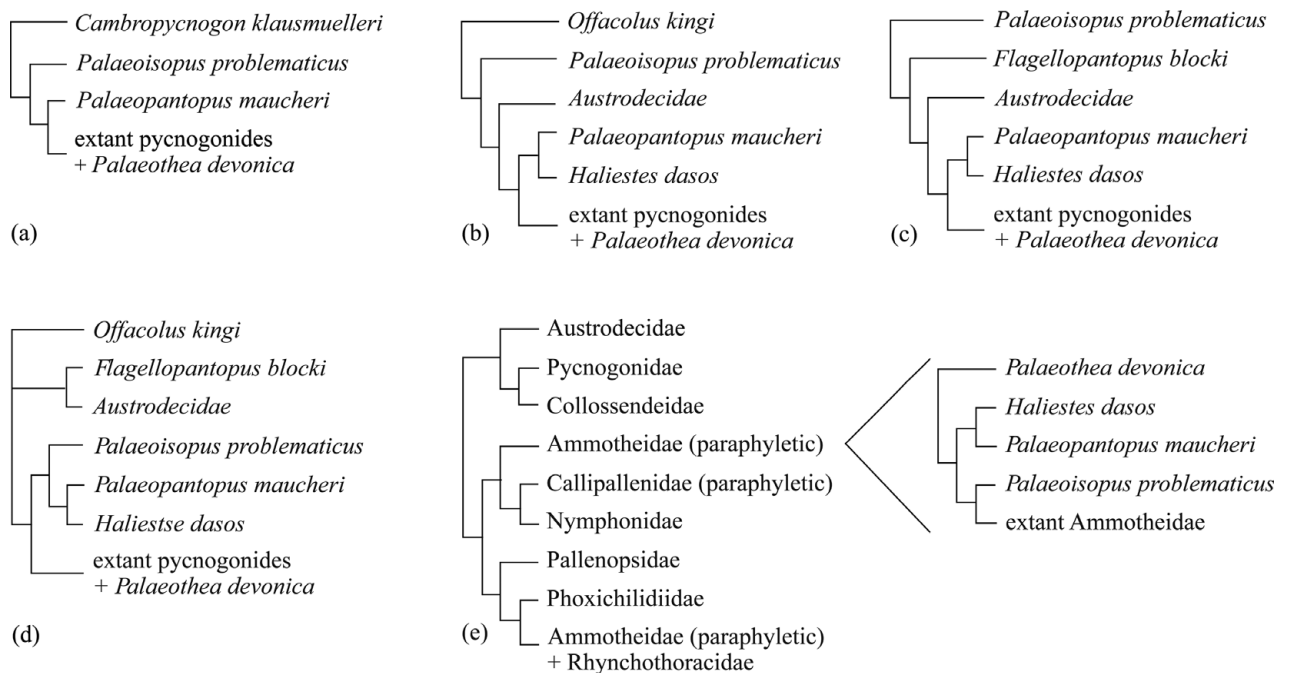


Figure 3. Published pycnogonid cladograms. (a) Waloszek & Dunlop (2002); (b) Siveter *et al.* (2004); (c) Poschmann & Dunlop (2006); (d) Charbonnier (2009); and (e) Arango & Wheeler (2007).

taxon to Recent pycnogonids including *Palaeothea devonica* (Fig. 3 a–c).

This concept follows Hedgpeth (1955) who supposed a stem lineage position of *P. problematicus* and *P. maucheri* with respect to the remaining Pycnogonida, with *P. problematicus* as the most basal taxon. This author suggested an evolutionary trend of the reduction of appendages, such as chelifores, palps or ovigers for more derived pycnogonids. The presence of a five and three segmented abdomen in *P. problematicus* and *P. maucheri* respectively was generally regarded as a plesiomorphic character state (Hedgpeth, 1955;

Bergström, Stürmer & Winter, 1980). Arango & Wheeler (2007) tested the concept of appendage reduction with a cladistic analysis based on molecular and morphological data and showed that there seems to be no such evolutionary trend within the Pycnogonida. Additionally, all fossil taxa were grouped within the extant, paraphyletic Ammotheidae with *P. problematicus* as direct sister taxon to the extant Ammotheidae, and *Palaeothea devonica* as most basal taxon of Ammotheidae (Fig. 3e). In contrast to these results, Charbonnier (2009; Fig. 3d) excluded most fossil pycnogonids from having a close relationship with the

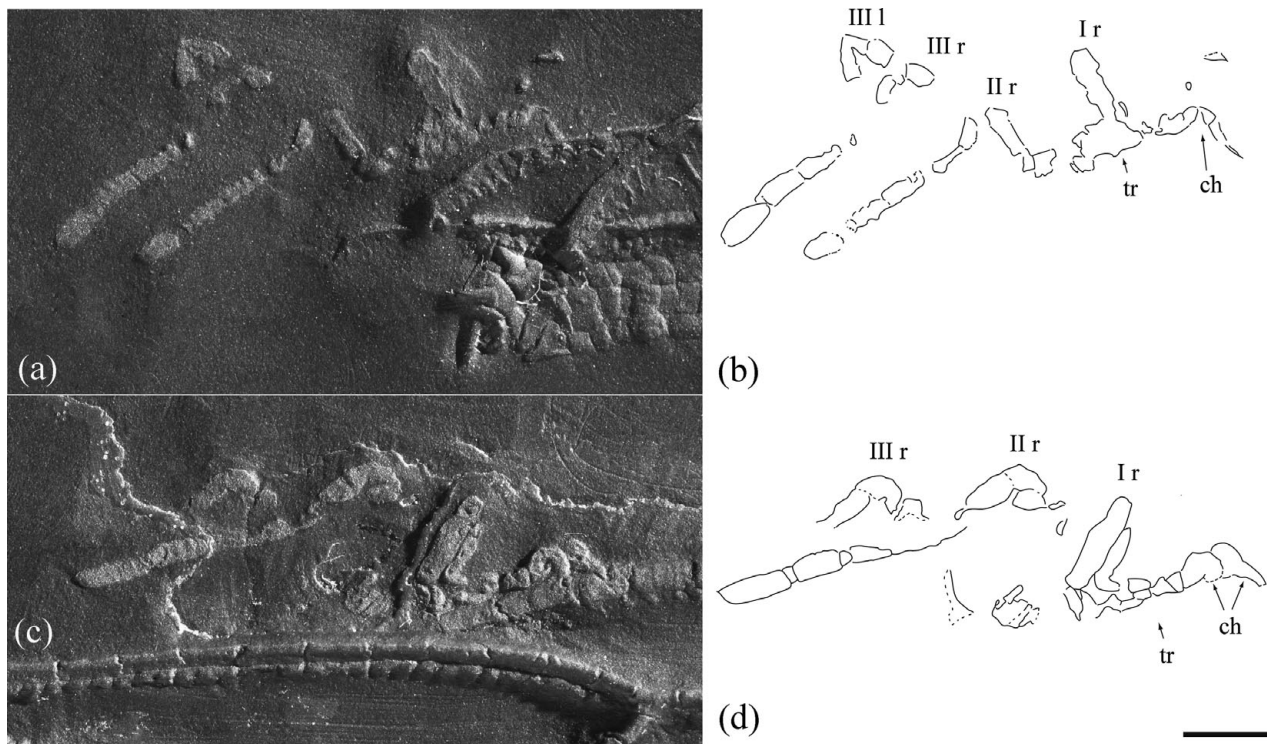


Figure 4. MNHM PWL2010/5-LS. (a, b) Undetermined pycnogonid near the anal tube of the crinoid *Parisangulocrinus zaeformis*; (c, d) undetermined pycnogonid attached to one arm of the crinoid *P. zaeformis*. Abbreviations: ch – chelifore; tr – trunk. Scale bar represents 1 mm.

extant taxa. He proposed a sister group relationship of *Flagellopantopus blocki* and the Austrodecidae in an unresolved relationship with *Offacolus kingi* Orr *et al.* 2000 (usually taken as the outgroup, e.g. Sutton *et al.* 2002) at the base of pycnogonids. The remaining fossil taxa *P. problematicus*, *P. maucheri* and *Haliestes dasos* are thus the sister taxa to the extant pycnogonids, including *P. devonica*.

Determining the phylogenetic position of *Pentapantopus vogteli* gen. et sp. nov. is difficult because of incomplete preservation and because the ontogenetic stage of the specimens is unclear (see discussion below). Nevertheless, three character states strongly support a position within the crown group. First, there is the presence of five pairs of walking legs. Although the full set of walking legs is preserved only on one side of the holotype specimen, we interpret the number of walking legs (5 pairs) as a true morphological trait of this new taxon, and not as a morphological abnormality. Five pairs of walking legs occur in the extant pycnogonid genera *Pentanympyon* (Nymphonidae), *Pentapycnon* (Pycnogonidae), *Pentacolossendeis* (Colossendeidae) and *Decolopoda* (Colossendeidae), but the phylogenetic significance of their polymery is unclear (Arango & Wheeler, 2007). However, as this character is unknown from any pycnogonid hitherto considered as basal, polymery might indicate a more derived phylogenetic position. This is also indicated by the reduction of the abdomen and telson in *P. vogteli* nov. gen. et sp., because a segmented abdomen (plus telson, if applicable) seems

to be the strongest argument for the inclusion of *Palaeoisopus problematicus*, *Flagellopantopus blocki* and *Haliestes dasos* in the pycnogonid stem lineage (Hedgpeth, 1955; Bergström, Stürmer & Winter, 1980; Waloszek & Dunlop, 2002; Siveter *et al.* 2004; Poschmann & Dunlop, 2006). On the other hand, the chelifores with a two-segmented scape, the flattened and setose distal leg podomeres, and the reduced trunk end may indicate a closer relationship of *P. vogteli* gen. et sp. nov., and the Silurian *H. dasos* (i.e. Nectopantopoda of Bamber, 2007), although the morphology of the trunk end is somewhat obscure in *H. dasos* (composed of three 'elements', but with no segment boundaries visible; Siveter *et al.* 2004).

## 7. Discussion

### 7.a. Larva or adult?

Because live observations of Recent pycnogonids are difficult to obtain, knowledge of their post-embryonic development is still limited, but the situation has been improved considerably in the last two decades (e.g. Nakamura, 1981; Bain, 2003a; Bogomolova, 2007; Bogomolova & Malakhov, 2004; Brenneis, Arango & Scholtz, 2011; Cano & López-González, 2009; Cano Sánchez & López-González, 2010; Vilpoux & Waloszek, 2003). These studies showed that larval development is not consistent within pycnogonids, which complicates the determination of the ontogenetic stage of isolated fossil material. Postembryonic development

in some pycnogonids (e.g. in *Austropallene cornigera*; Möbius, 1902), shows that the development of the walking legs is sequential, i.e. with each subsequent moult a further (more posterior) leg is added and the number of leg podomeres of the previous one increases until the full (adult) number of podomeres has been acquired (Bain, 2003b). In *Propallene longiceps* (Böhm, 1879) the sixth instar larva already has four pair of legs, and the chelifores. Up to the ninth instar, the larva develops the sexual organs and shows the complete sexual differentiation at this stage (Nakamura, 1981). Observations on postembryonic larval development in *Tanystylum orbiculare* Wilson, 1878 and *Achelia alaskensis* Cole, 1904 showed that the sixth or seventh instars can be distinguished from the eighth by an incomplete number of podomeres in their legs (Bain, 2003a). The new Hunsrück Slate pycnogonid has the complete set of appendages (assuming it is a decapodous form) with the full number of podomeres developed. Sexual differentiation cannot be determined. However, we are inclined to assume that the specimens are at least subadults. Based on the presence of five pairs of appendages in *Pentapantopus vogteli* gen. et sp. nov., it can be discounted that the pycnogonid is a juvenile form of one of the previously described Hunsrück Slate pycnogonids.

#### 7.b. Palp or oviger?

*Pentapantopus vogteli* gen. et sp. nov. is missing one pair of head appendages. The chelifores and the first pair of walking legs are easy to identify due to their morphology. The distinction between ovigers and palps is more difficult, because these appendages can be morphologically very similar. Usually, ovigers insert on the ventral side of the cephalosoma and are directed posteriorly. Palps insert laterally succeeding the chelifores. In *P. vogteli* gen. et sp. nov. the second pair of appendages seems to insert laterally, as the appendage base does not proceed to the ventral part of the cephalosoma. Hence, we conclude that the second pair of appendages in the cephalosoma of *P. vogteli* gen. et sp. nov. are palps. In the absence of further evidence for an additional pair of appendages in the cephalosoma, we conclude that the ovigers are not present. Whether their absence indicates sexual dimorphism, a subadult stage or a morphological character of this species cannot be determined.

#### 7.c. Life habits

A conspicuous morphological trait of *Pentapantopus* gen. nov. is the flattened distal leg podomeres not unlike those found in *Haliestes* or *Palaeoisopus*. These flattened podomeres might indicate that *Pentapantopus* gen. nov. was a fairly good swimmer, as has been assumed for *Palaeoisopus* by Bergström, Stürmer & Winter (1980). An occasional co-occurrence with crinoids is another feature that is shared by these two pycnogonid taxa (cf. Broili, 1933; Bergström, Stürmer & Winter, 1980). Pycnogonid feeding on echinoderms,

such as ophiuroids, echinoids and holothuroids has been reported several times (Helfer & Schlottke, 1935; Sloan, 1979; Arnaud & Bamber, 1987 and references therein). Furthermore, a co-occurrence of extant pycnogonids with crinoids has been reported by Carpenter (1908), but information concerning the nature of this interaction is lacking. Although the association of *Pentapantopus* gen. nov. with the crinoid *Parisangulocrinus* could be accidental, the association of Hunsrück Slate pycnogonids with crinoids is not uncommon and might possibly be related to the pycnogonids' mode of feeding, suggesting that both *Palaeoisopus* and *Pentapantopus* gen. nov. preyed upon crinoids. Recent re-investigation of fossil pycnogonid material showed, that predominantly smaller forms are associated with crinoids. Therefore the crinoid may also have provided shelter for smaller individuals.

#### 7.d. Two additional pycnogonids

The two specimens of *Pentapantopus vogteli* gen. et sp. nov. are associated with a crinoid and two additional pycnogonids, much smaller than the ones described above (Figs 1a, b; 4a, c). These two specimens are very poorly preserved, but the observable chelifores and their general habitus clearly identify these arthropods as pycnogonids. In both cases only three pairs of walking legs are preserved in addition to the chelifores, corresponding to the situation in the fifth instar larva of *Propallene longiceps* (Nakamura, 1981). But owing to their poor preservation, it is impossible to determine, whether the two additional specimens are juvenile stages of *P. vogteli* gen. et sp. nov., or of one of the earlier described Hunsrück Slate pycnogonids, or even represent a further new taxon. In the absence of any distinguishing characters there is some probability that they are younger individuals of our new species.

### 8. Conclusions

The association of a crinoid with four specimens of pycnogonids is described from the Lower Devonian Hunsrück Slate. Two specimens can be assigned to a new genus and species, *Pentapantopus vogteli*. The new taxon is morphologically quite different from previously described Hunsrück Slate pycnogonids and bears some resemblance to both modern representatives and the Silurian *Haliestes dasos*. It thus widens the known range of diversity for Devonian pycnogonids. Furthermore, the fossil association indicates that these Devonian pycnogonids possibly preyed upon crinoids. The putative phylogenetic position of *P. vogteli* gen. et sp. nov. among other crown group pycnogonids shows that the evolution of pycnogonid body plans must have taken place early in the Palaeozoic and that subsequent evolution of pycnogonid morphology was much more conservative.

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