



AN ORDOVICIAN PYCNOGONID (SEA SPIDER) WITH SERIALY SUBDIVIDED ‘HEAD’ REGION

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ABSTRACT—The bizarre morphology of living Pycnogonida, known colloquially as sea spiders, has long fueled dissent over their status within the arthropods. Pycnogonids figure prominently in recent analyses of anterior limb homologies and ancestral crown-group euarthropod relationships, with support for the concept of Pycnogonida as sister taxon to Euchelicerata now contested by proponents of a more basal position between Radiodonta and all other arthropods. A challenge to further elucidation of their phylogenetic position is the exceptional rarity and disjoint distribution of pycnogonids in the fossil record, due largely to their fragile unmineralized exoskeletons. New fossil discoveries therefore have the potential to add significantly to knowledge of their evolution, paleoecology, and paleobiogeography. Here we report the first known occurrence of fossil pycnogonids from rocks of Ordovician age, bridging a 65 Myr gap between controversial late Cambrian larval forms and a single documented Silurian specimen. The new taxon, *Palaeomarachne granulata* n. gen. n. sp., from the Upper Ordovician (ca. 450 Ma) William Lake Konservat-Lagerstätte deposit in Manitoba, Canada, is also the first reported from Laurentia. It is the only record thus far of a fossil sea spider in rocks of demonstrably shallow marine origin. Four incomplete, partially disarticulated molts represent a relatively large, robust animal with a series of five segment-like elements in a ‘head’ region that does not incorporate the first of four preserved limb-bearing trunk segments. This unique pattern may reflect the plesiomorphic condition prior to complete fusion of anterior ‘head’ elements and first trunk segment to form a cephalosoma, as seen in all eupycnogonids. *Palaeomarachne granulata* is interpreted as occupying a basal stem-group position in the Pycnogonida.

INTRODUCTION

SEA SPIDERS (Pycnogonida) are a clade of morphologically distinctive, yet highly variable, non-biomineralizing marine arthropods with a superficial resemblance to terrestrial aranean arachnids. Fewer than 1500 living species have been described (Arango and Wheeler, 2007), but these show an astounding and confusing range of ecological and anatomical adaptations, to such an extent that within-group relationships have remained subject to considerable controversy (Dunlop and Arango, 2005; Manuel et al., 2006). It has been an even greater challenge to determine an appropriate higher level taxonomic placement. Traditionally, pycnogonids have been allied most frequently with various chelicerate taxa (Bergström et al., 1980; Arnaud and Bamber, 1987). Recent embryological investigations (Machner and Scholtz, 2010) and studies on Hox gene expression (Jager et al., 2006; Brenneis et al., 2008) provided compelling evidence for Pycnogonida as a sister taxon to Euchelicerata (together comprising Chelicerata) on the basis of shared chelate first appendages innervated by the second neuromere (deutocerebrum), a conclusion that has garnered support in molecular phylogenies (Dunn et al., 2008; Rota-Stabelli et al., 2011). Other reports, however, have reasserted historical views of a more basal position as sister taxon to all extant arthropod groups (Giribet et al., 2001; Maxmen et al., 2005; Briggs et al., 2012; Legg et al., 2012). Efforts to unravel the origin and evolutionary significance of the novel pycnogonid body plan, and in particular the precise pattern of underlying anterior (‘head’) segmentation, limb homologies, and tagmatization (Vilpoux and Waloszek, 2003; Manuel et al., 2006), have been stymied by a notoriously poor and temporally disjoint fossil record (Waloszek and Dunlop, 2002; Siveter et al., 2004). Consequently, any newly discovered fossil sea spider

occurrences will have the potential to help constrain minimum ages for acquisition or loss of key character states, as well as advance the currently meager state of knowledge of their paleoecologic and paleogeographic distributions.

In this report, we describe the first pycnogonid fossils collected from rocks of Ordovician age. They are also the first to be documented from the Laurentian paleocontinent. These represent the geologically oldest (Late Ordovician, Katian) post-larval sea spiders so far discovered, and constitute the only known example of the group between the late Cambrian (Waloszek and Dunlop, 2002) and mid-Silurian (Wenlock) (Siveter et al., 2004). In contrast to all previously described occurrences of fossil pycnogonids, which are in deeper shelf to slope depositional settings (Sutcliffe et al., 2002; Waloszek and Dunlop, 2002; Siveter et al., 2004; Charbonnier et al., 2007), the new specimens were recovered from carbonate rocks of a shallow marine Konservat-Lagerstätte deposit in association with other non-biomineralizing chelicerates including eurypterids and xiphosurid horseshoe crabs, and with three-dimensionally preserved cnidarian medusae (jellyfish) (Young et al., 2007).

Although the new taxon is so far represented by incomplete molts only, dorsal features of the axial trunk and anteriormost ‘head’ region correspond closely to the highly distinctive Bauplan of the Pycnogonida and cannot be matched in any other known arthropod group. It differs, however, from all known adult pycnogonids (fossil and living) in having a serially subdivided ‘head’ that does not incorporate the anteriormost trunk limb-bearing segments into a single fused unit variously referred to as a cephalon (King, 1973; Arnaud and Bamber, 1987), or a cephalosoma (Heymons, 1901; Dunlop and Arango, 2005).

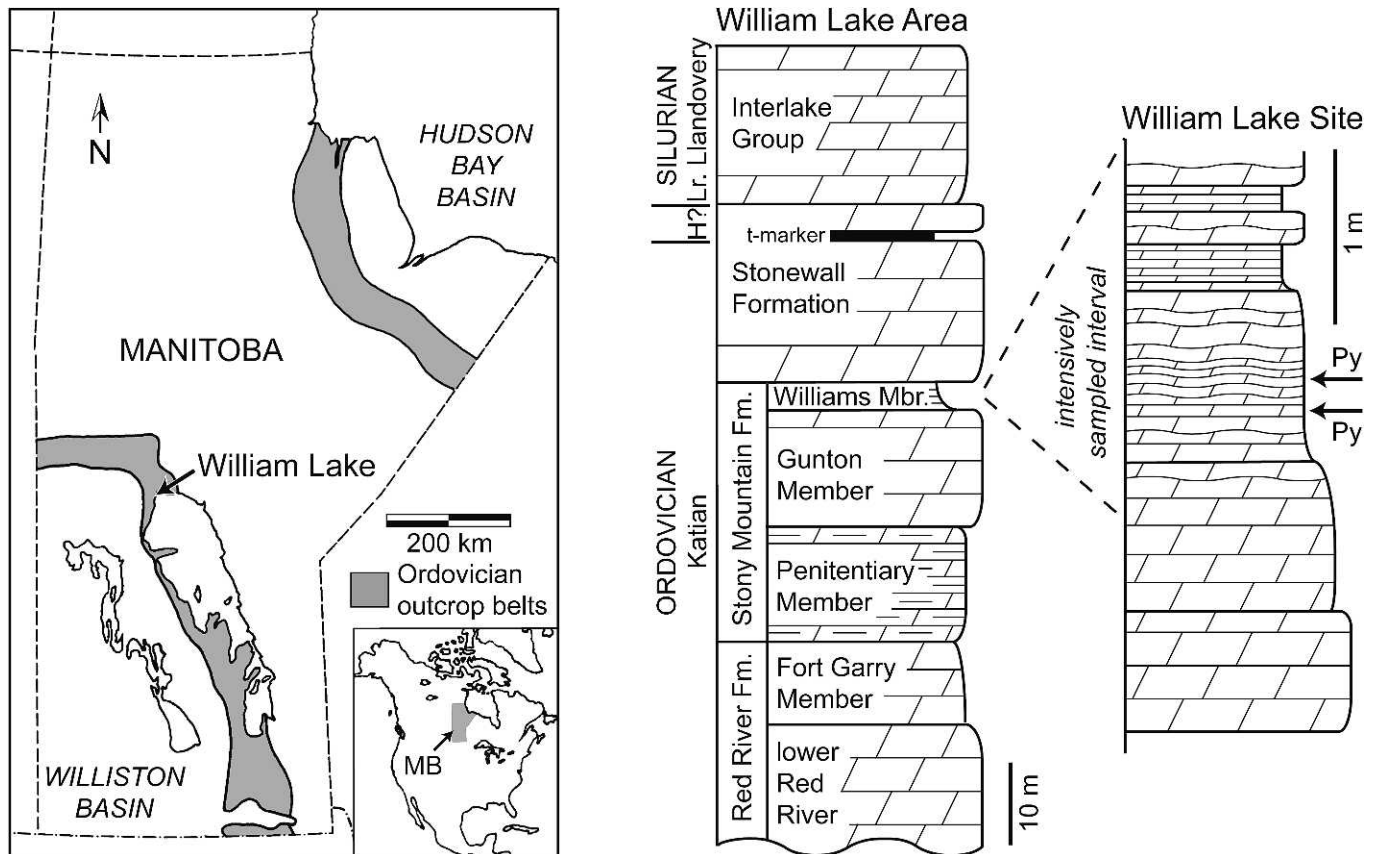


FIGURE 1—Location and stratigraphic context for the Upper Ordovician Williams Member (Stony Mountain Formation) near William Lake in central Manitoba, Canada. Arrows indicate the two levels from which specimens of *Palaeomarachne granulata* n. gen. n. sp. have been recovered. Abbreviations: H?=Hirnantian?, Lr.=Lower.

MATERIAL AND METHODS

A part and partial counterpart of a single incomplete pycnogonid molt (the holotype specimen, MM I-4282A) was first recovered in 2007 in well-delimited fossil collections from a thin subunit (Bed J) of the Upper Ordovician Williams Member (Stony Mountain Formation) excavated near William Lake in central Manitoba, Canada (Fig. 1). Two less complete molts (without counterparts) were discovered in 2011 during laboratory re-examination of 2007 collections from the same stratigraphic interval; a fourth disarticulated partial molt was subsequently found among material collected in 2009 from a bed about 15 cm lower in the section. The holotype was mechanically prepared under a binocular microscope using a needle-tipped percussion handpiece to reveal areas obscured by the tough dolostone matrix. The other specimens occur on weathered surfaces and are too fragile to undergo significant further preparation. Lack of color and texture differentiation between fossils and matrix renders accurate measurement of component elements difficult; the description below was developed through direct microscopic observation of the specimens (primarily the holotype) and latex peels, in close conjunction with careful study of hundreds of digital photographs taken under a wide variety of lighting conditions, including short wave and long wave ultraviolet radiation. The holotype specimen was imaged at various stages of preparation, dry and untreated, with a thin coating of ammonium chloride sublimate, and immersed in distilled water. Photos in this paper were taken using a Nikon D70s digital SLR mounting a Micro-Nikkor 55 mm 1:2.8 lens, and a Canon EOS. Image contrast,

brightness, and sharpness were adjusted in Adobe Photoshop CS4.

The holotype and three additional specimens are the only ones known—all are housed in The Manitoba Museum (Winnipeg, Manitoba) paleontology collections.

SYSTEMATIC PALEONTOLOGY

Class PYCNOGONIDA Latreille, 1810

Genus PALAEOMARACHNE new genus

Type species.—*Palaeomarachne granulata* n. sp. by monotypy.

Diagnosis.—As for type species.

Etymology.—*Palaeo* (Gr.), meaning ancient, *mar* from marinus (L.) referring to sea dwelling and *Arachne* (Gr.), from the mythological weaver magically transformed into a spider.

PALAEOMARACHNE GRANULATA new species

Figures 2, 3.2, 4–6

Diagnosis.—Large pycnogonid with discrete ‘head’ region of five serially heteromorphic elements separated externally by strong transverse furrows; anterior element largest, broadly anchor-shaped, with basal articulations for frontal chelifores and lateral palps. Robust trunk of at least four segments, anteriormost not incorporated into ‘head’ region to form a fused cephalosoma. Trunk segments with large lateral extensions set off from axial region by longitudinal furrows; axial and lateral portions showing narrower anterior band demarcated by shallow transverse furrow; axial section of fourth trunk segment narrowing posteriorly to about one-third maximum width (trans.). Dorsal cuticle with fine granulate prosopon or ornament; granules

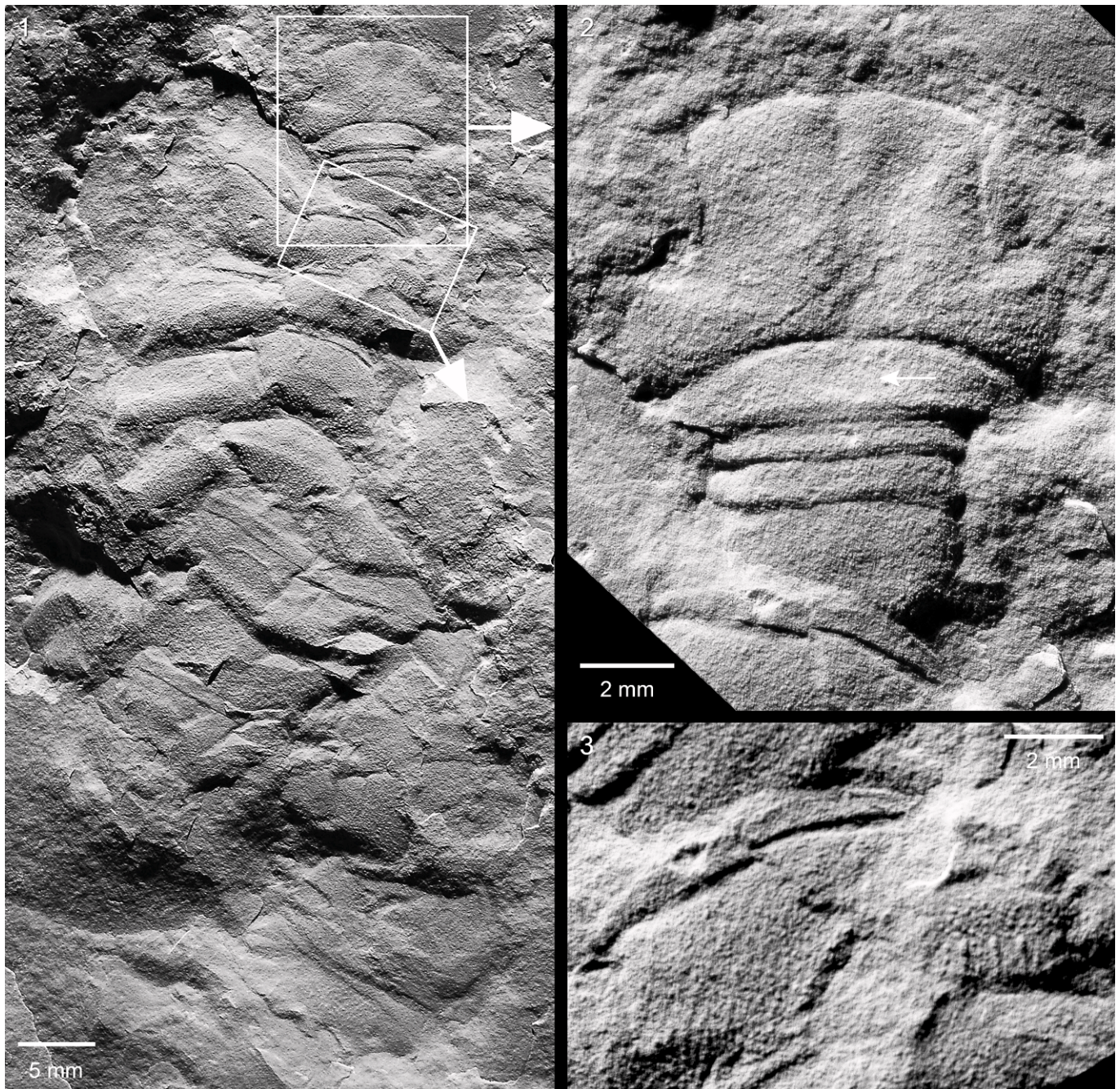


FIGURE 2—*Palaeomarachne granulata* n. gen. n. sp., holotype MM I-4282A, The Manitoba Museum, Winnipeg; part (positive) only, lightly coated with ammonium chloride sublimate; scale bars as indicated. 1, overall view of composite internal-external impressions and casts of dorsoventrally compressed and slightly disarticulated dorsal exoskeletal components, including multielement ‘head’ region (at top) and trunk segments, with impressions of additional cuticle fragments of unknown body parts below; 2, close up of ‘head’ region showing broad inverted T-shape of anteriormost element with shallow median furrow demarcating pair of forward facing articular bases for chelifores, and posterior pair of lateral projections forming articular bases for palps; second element with arrow indicating vague central subcircular depression, possibly representing position of median eye tubercle/ocular structure; 3, close up of medial area of first trunk segment with slightly displaced patch of cuticle bearing a row of three elongate granules; note finely granulate texture of background prosopon.

slightly larger, tending to elongation, and forming subtle longitudinal rows near posterior edges of axial segments of trunk.

Description.—The holotype specimen (MM I-4282A) comprises a dorsoventrally flattened and partially disarticulated dorsal cuticular exoskeleton with impressions of (probably) ventral cuticle fragments scattered posteriorly (Fig. 2.1). Recognizable appendage ‘sleeves’ are absent and there is no sign of a proboscis. This association is presumed to represent a molted individual in which the upper (dorsal) cuticle unit has

remained more or less intact and elements of the lower (ventral) piece have become separated, rotated, and inverted to lie behind and beneath. Due to incomplete exposure of elements and lack of sharp demarcating boundaries between fossil and matrix, all dimensions in the following description are best approximations. We herein use ‘head’ and ‘head region’ simply to denote the anteriormost set of five segment-like elements in *Palaeomarachne granulata* n. gen. n. sp., emphasizing that these terms do not imply any particular homologies or anatomical equivalence

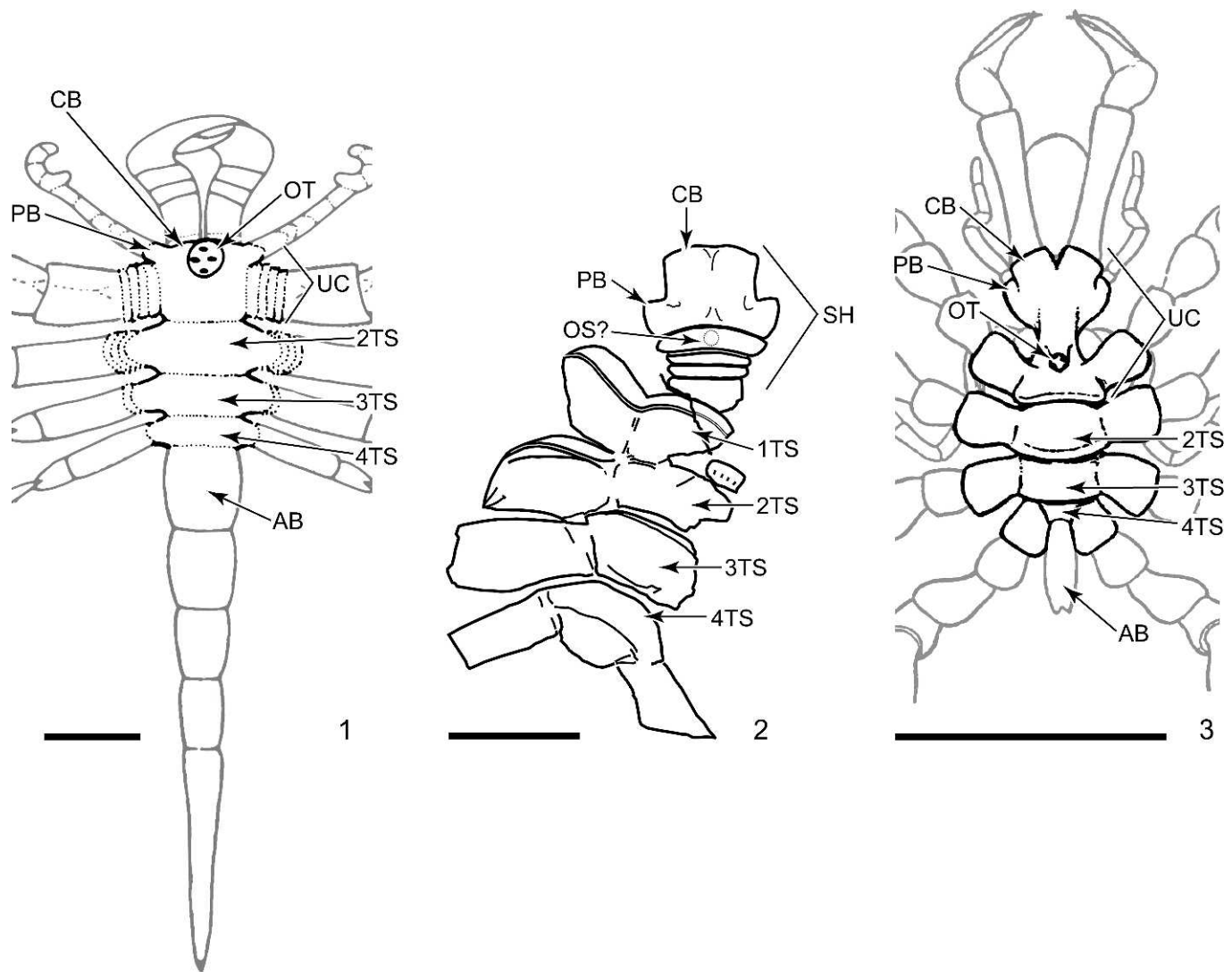


FIGURE 3—Outline cartoons comparing *Palaeomarachne granulata* n. gen. n. sp. with two other species. 1, the Early Devonian stem-group pycnogonid *Palaeoisopus problematicus* (modified from Bergström et al., 1980); 2, *Palaeomarachne granulata* n. gen. n. sp. (holotype MM I-4282A); 3, *Nymphon hirtipes* Bell, 1853, a representative modern crown-group pycnogonid (modified from Dunlop and Arango, 2005). In 1 and 3 the ‘head’ region comprises an unsegmented cephalosoma (UC) bearing paired chelifores and palps, a median ocular tubercle (OT), and the first pair of trunk limbs (proboscis, chelifores, palps, ovigers, truncated trunk limbs, and abdomen outlined in gray). In 2 the multielement ‘head’ region (SH) includes an anterior unit bearing articular bases for paired chelifores (CB) and palps (PB), and four shorter elements, the second of which shows a median depression that may represent an ocular structure (OS?). The first trunk segment is not fused into the ‘head’. Individual scale bars=10 mm; details of prosopon omitted from all. Abbreviations: AB=abdomen; TS=trunk segment (numbered 1 to 4, from anterior to posterior).

to what has been interpreted as a “head” or cephalic unit in other arthropods.

‘Head’ region of the holotype (Figs. 2.2, 3.2) comprises five serially arranged, heteromorphic, segment-like elements, with total length (sag.) of 12 mm. Anterior element largest, maximum width 9.8 mm (trans.) posteriorly, length 5.3 mm (sag.), roughly in the shape of a broad-shafted anchor or broad inverted ‘T’. Frontal portion (shaft, or stem of T) 6.5 mm wide anteriorly, approximately two-thirds of maximum element length (sag.), parallel-sided, with forwardly bowed anterior margin. Shallow median furrow extends backwards from margin about one-third maximum element length, demarcating pair of forward facing and slightly divergent articular bases for chelifores. Posterior one-third of element extended into pair of lateral projections (anchor arms, or cross-bar of T) to form articular bases for palps; lateral projections narrower at base, about 2 mm, expanding distally to 2.5 mm. Posterior margin of first element gently arcuate, concave

in posterior direction; articulation with second element shown by narrow, well impressed furrow. Short (sag.) second element (2 mm), almost as wide as first, with arcuate anterior margin marked by backwardly curving furrow, narrowing back to straight transverse posterior margin, 5.8 mm wide (trans.); possible position of median eye tubercle/ocular patch suggested by subtle subcircular depression centrally located on second element (Fig. 2.2, arrow). Third and fourth elements self-similar, each 5.8 mm wide (trans.) and ~1 mm long (sag.); fifth element same width (trans.) as third and fourth, but appears to be at least twice as long (2.8 mm, exsag.); posterior margin partially obscured by diagonal course of displaced anterior trunk segment.

Trunk region of holotype (Fig. 2.2, 2.3) is rotated clockwise with respect to ‘head,’ splayed, and incomplete on right side; total length (sag.) 20.4 mm. Four segments preserved, each consisting of a medial region flanked by what are interpreted as lateral extensions (Bergström et al., 1980) or lateral processes (Arnaud

and Bamber, 1987) (see also Fig. 3.2). Medial portions of anterior two segments more or less rectangular in outline (9 mm wide, 5 mm long); third segment subtrapezoidal medially, narrowing from 10 mm maximum width (trans.) to 6 mm posteriorly; fourth segment roughly diamond-shaped, 10 mm wide and 4.2 mm long. Median area of first through third segments has narrow anterior band set off by transverse furrow. First segment is flattened and appears to be ruptured at about midpoint, with slight offset; patch of cuticle bearing three larger elongate granules (Fig. 2.3), located on right posterior margin, may be displaced. Second segment shows slight anterior-posterior arching. Third segment flat anteriorly, bowed gently down towards posterior margin. Fourth segment shows slightly arcuate transverse ridge at about midlength, sloping evenly forward and backward to margins. Only left side of trunk shows the nature of the presumed lateral extensions, set off from median region by shallow, disjunct, parallel to posteriorly convergent axial furrows; each extension approximately as long as maximum (trans.) width of corresponding median portion; all apparently divergent with free anterior and posterior margins. Anteriormost rotated slightly forward, second through fourth rotated backwards at increasingly acute angle to longitudinal axis. Lateral extension of first trunk segment flattened, broadening abaxially to distal diagonal truncation; maximum preserved length (trans.) 6.5 mm. Broad blade-shaped anterior band demarcated by shallow transverse furrow curving backward distally. Second lateral extension of flattened hemicylindrical shape, widening toward curved truncation distally; maximum preserved length (trans.) 10 mm, narrow (long.) anterior band preserved over about half that distance from axial furrow. Lateral extension of third segment parallel-sided, flattened hemicylindrical shape, 10 mm long from axial furrow to distal truncation; short triangular section of anterior band visible adjacent to axial furrow, remainder obscured beneath second projection. Posteriormost lateral extension on left side lacking anterior band, flattened hemicylindrical shape, angled back about 60°; maximum preserved length 7.5 mm. Similar sized portion of lateral extension also present on right side.

There is no preserved evidence of an abdomen (“trunk end” of Vilpoux and Waloszek, 2003) extending posterior to the fourth trunk segment.

MM I-4457 is a negative impression. A positive latex peel (Figs. 4.1, 4.2, 6.1) shows most of the anterior four elements of the ‘head’ region in positive relief, with slight mutual rotation and separation; anteriormost element appears obliquely distorted, maximum posterior width (trans.) estimated at 6.8 mm; impressions of large granulate cuticular fragments showing arcuate rimmed margins lie posterior to ‘head’ region (Fig. 4.3). MM I-4456 (Figs. 5.1, 6.3) is an incomplete presumed molt consisting of the ‘head’ region and the first two trunk elements in a dorsoventrally compressed orientation. Right anterior corner of first ‘head’ element is broken away and posterior portion behind second element is abraded, obscured, and separated from trunk. Maximum width (trans.) of first “head” element 6.7 mm. MM I-4458 (Figs. 5.2, 6.2) exposes positive granulate surface of two broken and abraded medial trunk segments, the anterior bearing partial lateral flanges. Fragments in front of this may represent rotated and telescoped posterior elements of ‘head’. Maximum width (trans.) of most complete medial trunk segment approximately 9 mm.

Etymology.—*granulata* (fem.), from *granulum* (L.), grain and -*atus*, possessing, in reference to the finely granulate texture of the cuticle.

Holotype.—MM I-4282A, part and counterpart (The Manitoba Museum, Winnipeg); composite of partial internal and external impressions and casts of dorsoventrally compressed and slightly

disarticulated dorsal exoskeletal elements comprising ‘head’ region and trunk segments, with impressions of additional cuticle fragments of unknown body parts (Figs. 2, 3.2).

Other material includes MM I-4457, ventral view (negative part only) of incomplete dorsoventrally and obliquely compressed ‘head’ region, along with fragmentary posterior cuticle impressions (Figs. 4, 6.1); MM I-4456; positive (part only) of incomplete dorsoventrally compressed ‘head’ region and anterior-most trunk (Figs. 5.1, 6.3); MM I-4458; dorsal view (positive part only) of fragmentary posterior ‘head’ region and two incomplete dorsoventrally compressed medial trunk segments with partial lateral extensions (Figs. 5.2, 6.2).

Occurrence.—All material known only from Upper Ordovician (Richmondian=late Katian), Stony Mountain Formation, Williams Member (Bed J 25–32 and 43–49 cm interval); The Manitoba Museum Locality No. GR04-1, Grand Rapids Uplands, near William Lake, Manitoba, Canada (Fig. 1). The Richmondian age of the Williams Member at William Lake is established on the basis of an accompanying low diversity conodont fauna including *Rhipidognathus symmetricus*, *Drepanoistodus?* species, and *Aphelognathus?* (Young et al., 2007; Rudkin et al., 2008).

DISCUSSION

Affinities.—Prior to concluding that the only logically defensible phylogenetic placement for *Palaeomarachne granulata* n. sp. lies along the basal stem of Pycnogonida, we carefully considered and eliminated a variety of other potential early Paleozoic arthropod affiliations.

Trilobites, the most common marine arthropod fossils of Paleozoic age, have pervasively calcified dorsal exoskeletons (Scholtz and Edgecombe, 2005). No specimen of *P. granulata* shows evidence of original biomineralization and, solely on that basis, a trilobite relationship can be rejected. Furthermore, comparison of the anterior ‘head’ region of *P. granulata* with the cephalic shield in trilobites reveals only superficial similarities. No trilobite possesses a series of short, narrow axial elements forming a neck-like extension between the transverse posterior cephalic margin and first thoracic segment. Axial elements of the short compact trunk of *P. granulata*, particularly the posteriormost, have distinctly trapezoidal outlines, with furrows separating lateral processes converging backwards independently on each segment. These lateral processes do not conform to the structure of dorsal pleurae in trilobites, but most strongly resemble extensions of the trunk that articulate directly with basal limb elements, as in Pycnogonida; those on the anterior trunk segment are swept forwards, and on the three posterior segments they are angled progressively more towards the rear. Typical trilobite axial and pleural articulation structures are completely lacking in *P. granulata*, and although it possesses shallow transverse furrows parallel to the anterior margins of both the lateral processes and axial elements of the first two trunk segments, these are unlike the pleural furrows and articulating furrows of the mineralized dorsal thoracic exoskeleton in trilobites (Whittington, 1997).

Chelicerata comprises the only moderately diverse group of exclusively non-biomineralized arthropods with a post-Cambrian early Paleozoic marine record. At the William Lake site, euchelicerates are the most frequently encountered arthropod fossils, represented by eurypterids and xiphosurid horseshoe crabs (*Lunataspis aurora*). These are preserved as discrete sclerites, presumed molt configurations, and fully articulated individuals. *Palaeomarachne granulata* does not morphologically match complete or disarticulated specimens of either group (at William Lake or elsewhere), in dorsal or in ventral aspect. There are also differences in exoskeletal proportions. Whereas William Lake eurypterids and horseshoe crabs preserve no obvious external

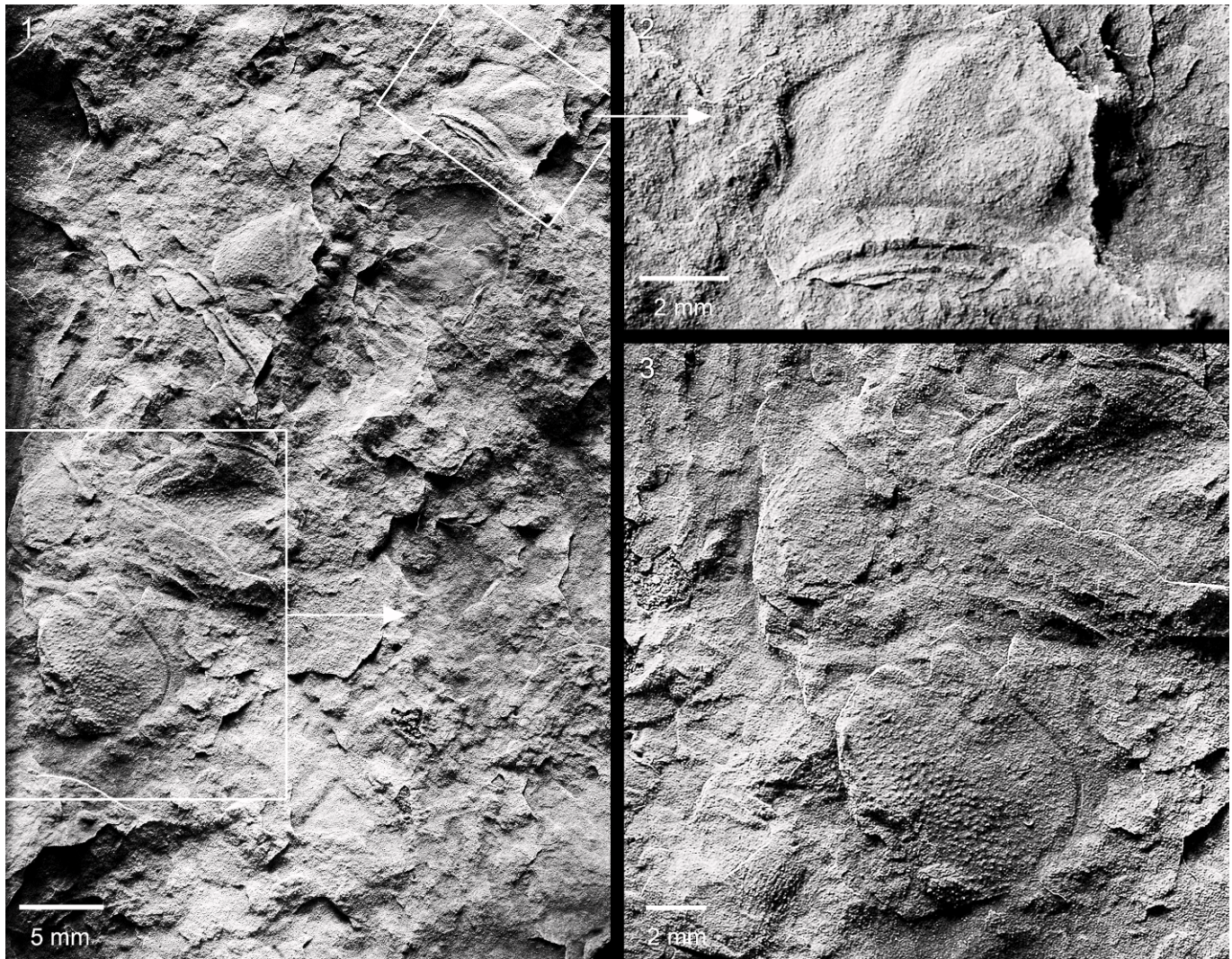


FIGURE 4—*Palaeomarachne granulata* n. gen. n. sp., MM I-4457, The Manitoba Museum, Winnipeg; latex peel of negative counterpart lightly coated with ammonium chloride sublimate; scale bars as indicated. 1, overall view of incomplete dorsoventrally and obliquely compressed ‘head’ region (three anterior elements only), along with numerous fragmentary posterior cuticle impressions; 2, close up view of ‘head’ region shows obliquely skewed median furrow of anterior element and distorted bases for chelifores and palps; 3, close up of fragmentary cuticle patches, presumably from dissociated elements of trunk region, showing variation in fine granulate prosopon.

cuticular textures, the appearance of *P. granulata* is quite striking. In this character it shows close similarity to a number of living pycnogonid species with densely granulate trunk surfaces, such as *Pycnogonum drumus* Arango (Arango, 2003, p. 2763, fig. 16). Other rare chelicerate taxa currently known from the Ordovician or Silurian (at other localities) include chasmataspidids, ‘synziphosurans’, and scorpions, but none shares a common anterior segmental pattern or trunk structure with *P. granulata*.

Likewise, comparison of *P. granulata* with marine representatives of other early Paleozoic groups, including crustaceans, euthycarcinoids, anomalocaridids, and aglaspids, yields no meaningful morphological correlations except for those that can be regarded as very basic primitive (symplesiomorphic) features shared by all arthropods. The post-Silurian Paleozoic record expands to include an array of new arthropod lineages associated with an initial transition to—and ultimately full exploitation of—terrestrial (including freshwater) environments. In none of these (representing Myriapoda [including Arthropleurida], Hexapoda, and arachnid chelicerates) can we find morphological evidence of a plausible phylogenetic relationship with *P. granulata*.

Conversely, as outlined in the description and elsewhere, we do see clear points of morphological correlation between *P. granulata* and those Paleozoic fossils now accepted as early pycnogonids; some minor external details can even be compared with extant crown-group species. Despite its apparently unique segmented ‘head’ region and lack of articulated appendages, the presumed molt remains of *P. granulata* are best accommodated as Late Ordovician stem-group Pycnogonida.

Molt interpretation.—Relatively little is known of molting in living sea spiders (King, 1973; Arnaud and Bamber, 1987; Tetlie et al., 2008) except through the larval to earliest adult stages of a few taxa that remain quite small at maturity (Nakamura, 1981; Vilpoux and Waloszek, 2003). Some pycnogonids apparently forgo a full ecdysial cycle as adults and instead periodically ‘peel’ off portions of degraded or fouled cuticle (Meyer and Bückmann, 1963; Lotz and Bückmann, 1968). In documented ecdysis for extant species of *Pycnogonum* and *Nymphon* (Lotz and Bückmann, 1968; King, 1973), ‘longitudinal’ (=circumarginal) sutures on each side of the body split apart yielding a dorsal and a ventral cuticle piece. In *Nymphon*, trunk legs and chelifores are molted as separate ‘sleeves’ and the dorsal

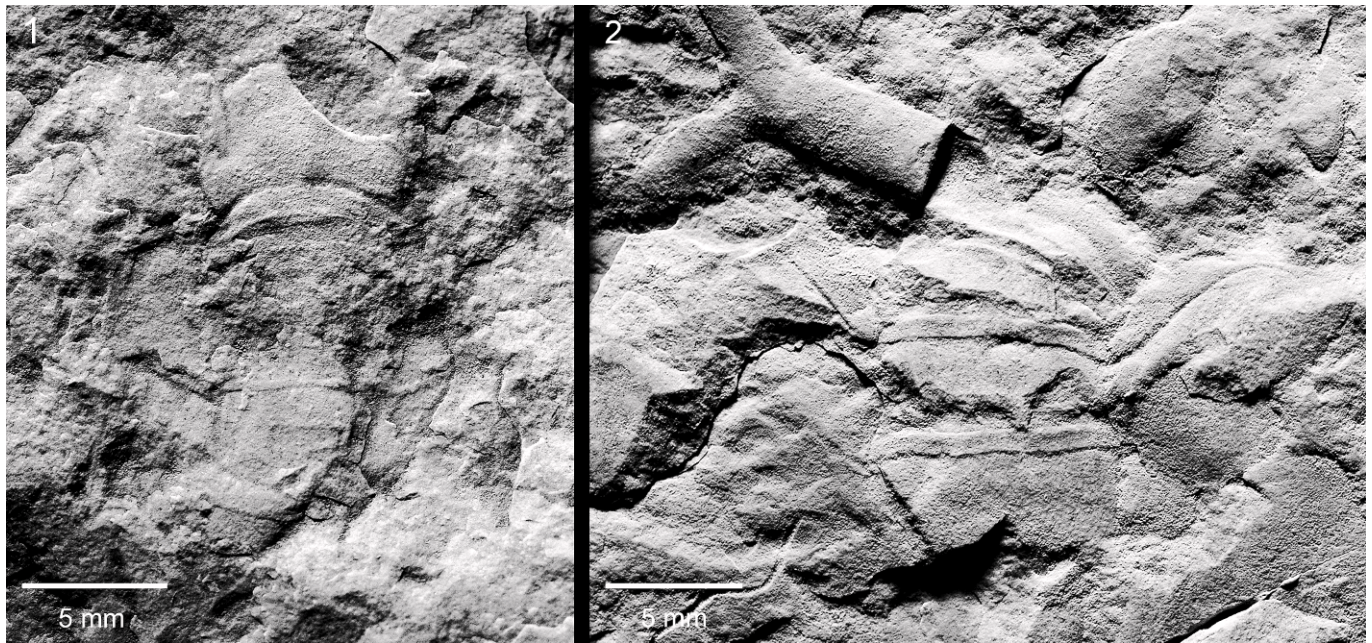


FIGURE 5—*Palaeomarachne granulata* n. gen. n. sp.; scale bars as indicated. 1, MM I-4456, The Manitoba Museum, Winnipeg; part (positive), lightly coated with ammonium chloride sublimate; incomplete dorsoventrally compressed 'head' region and anteriormost trunk segments; 2, MM I-4458, The Manitoba Museum; part (positive), lightly coated with ammonium chloride sublimate; dorsal view of fragmentary 'head' region and two incomplete dorsoventrally compressed medial trunk segments with partial lateral extensions; median area and lateral projections of the most complete trunk segment (probably the anteriormost by comparison with the holotype) clearly show narrow anterior bands set off by well-impressed transverse furrows; Y-shaped structure in upper left does not appear to be related to molt remains of *Palaeomarachne* and may represent a portion of a flattened horizontal burrow system.

cuticle piece retains the eye tubercle/covering, abdomen and hind gut lining; the ventral piece carries the entire proboscis, foregut lining, palps and ovigers. Thus the absence of verifiable chelifores, palps, ovigers, proboscis, and trunk limb elements in the four known specimens of *Palaeomarachne granulata* n. gen. n. sp. strongly suggests that they represent the dorsal cuticles of molted individuals (see King, 1973, fig. 11b for an outline drawing of a comparable dorsal cuticle piece in a species of *Nymphon*). This is supported by partial disarticulation and splaying of elements of the trunk and 'head' in the more complete holotype (Fig. 2). Fragmentary remnants of granulate cuticle scattered beneath and behind the posterior trunk region of the holotype (Fig. 2.1, 2.3) and in MM I-4457 (Fig. 4.1, 4.3) may be pieces of ventral cuticle sheet that were inverted during ecdysis or in post-molting transport. It has been suggested (Tetlie et al., 2008) that all previously known pycnogonid fossils likely represent carcasses due to the presumably more fragile nature of molted cuticle versus that of intact animals. Whereas we cannot rule out the possibility that one or more of the four known specimens of *P. granulata* is a partly decayed and disarticulated carcass from which the proboscis and all limb elements have been stripped by scavenging or transport, the weight of evidence argues for their molt status.

Paleoecology and taphonomy.—Thin-bedded dolomudstones of the Williams Member (Stony Mountain Formation) at the William Lake locality are interpreted as restricted, shallow marginal marine (mud flat to lagoon) deposits on the basis of sedimentological and paleontological evidence, as well as on their position near the top of a shallowing-upwards cycle (Young et al., 2007; Rudkin et al., 2008). Non-biomineralized fossils associated with *Palaeomarachne granulata* n. gen. n. sp. in Bed J include euchelicerate arthropods (eurypterids and horseshoe crabs), problematic large chitinous tubes, and numerous cnidarian medusae; a poorly preserved shelly fauna comprises abundant lingulide brachiopods, sparse gastropods, and ostracodes (Young et al., 2010). No trilobite sclerites have been recovered from this

interval. Co-occurring conodonts represent the *Rhipidognathus* Biofacies indicating shallowest conditions for the Late Ordovician of the intracratonic Williston Basin (Nowlan and Haidl, 2001). A significant number of modern pycnogonid species occupy intertidal and shallow subtidal habitats (Arnaud and Bamber, 1987; Arango and Wheeler, 2007), and it has been conjectured that colonization of shallow marine waters by primarily bathyal pycnogonids may have been delayed until sometime after the Jurassic (Charbonnier et al., 2007). The discovery of *P. granulata* in Late Ordovician sediments of demonstrably shallow water (perhaps lagoonal intertidal) origin indicates that at least some large sea spiders occupied near-shore environments about 300 Myr earlier. It is highly unlikely that molt remains or decayed carcasses of even comparatively big pycnogonids could survive transportation from a significantly deeper offshore setting onto a marginal marine mudflat.

The four known specimens of *P. granulata* represent incomplete flattened and partially disarticulated dorsal cuticular exoskeletons of large, robust adult animals. Particularly in the holotype, a subtle prosopon of fine granules (Fig. 2) is in places sharply replicated in the dolomudstone matrix and these regions are interpreted as representing the outer cuticle surface. Areas devoid of granules may represent unornamented external cuticle, impressions of the inner cuticle surface, or patches of degraded or abraded cuticle. The lack of any residual organic material, such as that seen in some co-occurring eurypterid specimens (Young et al., 2007; Young et al., 2010), and of early mineralization products, precludes differentiating between these alternatives. The flattened composite cast-mould preservation of partial axial exoskeletons without obvious secondary mineral replacement in *P. granulata* departs from that of all other known fossil pycnogonids, in which more or less complete limb-bearing individuals (presumed carcasses) are preserved, sometimes in full relief, as mineral replicates in pyrite (Bergström et al., 1980; Poschmann and Dunlop, 2006; Charbonnier et al., 2007), calcium

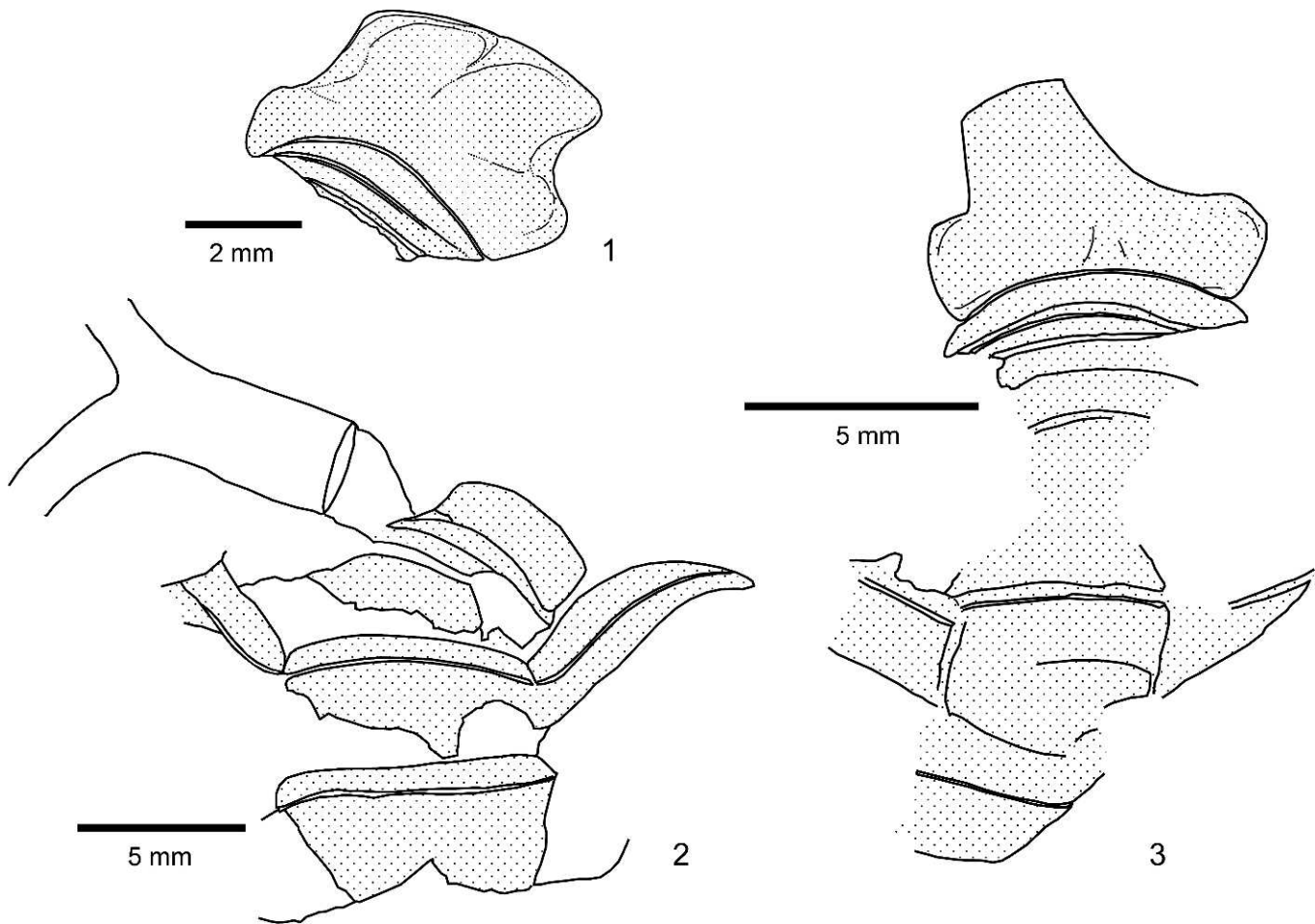


FIGURE 6—Outline drawings of *Palaeomarachne granulata* n. gen. n. sp.; scale bars as indicated. 1, MM I-4457, The Manitoba Museum, Winnipeg; based on latex peel of negative counterpart of incomplete dorsoventrally and obliquely compressed ‘head’ region shown in Figure 4.2; 2, MM I-4458, The Manitoba Museum, Winnipeg; based on dorsal view of fragmentary ‘head’ region and two incomplete dorsoventrally compressed medial trunk segments with partial lateral extensions shown in Figure 5.2; 3, MM I-4456, The Manitoba Museum, Winnipeg; based on incomplete dorsoventrally compressed ‘head’ region and anteriormost trunk segments shown in Figure 5.1.

phosphate (Waloszek and Dunlop, 2002), or calcite (Siveter et al., 2004). Preservation differences are attributable to variable factors operating early in burial history, including properties of the enclosing sediment and pore water chemistry, and availability of oxygen and organic matter.

Size and morphology.—The largest known fossil sea spider is *Palaeoisopus problematicus* Broili, 1928 from the Early Devonian. Overall length may exceed 125 mm, of which approximately two-thirds is accounted for by the elongate multisegmented abdomen (Fig. 3.1) unique to this taxon (Bergström et al., 1980). The combined length of cephalosoma (excluding proboscis and chelifores) and pre-abdominal trunk in the biggest individuals of *Palaeoisopus* is probably about 45 mm. In these large specimens maximum axial trunk width, measured across the lateral extensions, is approximately 25 mm. For the holotype of *Palaeomarachne granulata* n. gen. n. sp., combined length of the ‘head’ and preserved axial trunk region is at least 32 mm, and maximal trunk width (including presumed lateral extensions) is estimated at 24 mm. This places *Palaeomarachne granulata* within the upper range of corresponding body dimensions for *Palaeoisopus*. Although no comparisons can be made for actual appendage dimensions, broad articulating bases for chelifores and palps, and the relatively stout nature of the lateral extensions of trunk segments (Figs. 2.1, 5.2), suggest that *Palaeomarachne granulata* was overall a robust animal with

substantial feeding and walking limbs. Published sizes for “giant” living pycnogonids in the genus *Colossendeis* usually emphasize maximum leg span, which can exceed 500 mm, but the bodies of these animals are greatly reduced and maximum lengths (excluding proboscis and abdomen) are typically on the order of about 20–30 mm (Staples, 2007).

Paleobiogeography.—*Palaeomarachne granulata* n. gen. n. sp. is the only fossil pycnogonid so far documented from the Laurentian paleocontinent (a rumored occurrence of a possible sea spider in the upper Silurian Bertie Formation Lagerstätte of southern Ontario has yet to be verified). Other Paleozoic occurrences include *Cambropycnogon klausmuelleri* Waloszek and Dunlop, 2002 from ‘Orsten’ deposits of Baltica (Cambrian, Furongian), *Haliestes dasos* Siveter et al., 2004 from the Avalonian Herefordshire Lagerstätte (Silurian, Wenlock), and four species from the Hunsrück Slate (Lower Devonian, Emsian) of the Rheohercynian Basin (SE margin of Laurussia) (Bergström et al., 1980; Poschmann and Dunlop, 2006). More recently, the first confirmed pycnogonids of Mesozoic age were described from the La Voulte Lagerstätte of France, a setting on the Middle Jurassic (Callovian) margin of the western Tethys (Charbonnier et al., 2007).

Phylogenetic considerations.—Various hypotheses (Vilpoux and Waloszek, 2003; Manuel et al., 2006; Scholtz and Edgecombe, 2006; Bitsch and Bitsch, 2007) of ‘head’ segment allocation and homology of anterior appendages of Pycnogonida,

including chelifores, palps, ovigers, and first walking limbs (incorporated into the cephalosoma), have been proposed in efforts to clarify ancestral relationships, but the highly derived nature of even the supposed most “primitive” fossil adult forms has hampered progress (Arango and Wheeler, 2007). The current candidate for the oldest fossil sea spider is *Cambropycnogon klausmuelleri*, a minute late Cambrian protonymph-like form known from a small number of secondarily phosphatized ‘Orsten’ specimens (Waloszek and Dunlop, 2002; Vilpoux and Waloszek, 2003). *Cambropycnogon* shows no external demarcation of primary segment boundaries on the larval head/body, and its pycnogonid affinities have not been universally accepted (Arango, 2002; Bamber, 2007; Dunlop and Selden, 2009). *Haliestes dasos*, from the Silurian Herefordshire Lagerstätte, is based upon a single complete, three-dimensionally preserved adult individual of very small size (3.5 mm in length); the unique specimen was serially sectioned and digitally reconstructed in remarkable detail (Siveter et al., 2004). In most aspects of morphology, including fusion of the first limb-bearing trunk element with anterior ‘head’ elements to form an unsegmented cephalosoma, *Haliestes* is sufficiently like typical living sea spiders to result in a phylogenetic placement within the pycnogonid crown-group (Siveter et al., 2004; Arango and Wheeler, 2007). Similarly, all four pycnogonid species described from the Devonian Hunsrück Slate (Bergström et al., 1980; Poschmann and Dunlop, 2006) are adult forms and each clearly possesses a cephalosoma. In recent phylogenetic analyses two of these (*Palaeothea devonica* Bergström et al., 1980 and *Palaeopantopus maucheri*, Broili, 1928) consistently resolved within the crown-group of Pycnogonida (Siveter et al., 2004; Poschmann and Dunlop, 2006; Arango and Wheeler, 2007). A third species, *Palaeoisopus problematicus*, is unique in having a narrow and elongate five-segmented abdomen and is usually viewed as the most “primitive” of all sea spiders, occupying a stem-group position (Arango, 2002; Siveter et al., 2004; Poschmann and Dunlop, 2006; Dunlop, 2010) within the Eupycnogonida of Waloszek and Dunlop (2002). The most recently named Hunsrück species is *Flagellopantopus blocki* (Poschmann and Dunlop, 2006), described as having an extraordinary whip-like “telson” extending from the posterior trunk region. Despite showing an apomorphic loss of chelifores, it, too, is regarded as a possible stem-group representative (Poschmann and Dunlop, 2006). Three taxa of Jurassic age from the La Voulte-sur-Rhône Lagerstätte represent adult sea spiders that share far more in common with extant pycnogonid lineages, even to Family level, than with any described Paleozoic forms (Arango, 2002; Charbonnier et al., 2007; Dunlop and Selden, 2009).

The presence of five discrete serially heteromorphic segment-like elements in the ‘head’ of *Palaeomarachne granulata* n. gen. n. sp., anterior to the first of four unambiguous free limb-bearing trunk segments, is a unique condition among all known Pycnogonida (Fig. 3). We are unable to state with certainty, based on currently available material, which of these furrow-bounded elements might represent true segments corresponding to underlying somatic divisions. It is apparent from the configuration of basal articulations on the large anteriormost ‘head’ element (Figs. 2.2, 3.2) that it bore at least two pairs of limbs in the same position as chelifores and palps in most conventional pycnogonids. This implies that fusion of the first two limb-bearing post-antennal somites, corresponding to the cheliceral and parapalp segments of Vilpoux and Waloszek (2003), had been achieved by the Late Ordovician. Such a development presumably marks the initial stage in formation of a cephalosoma, suggesting that fusion may have proceeded by sequential capture of additional posterior units. The segmental identity of the four succeeding elements in *P. granulata*, and whether any bore ovigers or other limbs, remains unknown. The first of these shows

equivocal evidence of a medial circular depressed area (Figs. 2.2, 3.2) which might represent the position of an ocular structure. Even should this be confirmed, it will be of little help in identifying homologous regions in other pycnogonids, as median eye tubercle location in adults of living species that retain such a feature is highly variable, ranging from an extreme anterior to posterior placement on the cephalosoma (Arnaud and Bamber, 1987; Arango and Wheeler, 2007; Dunlop, 2010), to the first free trunk segment (King, 1973); where noted in fossil material, the anterior-posterior position of the eye tubercle also varies considerably (Bergström et al., 1980; Siveter et al., 2004; Poschmann and Dunlop, 2006; Charbonnier et al., 2007).

The next two elements in *P. granulata* are short (sag.) and relatively narrow (trans.), and are followed by an element of the same width but at least twice the length. Together, these three form a stalk-like connection between the anterior two elements and the first trunk segment. This arrangement superficially resembles the narrow ‘neck’-like region of the cephalosoma developed in some extant pycnogonid species. Bergström et al. (1980, fig. 5) illustrate one such example (in the genus *Nymphon*) that even shows a series of faint furrows demarcating three or four ring-like ‘segments’ between the anterior chelifore- and palp-bearing portion and the fused first trunk-limb bearing segment. In location and number, if not morphology and degree of expression, these ‘segments’ resemble the four posteriormost elements in the ‘head’ of *P. granulata* (we have found no explicit reference to this incipient segmentation in the literature on living pycnogonids, and cannot comment on its potential developmental or phylogenetic significance within the crown-group).

Fusion of the first limb-bearing trunk segment with an undivided ‘head’ region to form a cephalosoma, anterior to a separate trunk unit with walking legs (typically three pairs, rarely four or five) represents a derived adult state in all other pycnogonids, fossil and extant (Eupycnogonida of Waloszek and Dunlop, 2002).

Assuming the anteriormost element in *P. granulata* represents the fusion of separate cheliceral and parapalp segments, and if the succeeding four elements are also true segments, then six ‘head’ segments (posterior to the so-called “pre-antennal segment” of Vilpoux and Waloszek [2003]) may have been present in front of the first free limb-bearing trunk segment in an ancestral form. In so far as *P. granulata* represents the oldest known adult sea spider, its anterior multielement ‘head’ could be the plesiomorphic post-larval state for the group. Alternatively, the four elements between the large anterior unit and the first free trunk segment might instead be the result of autapomorphic duplication of one or more primary segments. Manuel et al. (2006) proposed a novel segmental duplication hypothesis to explain close morphological and ontogenetic similarities between palps (“pedipalps” in their terminology) and ovigers on the cephalosomas of eupycnogonids. Although the results of their study of Hox gene expression did not support this scenario, they suggested that segment duplication accounting for palp/oviger similarity could have occurred deeper in the tree, perhaps in “. . . a common ancestor of all extant arthropods . . .” (Manuel et al., 2006, p. 489). On the evidence provided by *P. granulata*, developmental duplication of anterior segments may have arisen along the basal stem-lineage of pycnogonids, only to be subsequently masked by fusion in the formation of the cephalosoma in Eupycnogonida.

Unfortunately, unless more complete specimens preserving intact appendages are recovered, the novel ‘head’ construction in *P. granulata* will remain largely uninformative in terms of helping decide which of numerous proposed segment homologies and phylogenetic scenarios (Waloszek and Dunlop, 2002; Vilpoux and Waloszek, 2003; Manuel et al., 2006) might apply

in reconciling the nature of the pycnogonid cephalosoma and the pattern of prosomal-opisthosomal tagmosis in euchelicerates.

SUMMARY

Palaeomarachne granulata n. gen. n. sp. is the geologically oldest post-larval fossil pycnogonid so far described, and the first sea spider known from Ordovician strata. Four sets of incomplete molt remains from relatively large animals were recovered from rocks of shallow marine origin representing deposition in a lagoonal setting in the Late Ordovician (Richmondian) Williston Basin of Laurentia. Its morphology clearly demonstrates that by Late Ordovician time pycnogonids had evolved at least part of the highly modified adult 'head' construction and anterior limb arrangement that sets the group apart from all other arthropods, but *P. granulata* uniquely retains four additional segment-like elements behind a chelifore and palp-bearing unit. This latter feature, plus the non-preservation of articulated limbs and unresolved nature of the region posterior to a robust four-segmented trunk, make it unreasonable to attempt assignment of *P. granulata* to anything other than a stem-lineage position, basal to the Late Devonian species *Palaeoisopus problematicus*, near the root of an already complicated pycnogonid tree (Arango, 2002).

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