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ONYCHOPHORAN-LIKE MYOANATOMY OF THE CAMBRIAN GILLED LOBOPODIAN, *PAMBDELURION WHITTINGTONI*

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Abstract: Arthropods are characterised by a rigid, articulating, exoskeleton operated by a lever-like system of segmentally arranged, antagonistic muscles. This skeletomuscular system evolved from an unsegmented body wall musculature acting on a hydrostatic skeleton, similar to that of the arthropods' close relatives, the soft-bodied onychophorans. Unfortunately, fossil evidence documenting this transition is scarce. Exceptionally-preserved panarthropods from the Cambrian Lagerstätte of Sirius Passet, Greenland, including the soft-bodied stem-arthropod, *Pambdelurion whittingtoni*, and the hard-bodied arthropods, *Kiisortoqia soperi* and *Campanamuta mantonae*, are unique in preserving extensive musculature. Here we show that *Pambdelurion*'s myoanatomy conforms closely to that of extant onychophorans, with unsegmented dorsal, ventral and longitudinal muscle groups in the trunk, and extrinsic and intrinsic muscles controlling the legs. *Pambdelurion* also possesses oblique musculature, which has previously been interpreted as an arthropodan characteristic. However, this oblique musculature appears confined to the cephalic region and first few body segments and does not represent a shift towards arthropodan myoanatomy. The Sirius Passet arthropods, *Kiisortoqia* and *Campanamuta*, also possess large longitudinal muscles in the trunk, although, unlike *Pambdelurion*, they are segmentally divided at the tergal boundaries. Thus, the transition towards an arthropodan myoanatomy from a lobopodian ancestor likely involved the division of the peripheral longitudinal muscle into segmented units.

Key words: Cambrian, Ecdysozoa, musculature, Onychophora, phosphatisation, Sirius Passet, taphonomy

INTRODUCTION

ARTHROPODS are characterised by a rigid, articulating, exoskeleton operated by a lever-like system of segmentally arranged muscles (Hessler 1964; Manton 1977). In contrast, the soft-bodied onychophorans, likely their closest relatives (Fig. 1; Andrew 2011; Campbell *et al.* 2011; Borner *et al.* 2014), possess an unsegmented body wall musculature which acts on a hydrostatic skeleton. Based on comparison between these groups and fossil evidence, it is believed that the arthropod skeletomuscular system evolved from an onychophoran-like state (Manton 1973, 1977; Budd 1998). However, the significant morphological and functional disparity between these two systems and the lack of any extant intermediary makes fossil stem-arthropods, which include many transitional taxa, crucial in understanding this evolutionary transition. Unfortunately, fossilised stem-arthropod musculature is rare, and in most instances preservation is poor (Hou *et al.* 2004; Gámez Vintaned *et al.* 2011) or confined to patches (Cong *et al.* 2014; Daley & Edgecombe 2014*a*). A major exception is the stem-arthropod *Pambdelurion whittingtoni* (Budd 1997), a common element of the Cambrian Lagerstätte of Sirius Passet in northern Greenland, which has a high frequency of specimens exhibiting exceptionally preserved musculature (Budd 1998). Its myoanatomy can be reconstructed in detail, providing significant insight into the evolution of arthropodan musculature.

Although there is a high degree of myoanatomical specialisation across different arthropod groups, the ground pattern of a "box-truss" system of trunk musculature is evident in crustaceans (Hessler 1964), myriapods (Hessler & Yager 1998), hexapods (Manton 1972; Birkett-Smith 1974), chelicerates (Shultz 2001) and seemingly trilobites (Cisne 1981). The box-truss system is composed of segmentally repeating, bilateral pairs of dorsal and ventral longitudinal, dorsoventral and, posterior and anterior oblique muscles (Figs. 2**,** 3; Shultz 2001). These muscles insert on specific internal, segmentally-arranged attachment points consisting of tendons or cuticular invaginations, forming an endoskeleton (Bitsch & Bitsch 2002). Lateral longitudinal muscles are also observed in some arthropod taxa, including the collembolan hexapods, diplopods and chilopods, but are absent in other arthropods (Manton 1977). The typical arthropod limb is controlled by both extrinsic muscles, which originate in the trunk and control the leg's stepping movement, and intrinsic muscles, which operate the joints of the leg (Fig. 3; Manton 1977). Together, the articulating sclerites and segmented muscles of arthropods form a complex system of interdependent elements, raising questions about the functioning of any intermediate system and the order of acquisition of these features.

The panarthropods (arthropods, onychophorans and tardigrades (Nielsen 1995)), are united in possessing distinct, paired dorsal, ventral and lateral longitudinal muscle groups and extrinsic limb musculature attaching dorsally and ventrally in the trunk (Fig. 3; Hoyle & Williams 1980; Schmidt-Rhaesa & Kulessa 2007; Halberg *et al.* 2009; Schulze & Schmidt-Rhaesa 2011; Marchioro *et al.* 2013; Smith & Jockusch 2014). Tardigrades and onychophorans thus possess the basic myoanatomical elements from which arthropodan musculature could be derived, with the exception of the dorsoventral and oblique elements of the arthropodan box-truss (Fig. 2). However, there are major functional and morphological differences in myoanatomy between the panarthropod phyla.

Unlike the arthropods, onychophoran longitudinal muscle does not exhibit segmentation (Hoyle & Williams 1980), and acts on a hydrostatic skeleton rather than manipulating a rigid, articulating exoskeleton. Moreover, onychophoran muscle fibres do not attach to apodemes, with the exception of those operating the claws of the feet and the jaws (Hoyle & Williams 1980). Rather, muscle fibres are attached directly or indirectly to the body wall by bundles of fine collagen fibres at several places along their length (Hoyle & Williams 1980).

Tardigrades similarly possess a hydrostatic muscular system, but unlike onychophorans their muscle fibres attach to the internal cuticle through specialised attachment points, comprised of interlocking muscle and epidermal cells (Shaw 1974). Whereas onychophoran longitudinal muscles extend the entire length of the body, tardigrade longitudinal muscles are composed of discrete fibres connecting at successive attachment points (Schmidt-Rhaesa & Kulessa 2007; Schulze & Schmidt-Rhaesa 2011; Marchioro *et al.* 2013).

The disparity between the tardigrade, onychophoran and arthropod muscular systems, and the lack of any extant intermediary, means that investigation of fossil stem-arthropods is required to confirm the primitive panarthropod condition and reveal how the arthropodan muscular system was derived. Cambrian stem-group arthropods possess varying combinations of lobopodian and arthropodan traits, such as *Pambdelurion whittingtoni* (Budd 1997), *Opabinia regalis* (Zhang & Briggs 2007), *Anomalocaris canadensis* (Whittington & Briggs 1985; Daley & Edgecombe 2014*b*) and *Fuxianhuia protensa* (Bergström *et al.* 2008), revealing a sequential acquisition of arthropod autapomorphies along the stem (Fig. 2; Legg *et al.* 2012, 2013). Hence, fossil stem-arthropods can potentially reveal when evolutionary developments in myoanatomy occurred relative to the acquisition of other arthropodan traits, such as arthropodisation (the development of a jointed limb) and arthrodisation (the sclerotising and segmentation of the exoskeleton).

Specimens from the Sirius Passet Cambrian Lagerstätte of northern Greenland, exhibit an unusually high frequency of exceptionally preserved musculature, which has been observed in annelids (Conway Morris & Peel 2008; L. Parry, pers. comm.), the stem loriciferan, *Sirilorica* (Peel *et al.* 2013), and, most relevantly, a variety of panarthropods, including both soft- (Budd 1998, 1999*a*) and hard-bodied taxa (Stein 2010; Budd 2011). Sirius Passet thus presents an opportunity to compare the myoanatomies of Cambrian stem and crown arthropods with important implications for the evolution of the arthropodan bodyplan.

Kerygmachela kierkegaardi (Budd 1993, 1999*a*) and *Pambdelurion whittingtoni* (Budd 1998), common elements of the Sirius Passet fauna, are soft-bodied "gilled lobopodians", distinguished by the possession of both lobopodous legs and dorsolateral flaps. Together with *Opabinia* and the anomalocaridids, the gilled lobopodians form a paraphyletic grade along the arthropod stem, which exhibit a progressive accumulation of arthropodan traits (Fig. 1; Daley *et al.* 2009; Legg *et al.* 2013; Smith & Ortega-Hernández 2014). Musculature is only rarely preserved in *Kerygmachela*, with no described specimens possessing longitudinal musculature and only limited evidence of circular musculature (Budd 1993, 1999*a*). In contrast, extensive musculature is frequently preserved in *Pambdelurion* allowing for detailed reconstruction of its myoanatomy (Budd 1997, 1998).

Pambdelurion's myoanatomy was examined by Budd (1998), who described a thick cylinder of unsegmented longitudinal muscle lining the body wall from which extrinsic limb musculature extends into the legs, confirming that the lower stem-group arthropods are characterised by onychophoran-like musculature. However, Budd (1998) also identified groups of oblique muscles which he interpreted as running through the body cavity, rather than peripherally, and forming a major component of the trunk musculature. Budd (1998) argued that *Pambdelurion's* possession of both peripheral longitudinal and internal, oblique muscle represents a system intermediate between the muscular hydrostatic skeleton possessed by onychophorans, and the arthropodan system of level-like muscles acting on sclerites, with limited peripheral muscle. The apparent presence of internal muscle in *Pambdelurion* implies that it developed before articulating external tergites, and was subsequently co-opted into its eventual role of acting on sclerites in arthropods. However, Budd's (1998) description of *Pambdelurion'*s myoanatomy was primarily based on very weathered and highly decayed specimens, which do not clearly demonstrate that the oblique musculature persists throughout the body or represents a significant, novel component of the trunk musculature.

Two arthropod taxa with segmented, sclerotised exoskeletons from Sirius Passet, *Kiisortoqia soperi* (Stein 2010) and *Campanamuta mantonae* (Budd 2011), also exhibit fossilised muscle tissue. *Kiisortoqia*, a basal arthropod (Stein & Selden 2012) or possible stem chelicerate (Legg *et al.* 2013; Stein *et al.* 2013), exhibits longitudinal muscle in the axial region, seemingly segmentally divided at the tergal boundaries (Stein 2010). *Campanamuta*, an artiopod (Stein *et al.* 2013), possesses dorsal bands of longitudinal muscle that extend from the anterior of the first tergite to about halfway into the caudal shield (Budd 2011). Transverse apodemes co-occur with the longitudinal muscle, which likely ran along the internal surface of the tergites, and, as in *Kiisortoqia*, appears segmentally divided at the tergal boundaries (Budd 2011). *Campanamuta* also possesses bundles of transverse muscle running from near the gut to the edge of the axial region, with a metameric arrangement corresponding in position to the tergal boundaries.

The preservation of muscle in *Pambdelurion*, *Kiisortoqia* and *Campanamuta*, allows for myoanatomical comparison between a soft-bodied, lobopodian stem-arthropod and early arthropods. In the present study, *Pambdelurion* material was re-examined to reconstruct its musculature in greater detail and to test for the presence of any arthropodan myoanatomical features. Many previously unpublished specimens, including new material collected in 2009 and 2011 and excavated from the outcrop itself, rather than the scree as in prior expeditions, supplemented this investigation. The new material is less weathered, retaining greater morphological detail and enabling a more complete reconstruction of *Pambdelurion'*s myoanatomy and morphology. Furthermore, newly collected and undescribed specimens of *Kiisortoqia* and *Campanamuta*, were examined to better reconstruct their myoanatomies, which are presently only partially documented (Stein 2010; Budd 2011). These taxa were examined for the presence of segmentation in the longitudinal musculature, and muscle groups potentially homologous to *Pambdelurion*'s oblique muscle. The musculature of these three taxa was further compared to that of extant ecdysozoans, with consideration as to how arthropodan myoanatomy could have been derived from a *Pambdelurion*-like lobopodian ancestor.

Sirius Passet fossils can also offer insight into the factors, biological and environmental, controlling soft-tissue preservation. Although muscle tissue decays quickly, in certain conditions it can be preserved through authigenic mineralisation, the rapid growth of minerals resulting from the activity of decay bacteria (Briggs *et al.* 1993). Microbial activity releases ions that can form minerals and generates geochemical gradients that lead to the diffusion of chemicals in and out of a carcass (Briggs 2003), with exceptional preservation of soft tissues requiring elevated microbial activity (Sagemann *et al.* 1999). Usually muscle preservation results from early phosphatisation in the form of apatite (Martill 1990; Briggs *et al.* 1993, 2005; Briggs & Wilby 1996). However, Sirius Passet fossils exhibit muscle tissue preserved in silica with phosphate absent (Budd 1998, 1999*a*, 2011). Whether these tissues were originally preserved in silica is uncertain. It is possible the musculature was originally preserved in phosphate which was later replaced by silica through metamorphic processes (Page *et al.* 2008). Furthermore, a nearby magmatic dyke (Ineson & Peel 2011*a*) could have led to hydrothermal alterations and dissolution and replacement by quartz. Here, we re-analysed mineralised muscle tissue in *Pambdelurion* and *Campanamuta* to confirm its chemical composition.

Preservation of soft tissue is highly variable between species, localities and even between parts of a carcass (Briggs 2003). The mineralisation of muscle tissue in apatite requires levels of phosphate concentration sufficient to inhibit the precipitation of calcite or aragonite (Allison 1988). This is normally determined by the build-up and release of phosphorous in the sediment and a reduced pH, with a point at which conditions switch to favour apatite precipitation (Allison 1988). Chemical gradients generated by decay, characterised by a drop in pH, have been shown experimentally to significantly impact mineral formation and consequently the preservation of soft tissues (Sagemann *et al.* 1999). This drop in pH needs to be maintained for apatite to precipitate and is generally more easily sustained near the centre of the body, favouring phosphatisation in these areas (Briggs & Wilby 1996). Biofilms formed by endogenous gut bacteria may also facilitate the preservation of internal soft tissues (Butler *et al.* 2015). It is suggested that after the decay of the gut wall, endogenous microbes enter the body cavity, consuming tissues and forming biofilms capable of mediating authigenic mineralisation, potentially explaining the frequent preservation of the gut, compared with the rare preservation of other internal structures (Butler *et al.* 2015).

To test for an influence of body size and the presence of certain organs on the diffusion gradients promoting mineralisation of soft-tissue, the patterns of preservation in *Pambdelurion* were examined for differences both between certain areas within a specimen and between specimens of varying sizes. Furthermore, the preservation of soft tissue in *Pambdelurion* was considered in light of the model proposed by Butler *et al.* (2015), to determine whether endogenous bacteria may be facilitating its preservation. The preservation of muscle tissue in *Pambdelurion* was further compared with that in *Kerygmachela*, *Kiisortoqia* and *Campanamuta* to test for interspecific taphonomic biases.

GEOLOGICAL SETTING

All material described in this study originates from Sirius Passet, an early Cambrian Lagerstätte in Peary Land, North Greenland (82°47.6´N, 42°13.7´W), first discovered in 1984 (Conway Morris et al. 1987). Sirius Passet correlates in age with the North American *Nevadella* Zone (Cambrian Series 2, Stage 3) (Babcock & Peel 2007). It is approximately contemporaneous with China's Chengjiang Lagerstätte and 10 Myr older than the Burgess Shale (Zhuravlev & Riding 2001). The Lagerstätte occurs in the marine mudstones of the siliciclastic Buen Formation deposited in a slope environment along the eroded scarp of an extensive carbonate platform, the Portfjeld Formation (Ineson & Peel 1997). The Lagerstätte consists of an 8.5 m thick succession of fine-grained, fossiliferous mudstones found in the Transitional Buen Formation, which have accumulated downslope from their point of origin (Ineson & Peel 2011). The organic-rich character and fine lamination of the sediment indicate poor oxygenation, inhibiting the decay of organic material (Ineson & Peel 2011*b*). This is supported by geochemical analysis (Le Boudec *et al.* 2014). However, the presence of narrow, irregular, horizontal burrows crossing many Sirius Passet fossils indicate the activity of a shallow burrowing, sediment-ingesting infauna (Peel 2010*a*), suggesting that the muds of Sirius Passet were not fully anoxic (Ineson & Peel 2011*b*). The organisms responsible for the trace fossils may have been feeding on sulphur bacteria, the growth of which was possibly promoted by carcasses and carapaces creating a barrier decreasing oxygen diffusion into the sediment (Mángano *et al.* 2012).

The Sirius Passet biota is an example of Burgess-Shale-type preservation (Butterfield 1995), being primarily organically preserved as carbonaceous compressions with mineralisation confined to specific regions such as the gut and digestive glands (Budd 1997; Vannier *et al.* 2014), or muscle (Budd 1998, 2011). Most carbonaceous material in the fossils has been lost due to exposure to chloritoid-grade metamorphism, though some organic matter appears to have been replaced by thin sheets of clay minerals (Budd 2011). The fossils are flattened, but show a higher degree of relief than those of the Burgess Shale. Two dimensional reflective films are associated with some specimens, preserving external features. Sirius Passet material is generally dark with little contrast in colour, although some specimens show tissue preserved in a pale, yellowish mineral.

In addition to the stem-group arthropods *Kerygmachela* (Budd 1993, 1999*a*) and *Pambdelurion* (Budd 1997), the Sirius Passet assemblage includes a number of euarthropods (Budd 1995, 1999*b*, 2011; Lagebro *et al.* 2009; Peel & Stein 2009; Stein 2010; Stein *et al.* 2013), an anomalocaridid (Daley & Peel 2010; Vinther *et al.* 2014), articulated halkieriids (Conway Morris & Peel 1990, 1995; Vinther & Nielsen 2005), the oldest recorded annelids (Conway Morris & Peel 2008; Vinther *et al.* 2011*a*), palaeoscolecidans (Conway Morris & Peel 2010), a stem loriciferan (Peel 2010*b*), hyoliths (Peel 2010*a*), vetulicolians (Vinther *et al.* 2011*b*).

MATERIALS AND METHODS

The Sirius Passet material here described was collected over several expeditions between 1985 and 2011 and is held by the Geological Museum of Copenhagen. Hundreds of specimens of *Pambdelurion*, *Kerygmachela*, *Kiisortoqia* and *Campanamuta* were examined, and those with well-preserved musculature or other structures were selected for further study. Where necessary, specimens were prepared mechanically with a pneumatic chisel to reveal obscured features. All specimens were washed in a solution of 10% HCl to remove loose sediment and weathering products. Because of the low relief and minimal colour contrast of Sirius Passet material, the specimens were drawn using a camera lucida attached to a microscope to identify, interpret and document obscure features. The direction and angle of illumination was varied to expose different features.

All specimens were imaged using Reflective Transformation Imaging (Malzbender *et al.* 2001). Specimens were photographed with 48 different lighting angles arranged in a dome shape, 25 cm in radius, around the subject with a Nikon D800 digital camera. These photographs were then processed with RTIBuilder 2.0.2 using the Hemispherical Harmonic algorithm (Wang *et al.* 2009) to produce an RTI file. Images were captured from the RTI file in RTIViewer 1.1.0 using the Specular Enhancement rendering mode to remove colour and enhance topographic contrast. The Specular Enhancement settings differed between specimens, but generally Specularity was set at approximately 25 and Highlight Size at approximately 10. Diffuse Colour was set to zero for all images. Fossils were illuminated from the northwest, except for images showing details where lighting was varied to best reveal the structure.

To test for a relationship between body size and the preservation of certain structures in *Pambdelurion*, an unpaired t-test was used to compare body width, excluding flaps, between specimens preserving longitudinal muscle and those with gut diverticulae. Using a ΣIGMA FESEM microscope, the ultrastructure of preserved muscle tissue in *Pambdelurion* and *Campanamuta* was examined using scanning electron microscopy (SEM) and energy-dispersive X-ray spectroscopy (EDX) analysis was performed to determine its elemental composition.

RESULTS

Taphonomy of Pambdelurion whittingtoni

All *Pambdelurion* specimens examined in the present study lie parallel to the bedding plane and are dorsoventrally flattened. Both dorsally and ventrally exposed specimens are known. A considerable size range was represented, with specimens ranging from 30 to 339 mm in length, and from 6 to 80 mm in body width, excluding flaps.

The external anatomy of *Pambdelurion* is usually poorly preserved and entirely absent in many specimens. External transverse annulations of the trunk and legs are occasionally preserved in low relief (Young & Vinther 2016, Fig. 1A). The lateral body-flaps are sometimes present as smooth areas lateral to the body, with very shallow relief marking the overlap with adjacent flaps. Frontal appendages are usually absent, but are occasionally preserved flattened, with low relief annulations (Young & Vinther 2016, Fig. 2). Occasionally, the body flaps, frontal appendages, and frontal appendage and cephalic spines are preserved as a reflective film, showing nearly the full body outline (Young & Vinther 2016, Fig. 1B).

In contrast to the generally poor preservation of the external anatomy, much of the internal anatomy is mineralised, preserving details of the gut and its diverticulae, the pharynx, and trunk and limb musculature. Electron microprobe analysis reveals that the mineralised musculature consists of silica, with phosphate absent (Table 1). Observation under SEM revealed that some, though not all, samples of mineralised muscle tissue preserved ultrastructural detail with individual myofibrils identifiable (Fig. 4A, B). Although some specimens show clear evidence of the longitudinal muscle having ruptured, generally the musculature in *Pambdelurion* shows relatively little decay.

The types of tissues preserved is size-dependant. Musculature is preserved in almost all smaller individuals but not larger specimens, with the largest individual preserving extensive musculature having a body width, excluding flaps, of 28 mm (Fig. 5). Gut diverticulae are only known from larger specimens, the smallest specimen preserving them having a body width of 40 mm (Fig. 5). There are no examples of trunk musculature preserved together with gut diverticulae. A t-test revealed a significant difference ($t_{32}=11.06$, $p<0.001$) in body width between specimens preserving longitudinal muscle (Mean=16.1, SE=8.54, *n*=30) and those preserving diverticulae (Mean=57.5, SE=0.90, *n*=4).

The more complete specimens of *Pambdelurion* reveal a pattern of differential preservation along the longitudinal axis. Trunk musculature and the gut are best preserved in the anterior half of the body, from immediatley posterior to the cephalic region to approximately the fifth or sixth trunk segment (Figs. 6, 7). In one exceptionally preserved specimen, the trunk musculature is mineralised up to approximately the ninth body segment (Fig. 6D). In the posterior region, the mineralisation of the trunk often ceases abruptly (Figs. 6, 7). However, many specimens retain an amorphously mineralised patch of apparent soft tissue located axially near the posterior of the body, even where all surrounding tissue is lost (Figs. 6, 7). Occasionally, traces of longitudinal striations, seemingly muscle, are associated with this patch of tissue (Fig. 6). There does not appear to be great lateral variation in the preservation of muscle, with both the axial region and lateral margins of the trunk often characterised by well-mineralised muscle tissue (Figs. 8**,** 9**,** 10).

Pambdelurion’s leg musculature has a strong tendency to fossilise, being preserved in almost all specimens that retain trunk musculature. With the exception of the last two and first pairs of legs usually being poorly preserved, there is little longitudinal variation in the preservation of the leg muscles. The leg musculature is frequently preserved in the posterior half even where the posterior trunk musculature is absent (Figs. 6, 7).

Musculature of Pambdelurion whittingtoni

Pambdelurion's musculature includes lateral longitudinal muscles, paired ventral and dorsal longitudinal muscles, extrinsic limb musculature, intrinsic limb musculature, extrinsic frontal appendage musculature and anteriorly-located, obliquely-orientated muscles (Fig. 11). Evidence for circular muscle is limited.

Lateral longitudinal muscles. Thick bundles of lateral longitudinal muscle along the left and right margins of *Pambdelurion's* body, which several specimens show as clearly distinct from other, more axial longitudinal muscle bands in the trunk (Figs. 8**,** 9). The lateral longitudinal muscle runs uninterrupted through the trunk, exhibiting no patterns of segmentation. Although usually poorly preserved in the anterior region, the lateral longitudinal muscles appear to originate near the anterior margin of the head (Young & Vinther 2016, Fig. 2). Along the trunk, the lateral longitudinal muscles gradually diverge laterally, following the cigar-shaped outline of the body, before converging posteriorly (Figs. 8**,** 10). Although no specimens preserve the posterior musculature of the trunk in great detail, the continuation of faint, fibrous depressions along the posterolateral margins in some specimens suggests that the lateral longitudinal muscles extend to the posterior end of the trunk, and spans the entire length of the animal (Fig. 8).

Dorsal and ventral longitudinal muscles. In many specimens, axially-located longitudinal muscle bands are preserved as separate from the lateral longitudinal muscle (Figs. 8**,** 9). These muscle groups are seen in both dorsally and ventrally exposed specimens (Figs. 9**,** 10), indicating the presence of both dorsal and ventral longitudinal muscles. These muscles appear sagittally divided into left and right pairs (Figs. 8; Young & Vinther 2016, Fig. 2). Like the lateral longitudinal muscle, the dorsal and ventral longitudinal muscles bear no trace of segmentation. Consistent with the generally poor preservation of the posterior, the dorsal and ventral longitudinal muscles are rarely preserved past roughly the 5th or 6th trunk segment and never past approximately the 8th segment (Figs. 6, 7). Their further longitudinal extent can only be inferred, but like the lateral longitudinal muscles they probably spanned the length of the body. Anteriorly, these muscles appear to extend to near the margin of the head (Young & Vinther 2016, Fig. 2).

Limb musculature. Limb musculature is preserved in the majority of *Pambdelurion* specimens as segmentally-arranged bundles of muscle extending distally from the lateral margins of the body wall (Figs. 8**,** 9**,** 10). In some specimens these fibres are observed running directly into the limb, marked by transverse annulations (Fig. 12D). In contrast, there is no evidence of any musculature directly associated with the lateral body flaps.

Generally, muscle bundles associated with the limbs are subtriangular with a broad base and distal taper (Fig. 12A, B, E), although in some specimens the bundles are splayed out distally (Fig. 12C). Details of the limb myoanatomy are often unclear, but many specimens show at least two distinct muscle bundles, one anterior and one posterior, entering a single leg (Fig. 12). Occasionally, three distinct muscle bundles appear to enter the limb (Figs. 12B, E). There is also evidence of intrinsic limb musculature in the form of obliquely-orientated fibres preserved either superimposed over the extrinsic limb musculature or extending between extrinsic bundles (Fig. 12A, F).

The proximal attachment points of the extrinsic limb musculature are uncertain, but appear to be located in the body wall. The limb muscles are sometimes seen extending about halfway into the lateral longitudinal muscle, forming a deep depression (Figs. 8**,** 9, 12A), suggesting that the extrinsic limb musculature may pass through the lateral longitudinal muscle. A single specimen potentially shows the continuation of the limb muscle past the lateral longitudinal muscle towards the more axial region of the trunk (Fig. 6B), although this may represent separate oblique musculature, discussed below. The distal insertion point of the extrinsic muscles is unclear because the musculature is usually preserved without the external limb morphology. However, the extrinsic limb musculature seems to extend to near the distal end of the leg (Fig. 12D).

Frontal appendage musculature. Despite their large size relative to the legs, the musculature of the frontal appendages is completely lost in all but a few specimens. In the exceptional cases it is present, the quality of preservation is poor compared with the limb musculature. The extrinsic frontal appendage musculature appears as a subtriangular bundle extending from the anterolateral region of the head into the base of the appendage (Young & Vinther 2016, Figs. 2C). It is never observed extending far into the appendage.

Oblique musculature. A number of specimens possess groups of well-developed, obliquely-oriented muscles located in the anterolateral region, set approximately 90° to the body axis, and clearly distinct from the longitudinal muscle (Figs. 9, 13). In some specimens these fibres extend between the lateral longitudinal muscles, and the dorsal and ventral longitudinal muscle groups, while they also occasionally overlie the longitudinal muscles, extending from near the body wall towards the gut (Fig. 13A-B). These fibres therefore appear to sit internally to the longitudinal muscle bands of the body wall. They never cross the sagittal line, with the margins of the gut appearing to be their greatest axial reach, and are arranged in separate left and right units, showing no evidence of segmentation. This musculature appears limited to the posterior half of the cephalic region and roughly the first trunk segment. The oblique fibres are present in approximately perpendicular sets, which are often preserved overlaying each other (Figs. 9, 13). In some specimens the oblique musculature appears closely associated with the pharynx (Fig. 13C-D). Occasionally, the fibres appear to curve anteriorly in the cephalic region (Fig. 13A-B).

In some specimens, a thin band with an oblique, fibrous structure lies between the lateral longitudinal muscle and the more axial longitudinal muscle (Fig. 14). While possibly a further example of oblique musculature, it does not appear to be a continuation of the oblique fibres discussed above, being narrower and not composed of perpendicular, conjugate sets. This structure cannot be unambiguously diagnosed as muscle, being poorly preserved in only a few specimens, and may instead represent some kind of connective tissue. One specimen preserves oblique muscle fibres extending between longitudinal muscle bands for approximately the first five body segments (Figs. 6B, 14A-B). However, these fibres appear to correspond closely with the extrinsic limb musculature, and are not present continuously along the trunk. It possible that they represent an axial extension of the extrinsic limb musculature rather than oblique trunk muscles.

Circular musculature. Evidence of circular musculature in *Pambdelurion* is ambiguous. The majority of specimens show no trace of circular muscle. Several specimens show widely-spaced (ca. 0.3 mm), transverse fibrous impressions spanning most of the trunk’s width, which potentially represent circular muscle (Young & Vinther 2016, Fig. 3). However, these structures cannot be diagnosed as muscle with any degree of certainty, possibly representing another kind of transverse structure such as vascular channels.

Gut and pharynx. A bulbous pharynx which sits in the cephalic region between the bases of the frontal appendages, occupying a large portion of the cephalic region (Fig. 15). Posterior to the pharynx, the gut is undifferentiated (Fig. 15D). Both the pharynx and the post-pharyngeal gut are marked by deep, transverse ridges.

Taphonomy and musculature of Kerygmachela kierkegaardi

Muscle tissue is rarely preserved in *Kerygmachela*, despite its close anatomical similarity to *Pambdelurion*. Rather, *Kerygmachela's* axial region is commonly preserved with a relatively high relief, commonly showing the gut, pharynx and occasionally diverticulae (Young & Vinther 2016, Fig. 5B). In the present study only a single *Kerygmachela* specimen, identified on the basis of large pygidial spines, exhibited extensive trunk musculature (Young & Vinther 2016, Fig. 4). As in *Pambdelurion*, the musculature is best preserved in the anterior half of the body.

Like *Pambdelurion*, the trunk is characterised by well-developed longitudinal muscles, which appear to sheath the entire body, tapering anteriorly and posteriorly as they follow the body outline (Young & Vinther 2016, Fig. 4). The extrinsic limb musculature is poorly preserved, but can be seen extending laterally from the body (Young & Vinther 2016, Fig. 4). There is evidence of obliquely-orientated muscle in the first trunk segment which extends anteriorly from the gut margin at roughly 45° to the body axis towards the body wall. These fibres are superimposed on the longitudinal muscle. In the posterior half, very faintly preserved fibres appear to run between longitudinal muscle bands at an oblique angle. Thin, widely-spaced (ca. 0.25 mm), individual fibrous structures run transversely across nearly the full width of the trunk and may represent circular muscle (Young & Vinther 2016, Fig. 5A). The gut emerges axially from the anterior of the trunk, appearing as a straight, transversely ridged structure, before expanding into an ovoid-shaped pharynx, also marked by transverse wrinkles.

Musculature of Kiisortoqia soperi

Muscle tissue is generally not well preserved in *Kiisortoqia soperi* and entirely absent in many specimens. Several specimens show a longitudinally striated surface with low relief in the axial region, which most likely represents the longitudinal muscle fibres of the trunk (Figs. 16**,** 17A, C). The most complete specimen shows the longitudinal muscle originating from the posterior of the second trunk tergite and appears to extend to the 16th tergite (Fig. 16). The longitudinal muscle tapers posteriorly, being particularly narrow in the final five tergites. In all cases the longitudinal muscle is restricted to the most axial regions of the body, occupying roughly one quarter of the width of the whole trunk.

Unlike in *Pambdelurion*, the longitudinal muscle does not appear to run continuously through the trunk. Rather, it is interrupted at the tergal boundaries and appears segmentally arranged

(Fig. 17A, C). Generally, the longitudinal muscle appears as a complex mass and is not easily divided into dorsal, ventral or lateral components. However, one laterally preserved specimen seems to possess a distinct group of dorsal, segmentally divided longitudinal muscles, in addition to less well-preserved ventral longitudinal muscles (Fig. 17C).

Transversely orientated muscle fibres with an apparently segmental arrangement are present in one specimen, but are very poorly preserved (Fig. 17B). These fibres appear to originate from the dorsolateral region of the trunk and extend ventrally. It is possible that they represent segmental, dorsoventral muscles. No specimens preserve extrinsic or intrinsic muscle associated with the appendages.

Due to the infrequent, incomplete and usually poor preservation of the musculature it is difficult to fully reconstruct the myoanatomy of *Kiisortoqia*. However, the trunk musculature appears to be primarily composed of segmentally-arranged longitudinal muscles, with both dorsal and ventral groups. There is also limited evidence of dorsolateral musculature within the trunk.

Musculature of Campanamuta mantonae

All investigated *Campanamuta mantonae* specimens were preserved dorsoventrally. Commonly, the external anatomy, including rounded head and caudal shields, and nine thoracic tergites, is preserved as a smooth area surrounding mineralised, internal soft tissue, including musculature (Fig. 18). Observations under SEM reveal that the muscle tissue retains ultrastructural detail, with individual myofibrils identifiable (Fig. 4C, D).

Longitudinal muscle runs through the trunk, although it is limited to the axial region, covering roughly one seventh on the total body-width. These muscles extend from the first tergite, continue through the entire thoracic region, and sometimes extend into the anterior region of the caudal shield (Young & Vinther 2016, Fig. 6). As in *Kiisortoqia*, the muscle does not run uninterrupted through the trunk, but appears to be divided into longitudinal segments at the thoracic tergal boundaries (Figs. 18**,** 19). It is not clear that the longitudinal muscle is divided sagittally, rather part of the muscle seems to run centrally through the trunk.

The trunk also contains transverse bands of muscle. These extend from an area just lateral to the body axis to the edge of the axial region (Young & Vinther 2016, Fig. 7). Although these groups of muscles are not generally well preserved, they appear segmental in arrangement, corresponding with the thoracic and caudal tergites.

Many specimens preserve a series of axial, striated structures that are segmentally repeated along either side of the body axis (Young & Vinther 2016, Fig. 8). These structures are angled slightly backwards and occupy depressions. They have the general appearance of muscle, but the striations are more clearly defined and regular compared to other examples of muscle in *Campanamuta*. Several pairs of these structures appear in the cephalic region, and they continue into the caudal area.

Musculature of an undescribed Sidneyia-like arthropod

A single specimen of an undescribed *Sidneyia*-like species (see Bruton 1981) from Sirius Passet shows well-mineralised longitudinal musculature through the trunk segments (Young & Vinther 2016, Fig. 10). Longitudinal muscle appears preserved from the second thoracic segment, through to the eighth. It is best preserved in thoracic segments four through seven and tapers posteriorly to a point at the ninth segment. As with other Sirius Passet arthropods, *Campanamuta* and *Kiisortoqia*, the longitudinal muscle appears divided into segments at the tergal boundaries. A raised, amorphously mineralised structure, likely representing the gut, runs axially through the trunk, dividing the longitudinal muscle sagittally. In the caudal region, the gut is visible as a deep depression. Extensive musculature is not preserved in other specimens.

DISCUSSION

Taphonomy of Pambdelurion whittingtoni

The generally poor preservation of *Pambdelurion*'s external anatomy when compared with euarthropods from Sirius Passet (e.g. *Campanamuta* (Budd 2011), *Kiisortoqia* (Peel & Stein 2009) and *Arthroaspis bergstroemi* (Stein *et al.* 2013)), suggests it possessed a weakly sclerotized cuticle. In contrast, the internal anatomy is often well preserved, particularly the musculature. Consistent with previous reports (Budd 1998, 1999*a*, 2011), EDX analysis revealed the musculature of *Pambdelurion* and *Campanamuta* to be preserved in silica. However, it is unlikely that this was the original mode of mineralisation. It is probable that the musculature was initially preserved in phosphate, as in most cases of mineralised muscle (Martill 1990; Briggs *et al.* 1993, 2005; Briggs & Wilby 1996), which was later replaced by silica. In support of the original phosphotisation of soft tissue at Sirius Passet, the gut diverticulae of *Pambdelurion* are reported as composed of calcium phosphate (Vannier *et al.* 2014). Additionally, geochemical analysis of Sirius Passet material suggests the loss of phosphate during diagenesis, revealed by a low Ca contents and the correlation between δ^{66}Zn and Mn/Zn (Le Boudec *et al.* 2014). While sufficient phosphorous to mineralise small areas of muscle tissue can be derived from the decaying organism itself (Briggs & Kear 1993), the extensive areas of mineralised muscle tissue in *Pambdelurion, Kiisortoqia* and *Campanamuta*, and in some polychaetes (Conway Morris & Peel 2008; L. Parry, pers. comm.), suggest an external source of phosphorous derived from the sediment.

In the carcasses of modern onychophorans, the closest extant anatomical analogue of *Pambdelurion*, the body wall muscles are the first structures to fully decay, beginning to deteriorate in three days before being completely lost within eight days, compared with the far more resistant cuticle which takes over 200 days to fully decay (Murdock *et al.* 2014). The frequency with which musculature is preserved in *Pambdelurion*, sometimes even where other, more resilient structures, such as the cuticle, are absent, is notable. The high frequency of *Pambdelurion* specimens with exposed musculature may, in part, be a result of their soft-cuticle. In the absence of hard cuticle, mineralised muscle tissue likely provides the greatest difference in lithology to the surrounding rock, acting as a plane of weakness along which the rock tends to split. Similar preservation appears in the putatively *Opabinia*-like *Myoscolex ateles* from the Emu Bay Shale, which frequently preserves the trunk musculature, but only rarely the external anatomy (Briggs & Nedin 1997) and the Cretaceous polychaete *Rollinschaeta myoplena*, which preserves extensive body musculature while mostly lacking the more recalcitrant external chaetae and cuticle (Parry *et al.* 2015). In such cases it appears the musculature was subject to microbially-induced mineralisation soon after decay commenced, resulting in a relatively high fidelity replication of these tissues. This contrasts with the Burgess Shale biota where the loss of musculature and most internal structures prior to fossilisation suggests bacterial decay was far more advanced, with often only the cuticle remaining.

The preservation of larger *Pambdelurion* specimens (body width excluding flaps >40 mm, Fig. 7E), where generally the only internal structures remaining are the gut and its diverticulae, appears to conform to Butler *et al.* (2015)'s suggestion that endogenous gut bacteria facilitate soft-tissue preservation. However, this is not the case for smaller *Pambdelurion* specimens (body width excluding flaps <20 mm), where longitudinal muscle is often mineralised in specimens where the gut is only partially preserved (Figs. 6**,** 7A-D). This suggests that, at least in smaller individuals, endogenous gut bacteria is less influential than exogenous bacteria in facilitating the preservation of soft-tissue in smaller individuals.

Rather than a pattern of reduced preservation moving abaxially from the gut, *Pambdelurion* generally shows differential preservation along the longitudinal axis (Figs. 6**,** 7A-D). A similar pattern is not observed in *Campanamuta*, *Kerygmachela* or *Myoscolex*, which are generally mineralised along the length of the trunk, suggesting this pattern may be caused by specifics of *Pambdelurion*'s anatomy. While the mechanisms are not entirely clear, it is potentially related to *Pambdelurion*'s gut diverticulae, which sit in the anterior half of the trunk (Vannier *et al.* 2014), the region of the body where soft tissues are best preserved.

Experiments (Briggs & Kear 1993) and fossil evidence (Briggs & Wilby 1996) reveal that conditions favourable for apatite precipitation may be restricted to specific regions within a carcass. In *Pambdelurion*, the presence of diverticulae may influence the potential for apatite precipitation, which generally requires a low pH (Allison 1988), by causing a local shift in the chemical gradients in their surrounding areas during decay (Sagemann *et al.* 1999). The decay of the diverticulae may have caused a reduced pH relative to other parts of the carcass. It is also possible these organs maintained a high concentration of phosphate which was released during decay. The frequent presence of an axial, amorphous patch of soft tissue in the posterior (Figs. 6**,** 7A-D), suggests similar processes may be operating to facilitate apatite precipitation in this area. Unfortunately, as detailed morphology of this posterior structure is almost always lost, it is difficult to identify it with certainty. However, its location and general shape suggest it may be part of the hindgut.

The tendency for *Pambdelurion*'s leg musculature to become mineralised in the posterior region, even where trunk musculature is lost, is inconsistent with a model of fossilisation mediated by gut-derived bacteria (Butler *et al.* 2015). The frequent preservation of leg musculature indicates an inhibition of decay in the limbs, possibly due to the legs having a more robust cuticle relative to the trunk, which might also act as a source of phosphorous (Briggs & Kear 1993).

Mineralisation of musculature in *Pambdelurion* is size dependent, with extensive musculature absent in all large specimens (body width excluding flaps > 40 mm). The reasons for this are not clear, but it appears that conditions favourable for muscle mineralisation (low pH and sufficiently high concentration of phosphate (Allison 1988; Briggs & Wilby 1996; Sagemann *et al.* 1999)) are difficult to maintain in a larger carcass, where it appears muscle tissue decays without undergoing mineralisation.

The general absence of preserved musculature in *Kerygmachela* specimens contrasts with its frequent preservation in *Pambdelurion* and is surprising given their close anatomical similarity. Such taxonomic biases in preservation between apparently morphologically similar taxa are also observed between species of fish at the Santana Formation of Brazil (Martill 1998) and annelid species at the Hakel and Hjoula localities of Lebanon (Wilson *et al.* 2016). Amongst South Australia's Emu Bay Shale biota, *Myoscolex* is unique in exhibiting exceptionally preserved trunk musculature (Glaessner 1979; Briggs & Nedin 1997). The taphonomic differences between *Pambdelurion* and *Kerygmachela* reinforce that preservation is a highly complex process that can be significantly affected by seemingly subtle differences in the nature of the target organism. One explanation for this taxonomic bias is a possible difference in the robustness of the cuticle, and subsequently the time taken for external microbes to invade the body (Wilby & Briggs 1997). *Kerygmachela* may possess a weaker cuticle than *Pambdelurion* leading to a faster decay of muscle tissue by exogenous bacteria. Interestingly, *Kerygmachela* conforms much more closely than *Pambdelurion* to Butler *et al.*'s (2015) model of fossilisation mediated by gut-bacteria, with the gut frequently being the only internal structure preserved (Young & Vinther 2016, Fig. 5B).

The onychophoran-like myoanatomy of Pambdelurion whittingtoni and Kerygmachela kierkegaardi

The myoanatomy of *Pambdelurion* conforms remarkably closely with that of extant onychophorans (Hoyle & Williams 1980), which molecular evidences suggests are the closest relatives of the arthropods (Fig. 1; Andrew 2011; Campbell *et al.* 2011; Borner *et al.* 2014), despite significant morphological evidence supporting an arthropod-tardigrade sister grouping (Budd 2001; Mayer *et al.* 2013; Smith & Ortega-Hernández 2014; Yang *et al.* 2016). The muscle groups that *Pambdelurion* shares with modern onychophorans include paired, unsegmented lateral, dorsal and ventral longitudinal muscles extending the length of the trunk, extrinsic leg musculature and, putatively, circular muscle (Figs. 3, 11). *Pambdelurion* is here reconstructed as also possessing a ventromedian longitudinal muscle located dorsally to the paired ventral longitudinal muscles, which is present in onychophorans (Hoyle & Williams 1980) and appears to be a primitive bilaterian character (Brunet *et al.* 2015). The onychophoran body wall musculature, however, is more complex than that observed in

Pambdelurion, with a layer of overlapping oblique fibres located between the outer circular and inner longitudinal muscle groups (Fig. 3).

Tardigrades exhibit a similar arrangement of longitudinal musculature to *Pambdelurion*, possessing dorsal, ventral and lateral groups extending the length of the body (Fig. 3; Schmidt-Rhaesa & Kulessa 2007; Schulze & Schmidt-Rhaesa 2011; Marchioro *et al.* 2013). However, due to their small size, the longitudinal muscles of tardigrades are reduced to thin bands composed of a few fibres, unlike the large body wall muscles of onychophorans and *Pambdelurion* which form a near-complete cylinder around the body. Moreover, based on analysis of the molecular identities of tardigrade segments, it appears that almost the entire tardigrade body is homologous to the head region of arthropods, further obscuring comparisons between tardigrade, *Pambdelurion* and arthropod myoanatomies (Smith *et al.* 2016). Nevertheless, tardigrade musculature resembles that of the arthropods in a number of important aspects. The longitudinal muscles of tardigrades are divided into separate units along the body which connect at successive attachment points (Marchioro *et al.* 2013), in contrast to the undivided longitudinal muscle units which run continuously throughout the length of the trunk in *Pambdelurion* and the onychophorans (Hoyle & Williams 1980). Echiniscoidean tardigrades are also characterised by segmented sclerotised dorsal cuticular plates, revealing a particularly striking convergence with the arthropods (Marchioro *et al.* 2013). Tardigrades further possess metamerically arranged dorsoventral and oblique muscles which connect the lateral and ventral muscle groups (Marchioro *et al.* 2013), bearing a resemblance to the arthropodan box-truss. The likely placement of the tardigrades as basal to *Pambdelurion* and the arthropods suggests that the similarities between tardigrade and arthropod musculature are a product of convergence.

Comparison with the cycloneuralians, a paraphyletic assemblage that includes the priapulids, kinorhynchs, nematodes, nematomorphs and loriciferans (Fig. 3; Campbell *et al.* 2011; Borner *et al.* 2014; Laumer *et al.* 2015; Yamasaki *et al.* 2015) which with the panarthropods form the Ecdysozoa (Aguinaldo *et al.* 1997; Budd & Telford 2009; Edgecombe 2009), suggests the presence of peripheral longitudinal muscle represents the primitive Ecdysozoan condition. However, longitudinal musculature varies widely in arrangement between the cycloneuralian phyla (Fig. 3; Carnevali & Ferraguti 1979; Müller *et al.* 2004; Rothe *et al.* 2006; Neves *et al.* 2013; Herranz *et al.* 2014) and further developmental studies are required to confirm homology of these muscles. It is possible that ancestral ecdysozoan possessed a cylinder of undifferentiated longitudinal muscle bands similar to that of modern priapulids (Webster *et al.* 2006) from which the distinct dorsal, ventral and lateral longitudinal muscle groups of the panarthropods, including those of *Pambdelurion* (Fig. 3), were derived. Remarkably, the kinorhynchs possess a highly segmented trunk musculature and hard cuticle, representing an independent transition from a vermiform to a segmented bodyplan, convergent with the arthropods (Kristensen & Higgins 1991; Herranz *et al.* 2014). Despite this convergence, the kinorhynchs and arthropods show disparate ontogenetic patterns of segmentation. The longitudinal muscles in juvenile kinorhynchs are continuous prior to developing the segmental pattern of the adult (Schmidt-Rhaesa & Rothe 2006). In contrast the arthropod mesoderm is divided into segmental regions very early during development (Scholtz 1997; Weisblad & Huang 2001).

The two extrinsic muscle bundles that enter the legs of *Pambdelurion* in an anterior-posterior arrangement likely represent protractor and retractor muscles, used to move the limb forwards and backwards. Where a third bundle is seen associated with the leg (Fig. 12B, E), this is likely either a levator or depressor muscle, which moves the leg up or down respectively. The extrinsic leg musculature of *Pambdelurion* closely resembles that of onychophorans which consists of five muscles: a protractor, retractor, levator, which attach high up on the body wall and two depressors (Hoyle & Williams 1980), which attach to metamerically arranged, ventral cuticular thickenings (de Sena Oliveira *et al.* 2013). Arthropod extrinsic limb muscles are similarly composed of promotor, remotor, levator and depressor groups, although consisting of more distinct muscles, which originate on the coxa and insert dorsally and ventrally in the trunk (Manton 1977). Likewise, the tardigrade leg is operated by up to 14 extrinsic muscles, originating from the dorsal, ventral and lateral muscle attachment points (Halberg *et al.* 2009; Marchioro *et al.* 2013). The presence of limbs operated by groups of extrinsic muscles extending from ventral and dorsal regions of the trunk therefore likely represents the primitive panarthropod condition (Fig. 3).

The attachment points of *Pambdelurion*'s extrinsic leg musculature are difficult to ascertain, but are likely located along the inner dorsal and ventral margins of the trunk as in arthropods (Manton 1977) and onychophorans (Hoyle & Williams 1980). The extrinsic leg musculature in *Pambdelurion* often forms a depression in the lateral longitudinal muscle (Fig. 12A), suggesting it may pass through the lateral longitudinal muscle as in onychophorans (Fig. 3**;** Hoyle & Williams 1980). The intrinsic musculature of *Pambdelurion*'s limbs is possibly homologous to the septal muscle of onychophorans, a complex mass of circular, longitudinal and oblique intrinsic muscles located in the leg, which stiffen it when contracted (Hoyle & Williams 1980).

The single specimen of *Kerygmachela* preserving extensive musculature shows a myoanatomy very similar to that of *Pambdelurion* and onychophorans, with well-developed longitudinal muscle sheathing the trunk, putative circular muscle and extrinsic limb muscle (Young & Vinther 2016, Figs. 4, 5A). No differences from *Pambdelurion*'s musculature were observed, although the discovery of further specimens may reveal unique aspects of *Kerygmachela's* myoanatomy.

The division of *Pambdelurion*'s digestive tract into a bulbous pharynx located between the frontal appendages, and an undifferentiated gut, both bearing transverse ridges, is a feature shared with *Kerygmachela* (Budd 1999*a*). The possession of a large, muscular pharynx is a character shared with onychophorans, tardigrades and the scalidophorans, and likely represents the primitive condition within Ecdysozoa (Smith & Caron 2015).

Lack of flap musculature in Pambdelurion whittingtoni

It has been postulated that *Pambdelurion* and *Kerygmachela* used their dorsolateral flaps in swimming via undulation (Budd 1999*a*; Hou & Bergström 2006; Gámez Vintaned *et al.* 2011; Liu & Dunlop 2014; Vannier *et al.* 2014). However, the lack of musculature associated with the flaps, and consequently any way to precisely control their movement suggests this was not the case. Furthermore, *Pambdelurion*'s flaps lack the high-relief, transverse lines seen in *Anomalocaris canadensis* which have been interpreted as support structures to assist in swimming (Daley *et al.* 2013; Daley & Edgecombe 2014*b*). *Anomalocaris* likely achieved propulsion through an undulating wave-like motion of its flaps (Usami 2006), similar to that seen in modern stingrays (Rosenberger & Westneat 1999). It seems unlikely that *Pambdelurion's* longitudinal musculature could achieve a similar motion. Hence, rather than being an actively swimming predator, *Pambdelurion* was probably restricted to a benthic lifestyle, with its gill-bearing flaps likely used for respiration (Budd 1997, 1999*a*).

Pambdelurion's lack of flap musculature is consistent with conclusions regarding arthropod limb evolution based on a giant anomalocaridid, *Aegirocassis benmoulae*, bearing both dorsal and ventral body flaps (Van Roy *et al.* 2015). The dorsal flaps of *Aegirocassis* were interpreted as homologous to the flaps of gilled lobopodians, with the ventral flaps homologous to the legs of lobopodians and the swimming flaps of other anomalocaridids. *Pambdelurion*’s lack of flap musculature supports the suggestion that it is the legs of *Pambdelurion*, rather than the flaps, that are homologous to the swimming flaps of the anomalocaridids. In *Anomalocaris*, transverse musculature at the base of the flaps has been interpreted as representing patches of more extensive transverse trunk muscle continuing along the longitudinal axis (Daley & Edgecombe 2014*a*). However, these muscles are very similar in appearance to the limb musculature of *Pambdelurion* and more likely represent the extrinsic musculature of *Anomalocaris’* swimming flaps, homologous to *Pambdelurion*’s extrinsic limb muscles.

Frontal appendage musculature in Pambdelurion whittingtoni

Pambdelurion’s frontal appendage musculature, although rarely preserved, is broadly similar to that of the legs, being composed of extrinsic bundles extending from the trunk into the appendage (Young & Vinther 2016, Fig. 2). However, the extent of the musculature is limited relative to the large size of the frontal appendages compared with the legs. This may be a taphonomic artefact, consistent with the overall poor preservation of musculature in the cephalic region. However, the legs, which appear to be constructed very similarly to the frontal appendages, often show well preserved musculature, even where trunk musculature is not preserved. Furthermore, the musculature of the frontal appendage is minimal even in specimens where the cephalic region is well-preserved (Young & Vinther 2016, Fig. 2). The limited, and often absent, myoanatomy of the frontal appendages in *Pambdelurion*, therefore, likely reflects an actual reduced musculature in the frontal appendage, casting doubt on the extent to which they functioned raptorially. The frontal appendages appear highly flexible, and relatively soft (Young & Vinther 2016, Fig. 9), in contrast to the rigidly articulating, sclerotised frontal appendages of the anomalocaridids which were almost certainly raptorial (Whittington & Briggs 1985; Chen *et al.* 1994; Daley *et al.* 2009; Daley & Edgecombe 2014*b*). While, *Pambdelurion*’s frontal appendages may have had a weakly raptorial function, it is possible they were predominantly sensory. In particular, the highly elongated, thin distal spines of the frontal appendage (Young & Vinther 2016, Fig. 9), would have little raptorial use and were very likely sensory.

Pambdelurion whittingtoni lacks any uniquely arthropodan musculature

The major ways in which *Pambdelurion’*s myoanatomy differs from modern onychophorans are (1) the apparent lack of circular muscle and (2) the presence of oblique musculature. Budd

(1998) considered these differences as representing a significant shift in the arthropod stem group towards a more arthropodan musculature. Budd (1998) interpreted *Pambdelurion*'s oblique musculature as continuing throughout the trunk and representing a shift away from a reliance on peripheral muscle acting on a hydrostatic skeleton, as seen in onychophorans, towards muscle running through the trunk as in arthropods. Consequently, Budd (1998) concluded that *Pambdelurion*'s myoanatomy indicates that an arthropodan musculature developed prior to the evolution of sclerotised, articulating tergites.

However, our present findings put Budd's (1998) interpretation into question. Firstly, the limited evidence for circular muscle in *Pambdelurion* may be a taphonomic artefact. In onychophorans the circular muscle, which antagonises the longitudinal muscle and elongates the body, is extremely thin, being just one layer deep, and is the most peripheral muscle group (Hoyle & Williams 1980). If circular muscle in *Pambdelurion* is similarly underdeveloped, it likely decayed rapidly and had minimal fossilisation potential. This is consistent with circular muscle rarely being preserved in Sirius Passet polychaetes, despite likely being an important part of their myoanatomy (Conway Morris & Peel 2008; L. Parry, pers. comm.). Likewise, in the Cretaceous polychaete *Rollinschaeta myoplena* longitudinal and parapodial muscle is preserved to a far greater degree than circular muscle, which is observed in only a few specimens (Wilson *et al.* 2016).

The transverse, fibrous impressions observed in *Pambdelurion* are reasonably interpreted as representing a thin layer of circular muscle (Young & Vinther 2016, Fig. 3). Furthermore, apparent circular muscle has been observed in *Kerygmachela* both in the present study (Young & Vinther 2016, Fig. 5A) and previous investigations (Budd 1993, 1999*a*). Given the overall similarity of *Kerygmachela's* myoanatomy with *Pambdelurion's*, and the need for unsegmented longitudinal muscles acting on a haemocoel to be properly antagonised, it appears likely that *Pambdelurion* possessed a thin layer of circular muscle.

Secondly, although Budd (1998) interpreted the oblique musculature of *Pambdelurion* as persisting through the whole trunk, and constituting a significant component of the body musculature, this is not apparent in the material. Rather, the well-developed groups of perpendicularly orientated oblique muscles appear restricted to the cephalic region and the first few trunk segments (Fig. 13). It is unlikely that these muscles had a significant role in locomotion, or in cross-bracing the body as previously suggested (Budd 1998). No obvious homologue to these muscles is found in onychophorans. Onychophorans do possess a pair of overlapping, perpendicularly arranged, oblique muscles, which sit between the outer circular and longitudinal muscles, persisting throughout the trunk and forming a major part of the body wall (Fig. 3). However, *Pambdelurion's* oblique musculature appears to lay interior to the longitudinal muscle and likely bears no relation to the oblique muscles of onychophorans. Furthermore, the highly derived nature of the onychophoran mouth, which is not homologous to the mouths of other ecdysozoans, (Ou *et al.* 2012), makes it difficult to identify homologous musculature in the onychophoran head.

Musculature potentially homologous to the anterior oblique musculature of *Pambdelurion* must be sought amongst other ecdysozoan taxa. Most cycloneuralian phyla, including the priapulids (Storch *et al.* 1990), kinorhynchs (Herranz *et al.* 2014), loriciferans (Neves *et al.* 2013) and larval nematomorphs (Müller *et al.* 2004) possess a retractable introvert. The introvert is controlled by retractor muscles, and in some cases protractors, which extend from the body wall and attach to the introvert controlling its retraction and protrusion, although, between the phyla, the retractor muscles differ in number, arrangement and attachment points. The anterior oblique muscles of *Pambdelurion*, which seem to insert on the body wall, appear associated with the pharynx (Fig. 13), may have controlled the protrusion of an eversible pharynx and mouth cone either directly or through hydrostatic pressure, with the posteriorly directed oblique muscles responsible for retraction. Comparable muscles are not present in the tardigrades, onychophorans and arthropods, which lack an introvert. *Pambdelurion*, however, possessed a highly conserved, introvert-like mouth apparatus, with radially arranged plates and pharyngeal teeth homologous to mouth parts found in cycloneuralians (Vinther et al, 2016). Similar homologies have been identified in the mouth parts of the stem-group onychophoran *Hallucigenia* (Smith & Caron 2015) and the stem-group arthropod *Jianshanopodia* (Vannier *et al.* 2014), suggesting the radial oral mouth cone is a shared derived character of the Ecdysozoa. Alternatively, these anterior oblique muscles may act as pharyngeal dilators, similar to those in *Limulus polyphemus* (Shultz 2001), serving to expand the pharynx.

The thin band of oblique fibres that sits between the lateral and axial longitudinal muscle groups appears to be a separate structure from the larger anterior oblique muscles. Preserved in only a few specimens, their longitudinal extent is difficult to determine, but they appear restricted to the anterior half of the trunk (Fig. 14). In one specimen they possibly represent an axial continuation of the extrinsic limb musculature (Fig. 14A, B), but in other specimens they clearly constitute a separate group of oblique fibres (Fig. 14C, D). Poor preservation makes it difficult to classify this tissue as muscle with any certainty, and it is often coarser and more roughly striated than is typical of preserved muscle in *Pambdelurion*. If this does represent muscle extending between longitudinal muscle bands, it is difficult to infer its function. Onychophorans possess inner circular musculature, which lies interior of the longitudinal muscle and passes between the dorsal and lateral longitudinal muscles (Fig. 3), which is possibly homologous.

Neither the anterior oblique musculature nor oblique bands extending between longitudinal muscle groups constitute strong evidence for a shift towards more arthropodan musculature in *Pambdelurion*. While "oblique" musculature is an important element of the box-truss system which seems to be a shared derived character for arthropods (Fig. 2**;** Shultz, 2001), these muscles are oblique relative to the dorsoventral axis, not the lateral axis and bear no relation to *Pambdelurion*'s oblique musculature.

Myoanatomical comparisons between Pambdelurion whittingtoni and the euarthropods, Kiisortoqia soperi and Campanamuta mantonae

A lack of specimens preserving musculature and generally poor preservation relative to *Pambdelurion* makes it difficult to reconstruct the myoanatomy of the Sirius Passet euarthropods, *Kiisortoqia*, *Campanamuta* and the *Sidneyia*-like arthropod in detail. *Kiisortoqia* appears to possess separate dorsal and ventral longitudinal muscle (Fig. 17), although other muscle groups, including limb musculature, were not identified. Muscle tissue in *Campanamuta* is generally better preserved than in *Kiisortoqia*, with transverse fibres identified in the trunk (Young & Vinther 2016, Fig. 7) in addition to longitudinal musculature (Fig. 19), consistent with previous reports (Budd 2011). However, the precise nature and function of these transverse fibres remains unclear. Extending from near the margin of the gut to the edge of the axial region in a segmental arrangement, it is possible they represent extrinsic appendage musculature, homologous to the coxal muscles of extant arthropods (Manton 1977). Separate, transversely-striated axial structures, angled posteriorly at 45° to the body axis potentially represent a distinct group of muscles (Young & Vinther 2016, Fig. 8). Although similar in appearance to muscle tissue, the striations of these structures are far more well-defined and regular than is characteristic of preserved musculature. These structures were diagnosed by Budd (2011) as gut diverticulae, rather than muscle, and this is likely the correct interpretation.

Neither *Kiisortoqia*, *Campanamuta* nor the *Sidneyia*-like arthropod, possess obliquely orientated muscle in the trunk (Figs. 17, 19; Young & Vinther 2016, Fig. 10), further supporting the conclusion that *Pambdelurion's* oblique musculature is not an arthropodan trait. Instead, like in *Pambdelurion, Kerygmachela* and the onychophorans, longitudinal muscle is the dominant myoanatomical element in these taxa. The major myoanatomical difference between the gilled lobopods, *Pambdelurion* and *Kerygmachela*, and the Sirius Passet euarthropods, is the segmental division of the longitudinal musculature at the tergal boundaries seen in the euarthropods (Figs. 17-19; Young & Vinther 2016, Fig. 10). This suggests that the transition to an arthropodan myoanatomy did not involve a reduced reliance on peripheral muscle and an increased reliance on internal muscle as Budd (1998) argues. Rather, it seems the primitive peripheral longitudinal muscle, homologous to that present in *Pambdelurion* and modern onychophorans, was conserved, but was fundamentally modified by being divided into segments.

When this segmentation occurs in relation to the evolution of segmented, articulating tergites remains a fundamental problem. Amongst the Sirius Passet panarthropods, segmented longitudinal muscles only appear in taxa possessing articulating sclerites, leaving the question open. Unfortunately, examples of preserved musculature amongst Cambrian stem-group arthropods are rare. *Myoscolex*, which has been suggested as an *Opabinia*-like animal (Briggs & Nedin 1997), despite objections from Dzik (2004), is one potential exception. *Myoscolex* has been described as possessing dorsal and ventral longitudinal muscles and dorsoventral muscles extending between them, while having a soft cuticle and lacking externally segmented, articulating sclerites (Briggs & Nedin 1997). The dorsoventral muscles appear metameric in arrangement and the longitudinal muscles are described as separated by segmental boundaries (Briggs & Nedin 1997). However, further work is required to confirm *Myoscolex's* precise affinities.

CONCLUSIONS

The myoanatomies of the three extant panarthropod phyla, tardigrades, onychophorans, and arthropods are all characterised by dorsal, ventral and lateral longitudinal muscle groups and extrinsic leg musculature (Fig. 3). The stem-arthropod, *Pambdelurion*, exhibits all of these muscles groups, with its myoanatomy conforming closely to that of onychophorans, being characterised by unsegmented longitudinal musculature and relatively simple, unsegmented groups of extrinsic limb muscles. An onychophoran-like musculature, therefore, likely represents the primitive condition in the panarthropods and appears to have persisted crown-wards along the arthropod stem to at least the gilled lobopodian grade.

Comparisons between the myoanatomy of *Pambdelurion* and Sirius Passet euarthropods suggest that the transition towards an arthropodan myoanatomy was likely achieved through the segmentation of the longitudinal muscle groups, which then inserted at the tergal and sternal boundaries. Similarly, the extrinsic muscles of the arthropod limb broadly correspond in arrangement to those of the onychophorans and *Pambdelurion*, being composed of separate promotor, remotor, levator and depressor muscles. The intrinsic limb muscles of the arthropod leg could be derived from the division of extrinsic lobopod musculature into separate intrinsic components operating the joints of the limb. As previously suggested by Manton (1977), the transition towards an arthropodan myoanatomy appears to have involved a division of continuous muscle groups, in both the limbs and trunk, into segmented units connected, either directly or through an endoskeleton, to hardened, articulating sclerites, with a reduced dependence on the haemocoel for transmitting force.

The major novel muscle groups in the arthropodan box-truss system are the dorsoventral and oblique muscles (Shultz 2001), neither of which appear homologous to the oblique musculature of *Pambdelurion*, which does not exhibit any arthropodan characteristics. It is possible the dinocaridids, which lie crown-ward of *Pambdelurion*, possessed a musculature with distinctly arthropodan features. Unfortunately, with the possible exception of *Myoscolex*, there are presently no dinocaridid taxa exhibiting musculature that can be reconstructed in detail. A full understanding of the transition from an onychophoran to an arthropodan myoanatomy, and the development of the novel muscle groups associated with the box-truss system, may not be possible until further fossil evidence emerges

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FIGURES

FIG. 1. Simplified cladogram of extant and fossil ecdysozoans based on recent studies (Campbell *et al.* 2011; Legg *et al.* 2012, 2013; Stein *et al.* 2013; Borner *et al.* 2014; Smith & Ortega-Hernández 2014; Laumer *et al*. 2015; Yamasaki *et al.* 2015). Width: 80 mm.

FIG. 2. The box-truss trunk musculature system, representing the primitive condition in arthropods, showing four trunk segments and their major muscle groups. Abbreviations: aom, anterior oblique muscle; dlm, dorsal longitudinal muscle; dvm, dorsoventral muscle; pom, posterior oblique muscle; teb, transverse endoskeletal bar; vlm, ventral longitudinal muscle. Adapted from Shultz (2001). Width: 80 mm.

FIG. 3. Simplified cladogram showing *Pambdelurion whittingtoni* and extant ecdysozoans based on recent studies (Campbell *et al.* 2011; Borner *et al.* 2014; Laumer *et al*. 2015; Yamasaki *et al.* 2015), with schematic cross-sections through the trunk showing myoanatomy. Myoanatomy is simplified for all taxa to show only the major muscle groups. Note the common elements shared by tardigrades, onychophorans, *Pambdelurion* and arthropods: dorsal, ventral and lateral longitudinal muscle and multiple bundles of extrinsic limb muscle. *Pambdelurion* is shown with circular musculature, although this is uncertain. Arthropod cross-section shows the centipede *Lithobius forficatus* adapted from Manton (1977). Muscles with similar orientations and position are coloured identically, although they are not necessarily homologous: dark blue, longitudinal

muscle; light blue, arthropod oblique muscle; brown, dorsoventral muscle; green, onychophoran oblique muscle; orange, gut and pharynx; purple, circular muscle; red, limb musculature; yellow, extrinsic frontal appendage musculature. Width: 166 mm.

Table 1. EDAX analysis of *Pambdelurion whittingtoni* musculature sample pictured in Fig. 4A, showing silica composition and absence of phosphate. Gold content is due to the coating applied to the specimen.

Element	Weight %	Atomic %	Net Int.	Error %	Kratio
O K	38.27	57.86	3907.87	6.33	0.2459
FeL	4.54	1.97	156.80	7.37	0.0243
MgK	4.06	4.04	637.22	4.60	0.0337
AlK	8.66	7.77	1304.45	3.82	0.0742
SiK	28.93	24.92	4117.23	3.51	0.2587
AuM	12.51	1.54	537.51	4.33	0.0834
ClK	0.99	0.68	79.68	7.69	0.0083
K K	0.94	0.58	54.51	15.97	0.0083
CaK	1.08	0.65	48.67	12.14	0.0099

FIG. 4. SEM images of preserved musculature in: A, B, *Pambdelurion whittingtoni*; C, D, *Campanamuta mantonae*. A, Longitudinal trunk musculature from MGUH 31527. B, Limb musculature from MGUH 31528. C, Transverse muscle from the axial region of the trunk in MGUH 31529. D, Close up of C, showing individual myofibrils. Scale bars represent: 20 µm (A-C); 2 µm (D). Width: 110 mm.

FIG. 5. Size distribution of *Pambdelurion whittingtoni* specimens preserving longitudinal muscle gut diverticulae. Longitudinal muscle is preserved exclusively in smaller specimens and gut diverticulae in larger individuals, with no specimens preserving both structures. There is a significant difference (t_{32}=11.06, p<0.001) in body width between specimens preserving longitudinal muscle (Mean=16.1, SE=8.54, *n*=30) and those preserving diverticulae (Mean=57.5, SE=0.90, *n*=4). Width: 80 mm.

FIG. 6. *Pambdelurion whittingtoni*: A, MGUH 31530; B, MGUH 24.577; C, MGUH 31531; D, MGUH 31532. A-D, show a typical mode of preservation, with musculature well mineralised in the anterior half, but absent posteriorly. Isolated bundles of limb musculature characterise the posterior, along with an axial patch of amorphous, mineralised soft tissue (c.f. Fig. 7). A-D shows an increasing longitudinal extent of mineralised musculature, with D showing the maximum extent of mineralisation observed. Abbreviations: hg, hindgut; lm, longitudinal muscle; lim, extrinsic limb muscle. All scale bars represent 10 mm. Width: 166 mm.

FIG. 7. Schematic representations of the variation in preservation between *Pambdelurion* specimens showing a ventral view (cf. Fig. 6). A-D, range of preservation in smaller specimens (~<30 mm body width), showing differential mineralisation of muscle along the longitudinal axis. E, typical preservation in larger specimens (~>40 mm body width, cf. Fig. 6). Dotted lines indicate poorer preservation. Note: specimens are never so complete, often being broken or poorly preserved in certain areas. Abbreviations: an, annulations; cs, cephalic spine; dg, digestive gland; fa, frontal appendage; fas, frontal appendage spine; fl, flap; gu, gut; hg, hindgut; lm, longitudinal muscle; lim, extrinsic limb muscle; m, mouthparts; ph, pharynx. Width: 110 mm.

FIG. 8. *Pambdelurion whittingtoni*: A, MGUH 31533, showing a sagittal division of the longitudinal musculature and its continuation to almost the posterior of the animal. B, drawing of MGUH 31533. Boxed area shows pharynx and frontal appendages and is enlarged in Fig. 15A. Abbreviations: a, anus; an, annulations; fa, frontal appendage; gu, gut. See appendix for colour coding of muscle groups. All scale bars represent 5 mm. Width: 110 mm.

FIG. 9. *Pambdelurion whittingtoni*: A, MGUH 31534, showing two bundles of muscle entering each limb, well-developed, anterior oblique muscle and a band of striated tissue between the lateral and axial longitudinal muscle. B, drawing of MGUH 31534. C, Anterior oblique musculature, enlarged in Fig. 13C. D, limb musculature, enlarged in Fig. 12A. E, oblique fibres extending between lateral and axial longitudinal muscles, enlarged in Fig. 14D. See appendix for colour coding of muscle groups. All scale bars represent 5 mm. Width: 110 mm.

FIG. 10. *Pambdelurion whittingtoni*: A, MGUH 31532. B, drawing of MGUH 31532, dotted line represents reflective film preserving body flaps, frontal appendages and cephalic spines. Boxed area encloses limb musculature and is enlarged in Fig.

12C. Abbreviations: cs, cephalic spines; fa, frontal appendage; fas, frontal appendage spines; fl, flaps; hg, hindgut. See appendix for colour coding of muscle groups. All scale bars represent 10 mm. Width: 166 mm.

FIG. 11. Schematic reconstruction of the myoanatomy of *Pambdelurion*, dorsal view. The dorsolateral flaps are rendered as transparent to reveal the ventral limbs and their musculature. The extrinsic limb musculature is simplified to only show the protractor and retractor muscle. For visual clarity, circular musculature is omitted. See Fig. 3F for cross-sectional view. Abbreviations: an, annulations; cs, cephalic spines; fa, frontal appendage; fam, frontal appendage musculature; fas, frontal appendage spines; fl, flaps; ilim, intrinsic limb musculature; lm, longitudinal muscle; ob, oblique fibres; om, oblique musculature; pr, promotor; re, remotor. Width: 80 mm.

FIG. 12. Limb musculature in *Pambdelurion whittingtoni*. A, MGUH 31534, enlargement of Fig. 9D, showing two distinct bundles of extrinsic muscle associated with each limb. Arrow marks intrinsic limb musculature. B, MGUH 31535, arrows mark each of three distinct muscle bundles associated with a single limb. C, MGUH 31532, enlargement boxed area in Fig. 10A**.** D, MGUH 31536, showing musculature entering a limb which is marked by transverse annulations. E, MGUH 31537, arrows mark three distinct bundles associated with a single limb. F, MGUH 31538, arrows mark intrinsic oblique muscles. All scale bars represent 2 mm. Width: 110 mm.

FIG. 13. Anterior oblique muscle in *Pambdelurion whittingtoni*. A, MGUH 24.56, cephalic region showing the oblique musculature overlaying longitudinal muscle. B, drawing of MGUH 24.56. C, MGUH 31534, enlargement of Fig**.** 9C, and D, MGUH 31537, show oblique musculature in close association with the pharynx and composed of perpendicularly-arranged, overlapping fibres. Abbreviations: lm, longitudinal muscle; om, oblique muscle; ph, pharynx. All scale bars represent 5 mm. Width: 166 mm.

FIG. 14. Oblique fibres extending between lateral and axial longitudinal muscles in *Pambdelurion whittingtoni*. A, B, MGUH 24.577, showing oblique fibres possibly representing extensions of the extrinsic limb musculature. C, MGUH 31535. D, MGUH 31534, enlargement of Fig**.** 9E, showing a thin continuous band of fibres which may represent muscle, or some other type of tissue. Abbreviations: lm, longitudinal muscle; lim, extrinsic limb muscle; om, oblique fibres. All scale bars represent 2 mm. Width: 80 mm.

FIG. 15. Gut and pharynx of *Pambdelurion whittingtoni*: A, MGUH 31536. B, MGUH 31539. C, MGUH 31533, enlargement of boxed area in Fig. 8A, showing the pharynx as a bulbous structure marked by deep transverse ridges, sitting between the bases of the frontal appendages. D, MGUH 31540, showing the gut as undifferentiated, before expanding at the pharynx. Abbreviations: fa, frontal appendage; gu, gut; ph, pharynx. All scale bars represent 4 mm. Width: 80 mm.

FIG. 16. *Kiisortoqia soperi*: A, MGUH 31541, dorsoventrally preserved specimen showing segmentally-arranged, axial longitudinal trunk musculature, cephalic shield and trunk tergites. B, drawing of MGUH 31541. Boxed area encloses the segmented longitudinal musclulature and is enlarged in Fig. 17A. Abbreviations: ces, cephalic shield; lm, longitudinal muscle; tg, tergite. All scale bars represent 10 mm. Width: 110 mm.

FIG. 17. Trunk musculature in *Kiisortoqia soperi*: A, MGUH 31541, enlargement of boxed area in Fig. 16A, showing segmented longitudinal muscle. B, MGUH 31542, detail showing transversely orientated muscle fibres. C, MGUH 31543, showing clearly segmented dorsal longitudinal musculature. Arrows mark segmental boundaries in the muscle. All scale bars represent 3 mm. Width: 80 mm.

FIG. 18. *Campanamuta mantonae*: A, MGUH 31544, showing segmented longitudinal musculature. B, drawing of MGUH 31544. Boxed area encloses the segmented longitudinal musculature, enlarged in Fig. 19A. Abbreviations: cas, caudal shield; ces, cephalic shield; gu, gut; lm, longitudinal muscle; oe, oesophagus; tg, tergite. All scale bars represent 10 mm. Width: 110 mm.

FIG. 19. Segmented longitudinal trunk musculature in *Campanamuta mantonae*: A, MGUH 31544, enlargement of boxed area in Fig. 18A; B, MGUH 31545. Arrows mark segmental boundaries of muscle. All scale bars represent 2 mm. Width: 80 mm.

Dryad figures

FIG. 1. Preservation of external anatomy in *Pambdelurion whittingtoni*: A, MGUH 31546, showing external annulations of legs, frontals appendages and trunk in low relief. B, MGUH 31553 showing frontal appendage and its spines, rounded outline of the head and associated spine and lateral flaps, all preserved as a two-dimensional reflective film. See appendix for abbreviations. Abbreviations: an, annulations; cs, cephalic spine; fa, frontal appendage; fas, frontal appendage spine; fl, flap; lg, leg. All scale bars represent 10 mm.

FIG. 2. *Pambdelurion whittingtoni*: A, MGUH 31547, showing well-preserved longitudinal muscle in the cephalic region, frontal appendages and associated musculature. B, drawing of MGUH 31547. C, enlargement of boxed area in A, showing

extrinsic frontal appendage musculature. Abbreviations: an, annulations; fa, frontal appendage. See appendix for colour coding of muscle groups. Scale bars represent: 10 mm (A, B); 1 mm (C).

FIG. 3. Putative circular musculature in *Pambdelurion whittingtoni*: MGUH 31531, showing transverse, widely-spaced fibrous impressions crossing the trunk in a crescent-shape path. Scale bar represents 5 mm.

FIG. 4. *Kerygmachela kierkegaardi*: A, MGUH 31548. B, drawing of MGUH 31548. Boxed area enlarged in Fig. 5A. Abbreviations: lm, longitudinal muscle, annulations; cm, circular muscle; fa, frontal appendage. See appendix for colour coding of muscle groups. All scale bars represent 10 mm.

FIG. 5. *Kerygmachela kierkegaardi*: A, MGUH 31548, enlargement of boxed area in Fig. 4, trunk region showing faint, fibrous transverse impressions, possibly representing circular muscle. B, MGUH 31549, typical preservation showing pharynx and gut, but no musculature. All scale bars represent 10 mm.

FIG. 6. *Campanamuta mantonae*: A, MGUH 31545, showing extensive axial longitudinal musculature, caudal and cephalic shields and thoracic tergites. B, drawing of MGUH 31545. Boxed area enlarged in Fig. 20B. Abbreviations: cas, caudal shield; ces, cephalic shield; gu, gut; lm, longitudinal muscle; tg, tergite. All scale bars represent 10 mm.

FIG. 7. *Campanamuta mantonae*, A, MGUH 31529, showing transverse musculature. B, drawing of MGUH 31529. Abbreviations: oe, oesophagus; tg, tergite; tm, transverse muscle. All scale bars represent 5 mm.

FIG. 8. *Campanamuta mantonae*: A, MGUH 31550, showing axial striated structures representing either gut diverticulae or musculature. B, drawing of MGUH 31550. C, close-up of area enclosed by white box, showing axial, striated structures. Abbreviations: fg, foregut; gu, gut; tg, tergite. Scale bars represent: 10 mm (A, B); 2 mm (C).

FIG. 9. *Pambdelurion whittingtoni*, MGUH 31551 showing frontal appendages and head preserved as a reflective film. The right appendage reveals a high degree of flexibility, stretching over the left appendage. The spines emerging from the distal end of the appendage are narrow and extremely elongated. Abbreviations: an, annulations; cs, cephalic spines; fa, frontal appendage; fas, frontal appendage spines. Scale bar represents 10 mm.

FIG. 10. Undescribed *Sidneyia*-like arthropod from Sirius Passet: A, MGUH 31552, showing segmented longitudinal musculature in the thorax. B, drawing of MGUH 31552. Arrows mark segmental boundaries of muscle. Abbreviations: ces, cephalic shield; gu, gut; lm, longitudinal muscle. All scale bars represent 10 mm.