A new species of *Markuelia* from the Middle Cambrian of Australia

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We describe a new species of *Markuelia* from the Middle Cambrian of Australia, a taxon based exclusively on embryonic specimens. The two likewise putatively embryonic specimens of the new species named *Markuelia lauriei* sp. nov. have been discovered amongst material collected in 1986 in an area approximately 160 km south of Mt. Isa, Queensland, Australia. The specimens differ from the previously described species of *Markuelia* not only in size (they are significantly smaller), but also in the presence of an abaxial row of four soft, slim, elongate, tubulous outgrowths dorsally in the anterior region with more being irregularly distributed all over the dorsal surface. The extremely fine preservation of the new specimens adds significantly to the known morphological variation within the taxon *Markuelia*.

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‘ORSTEN’-TYPE preservation yields three-dimensionally preserved, uncompressed, phosphatised fossils with even the finest details preserved. ‘Orsten’ fossils have become famous for not only representing adult arthropods with “soft” parts such as eye structures or complete appendages with even the membranous areas, setae and setules (Müller 1983; Müller & Walossek 1985a) but also larvae (Müller & Walossek 1986b, Walossek & Müller 1989). For nine arthropod species it was even possible to reconstruct ontogenetic sequences (Müller & Walossek 1986b, 1987, 1988; Walossek 1993; Maas et al. 2003; Stein et al. 2008; Haug et al. in press, submitted) with up to 30 successive instars (Walogsek 1993). Although ‘Orsten’-type localities are now known from all over the world (Maas et al. 2006) only the middle Cambrian of Australia has yielded members of the Nemathelminthes.

Palaeoscolecid worms occurring here as isolated cuticular remains (Müller & Hinz-Schallreuter 1993) have been assigned to Sciodophora, a group comprising the species-poor taxa Loricifera, Priapulida and Kinorhyncha. Complete specimens are known from the Cambrian Chengjiang Lagerstätte, China (e.g. *Palaeoscolex sinensis* Hou & Sun, 1988). Other Nemathelminthes from this locality are the single, possibly immature specimen of *Shergoldana australiensis* Maas, Waloszek, Haug & Müller, 2007, which was proposed to represent a stem scalidophoran or stem cycloneuralian (Maas et al. 2007a), and also small loricate larvae interpreted as representatives of a sister species to Loricifera (Maas et al., this volume). Among the Nemathelminthes from this locality are two specimens with affinities to the microfossil *Markuelia* Valkov, 1983. This is known from small ball-shaped specimens preserved in calcium phosphate (Donoghue et al. 2006a) with a wide stratigraphic range from the Lower Cambrian to the Lower Ordovician. The first specimens were discovered in Siberia (Valkov 1983), but more have been found in many locations all over the world, such as China (Dong et al. 2004, 2005; Donoghue 2006a, b), North America (Donoghue et al. 2006a) and Australia (Donoghue et al. 2006a; Maas et al. 2007).

The specimens of all *Markuelia* species known so far are, most likely, the embryonic stage of a bilateral annulated worm-shaped organism (Bengtson & Yue 1997). While *Markuelia* has been assigned to arthropods, lobopodians,
annelids and even halkeriids, it was later identified as a nemathelminth round worm, more precisely, belonging to the Scalidophora (Dong et al. 2004). Two valid species of the taxon *Markuelia* have been formally described: *M. secunda* Valkov 1983 and *M. hunanensis* Dong & Donoghue, 2004 (Donoghue et al. 2006a). For *M. hunanensis* it was even possible to document developmental changes during the time within the egg envelope, i.e. the late embryonic phase (Dong 2007). Thus, the embryology of a fossil (putative) scalidophoran is well documented while that of living species remained, to that time, limited. Although the lack of knowledge of living species was partially overcome through the studies of Kozloff (2007), Wennberg et al. (2008, 2009) and Heiner & Christensen (2009), the detailed knowledge of the development of a Cambrian nemathelminth remains an impressive example of the fossil preservation of ontogenetic information, even though knowledge of the adult is still lacking.

The description of a new species of *Markuelia* herein adds to the diversity of the taxon. Despite the fact that the general fossil record of Nemathelminthes is relatively poor, that of Cambrian species is astonishingly good (for details see Maas et al. 2007a, b; Maas et al., this volume).

**MATERIAL AND METHODS**

**Material**

The two specimens, CPC 39947 (Fig. 1A) and CPC 39946 (Fig. 1B) were collected by one of us (DW) in 1986. The locality is in the Middle Cambrian Monastery Creek Formation (late Templetonian), 250m south of the telegraph line, to the north of Rogers Ridge, in the Duchess Embayment of the Georgina Basin, Queensland (Müller & Hinz-Schallreuter 1993; Walossek et al. 1993). Unfortunately, CPC 39946 was lost during processing. CPC 39947 is deposited in the Commonwealth Palaeontological Collection of Geoscience Australia, Canberra.

**Preservation**

The two specimens are preserved as uncompressed fossils impregnated by calcium phosphate. In specimen CPC 39947 the surface appears to be eroded in certain areas (Fig. 2A), and no surface ornament or structures could be identified. Additionally, in some areas the glue that was used to fix the specimen on the stub has moved up the specimen through adhesive effects now partly concealing details, e.g. parts of the tail end (Fig. 2B).

Specimen CPC 39946 was better preserved. The surface was only partially eroded in some areas very close to the point were the specimen is glued onto the stub. Elsewhere, the surface has retained true ornamentation structures and the small tubulous outgrowths (Fig. 3A, D).

**Processing**

To extract phosphatised fossils from the matrix, the rocks were etched with 15% acetic acid (the process has been described in detail by Müller & Walossek 1985b). Residues were graded in size during the dissolution process on two sieves. The described specimens were picked from the finest fraction.

**Methods**

The two specimens have been investigated using a Scanning Electron Microscope (SEM). Both were mounted on SEM stubs and gold coated. Images were produced digitally on a Zeiss DSM 962 SEM.

Further image processing was done using Adobe Photoshop CS3. A simplified 3D model of one specimen was produced using the open source 3D modelling software Blender. This 3D model was rotated around the vertical axis in 60° steps. Line drawings of these six views were produced using the vector graphics program Adobe Illustrator CS3.

**Terminology**

Although *Markuelia* has repeatedly been assigned to the stem-lineage of the Scalidophora or even Priapulida, we feel that this assignment remains...
Fig. 2. **A-C, E-G.** Holotype CPC 39947. **A.** Detail of the holotype, exhibiting the eroded surface (arrow). **B.** Tail end (te) with tail hooks exhibited but covered by glue. Due to the fixation of the specimen on the stub, the anterior end curves around the tail end and to the left underneath, thus is disguised. Glue partially conceals details of the tail end. **C.** Anti-S shaped curvature of the trunk of the holotype. **E-G.** Three views illustrating the curling pattern. **D.** CPC 39946. Anterior end (ae) on top pointing to the left and tail end (te) curving around it and pointing to the right well exposed. Note that the tail end points into the same direction as in B, but here the anterior end (ae) is above the tail end, demonstrating that the two specimens are mirror morphs.
to be validated. Hence, application of the specific terminology used for these taxa is premature. We therefore attempt to use a more neutral terminology. The backward pointing tooth-like structures in the anterior region have been referred to as scalids by other authors. However backward pointing tooth-like or hook-like structures occur also in other Nemathelminthes and have been referred to under different names there (see discussion below). We therefore do not to use the term scalid for these structures. Dong et al. (2005) have argued for homology of the spines in *Markuelia* and scalids, because the spines in *Markuelia* appear to be hollow. This hints at a possible scalidophoran affinity. We also refrain from applying the term tubuli for the fine, elongate structures on the dorsal side of the specimens, because this is a specific priapulid term. The term ‘tubulous outgrowth’ is used instead to refer to the small backward-pointing structures in preference to the term ‘protuberances’ proposed by Donoghue et al. (2006b). Indeed, these structures appear to be very similar to the tubuli on the loricae of larval priapulids, but we do not want to make any assumptions about homology of these structures, since neither annulations occur on the loricae, nor can their position be homologised.

**SYSTEMATIC PALAEOONTOLOGY**

**NEMATHELMINTHES** (sensu Ahlrichs 1995)  
Gegenbaur, 1859 (= Aschelminthes Grobben, 1910)  
**CYCLONEURALIA** Ahlrichs, 1995 (= Introverta Nielsen, 1995)

*Markuelia* Valkov, 1983

**Type species.** *Markuelia secunda* Valkov, 1983

*Markuelia lauriei* sp. nov.

. 2006 embryos from the middle Cambrian of Australia; Donoghue et al. a, p. 233–235.  
. 2006 specimens from the middle Cambrian of Australia; Donoghue et al. a, p. 233.  
. 2006 Australian specimens; Donoghue et al. a, p. 234.

v 2007 *Markuelia* n. sp.; Donoghue et al. a, figs. 1A–D, 2 [CPC 39946, 39947].  
v 2006 species of *Markuelia*; Maas et al., p. 278.

v 2006 *Markuelia* sp.; Maas et al., fig. 6A [CPC 39947, as UB W 132], 6B [CPC 39946, as UB W 133].  
. 2007 several specimens of *Markuelia*....from Middle Cambrian in Georgina Basin, northern Australia; Dong, p. 930.

v 2007 *Markuelia* sp.; Maas et al. a, p. 499, 509, 513; fig 7A [CPC 39946].  
. 2007 Two specimens of *Markuelia*; Maas et al. a, p. 501.

v 2007 Cambrian fossils interpreted as embryos from the lineage leading to the Priapulida; Webster et al., p. 503

v 2007 *Markuelia* sp.; Webster et al. fig. 1C (CPC 39946)

v this volume Still undescribed species of *Markuelia* Valkov, 1984; Maas et al., fig. 2. [CPC 39946].

**Derivation of the name.** After John R. Laurie, Canberra, Australia, who was member of the expedition team recovering the material described herein.

**Type Locality.** Middle Cambrian of Queensland, Duchess Embayment, of the Georgina Basin North of Rogers Ridge, 250m south of telegraph line, Monastery Creek Formation (late Templetonian).

**Holotype.** CPC 39947.

**Additional Material.** One specimen, CPC 39946, lost during investigation.

**Remarks.** Since this species is known only from a late embryonic stage putatively close to hatching, diagnosis and description refer to that developmental stage.

**Diagnosis.** Elongated worm-shaped nemathelminth with an annulated body of about 90 annuli. Anterior region with two weakly defined annuli dorsally. Second annulus with an abaxial row of four straight, backward-pointing, tubulous outgrowths that appear rather soft. Many annuli of the remaining body also carrying such tubulous outgrowths dorsally or laterally, pattern appears irregular. Tubulous outgrowths bipartite. Proximal portion slightly wider in diameter and with 3–4 tiny spinules distally arising in a corona around the slightly slimmer distal part. Posterior end carrying six backward orientated, ventro-laterally pointing hooks. The medio-dorsal two of these hooks are smaller than the other four and bear a tiny spinule closer to the tip.

**Description.** The two specimens both have a maximum diameter of approximately 320 µm and a minimum diameter of 230 µm. The elongate, worm-shaped body is folded in a special way to form a globule inside an egg-shell, which is not quite spherical but slightly compressed from two sides and therefore more like a tyre. To facilitate
the three-dimensional aspect, we approximate the shape to a ball in our model and description. The special pattern was already recognised by Bengtson & Yue (1997) and also described by Donoghue et al. (2006a). The latter authors have also noted the existence of two mirror-symmetric morphs in our Markuelia specimens, which they called S-curled and anti-S-curled: the holotype, CPC 39947, is an anti-S morph, CPC 39946 is an S morph. The differences of the two morphs can be recognised when comparing Fig. 2B and 2D. Here, both specimens are depicted with the tail end (te) pointing to the right. In CPC 39947 (Fig. 2B) the head parallels the right side of the tail end, while in CPC 39946 (Fig. 2D) the anterior end parallels the left side. Figure 2C documents the anti-S curling of CPC 34497 on the opposite side of the head-tail connection.

Since the curvature pattern is difficult to understand, we modelled the pattern for an S morph in Figure 3 and rotated the model in steps of 60°. Figure 4 displays a step-wise ‘unfolding’ of the S-morph egg larva. Within the egg envelope, the posterior end of the animal lies adjacent to the left side of the anterior end over a little more than 100 µm, but facing to the opposite direction. Starting from the anterior end, the body extends backwards following the curvature of the sphere. After reaching about half of the outline of the sphere the body curves sharply to the right and runs straight back into the opposite direction, i.e. towards the anterior. Because of the annulations and since the inner margin is straight while the outer is more curved, this part has the appearance of a symmetrical lappet (Fig. 2F). After the same distance another sharp curvature follows, repeating the lappet pattern but on the opposite side of the sphere. This pattern forming a pronounced S shape was eponymous to this morph, while the mirror image was named anti-S. After the second turn the body follows again the curvature of the sphere until the tail end comes to lie next to the anterior end. The area where head and tail end approach the S and each other is somewhat shallower so that the sphere is compressed on these opposing sides and appears more like a rounded tyre, distinctly recognisable in the holotype (Fig. 2E, G).

Because of the specific folding of the body, apparently to fit into an egg envelope, as in other material of Markuelia (Bengtson & Yue 1997), the probable tubular body of the embryo (we prefer the term ‘egg-larva’; see discussion), was deformed. This deformation resulted in a slightly convex outer surface, while the inner parts were squeezed to fit into a sphere. With this, the entire dorsal side is almost flat throughout the curved body, with sharp inward deflections of the sides. Accordingly, the annulations appear more like bars with clearly marked lateral edges rather than supporting the impression of a tubular organism.

The anterior region of the body is about 160 µm wide and 85 µm long. At the anterior rim, at
least four stout and apparently slightly backward pointing and laterally compressed spines are positioned (marked with 3 in Fig. 5A). The spines are about 35 µm long and are about 25 µm wide at their base. Right at the anterior rim, at least five more similar spines are exhibited (three of them marked with 2 in Fig. 5B). These point almost anteriorly, most likely because the supposed anterior opening of the animal is partly introverted. The opposite side of the opening is mainly concealed. This interpretation is supported by infoldings on the dorsal side of the anterior region (owing to collapse of the animal at death) suggesting that the entire area was more tubular and that the anterior opening might have been rather circular. The size of this more anterior row of spines corresponds to that of the backward-pointing more posterior ones. A faint view deeper into the opening reveals the presence of another set of spines, three visible in CPC 39946 (marked...
with 1 in Fig. 5B), which arise from even further inside, in fact, topologically from more anterior. These appear to be more pointed and fragile than the spines of the two more posterior rows, but their corresponding sharp tips may simply be broken off. At least for one of the presumably most anterior spines, two associated spinules can be recognised flanking the central spine on either side (arrows in Fig. 5C).

Two transverse demarcations are present on the anterior region, but these are less pronounced compared to those of the rest of the body (Fig. 5A). At the rear of the second annulus four slim tubulous outgrowths point postero-distally (arrows in Fig. 5A). These tubulous outgrowths appear to be have been rather soft in life since they show evidence of flexibility through folding. They are up to 14 µm long and are slightly less than 5 µm in diameter at their base, tapering distally. Half way up there arise a few small spinules in a circle around the slender distal part of outgrowths (arrow in Fig. 5D). These tiny spinules are only about 1 µm long and also are 1 µm wide at their base tapering distally to a tip. Based on the visible spines, a complete surrounding corona may have comprised three or four spinules.

Behind the anterior region, the body has about 90 annuli (both specimens, calculated from various views). Each annulus is about 175 µm wide and about 15 µm long. Accordingly, the total length of the annulated region would have been about 1.35 mm. The annuli (Fig. 5A, D) are interpreted as an external cuticular ornament rather than as segments. In addition there is a subordinate pattern of fine meandering folds or wrinkles (Fig. 5D). These folds are less then 1 µm wide and appear to be a real subordinate cuticular structure and not a preservational artefact.

More tubulous outgrowths arise from the annuli (Fig. 5A) but are more irregularly distributed. The second annulus (counted from anterior) has one on its left lateral side; the third has one on its right lateral edge. The fourth annulus also has one almost medially, the fifth appears to have two, both arising from about one third of the median-lateral distance measured from the midline. The sixth one has one outgrowth on the right side about two thirds of the distance measured from the midline. It is unfortunately not possible to follow the complete pattern further from this side because of preservation and mounting of the specimens. From the posterior end the fourth annulus (counted from the posterior) has a lateral outgrowth, the fifth a dorsal one, the eleventh a lateral one. The twelfth annulus has an outgrowth dorso-laterally. Also here the pattern of the outgrowths could not be documented further and the given position of these structures must remain
Close to the posterior end the body becomes narrower and, counted from about the 12th annulus from the posterior, forms a short constriction. The fourth annulus counted from the posterior has the smallest width of just about 70 µm (marked by arrows in Fig. 6A). Thereafter the body widens again. Figure 6B shows that the annulations surround the entire body. The posterior end of 85 µm length and 115 µm maximum width is dorsally smooth and caudally armed with 6 hooks, oriented backward, but pointing ventro-laterally (Fig. 6B). Two of these are smaller than the other four (5th in Fig. 6B). Assuming (based on other species of Markuelia) that the two smaller hooks mark the dorsal midline (dm in Fig. 6B), the posterior end appears to be somewhat rotated in its position not exhibiting the true dorsal surface but mainly the left body side. According to this orientation the hooks curve effectively ventro-laterally, although the visible hooks of the left body side appear to curve outwards. The complete length of the embryo can be reconstructed as being 1.52 mm.

The length of the shorter median hooks (based on the left one) is 55 µm, the base of such a hook is 35 µm wide. Due to the curvature of the hook the tip is about 15 µm laterally to the midline of the base and forms an angle of about 60° to the perpendicular bisector of the base. The left hook also has a small spinule on the lateral (functional ventral) side (arrow in Fig. 6B), slightly more than 6 µm below the tip. It is less than 2 µm in diameter and appears to be broken after a length of also 2 µm. The shape of the four larger hooks is similar to that of the small ones but their length is 85 µm. The base of the larger hook is partly concealed by the base of the small hook. The more dorsal one of the larger hooks appears to conceal parts of the ventral one in the same manner.

**Remarks.** Markuelia lauriei sp. nov. differs in several aspects from the other species of the taxon Markuelia. Already Donoghue et al. (2006a) have pointed out that the two Australian specimens are significantly smaller than the specimens of all other species of Markuelia. Donoghue et al. (2006a) also recognised the absence of what they named “conical protuberances” in M. hunanensis, while such structures should be present in M. secunda and in the Australian specimens, but they also remark upon the difference of these protuberances in the two forms. Those in the specimens we refer to as M. lauriei are less numerous and more slender, whereas those of M. secunda appear quite robust and different in shape being slightly depressed lobate humps proximally that taper rapidly to a pointed tip. We refer to the “conical protuberances” in M. lauriei as slim, elongate tubulous outgrowths. Additionally these outgrowths exhibit associated features such as a reduction in diameter half way up and a corona of fine spinules on the distal edge of the proximal part, not present in M. secunda. The fine, subordinate, wrinkled surface ornamentation is also encountered in M. hunanensis (Dong et al. 2004) and the spinules on the backward pointing spines of the innermost ring in the anterior region are similar to the condition in specimens described by Dong et al. (2005). In M. lauriei, the two dorsal tail hooks are shorter than the other four and have a small spinule close to the tip. In other Markuelia species differing lengths of the tail hooks have not been described; also spinules on these are unknown.

Donoghue et al. (2006a) speculated that the specimens of M. lauriei might be representatives of two different species, based on certain variation of the tail hooks. This cannot be completely ruled out, but the really small difference between the two specimens may easily be explained by the apparent differences in preservation. Hence, we keep a more conservative view and consider the specimens as conspecific. In all, the differences in the tubulous outgrowths, the distinct size differences, details of the tail hooks and fine structure of backward pointing spines of the anterior region and the geographical separation justifies, in our view, the erection of the new species.

**DISCUSSION**

The newly described species is the third valid one of the taxon Markuelia, as Donoghue et al. (2006a) indicate the invalidity of Markuelia prima Valkov, 1983. Further species might be represented by specimens from North America noted by Donoghue et al. (2006a). The material appears to be more widespread in the fossil record than previously thought (Donoghue et al. 2006a). New investigation methods for inferring details of these minute fossils have been established (Donoghue et al. 2006b). Yet, many details of Markuelia are not completely understood.

Formally describing the species presented here is seen as an important step in aiding further investigations on these species. Again, recently, Dong (2007) has made further attempts in describing the developmental sequence of Markuelia hunanensis. According to his scheme, the known specimens of M. lauriei might correspond to his stage 2 (“The later period during the pre-hatching stage”). In this stage the tail hooks are well developed, but the backward pointing spines of the anterior region are not yet fully developed. In our specimens, we can observe only a single ring of these
spines directly externally (two further rings are visible “internally”), whereas older specimens should exhibit more than one ring (Dong 2007). Unfortunately, Dong (2007) did not make any statements about the number of annuli for his stage 2. His stage 1 has about 62 annuli, stage 4 about 216. The presence of about 90 annuli in our specimens would therefore be suitable for a corresponding stage 2.

As Dong (2007) has demonstrated, _Markuelia_ appears to reach a degree of differentiation that is comparable to a free-living organism. Nevertheless, it is clear from other observations that the specimens had remained within an egg envelope for a longer time and developed further. Yet, because of the differentiated status of the animal we feel that it is of course appropriate to speak of an embryo, but as _Markuelia_ appears more likely as a larva resting inside an egg case, the term ‘egg-larva’ might suit these fossils much more than the term ‘embryo’. Also, the conclusions of Dong et al. (2005) that the ground pattern of Scalidophora is characterised by direct development, based on the developmental mode of _Markuelia_, cannot be supported here. As we do not yet know the adult form, we cannot judge whether the hatching stage of any _Markuelia_ species is a larval or juvenile one. Size alone cannot be a criterion here, as not only larvae of recent cycloneuralian species are significantly smaller than _Markuelia_ specimens. This is true also for the juveniles of direct developers such as nematodes when hatching.

Another counter-argument is seen in the more recent discoveries of additional larval nemathelmints in the 3D-preserved Cambrian material from Australia. In fact, _Shergoldana australiensis_ (Maas et al. 2007a) and _Orstenoloricus shergoldii_ (Maas, Haug, Waloszek & Müller (Maas et al. this volume). Other morphological details on the other hand might also link _Markuelia_ to Nematomorpha. The anterior region of nematomorph larvae bears striking similarities to that of the _Markuelia lauriei_ specimens. Especially the partially introverted second ring of spines perfectly resembles the second ring of spines of the larva of _Chordodes morgani_ Montgomery, 1898 as depicted by Bohall et al. (1997, their fig. 2; also shown by Maas et al. 2007, fig. 9A). This larva also has an annulated body, although with less annuli than any species of _Markuelia_. Furthermore the nematomorph larvae also possess a set of tail spines that resemble the tail hooks of _Markuelia lauriei_ to some degree. The shape of the tail hooks in _M. lauriei_ also resembles other structures in Nemathelmintes such as the scalids in Priapulida (compare Lemburg 1999, especially his fig. 25A-C). Although positional differences
make it difficult to establish homology here, one could speculate that body outgrowths including tail hooks and scalids have basically the same evolutionary origin.

CONCLUSIONS
Markuelia lauriei sp. nov., described herein as the third species of Markuelia, differs from M. hunanensis in the presence of tubulous outgrowths. Related structures, so-called “conical protuberances”, are also present in M. secunda, but clearly differ in shape and greater number. Those of M. lauriei are not only much thinner and have tubulous shape but also appear softer. Additionally, in M. secunda, they are differentiated into a proximal and distal part with a corona of small spines arising from the distal end of the proximal part. Other differences include the presence of spinules on spines of the anterior region and the tail hooks. Furthermore, the specimens of M. lauriei are significantly smaller than those of all other Markuelia specimens, and M. lauriei is also geographically isolated from other occurrences. Markuelia lauriei exhibits many details hitherto unknown in other species of Markuelia and expands the morphological disparity of the taxon.

In conclusion, we can state that the morphological details exhibited by M. lauriei add new characters for comparison with other Nemathelminthes. Some characters indicate it is closer to Scalidophora (tubulous outgrowths) but others to Nematomorpha (anterior region, annuli, tail hooks). This either indicates that more of these structures might have been present in the ground pattern of Cycloneuralia or that they have been convergently evolved in different lineages.

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