

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 1986a, 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 (Walossek 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 Nematelminthes.

Palaeoscolecid worms occurring here as isolated cuticular remains (Müller & Hinz-Schallreuter 1993) have been assigned to Scalidophora, 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 Nematelminthes 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 Nematelminthes 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,

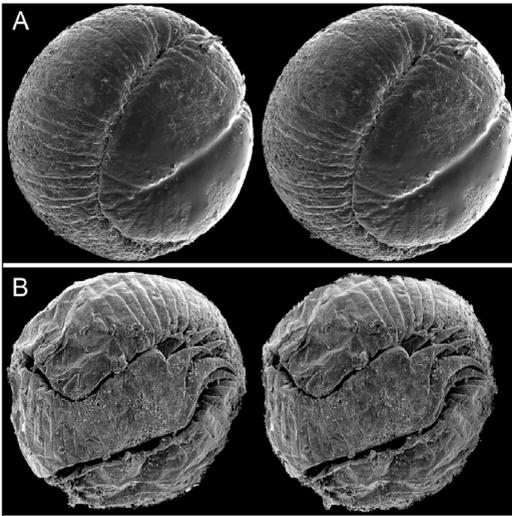


Fig. 1. Stereo images of the two available specimens of *Markuelia lauriei* sp. nov. **A.** Holotype, CPC 39947 (head would be underneath, tail end on opposite side). **B.** CPC 39946 (head pointing to lower left, tail end parallel to it but facing the opposite side; specimen lost during processing).

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 where 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

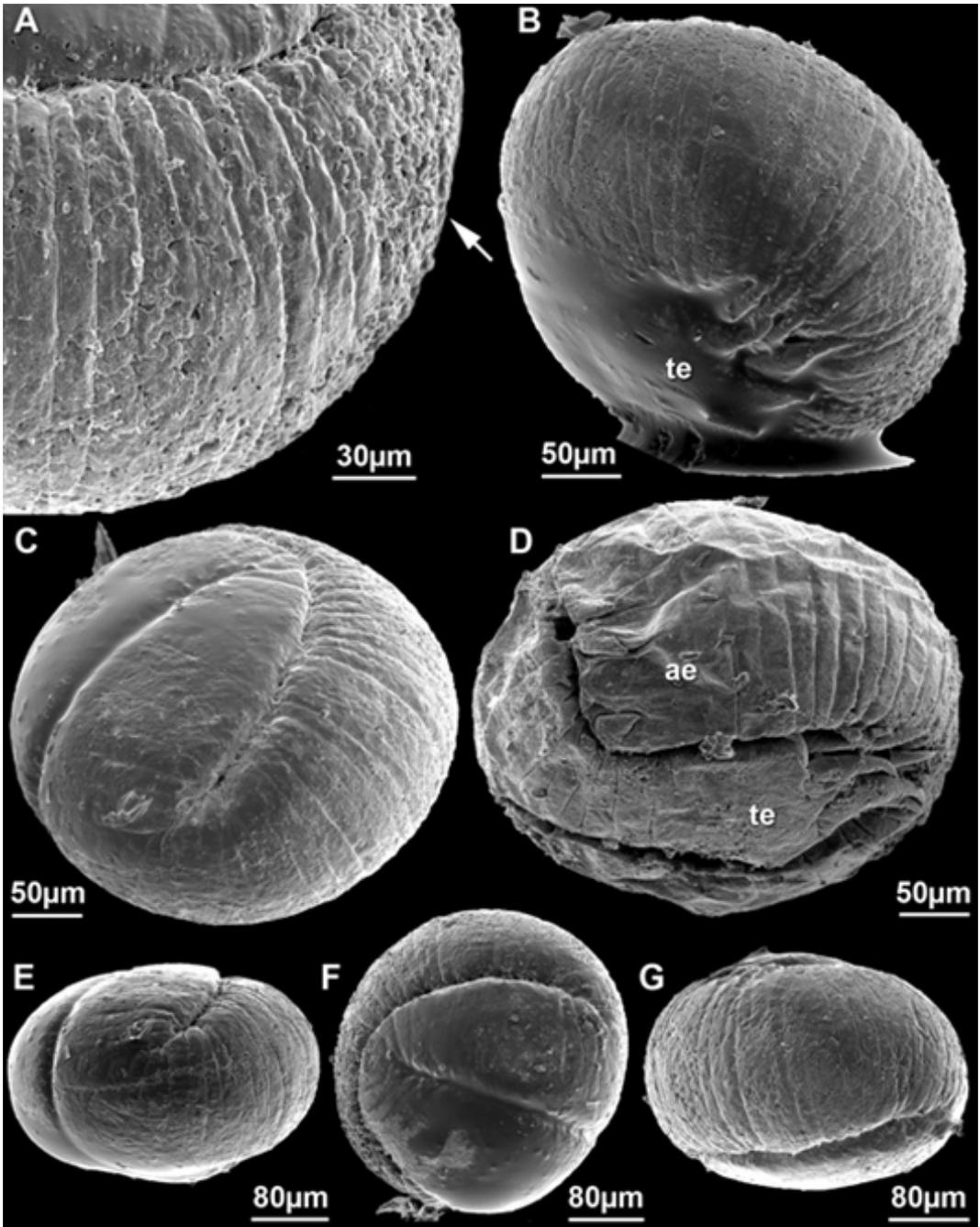


Fig. 2. A-C, E-G. Holotype CPC 39947. A. Detail of the holotype, exhibiting the eroded surface (arrow). B. Tail end (te) with tail hooks exhibited but covered by glue. Due to the fixation of the specimen on the stub, the anterior end curves around the tail end and to the left underneath, thus is disguised. 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 Nematelminthes and have been referred to under different names there (see discussion below). We therefore do not 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 PALAEOLOGY

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 2006 *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 nematelmint 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

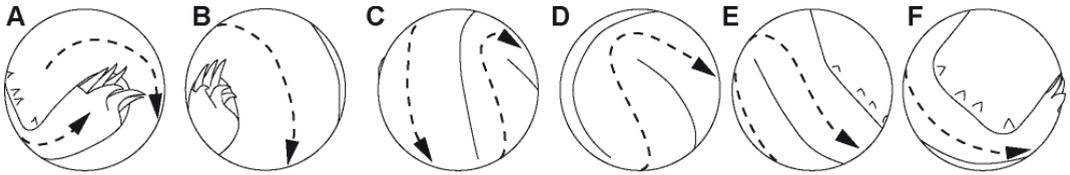


Fig. 3. Line drawings based on a 3D-model showing the curling pattern of an S-curved *Markuelia* specimen. The images depict the model in different positions, rotated around the vertical axis. From step to step the model was rotated 60° . The arrow gives the direction from anterior to posterior. **A.** The anterior and posterior ends are visible (compare Fig. 1B). **B.** In the next step only the posterior end is visible. **C.** Third step exhibits first part of the S curl. **D.** Fourth step depicts both loops of the S curl. **E.** In the fifth step the second loop of the S curl is still visible while additionally the anterior end is now exhibited. **F.** Anterior end and part of the tail end visible.

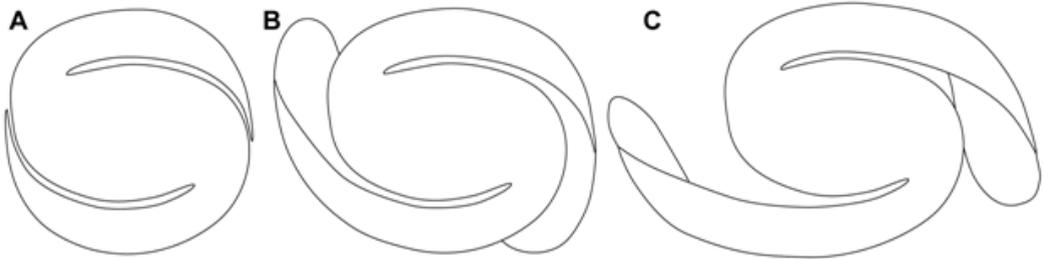


Fig. 4. Line drawings of a step-wise unrolling 3D model of an S-morph of *Markuelia lauriei* sp. nov., exhibiting the enrolling pattern. **A.** Completely enrolled specimen. The S-shaped curvature is apparent. **B.** Anterior and posterior end are partially unfolded. **C.** Anterior and posterior end are further unfolded.

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-curved and anti-S-curved: 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 $100\ \mu\text{m}$, 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 $160\ \mu\text{m}$ wide and $85\ \mu\text{m}$ long. At the anterior rim, at

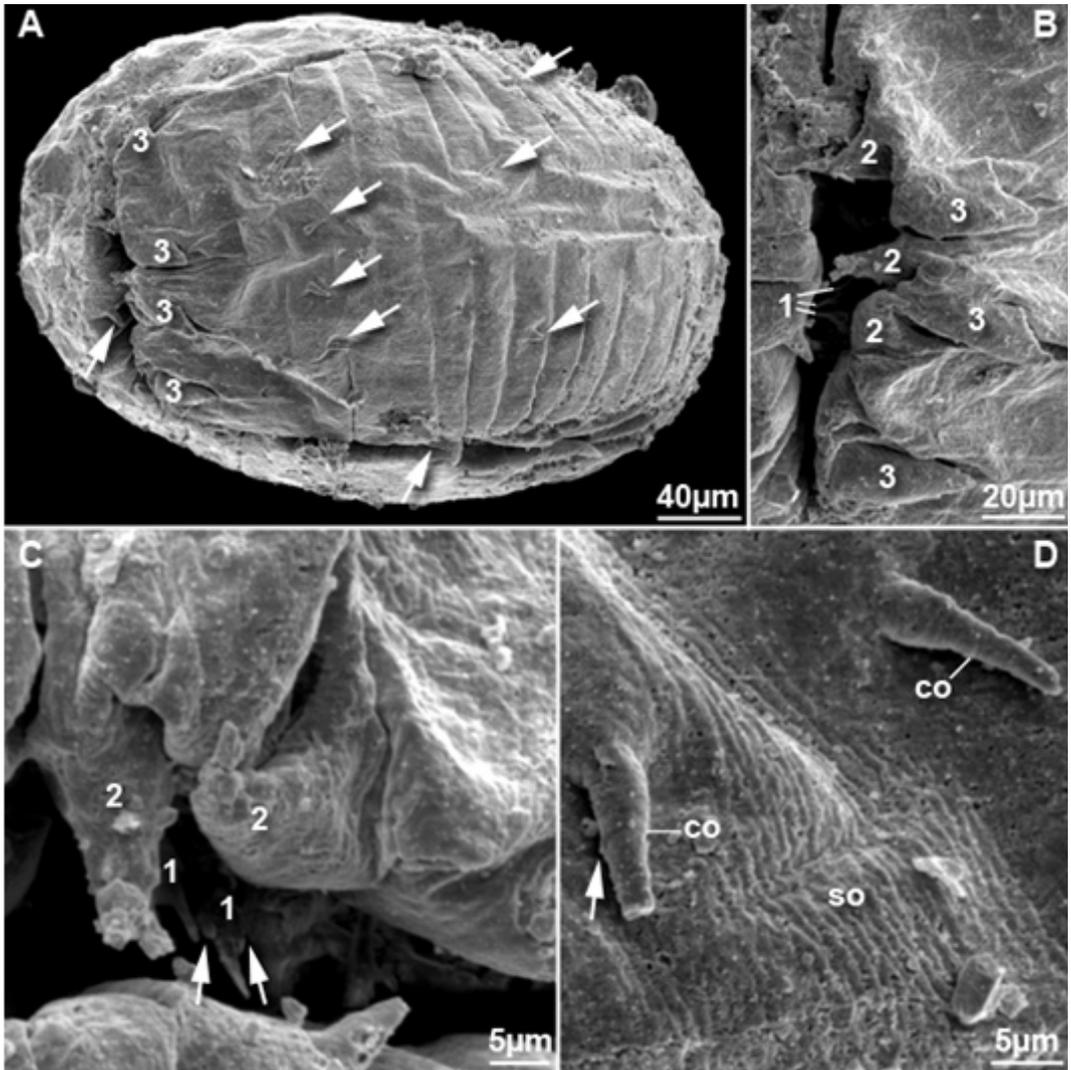


Fig. 5. CPC 39946. Details of the anterior region. **A.** Specimen positioned to exhibit the anterior end. One row of backward pointing spines is exhibited. Spines marked with 3. Arrows point to tubulous outgrowths. Note the row of four tubulous outgrowths on the posterior portion of the anterior area close to the annulated trunk region. **B.** Detail of the anterior opening. Three rows of spines are apparent. The innermost ones are marked with 1, the spines of the next row with two, the ones of the outermost row with 3 (as in A). **C.** Detail of the two anterior rows of spines. Spines of the innermost row marked with 1, the ones of the next outer row with two. Arrows mark the two spinules of one spine of the innermost row. **D.** Details of the tubulous outgrowths (co) and the surface ornament (so). Arrow marks one small spine of the corona surrounding the distal part of the tubulous outgrowth.

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

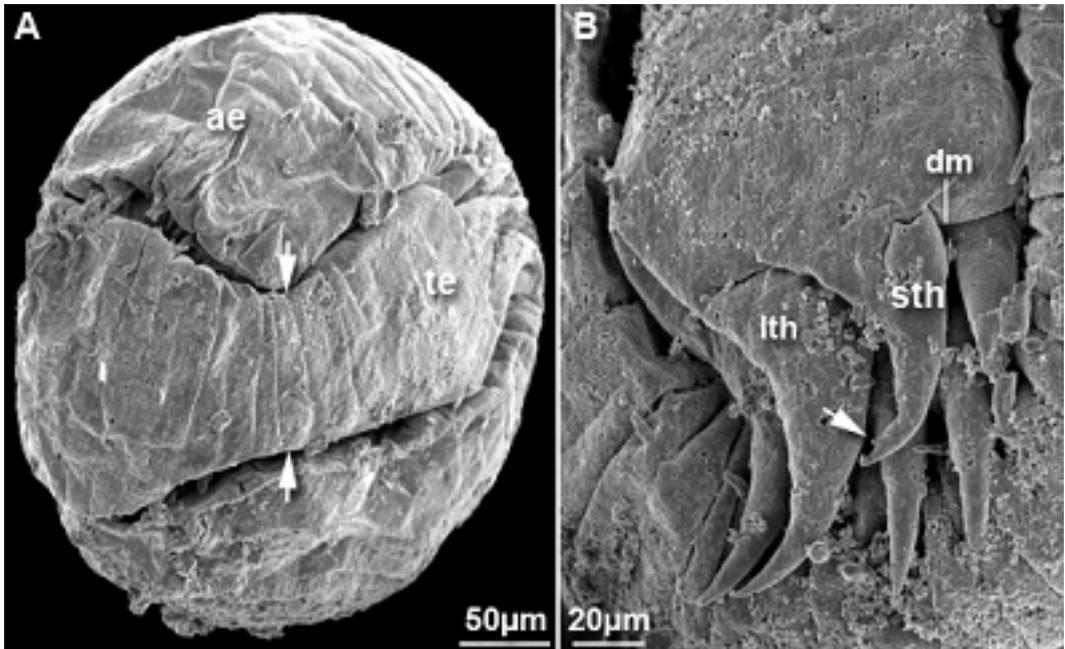


Fig. 6. CPC 39946. Details of the tail end. **A.** Specimen positioned to exhibit the constriction anterior to the tail end (te). Two arrows mark the narrowest width of the constriction. Note how the anterior area (ae) occupies the space made available through the constriction. **B.** Details of the tail hooks. The short tail hook (sth) carries a spinule (arrow). No such structure is seen on the large tail hooks (lth). The presumed dorsal midline (dm) is slightly shifted, indicating a somewhat twisted tail end.

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 slimmer 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 than 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

preliminary.

Closer 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 (sth 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 justify, 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 nemathelminths 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), representing either sister species to Cycloneuralia, Scalidophora or Loricifera, rather point to the presence of larval instead of direct development in the ground pattern of Cycloneuralia and/or Scalidophora.

Furthermore, the placement of *Markuelia* as the sister group to Scalidophora, or even as a stem-priapulid, may be questioned. While the backward-pointing spines in the possible larval specimen of *Shergoldana australiensis* exhibit detailed structural similarities to structures of Scalidophora the homology of the structures in *Markuelia* with scalids is still equivocal. Backward pointing spine-like structures can also be found in non-scalidophoran Nematelminthes, i.e. Nematoida, such as Nematomorpha (e.g. Bohall *et al.* 1997) and Nematoda (e.g. Ward 1995). A placement of *Markuelia* within Cycloneuralia

is thus in any case valid, but for assigning it to Scalidophora (or its stem group) more convincing characters have to be found. The presence of a possible 8, 8, 9 pattern in the supposed introvert in a specimen investigated by Donoghue *et al.* (2006b) might be seen as an indication to a close relationship to Priapulida, which exhibit a related, but slightly different pattern of 8, 9, 8+8+9 scalids in the anterior three rings (Adrianov & Malakhov 2001).

Recent investigations have shown that not only the six-based patterns of Nematomorpha (and Nematoda), an eight-based pattern as in Priapulida (and Loricifera) and a ten-based pattern in Kinorhyncha, but also a seven-based pattern, is possible. This could be found in the fossil species, *Shergoldana australiensis* (Maas *et al.* 2007a) as well as in a larval priapulid (Wennberg *et al.* 2009), demonstrating that sorting out the correct ground pattern conditions for various taxa still needs to be done, and a simple similarity of numbers is only weak support for homology of the tooth-like structures on the anterior regions of Cycloneuralia. Even if the backward pointing spines are indeed scalids, as they are hollow (Dong *et al.* 2005), this still does not allow a final decision. If the backward pointing spines of Nematoida and the scalids of Scalidophora are homologous structures, it remains unclear whether hollow spines as scalids or massive spines as in nematoids are plesiomorphic. *Markuelia* could thus still be a stem-nematoid, which still possesses hollow spines.

One morphological detail of *Markuelia lauriei* might strengthen assumed scalidophoran affinities, namely the tubulous outgrowths. Apparently similar outgrowths are known from Kinorhyncha (Neuhaus & Higgins 2002), Loricifera and loricate priapulid larvae (compare 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 Nematelminthes 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 scalds 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 Nematelminthes. Some characters indicate it is closer to Scalidophora (tubulous outgrowths) but others to Nematoida, more precisely 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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