Onychophoran-like musculature in a phosphatized Cambrian lobopodian

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1. Introduction

The restricted, exclusively terrestrial distribution of modern Onychophora contrasts strikingly with the rich diversity of onychophoran-like fossils preserved in marine Cambrian Lagerstätten. The transition from these early forebears to the modern onychophoran body plan is poorly constrained, in part owing to the absence of fossils preserving details of the soft anatomy. Here, we report muscle tissue in a new early Cambrian (Stage 3) lobopodian, Tritonychus phanerosarkus gen. et sp. nov., preserved in the Orsten fashion by three-dimensional replication in phosphate. This first report of Palaeozoic onychophoran musculature establishes peripheral musculature as a characteristic of the ancestral panarthropod, but documents an unexpected muscular configuration. Phylogenetic analysis reconstructs T. phanerosarkus as one of a few members of the main onychophoran lineage—which was as rare and as cryptic in the Cambrian period as it is today.

2. Material and methods

The specimen was recovered by 5% acetic acid digestion of carbonate nodules from black shales, and is deposited at the Key Laboratory for Palaeobiology.
Yunnan University, Kunming, China (YKLP). Phylogenetic analysis was conducted in TNT [10], using the methods of Smith & Ortega Hernández [1], on a revised matrix of 49 taxa and 115 unordered characters, integrating data from recent lobopodian analyses [1,3,9,11] (data and scripts available at Dryad [12]). Parsimony analysis employed implied weights, with 99 values of Goloboff’s concavity constant [13] picked from a lognormal distribution (range: 1.061–259.4; R function qlnorm((1 : 99)/100, meanlog = log(4), sdlog = log(6)) + 1), and equal weights, with a consensus tree generated from all most parsimonious topologies [14]. Extended implied weighting [15] does not affect the consensus tree.

3. Results

(a) Systematic palaeontology
Superphylum Ecdysozoa, Aguinaldo et al. [16].
Stem-group Onychophora, Grube [17].
Genus Tritonychus Zhang et Smith, gen. nov.
LSID. urn:lsid:zoobank.org:act:959A47D4-3323-47CB-ADB2-B6A8F5B945A0.

Etymology. In reference to the third (τρίτος, tritoς) claw (ὀνυχός, onychos), a unique feature among lobopodians.

Diagnosis. Lobopodous appendages paired, 10 times longer than wide, four times narrower than trunk, each ending with three anteriorly directed claws. Trunk and appendages ornamented with bifurcating circumferential wrinkles and bearing dermal papillae. Two discrete layers of longitudinal fibres peripheral to body cavity.

Type species.
Tritonychus phanerosarkus Zhang et Smith gen. et sp. nov.
LSID. urn:lsid:zoobank.org:act:1715A32E-C258-4EC2-A44D-EC1A1E3DC23E.

Etymology. φανέρως, phaneros, well-displayed, σαρκός, sarkos, muscle, flesh.

Holotype. YKLP 12335 (figure 1), the only known specimen.

Occurrence. Yu’anshan Formation (Eoredlichia–Wutingaspis Biozone, approximately late Atdabanian = Cambrian Series 2, Stage 3), Xiaotan section, Yongshan, Yunnan Province.

Diagnosis. As genus.

Description. The specimen is a millimetre-long section of lobopodian trunk that is folded at its midpoint and bears a pair of lobopods on its ventral surface near the presumed

Figure 1. The Cambrian Stage 3 lobopodian Tritonychus phanerosarkus gen. et sp. nov. from China (YKLP 12335). (a) Overall morphology. (b) Surface ornament; circumferential wrinkles irregularly bifurcate and merge (white arrows) and bear papillae (black arrow). (c) Close up of musculature in panel (a). (d) Three layers of three-dimensionally preserved muscle fibres (myofibrils). Colours denote structures interpreted as: white, ventral longitudinal muscles; cyan, outer layer of longitudinal muscles, parting to leave gap (arrow); crimson/mauve, interwoven layer of oblique muscles; yellow, inner layer of circular muscles; green, point of leg levator insertion. (e) Details of linear fibres subparallel (black arrows) and perpendicular (white arrows) to the body axis. (f) Left appendage tip, bearing impressions of three claws. (g) Right appendage, showing the reverse side of claws. (h) Papillae of different sizes (arrows) on the surface of right appendage.
The posterior margin (figure 1a). It is incomplete at each end, and lacks most of its dorsal surface.

The trunk is ornamented with circumferential wrinkles, spaced at 10 μm, which bifurcate and merge in an irregular fashion (figure 1b). Irregularly positioned conical projections, 5 μm in diameter and 7 μm in height and situated on a round cuticular base (figure 1b), presumably correspond to the dermal papillae of Orstenotubulus and extant Onychophora [8]. Moving distally along each appendage, the cuticle wrinkles give way to a reticulate pattern of polygonally arranged ridges that conceivably correspond to cell boundaries, and the papillae are less frequently expressed (figure 1f–h).

The trunk is lined with three layers of fibrous tissue, each around 10 μm thick, which we interpret as muscles. The outer layer (figure 1c–e, cyan) comprises 5–10 μm wide longitudinal fibres; it parts between the appendages to leave a 60 μm wide gap, through which a separate bundle of longitudinal fibres (white in figure 1d) passes. The fibres part again to the right of this point (green in figure 1d), perhaps reflecting the insertion of leg levator musculature. A second layer of interwoven oblique fibres (crimson and mauve in figure 1d) sits within the first, and within that layer lie further fibres oriented perpendicular to the body axis (yellow in figure 1d), presumably representing decayed remnants of an originally extensive layer of circular musculature.

Each of the two appendages is 800 μm long and a uniform 80 μm in diameter, with a circular cross section that is distorted in places by flattening. Each bears the impressions of three terminal claws, separated by 45°; the raised central bosses of these impressions denote an originally hollow claw (figure 1f,g). No distinct foot is present. Assuming the claws to be directed forwards (as in other lobopodians), the legs occupy the posterior limit of the fragment. The ventrolateral location of the appendages suggests that they served a conventional locomotory role, contrasting with the intriguing lateral position of appendages of Orstenotubulus [8].

4. Discussion

The preservation of muscular tissue is in some respects surprising, as body wall musculature is the first feature to decay when onychophorans are rotted in isotonic saline solution [18]. The absence of both labile (gonads, gut) and recalcitrant (claws) tissues in T. phanerosarkus indicates that the sequence of decay in salt water is a poor guide to the sequence of preservation in this fossil material. Here, early phosphatization initiated at the cuticle (evinced by the decreasing quality of preservation away from the body wall) clearly led to enhanced preservation of peripheral tissue (cf. [19]).

More generally, muscle tissue is atypical in phosphatized (‘Orsten-type’) microfossils (reference [20] provides a rare example), and though it may be concealed by overlying tissue layers in some cases [21], in most—including
palaeoscolecid cuticles that occur alongside _T. phanerosarkus_—its absence is genuine. Muscle preservation is no less unusual in Burgess Shale-type settings [22]. The exception is Sirius Passet, where early diagenetic phosphatization records the evolution of muscle anatomy in stem-group Euarthropoda—documenting a conceived transition from peripheral musculature deep in the stem group ( _Kerygrychus_), via peripheral + skeletal muscle (in _Pambdelurion_), to the skeletal muscle arrangement of crown group euarthropods (and tardigrades) [2]. The presence of peripheral musculature in _T. phanerosarkus_ confirms that peripheral musculature was also ancestral within onychophorans, and thus for panarthropods as a whole.

Nevertheless, the derivation of three-layered musculature from the presumably ancestral twin layers observed in priapulids [23] is not straightforward. In priapulids and extant onychophorans, the outermost muscles are circular and the innermost longitudinal, with onychophorans incorporating an intermediate layer of interwoven oblique muscles [24,25]. *Trionycus phanerosarkus* exhibits equivalent layers—though their order is reversed, leaving the homology of each layer with those in other panarthropods unclear, and revealing an unexpected diversity of muscle arrangement in early panarthropods.

A position within Onychophora is nonetheless robustly supported by phylogenetic analysis, which consistently places the new lobopodian in a clade comprising *Orstenotubulus*, *Antennacanthopoda*, *Helenovora* and crown group Onychophora (electronic supplementary material, summarized in figure 2). This ‘onychophoran-like’ clade is sister to all other Cambrian stem-group onychophorans, with the exception of *Onychodictyon gracilis*. It reflects curricular similarities between _T. phanerosarkus_, *Orstenotubulus* [8] and extant onychophorans: bifurcating circumferential wrinkles, spineose projections mounted on with circular bases, and (in places) hexagonal patterning.

The new fossil extends the record of these features of the modern onychophoran cuticle into the lower Cambrian (Stage 3), along with other characteristics of the onychophoran body plan: the peripheral disposition of multiple muscular layers, the ventrolateral appendage location and conceivably a gonopore—one possible interpretation of the intra-appendicular gap in musculature, suggested by equivalent openings in *Orstenotubulus* and extant onychophorans [8].

Despite the early evolutionary origin of this suite of onychophoran features, it is striking that the ‘onychophoran-like’ clade is so poorly represented in the fossil record: only six specimens have yet been recovered, four of which are Orsten-type fragments. Whether or not the distinctively onychophoran-like features of the new fossil were also present in other Cambrian lobopodians, the lineage leading to modern Onychophora seems to have been as rare and depauperate during the formative stages of its evolution as it is today.

Data accessibility. Phylogenetic data: TreeBASE accession number S18871 [26]. Description of characters and detailed phylogenetic results: Dryad: http://dx.doi.org/10.5061/dryad.7r10b [12]. This published work and the nomenclatural acts it contains have been registered in ZooBank: http://zoobank.org/References/D56C681C-2EEB-41CD-BE92-48927554810D.

**Authors’ contributions.** X.G.Z. and M.R.S. conceived the study. X.G.Z., J.Y. and J.B.H. collected the material. M.R.S. performed the phylogenetic analysis. J.Y. took the SEM photos. X.G.Z. and M.R.S. made the phylogenetic tree and published work and the nomenclatural acts it contains have been approved the final version of the manuscript. All authors have agreed to be held accountable for the content and approved the final version of the manuscript.

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**References**


