

Research

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e-mail: jortegahernandez@fas.harvard.eduElectronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.7130009>.Post-Cambrian survival of the tubicolous scalidophoran *Selkirkia*

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Scalidophoran worms represent common infaunal components of early and middle Cambrian Burgess Shale-type fossil biotas. Early scalidophorans resemble extant priapulids based on overall morphology, but the genus *Selkirkia* represents the earliest record of tube dwelling for the group. Despite its ubiquitous presence in exceptional marine deposits, whether the exclusively Cambrian occurrence of *Selkirkia* reflects its entire evolutionary history or is affected by taphonomic biases remains unresolved. Here, we demonstrate the post-Cambrian survival of *Selkirkia* based on new material from the Lower Ordovician Fezouata Shale biota of Morocco. The discovery of *Selkirkia* in the Fezouata Shale extends the biostratigraphic range of the genus by 25 million years and its palaeobiogeographic occurrence to the high latitudes of Gondwana, strengthens the evolutionary links between Cambrian and Ordovician Burgess Shale-type biotas and increases scalidophoran diversity for the Fezouata Shale biota otherwise consisting exclusively of the palaeoscolecoid *Palaeoscolex? tenensis*. The tube of *Selkirkia* underwent negligible external change for over 40 million years, indicating a high degree of morphological stasis during the Early Palaeozoic. A tubicolous mode of life is rare among extant priapulids and expressed only in *Maccabeus*, which forms a delicate tube from agglutinated plant debris, unlike the macroscopic secreted cuticular tube of *Selkirkia*.

1. Introduction

Burgess Shale-type (BST) biotas fundamentally inform the biodiversity of animal-dominated communities during the early stages of the Phanerozoic. These extraordinary deposits contain diverse non-biomineralized organisms that would normally be absent from the shelly fossil record, offer insights into the ancestral morphology of extant groups, and illuminate the autecology of the earliest complex animals [1–3]. Cambrian BST biotas indicate that the scalidophorans, vermiform organisms characterized by the presence of an eversible introvert lined with pharyngeal teeth and cuticular specializations known as scalids with diverse morphologies, were some of the most diverse and common infaunal elements in early marine animal-dominated communities as carnivorous predators and scavengers [4–6]. Although Cambrian scalidophorans are mostly known from exceptionally preserved cuticular macrofossils [4,7–9], their microfossil record includes spectacular instances of phosphatized (e.g. armored kinorhynch-like species from South China [10], *Markuelia* from Cambrian sites in Siberia, North America, Australia and China [11]) and even carbonaceous remains (e.g. small carbonaceous fossils pharyngeal teeth [6], complete loriciferans [12]). Critically, exceptionally preserved microfossils from the Kuanchuanpu Formation biota in south China capture the stratigraphically oldest record of scalidophorans during the Fortunian (ca 535 Ma) [10,13]. Cambrian scalidophorans had a similar degree of overall morphological disparity relative to their extant representatives [14,15], which include priapulids, kinorhynchs and loriciferans, but some of these early representatives featured anatomical adaptations and modes of life that are rarer, even absent, in modern counterparts. For instance, selkirkiid scalidophorans are

spatiotemporally widespread in the Cambrian, with records from BST biotas in North America and South China ranging from Stage 3 (e.g. Chengjiang, Xiaoshiba, Buen Formation), to Wuliuan (e.g. Burgess Shale, Kaili, Spence Shale) and Guzhangian (e.g. Weeks, Pika) (electronic supplementary material, table S1). Selkirkiids feature a secreted ornamented tube around the body, an eversible scalid-bearing introvert, and a simple gut. By contrast, tube dwelling is only expressed in the small bodied (less than 3 mm in length) genus *Maccabeus* among extant priapulids [16,17], although in this case the tube is extremely delicate and the result of agglutinated plant debris rather than being secreted by the organism itself. Some larval priapulids and loriciferans bear a lorica [12,16,17], which consists of a series of cuticular sheaths for protection, but these structures do not form an enclosed tube proper.

Selkirkiids comprise two genera, *Selkirkia* which embodies most of the diversity and spatio-temporal distribution of the group [4,18,19], and the controversial *Sullulika* that is only known from Greenland's Stage 3 Buen Formation [20]. Although selkirkiids represent common infaunal components of BST biotas during the Cambrian thanks to the preservation potential of their robust secreted tubes, these organisms have not been recorded from younger deposits with soft tissue preservation that have produced evidence for scalidophoran macrofossils [21–23]. Whether the absence of post-Cambrian tube forming scalidophorans is a legitimate or a taphonomic bias remains unresolved. Here, we describe a new species of *Selkirkia* from the Lower Ordovician Fezouata Shale biota of Morocco [24,25] that demonstrates the post-Cambrian survival of tubicolous scalidophorans and significantly expands the distribution of the genus both in terms of its biostratigraphic and palaeobiogeographic occurrence during the Early Palaeozoic.

2. Systematic palaeontology

Scalidophora Lemberg, 1995

Phylum Priapulida Delage & Herouard, 1897

Order Selkirkiimorpha Adrianov & Malakhov, 1995

Family Selkirkiidae Conway-Morris, 1977

(a) Genus

Selkirkia Walcott, 1911

Selkirkia tsering nov.

Zoobank identifier B523E00B-59BF-4BC0-9D05-FB62474CB64F

(i) Etymology

Derived from the Tibetan word 'tsering' meaning 'long life'.

(ii) Type material

Holotype (MCZ.IP.201003). Paratypes (MCZ.IP.201004, MCZ.IP.201005, MCZ.IP.202502). Other material (YPM.IP.521504, YPM.IP.521909, YPM.IP.524887). All studied and figured material is deposited at the Invertebrate Paleontology collections at the Museum of Comparative Zoology (MCZ.IP), Harvard University (Cambridge, USA), and the Invertebrate Paleontology collections at the Yale Peabody Museum of Natural History (YPM.IP), Yale University (New Haven, USA).

(iii) Locality and age

Lower Fezouata Shale Formation in the Draa Valley, Zagora region of Morocco. Georeferenced sub-locality information is curated with the specimens in their respective collections. The co-occurrence of the planktic graptolites *Kiaerograptus* and *Tetragraptus* from the same sub-locality as *Selkirkia tsering* indicate a late Tremadocian age as part of the *Araneograptus murrayi* biozone [26].

(iv) Diagnosis

Medium-sized *Selkirkia* (27.9 mm average tube length) with tube bearing evenly spaced transverse ornamentation with a density of six annulations per millimetre. Tube with low opening angle conveying a sub-parallel outline that gently tapers posteriorly to a blunt termination.

(v) Description

The studied specimens ($n=7$) consist of cone-shaped tubes with a low opening angle that conveys a sub-parallel appearance throughout (figure 1), with complete specimens ranging in length from 19.95 to 34.24 mm, and maximum width from 2.73 to 3.8 mm measured at the anterior opening (electronic supplementary material, table S2). The orientation of the specimens does not allow us to evaluate whether the posterior end is open, but most of the studied tubes are complete and show a blunt posterior termination (figure 1). The tubes are ornamented with highly regular transverse annulations, with a density of six annulations per millimetre measured at the level of the mid length where the ornamentation is best expressed (figure 2g). The holotype (MCZ.IP.201003) preserves evidence of soft tissues in the form of a partially everted subtriangular introvert that is found extending forward from the anterior tube margin (figures 1d,e and 2a,b). The paratype (MCZ.IP.201005) also preserves soft tissues anteriorly, possibly remains of the introvert, as well as elongate morphological structures within the tube walls with a slightly darker coloration in a more posterior position within the trunk (figures 1a and 2d–f). The fact that these structures show a slight degree of

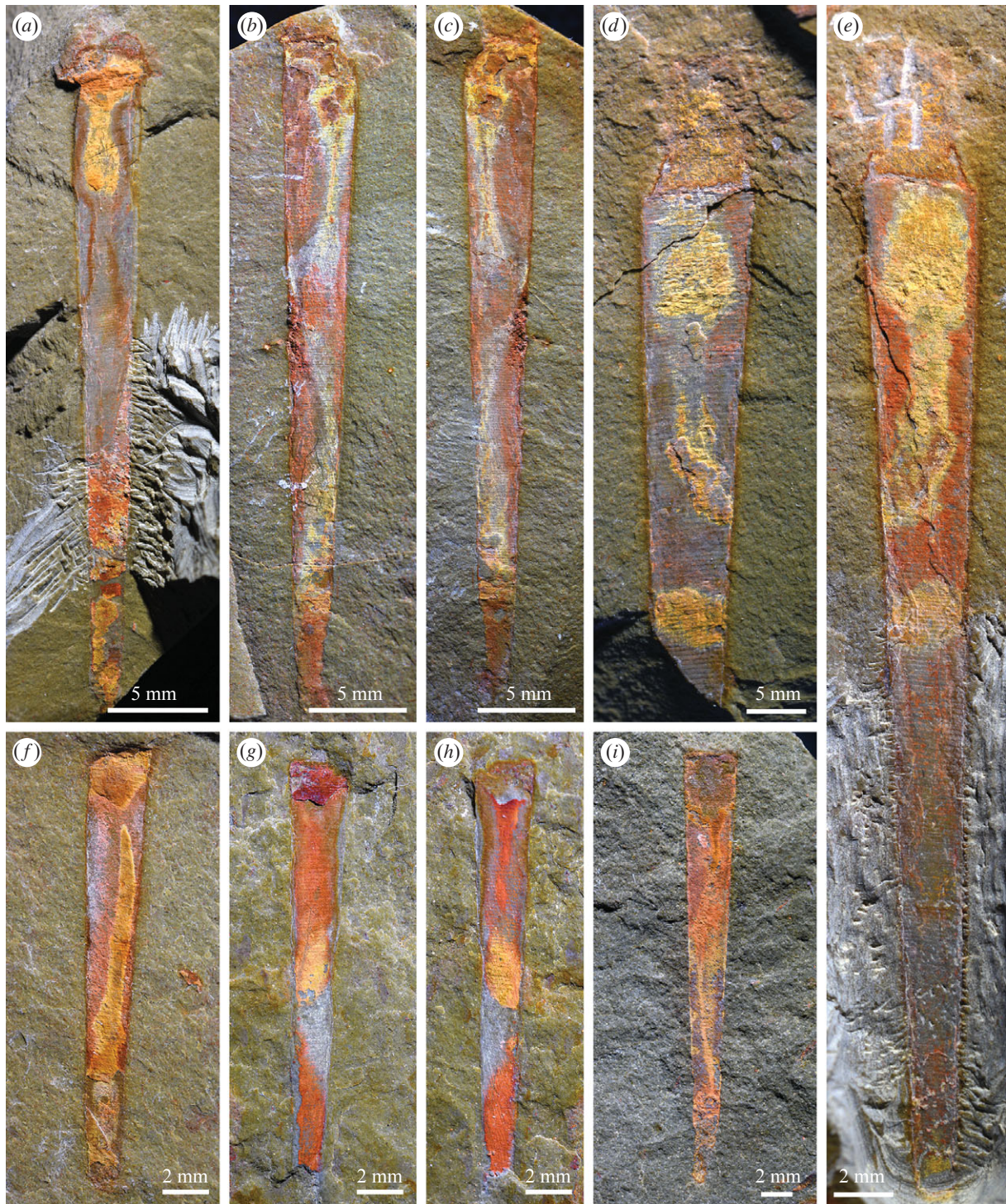


Figure 1. The tubicolous scalidophoran *Selkirkia tsering* nov. from the Lower Ordovician (Tremadocian) Lower Fezouata Shale of Morocco. (a) Paratype MCZ.IP.201005, complete individual with preserved soft tissues and transverse tube annulations. (b) Paratype MCZ.IP.201004a, part, complete tube with well-preserved transverse annulations. (c) Paratype MCZ.IP.201004b, counterpart. (d) Holotype MCZ.IP.201003a, part, fragmentary individual with remains of introvert and well-preserved transverse tube annulations. (e) Holotype MCZ.IP.201003b, counterpart, complete individual. (f) YPM.IP.521909, isolated tube with transverse annulations. (g) YPM.IP.524887a, isolated tube. (h) YPM.IP.524887b, counterpart. (i) Paratype, MCZ.IP.202502, isolated tube with transverse annulations.

three-dimensionality relative to the rest of the fossil specimen suggests that they might have been robust and possibly sclerotized, which would be consistent with their interpretation as pharyngeal teeth based on their similar position to the pharyngeal teeth of extant priapulids when the introvert is retracted [16,17,27]. The everted introvert has a broadly subtriangular tapering appearance (figure 2a,b), and although finer details such as the teeth circlets are not well preserved, it is similar in size and shape to that observed in the early Cambrian *Selkirkia sinica* from Chengjiang and Xiaoshiba [4,18,28] and the mid-Cambrian Burgess Shale *S. columbia* (figure 2c) [6]. MCZ.IP.201003 also shows evidence of a long and simple gut tract consistent with other Cambrian *Selkirkia* species (figure 2a–e). The Fezouata Shale specimens consistently show an enlarged anterior area of the gut tract within the tube walls defined by the selective accumulation of yellow to bright orange iron oxides (figure 2a,b,d–f); we interpret this as a specialization of the gut tract, possibly the pharynx based on its position and shape, that might have been involved in digestion and formation of faecal pellets, as also observed in well preserved specimens of *S. sinica* from Chengjiang and Xiaoshiba [4,18].

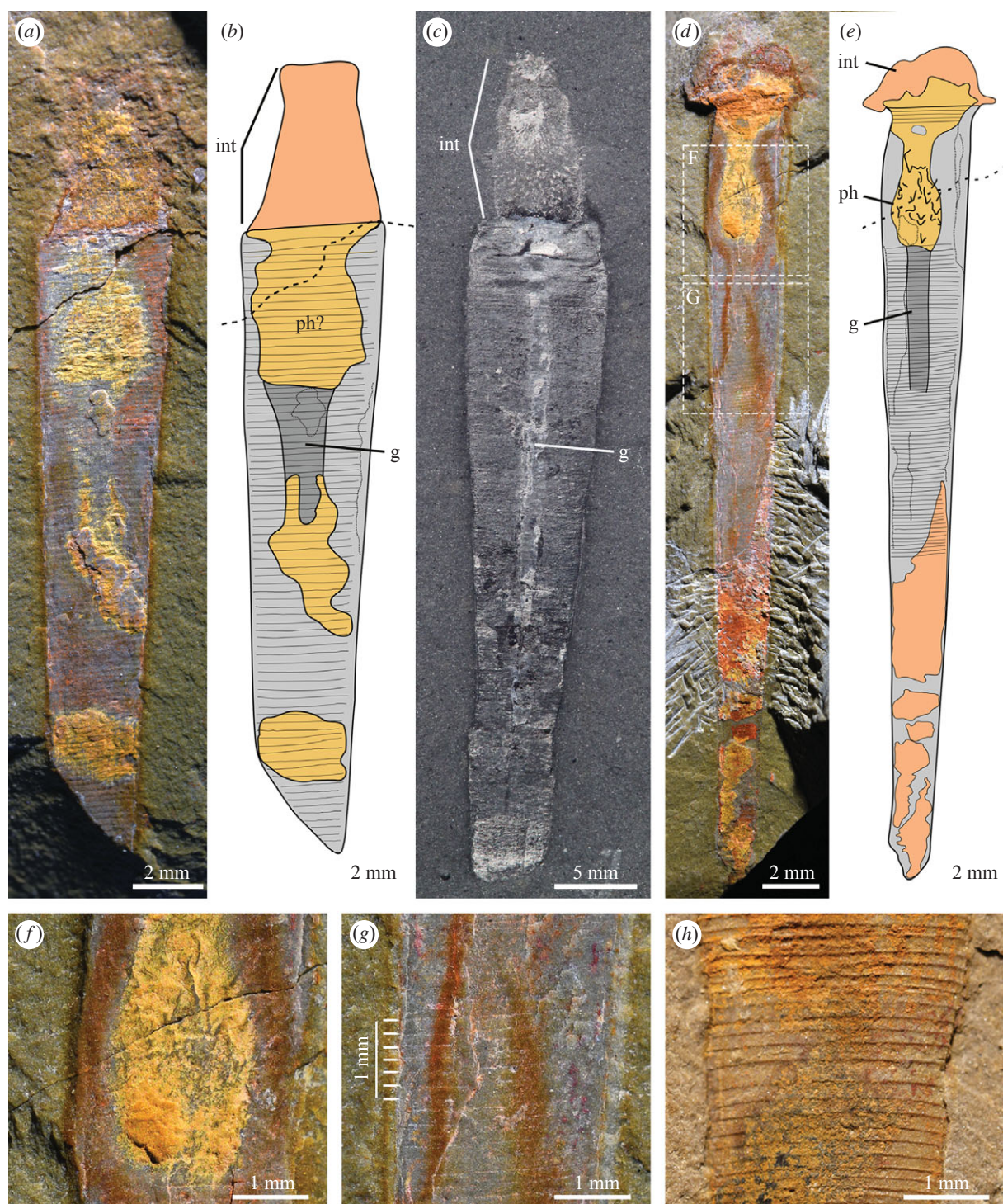


Figure 2. Morphological comparison of Cambrian and Ordovician selkirkid scaldiphorans. (a) *Selkirkia tsering* sp. nov. (holotype MCZ-IP-201003) from the Lower Ordovician Fezouata Shale with well-preserved annulated tube, gut tract, and outstretched introvert. (b) Interpretative diagram of MCZ-IP-201003. (c) *Selkirkia columbia* (ROMIP 63195) from the mid-Cambrian Burgess Shale with well-preserved annulated tube, gut tract and outstretched introvert. (d) *Selkirkia tsering* sp. nov. (MCZ-IP-201005) from the Lower Ordovician Fezouata Shale with retracted the introvert. (e) Interpretative diagram of MCZ-IP-201005. (f) Close-up of pharyngeal teeth-like impressions in MCZ-IP-201005. (g) Close up of well-preserved tube annulations in MCZ-IP-201005. (h) Close up of the tube annulations in *Selkirkia transita* from the early Cambrian Chengjiang (ELI-0000604). g, gut; int, introvert; ph, pharynx.

(vi) Remarks

Selkirkia tsering bears the greatest resemblance to the Chengjiang *S. transita* in terms of overall tube size and annulation density [4]. However, the tube of the Fezouata Shale species differs from *S. transita* and other selkirkids in having a lower opening angle that tapers posteriorly more gently, conveying an almost parallel-sided appearance. *Selkirkia tsering* also shows a more consistent ornamentation pattern consisting of six annulations per millimetre measured at the mid-length of the tube (figure 2g), whereas there is some variability in other taxa (see [4]). Although the information on the introvert structure in *S. tsering* is not well preserved which hampers detailed morphological comparisons with *S. transita*, we consider that the status of the former as a new and distinct species could be partly justified given the considerable age gap (ca 40 million years) and palaeobiogeographic distance (low versus high palaeolatitudes) between the Chengjiang and Fezouata Shale biotas. *Selkirkia tsering* is morphologically distinguished from *S. sinica* (Chengjiang and Xiaoshiba in South China) by its larger average size (*S. sinica* tube size between 8 to 19 mm) and

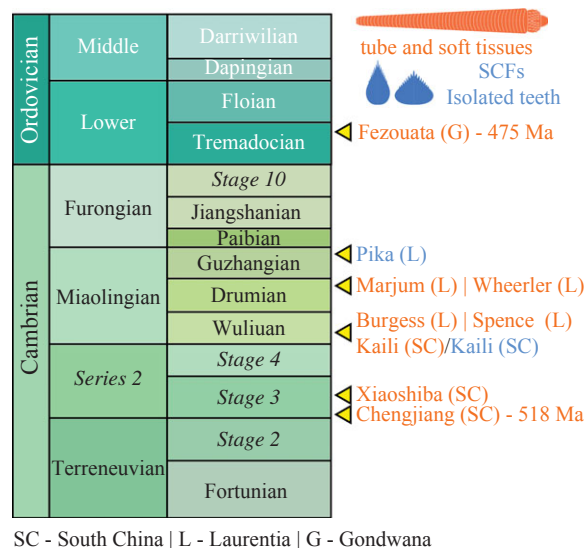


Figure 3. Spatio-temporal distribution of selkirkid scalidophorans. SCF, small carbonaceous fossils. See electronic supplementary material, table S1 for detailed biostratigraphic occurrence data.

lower annulation density (8 to 14 annulations/mm in *S. sinica*) [4,18]. We also distinguish *S. tsering* from *S. columbia* (Burgess Shale, Wheeler) by its smaller average size (*S. columbia* tube size between 20 to 50 mm) and lower annulation density (40 annulations/mm in *S. columbia*) [4,29]. Comparisons with other *Selkirkia* species are more challenging due to poor preservation of the tube ornamentation, but *S. tsering* is larger than *S. willoughbyi* (16 mm average length) from the Marjum and Wheeler Formations in Utah [7,30], but smaller than *S. spencei* (at least 73 mm length) from the Spence Shale [7]. Comparisons with other putative *Selkirkia* from Laurentia are not possible as they consist of broken isolated tubes without clearly preserved ornamentation (electronic supplementary material, table S1).

We can confidently rule out alternative phylogenetic affinities for *S. tsering* through comparisons with cone-shaped taxa from the Fezouata Shale and other Lower Palaeozoic deposits. The new material is readily distinguished from Fezouata Shale hyoliths with soft tissues [31] based on the more elongate shape of the tube in *S. tsering*, presence of an introvert and straight gut tract. Furthermore, our material lacks evidence of an operculum or helens, despite its good preservation quality. Similar arguments apply to cnidarians that are relatively common in the Fezouata Shale Formation, such as *Sphenothallus* and conulariids [32]. *Sphenothallus* has a stronger tapering profile, a curved median axis and outline, as well as lateral tube wall reinforcements, all of which are missing in *S. tsering*. Likewise, Fezouata conulariids have a much higher width to length ratio, higher opening angle, and feature axial longitudinal keel-like structures that are not observed in any of the specimens of *S. tsering* (figure 1). Similar arguments apply to comparisons with other Lower Palaeozoic cnidarians that have a tube-like habitus and transverse ornamentations, such as Cambrian and Ordovician species of *Byronia* [33,34] or the recently redescribed *Gangtoucunia* from the Stage 4 Guanshan biota in South China [35]. Despite the presence of transverse annulations, the growth pattern of these cnidarians does not consistently produce a tube with a straight median axis, but instead results in a gently curving or meandering overall morphology. Coupled with the preservation of a straight gut tract, introvert and possibly pharyngeal teeth in the studied material of *S. tsering* (figure 2), we consider that an alternative phylogenetic hypothesis as a cnidarian is unlikely.

3. Discussion

(a) Selkirkid fossil record and spatio-temporal distribution

The discovery of *Selkirkia tsering* from the Fezouata Shale carries several implications for early scalidophoran evolution. Scalidophorans are known from several early to mid-Cambrian sites with exceptional preservation with a circum-equatorial distribution in Laurentia and South China (figure 3; electronic supplementary material, table S1), represented by soft-bodied macrofossils [4,7,30] and either phosphatized [10,11] or carbonaceous microfossils [6,12]. *Selkirkia tsering* is the only selkirkid reported from a post-Cambrian deposit to date, expanding the macroscopic stratigraphic range of the genus by approximately 25 million years, and represents the first record of these organisms from the high latitudes of Gondwana (figure 3; electronic supplementary material, table S1), similarly to other typically Cambrian organisms recovered from the Fezouata Shale [24,25]. Thus, *Selkirkia* had a significantly more widespread geographical distribution overall in the context of its entire evolutionary history, implying substantial dispersal capabilities greater than those suggested by Cambrian sites of exceptional preservation alone, all of which are restricted to low palaeolatitudes. However, the paucity of additional occurrences does not allow us to conclusively determine whether *Selkirkia* was also distributed in high palaeolatitudes during the Cambrian, or if this pattern is exclusive to younger Ordovician deposits. New discoveries of scalidophoran macrofossils from post-Cambrian marine sites of exceptional preservation, such as those from the Ordovician of Morocco [21,22], China [36–38], Wales [23,39,40], Czech Republic [41], and North America [42] are needed to answer this question. The fact that no other selkirkids have been discovered from these multitude of Ordovician sites with soft tissue preservation worldwide, despite their durable tube construction, suggests that the polar distribution of *S. tsering* might be legitimate rather than a preservation artefact. We hypothesize that selkirkids might have shrunk their Cambrian low

latitude worldwide distribution into a single high latitude Ordovician refuge as a consequence of the increased ecological pressure during the initial series of Early Ordovician radiations preceding the Great Ordovician Biodiversification Event [43,44]. Palaeoscolecid sponges appear to have been much less affected by comparison based on their much broader palaeobiogeographic distribution during the Ordovician including Gondwana [21,22,41], Laurentia [42], South China [36–38] and Avalonia [23,39,40], which suggests a degree of ecological selectivity in the survival of Early Palaeozoic scalidophorans. It is also possible that the evolutionary trade-off of living in a protective tube but at the cost of greatly reduced motility [4] was a compounding factor for the highly restricted distribution of Ordovician selkirkids, and possibly even the demise of this mode of life for macroscopic scalidophorans among modern representatives.

(b) Ecological implications

Our results highlight the marked rarity of scalidophorans in the Fezouata Shale biota. Both the palaeoscolecid *Palaeoscolex? tenensis* [21] and *Selkirkia tsering* have been recovered from the late Tremadocian *Araneograptus murrayi* biozone [26], and thus appear to be highly localized in terms of their biostratigraphic distribution within the Fezouata Shale Formation. Given the fossilization potential of both selkirkid tubes and palaeoscolecid phosphatized sclerites coupled with the good representation of diverse ecological modes of life in the Fezouata Shale biota [45], we regard the paucity of infaunal scalidophorans as an authentic biological signal. Although some degree of taphonomic bias cannot be completely ruled out, we consider that a combination of the recalcitrant nature of selkirkid tubes and palaeoscolecid sclerites and the availability and examination of thousands of fossils from the Fezouata Shale (from the Invertebrate Paleontology collections at MCZ and YPM) support the interpretation that their rarity is legitimate rather than solely an artefact of preservation. The low scalidophoran species diversity of the Fezouata Shale biota is a stark contrast with the higher biodiversity and abundance of these organisms in Cambrian BST deposits in Laurentia and South China, which in addition to several palaeoscolecid and selkirkid species also includes diverse archeopriapulids such as *Ottoia* [5–9,46]. The rarity of infaunal scalidophorans in the Fezouata Shale likely reflects a combination of its shallower depositional environment and some degree of decay prior to final burial that typifies this exceptional site [45]. Critically, the fact that the distribution of exceptionally well-preserved fossils in the Fezouata Shale is partly controlled by tempestites (i.e. storm deposits) [47], likely negatively impacted the ability of infaunal scalidophorans to settle and proliferate more broadly within this marine deposit located below storm-wave base.

A possible counterpoint to this ecological interpretation is the fact that, unlike the strictly open marine conditions that typify Cambrian BST sites that have yielded infaunal scalidophorans [1–7,9,18,20,28–30], the Ordovician Period boasts several biotas with exceptional preservation that reflect a broader range of marine depositional environments. Examples include the near shore coarse sandstones of the Llandegley Rocks [48], cases of lagoonal or embayment deposits such as Winneshiek [49] and the Soom Shale [50], the deep-water mudstones of Beecher's Bed [51] and Llanfallteg [40], or the distal ramp carbonates of the Walcott-Rust Quarry [52]. It is conceivable that selkirkids and other scalidophorans might have also inhabited at least some of these environments, but that the peculiarities of these deposits would not record the presence of these organisms relative to the more favourable conditions for their fossilization during the Cambrian. Alternatively, this observation might point to the fact that Early Palaeozoic scalidophorans preferentially inhabited open marine conditions at variable depths (e.g. storm-wave base to deep marine), and that the occurrence of extant scalidophorans in shallower and marginal environments today represents a more recent event in their evolutionary history [53].

(c) Tubicolous scalidophoran evolution

Selkirkia tsering demonstrates that the construction of the secreted tube in this tubicolous scalidophoran underwent negligible macroevolutionary change over its 40-million-year history considering its first appearance in the Stage 3 Chengjiang biota (ca 518 million years ago; [4]) and its extension into the late Tremadocian (ca 475 million years ago) (figure 3). *Selkirkia* joins the roster of 'Cambrian survivors' that persisted into the Ordovician as informed by the Fezouata Shale biota [24,25] and other sites around the world [21,22,36–42] (e.g. radiodonts, artiopods, lobopodians), and demonstrates the ecological success and stability of the tubicolous mode of life for scalidophorans during the Early Palaeozoic. By contrast, tube-dwelling is comparatively much rarer in extant priapulids, being only known in the genus *Maccabeus*, which contains only two described species [16,17,54]. The ecological similarities between *Selkirkia* and *Maccabeus* are only superficial, however, as these taxa differ in several key aspects that affect their mode of life. First, the tube of *Selkirkia* was entirely secreted by the animal during growth, and likely entirely replaced during ecdysis [4], whereas the tube of *Maccabeus* consists of agglutinated plant debris from the environment that is encased in a longitudinal pattern thanks to secretions of the glandular spines [16,17]. Second, whereas there is interspecific and ontogenetic variation in size in *Selkirkia* species ranging from 3 to 75 mm in body length, *Maccabeus* is diminutive with an adult body length below 3 mm. These differences in body size would directly impact their mode of life, as *Selkirkia* would be capable of carnivory and/or scavenging of larger food items as evidenced by the presence of gut pellets in Cambrian specimens [4,18], whereas *Maccabeus* is restricted to a specialized type of 'trap-feeding' of meiofaunal or microscopic organisms. Finally, *Selkirkia* bore differentiated circlets of pharyngeal teeth and scalids on the introvert [6], whereas the mouthparts of *Maccabeus* consist of sets of elongate oral spines involved in the trap-feeding strategy [16]. Taken together, although both the Cambro-Ordovician *Selkirkia* and extant *Maccabeus* broadly represent cases of tube-dwelling scalidophorans, the precise adaptations to this mode of life differ substantially between these taxa. Although some extant scalidophorans bear a cuticular lorica composed of several articulating sheets that have a protective role similar to that of the tube in *Selkirkia* [12,16,17], this adaptation is also only expressed in small meiofaunal organisms (loriciferans) or during the early larval stages of otherwise macroscopic organisms (priapulids). Thus, *Selkirkia* demonstrates that macroscopic tube building was an effective strategy during the Cambrian that appears to have become much more palaeobiogeographically restricted during the Ordovician based on the available fossil data from the Fezouata Shale

and the growing number of Ordovician sites with soft tissue preservation around the world [21,22,36–42]. While the protection conveyed by tube-dwelling likely facilitated the Cambrian diversity and worldwide distribution of selkirkiids (figure 3; electronic supplementary material, table S1), the downside caused by the loss of motility might have negatively affected their evolutionary and ecological success during the Ordovician, particularly when compared with palaeoscolecid worms with a vagrant mode of life. By contrast, tube dwelling in extant scalidophorans represents a highly restricted, and most likely convergent, strategy that is only known from meiofaunal *Maccabeus* species, and which are only found in the Mediterranean Sea and the Indian Ocean [16,54].

Ethics. The specimens are part of a larger collection produced by Mohammed ‘Ou Said’ Ben Moula from the Draa Valley in the Zagora region of Morocco, purchased in 2019 from Lahcen Ben Moula (address in Morocco: Ksar Taichouta, Alnif, Tinghuir), and exported by Brahim Tahiri (108 Cite Essalem, Erfoud, Morocco) with the approval of the Ministry of Mines in Rabat (invoice no. 92/E/21).

Data accessibility. All studied and figured material is deposited and publicly accessible at the Invertebrate Paleontology collections at the Museum of Comparative Zoology, Harvard University (MCZ.IP, Cambridge, USA), and the Invertebrate Paleontology collections at the Yale Peabody Museum of Natural History, Yale University (YPM.IP, New Haven, USA).

Supplementary material is available online [55].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors’ contributions. K.N.: conceptualization, investigation, writing—original draft; J.O.-H.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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