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Brachiopods hitching a ride: an early case of commensalism in the middle Cambrian Burgess Shale

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Ecological interactions, including symbiotic associations such as mutualism, parasitism and commensalism are crucial factors in generating evolutionary novelties and strategies. Direct examples of species interactions in the fossil record generally involve organisms attached to sessile organisms in an epibiont or macroboring relationship. Here we provide support for an intimate ecological association between a calcareous brachiopod (*Nisusia*) and the stem group mollusc *Wiwaxia* from the Burgess Shale. Brachiopod specimens are fixed to *Wiwaxia* scleritomes, the latter showing no signs of decay and disarticulation, suggesting a live association. We interpret this association as the oldest unambiguous example of a facultative ectosymbiosis between a sessile organism and a mobile benthic animal in the fossil record. The potential evolutionary advantage of this association is discussed, brachiopods benefiting from ease of attachment, increased food supply, avoidance of turbid benthic conditions, biofoul and possible protection from predators, suggesting commensalism (benefiting the symbiont with no impact for the host). While Cambrian brachiopods are relatively common epibionts, in particular on sponges, the association of *Nisusia* with the motile *Wiwaxia* is rare for a brachiopod species, fossil or living, and suggests that symbiotic associations were already well established and diversified by the “middle” (Series 3, Stage 5) Cambrian.

Symbiosis in a broad sense refers to the intimate physical association between two organisms, commonly one species (symbiont) living with a host species¹, associations that are notoriously difficult to detect in the fossil record. Seen as a crucial factor in the evolution of organisms², symbiotic relationships are displayed by millions of modern day organisms canvassing the terrestrial and marine realms. Associations can take a number of forms, generally categorized based on the impact incurred by the host³, including parasitism (negative impact on the host), mutualism (positive impacts for both host and symbiont) and commensalism (no direct impact for host but positive for the symbiont). Symbiosis is a poorly studied aspect of the fossil record, owing largely to taphonomic biases that inconveniently inhibit preservation of direct interaction between two or more organisms in life. Despite the difficulties, various forms of symbiosis have been identified in the fossil record, principally from Ordovician and younger strata and predominantly dealing with epibiont and macroboring organisms⁴.

Brachiopods, one of the dominant filter feeders of the Palaeozoic, frequently play both roles, acting as symbionts and as hosts. Attaching themselves to various sessile organisms for support⁵ and having a range of organisms living on^{6,7} and to some extent inside their shell^{8,9}. Brachiopods generally attach to hard substrates by means of a pedicle, this includes substrates such as, sponges¹⁰, algae⁵, other brachiopods¹¹, disarticulated skeletal elements¹², an attachment strategy that has not significantly changed since the phylum arose in the Cambrian¹³. Brachiopods have, in rare instances, been documented attached to the spines of live echinoids from the Carboniferous (Pennsylvanian) echinoderm Lagerstätte in the Winchell Formation of Texas¹⁴. Exceptionally preserved *in situ* records of Cambrian brachiopods attached to other organisms have been reported from Burgess Shale-type deposits^{5,10}, and such associations generally involve other sessile organisms such as sponges and algae. Enigmatic shells (possibly brachiopods) attached to the disk of the eldoniid *Rotadiscus*¹⁵, have also been reported, but it is not clear whether eldoniids had a semi-vagrant lifestyle¹⁶ or were entirely sessile¹⁵. A couple of occurrences of brachiopods possibly attached to unambiguous vagile organisms have also been noted from the Burgess Shale, including on the arthropod *Sidneyia inexpectans*¹⁷ and on an isolated sclerite of the stem group mollusk *Wiwaxia corrugata*¹⁸. However, in both cases the possible attachments occurred on disarticulated body elements suggesting the hosts represented molts or carcasses and not live animals. One other example involved a complete and

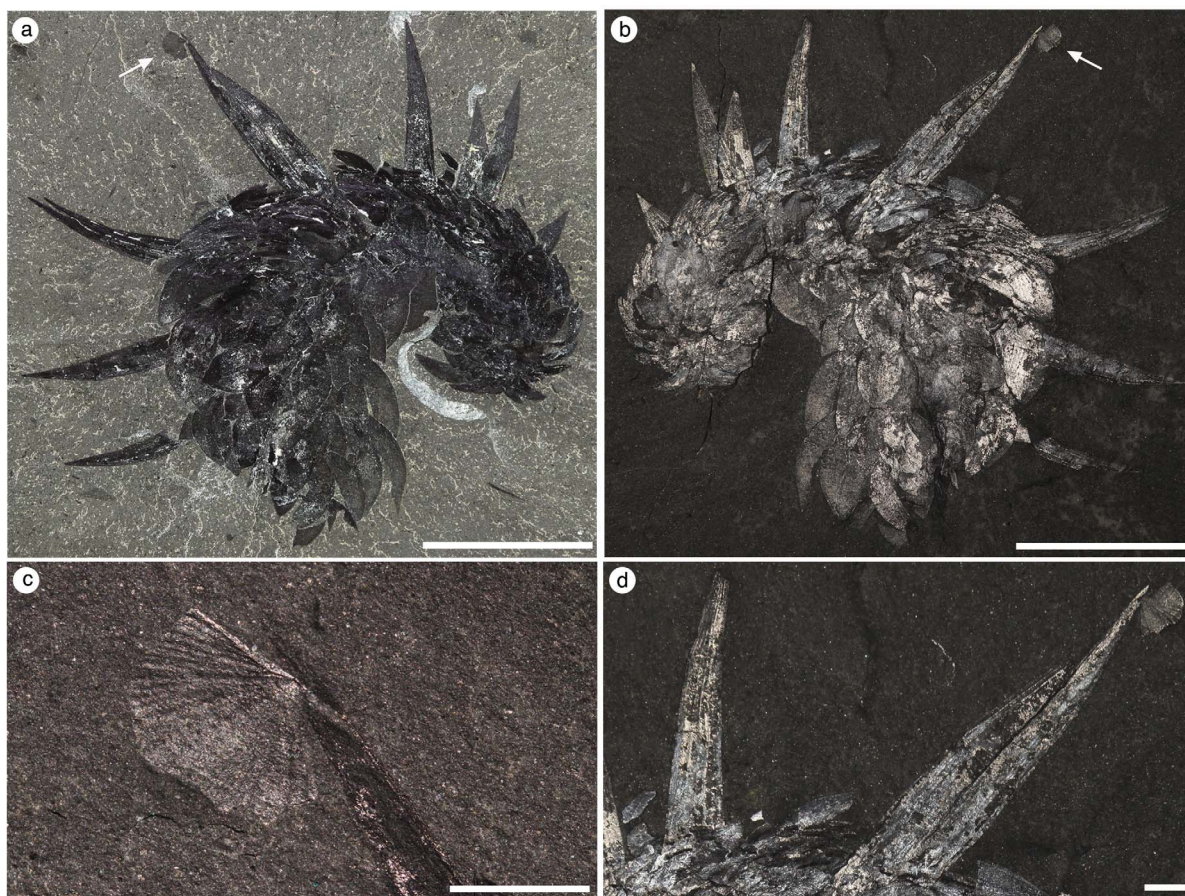


Figure 1 | Specimen of *Nisusia* attached to the dorsal spine of *Wiwaxia*, from the “middle” (Series 3, Stage 5) Cambrian Burgess Shale, ROM 61116. (a–b) Plan views, scale bars 15 mm, (c–d) Close up views of *Nisusia* attached to dorsal spine, scale bars 2 mm.

articulated specimen of *Wiwaxia*, but this association had remained tentative and difficult to separate from chance superposition during burial¹⁸. Here we report the discovery of a second *Nisusia* specimen attached to an articulated *Wiwaxia* specimen also from the Burgess Shale. This new evidence combined with a reevaluation of previous material using modern photographic techniques, reinforces the interpretation that such associations are ecologically genuine, suggesting that symbiotic associations had diversified early on during the Cambrian period.

Results

Wiwaxia is a non-mineralized, cataphract animal, with articulated specimens principally documented from the Burgess Shale^{18,20,21} and the Xiaoshi Lagerstätte of south China²². The dorsal and lateral surface of *Wiwaxia* is covered with imbricating leaf-shaped sclerites together with a variable number of elongate spines that emerge in later growth stages from the dorsolateral regions on each side of adult specimens²¹. Evidence of kinks of the originally chitinous, individual sclerites and spines suggests a relative flexible nature^{18,20}. Sclerites and spines grew to a fixed size by basal accretion and were periodically shed and replaced^{21,22}.

The affinities of *Wiwaxia* are still very much controversial^{20,23,25}, recent studies seem to be leaning towards placing the genus together with *Odontogriphus*²³ and *Orthrozanclus*²⁴ in a stem group of slug-like lophotrochozoans, called the halwaxiids, which is considered closer to molluscs than annelids²⁵. Possession of a radula^{23,26} and evidence of a foot²³, suggest this clade of organism to be well adapted to an epifaunal vagrant grazing lifestyle. Regardless of its exact phylogenetic position, *Wiwaxia* has always been interpreted as a facultatively motile creature.

Here we document one new specimen of *Nisusia burgessensis*²⁷ attached to a completely articulated *Wiwaxia* specimen (fig. 1) and critically reevaluate an additional association involving *Nisusia* attached to a separate articulated *Wiwaxia* specimen (figure 2a–d). Specimen 1 is attached to the apical region of one of the dorsal spines (ROM 61116, fig. 1) and specimen 2, previously interpreted to belong to *Diraphora bellicostata*¹⁸ is attached to a lateral sclerite (USNM 83938 and fig. 2a–b). The individuals are only 2.7 mm (fig. 1) and 2.3 mm (fig. 2a–d) in width and most likely represent juveniles, as specimens of *N. burgessensis* reaching over 20 mm in width are known from the Burgess Shale²⁸. Specimen 1 is attached approximately 0.5 mm from the apex of the spine and its notothyrium (where the pedicle emerges) is centered on the mid-area of the spine (fig. 1c). The dorsal spine is located approximately mid-length along the body, corresponding to the location where the greatest height above the substrate would be achieved, with the brachiopod having been perched at least 20 mm above the substrate, based on the distance from the base of the dorsal spine to the location of the brachiopod. Specimen 2 is attached approximately 3 mm from the apex of the dorsal surface of a lateral sclerite and its notothyrium is also centered on the mid-area (fig. 2b–d). Unfortunately, the dorso-ventral preservation of the specimen does not allow for an accurate measurement regarding the attachment height of the brachiopod above the substrate.

Admittedly, these occurrences could be related to fortuitous superposition during burial¹⁸, or possibly represent attachment by the brachiopod specimens on *Wiwaxia* carcasses before complete burial. Burgess Shale assemblages are typically composed of a combination of articulated and disarticulated organisms, where articulated specimens represent animals buried alive and dissociated

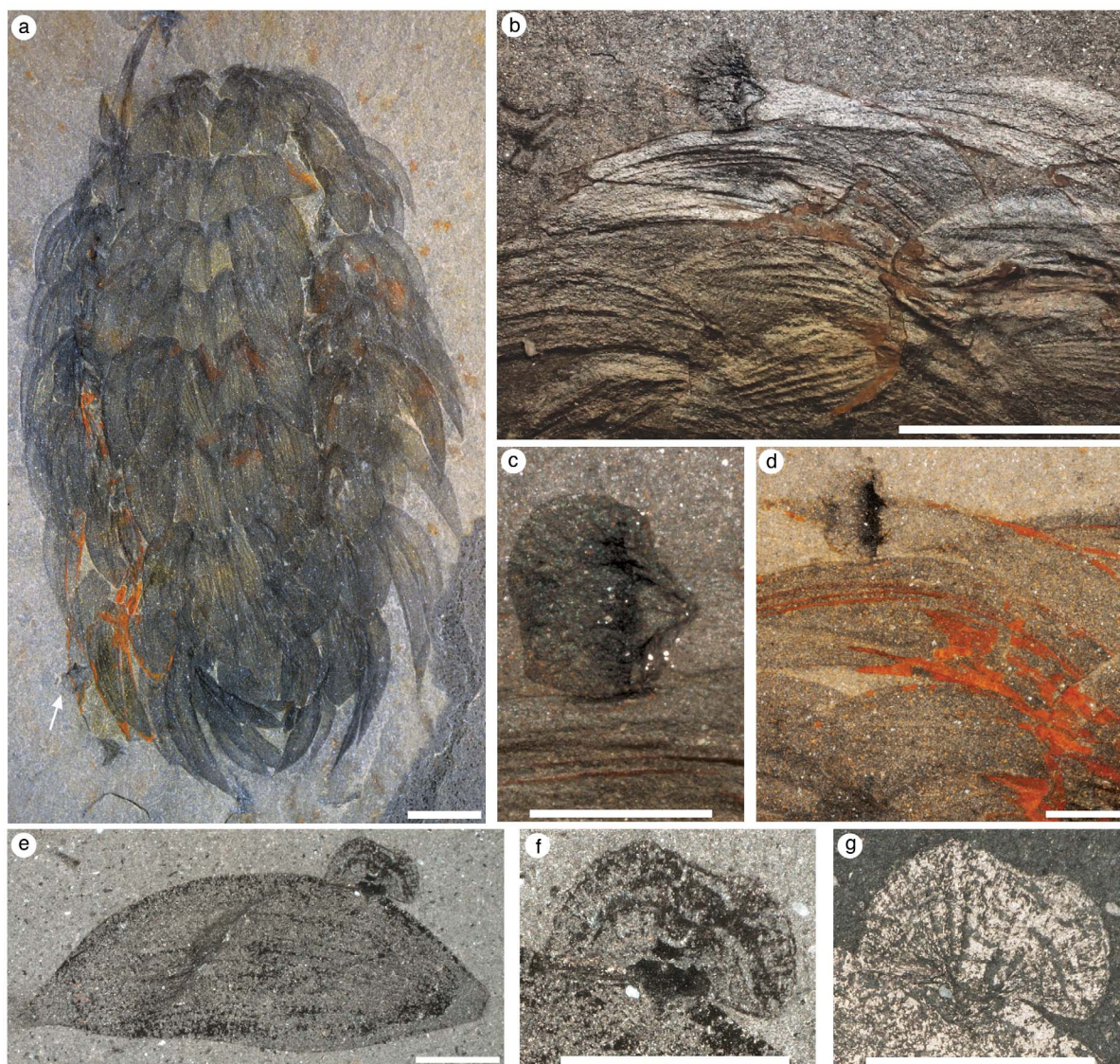


Figure 2 | Specimens of *Nisusia* attached to *Wiwaxia*, from the “middle” (Series 3, Stage 5) Cambrian Burgess Shale. (a–d) *Nisusia* attached to ventro-lateral sclerite of *Wiwaxia*, USNM 83938. (a) Plan view, scale bar 5 mm (b–d) Close up views of *Nisusia* attached to dorsal sclerite, scale bars 2 mm; (e–g) *Nisusia* attached to detached *Wiwaxia* sclerite, USNM 199960. (e) Plan view (f–g) Close up views, scale bars 2 mm.

animals probably represent organisms that died shortly before burial²⁷. Sclerites of *Wiwaxia* although remaining in transverse rows upon death, clearly become disassociated as the specimen disintegrates²⁹. The *Wiwaxia* specimens herein are perfectly articulated indicating rapid and complete burial with no signs of pre or post burial decay. One specimen (ROM 61116, fig. 1) is also unusually contorted, consistent with a possible reaction to burial indicating this animal was probably alive at the time of burial. Growth rates of modern brachiopods are dependent on many biological, ecological and environmental factors, the latter include temperature, salinity, turbulence and intensity of incident light^{30,31} and without knowledge of these factors, growth rates of Cambrian brachiopods is largely speculative. However, comparisons with growth rates of recent taxa, from Scotland (2.75 mm growth 3 months after settling in *Terebratulina*)³⁰ and New Zealand (3 mm annual growth in *Wahonia*)³¹ suggests these *Nisusia* individuals (2.19 mm and 2.13 mm in length) must have been attached for a number of months before burial. It is highly improbable that these brachiopods attached themselves to carcasses for this length of time without the carcasses showing any signs of disintegration. Consequently we concur with Conway Morris¹⁸ that such associations are more likely ecological

and probably occurred on live specimens rather than carcasses. As suggested¹⁸, the specimen of *Nisusia* (1.5 mm in length) associated with an isolated sclerite (fig. 2e–g) may have possibly attached itself after death and disarticulation of *Wiwaxia*. However since there are no signs of decay of this sclerite, an alternative hypothesis is that the brachiopod was attached when *Wiwaxia* was alive and eventually became isolated after moulting.

Discussion

Perhaps one of the most important adaptations of Cambrian brachiopods was the ability to attach to hard substrates, in particular sponges^{6,11,19}, raising the individuals above the seafloor to avoid bio-fouling, turbidity and lowering competition by implementing a tiering system. Attachment to larger motile organisms would not only provide the advantages listed above, but could potentially increase nutrient availability by transporting the individuals to more habitable parts of the benthic environment where both hosts and symbionts would benefit from low turbidity levels and higher access to food sources (i.e., in areas with bacterial mats uncovered by silt in the case of *Wiwaxia*). The current generated by the movement of *Wiwaxia* may have also been sufficient to improve the food supply



and remove waste products produced by the brachiopod. In addition, brachiopods have been documented in unidentified coprolites and in the gut of *Ottoia prolifica*³², a priapulid worm from the Burgess Shale³² suggesting brachiopods were common prey items. *Wiwaxia* sclerites were also identified in the gut contents of *Ottoia*, however, based on size inconsistencies it was suggested that *Ottoia* scavenged on decaying wiwaxiids rather than preying on live specimens³³. Attaching to larger, motile animals, such as *Wiwaxia* would have certainly acted as a deterrent and made it more challenging for benthic predators to eat the brachiopods.

This relationship also sheds some indirect light on the timing and mode of growth of the scleritome of *Wiwaxia* and points to the uniqueness and limitations of this scleritome for brachiopods to attach to it. All *Wiwaxia* specimens described herein are well over 25 mm in length, a dimension considered to represent the beginning of the adult phase when the scleritome becomes less variable^{21,26}. Assuming that the attached brachiopods are a few months old, this puts some minimal time constraints between two consecutive molting events in adult *Wiwaxia* specimens. This also suggests that juvenile *Wiwaxia* specimens were less likely to be suitable habitats for brachiopods presumably because the rate of shedding and replacing sclerites was higher in smaller individuals to accommodate for an increased number and variety of sclerites²⁶, thus reducing the time for larval brachiopods to settle. In addition, the size of the three attached brachiopod shells are comparable possibly suggesting that other *Nisusia* specimens, larger than the ones already documented, are unlikely to be found in association with other *Wiwaxia* scleritomes. Owing to the fact that such associations remain extremely rare (i.e. among hundreds of articulated *Wiwaxia* specimens, only three occurrences exist, a fourth specimen housed at the Cincinnati Museum¹⁸ is inconclusive), points out to the nature of the symbiosis, which must have been facultative for both species and of limited evolutionary advantage for the brachiopod, since growth to adult stage might not have been possible due to periodic shedding of the sclerites.

Attachment of invertebrates to mobile organisms, although considerably rare in the fossil record, is a strategy adopted by a wide variety of organisms in modern marine communities. Bryozoans in particular are common epibionts on motile organisms, attaching themselves to crabs^{34,35}, cephalopods³⁶, sea turtles³⁷ and sea snakes³⁸. Poriferans, hydrozoans, scyphozoans, sea anemones, anthozoans, nematodes, nemertians, annelids, barnacles, molluscs and echinoderms have also been reported in modern marine settings as epibionts on copepods, crabs, isopods, lobsters and shrimp as well as on gastropod shells³⁴. No records of extant brachiopods living as epibionts on mobile hosts has been found, instead extant brachiopods have been reported predominantly acting as the role of host and are commonly encrusted by bryozoans³⁹, bivalves⁴⁰, polychaetes⁴¹ and internally inhabited by crustaceans⁴².

Many of the mobile hosts mentioned above are arthropods (e.g. crabs, lobsters, isopods) and the frequent moulting of the arthropod host would obviously have a negative impact on the attached epibiont, as the exoskeleton is removed. The benefits that may accrue from attaching to a moulting organism to some degree must offset the potential shortened life span, at least in the bryozoan/crab symbiotic relationship that appears to have repeatedly evolved, suggesting that a real benefit exists for the bryozoans^{34,43}. A moulting episode would not necessarily lead directly to the death of the symbiont, but it would increase the symbiont's exposure to scavengers and other organisms that may consume the moulted shell. Competition for suitable substrate space is intense in modern communities^{43,44} and exploitation of mobile hosts may lessen the competition for substrate by providing additional unoccupied substrate space. Mobile hosts, due to the difficulty of settling on a free moving organism, are typically less occupied, (in terms of the number of epibionts and percentage of the host covered by epibionts) when compared to sessile

substrates^{34,38,43} providing a substrate where interactions with other attached organisms will be minimal⁴⁵.

It is difficult to determine if the pelagic larvae of *Nisusia* actively sought out *Wiwaxia* for settlement rather than fortuitously settling on *Wiwaxia* because the sclerite provided a suitable attachment surface. Over 200 specimens of *Nisusia* from the Burgess Shale Formation have been examined and only 18 individuals are preserved directly attached to a form of substrate. Of those 18 individuals, attachment to the sponge *Pirania* is the most common (67%, 12 of the 18 specimens) and three specimens are attached to *Hazelia*, *Chancelloria* and a tube belonging to *Selkirkia* (one specimen on each substrate type). The three *Nisusia* specimens attached to *Wiwaxia* (17% of total attached *Nisusia* specimens) represent the second most favoured substrate of the preserved specimens available. The most common brachiopod in the Burgess Shale Formation preserved attached to substrate, is the paterinate brachiopod *Micromitra*, where over 50 specimens have been recorded (Topper, unpublished). *Pirania* once again, is the most heavily favoured substrate with over 60% of *Micromitra* individuals attached to the sponge. Despite the abundance of *Micromitra* specimens, no individuals are attached to *Wiwaxia* sclerites, in fact *N. burgessensis* is the only species that is found to be directly attached to *Wiwaxia* out of the eight species of brachiopods documented from the Burgess Shale Formation.

In total, out of the 87 specimens of brachiopod (across all brachiopod species documented from the Burgess Shale) found to be directly attached to substrate, 57 specimens are attached to the sponge *Pirania*. Brachiopod specimens are also attached to a variety of disarticulated skeletal elements and to other brachiopod individuals, however *Wiwaxia* is the only mobile organism in the community that is preserved with brachiopods attached. Other organisms in the Burgess Shale community may have moved too rapidly or lived too high in the water column to allow settlement (free swimmers like the anomalocaridids), lacked appropriate sclerites to attach to (soft bodied organisms such as *Nectocaris* and *Odontogriphus*) or been too small to allow settlement and development (e.g. *Marrella* and *Scenella*). Admittedly this is but a few examples of the some 170 species documented from the Burgess Shale¹⁸, however it does accentuate the combination of characters possessed by *Wiwaxia* that would have allowed for a suitable settlement point for brachiopod larvae.

Conclusions. This unique association of brachiopods attaching onto *Wiwaxia* represents the oldest commensal relationship of sessile organisms fixed on a mobile organism in the fossil record, predating the previous oldest occurrence by approximately 200 million years¹⁴. This commensal and facultative relationship would have benefited the brachiopod in a variety of ways but would have been temporary and potentially limited by the timing of scleritome ecdysis. Possible advantages include; (1) obtaining an attachment on a hard substratum, (2) reaching an elevated position above the sediment surface and a variety of potential food supplies due to locomotion of the host (3) avoidance of biofouling and sedimentary disturbance (4) less competition by settlement on unoccupied space and (5) added protection. It would be hard to imagine given the small size of the brachiopods relative to the size of *Wiwaxia* that the symbiont negatively impacted the host, especially with *Wiwaxia* episodically shedding its sclerites and spines. This commensal association is unique for a species of brachiopod, fossil or living and suggests that complex forms of symbiotic relationships were already well established by the Cambrian period.

Methods

All specimens come from the Cambrian (Series 3, Stage 5) Burgess Shale Formation, Walcott Quarry Shale Member on Fossil Ridge, Yoho National Park, Canada. Two (USNM 83938 and 199960) specimens¹⁷ were collected in the original Walcott Quarry ("Phyllopod Bed") and one (ROM 61116) specimen from level -210 (approximately 210 centimeters below the base of the original Walcott Quarry



floor¹⁸). Specimens were photographed under normal and cross-polarized light and wet and dry conditions using an Olympus DSX 100 opto-digital microscope (USNM 83938 and 199960) and a Canon EOS5D digital SLR camera (ROM 61116). The studied specimens are housed at the Royal Ontario Museum (acronym: ROM) in Toronto, Canada (ROM 61116) and the National Museum of Natural History, Smithsonian Institution (acronym: USNM) in Washington D.C., USA (USNM 83938 and 199960).

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Author contributions

All authors participated in the discussion and analysis of these fossils. The material was made available by J.-B.C. and one specimen was photographed by J.-B.C. T.T. prepared the earlier manuscript and figures. All authors (T.T., L.H. and J.-B.C.) reviewed the manuscript and improved the final version.

Additional information

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