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Sclerites and possible mouthparts of *Wiwaxia* from the temperate palaeolatitudes of Colombia, South America

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Abstract

The problematic mollusc *Wiwaxia* is perhaps the most widely distributed non-mineralized Cambrian metazoan, but has only been reported from palaeotropical latitudes. Here we describe mid-Cambrian (Drumian, c. 504 Ma) sclerites and possible tooth arrays from the northern Llanos Basin, Colombia, recovered from drilled ditch cuttings by palynological processing – demonstrating that pristine material and low-manipulation processing are not essential to the recovery of Small Carbonaceous Fossils. This, the first report of *Wiwaxia* from South America, substantially expands *Wiwaxia*'s geographic range into the high palaeolatitudes.

Cambrian lagerstätten such as the Burgess Shale are renowned for their exceptionally preserved non-mineralized metazoans. Among the most iconic of these animals is *Wiwaxia*, a problematic slug-like mollusc covered in imbricating scales and spines. Originally interpreted as an annelid worm (Walcott 1911; Butterfield 1990), *Wiwaxia* is now recognized as a mollusc based on its radula, creeping ventral foot, and aculiferan-like scleritome (Conway Morris 1985; Smith 2012, 2014), although its precise position within total-group Mollusca remains unclear.

The anatomy of *Wiwaxia* has been reconstructed from articulated specimens, known from four Burgess Shale-type deposits in North America and China (Conway Morris 1985; Zhao *et al.* 1994; Yang *et al.* 2014; Conway Morris *et al.* 2015). The organism bears four sclerite morphologies (Conway Morris 1985): depending on their position, sclerites are asymmetric (dorsal), rounded and symmetrical (upper lateral and anterior), elongate and symmetrical (lower lateral) or sickle-shaped (ventral). Mature *Wiwaxia* specimens also exhibit elongate dorso-lateral spines.

Sclerites bear a variable number of ribs and express a thickened margin and a microvillar construction (Butterfield 1990; Smith 2014). They are constructed from a broad oval blade and narrow, hollow root; this distinctive outline means that isolated *Wiwaxia* sclerites are readily identified (Conway Morris 1985; Butterfield 1990).

Indeed, lone *Wiwaxia* sclerites have been reported on bedding-surfaces (Ivantsov *et al.* 2005; Fatka *et al.* 2011; Sun *et al.* 2014; Zhao *et al.* 2015), as phosphatic casts (Porter 2004), and – most importantly – as Small Carbonaceous Fossils (SCFs) (Butterfield & Harvey 2012; Harvey *et al.* 2012; Pedder 2012).

SCFs are robust carbon films, typically extracted from pristine siliciclastic mudstones and siltstones through the hand-picking of sieved macerates (Butterfield & Harvey 2012). Owing to their small size and taphonomic recalcitrance, they are widely distributed in space and time, and extend the record of *Wiwaxia* across the modern globe (Fig. 1). Nevertheless, *Wiwaxia* has not been reported outside the low palaeolatitudes – possibly reflecting the increased sampling effort applied to low-palaeolatitude continents. Our material from the Llanos Basin of Colombia, South America, was deposited at a latitude between 50–90° S (McKerrow *et al.* 1992; Torsvik & Cocks 2013), providing the first sampling of SCFs from high palaeolatitudes.

Materials and methods

Mudstone samples were obtained from washed and dried ditch cuttings from the Chigüiro-1 well, which was drilled in 1985 in the northern Llanos Basin, north-east Colombia. Ditch cuttings were produced by the rotational grinding action of the drill bit and brought to the surface by the conveyor-belt action of circulating drilling fluid. Samples were collected and bagged at regular intervals; each sample thus represents the depth of rock drilled since the last sample was taken. Over the *Wiwaxia*-yielding interval (8750–9710 ft), each sample typically corresponds to an interval of 20–30 ft (6–10 m) of rock; each quoted sample depth denotes the bottom of the sampled interval.

5–20 g of each sample was prepared either by standard palynological procedures – maceration by successive applications of HCl and HF, followed by heavy mineral separation in LST FastFloat™, sieving through a 10 µm mesh, and strew mounting (56 samples in total; 20 from the *Wiwaxia*-bearing interval, of which 12 yielded *Wiwaxia*) – or a low-manipulation procedure incorporating gentle dissolution in HF, sieving through a 63 µm gauze, and manual mounting onto glass slides by pipette (21 samples from the *Wiwaxia*-bearing interval, 4 yielding *Wiwaxia*).

Light micrographs from multiple focal planes were combined using *TuFuse* (tawbaware.com); backgrounds and extraneous objects have been removed. Measurements were recorded digitally from micrographs. SCFs are deposited at the Sedgwick Museum of Earth Sciences, Cambridge (CAMSM); comparative macrofossil material is accessioned at the Smithsonian Institute National Museum of Natural History (NMNH) and the Royal Ontario Museum (ROM).

Geological setting

Co-occurring acritarchs (in particular *Retisphaeridium dichamerum, Eliasum llaniscum, Adara matutina* and *Cristallinium cambriense*), together with the first downhole occurrence of the acritarch *Vulcanisphaera lanugo* in the interval below the last persistent downhole occurrence of *Wiwaxia* sclerites, confine the range of *Wiwaxia* sclerites to within the *Rugasphaera terranovana* acritarch zone (Martin & Dean 1988), corresponding to the *Ptychagnostus atavus / Tomagnostus fissus* trilobite zone and an approximate age of 504 Ma.

The frequent-to-superabundant occurrences of *Siphonophycus* spp. (stromatolite filaments) throughout the *Wiwaxia*-bearing interval indicate a shallow water depositional environment (Butterfield & Chandler 1992), whereas the regional geology indicates a distal shelf setting (Torsvik & Cocks 2013).

Sclerites

Twenty-five sclerites were recovered: eighteen through palynological preparations and seven through manual extraction, in approximate proportion to the amount of sample processed by each method. Sclerites ranged from 100–500 µm in maximum dimension; neither the typical size nor the sclerite integrity exhibited meaningful variation between the two extraction methods.

Sclerites could be identified as *Wiwaxia* scales based on their construction from a broad, ribbed blade and hollow root, and by the presence of microvillar chambers (Fig. 2). Sclerites can further be designated as: ventro-lateral (two, Fig. 2a, e), based on a siculate habit; lower lateral (five, Fig. 2b, f), based on an elongate aspect and symmetrical shape; upper lateral (four, Fig. 2c, g), based on their rounded profile and 1:1 height:width ratio; and dorsal (four, Fig. 2d, h), based on their marked asymmetry. Ten incomplete sclerites are insufficiently preserved for a confident assignation. Overall, the sclerites' shape and dimensions correspond to those of articulated *Wiwaxia corrugata* juveniles (Fig. 2k), though the sample size is insufficient to attempt species-level taxonomy. Three specimens displayed superficial pustules with an irregular appearance and distribution that conceivably correspond to surface ornament (Fig. 2i–j).

Mouthparts

Sclerites are not the only tough component of *Wiwaxia*: its mouthparts also have a robust carbonaceous construction and could in principle be preserved as SCFs (Smith 2012). The mouthparts were originally understood to represent a series of two to three denticulate bars (Conway Morris 1985), and on this basis various SCFs from the Mount Cap formation (mid-Cambrian of Canada) were compared with the rows of teeth in *Wiwaxia* (Harvey & Butterfield 2011). However, a more detailed morphological interpretation demonstrates that each 'bar' in fact represents an array of around two dozen shoehorn-shaped teeth arranged symmetrically about a triangular central tooth (Smith 2012), undermining the comparison with the Mount Cap SCFs. Despite the robust nature of the teeth, therefore, no convincing representatives are available from the SCF record.

Our palynological samples contained four SCF elements that correspond to the morphology of the *Wiwaxia* radula (Fig. 3). These comprise 100–250 μm long series of four to six teeth – equivalent in size to the mouthparts of the smallest articulated *Wiwaxia* specimens (Smith 2012; Zhang *et al.* forthcoming). Each tooth has a narrow root that tapers into a broad, flat-ended scoop. Teeth are attached by a basal membrane (Fig. 3). In the context of the co-occurring *Wiwaxia* sclerites and the absence of other metazoan components, the tooth rows' distinctive morphology identifies them as candidate *Wiwaxia* mouthparts.

Discussion

Wiwaxia-like mouthparts.—*Wiwaxia*-like mouthparts have not been convincingly reported as SCFs – despite the robust construction indicated by the thickness of the carbon films and (unlike their co-occurring scales) their association with traces of phosphorous (Smith 2012). Phosphorous seemingly typifies the most recalcitrant components of Burgess Shale-type organisms; it is also associated with the tough dorsal armature of *Hallucigenia* and the most robust teeth in *Ottoia*, both of which occur as SCFs (Caron *et al.* 2013; Smith *et al.* in press).

The recovery of probable *Wiwaxia* mouthparts from the Llanos basin confirms this taphonomic potential. The rarity of mouthpart SCFs relative to sclerites may partly reflect the less distinctive morphology of the tooth rows, but it is also likely that sclerites – which are periodically shed into the water column (Smith 2014) – were originally more abundant than mouthparts, which were swallowed when they were moulted (Smith 2014) and presumably disarticulate during digestion.

Distribution of Wiwaxia.—Although early reconstructions placed Colombia at equatorial palaeolatitudes (Scotese & McKerrow 1990), current palaeogeographic maps indicate a location in a cooler climate belt, whether in a polar (McKerrow *et al.* 1992; Scotese *et al.* 1999; Meert & Lieberman 2004) or temperate (Torsvik & Cocks 2013) setting. Our report of *Wiwaxia* from South America thus represents the first data on its distribution at higher latitudes. The equatorial distribution suggested by previous occurrences of *Wiwaxia* (Fig. 1) thus reflects an acquisition bias – higher latitudes are only represented by the poorly sampled terranes of Africa, Antarctica and South America. As such, *Wiwaxia* seems to represent an environmental generalist, able to colonize habitats regardless of ecological, geographical or climatic constraints.

Implications for microfossil recovery.—SCFs are generally recovered through the manual manipulation of pristine mudstones, reflecting the belief that SCFs are too large or too delicate for recovery by traditional palynological techniques (Butterfield &

Harvey 2012). There is only one report of SCF recovery through palynological preparation: copepod mandibles and *Wiwaxia* sclerite fragments from the Cambrian Nolichucky Shale (Pedder 2012; Harvey & Pedder 2013). These specimens are uniformly smaller than 80 µm, around the minimum size that can be recovered by the manual manipulation approach. Corresponding copepod mandibles recovered from the Deadwood Formation by manual manipulation occupy the 100–500 µm size bracket; this seems to suggest that elements in this larger size range disintegrate during centrifugation, prohibiting their recovery by the palynological technique (Harvey & Pedder 2013).

Our study, however, demonstrates that certain SCFs – *Wiwaxia* sclerites and mouthparts – are robust to palynological processing, even in the 100–500 µm size range. If this is representative of SCFs more generally, processing method alone cannot account for the scarcity of recognizable metazoan microfossils in palynological preparations.

Moreover, this report represents the first recovery of SCFs from washed and dried ditch cuttings, a sampling and preparation method that substantially disaggregates the rock; conventionally, samples from outcrop or pristine cores are preferred. The unrecognized potential of low-grade but abundant ditch cuttings for SCF recovery opens the possibility of a systematic high-throughput sampling of Cambrian wellbore material.

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Figure 1. Stratigraphic and geographical distribution of *Wiwaxia*. Silhouettes denote whether sites preserve articulated specimens or isolated sclerites. 'Wiwaxiid' material from Sinsk (Ivantsov *et al.* 2005) has not been figured or described and its identity is therefore uncertain. A reported occurrence in South Australia (Emu Bay Shale, Porter 2004) is based on unpublished material and is thus not depicted. The palaeogeographic reconstruction is based on true polar wander data (after Torsvik & Cocks 2013). Colour online.

Figure 2. Sclerites of *Wiwaxia* from the Llanos Basin, Colombia. (a–d), sclerites recovered by manual extraction: (a), CAMSX ####1a (−9130'), ventro-lateral sclerite; (b), CAMSX ####2a (−9050'), lower lateral sclerite; (c), CAMSX ####3a (−9100'), upper lateral sclerite; (d) CAMSX ####3b (−9100'), dorsal sclerite. (e–i), sclerites recovered by palynological processing: (e), CAMSX ####4a (−8750'), ventro-lateral sclerite; (f), CAMSX ####5a (−9810'), lower lateral sclerite; (g), CAMSX ####6a (−9710'), upper lateral or anterior sclerite; (h), CAMSX ####7a (−9650'), dorsal sclerite; (i), CAMSX ####4a (−8750'), enlargement of boxed area in e, demonstrating oval pustules. (j), CAMSX ####2b (−9050'), upper lateral sclerite recovered by

manual extraction; enlargement of boxed area demonstrates microvillar construction and superficial pustules. (k), NMNH 229901, showing position of sclerites on articulated juvenile of *Wiwaxia corrugata*. Scale bars = 100 µm except panels marked +, 70 µm. Colour online.

Figure 3. Possible *Wiwaxia* tooth rows from the Llanos Basin, Colombia, recovered through palynological processing; (a), CAMSX ####10a (−9140'); (b), CAMSX ####8a (−9010'); (c), CAMSX ####9a (−8990'); (d), CAMSX ####11a (−8440'). Colour online.

References

Butterfield, N.J. 1990: A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. *Paleobiology 16*, 287–303.

Butterfield, N.J. and Chandler, F.W. 1992: Palaeoenvironmental distribution of Proterozoic microfossils, with an example from the Agu Bay Formation, Baffin Island. *Palaeontology 35*, 943–957.

Butterfield, N.J. and Harvey, T.H.P. 2012: Small Carbonaceous Fossils (SCFs): a new measure of early Paleozoic paleobiology. *Geology 40*, 71–74.

Caron, J.-B., Smith, M.R. and Harvey, T.H.P. 2013: Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians. *Proceedings of the Royal Society B: Biological Sciences 280*, 20131613.

Conway Morris, S. 1985: The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada. *Philosophical Transactions of the Royal Society of London B: Biological Sciences 307*, 507–582.

Conway Morris, S., Selden, P.A., Gunther, G., Jamison, P.M. and Robison, R.A. 2015: New records of Burgess Shale-type taxa from the middle Cambrian of Utah. *Journal of Paleontology*, in press.

Fatka, O., Kraft, P. and Szabad, M. 2011: Shallow-water occurrence of *Wiwaxia* in the Middle Cambrian of the Barrandian area (Czech Republic). *Acta Palaeontologica Polonica 56*, 871–875.

Harvey, T.H.P. and Butterfield, N.J. 2011: Macro- and microfossils of the Mount Cap Formation (Early and Middle Cambrian, Northwest Territories). *Geoscience Canada 38*, 165–173.

Harvey, T.H.P. and Pedder, B.E. 2013: Copepod mandible palynomorphs from the Nolichucky Shale (Cambrian, Tennessee): implications for the taphonomy and recovery of Small Carbonaceous Fossils. *Palaios 28*, 278–284.

Harvey, T.H.P., Ortega-Hernández, J., Lin, J.-P., Zhao, Y.-L. and Butterfield, N.J. 2012: Burgess Shale-type microfossils from the middle Cambrian Kaili Formation, Guizhou Province, China. *Acta Palaeontologica Polonica 57*, 423–436.

Ivantsov, A.Yu., Zhuravlev, A.Yu., Leguta, A.V., Krassilov, V.A., Melnikova, L.M. and Ushatinskaya, G.T. 2005: Palaeoecology of the Early Cambrian Sinsk biota from the Siberian Platform. *Palaeogeography, Palaeoclimatology, Palaeoecology 220*, 69–88.

Martin, F. and Dean, W.T. 1988: Middle and Upper Cambrian acritarch and trilobite zonation at Manuels River and Random Island, eastern Newfoundland. *Geological Survey of Canada, Ottawa, Bulletins 381*, 1–91.

McKerrow, W.S., Scotese, C.R. and Brasier, M.D. 1992: Early Cambrian continental reconstructions. *Journal of the Geological Society 149*, 599–606.

Meert, J.G. and Lieberman, B.S. 2004: A palaeomagnetic and palaeobiogeographical perspective on latest Neoproterozoic and early Cambrian tectonic events. *Journal of the Geological Society 161*, 477–487.

Pedder, B.E. 2012: The palynology and stratigraphy of the Cambrian Nolichucky Shale and associated formations at Thorn Hill, Tennessee, USA. University of Sheffield, 231 pp.

Porter, S.M. 2004: Halkieriids in Middle Cambrian phosphatic limestones from Australia. *Journal of Paleontology 78*, 574–590.

Scotese, C.R., Boucot, A.J. and McKerrow, W.S. 1999: Gondwanan palaeogeography and palaeoclimatology. *Journal of African Earth Sciences 28*, 98–114.

Scotese, C.R. and McKerrow, W.S. 1990: Revised world maps and introduction. *In* McKerrow, W.S., Scotese, C.R. (eds.), *Paleozoic Paleogeography and Biogeography,* 1–21. Geological Society of London, Memoir 12.

Smith, M.R. 2012: Mouthparts of the Burgess Shale fossils *Odontogriphus* and *Wiwaxia*: implications for the ancestral molluscan radula. *Proceedings of the Royal Society B: Biological Sciences 279*, 4287–4295.

Smith, M.R. 2014: Ontogeny, morphology and taxonomy of the soft-bodied Cambrian 'mollusc' *Wiwaxia*. *Palaeontology 57*, 215–229.

Smith, M.R., Harvey, T.H.P. and Butterfield, N.J. 2015: The macro- and microfossil record of the middle Cambrian priapulid *Ottoia*. *Palaeontology,* in press.

Sun, H.-J., Zhao, Y.-L., Peng, J. and Yang, Y.-N. 2014: New *Wiwaxia* material from the Tsinghsutung Formation (Cambrian Series 2) of Eastern Guizhou, China. *Geological Magazine 151*, 339–348.

Torsvik, T.H. and Cocks, L.R.M. 2013: Gondwana from top to base in space and time. *Gondwana Research 24*, 999–1030.

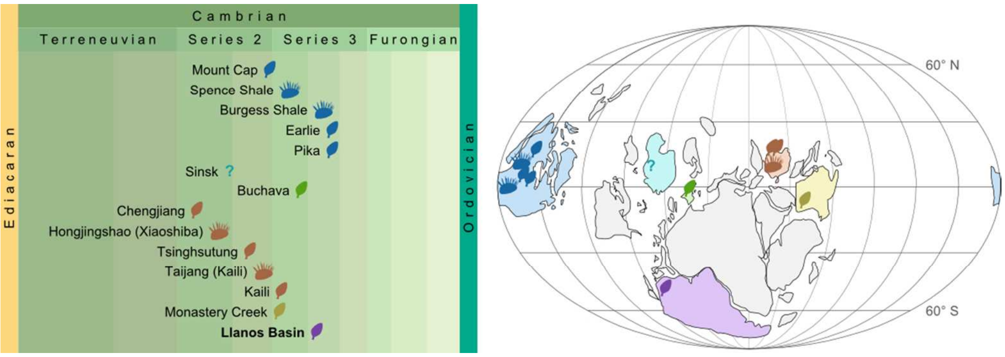
Walcott, C.D. 1911: Cambrian Geology and Paleontology II, no. 5. Middle Cambrian annelids. *Smithsonian Miscellaneous Collections 57*, 109–144.

Yang, J., Smith, M.R., Lan, T., Hou, J. and Zhang, X. 2014: Articulated *Wiwaxia* from the Cambrian Stage 3 Xiaoshiba Lagerstätte. *Scientific Reports 4*, 4643.

Zhang, Z., Smith, M.R. and Shu, D. in review: New reconstruction of the *Wiwaxia* scleritome, with data from Chengjiang juveniles. *Scientific Reports*.

Zhao, F., Smith, M.R., Yin, Z.-J., Zeng, H., Hu, S.-X., Li, G.-X. and Zhu, M.-Y. 2015: First report of *Wiwaxia* from the Cambrian Chengjiang Lagerstätte. *Geological Magazine 152*, 378–382.

Zhao, Y.-L., Qian, Y. and Li, X.S. 1994: *Wiwaxia* from Early-Middle Cambrian Kaili Formation in Taijiang, Guizhou. *Acta Palaeontologica Sinica 33*, 359–366.



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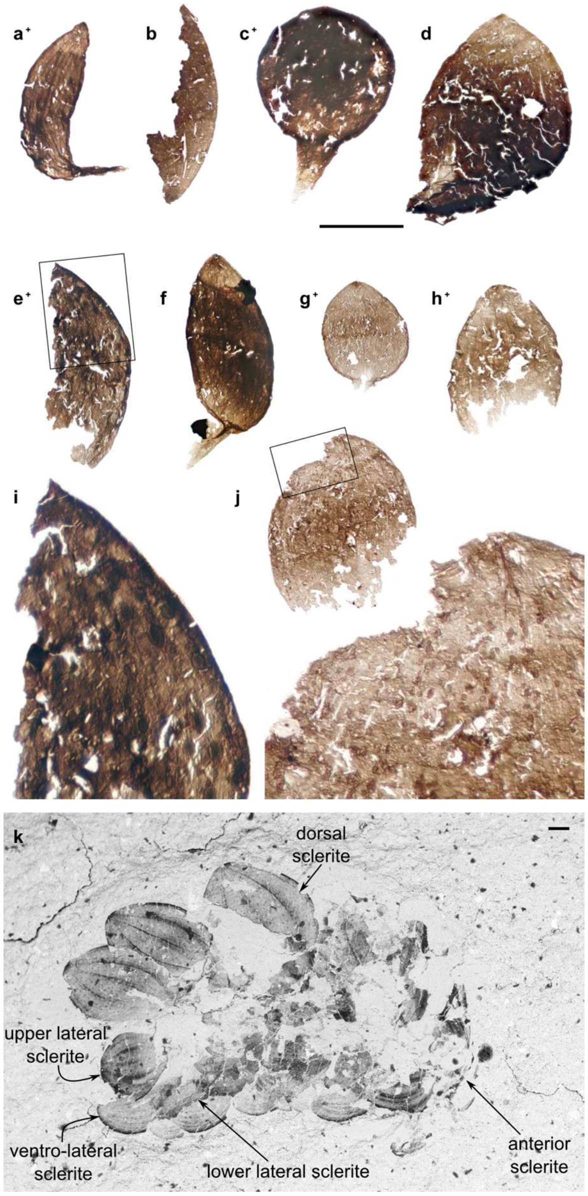

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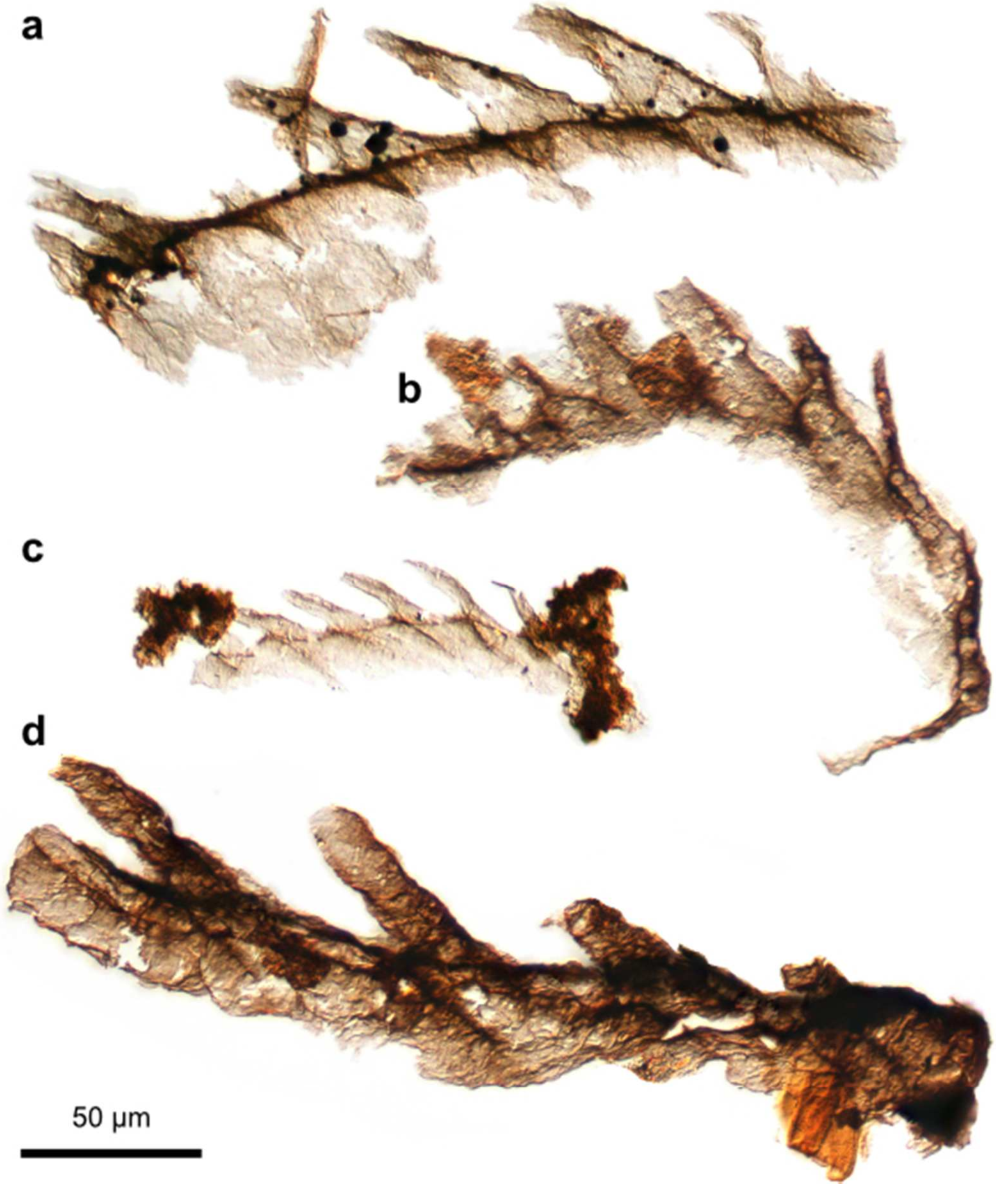

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