On the margins: exceptionally preserved small carbonaceous fossils (SCFs) from Silurian marginal marine strata of southern China

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Small carbonaceous fossils (SCFs) have recently emerged as a novel means to track the evolution of non-mineralized animals throughout the early Palaeozoic. Currently however, records are largely concentrated in Cambrian-age strata, and little is known of the post-Cambrian extent of this style of preservation. Here, a previously unknown variety of SCFs are reported from shallow marine sediments of the Silurian (Ludlow to Pridoli) age Xiaoxi Formation, revealing exceptionally preserved microscopic anatomical remains of animals in what is otherwise a relatively unfossiliferous package of clastic rocks. Recovered SCFs encompass cuticular structures derived from eurypterid arthropods, including exquisitely preserved respiratory organs (kiemenplatten and lamellate book gills), sensory setae, fragments from other euarthropods, jaws of eunicid polychaete annelids (scolecodonts), a range of ornamented cuticles and spines of unknown affinity, and delicate protistan remains assigned to the possible euglenid *Moyeria*. Discovery of a range of animal-derived SCFs in the Xiaoxi Formation demonstrates that this style of fossil extraction and processing might be successfully developed and expanded into comparable upper Palaeozoic strata and deposits where the biota is similarly otherwise known only via trace fossil evidence. A concerted effort to expand this record has the potential to enrich our knowledge of otherwise poorly documented non-mineralized fossil taxa in shallow marine settings throughout the Palaeozoic.

Key words: Arthropoda, Eurypterida, Euglenida, *Moyeria*, scolecodonts, taphonomy, exceptional preservation, small carbonaceous fossils, Silurian, China.

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Introduction

Outside Lagerstätten, the bulk of the marine animal fossil record comes from conventional "shelly" fossils representing biomineralized organisms, or trace fossils which record animal behavior imparted in sediments. A third and increasingly explored source of information are so-called "small carbonaceous fossils" (SCFs) (Butterfield and Harvey 2012). These are the organically-preserved fragmentary remains of animals and other organisms, that can be extracted from siliciclastic sediments using gentle palynological processing. An advantage of SCFs is their capacity to reveal non-biomineralized elements of the fauna that are otherwise severely underrepresented in the wider fossil record.

To date, the focus of SCF research has primarily centred on tracking the earliest phases of animal evolution, and has therefore largely seen the targeting of Cambrian age sediments (ca. 538.8–458 Ma) or underlying Ediacaran strata (Slater and Bohlin 2022). A handful of studies have

nevertheless successfully employed SCF-extraction techniques in younger Phanerozoic strata, notably from the Ordovician (e.g., Nowak et al. 2018; and more recently, exceptionally diverse SCF assemblages have been reported from the Ordovician (Tremadocian and Darriwilian) of North America; Mussini and Butterfield 2025), yet it remains unclear how stratigraphically extensive SCF preservation is, particularly in shallow-water nearshore depositional environments. Although organic fragments sourced from animals have long been noted in palynological studies of later Phanerozoic strata, for the most part these entail fortuitous and scattered recovery among preparations targeting more conventional microfossil groups (e.g., spores, pollen, dinoflagellates).

To test the stratigraphic continuity of this preservation style in younger Palaeozoic strata, we investigated SCF preservation in a late Silurian shallow-water deposit from southern China, the Xiaoxi Formation. To date, palynomorphs reported from the Xiaoxi assemblage include cuticle-like sheets possibly derived from land plants (Wang et al. 2023), smooth-walled tubes (*Laevitubulus tenuis* Burgess & Edwards, 1991), acritarchs (e.g., *Veryhachium*, *Micrhystridium*, and *Domasia*) (Wang and Zhang 1985; Wang et al. 2010, 2011), and biostratigraphically informative chitinozoans (e.g., *Eisenackitina rimosa* Umnova, 1976) (Geng et al. 1997). Processing here has further revealed a diverse assortment of exceptionally detailed fragments of non-mineralized metazoans. Significantly, this points to persistent SCF preservation throughout equivalent Palaeozoic strata, with important implications for enhancing our understanding of animal evolution in shallow marine settings.

Institutional abbreviations.— NIGPAS, CAS, Experimental Technologies Center of Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Geological setting

The Xiaoxi Formation (Ludlow–Pridoli, Silurian) is a ca. 3–360m-thick succession of clastic rocks, in unconformable contact with both the underlying Xiushan or Huixingshao formations (Telychian, Silurian) and overlying Yuntaiguan (Middle Devonian) or Liangshan (Lower Permian) formations (Wang et al. 2023). Deposited within the interior of the Yangtze Block, the Xiaoxi Formation has been well recorded from numerous well exposed outcrops in Guizhou, Chongqing, Hu'nan, Hubei, and Anhui provinces of southern China (Fig. 1). This formation mainly consists of yellow-green thinly layered silty shales with greyish-green fine-grained sandstone interlayers. Prominent sedimentary structures include ripple marks, ripple cross-lamination, hummocky cross-stratification and trace fossils, which occur throughout the formation (Wang et al. 2010; Zhang et al. 2024). The ichnofossils are diverse, and several taxa have been recognized, such as *Cruziana*, *Dimorphichnus*, *Lockeia*, *Phycodes*, *Planolites*, *Ptychoplasma*, *Rusophycus*, and *Thalassinoides* (Wang et al. 2024; Zhang et al. 2024). Among them, the most abundant is *Thalassinoides*, of-

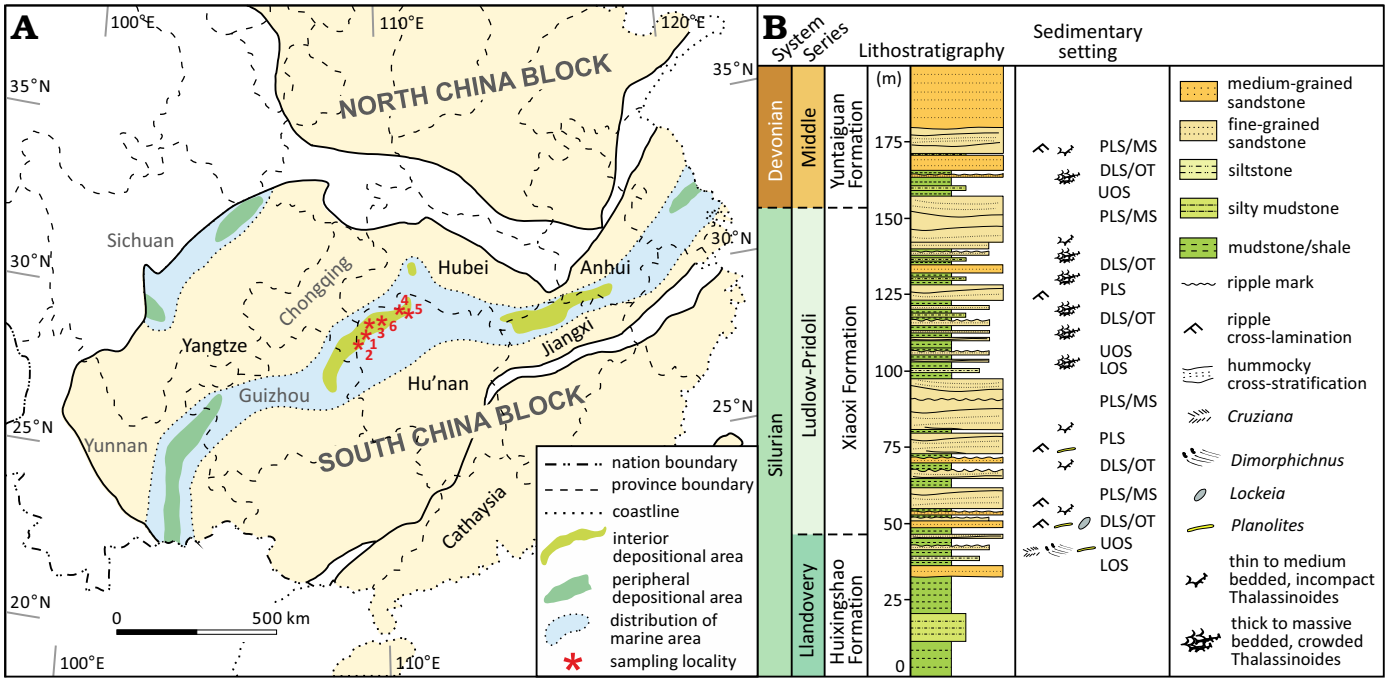

Fig. 1. Geological information. **A**. Distribution of the upper Silurian and sampling localities (after Wang et al. 2023). Outcrop sections: 1, Yayu; 2, Kapeng Reservoir; 3, Malao; 4, Shizinao; 5, Fengheshan; 6, Tongchaku. The light-yellow shaded areas denote the major tectonic blocks. **B**. Stratigraphic division, lithology, and sedimentary setting of Xiaoxi Formation at type section Yutan Reservoir (after Zhang et al. 2024). DLS, distal lower shoreface; LOS, lower offshore; MS, middle shoreface; OT, offshore transition; PLS, proximal lower shoreface; UOS, upper offshore.

ten ascribed to euarthropods such as decapod crustaceans (Knaust 2021; Zhang et al. 2024). Some eurypterid body fossils, such as *Adelophthalmus* cf. *mansfieldi* Hall, 1877, *Parahughmilleria* sp., *Hughmilleria viriosa* Lei, 2022, and *Erettopterus* sp., have also been reported from the Xiaoxi Formation (Lei 2022), along with occasional vertebrate fish remains (e.g., galeaspids belonging to the genus *Dunyu*) (Li et al. 2024). Recent studies on trace fossils and sedimentary fabrics of the Xiaoxi Formation have revealed a sequence from the lower offshore to middle shoreface, associated with storm activity (Zhang et al. 2024). In addition, previous palaeobotanical and palynological studies have produced abundant nematophyte body fossils (*Prototaxites*? sp.), cuticle-like sheets (resembling categories 1–3 in the scheme of Edwards 1982), and tubular palynomorphs that can be assigned to the *Laevitubulus–Porcatitubulus–Constrictitubulus* association (Wang et al. 2010, 2011, 2017, 2023), indicating significant terrestrial input. Collectively, the Xiaoxi Formation represents deposits formed in shallow marine settings above the storm wave base, with inputs of terrestrial organic matter (Wang et al. 2011, 2023). A late Silurian age for the Xiaoxi Formation has previously been suggested based on its relationship to adjacent, overlying and underlying strata, and on biostratigraphic grounds (Wang et al. 2010). The corresponding adjacent Chejiaba Formation has notably been constrained to a late Ludlow age using conodonts (e.g., *Ozarkodina snajdri* Walliser, 1964, and *Ozarkodina crispa* Walliser, 1964) (Tang et al. 2010). In particular, chitinozoans reported from the Xiaoxi Formation (e.g., *Eisenackitina rimosa*) are strongly suggestive of a late Silurian age (Geng et al. 1997), as are reports of vertebrate fish assignable to late Silurian taxa from the Galeaspida (e.g., Li et al. 2024), along with the presence of distinctive cuticle-like sheets recovered among the palynomorph assemblage that are elsewhere known only from strata of late Ludlow to early Pridoli age (Wang et al. 2010, 2011, 2017).

Material and methods

Ten samples of silty shales collected from the upper Silurian Xiaoxi Formation at six sections in southern China (Fig. 1; sample details in SOM: table S1, Supplementary Online Material available at http://app.pan.pl/SOM/app71-Wang_etal_SOM.pdf) were prepared using HCl-HF-HCl acid maceration (Wood et al. 1996) at the microfossil lab of NIGPAS, CAS. Microfossils were mounted in glycerol jelly and sealed with paraffin wax for examination with an Olympus BX53 light microscope. Figured specimens are located on slides using England Finder (EF) Coordinates and stored at NIGPAS, CAS. The slide numbers and EF coordinates for each of the specimens are provided in SOM: table S2 (material mounted on 15 slides, with repository numbers: SZXL-1-1–5, 45, 76; SZXL-2-1, 2; HBKP-3-1–3; HBKP-10-1, 2; LSLM-S-3).

Results

Extraction recovered hundreds of well-preserved organic microfossils. Among the recovered microfossils were previously detected non-animal cuticle-like sheets, tubular palynomorphs (e.g., *Laevitubulus*), and acritarchs, with newly detected animal-derived components being present as a comparatively less numerous subset of the assemblage. Also detected in this assemblage were dispersed plant spores, for which a specialised investigation is underway. The focus here is on metazoan remains, alongside possible protistan fossils, delineated into the following categories.

Kiemenplatten.—Among the recovered SCFs are a distinct set of isolated cuticular fragments sharing a characteristic hexagonal microstructure (Fig. 2A–G, O). In specimens with intact tips, these cuticles terminate in a sclerotized and optically-dense spine tapering to an acute point (10–27 μm length, $\bar{x}$ = 15.8 μm, n = 5; 3.3–14.6 μm basal width, $\bar{x}$ = 6.6 μm, n = 5: Fig. 2A–D). Examination of the margins (Fig. 2A, D, G) reveals the hexagonal ornament is composed of triradial projections or columns that interlock to form the characteristic hexagonal pattern (3.5–13 μm in diameter, $\bar{x}$ = 7.1 μm, n = 69).

These distinctive SCFs are identifiable as eurypterid respiratory organs known as "kiemenplatten" (Manning and Dunlop 1995). Such structures described as "gill-tracts" or "spinules" are found in situ on eurypterid macrofossils (Wills 1965), and have since been identified among acid-isolated fragments from several Palaeozoic deposits including the Ludlow, upper Silurian of Canada (McGregor and Narbonne 1978), Pridoli, upper Silurian of Shropshire, UK (Manning and Dunlop 1995), Lower Devonian of Ukraine (Filipiak et al. 2012) and Poland (Filipiak and Zatoń 2011; Filipiak et al. 2022; Kondas et al. 2025). Eurypterid kiemenplatten have also recently been detected among SCFs from the lower Osterberg biota of North Dakota (Mussini and Butterfield 2025) alongside a range of eurypterid cuticular fragments, extending the record of this clade back to the Tremadocian within the lowermost Ordovician (though fragmentary bedding-plane eurypterid remains have now also recently been reported among bedding-plane macrofossils from the upper Tremadocian, Ordovician, Fezouata Lagerstätten of Morocco; Van Roy et al. 2025).

Lamellate book gills?—Several recovered SCFs occur as bi-layered sheets bearing diamond-shaped reticulation (2.2–6.8 μm in diameter, $\bar{x}$ = 4.6 μm, n = 31; Fig. 2H–J). Ribs forming the reticulation are 0.9–3.6 μm wide ($\bar{x}$ = 1.5 μm, n = 29) and are developed on a thin underlying cuticle (clearest in Fig. 2H). One relatively large specimen suggests these sheets were broadly rectangular in overall shape (Fig. 2J).

This morphology is reminiscent of lamellate book gills described from the Pridoli, upper Silurian of UK (Manning and Dunlop 1995), though in the latter ribs are near-parallel and irregularly connected by narrow cross-bars. Such book gills are also reported from articulated eurypterid macrofossils (Braddy et al. 1999).

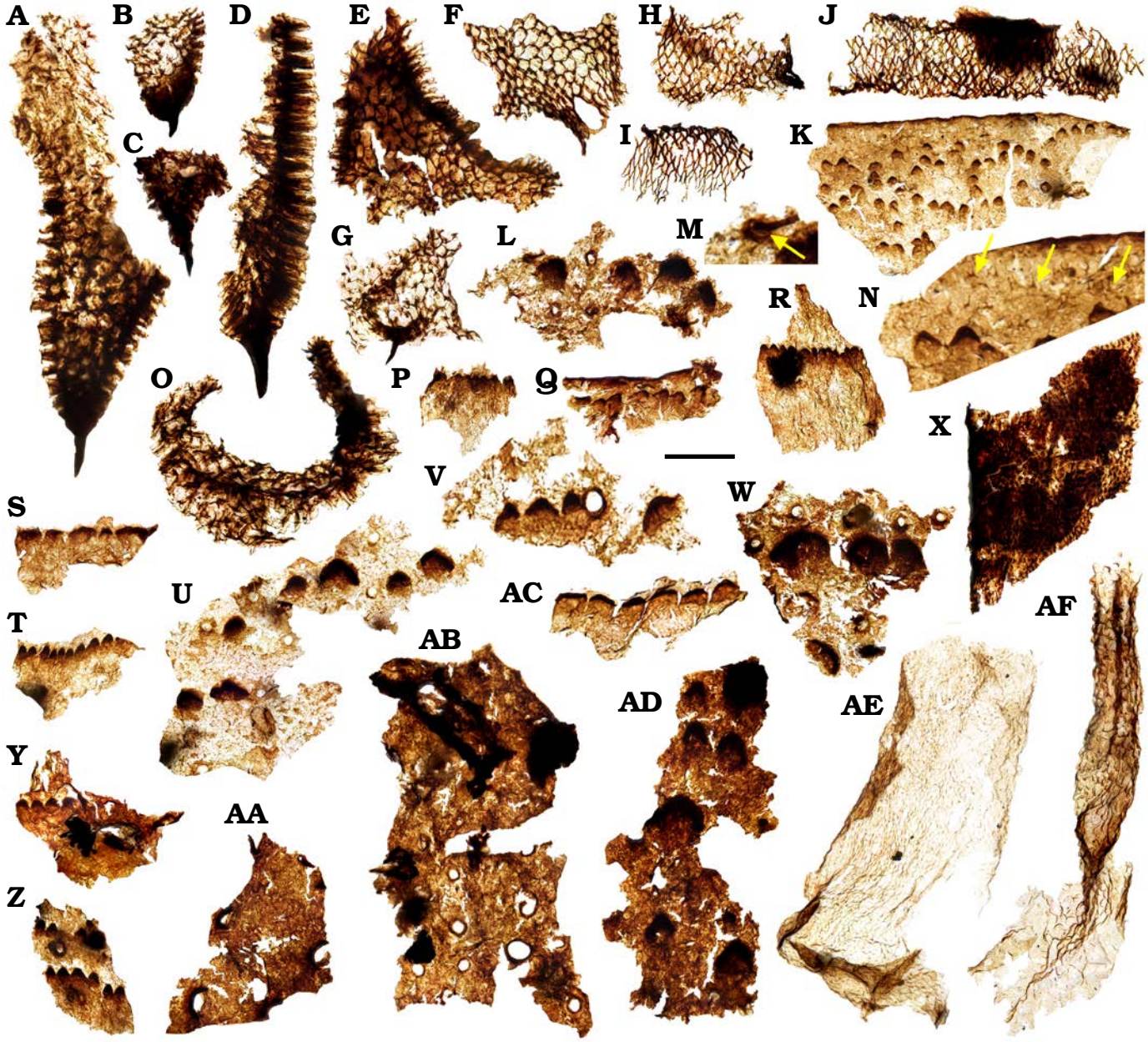

Fig. 2. SCFs from the Silurian Xiaoxi Formation of Hu'nan, southern China. **A**–**G**, **O**. Kiemenplatten (eurypterid respiratory organs). **H**–**J**. Lamellate book gills? **K**–**N**, **P**–**AF**. Ornamented cuticles. M, close up of L, showing truncated seta attached to circular perforation (yellow arrow); N close up of K, detailing minute cuticular spines (yellow arrows). Scale bar: A–L, O–AF, 50 μm; M, N, 20 μm. Repository numbers provided in SOM: table 2.

Ornamented cuticles.—Xiaoxi SCFs also include ornamented cuticles covered with short blunt cones (5–33 μm at basal width, $\bar{x}$ = 12 μm, n = 58; Fig. 2K–N, P–W, Y, Z, AD) or crescent-shaped structures (2–7 μm at basal width, $\bar{x}$ = 4 μm, n = 37; Fig. 2X, AE, AF).

Comparisons can be drawn with similarly ornamented eurypterid and/or scorpion cuticle reported among acid-macerals elsewhere, for instance the Lower Devonian of Poland (Filipiak et al. 2022) and Egypt (Makled et al. 2021). The short cones covering the Xiaoxi Formation specimens are also reminiscent of those adorning the surface of known eurypterid taxa, for example, from the mesosomal and metasomal tergites of the Ordovician *Pentecopterus decorahensis* Lamsdell et al., 2015, of the Winneshiek Lagerstätten (Iowa), which exhibits similar rows of sub-rounded scale ornamentation (Lamsdell et al. 2015).

A subset of these SCF cuticles bear distinct elliptical-circular perforations or lacunae (4.5–16 μm diameter, $\bar{x}$ = 7 μm, n = 16; Fig. 2L, U, W, AA, prominent in Fig. 2AB). Such cuticles are known from several Devonian deposits, and typically ascribed to eurypterids (Filipiak and Zatoń 2011; Filipiak et al. 2012, 2022; Makled et al. 2021).

Setae-bearing cuticles.—Some cuticular SCFs in the Xiaoxi assemblage can be discerned by a densely-distributed covering of fine setae (5.5–14.6 μm length, $\bar{x}$ = 10.2 μm, n = 23;

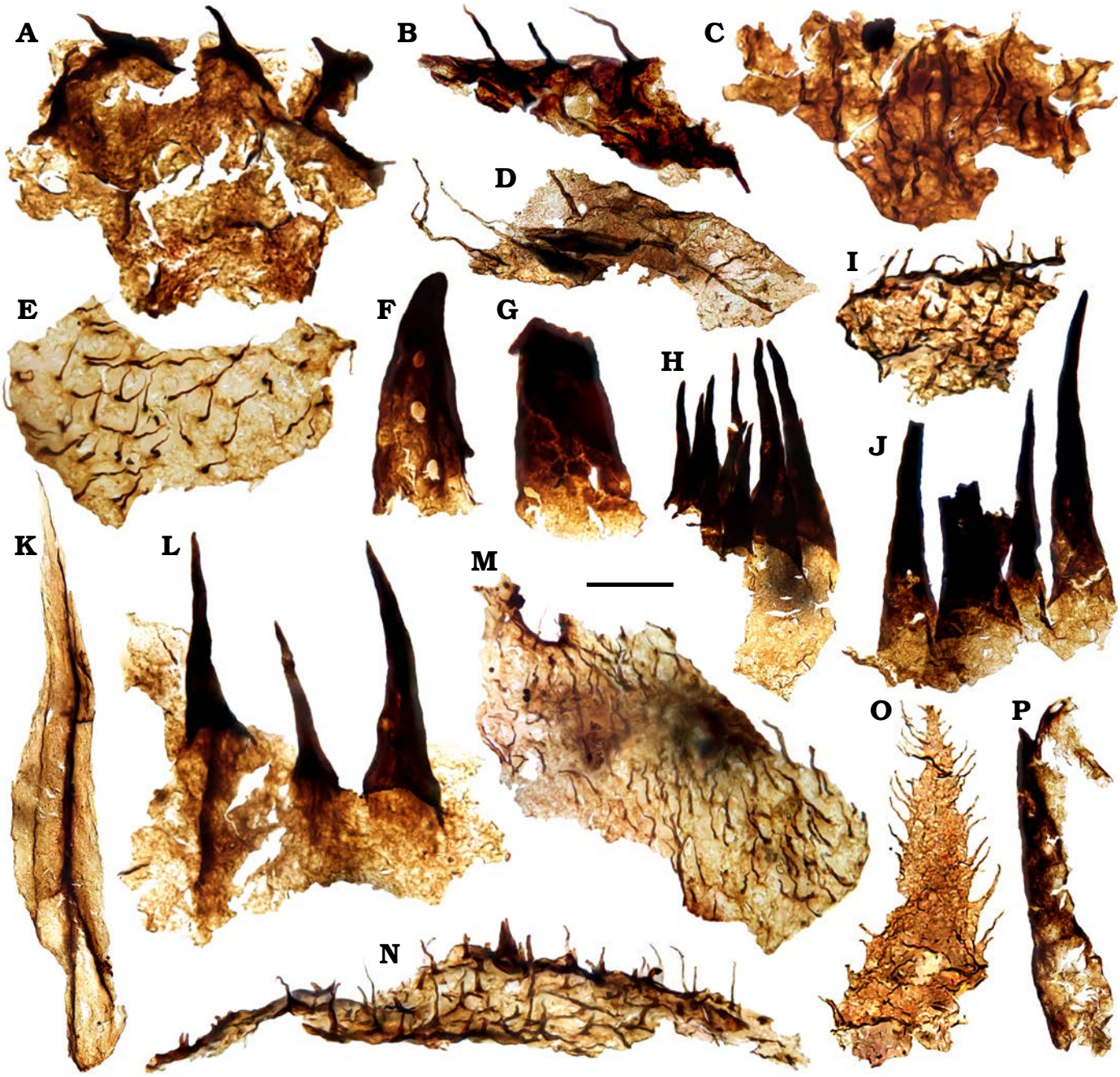

Fig. 3. SCFs from the Silurian Xiaoxi Formation of Hu'nan, southern China. **A**, **H**, **J**, **L**. Sclerotized spines. **B**–**E**, **I**, **M**, **N**. Setae-bearing cuticles. **F**, **G**, **K**. Spines. **O**. Fragment with symmetrical marginal spines. **P**. Unidentified fragment. Scale bar B, D, H, J, K, P 40 μm; A, C, E–G, I, L–O 20 μm. Repository numbers provided in SOM: table 2.

0.75–3.1 μm basal width, $\bar{x}$ = 1.4 μm, n = 39; Fig. 3C, E, I, M, N).

Cuticles bearing similar fine setae are figured among younger acid-isolated fragments from the Emsian, lower Devonian of Poland (Filipiak and Zatoń 2011; Filipiak et al. 2022) and the upper Devonian Ora Formation of Iraq, where they are attributed to eurypterids, though the latter possess somewhat stouter setae (Makled et al. 2025).

Sclerotized spines.—Among the various spinose SCFs detected here are a subset of robust sclerotized spines with an ovoid basal opening (39–141 μm length, $\bar{x}$ = 81 μm, n = 10; 10–38 μm basal width, $\bar{x}$ = 20.4 μm, n = 9; Fig. 3H, J, L) found in clusters of 3–6 individual spines connected by a basal cuticle. Adjacent spines tend to increase in length sequentially in one direction (Fig. 3H).

Comparable SCF sclerotized spines have been reported from younger Palaeozoic deposits, including the Emsian, Lower Devonian of Poland (Filipiak et al. 2022; Filipiak and Zatoń 2011), and Lower Devonian of Podolia, Ukraine (Filipiak et al. 2012). Elongate spines of a similar construction have also been detected in the Lower Devonian of Egypt

Fig. 4. SCFs likely representing arthropod sensory setae from the Silurian Xiaoxi Formation of Hu'nan, southern China. Scale bars: D, K, L, 30 μm; A, I, M, 25 μm; B, C, E–H, J, O, P, 20 μm; N, 10 μm. Repository numbers provided in SOM: table 2.

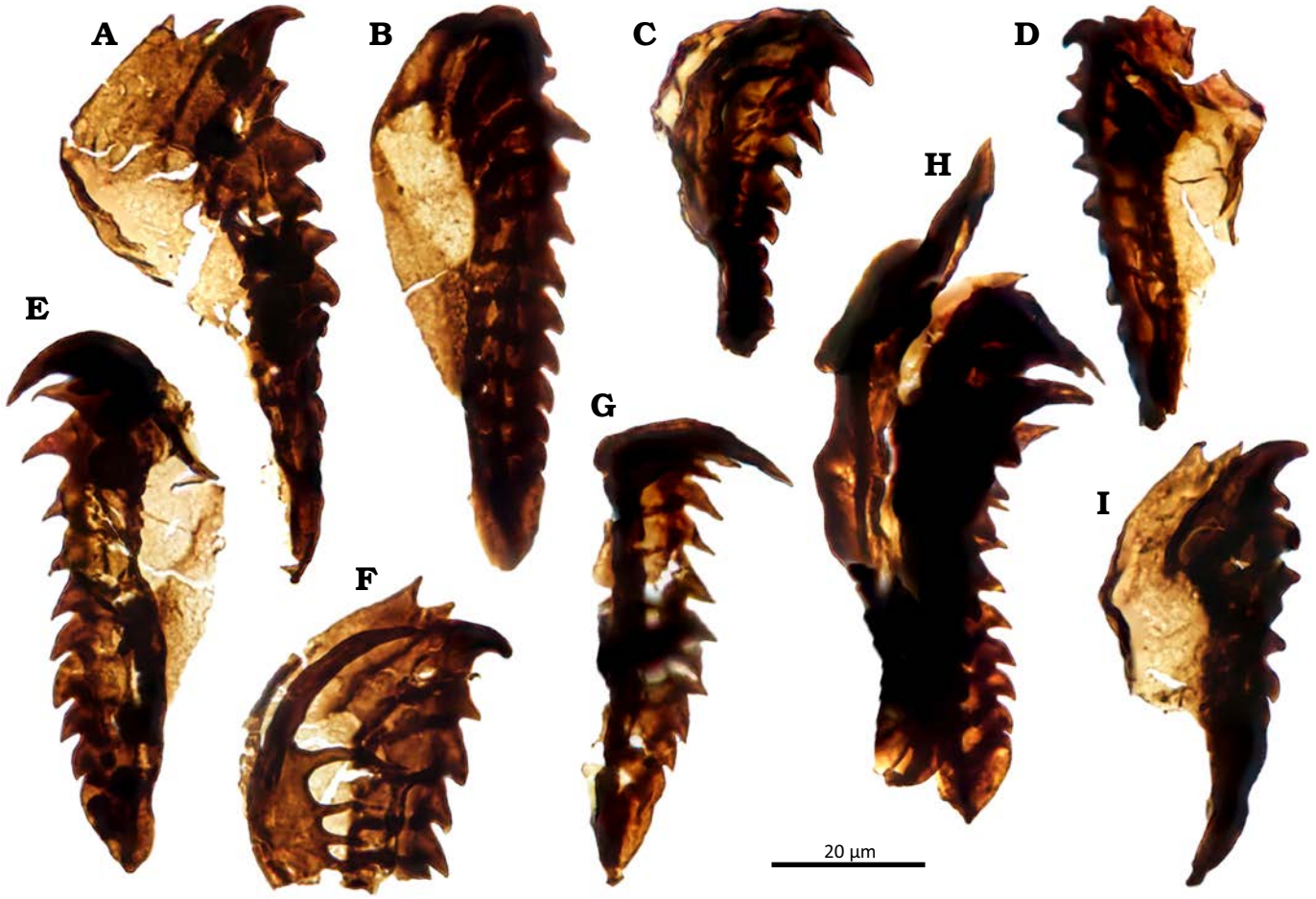

Fig. 5. Scolecodonts (jaws of eunicid polychaete annelids) from the Silurian Xiaoxi Formation of Hu'nan, southern China. *Oenonites*-like specimens. **A**. Right MI? **B**. Left MI? **C**. Left MII with its anterior part broken. **D**. Right MI? with its anterior part broken. **E**. Left MI in ventral view. **F**. Scolecodonta indet. **G**. A specimen with its myocoele opening broken. **H**. Left MI in dorsal view. **I**. Left MI in dorsal view. Scale bar 20 μm. Repository numbers provided in SOM: table 2.

(Makled et al. 2021) where they are again attributed to eurypterids. More broadly, SCF spines of a similar type are found in anatomical connection with arthropod cuticles exhibiting perforations or lacunae in various Cambrian deposits (e.g., Harvey and Butterfield 2022), and in association with acid-extracted phyllocarid crustacean cuticle directly macerated from macrofossil specimens found in Ordovician and Silurian strata of the Czech Republic (Kovář et al. 2024). The presence of comparable spines among a phylogenetically diverse array of clades suggests that such spines/cuticles could in principle be sourced from a wide variety of euarthropods.

Arthropod tactile setae.—A further distinct SCF morphotype recovered here comprise elongate ribbon-like shafts (70–395 μm length, n = 15; 4.6–18.4 μm maximum width, $\bar{x}$ = 9.8 μm, n = 15) with margins fringed by densely packed spinose ornament oriented toward the apical portion (Fig. 4). The distal tip is often missing, but where intact appears as either a tapering point lacking fringing ornamentation (Fig. 4C, J, M), or as a second morphotype that terminates in a blunt rectangular truncation with spinose ornamentation identical to that fringing the shaft (Fig. 4H). The basal portion of these ribbon-like spinose shafts is frequently broken, but where complete is unornamented, and tapers to a constricted portion approximately a half to quarter the width of the main shaft (Fig. 4O). In one specimen, the density of spinose ornamentation is markedly sparser along the entire length (Fig. 4F).

These SCFs find their closest comparison with fragmentary "seta-like structures" previously described from the early Silurian Tuscarora Formation of Pennsylvania (Gray and Shear 1992). Gray and Boucot (1994) note these fragments are particularly reminiscent of the bipectinate tactile sensory setae possessed by a range of arthropods.

Scolecodonts (jaws of polychaete annelids).—Organically preserved scolecodonts (i.e., the disarticulated jaws of polychaete annelids) recovered among the Xiaoxi SCFs are represented by several maxillary elements that share similar morphological characters (Fig. 5). They are bluntly rounded at the anterior part and distinctly tapered at the posterior portion (46–74 μm length, $\bar{x}$ = 63.4 μm, n = 8; 20–32 μm maximum width, $\bar{x}$ = 25.3 μm, n = 7). Myocoeles are visible, with the opening measuring two-thirds of the jaw in length. Approximately 8–10 denticles are arranged along

Fig. 6. Possible euglenid *Moyeria cabottii* (Cramer) Miller & Eames, 1982, from the Silurian Xiaoxi Formation of Hu'nan, southern China. Presence of well-preserved euglenids suggests significant terrestrial input for the Xiaoxi Formation. Scale bar 20 µm. Repository numbers provided in SOM: table 2.

the margin, showing a decrease in size toward the posterior part of the jaw.

Occurrences of scolecodonts in coeval rocks of China are known from the Yanglugou Formation of the western Qinling Mountains (Ye 1994) and the Miaogao Formation of Yunnan (Gao et al. 2025). In comparison to these previously reports, the Xiaoxi scolecodonts are of a much smaller size. Although certain forms in the Yanglugou Formation (e.g., *Anisocerasites cheles* Ye, 1994, and *Lunoprionella lepida* Ye, 1994) are less than 60 µm in length, they are either

morphologically distinctly different from the Xiaoxi specimens, or they are poorly preserved, hampering any detailed comparison. Scolecodonts recovered here from the Xiaoxi Formation bear a close resemblance to known some known species of *Oenonites* (Polychaetaspidae), as exemplified by those from the lower Silurian of Gotland, Sweden (Eriksson 1997). Especially noteworthy is a specimen identified as a possible *Oenonites* from the Devonian (Eifelian) of Egypt, which exhibits an overall similar morphology to the Xiaoxi scolecodonts, except for being only slightly larger in size (108 μm in length) (El Shamma et al. 2019: pl. 1: 2).

Possible euglenids (flagellate eukaryotes).—Alongside the diverse range of animal-derived SCFs, processing of the Xiaoxi Formation material also recovered a distinctive set of ovoid vesicular fossils of probable protistan origin (Fig. 6), which were among the more common elements of the recovered assemblage. These specimens are united by their characteristic wall architecture, comprising a set of parallel striae that are arranged in a helical construction, where the striae converge at opposing apical poles (Fig. 6). These features identify these fossils as the taxon *Moyeria* (Thusu 1973; Gray and Boucot 1989; Strother et al. 2020, 2025), and specifically *Moyeria cabottii* (Cramer) Miller & Eames, 1982, based on the manner in which the pellicle strips form a crenelated margin to the overall vesicle (Strother et al. 2025). *Moyeria* is a former "acritarch" known from mid-Ordovician through Silurian strata, that has since been suggested to represent the remains of eukaryotic flagellates assignable to the photosynthetic euglenids, based on their overall euglenid-like construction (Gray and Boucot 1989) and diagnostic pellicle ultrastructure (Strother et al. 2020). Despite the compelling structural similarity between *Moyeria* and euglenids, it is nevertheless difficult to explain on taphonomic grounds how a flagellated protist like a euglenid would preserve as a robust organic-walled fossil (see discussion on the preservation potential of unwalled protists as carbonaceous microfossils in Butterfield 2003, 2015a, b; Slater et al. 2020; Slater and Bohlin 2022). Proteinaceous euglenid pellicles are notably more robust than other cellular components, and can be isolated for study, in at least one incidence, taxa that produce a lorica (e.g., *Trachelomonas*) have been shown to survive acetolysis (Lindgren 1981; Strother et al. 2020). Delicate structures are known to preserve as organic fossils via fusion or imprinting into extraneous organic material prior to degradation (e.g., Slater et al. 2020; Slater et al. 2022), including even ciliates (e.g., Bomfleur et al. 2012), yet it remains unresolved whether a euglenid pellicle would preserve among acid-extractable palynomorphs. Alternative comparisons for the affinities of *Moyeria* include the spirally ornamented oogonia of charophyte algae (e.g., Soulié-Märsche and García 2015). Among organic microfossils, *Moyeria* has been compared to acritarchs of the Mesoproterozoic Kaltasy Formation from the Volgo-Ural region of Russia (Sergeev et al. 2016: fig. 5.10–12), it also shares features with the late Palaeoproterozoic taxon *Filinexum torsivum* Riedman et al., 2023 (Riedman et al. 2023: fig. 5) which exhibits a similar spirally twisted wall construction, and can also be compared to a relatively large ovoid SCF from the Terreneuvian, Cambrian age Voosi Formation of Estonia (Slater et al. 2018: fig. 9a) which likewise displays a helical wall architecture.

The presence of *Moyeria* further points to a freshwater influence in the deposition of the Xiaoxi Formation, complementing the sedimentological evidence suggesting that the Xiaoxi Formation was deposited in a nearshore setting. Indeed, based on its known fossil occurrence being restricted to terrestrial and nearshore palaeoenvironments (Gray and Boucot 1989; Strother et al. 2025), the frequent occurrence of *Moyeria* in the Xiaoxi Formation is consistent with the interpretation that this SCF assemblage is influenced by a terrestrial input.

Discussion

SCF sampling of shallow marine environments.—The fossil record is our primary resource for understanding ancient ecosystems. Fossilisation potential, however, varies widely across environments (Shaw et al. 2021), and is also strongly biased in favor of more easily preserved biomineralized organisms. SCFs can counter some of this bias by accessing novel data on non-mineralized animals from depositional environments not typically associated with the preservation of delicate non-mineralized taxa (such as shallow marine facies). The Xiaoxi Formation was deposited in a shallow marine setting (Wang et al. 2023). In shallow marine siliciclastic deposits of this kind, trace fossils are often the primary source of palaeobiological evidence. The Xiaoxi Formation is no exception, as evidenced by abundant arthropod traces such as *Cruziana*, *Dimorphichnus*, and *Thalassinoides* burrows (Zhang et al. 2024). It is plausible that eurypterid and other arthropod SCFs detected here from the Xiaoxi Formation may even be sourced from some of the taxa generating these traces (arthropod surface trackways). Outside trace fossils, SCFs are a novel way to acquire body-fossil information from otherwise poorly fossiliferous shallow marine sandstones, shales and mudrocks (Slater 2024) or even deposits with relatively rich shelly fossils. Indeed, it is to some extent rare to acquire body-fossil information in the same unit as trace fossils, and so SCFs are one means of bridging this gap, as has recently been demonstrated using SCFs in older shallow marine Cambrian deposits (Slater 2024; Mussini et al. 2025).

Moreover, an added benefit of targeting shallow marine deposits is that they have the advantage of sampling not only marine organisms, but also freshwater and terrestrial taxa that have been transported into littoral settings. This is particularly important since pre-Devonian terrestrial deposits (e.g., the Silurian Downton Castle Sandstone Formation, Jeram et al. 1990 and the littoral Burgsvik Sandstone, Smith and Butterfield 2013, which exhibits significant terrestrial input) remain comparatively rare. By the Silurian, terres-

trial animals (primarily arthropods) begin to appear in the fossil record (Gray and Boucot 1994), and have been well documented occurring among organic microfossils in a select handful of terrestrial deposits (e.g., Jeram et al. 1990). SCF extraction from shallow marine deposits may therefore be considered an underexploited means of accessing a measure of terrestrial diversity, a property that may prove especially useful in regions and time windows where terrestrial deposits are lacking (or where dominated by poorly-fossiliferous red beds). Indeed, certain Xiaoxi Formation SCFs exhibit morphological adaptations to at least limited terrestrial excursions. Eurypterid respiratory organs for instance have been suggested to have served as air-breathing organs (Lamsdell et al. 2020). The hypothesized function of these structures being to retain water/moisture in order to facilitate respiration during temporary terrestrial activity (Manning and Dunlop 1995). In addition, a case can be made that the numerous arthropod sensory setae recovered here (Fig. 4) may even derive from terrestrial arthropods, notably such structures have previously only been found co-occurring with land plant spores and phytodebris (Gray and Shear 1992) indicating a potentially terrestrial origin. Frequently occurring nematophytes of *Prototaxites*? sp., as well as some cuticle-like sheets and tubes, have been reported from the Xiaoxi Formation (Wang et al. 2023). These fossils have been widely considered by palaeobotanists to originate from organisms inhabiting early terrestrial ecosystems (Edwards et al. 2013, 2018), though certain cuticular nematophytes have alternately been reconstructed as the remains of extinct rhodophytes (Smith and Butterfield 2013) and would therefore represent marine components found alongside terrestrial-derived spores and other phytodebris in Silurian marginal marine depositional settings. In this study, the case for a potential terrestrial/non-marine influence among the Xiaoxi SCF assemblage is further bolstered by the presence of abundant *Moyeria*. Indeed, if viewed as a photosynthetic euglenid (but keeping in mind the proviso that preservation of euglenids as organic microfossils has not yet been adequately explained) it is worth noting the overwhelmingly obligate freshwater (stenohaline) nature of extant euglenids (Gojdics 1953; Strother et al. 2020), offering a possible ecophysiological explanation for *Moyeria* being indicative of freshwater, and of a non-marine provenance (Gray and Boucot 1989; Strother et al. 2020).

The high quality of preservation among the Xiaoxi SCFs enables the resolution of fine-scale submicron anatomical details, and the study of semi-articulated clusters of spines and extensive portions of cuticle. In terms of taxonomy, the Xiaoxi SCFs are broadly comparable to other mid-Palaeozoic biotas where organic microfossils sourced from animals have been detected. Overall, the assemblage is predominantly composed of particularly recalcitrant organic structures that exhibit a somewhat lower threshold for preservation compared to the most delicate SCFs. These more robust structures include the cuticles of eurypterids and heavily sclerotized elements of the scolecodont jaw apparatus. In part, this may reflect the higher-energy depositional palaeoenvironment evident at the Xiaoxi Formation from the abundant ripple marks, ripple cross-laminations, and the presence of hummocky cross-stratification, attesting to substantial reworking of the sediments. However, the co-occurrence of intact elongate setae (Fig. 4), fragile Keimenplatten (Fig. 2A–G, O), a few weakly-sclerotized spines (e.g., Fig. 3O), and more extensive portions of cuticle show that SCF processing is also capable of capturing a broader array of more delicate animal structures even from such relatively higher-energy deposits.

Linking Early and Middle Palaeozoic SCF faunas.—Since there are relatively few reports or studies of SCFs from Silurian deposits when compared to younger Devonian and older Cambro-Ordovician rocks, the Silurian age of the Xiaoxi Formation is noteworthy. In part, this pattern mirrors the paucity of Silurian Lagerstätten noted in comparison to other periods of the Palaeozoic (Schiffbauer and Laflamme 2012). In Cambrian rocks, small organic fragments of animals constitute a relatively common component of palynological residues (Slater and Bohlin 2022). Recent increased attention toward Cambrian SCFs has helped expand the fossil records of a wide variety of metazoan groups, including the oldest occurrence data for multiple key clades (e.g. Chaetognatha, Annelida, Panarthropoda, stem-Crustacea, and Pterobranchia) (Slater 2025; Slater et al. 2018; Slater and Willman 2019; Palacios et al. 2018; Jankauskas et al. 1989; Harvey and Butterfield 2008; Harvey et al. 2012; Wallet et al. 2021; Kovář 2020; Kovář and Fatka 2025). Aside from scolecodonts (polychaete jaws), studies of Ordovician SCFs remain few, but are perhaps best represented by crustacean and chelicerate fragments of the Middle Ordovician Winneshiek Shale (Nowak et al. 2018), and the recently reported diverse SCF assemblages recovered from Cambro-Ordovician parts of the Deadwood Formation and Darriwilian age Winnipeg Formation of North Dakota (Mussini and Butterfield 2025). Reports from Silurian marine strata are arguably more limited still, consisting chiefly of rare eurypterid cuticles (e.g., Manning and Dunlop 1995), and a few crustacean derived fragments (Rolfe 1962; Kovář et al. 2024). The principal exception to this is perhaps the relatively diverse assemblage of terrestrially-sourced arthropod cuticles that have been extracted as organic remains from the Downton Castle Sandstone Formation at the base of the Pridoli at Ludlow Lane in Shropshire, UK (above the famous "Ludlow bone bed"; Jeram et al. 1990), a deposit that is more-or-less contemporaneous with that of the Xiaoxi assemblage recorded here (interestingly, both the Xiaoxi Formation and Ludlow Lane exhibit comparable sedimentology and depositional features, including an abundance of ripple marks, ripple cross-lamination, and hummocky cross-stratification). By contrast, reports from the Devonian are more extensive, where a number of groups, including eurypterids, arachnids, centipedes, and even insects are counted among organic microfossils (Shear et al. 1984, 1989; Labandeira et al. 1988;

Makled et al. 2021; Filipiak et al. 2022). It is thus noteworthy that current Palaeozoic SCF records are not only temporally discontinuous but also represent two distinct locales of preservation, one restricted to marine deposits (Cambro-Ordovician) while younger Palaeozoic SCFs (Devonian) are chiefly derived from non-marine deposits. In this light, these newly detected Silurian SCFs bridge both a prominent stratigraphic gap, but also a major palaeoenvironmental divide by offering crucial insights into otherwise poorly understood Palaeozoic marginal marine faunas.

Conclusions

Processing for small carbonaceous fossils from the upper Silurian Xiaoxi Formation has yielded a rich assortment of exceptionally preserved metazoan remains, including eurypterid cuticles, respiratory organs (kiemenplatten), lamellate book gills, sensory setae, fragments from other euarthropods, scolecodonts, and a variety of unknown metazoans. Such fossils emphasize the largely untapped potential for SCFs in tracing macroevolutionary patterns among soft-bodied marine animals in post-Cambrian strata. In particular, the Xiaoxi Formation SCFs strongly suggest this style of preservation will become increasingly useful in capturing highly detailed remains of non-mineralized metazoans from Palaeozoic marginal marine settings, where Lagerstätten are lacking. Preservation of shallow water Silurian SCFs here is of particular significance, since only a limited set of post-Cambrian SCFs are reported from marine strata, but also because marginal marine settings may capture elements of the early terrestrial biota. The extent to which a broader SCF record can be developed among Silurian marine deposits remains to be seen, but their abundance in an otherwise poorly-fossiliferous, shallow-marine siliciclastic formation here hints that taphonomic demands are relatively relaxed, and that SCF preservation is substantially more widespread than previously expected.

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