Herpetogaster collinsi from the Cambrian of China elucidates the dispersal and palaeogeographic distribution of early deuterostomes

Xianfeng Yang Corresp., 1, 2, 3 , **Julien Kimmig** Corresp., 4, 5 , **James D Schiffbauer** 6, 7 , **Shanchi Peng** 3

1 Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China
2 MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, Kunming, China
3 State Key Laboratory of Palaeobiology and Stratigraphy, Chinese Academy of Sciences, Nanjing, China
4 Paläontologie und Evolutionsforschung, Abteilung Geowissenschaften, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany
5 The Harold Hamm School of Geology & Geological Engineering, University of North Dakota, Grand Forks, North Dakota, United States
6 Department of Geological Sciences, University of Missouri - Columbia, Columbia, Missouri, United States
7 X-ray Microanalysis Laboratory, University of Missouri - Columbia, Columbia, Missouri, United States

Corresponding Authors: Xianfeng Yang, Julien Kimmig
Email address: yangxf@ynu.edu.cn, jkimmig@psu.edu

The Cambrian Radiation represents one of the largest diversification events in Earth history. While the resulting taxonomic diversity is exceptional, relatively few of these novel species can be traced outside the boundaries of a single palaeocontinent. Those species with cosmopolitan distributions were likely active swimmers, presenting opportunity and means to conquer new areas, but this would not have been the case for sessile organisms. *Herpetogaster* is a genus of sessile, stalked, filter-feeding deuterostomes with two species, *H. collinsi* and *H. haiyanensis*, known from the lower to middle Cambrian (Series 2–Miaolingian, Stage 3–Wuliuan) of Laurentia and Gondwana. Here, we expand the distribution of *H. collinsi* to Gondwana with newly discovered specimens from the Balang Formation of Hunan, China. This discovery raises questions on the origin of the genus and how sessile organisms were able to disperse over such a broad distance in the lower Cambrian.

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Xianfeng Yang[1,2,3], Julien Kimmig[4,5], James D. Schiffbauer[6,7], Shanchi Peng[3]

[1]Yunnan Key Laboratory for Palaeobiology, Yunnan University, North Cuihu Road 2, 650091, Kunming, China

[2]MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Yunnan University, 650091, Kunming, China

[3]State Key Laboratory of Palaeobiology and Stratigraphy, Chinese Academy of Sciences, Nanjing, 210008, China

[4]Paläontologie und Evolutionsforschung, Abteilung Geowissenschaften, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, 76133, Germany

[5]The Harold Hamm School of Geology & Geological Engineering, University of North Dakota, Grand Forks, ND 58202, USA.

[6]Department of Geological Sciences, University of Missouri, Columbia, MO 65211, USA

[7]X-ray Microanalysis Laboratory, University of Missouri, Columbia, MO 65211, USA

Corresponding Authors:

Xianfeng Yang

Yunnan Key Laboratory for Palaeobiology, Yunnan University, North Cuihu Road 2, 650091, Kunming, China

Email address: yangxf@ynu.edu.cn

Julien Kimmig
Paläontologie und Evolutionsforschung, Abteilung Geowissenschaften, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, 76133, Germany
Email address: julien.kimmig@smnk.de

Abstract

The Cambrian Radiation represents one of the largest diversification events in Earth history. While the resulting taxonomic diversity is exceptional, relatively few of these novel species can be traced outside the boundaries of a single palaeocontinent. Those species with cosmopolitan distributions were likely active swimmers, presenting opportunity and means to conquer new areas, but this would not have been the case for sessile organisms. *Herpetogaster* is a genus of sessile, stalked, filter-feeding deuterostomes with two species, *H. collinsi* and *H. haiyanensis*, known from the lower to middle Cambrian (Series 2–Miaolingian, Stage 3–Wuliuan) of Laurentia and Gondwana. Here, we expand the distribution of *H. collinsi* to Gondwana with newly discovered specimens from the Balang Formation of Hunan, China. This discovery raises questions on the origin of the genus and how sessile organisms were able to disperse over such a broad distance in the lower Cambrian.

Subjects Biodiversity, Developmental Biology, Ecosystem Science, Paleontology, Taxonomy

Keywords Deuterostomia, Ambulacraria, *Herpetogaster*, Lifestyle, Dispersal, Cambrian Stage 4, Exceptional preservation, Larvae, Palaeoecology, Palaeogeography

Introduction

During the Cambrian Radiation, hundreds of metazoan species, representing nearly all known modern phyla, appear in the fossil record and can be found throughout rich fossil deposits around the world (Paterson et al., 2016; Fu et al., 2019; Harper et al., 2019; Kimmig et al., 2019; Nanglu, Caron & Gaines, 2020; Yang et al., 2021). While there is an excellent record of soft-bodied fossils from globally distributed Burgess Shale-type Lagerstätten as early as Cambrian Stage 3 (~521–514 Ma, not formally ratified), few species can be found crossing palaeocontinental boundaries (Paterson et al., 2016; Fu et al., 2019; Harper et al., 2019; Kimmig et al., 2019; Nanglu, Caron & Gaines, 2020; Yang et al., 2021). This pattern of species distribution not only begs important questions about modes of reproduction and broader-scale mobility or migration of species in the early Cambrian, but also how the few species with cosmopolitan distributions were able to accomplish this feat. Based on newly discovered fossils presented herein, one species that had successfully trekked and established a foothold on multiple palaeocontinents is *Herpetogaster collinsi* Caron et al. 2010.

Herpetogaster, one of the earliest-known representatives of the invertebrate deuterostomes, is a stalked filter feeder grouped with the informal cambroernid clade. The genus is represented by two species found in the lower to middle Cambrian (Series 2–Miaolingian, Stage 3–Wuliuan) of Gondwana and Laurentia (Caron, Conway Morris & Shu, 2010; Kimmig, Meyer & Lieberman, 2019; Yang et al., 2020; Nanglu et al., 2022; Pari, Briggs & Gaines, 2022). To date, its two species have been observed to be restricted to their respective palaeocontinents: *H. haiyanensis* to Series 2 deposits in Gondwana and *H. collinsi* to generally younger Miaolingian deposits in Laurentia (with the exception of the Series 2 Pioche Formation). From all known fossils of the genus, *Herpetogaster* appears to have been a sessile organism, with a stolon and a basal discoidal holdfast. While the stolon may have been contractible, its likely function was to anchor the organism in place within the sediment. Neither of the two species preserve swimming appendages, and thus the presumed mechanism of expanding its distribution would have been through passive transport by ocean currents. Recent flume experiments have shown that soft-bodied animals can hypothetically be transported over tens of kilometers by current flow (Bath Enright et al., 2021), but this is an improbable explanation for the occurrence of the same species separated by thousands of kilometers and within deposits of different ages. With specimens of *H. collinsi* reported here from the Balang Formation, Hunan, China, along with possible larval fossils, we propose that these organisms possessed a motile larval stage that provided the means for broad dispersal and migration.

Thus far, we have collected more than 60 new specimens of *H. collinsi* from the lower Cambrian (Series 2, Stage 4) Balang Formation. Here, we provide detail of 19 of the best-preserved new specimens, explore the distribution of the genus in time and space, and postulate mechanisms that might have led to its success.

Materials & Methods

The 19 new specimens of *Herpetogaster collinsi* described here are reposited in the collections of the Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming, China (YKLP), with specimen numbers YKLP 14570–14588. Specimens with the prefix ROM are housed in the Royal Ontario Museum, Ontario, Canada, with the prefix KUMIP at the Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas, and with the prefix YPM at the Yale Peabody Museum of Natural History.

Imaging

The specimens were photographed using a Canon EOS 5D digital SLR camera with a Canon 50 mm macro lens and cross-polarized lighting. Close-ups were captured using a Leica DFC 500 digital camera mounted on a Leica M205-C stereoscope. All specimens were submerged in alcohol to increase contrast. The contrast, colour space, and brightness were adjusted using Adobe Photoshop CC.

Scanning electron microscopy and energy-dispersive X-ray spectroscopy analyses.

The backscattered electron (BSE) imaging and energy-dispersive X-ray spectroscopy **(**EDS) of uncoated specimens was conducted with a FEI Quanta 650 FEG field emission scanning electron microscope (SEM) at the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, China (YKLP). All imaging analyses were conducted with the following operating conditions: 14 mm ± 1 mm working distance (minor differences to allow for variation in sample thickness or topography) for basic imaging and EDS, 20 keV beam accelerating voltage, 10 nA beam current, 20 Pa chamber pressure (low vacuum), 50 µm aperture for imaging, and 40 µm aperture for EDS analysis.

Geological setting

The specimens described herein were collected from the lower part of the Balang Formation in northwestern Hunan, China (Fig. 1A–D). The Balang Formation is part of a conformable lower Cambrian sequence, positioned between the Niutitang Formation below and the Chinghsutung Formation above (Fig. 1E). The presence of the trilobite *Oryctocarella duyunensis* confirms that the collection interval is positioned within Series 2, Stage 4 of the Cambrian System (Peng et al., 2017; National Commission on Stratigraphy of China, 2018; Zhao et al., 2019; Dai et al., 2021). In the context of other well-known Chinese Cambrian Lagerstätten, the Balang biota is situated in age between the slightly older Chengjiang biota (Series 2, Stage 3) and younger Kaili biota (Miaolingian, Wuliuan). The sampled outcrop, located approximately 32 km south-west of Huayuan town, is composed of finely laminated dark grey calcareous mudstone intervals, interbedded with silty mudstone and silty shale (Fig. 1B).

Results

Systematic paleontology

Superphylum: Deuterostomia Grobben, 1908
Clade: Ambulacraria Metschnikoff 1881
Unranked stem-group: Cambroernida Caron, Conway Morris & Shu, 2010

Genus *Herpetogaster* Caron, Conway Morris & Shu, 2010

Herpetogaster collinsi Caron, Conway Morris & Shu, 2010

Holotype. ROM 58051

New Material. YKLP 14570–14588

Provenance. Balang Formation, lower Cambrian (Series 2, Stage 4), *Oryctocarella duyunensis* biozone, Mozi village, Paiwu township, approximately 32 km south-west of Huayuan town, Hunan Province, China. Pioche Formation, Comet Shale Member; lower Cambrian (Series 2, Stage 4), *Nephrolenellus multinodus* biozone; Ruin Wash, NW ¼ SW ¼ sec. 15, R65E T2S, 17 km west of Panaca, Lincoln County, Nevada (see Palmer 1998, and Lieberman, 2003 for greater discussion of the locality). Burgess Shale and Stephen Shale Formations; middle Cambrian (Miaolingian, Wuliuan); Yoho and Kootenay National Parks, British Columbia, Canada.

Diagnosis. Segmented body, coiled dextrally. Short head bearing prominent bilateral anterior dendritic tentacles of sub-equal length and in two-by-two arrangement with pharyngeal structures, possibly lateral pores. Trunk subcylindrical, divided into two subsections, narrowing posteriorly. Ventral and contractile adhesive stolon, sometimes with terminal disc. Digestive tract with anterior mouth, pharynx, voluminous stomach, and narrow intestine with terminal anus. Stomach and intestine of sub-equal lengths, un-looped, with triangular mesenterial insertions (from Caron, Conway Morris & Shu 2010).

Description. Most of the specimens are complete and range in length from 8.4 to 53.6 mm and from 2.3 mm to 7.9 mm in width. The body is curved, some specimens show fine segmentation along the trunk (Figs. 2E,J and 3C,F), and ends in an anus (Figs. 2D–H and 3C,D,F–H).

The head has a maximum width of 7.4 mm and a maximum length of 3.9 mm. The pharynx is visible in 9 specimens. Two tentacles emerge from the corners of the head, they reach up to 14.3 mm in length, bifurcate at 0.6 to 5 mm and preserve between 10 and 11 branches.

The trunk ranges from 4.8 to 36.1 mm in length, which equates to about three-quarters of the total body length of the animal. The other quarter represents the pharynx, 0.7 to 3.6 mm in length. Some specimens (n = 9; Figs. 2E,I,J and 3A–C,E,F,I) preserve a darker internal structure, which is interpreted as the stomach and digestive tract as it reaches the anus in YXLP 14574 and YKLP14610 (Fig. 2E,J). The soft-tissue surrounding the stomach and intestine preserves fine segmentation (Figs. 2E,G,J and 3C,F), separating the trunk into 13 segments.

The stolon extends from the final third of the trunk, around the ninth or tenth segment (Figs. 2E,J and 3C,F), and varies in length (1.5 to 14.3 mm) and width (0.4 to 1.8 mm). This suggests that the stolon may have been contractible. Some specimens preserve a terminal disk at the end of the stolon, interpreted as the holdfast (Figs. 2G,I and 3C,H,I).

The Balang specimens appear to have been gregarious or living in close proximity; up to six specimens have been found on a single slab (Fig. 3C,F).

Preservation. Balang Formation specimens are usually regarded as carbonaceous compressions preserved within carbonaceous mudstones, similar to those of other Cambrian Burgess Shale-type deposits (e.g., Wen et al. 2019). Two specimens of *Herpetogaster collinsi* were analysed using SEM-EDS (Fig. 4). The first specimen (YKLP 14583) has a distinctive, if not continuous carbon signature (Fig. 4L), whereas the other specimen (YKLP 14573) did not provide a strong carbon signature, but a more continuous film (Fig. 4E). The analyses also show enrichment of iron and phosphate in the host rock, though neither elemental signature appears to be associated with the fossils themselves. This suggests that that diagenesis played a vital role in the preservation of carbon in the Balang Formation, but also suggests that all the *Herpetogaster* specimens underwent the same taphonomic process. The carbon signature in YKLP 14573 correlates spatially with calcium (Fig. 4C), suggesting that some of the signal is likely derived from the host rock; however, these elemental signatures do not correlate in YKLP 14583. A similar observation to YKLP 14573 has been made with fossils from the Marjum Formation of Utah (Broce & Schiffbauer, 2017; Leibach et al., 2021). These studies inferred that the higher carbon concentration observed locally stemmed from accumulation of carbonaceous material within interstitial spaces between grains of the host rock. The absence of detectable carbonaceous films or local enrichments of carbon in YKLP 14573 might indicate a few possible taphonomic scenarios involving the complete removal of organic carbon. For example, given their infaunal nature, the organisms likely died within the uppermost oxic- to sub-oxic layers of sediment, allowing for efficient decay by oxygenic microbes. Burial occurred rapidly after death, as indicated by their mostly complete preservation and the presence of preserved labile structures (e.g., tentacles, stolon, gut). Organic carbon removal/dispersion could have continued through diagenesis as well.

An interesting feature of the Balang specimens is that several have a relatively uniform preservational coloration (Figs. 2A,C,D and 3G,H) as compared to representatives of the genus in other deposits. This may be a result of additional decomposition of the specimens after burial, leading to decay of the internal organs, and a generally more homogeneous, black-film appearance. Additionally, rather than all dendritic in form, the tentacles are preserved in different morphologies, as opposed to the Burgess Shale and Pioche Formation specimens (Fig. 5). Enhanced decomposition may again be the culprit for this lack of dendritic detail; overlapping tentacles may also reduce the appearance of finer details, though this is not expected to be the case in all the examined Balang specimens.

Remarks. The Balang Formation specimens are assigned to *H. collinsi.* Though there are taphonomic differences as described above, these specimens appear to be nearly morphologically identical to those described from the Burgess Shale (Caron, Conway Morris & Shu 2010) and the Pioche Formation (Kimmig, Meyer & Lieberman 2019), preserving the dextrally coiled body, anterior dendritic tentacles, pharyngeal structures, stolon, terminal disc, and digestive tract. Segmentation is also prominent in some of the Balang specimens (Figs. 2D,E;,G,H,J and 3A,C,E,F), with segmentation lines visible in 9 of 19 closely examined specimens.

These Balang specimens visibly differ from *H. haiyanensis*, which has over one hundred branches per tentacle, a single layered stolon, and preserved inner and outer layers (Yang et al., 2020)—none of which can be explained by taphonomic differentiation though were plausibly beneficial adaptations to the deltaic environment which they occupied (Peng 2009; Saleh et al. 2022).

Discussion

The oldest-known occurrence of the *Herpetogaster* genus is from the lower Cambrian (Series 2, Stage 3) Chengjiang biota of China (Yang et al., 2020, 2021). The Chengjiang specimens, however, belong to *H. haiyanensis*, which were found in the Haiyan Lagerstätte. From the Haiyan locality, a total of eight specimens, including a juvenile specimen, were described (Yang et al., 2020). The subsequent occurrences are all representatives of *H. collinsi*, and include specimens from the Comet Shale, Nevada (Kimmig, Meyer & Lieberman, 2019), a possible specimen from the Parker Quarry, Vermont (Pari, Briggs & Gaines 2022), and now the specimens reported herein from the Balang Formation (Fig. 5). The youngest representatives known to-date are also specimens of *H. collinsi*, recovered from the Burgess Shale (Caron, Conway Morris & Shu 2010). While this is likely not yet a complete picture of the distribution and diversity of *Herpetogaster* through time and space, it suggests that the genus might have originated in Gondwana sometime around Cambrian Stage 3 and had likely spread globally, at least in the equatorial range (Fig. 1F), by Cambrian Stage 4. The current fossil record, with the oldest representatives from the Chengjiang biota (Yang et al., 2020, 2021), support the origin of the genus in Gondwana; however, the addition of the new specimens from the Balang biota also suggest that *H. collinsi* originated in Gondwana. Li et al. (2023) suggested *Herpetogaster* is the earliest-diverging cambroernid, and phylogenetically positioned at the base of the Ambulacraria, which aligns well with the origin of the genus on the timeline observed.

This discovery of *H. collinsi* in Laurentia and Gondwana around the same time (Cambrian Stage 4) implores consideration of how these sessile organisms, with no known swimming appendages or mechanisms for motility over broad distances, managed to establish themselves on the shelf of two palaeocontinents separated by thousands of kilometers of open ocean (Fig. 1F). There are many challenges that must have been overcome for this migration to have taken place, not least including the distance, but also predation, and changing water temperatures and oxygenation.

Even with an expansive fossil record and a wealth of soft-bodied organisms from the global distribution of Konservat-Lagerstätten known in the Cambrian (Muscente et al., 2017), it is rare that the same species is found in both Gondwana and Laurentia. In most cases when a Laurentian species has been proposed to occur in a Gondwanan deposit, or vice versa, it has later been revised and given a new species name, or even a new genus (Yang et al., 2021; Hou et al., 2017). However, most of the genera that are shared between the Gondwanan (e.g., Balang, Chengjiang, Emu Bay, Guanshan, and Kaili) and the Laurentian (e.g., Burgess Shale, Parker Quarry, Pioche Formation, Rockslide Formation, Sirius Passet, Spence Shale, Wheeler Formation, Marjum Formation, and Weeks Formation) biotas are arthropods. Many of these arthropods were pelagic and motile swimmers, and could have been actively seeking new habitats with new or greater resources (Legg & Vannier, 2013; Kimmig & Pratt, 2015; Robison, Babcock & Gunther, 2015; Foster & Gaines, 2016; Paterson et al., 2016; Hou et al., 2017; Lerosey-Aubril et al., 2018, 2020; Fu et al., 2019; Harper et al., 2019; Kimmig et al., 2019; 2023; Ma et al., 2020; Nanglu, Caron & Gaines, 2020; Yang et al., 2021). However, *Herpetogaster*, as a substrate-anchored deuterostome, requires fundamentally different considerations.

An equally plausible alternative for the palaeogeographic distribution of arthropods considers their larvae; the small size and zooplankton-like habit of the post-embryonic nauplius larval stages of arthropods could have traversed long distances by ocean currents (Müller & Walossek, 1986; Zhang & Pratt, 1993; Waloszek & Dunlop, 2002). Therefore, it follows that we should also consider the life cycle of *Herpetogaster,* or at least what we can infer from modern analogues. Though we have numerous fossils of the genus, much remains unknown about its ontogenesis. We can make some assumptions from modern ambulacrarian species; for example, most reproduce sexually, and many develop through a ciliated, free-swimming and feeding larval stage before settling and attachment. Depending on taxon, this motile larval form goes by numerous names, for example, tornaria for enteropneusts, pluteus for echinoids, auricularia for holothurians, and doliolaria for crinoids. These larvae bear little anatomical resemblance to the adult forms, undergoing considerable morphological change before entering their respective adult life stages (Ettensohn, Wessel & Wray 2004). One could suggest from the close affinity of *Herpetogaster* to modern invertebrate deuterostomes (Caron, Conway Morris & Shu 2010; Nanglu et al., 2022) that it might have also had a planktonic larval stage. Some evidence for the presence of planktonic larvae has been found in acorn worms from the Chengjiang biota (Yang et al., 2022), thus making this a tantalizing hypothesis. As *Herpetogaster* has been recovered at the base of the Ambulacrarian tree in recent phylogenies (Li et al., 2023), it suggests that the last common ancestor of the clade might have already had a planktonic larval stage, or alternatively that it developed several times within the Ambulacraria.

In addition to suggestions from phylogenetic affinity, another indication of plausible larval dispersal in *Herpetogaster* may come from their gregarious life habit. As noted, we observed some of the *H. collinsi* specimens from the Balang Formation found together on a single slab (Fig. 3C,F), which lends support to former suggestions of a gregarious lifestyle (Caron, Conway Morris & Shu 2010; Kimmig, Meyer & Lieberman, 2019). A planktonic larval stage is common in many other modern gregarious marine invertebrates (Pechenik, 1999; Toonen & Pawlik, 2001), with dispersal and global connectivity well-modeled from broadcast spawning of corals (Wood et al., 2014), and has been hypothesized for more ancient gregarious taxa as well (Cortijo et al., 2015; Schiffbauer et al., 2016). The gregarious lifestyle of *H. collinsi* may indicate that it, too, was a broadcast spawner, where fertilization and development of the offspring happened externally, promoting wide dispersal of embryos and larvae and resulting in a broad distribution of offspring. While more evidence is necessary to confirm our interpretation, we observed a single millimetric ovoid structure in close proximity to an adult *Herpetogaster* specimen (Fig. 3A). From hints of a lateral band extending around this ovoid, we offer a tentative suggestion that it may be a possible larva (Fig. 3B), as it is comparable in size and form to those of modern acorn worms or other echinoderms (e.g., Yang et al., 2022). This potential larva is understandably speculative, as it does not preserve enough details to be definitively identified, and other examples within this deposit have not yet been identified. However, previous authors have argued that larvae (*sensu* Hickmann, 1999; Haug, 2018) were likely the key to the worldwide distribution of deuterostomes from Burgess Shale-type biotas (e.g., Han, Zhang & Liu, 2008; Yang et al., 2022), and larvae are already known to play a vital role in Cambrian arthropod development and dispersal (e.g., Liu et al. 2016; Lerosey-Aubril & Laibl, 2021)—both of which urge the continued search for more possible larval fossils from the Balang.

We suggest that *Herpetogaster* having a planktonic larval stage and reproduction through broadcast spawning would have permitted dispersal of this genus over long distances, enabling them to establish a foothold in both Laurentia and Gondwana and providing a logical explanation for the sum of our observations. The question that remains is whether planktonic larvae were shared across the *Herpetogaster* genus, or if they developed later in *H. collinsi*. Testing this hypothesis, however, will require further discoveries of *H. haiyanensis* outside of the Chengjiang region or additional species elsewhere in the Cambrian. Continued investigation of the Balang biota is necessary to confirm or adapt our provisional inferences based on the presence of the tentative but promising tornaria-like larva.

Conclusions

The discovery of *H. collinsi* from the Balang Formation of China represents the first report of this species from Gondwana. Most specimens are complete and the detailed preservation, which required exceptional depositional circumstances, makes an assignment to the species unquestionable. However, the presence of the same sessile species in Laurentia and Gondwana poses the question as to how these organisms managed to colonize two distant parts of the world. We suggest that the most likely scenario sees *Herpetogaster* with a planktonic larval stage and reproduction through broadcast spawning, which would have permitted dispersal over long distances and enabled *H. collinsi* to establish a foothold in both Laurentia and Gondwana. As *Herpetogaster* is already known from Cambrian Stage 3 in Gondwana, it would suggest a possible origination of the genus there, but the limited record of the genus at that time does not yet allow for a definite conclusion.

Competing Interest

The authors declare no competing interest.

Author Contributions

Xianfeng Yang conceived and designed the study, collected specimens, performed the data analyses, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

Julien Kimmig and **James D. Schiffbauer** conceived and designed the study, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.

Shanchi Peng collected specimens, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.

Data availability

All data used in the analyses are as part of the text or electronic supplementary material.

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References

Bath Enright OG, Minter NJ, Sumner EJ, Mángano MG, Buatois LA. 2021. Flume experiments reveal flows in the Burgess Shale can sample and transport organisms across substantial distances. *Communications Earth & Environment* **2**:104 DOI 10.1038/s43247-021-00176-w.

Broce JS, Schiffbauer JD. 2017. Taphonomic analysis of Cambrian vermiform fossils of Utah and Nevada, and implications for the chemistry of Burgess Shale-type preservation of vermiform fossils. *Palaios* **32**:600–619 DOI 10.2110/palo.2017.011.

Caron J-B, Conway Morris S, Shu D. 2010. Tentaculate fossils from the Cambrian of Canada (British Columbia) and China (Yunnan) interpreted as primitive Deuterostomes. *PLoS One* **5**:e9586 DOI 10.1371/journal.pone.0009586.

Cortijo I, Cai Y, Hua H, Schiffbauer JD, Xiao S. 2015. Life history and autecology of an Ediacaran index fossil: Development and dispersal of Cloudina. *Gondwana Research* **28**:419–424 DOI 10.1016/j.gr.2014.05.001.

Dai T, Hughes NC, Zhang X, Fusco G. 2021. Absolute axial growth and trunk segmentation in the early Cambrian trilobite *Oryctocarella duyunensis*. *Paleobiology* **47**:517–532 DOI 10.1017/pab.2020.63.

Ettensohn CA, Wessel GM, Wray GA. 2004. The invertebrate deuterostomes: an introduction to their phylogeny, reproduction, development, and genomics. *Methods in Cell Biology* **74**:1–13 DOI 10.1016/ S0091679X04740017.

Foster JR, Gaines RR. 2016. Taphonomy and Paleoecology of the Middle Cambrian (Series 3) Formations in Utah's West Desert: recent finds and new data. 291–336. In: Comer JB, Inkenbrandt PC, Krahulec KA, Pinnell ML, eds. *Resources and Geology of Utah's West Desert*. Vol. 45. Salt Lake City: Utah Geological Association Publication, 377.

Fu D, Tong G, Dai T, Liu W, Yang Y, Zhang Y, Cui L, Li L, Yun H, Wu Y, Sun A, Cong L, Pei W, Gaines RR, Zhang X. 2019. The Qingjiang biota: a Burgess Shale-type fossil Lagerstätte from the early Cambrian of South China. *Science* **363**(6433):1338–1342 DOI 10.1126/science.aau8800.

Grobben K. 1908. Die systematische Einteilung des Tierreiches. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* **58**:491–511.

Harper DAT, Hammarlund EU, Topper TP, Nielsen AT, Rasmussen JA, Park T-YS, Smith MP. 2019. The Sirius Passet Lagerstätte of North Greenland: a remote window on the Cambrian Explosion. *Journal of the Geological Society* **176**, 1023–1037 DOI 10.1144/jgs2019-043.

Haug JT. 2018. Why the term "larva" is ambiguous, or what makes a larva? *Acta Zoologica* **101**:167–188 DOI 10.1111/azo.12283.

Hickman CS. 1999. Larvae in invertebrate development and evolution. In: Hall BK, Wake MH, eds. *The origin and evolution of larval forms*. San Diego: Academic Press. 21–59.

Hou X-G, Siveter DJ, Siveter DJ, Aldridge RJ, Cong P-Y, Gabbott SE, Ma X-Y, Purnell M, Williams M. 2017. *The Cambrian fossils of Chengjiang, China: the flowering of early animal life*, 2nd edn. Oxford, UK: Wiley Blackwell. 328

Kimmig J, Pratt BR. 2015. Soft-bodied biota from the middle Cambrian (Drumian) Rockslide Formation, Mackenzie Mountains, northwestern Canada. *Journal of Paleontology* **89**:51–71 DOI 10.1017/jpa.2014.5.

Kimmig J, Meyer RC, Lieberman BS. 2019a. *Herpetogaster* from the early Cambrian of Nevada (series 2, stage 4) and its implications for the evolution of deuterostomes. *Geological Magazine* **156**:172–178 DOI 10.1017/S0016756818000389.

Kimmig J, Strotz LC, Kimmig SR, Egenhoff SO, Lieberman BS. 2019b. The Spence Shale Lagerstätte: an important window into Cambrian biodiversity: *Journal of the Geological Society* **176**:609–619 DOI 10.1144/jgs2018-195.

Kimmig J, Pates S, LaVine RJ, Krumenacker LJ, Whitaker AF, Strotz LC, Jamison PG, Gunther VG, Gunther G, Witte M, Daley AC, Lieberman BS. 2023. New soft-bodied panarthropods from diverse Spence Shale (Cambrian; Miaolingian; Wuliuan) depositional environments. *Journal of Paleontology* DOI 10.1017/jpa.2023.24.

Legg DA, Vannier J. 2013. The affinities of the cosmopolitan arthropod *Isoxys* and its implications for the origin of arthropods. *Lethaia* **46**:540–550 DOI 10.1111/let.12032.

Leibach WW, Lerosey-Aubril R, Whitaker AF, Schiffbauer JD, Kimmig J. 2021. First palaeoscolecid from the Cambrian (Drumian, Miaolingian) Marjum Formation of western Utah, USA. *Acta Palaeontologica Polonica* **66**:663–678 DOI 10.4202/app.00875.2021.

Lerosey-Aubril R, Laibl L. 2021. Protaspid larvae are unique to trilobites. *Arthropod Structure and Development* **63**:101059 DOI 10.1016/j.asd.2021.101059.

Lerosey-Aubril R, Gaines RR, Hegna TA, Ortega-Hernández J, Van Roy P, Kier C, Bonino E. 2018. The Weeks Formation Konservat-Lagerstätte and the evolutionary transition of Cambrian marine life. *Journal of the Geological Society* **175**:705–715 DOI 10.1144/jgs2018-042.

Lerosey-Aubril R, Kimmig J, Pates S, Skabelund J, Weug A, Ortega-Hernández J. 2020. New exceptionally preserved panarthropods from the Drumian Wheeler Konservat- Lagerstätte of the House Range Utah. *Papers in Palaeontology* **6**:501–531 DOI 10.1002/spp2.1307.

Li Y, Dunn FS, Murdock DJ, Guo J, Rahman IA, Cong P. 2023. Cambrian stem-group ambulacrarians and the nature of the ancestral deuterostome. *Current Biology* DOI 10.1016/j.cub.2023.04.048.

Lieberman BS. 2003. A new soft-bodied fauna: The Pioche Formation of Nevada. *Journal of Paleontology* **77**:674–690 DOI 10.1666/0022-3360(2003)077<0674:ANSFTP>2.0.CO;2-

Liu Y, Melzer RR, Haug JT, Haug C, Briggs DEG, Hörnig MK, He Y, Hou X. 2016. Three-dimensionally preserved minute larva of a great-appendage euarthropod from the early Cambrian Chengjiang biota. *Proceedings of the National Academy of Sciences, USA* **113**, 5542–5546 DOI 10.1073/pnas.1522899113.

Ma J, Lin W, Liu C, Sun A, Wu Y, Wu Y, Fu D. 2020. A new bivalved arthropod from the Cambrian (Stage 3) Qingjiang biota expands the palaeogeographical distribution and increases the diversity of Tuzoiida. *Journal of the Geological Society* **179**:jgs2020-229 DOI 10.1144/jgs2020-229.

Metschnikoff VE. 1881. Über die systematische Stellung von *Balanoglossus*. *Zoologischer Anzeiger* **4**:139–157.

Müller KJ, Walossek D. 1986. Arthropod larvae from the Upper Cambrian of Sweden. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **77**:157–179 DOI 10.1017/S0263593300010804.

Muscente AD, Schiffbauer JD, Broce J, Laflamme M, O'Donnell K, Boag TH, Meyer M, Hawkins AD, Huntley JW, McNamara M, MacKenzie LA, Stanley GD, Hinman NW, Hofmann MH, Xiao S. 2017. Exceptionally preserved fossil assemblages through geologic time and space. *Gondwana Research* **48**:164–188 DOI 10.1016/j.gr.2017.04.020.

Nanglu K, Caron J-B, Gaines RR. 2020. The Burgess Shale paleocommunity with new insights from Marble Canyon, British Columbia. *Paleobiology* **46**:58–81 DOI 10.1017/pab.2019.42.

Nanglu K, Cole SR, Wright DF, Souto C. 2022. Worms and gills, plates and spines: the evolutionary origins and incredible disparity of deuterostomes revealed by fossils, genes, and development. *Biological Reviews* **98**:316–351 DOI 10.1111/brv.12908.

National Commission on Stratigraphy of China. 2018. *Explanations of stratigraphic chart of China (2014)*. Beijing, China: Geological Publishing House [in Chinese].

Palmer AR. 1998. Terminal Early Cambrian extinction of the *Olenellina*: Documentation from the Pioche Formation, Nevada. *Journal of Paleontology* **72**:650–672 DOI 10.1017/S0022336000040373.

Pari G, Briggs DEG, Gaines RR. 2022. The soft-bodied biota of the Cambrian Series 2 Parker Quarry Lagerstätte of northwestern Vermont, USA. *Journal of Paleontology* **96**:770–790 DOI 10.1017/jpa.2021.125.

Paterson, JR, García-Bellido DC, Jago JB, Gehling JG, Lee MSY, Edgecombe GD. 2016. The Emu Bay Shale Konservat-Lagerstätte: a view of Cambrian life from East Gondwana. *Journal of the Geological Society* **173**:1–11 DOI 10.1144/jgs2015-083.

Pechenik JA. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology - Progress Series* **177**:269–297 DOI 10.3354/meps177269.

Peng S-C. 2009. Review on the studies of Cambrian trilobite faunas from Jiangnan slope belt, South China, with notes on Cambrian correlations between South and North China. *Acta Palaeontologica Sinica* **48**:437–452 (in Chinese with English abstract).

Peng S, Babcock LE, Zhu X, Lei Q, Dai T. 2017. Revision of the oryctocephalid trilobite genera *Arthricocephalus* Bergeron and *Oryctocarella* Tomashpolskaya and Karpinski (Cambrian) from South China and Siberia. *Journal of Paleontology* **91**:933–959 DOI 10.1017/jpa.2017.44.

Robison RA, Babcock, LE, Gunther, VG. 2015. Exceptional Cambrian fossils from Utah: a window into the age of trilobites. *Utah Geological Survey, Salt Lake City, Miscellaneous Publication* **15–1**:1-97.

Saleh F, Qi C, Buatois LA, Mángano MG, Paz M, Vaucher R, Zheng Q, Hou X–G, Gabbott SE, Ma X–Y. 2022. The Chengjiang Biota inhabited a deltaic environment. *Nature Communications* **13**:1569 DOI 10.1038/s41467-022-29246-z.

Schiffbauer JD, Huntley JW, O'Neil GR, Darroch SAF, Laflamme M, Cai Y. 2016. The latest Ediacaran Wormworld fauna: Setting the ecological stage for the Cambrian Explosion. *GSA Today* **26**:4–11 DOI 10.1130/GSATG265A.1.

Streng M, Geyer G. 2019. Middle Cambrian Bradoriida (Arthropoda) from the Franconian Forest, Germany, with a review of the bradoriids described from West Gondwana and a revision of material from Baltica. *PalZ* **93**:567–591 DOI 10.1007/s12542-019-00448-z.

Toonen RJ, Pawlik, JR. 2001. Foundations of gregariousness: a dispersal polymorphism among the planktonic larvae of a marine invertebrate. *Evolution* **55**:2439–2454 DOI 10.1111/j.0014-3820.2001.tb00759.x.

Waloszek D, Dunlop JA. 2002. A larval sea spider (Arthropoda: Pycnogonida) from the Upper Cambrian 'Orsten' of Sweden, and the phylogenetic position of pycnogonids. *Palaeontology* **45**:421–446 DOI 10.1111/1475-4983.00244.

Wen R, Babcock LE, Peng J, Liu S, Liang BY. 2019. The bivalved arthropod *Tuzoia* from the Balang Formation (Cambrian Stage 4) of Guizhou, China, and new observations on comparative species. *Papers in Palaeontology* **5(4)**:719-742 DOI 10.1002/spp2.1262.

Wood S, Paris CB, Ridgwell A, Hendy EJ. 2014. Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Global Ecology and Biogeography* **23**:1–11 DOI 10.1111/geb.12101.

Yang X, Kimmig J, Lieberman BS, Peng S. 2020. A new species of the deuterostome *Herpetogaster* from the early Cambrian Chengjiang biota of South China. *Science of Nature* **107**:37 DOI 10. 1007/s00114-020-01695-w.

Yang X, Kimmig J, Zhai D, Liu Y, Kimmig SR, Peng, S. 2021. A juvenile-rich palaeocommunity of the lower Cambrian Chengjiang biota sheds light on palaeo-boom or palaeo-bust environments. *Nature Ecology and Evolution* **5**:1082–1090 DOI 10.1038/s41559-021-01490-4.

Yang X, Kimmig J, Cameron CB, Nanglu K, Kimmig SR, Zhang C, Yu M, Peng, S. preprint 2022. An Early Cambrian Pelago-Benthic Acorn Worm and the Origin of the Hemichordate Larva. *SSRN* DOI 10.2139/ssrn.4206625.

Zhang X-G, Pratt BR. 1993. Early Cambrian ostracode larvae with a univalved carapace. *Science* **262**:93–94 DOI 10.1126/science.262.5130.93.

Zhao Y, Peng S, Yuan J, Esteve J, Yang X, Wu M, Chen Z. 2019. The trilobite biostratigraphy for the Balang and "Tsinghsutung" formations, Cambrian Series 2, Stage 4 in the Balang area, Jianhe, Guizhou, South China. *Estudios Geológicos* **75**:28–31 DOI 10.3989/egeol.43595.574.

Figures

Figure 1: Distribution of *Herpetogaster*.

(A) Location of the studied section of the Balang Formation located approximately 32 km south-west of Huayuan town, Hunan Province, South China. (B) Generalized stratigraphy of the Balang Formation at this location. (C) Palaeogeographical distribution of *Herpetogaster* during Cambrian Stages 3–4 and during the Wuliuan (modified from Streng and Geyer 2019). 1. *H. hanyanensis* (Chengjiang biota, China, Stage 3), 2. *H. collinsi* (Balang biota, China, Stage 4), 3. *H. collinsi* (Burgess Shale, Canada, Wuliuan), 4. *H. collinsi* (Pioche Formation, Nevada, USA, Stage 4), 5. *H.* sp. (Parker Formation, Vermont, USA, Stage 4). Abbreviations: Ni., Niutitang Formation; Chi, Chinghsutung Formation.

Figure 2: Complete specimens of *Herpetogaster collinsi* Caron et al. 2010 from the Balang Formation of China.

(A) YKLP 14570 a small, likely juvenile specimen, preserving showing slim paired tentacles and the extended stolon. (B–C) YKLP 14571 and YKLP 14572 part and counterpart of a likely sub-adult specimen, the trunk is almost completely preserved as a black carbonaceous film, with the detail of dendritic symmetrical tentacle and a stolon. (D) YKLP 14573, a large adult specimen, with the showing the branching tentacles. Co-occurring with a relative individual. (E) YKLP 14574, adult specimen with prominent segments and segment boundaries (indicated by arrows). (F) YKLP 14575, adult specimen coiled with stolon. (G) YKLP 14576, adult specimen with well-preserved anus and terminal disc. (H) YKLP 14577, adult specimen with both tentacles and well-preserved anus. (I) YKLP 14578, sub-adult specimen with well-preserved branching tentacle. (J)

YKLP 14610, adult specimen with showing segments and segment boundaries. Scale bars: (A) 2mm; (B–J) 5mm. Abbreviations: an, anus; in, intestine; p?, putative pharyngeal pores; ph, pharynx; seg, segment boundary?; st, stolon; stom, stomach; td, terminal disc; te, tentacle.

Figure 3: Gregarious specimens of *Herpetogaster collinsi* from the Balang Formation of China.

(A) YKLP 14580, large adult specimen is found co-occurring with associated plankton, possibly larvae. (B) YKLP 14581, close-up of the associated tonaria-like structure, which shows similarities to extant early stage ambrulacarian larvae. (C) YKLP 14582, at least six specimens of *H. collinsi* on a single slab. (D) YKLP 14584, two adult specimens with almost complete paired tentacles. (E) YKLP 14585, two adult specimens. (F) YKLP 14583, counterpart of (C). (G) YKLP 14586, two complete adult specimens. (H) YKLP 14587, three specimens with almost complete paired tentacles, one preserving the stolon and terminal disc. (I) YKLP 14588, at least two adult specimens. Scale bars: (B) 1mm; (A, C–I) 5mm. Abbreviations: an, anusph, pharynx; seg, segment boundary?; st, stolon; td, terminal disc; te, tentacle.

Figure 4: SEM micrograph and SEM-EDS elemental maps of *Herpetogaster collinsi* from the Balang Formation of China.

(A–G) YKLP 14573. (A) Picture of the specimen indicating the analyzed area (dashed rectangle). (B) Detailed view of the analyzed area. (C–G) SEM-EDS elemental maps of Ca, Fe, C, P, S, respectively. (H–N) YKLP 14583. (H) Picture of the specimen indicating the analyzed area (dashed rectangle). (I) Detailed view of the analyzed area. (J–N) SEM-EDS elemental maps of Ca, Fe, C, P, S, respectively. Scale bars: (A, H) 5mm; (C–G, J–N) 1mm.

Figure 5: All known *Herpetogaster* species from Gondwana and Laurentia.

(A) YKLP 14404, holotype of *Herpetogaster haiyanensis* from the Chengjiang biota (Cambrian; Series 2; Stage 3) of Yunnan, China; (B) YPM IP 239054, ?*Herpetogaster* sp. from the Parker Formation (Cambrian; Series 2; Stage 4) of Vermont, USA; (C) YKLP 14576, *Herpetogaster collinsi* from the Balang Formation (Cambrian; Series 2; Stage 4) of China; (D) KUMIP 482878, *Herpetogaster collinsi* from the Pioche Formation (Cambrian; Series 2; Stage 4) of Nevada, USA; (E) ROM 58051, holotype of *Herpetogaster collinsi* from the Burgess Shale (Cambrian; Miaolingian; Wuliuan) of British Columbia, Canada. Scale bars: 5mm.

Tables

Supplementary Table 1. Measurements of the Balang Formation specimens

Figure 1

Distribution of *Herpetogaster*.

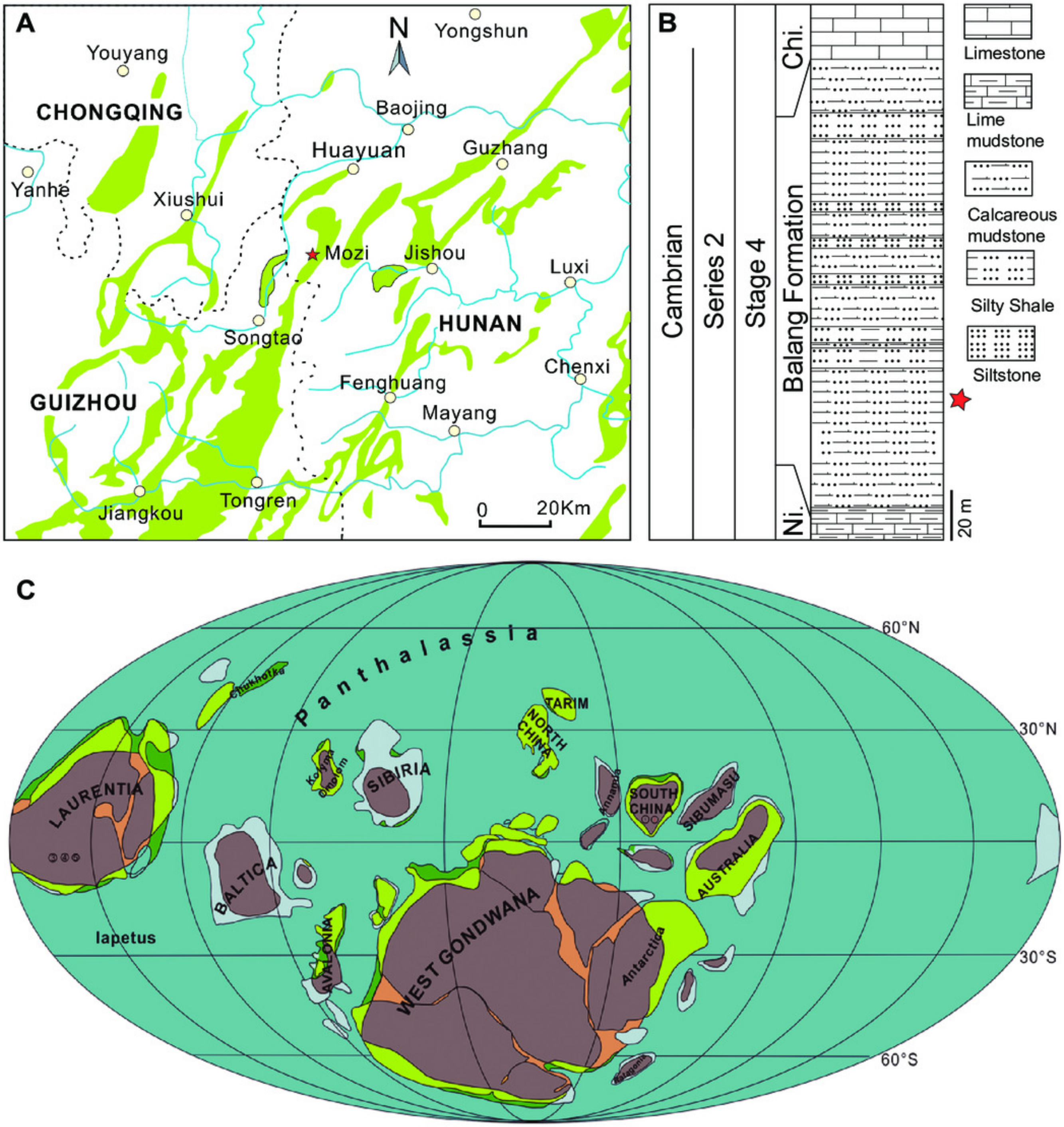

Figure 2

Complete specimens of *Herpetogaster collinsi* Caron et al. 2010 from the Balang Formation of China.

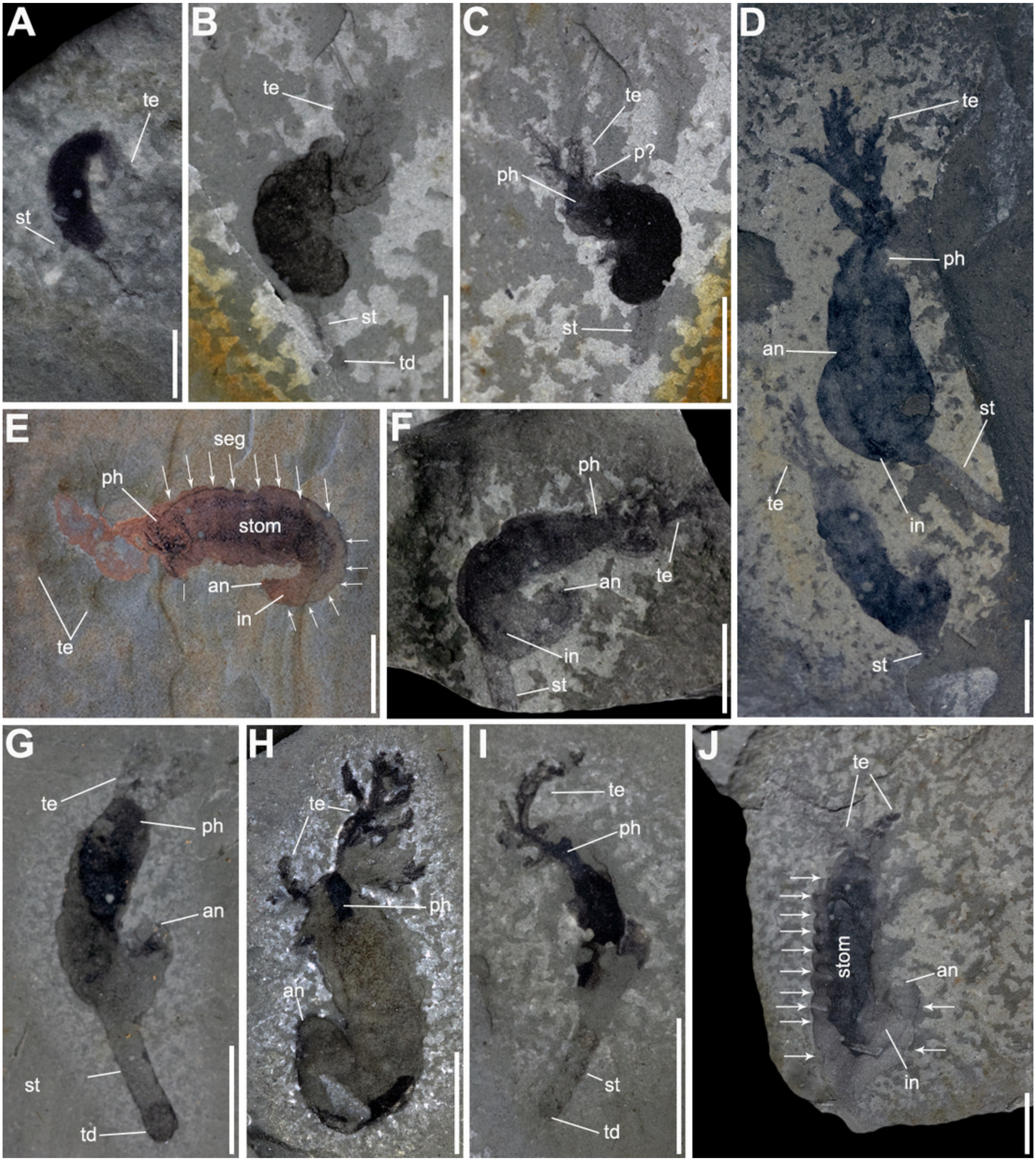
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Figure 3

Gregarious specimens of *Herpetogaster collinsi* from the Balang Formation of China.

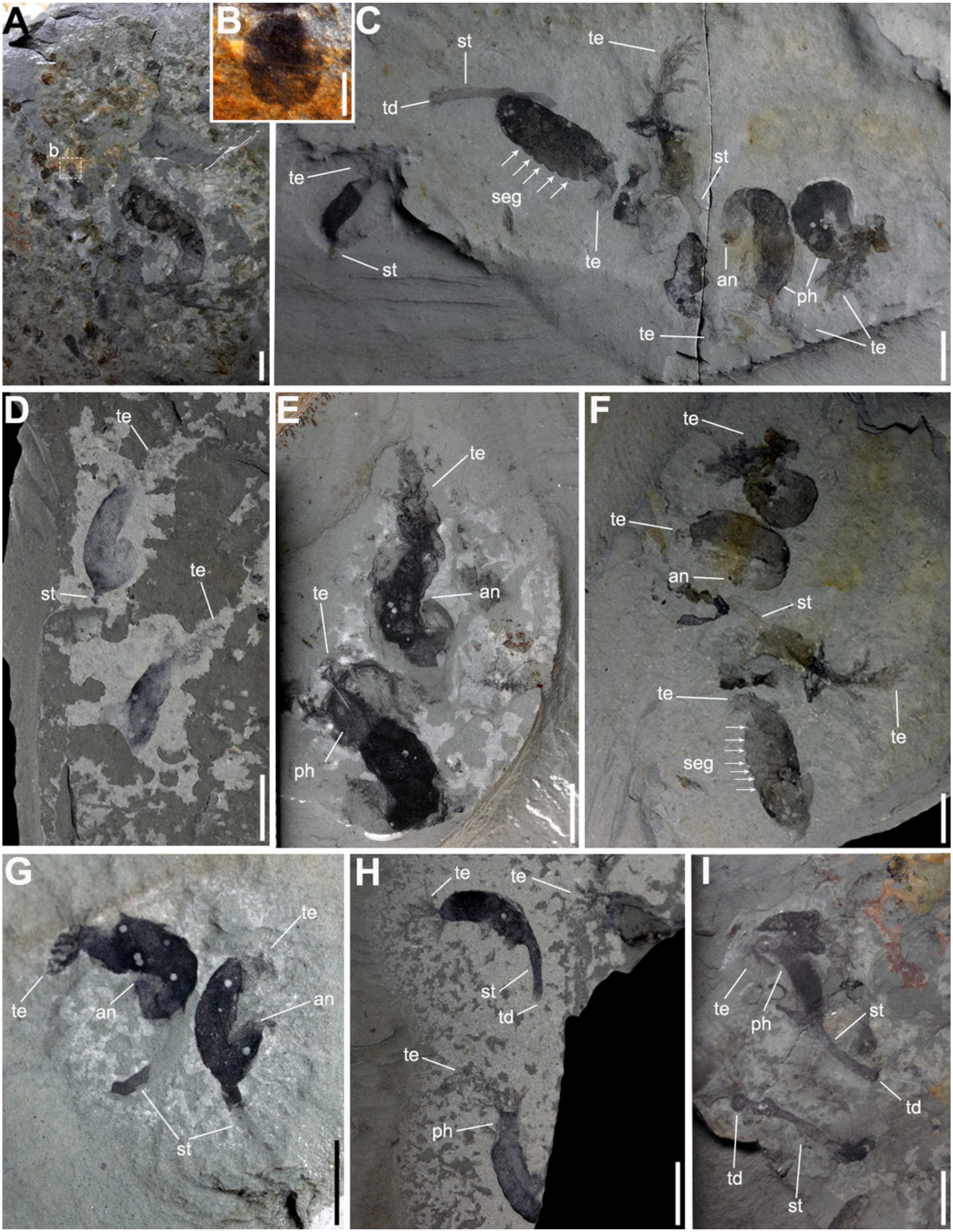
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Figure 4

SEM micrograph and SEM-EDS elemental maps of *Herpetogaster collinsi* from the Balang Formation of China.

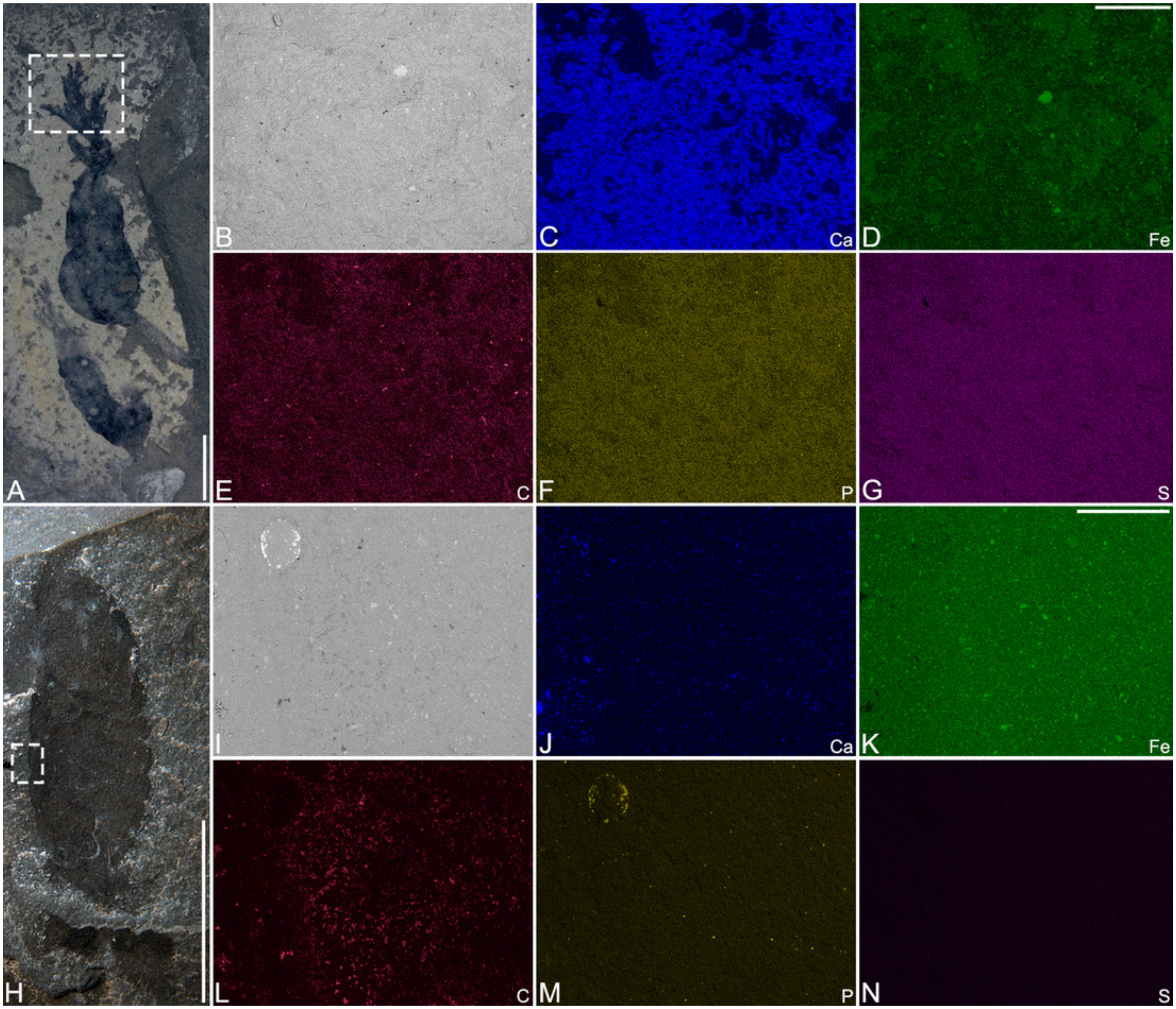

Figure 5

All known *Herpetogaster* species from Gondwana and Laurentia.