

New evolutionary and ecological advances in deciphering the Cambrian explosion of animal life

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The Cambrian explosion represents the most profound animal diversification event in Earth history. This astonishing evolutionary milieu produced arthropods with complex compound eyes (Paterson et al., 2011), burrowing worms (Mángano and Buatois, 2017), and a variety of swift predators that could capture and crush prey with tooth-rimmed jaws (Bicknell and Paterson, 2017). The origin and evolutionary diversification of novel animal body plans led directly to increased ecological complexity, and the roots of present-day biodiversity can be traced back to this half-billion-year-old evolutionary crucible. Alongside familiar living body plans (phyla), there are bizarre Cambrian forms that can be placed in the stem lineages of modern phyla (Budd and Jensen, 2000), allowing us to piece together the macroevolutionary heritage and timing of character trait assembly in many higher groups. The greatest advances in understanding the history of early animal evolution on Earth have been achieved through investigation of exceptionally preserved biotas (Könservat-Lagerstätten). While the Cambrian fossil record is deeply skewed in favor of shelly fossils, exceptionally preserved Cambrian Könservat-Lagerstätten, such as Chengjiang, Guanshan, Emu Bay Shale, Kaili, Burgess Shale, and the Lower Ordovician Fezouata Biota, yield a remarkable array of soft-body/tissue information. Exceptional preservation at these sites provides ‘snapshots’ of the anatomy, body organization, neural evolution, feeding modes, and community structures of the earliest animals that inhabited our planet during the Cambrian Period (541–485 Ma).

The fossils dealt with in this special issue come from Laurentian (Greenland and Labrador, Cambrian Stage 4) and middle Cambrian (Series 3) rocks of Utah; East Gondwana (Emu Bay Shale, Cambrian Stage 4) of South Australia; and a series of Könservat-Lagerstätte from China (in ascending order): the Kuanchuangpu Biota (Fortunian Stage), Chengjiang (Stage 3), Guanshan (Stage 4), Kaili (early Stage 5), and Wangcun (Paibian Stage) biotas.

A systematic examination of fossil assemblages across Cambrian continents demonstrates that the appearance of metazoans during the early Cambrian is not completely synchronous. In the earliest Cambrian Terreneuvian Series (Fortunian and unnamed Stage 2), the fossils are represented by abundant, mostly millimetric, small shelly fossils (SSFs), most of which belong in the superphylum Lophotrochozoa (e.g., Kouchinsky et al., 2012). Apart from a few contentious Terreneuvian ecdysozoans (Liu et al., 2014; Zhang et al., 2015),

the body fossil record of ecdysozoans and deuterostomes is very poorly known during this time, potentially the result of a distinct lack of exceptionally preserved faunas in the Terreneuvian (Fortunian and the unnamed Stage 2). However, this taxonomic ‘gap’ has been partially filled with the discovery of exceptionally well-preserved stem group organisms in the Kuanchuanpu Formation (Fortunian Stage, ca. 535 Ma) from Ningqiang County, southern Shaanxi Province of central China. High diversity and disparity of soft-bodied cnidarians (see Han et al., 2017b) and scalidophoran worms (Zhang et al., 2017) are revealed to complement previously reported basal deuterostomes (Han et al., 2017a). The ecological dominance during the Fortunian is largely represented by abundant radiate clades, especially cnidarians and ctenophores, along with an array of tubes or conical fossils mainly belonging to lophotrochozoans that make up a ‘tube world’ sensu Budd and Jackson (2016).

During Cambrian Stage 3, ecdysozoans, especially trilobites, bivalved arthropods, priapulids, and lobopodians, underwent grand diversification, occupying more than 80% of fossil diversity in the Chengjiang fauna of South China. A diversity of deuterostomes, including the earliest-known agnathan *Haikouichthys* (Shu et al., 2003) and the enigmatic vetulicolians (Ou et al., 2012), also underwent an explosive radiation as demonstrated by the faunas in the Chengjiang Könservat-Lagerstätte. Hu et al. (2017) reinterpret the enigmatic fossil *Malongitubus kuanshanensis* Hu, 2005 as a potential hemichordate pterobranch. If interpreted correctly, this stretches the lineage of pterobranchs back to the early Cambrian Stage 3, much earlier than previously thought. Utilizing fossil specimens from the middle Cambrian Burgess Shale and the Late Ordovician of Canada, Holmer et al. (2017) restudied the Chengjiang specimens of *Kutorgina chengjiangensis* Zhang et al., 2007 and determined that there were two apical openings in the earliest calcareous-shelled brachiopods with the apical foramen representing larval attachment subsequently becoming nonfunctional through ontogeny.

In the slightly younger Guanshan fauna (Stage 4), Zeng et al. (2017) present the first report of a new radiodontan oral cone with a unique combination of anatomical features, shedding new light on the feeding strategy and phylogeny of anomalocaridids. The approximately cotemporary soft-body fossils of priapulids are also documented for the first time in details from the Yanwangbian Formation of southern Shaanxi, along the northern margin of the Yangtze platform (Yang et al., 2017). These fossils, together with

some sclerites of *Microdictyon* from the southern margin of North China (Pan et al., 2017), herald a rapid generic diversification and ecological expansion of ecdysozoans (priapulids, lobopodians, and arthropods). Skovsted and Topper (2017) provide insight into the enigmatic tubular fossils of mobergellans from the early Cambrian (Stage 4?) of Greenland and Labrador and address the contradictory issues on the muscle scars and their functional morphology. The presence of enigmatic eldonioids with associated trace fossils is documented by Schroeder et al. (2017) from the lower Cambrian Emu Bay Shale Konservat-Lagerstätte of South Australia, providing the first record of the group for the Cambrian of East Gondwana.

After early Cambrian Stage 4, exceptionally preserved biotas generally become less abundant, but Liu et al. (2017) describe new three-dimensional phosphatized cycloneurians from the Paibian of South China. A detailed investigation by Pates et al. (2017) of hurdiid specimens from the Spence Shale Member, Langston Formation, and the Wheeler and Marjum formations of Utah greatly expands knowledge of Laurentian hurdiids, extending the range of the group above and below the Burgess Shale, which has implications for paleogeographic and temporal analyses of hurdiid distribution.

The 11 papers presented in this special issue focus on a wide range of themes that collectively address important evolutionary and ecological aspects of the Cambrian radiation, the greatest animal radiation event in the history of life.

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