



Early fossil record of Euarthropoda and the Cambrian Explosion

Allison C. Daley^{a,b,c,1}, Jonathan B. Antcliffe^{a,b,c}, Harriet B. Drage^{a,b,c}, and Stephen Pates^{a,b}

Edited by Neil H. Shubin, University of Chicago, Chicago, IL, and approved April 6, 2018 (received for review December 20, 2017)

Euarthropoda is one of the best-preserved fossil animal groups and has been the most diverse animal phylum for over 500 million years. Fossil Konservat-Lagerstätten, such as Burgess Shale-type deposits (BSTs), show the evolution of the euarthropod stem lineage during the Cambrian from 518 million years ago (Ma). The stem lineage includes nonbiomineralized groups, such as Radiodonta (e.g., *Anomalocaris*) that provide insight into the step-by-step construction of euarthropod morphology, including the exoskeleton, biramous limbs, segmentation, and cephalic structures. Trilobites are crown group euarthropods that appear in the fossil record at 521 Ma, before the stem lineage fossils, implying a ghost lineage that needs to be constrained. These constraints come from the trace fossil record, which show the first evidence for total group Euarthropoda (e.g., *Cruziana*, *Rusophycus*) at around 537 Ma. A deep Precambrian root to the euarthropod evolutionary lineage is disproven by a comparison of Ediacaran and Cambrian lagerstätten. BSTs from the latest Ediacaran Period (e.g., Miaohu biota, 550 Ma) are abundantly fossiliferous with algae but completely lack animals, which are also missing from other Ediacaran windows, such as phosphate deposits (e.g., Doushantuo, 560 Ma). This constrains the appearance of the euarthropod stem lineage to no older than 550 Ma. While each of the major types of fossil evidence (BSTs, trace fossils, and biomineralized preservation) have their limitations and are incomplete in different ways, when taken together they allow a coherent picture to emerge of the origin and subsequent radiation of total group Euarthropoda during the Cambrian.

paleontology | Paleozoic | evolution | Arthropoda | Cambrian explosion

Euarthropoda (in the sense of ref. 1), consisting of the extant groups Chelicerata and Mandibulata, is the most abundant and diverse animal phylum, and is one of the best-studied in modern biology. For over 500 million years, euarthropods have been major components of animal ecosystems, as indicated by their rich fossil record (2, 3). The earliest fossil assemblages of euarthropods show a range of preservation types, and they provide the most complete metazoan example of phylum-level anatomical construction in the early evolutionary lineage (2, 4). Euarthropod fossils have been key for examining the dynamics of the rapid early radiation of animals during the Cambrian explosion (2, 4–7). This event is documented by the Cambrian fossil record, which depicts a coherent sequence of events, including the origins of bioturbation, biomineralization, animal reef systems, zooplankton, and the appearance

of all major animal phyla in the 30 or so million years following the Ediacaran–Cambrian boundary (2, 7–10). However, Precambrian ancestors to the Metazoa have long been sought (11–13), with exploration efforts yielding numerous and diverse paleontological discoveries in this interval of time (8, 14).

We here examine the early fossil record of euarthropods (Fig. 1), and use it as a model to explore the quality of the fossil data as it relates to the Cambrian explosion. Numerous types of fossil preservation, including soft-bodied macrofossils from Burgess Shale-type (BST) localities, biomineralized exoskeletons, microfossils (phosphatic, siliceous, and carbonaceous), and trace fossils are compared and contrasted across the Ediacaran–Cambrian boundary to constrain when euarthropods first evolved. In congruence with the most recent analyses from molecular paleobiology

^aInstitute of Earth Sciences, University of Lausanne, Géopolis, CH-1015 Lausanne, Switzerland; ^bDepartment of Zoology, University of Oxford, OX1 3PS Oxford, United Kingdom; and ^cOxford University Museum of Natural History, OX1 3PW Oxford, United Kingdom

Author contributions: A.C.D. and J.B.A. designed research; A.C.D. and J.B.A. performed research; A.C.D., J.B.A., H.B.D., and S.P. analyzed data; and A.C.D., J.B.A., H.B.D., and S.P. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

¹To whom correspondence should be addressed. Email: allison.daley@unil.ch.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1719962115/-DCSupplemental.

Published online May 21, 2018.

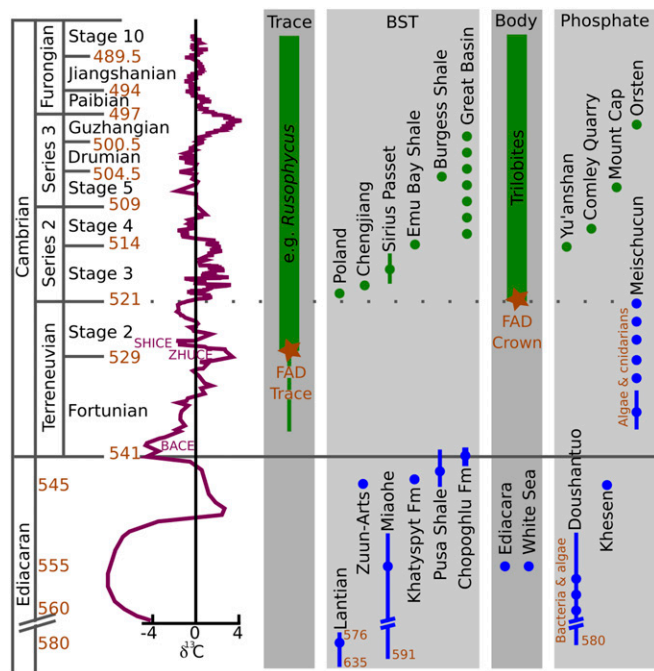


Fig. 1. Timescale of the Cambrian fossil evidence of euarthropods. Age of important localities shown in columns for trace fossils, BSTs, body fossils, and phosphatic microfossils. Localities in green show evidence of euarthropods, localities in blue do not. Orange stars indicate the FAD of total group Euarthropoda (FAD Trace) and crown group euarthropods (FAD Crown). Time in millions of years (red writing). Data from refs. 128 and 129.

(15–17), our comprehensive fossil dataset suggests an entirely Cambrian evolution for this phylum, as described below.

Cambrian BST Localities Reveal the Euarthropod Stem Lineage

The most renowned fossils of the Cambrian explosion are the diverse animal assemblages found at BST localities (Fig. 2), where soft-bodied fossils are preserved as compressions and carbonaceous films in fine-grained mudstones (18, 19). Euarthropods dominate Cambrian BSTs, and many possess morphologies that differ greatly from extant taxa. The stem and crown group concept (2) integrates Cambrian taxa into modern animal phylogeny, with the monophyletic crown group consisting of all extant members and their extant and extinct descendants of the last single-common ancestor uniting them. Stem lineage members are extinct taxa closely related to a crown group, but outside of it because they lack defining morphological characteristics of the crown (2). When stem taxa are arranged in a paraphyletic lineage leading to a crown group, they reveal the order of character acquisition and indicate homologies between living taxa.

Crown group euarthropods possess an exoskeleton, segmented body, jointed paired appendages, tagmosis, and specialized head appendages. A consensus view of how these characteristics were acquired along the euarthropod stem lineage is emerging (Fig. 3), although the interrelationships are often debated (1, 3, 4, 6). The base of the panarthropod tree is occupied by Onychophora, Tardigrada, and a grade of Cambrian lobopodians, including *Aysheaia* (Fig. 2A). The euarthropod lower stem lineage includes *Jianshanopodia* and *Megadictyon*, which have annulated bodies with unjointed lobopod walking limbs (3,

20). Next are the “gilled lobopodians” from Sirius Passet, *Kerygmachela*, and *Pambdelurion* (21), which possess lateral flaps and unsclerotized frontal appendages in addition to lobopod walking limbs. *Pambdelurion* also has sclerotized plates surrounding the ventral-facing mouth (21). The Burgess Shale taxon *Opabinia* (Fig. 2B) has a similar body morphology to the gilled lobopodians (22, 23), but a more developed head with compound eyes, a posterior-facing mouth, and a grasping appendage (24).

Radiodonta is a large clade (Fig. 2 C–E) that includes *Anomalocaris* and occupies the uppermost lower stem lineage position (4). Radiodonts lack lobopods and have a body with lateral flaps and setal blades, and a head with a pair of sclerotized appendages, circular mouthparts, and paired stalked compound eyes (4, 25–27). With over 20 taxa described, it is possible to examine ecological and evolutionary trends within this diverse and globally distributed clade. For example, radiodont frontal appendages (Fig. 2D) and mouthparts (Fig. 2C) were specialized either for active predation, scavenging, or filter feeding, so ecological dynamics can be examined (26, 27). Radiodonta also provide insight into euarthropod anatomical innovation. The evolutionary importance of the radiodont frontal appendage is seen in its homology to the labrum of modern euarthropods (6, 28). Important information is also revealed about the origin of the euarthropod biramous limb, a unique two-branched limb found in crustaceans and trilobites that is hypothesized to have formed from the fusion of two separate appendages (4, 22). The two pairs of swim flaps in radiodonts (27) indicate that the endopod (walking branch) and exopod (gill branch) of the biramous limb are homologous to a ventral set of walking limbs (in lobopodians, “gilled lobopodians,” *Opabinia*) or ventral flaps (in radiodonts) and a dorsal set of flaps with setal structures, respectively. The paired flaps of radiodonts were used for swimming, as indicated by the prominent euarthropod-like musculature found at the bases of the flaps in *Anomalocaris* (white arrows in Fig. 2E) (29). Other euarthropod features of radiodonts include paired compound eyes of *Anomalocaris* from the Emu Bay Shale, each with 16,000 hexagonally packed ommatidial lenses (30), and complex cephalic carapaces, which reveal the segmental architecture of the euarthropod head region (4, 31). Radiodont anatomy also informs on the evolution of the euarthropod digestive system, with prominent gut glands (black arrows in Fig. 2E) indicating complexity in their feeding behavior (20). Radiodonts exemplify the importance of studying fossil stem lineage taxa to understand the anatomical innovation that led to the evolutionary success of the euarthropods.

Crownwards of Radiodonta is the Deuteropoda, a monophyletic clade that includes the upper stem and crown group Euarthropoda, and consists of a wide variety of taxa with contested interrelationships (1). Upper stem lineage euarthropods include the fuxianhuiids (32), *Leanchoilia* and other megacheirans (“great appendage” euarthropods) (33) (Fig. 2F), and bivalved taxa, such as *Canadaspis*, *Isoxys*, and *Perspicaris* (34) (Fig. 2G), all of which have a segmented body bearing biramous limbs and a multisegmented head with specialized appendages (1), although not all crown group head structures are seen. Some megacheirans have alternatively been placed within the crown as stem-lineage chelicerates (35). The euarthropod crown likely also includes the trilobites (33, 36, 37), trilobite-like taxa (Trilobitomorpha) such as *Helmetia* (Fig. 2H), and the vicissicaudates (38), including aglaspidids and taxa such as *Sidneyia* (Fig. 2I) and *Emeraldella* (Fig. 2J). Vicissicaudata and Trilobitomorpha are often united in the clade Artiopoda (Fig. 3), which has alternatively been aligned with the mandibulates (37) or the chelicerates (33).

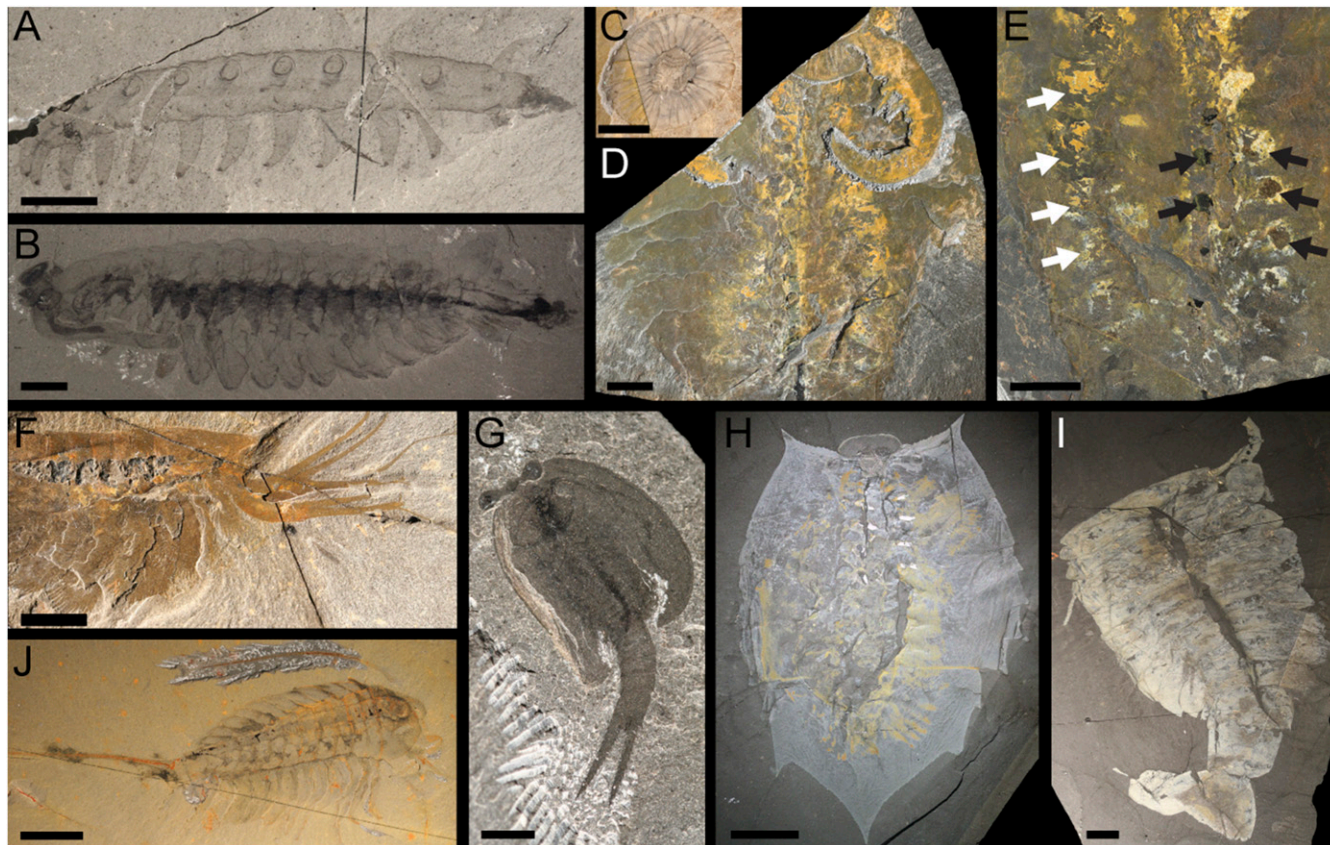


Fig. 2. Panarthropod fossils from the Burgess Shale. (A) Lobopodian *Aysheaia pedunculata*, USNM 83942. (B–E) Lower stem group euarthropods. (B) *Opabinia regalis*, USNM 155600. (C–E) Radiodont fossils. (C) *Hurdia* mouthpart, USNM 368583. (D) *Anomalocaris canadensis* body fossil, GSC 75535A. (E) *Anomalocaris canadensis* from D with musculature (white arrows) and gut glands (black arrows). (F and G) Upper stem group euarthropods. (F) Megacheiran *Leanchoilia superlata*, USNM 250299. (G) Bivalved arthropod *Perspicaris dictynna*, USNM 189245. (H–J) Crown euarthropods, artiopodans. (H) Trilobitomorph *Helmetia expansa*, USNM 83952. (I and J) Vicissicaudates. (I) *Sidneyia inexpectans*, USNM 250208. (J) *Emeraldella brocki*, USNM 57702. (Scale bars: 5 mm in A; 10 mm in B–F and H–J; 3 mm in G.)

The euarthropod stem lineage depicts a clear scenario of character acquisition, from the basal condition of an annulated body with lobopodous limbs through increasing levels of arthropodization. Stem lineage taxa originate from multiple BSTs, with the oldest being a single radiodont appendage from central Poland (39), which is only 1–2 million years older than the abundant and diverse arthropod assemblage of the Chengjiang biota at 518 million years old (40) (Fig. 1).

Microscopic Fossils of Extant Crown Group Euarthropods in the Cambrian

Microscopic fossils, such as small carbonaceous fossils (SCFs) and phosphatized “Orsten-type” fossils provide the earliest evidence of extant crown group euarthropods in the form of crustacean larvae and fragments. Three-dimensional phosphatic preservation is well known from the Upper Cambrian Orsten limestones of Sweden, and the Orsten-type preservational mode is widespread both temporally and geographically (41). The earliest crustaceans are *Yicaris dianensis* (Fig. 4E) and *Wujicaris muelleri* from the phosphatic Yu’anshan Formation, China (42, 43) and are at least 514 Ma (44). These taxa are comparable to larvae of crown group crustaceans such as cephalocarids, branchiopods, and maxillopods (43). The oldest nonlarval crown-group fossil crustacean is *Klausmuelleria salopensis* reported from the 511 Ma *Protolenus* Limestone, Comley, Shropshire, United Kingdom. *Klausmuelleria*

is a phosphatocopid euarthropod, with paired appendages, a labrum, and a sternum preserved inside two carapaces (10).

The slightly younger Mount Cap and Deadwood Formations in western Canada preserve euarthropod appendage fragments as 3D microscopic SCFs (Fig. 4 A–D). These contain a variety of spines, setae, and setules for filter feeding (Fig. 4 A–C), and the molar surface of grinding mandibles (Fig. 4D) (45, 46). Comparison with modern phyla links the Mount Cap and Deadwood fossils to extant crustaceans, including branchiopods and malacostracans (45, 46). Similar fossils of copepod mandibles are reported from the Nolichucky Shale (Cambrian Series 3 to Furongian in age) of Tennessee (47).

Trilobites Appear Earlier than the BSTs and Microfossils

Crown group euarthropods appear even earlier in the Cambrian, at 521 Ma, in the form of trilobite body fossils (48) (Fig. 4G). The extinct trilobites are placed within crown group Euarthropoda (33, 36, 49) (Fig. 3) based on the presence of derived morphological features, such as biramous limbs, deutocerebral antennae (36), diverse feeding specializations, and a heavily biomineralized calcitic exoskeleton (36, 49). Their position within Euarthropoda is uncertain, with trilobites (and other Trilobitomorpha) being aligned with the Chelicerata, creating clade “Arachnomorpha” (33, 50, 51), or placed within the clade Mandibulata (15, 36, 37, 52).

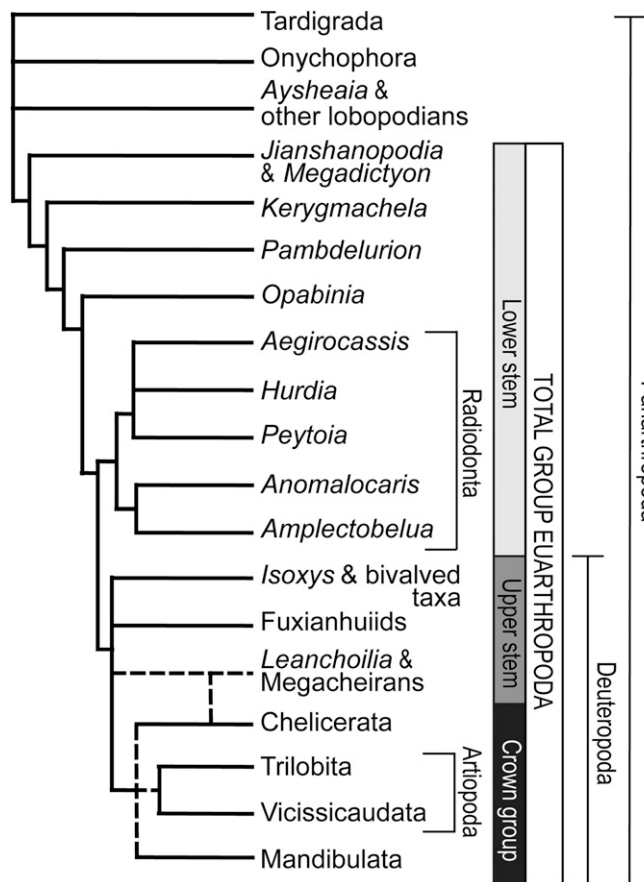


Fig. 3. A generalized phylogeny of panarthropod relationships, distinguishing the crown group Euarthropoda from the lower and upper stem lineage euarthropod taxa. Dashed lines indicate the uncertain phylogenetic placements of Megacheira and Artiopoda. Data from refs. 1, 4, 27, 31, 34, and 37.

The oldest trilobites currently define the beginning of Cambrian Series 2 Stage 3 at approximately 521 Ma (53) (Fig. 1), although formal designation has yet to be finalized for this boundary and the use of other sources (e.g., acritarch or molluscan biostratigraphy, isotopic curves) may mean the first appearance date (FAD) of trilobites could fall marginally into the latest Terreneuvian (54, 55). The oldest trilobites appear coevally at multiple localities, and include *Profallogaspis jakutensis* and *Profallogaspis tyusserica* from Siberia (48, 50, 56), *Hupetina antiqua* and fallotaspids (Fig. 4G) from the lowest Igoudine Formation of Morocco (55), *Lunagraulos tamamensis* from the lowermost Ovetian of Spain (57), and *Fritzaspis generalis* from Laurentia (48), meaning that disparate clades appear simultaneously (54). These are rapidly followed by the earliest trilobites from Australia and China, *Abadiella* and *Parabadiella* (48, 53, 54, 58), and within a few million years, trilobite fossils can be found globally in vast numbers, showing high ecological and morphological diversity (54, 55). This rapid global distribution may be a result of a planktonic larval stage and adult stages (59), and was controlled by factors such as paleoclimatic variation and paleogeographical conditions, including carbonate productivity and periods of anoxia (60). Distribution was likely facilitated by patterns of oceanic circulation (faster equatorial flow and more open circulation) and newly developed environments resulting from Cambrian transgression (57, 60), such that if oceanic turnover time was

similar to the present (20,000 to 30,000 years), trilobite diversification and dispersal would appear almost instantaneous given the resolution of the fossil record. Based on distribution patterns alone, there is no reason to suppose the existence of trilobites before their first appearance in the fossil record at 521 Ma (contrasting ref. 61).

It may seem counter-intuitive that crown group euarthropods appear at 521 Ma, while the first appearance of stem lineage euarthropods is not until 518 Ma. This makes sense in light of two points. First, trilobites have easily preserved, biomineralized skeletal elements, while stem lineage euarthropods lack biomineralized exoskeletons and require preservation of soft tissues in BSTs. Second, stem lineage euarthropod fossils do not represent the morphology at the divergence point to crown euarthropods, but are instead end members on a lineage that has undergone evolution since branching off from the lineage that led to crown Euarthropoda. However, stem lineage euarthropods would have evolved before trilobites, even if they are not preserved, so the real question is how much earlier

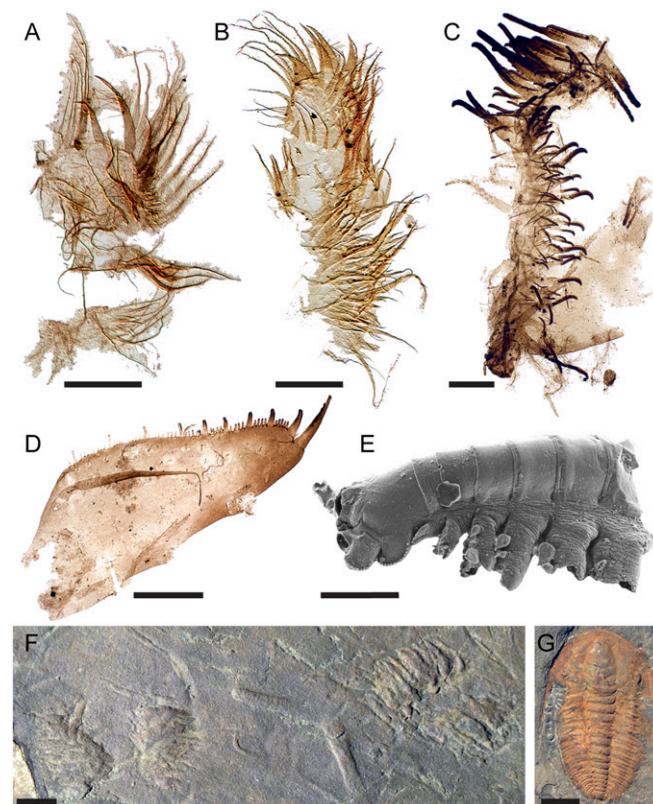


Fig. 4. Earliest fossil evidence of total group Euarthropoda, and extinct and extant crown group Euarthropoda. (A–D) SCFs of early crustaceans. Images courtesy of T. Harvey (University of Leicester, Leicester, United Kingdom) and N. Butterfield (University of Cambridge, Cambridge, United Kingdom). (A and B) Comparison of branchiopod filter plates from early Cambrian Mount Cap (A) and middle Cambrian Deadwood Formations (B, GSC 135392). (Scale bars, 50 μ m.) (C) Appendage setae from Mount Cap, GSC 34928. (Scale bar, 70 μ m.) (D) Branchiopod mandible from Mount Cap, GSC 34931. (Scale bar, 100 μ m.) (E) Oldest crustacean *Yicaris dianensis*, YKLP 10840. (Scale bar, 150 μ m.) (F) Earliest total group euarthropod evidence, *Rusophycus* trace fossil, GSC 85983. E and F reprinted with permission from ref. 44. (Scale bar, 20 mm.) (G) Fallotaspid trilobite from Morocco, OUMNH AX.27. (Scale bar, 10 mm.)

than 521 Ma did they appear? The answer comes from the trace fossil record.

Oldest Euarthropod Evidence Comes from the Earliest Cambrian Trace Fossil Record

Trace fossils record the activities of animals as they interact with sediment, and can include tracks, burrows, feeding marks, and even death throws. Before the first appearance of trilobites at 521 Ma, there are 20 million years of the Terreneuvian for which trace fossils are abundant (9) (Fig. 1), including the euarthropod traces *Rusophycus*, *Diplichnites*, *Cruziana*, *Asaphoidichnus*, *Tasmanadia*, and *Cheiihnus*.

The general order for the first appearance of euarthropod traces has been described as *Monomorphichnus*, *Diplichnites*, *Rusophycus*, and *Cruziana* (62). Although *Monomorphichnus* appears coevally with *Treptichnus* at the base of the Cambrian, the latter's affinity as an euarthropod trace (62, 63) can be doubted because it consists of a single row of traces rather than being paired. In contrast, *Rusophycus* (Fig. 4F) provides definitive evidence of crown group Euarthropoda (44) as it records the activity of paired limbs across a bilaterally symmetrical body plan and are "undoubtedly resting excavations made by trilobites" (ref. 64, p. W101). Some specimens of *Rusophycus* have been found with the trilobite trace maker in situ (65). While *Rusophycus* appears later than *Diplichnites* in many sections worldwide, it appears before *Diplichnites* immediately above the basal Cambrian golden spike in the Chapel Island Formation of Newfoundland (Fig. 4F) (66) and immediately above *Treptichnus* in the Breidvika Formation of northern Norway (67). This makes *Rusophycus* the oldest euarthropod trace globally (see [SI Appendix](#) for details of other Terreneuvian euarthropod traces).

During the Ediacaran period, euarthropod trace fossils are "strikingly absent" (ref. 9, p. 3), but it is clear that euarthropod activity is abundant, diverse, and global before 528 Ma (based on correlations to the FAD of the marker *Watsonella crosbyi* at the base of Stage 2). *Rusophycus* likely appeared early in the Fortunian (53) based on biozone correlations (55). However, precise dates for these traces suffer from difficulties in correlating biostratigraphic information in the Fortunian and Cambrian Stage 2 and an absence of absolute dates in this interval ([SI Appendix](#)), but we can be confident that euarthropod traces appear substantially before the first appearance of euarthropod body fossils.

Modes of Fossil Preservation Are Comparable in the Cambrian and Precambrian

To search for euarthropod fossils earlier in the rock record requires comparable fossil preservation modes in the Precambrian, where exceptional preservation of soft-tissues abounds (14). Of the fossils described above, BST and phosphatic microfossil preservation are abundant in the Precambrian, and other modes of relevance include siliciclastic moldic and chert preservation ([SI Appendix](#)). These cover a wide variety of depositional environments, and preserve hard and soft organisms on macroscopic and microscopic scales.

BST preservation is characterized as organic preservation of soft-bodied macrofossils as carbonaceous films preserving primary tissues, rather than early authigenic mineral replacement (18, 19, 68). Later Phanerozoic carbonaceous fossils, such as algae, plants, graptolites, and eurypterid cuticle (68) preserve only selected refractory tissues and do not reach the same level of anatomical fidelity, abundance, or diversity as the Cambrian BSTs (69). Carbonaceous fossils are also abundant in Proterozoic mudrocks, and

although detailed investigations of the depositional and diagenetic regimes of these localities are lacking, their preservation appears to be very similar to the Cambrian BSTs. Proterozoic carbonaceous compression fossils are seen, for example, in the Miaohu and Lantian biotas of South China (70, 71), Jinxian biota of North China (72), Pusa Shale of Spain (73, 74), Chopoghlu Shale of Iran (75), Khatyspyt Formation of Siberia (76), and Zuun-Arts biota of western Mongolia (77) (Fig. 1). The last four localities are latest Ediacaran in age (ca. 545 Ma), and BST preservation is then absent from the rock record until Cambrian Series 2, representing a gap of at least 20 million years (69). In Cambrian Series 2 and 3, as many as 50 BST localities are known (69), but BSTs are largely absent from the post-Cambrian rock record (68), a pattern that results from a combination of factors unique in Earth's history. Preservation is enabled by rapid accumulation of clays and silts beneath poorly oxygenated water masses, with stagnant anoxic conditions that reduce rates of microbial decay and bioturbation (18, 19, 78, 79), and the rapid early sealing of these entombing sediments by pervasive carbonate cements (80). Carbonate availability was likely amplified by enhanced weathering of continental basement rocks during the basal Cambrian marine transgression (79). Taken together with the increased use of carbonate as a biomineral during the Cambrian (14), these data show that carbonate became dramatically less available as a direct chemical cement by the end of the Cambrian, closing this taphonomic window.

Phosphatic microfossil preservation of soft tissues reached its greatest extent during the late Precambrian to early Cambrian (14, 81, 82). Phosphate precipitates on the seafloor within the photic zone under reducing conditions (82), when anoxic nutrient-rich water masses up-well into shallow water carbonate lagoons (14). It appears in the Ediacaran (14) as interbedded stratiform phosphate and chert layers in shallow water shale and limestone sequences (83) that formed along the northern margins of a vast ocean that now outcrops from south China through to Mongolia, west to the Arabian Peninsula, and into Oman (55). Numerous sections span the Ediacaran–Cambrian boundary and contain abundant bedded phosphates that are taphonomically, compositionally, and depositionally identical. High-quality post-Ordovician marine phosphate is unknown (14), indicating that the phosphorite preservation window is similar in length to that of BST deposits. This is because the phosphorus-rich redox boundary layer was shallow in Ediacaran oceans, allowing for early and rapid phosphatization within the photic zone, but during the Cambrian oxygen levels were increased in the water column by nekton and zooplankton (84, 85) and in the sediment by bioturbation (86), which forced the phosphogenic zone downward, through the water column and into the sediment profile.

Siliciclastic moldic preservation is associated with Ediacaran biota fossils, where fine to coarse sediments preserve external molds of soft organisms in open marine conditions. This preservation is abundant and widespread during the latest Ediacaran Period (87). At Ediacara in South Australia, rapid silicate lithification of overlying event sands preserve communities in situ by molding their upper surfaces (87), with the sands being stabilized through pervasive trapping and binding by microbial mats (87), which are preserved in detail in siltstones in Brazil (88) ([SI Appendix](#)). In sites across the Avalonian paleogeographic terrane, such as Mistaken Point, Newfoundland, Canada and Charnwood Forest, Leicestershire, United Kingdom, the lower surfaces of organisms are molded by smothering volcanic ash (87) and binding by microbial mats (89). Elsewhere, molds are formed from the rapid lithification of carbonates (White Sea, Russia) (90), or as

infaunal whole-body 3D preservation (Namibia) (91). Moldic preservation becomes less common at the start of the Cambrian (92–94) and rare later in the Phanerozoic, never again replicating the worldwide distribution seen in the Ediacaran (14), correlating with the decline and eventual disappearance of pervasive microbial mats during the Cambrian (14, 95).

These examples make it clear that the Cambrian is much more like the late Precambrian in terms of its taphonomy than it is like the rest of the Phanerozoic (14). A similar trend is also observed in chert deposits of cellular preservation (14) (*SI Appendix*), with high quality Precambrian and Cambrian preservation of soft tissues declining markedly in abundance and fidelity in post-Cambrian deposits. The differences between Ediacaran and Cambrian lagerstätten is mainly one of proportion rather than mode of preservation (14), for which numerous factors are responsible, as is also true for their decline after the Cambrian. The major factors are: alteration of ocean pH and Eh; dramatic reduction of phosphate, carbonate, and silica ion saturation in the seawater linked to abundant biomineralization in the Cambrian; oxygenation of upper sediment layers from increasing animal burrowing; lowering of the phosphate precipitation zone into deep sediment layers; and major erosional and facies differences related to global tectonics, which altered chemical availability for cement formation and changed ocean shelf areas (14, 78–80).

Ediacaran Biota Euarthropod Candidate Fossils Cannot Be Substantiated

Putative animals, including two euarthropod taxa, have been suggested from the siliciclastic moldic fossils of the Ediacaran biota, which consists of enigmatic discs and fronds (14). Animal affinities for the Ediacaran biota have been extensively debated (2, 11, 96). For example, although discoidal fossils were long regarded as cnidarian jellyfish (12), they are now known to instead consist of a mélange of microbialites, tool marks, gas escape structures, soft sediment deformation, and holdfasts (97). The suggested Pennatulacean affinity for Ediacaran rangeomorphs (11) has also been shown to be without any basis (98, 99). The numerous proposed affinities for *Dickinsonia* include Annelida (11), Placozoa (100), an extinct higher animal clade (Proarticulata) (101), Foraminifera (102), or an extinct eukaryotic kingdom (Vendobionta) (96). It is not our aim to review every enigmatic taxon, but only to emphasize the enigmatic nature of the Ediacaran biota and discuss putative euarthropod taxa.

Candidate euarthropod fossils include *Spriggina* and *Parvancorina* from the Ediacara Member in Australia and the White Sea locality in Russia (Fig. 1) (11, 12). No definitive characters have yet been identified that allow us to confidently place these fossils within Euarthropoda (or even within Metazoa). *Spriggina*, for example, does not possess bilateral symmetry, but instead has a marked offset along the midline (103), and this alone is sufficient to reject a euarthropod affinity. This mode of construction is common in the Ediacaran biota, and we emphasize that fossils should be analyzed in the context of their cooccurring biota to identify reliable characteristics for phylogenetic placement. *Spriggina* was also compared with *Metaspriggina* from the Cambrian Burgess Shale, with both considered euarthropods (104). *Metaspriggina* has since been shown to be a chordate (105, 106) and is unrelated to *Spriggina*, the affinity of which remains unknown.

Parvancorina has been compared with the Burgess Shale euarthropod *Skania* (104, 107) and the related marrellomorphs (13) based on similarity of the anchor-shaped anterior region, and

coding these characters as homologous in a phylogenetic analysis resolves *Parvancorina* as a stem group euarthropod (108). However, the anchor of *Parvancorina* lacks the anterior doublure and medial keel of the cephalic structure of *Skania*, meaning these structures are not homologous (109). The growth trajectory of *Parvancorina* does not match that of *Skania* (109, 110), and neither do the segmentation arrangement and attachment location of the supposed appendages (13, 109, 111). The Ediacaran taxa *Vendia* and *Praecambrium* were also suggested to have euarthropod-like guts, gonads, and intestinal caeca (112), but these are better understood as postdeath wrinkling and osmotic contractions, in concert with xenomorphism of the thin bodied organism over the irregular sediment surface, comparable to the taphonomy of other taxa from the White Sea and global specimens of *Dickinsonia* (113). No euarthropod claim from the Ediacaran biota can therefore be substantiated.

There Are No Euarthropods Preserved in Ediacaran BSTs, Phosphorites, or Cherts

The lack of euarthropod body fossils in the Ediacaran biota is mirrored in all other preservational regimes in the Precambrian, including BSTs, phosphatised microfossils, and chert deposits (Fig. 1 and *SI Appendix*). Numerous Precambrian BSTs (70–77) contain disk-shaped fossils of prokaryote colonies (71), such as *Beltanelloides* (73), or various carbonaceous ribbons and filaments interpreted as algae (14, 71). Over 15 algal taxa are known from the Miaohé assemblage of the Doushantuo Formation of China (71) and the Lantian Formation, a basal equivalent of the Doushantuo Formation (70). These are comparable to compressions of multicellular benthic algae found from the Ediacaran–Cambrian transition in Avalonia and Baltica (114). As discussed above, these algal-bearing Ediacaran sites exhibit the same preservation as the Cambrian BSTs, which also preserve metazoans (18, 19). *Eoandromeda* is the only known Ediacaran fossil found in both BST preservation and siliciclastic moldic preservation (115), but this crossing of taphonomic windows does not illuminate its affinity, which is thought by some (115) but not all (116) to be a putative ctenophore.

While BSTs preserve macroscopic soft-bodied fossils, phosphorites replicate microscopic organisms, preserving a different part of the biosphere. The biological content of abundant late Precambrian phosphorites (14, 81, 82) has been the subject of much debate. The Doushantuo Formation of China (~580 Ma) (117) was thought to contain animal embryos; however, these structures have now been shown to be nonmetazoan, containing algal thalli, acritarch vesicles, and nonmetazoan cell clusters (118). Some may even be nonbiological, as comparable structures can be generated during experimental precipitation of apatite (119). Other late Precambrian phosphate deposits contain a similar suite of single-celled/colonial eukarya and bacteria (81–83, 117), and even in the Khesen Formation of Mongolia, which is immediately below the base of the Cambrian, no metazoan remains are found (120, 121). The Doushantuo is continuous with the early Cambrian Meischucun phosphorites of South China, which preserve embryos and hatchlings of cnidarians (122). Rare examples of phosphatized animal embryos are also found throughout the middle and late Cambrian and early Ordovician (122). While Ediacaran phosphorites preserve only single-celled/colonial eukarya and bacteria, Cambrian localities with identical preservation contain metazoans. Phosphatic preservation of clustered coccoid benthic algae and photoautotrophs is rare from the base of the Cambrian onwards (14), with filaments distorted in a way that suggests

metazoan fecal processing (14). As outlined earlier, euarthropods are preserved in several Cambrian phosphorites, including the 514 Ma Yu'anshan Formation, China (42–44), the 511 Ma Comley Quarry limestone, United Kingdom (10), and the Upper Cambrian Orsten limestone, Sweden (41), but none has been reported from earlier in the Cambrian (i.e., Euarthropods are absent from Fortunian and Stage 2 Small Shelly Fossils) (*SI Appendix*) or the Precambrian.

When Did Euarthropods First Evolve?

The exact timing of the origination of animals has long been the subject of debate, with many claims being made for Ediacaran age animals (12, 13), including euarthropods (11, 103, 112). The development of molecular clocks during the 1990s (123) provided a stimulus for investigating the late Precambrian record for the earliest evolution of animals, as did the biomolecular preservation of sterols from approximately 640 Ma or younger (124, 125) (*SI Appendix*). This inspired field exploration efforts that led to the discovery of at least 30 new Ediacaran age lagerstätten in the last 20 years across the full range of taphonomic possibilities (siliciclastics, chert, phosphate, BST). These allow us to test the hypothesis of deep time euarthropods, as suggested by the earliest molecular clocks, which originally suggested the euarthropod divergence occurred at 1,200 Ma (123) to 610–700 Ma (8, 126). More recent molecular clocks place the euarthropod split in the late Ediacaran (15, 17), or constrained between 561–530 Ma and thereby spanning into the Cambrian (16), showing remarkable congruence with the fossil record. Divergence time analyses using morphological data also recover a Cambrian origin for Euarthropoda (127). These analyses benefit from refined analytical techniques (15–17) and the inclusion of well-defined and dated fossil calibrations (44), leading to increasingly precise results. Such divergence estimates require greatly enhanced rates of evolution in comparison with the Phanerozoic norm because it is not until ~940 Ma that rate parity would be achieved (7), but confining euarthropod evolution to the late Precambrian or early Cambrian only requires a fractionally more elevated evolutionary rate than having the origination at 680 Ma (7).

The early fossil record of euarthropods presents a robust and coherent picture of evolutionary processes at this time. The first arthropod traces (*Rusophycus*) appear at approximately 537 Ma, shortly after the start of the Cambrian at approximately 540 Ma. Crown group euarthropods (trilobites) appear at 521 Ma and crustacean microfossils at 514 Ma, with soft-bodied stem lineage fossils illustrating the sequence of character acquisition in BSTs starting from 518 Ma. In contrast, BSTs of latest Ediacaran age (e.g., Miaohe, 555 Ma) are abundantly fossiliferous with single-celled/colonial eukarya but completely lack any evidence of euarthropods. Other windows of preservation, such as phosphatic

microfossils, also lack any evidence of euarthropods in the Ediacaran yet contain abundant euarthropods in the Cambrian. Claims of Ediacaran age euarthropods, such as *Spriggina* and *Parvancorina*, all lack compelling euarthropod, or even animal, characters. Taken together, these data provide a convincing argument to reject the hypothesis of euarthropods originating before the Cambrian. The absence of animals from Ediacaran age rocks has been explained by either poor fossilization at this time (8) or by being too small to fossilize (e.g., the meiofauna of ref. 5) (88). Hypotheses that regard Precambrian preservation as insufficient to preserve euarthropods can no longer be sustained, given the abundant lagerstätten from the Ediacaran Period. Similarly, claims that euarthropods evolved as a tiny and soft-bodied meiofauna that escaped preservation cannot be substantiated because of how commonly the phosphate window is found in the Ediacaran and lower Cambrian, with microscopic euarthropods not appearing until 514 Ma.

The abundant sources of geological data spanning the Ediacaran and lower Cambrian can be used to constrain the origin of euarthropods. If it is accepted that as active motile organisms euarthropods are marked by their first appearance in the trace fossil record of sediment disturbance, then this constrains the first appearance date of total group Euarthropoda to near the base of the Cambrian at ~541 Ma. The taphonomic evidence of the lack of euarthropods in Ediacaran lagerstätten conservatively constrain the appearance of total group Euarthropoda to younger than ~550 Ma. Even the conservative estimate of 541 Ma would then allow around 20 million years for the evolution of the first crown group euarthropods at the base of Cambrian Stage 3.

Each of the major types of fossil evidence (BSTs, trace fossils, and biomineralized hard parts) have their limitations and are incomplete in different ways, but when they are taken together they are mutually illuminating and allow a coherent picture to emerge of the origin and radiation of total group Euarthropoda during the lower to middle Cambrian. The fossil record of euarthropods provides our most complete view of the origin and radiation of a major phylum during the Cambrian explosion. Rather than being a sudden event, this diversification unfolded gradually over the ~40 million years of the lower to middle Cambrian, with no evidence of a deep Precambrian history.

Acknowledgments

This paper results from the “Gene Regulatory Networks and Network Models in Development and Evolution” Sackler Colloquium, organized by N. Shubin, E. V. Rotherberg, and D. H. Erwin. We thank G. Edgecombe, J. Wolfe, D. Legg, L. Laibl, and J. Paterson for discussions; T. Harvey, N. Butterfield, M. Coyne, and X. Zhang supplied images used in Fig. 4. Support for this work was provided by the Oxford University Museum of Natural History; a Natural Environment Research Council Doctoral Training Partnership (H.B.D.) (NE/L002612/1); and an Oxford-St Catherine’s Brade-Natural Motion scholarship (to S.P.).

- 1 Ortega-Hernández J (2016) Making sense of ‘lower’ and ‘upper’ stem-group Euarthropoda, with comments on the strict use of the name Arthropoda von Siebold, 1848. *Biol Rev Camb Philos Soc* 91:255–273.
- 2 Budd GE, Jensen S (2000) A critical reappraisal of the fossil record of the bilaterian phyla. *Biol Rev Camb Philos Soc* 75:253–295.
- 3 Edgecombe GD, Legg DA (2014) Origins and early evolution of arthropods. *Palaeontology* 57:457–468.
- 4 Daley AC, Budd GE, Caron JB, Edgecombe GD, Collins D (2009) The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. *Science* 323:1597–1600.
- 5 Fortey RA, Briggs DEG, Wills MA (1996) The Cambrian evolutionary ‘explosion’: Decoupling cladogenesis from morphological disparity. *Biol J Linn Soc Lond* 57:13–33.
- 6 Budd GE (2002) A palaeontological solution to the arthropod head problem. *Nature* 417:271–275.
- 7 Lee MSY, Soubrier J, Edgecombe GD (2013) Rates of phenotypic and genomic evolution during the Cambrian explosion. *Curr Biol* 23:1889–1895.
- 8 Erwin DH, et al. (2011) The Cambrian conundrum: Early divergence and later ecological success in the early history of animals. *Science* 334:1091–1097.
- 9 Mángano MG, Buatois LA (2014) Decoupling of body-plan diversification and ecological structuring during the Ediacaran-Cambrian transition: Evolutionary and geobiological feedbacks. *Proc Biol Sci* 281:20140038.
- 10 Siveter DJ, Williams M, Waloszek D (2001) A phosphatocopid crustacean with appendages from the lower Cambrian. *Science* 293:479–481.
- 11 Gehling JG (1991) The case for the Ediacaran fossil roots to the metazoan tree. *Geol Soc India Mem* 20:181–224.

- 12 Glaessner MF (1985) *The Dawn of Animal Life: A Biohistorical Study* (Cambridge Univ Press, Cambridge, UK).
- 13 Glaessner MF (1980) *Parvancorina*—An arthropod from the late Precambrian of South Australia. *Ann Naturhist Mus Wien* 83:83–90.
- 14 Brasier MD, Antcliffe JB, Callow R (2011) Evolutionary trends in remarkable fossil preservation across the Ediacaran–Cambrian transition and the impact of metazoan mixing. *Taphonomy: Bias and Process Through Time*, eds Allison PA, Bottjer D (Springer, Amsterdam), pp 519–567.
- 15 Rota-Stabelli O, Daley AC, Pisani D (2013) Molecular timetrees reveal a Cambrian colonization of land and a new scenario for ecdysozoan evolution. *Curr Biol* 23:392–398.
- 16 dos Reis M, et al. (2015) Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. *Curr Biol* 25:2939–2950.
- 17 Lozano-Fernandez J, et al. (2016) A molecular palaeobiological exploration of arthropod terrestrialization. *Philos Trans R Soc Lond B Biol Sci* 371:20150133.
- 18 Gaines RR, Briggs DEG, Yuanlong Z (2008) Cambrian Burgess Shale-type deposits share a common mode of fossilization. *Geology* 36:755–758.
- 19 Butterfield NJ (2003) Exceptional fossil preservation and the Cambrian explosion. *Integr Comp Biol* 43:166–177.
- 20 Vannier J, Liu J, Lerosee-Aubril R, Vinther J, Daley AC (2014) Sophisticated digestive systems in early arthropods. *Nat Commun* 5:3641.
- 21 Budd GE (1998) Stem group arthropods from the lower Cambrian Sirius Passet fauna of North Greenland. *Arthropod Relationships, Systematics Association Special Volume*, eds Fortey RA, Thomas RH (Chapman and Hall, London), pp 25–138.
- 22 Budd GE (1996) The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. *Lethaia* 29:1–14.
- 23 Budd GE, Daley AC (2011) The lobes and lobopods of *Opabinia regalis* from the middle Cambrian Burgess Shale. *Lethaia* 45:83–95.
- 24 Whittington HB (1975) The enigmatic animal *Opabinia regalis*, middle Cambrian Burgess Shale, British Columbia. *Philos Trans R Soc B* 271:1–43.
- 25 Whittington HB, Briggs DEG (1985) The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British-Columbia. *Philos Trans R Soc B* 309:569–609.
- 26 Daley AC, Budd GE (2010) New anomalocaridid appendages from the Burgess Shale, Canada. *Palaeontology* 53:721–738.
- 27 Van Roy P, Daley AC, Briggs DEG (2015) Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. *Nature* 522:77–80.
- 28 Cong P, Ma X, Hou X, Edgecombe GD, Strausfeld NJ (2014) Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature* 513:538–542.
- 29 Daley AC, Edgecombe GD (2014) Morphology of *Anomalocaris canadensis* from the Burgess Shale. *J Paleontol* 88:68–91.
- 30 Paterson JR, et al. (2011) Acute vision in the giant Cambrian predator *Anomalocaris* and the origin of compound eyes. *Nature* 480:237–240.
- 31 Ortega-Hernández J (2015) Homology of head sclerites in Burgess Shale euarthropods. *Curr Biol* 25:1625–1631.
- 32 Yang J, Ortega-Hernández J, Butterfield NJ, Zhang XG (2013) Specialized appendages in fuxianhuids and the head organization of early euarthropods. *Nature* 494:468–471.
- 33 Legg DA, Sutton MD, Edgecombe GD (2013) Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nat Commun* 4:2485.
- 34 Legg DA, Caron JB (2013) New middle Cambrian bivalved arthropods from the Burgess Shale (British Columbia, Canada). *Palaeontology* 57:691–711.
- 35 Tanaka G, Hou X, Ma X, Edgecombe GD, Strausfeld NJ (2013) Chelicerate neural ground pattern in a Cambrian great appendage arthropod. *Nature* 502:364–367.
- 36 Scholtz G, Edgecombe GD (2005) Heads, Hox and the phylogenetic position of trilobites. *Crustacea and Arthropod Relationships, Crustacean Issues*, eds Koenemann S, Jenner RA (CRC Press Taylor & Francis, London), Vol 16, pp 139–165.
- 37 Ortega-Hernández J, Legg DA, Braddy SJ (2013) The phylogeny of aglaspidid arthropods and the internal relationships within Artiopoda. *Cladistics* 29:15–45.
- 38 Lerosee-Aubril R, Zhu X, Ortega-Hernández J (2017) The Vicissicaudata revisited—Insights from a new aglaspidid arthropod with caudal appendages from the Furongian of China. *Sci Rep* 7:11117.
- 39 Daley AC, Legg DA (2015) A morphological and taxonomic appraisal of the oldest anomalocaridid from the lower Cambrian of Poland. *Geol Mag* 152:949–955.
- 40 Zhao F, et al. (2014) Diversity and species abundance patterns in the early Cambrian (series 2, stage 3) Chengjiang biota of China. *Paleobiology* 40:50–69.
- 41 Maas A, et al. (2006) The ‘Orsten’—More than a Cambrian konservat-lagerstätte yielding exceptional preservation. *Palaeoworld* 15:266–282.
- 42 Zhang XG, Siveter DJ, Waloszek D, Maas A (2007) An epidote-bearing crown-group crustacean from the lower Cambrian. *Nature* 449:595–598.
- 43 Zhang XG, Maas A, Haug JT, Siveter DJ, Waloszek D (2010) A eucrustacean metanauplius from the lower Cambrian. *Curr Biol* 20:1075–1079.
- 44 Wolfe JM, Daley AC, Legg DA, Edgecombe GD (2016) Fossil calibrations for the arthropod Tree of Life. *Earth Sci Rev* 160:43–110.
- 45 Harvey THP, Butterfield NJ (2008) Sophisticated particle-feeding in a large early Cambrian crustacean. *Nature* 452:868–871.
- 46 Harvey THP, Vélez MI, Butterfield NJ (2012) Exceptionally preserved crustaceans from western Canada reveal a cryptic Cambrian radiation. *Proc Natl Acad Sci USA* 109:1589–1594.
- 47 Harvey THP, Pedder BE (2013) Copepod mandible palynomorphs from the Nolichucky Shale (Cambrian, Tennessee): Implications for the taphonomy and recovery of small carbonaceous fossils. *Palaios* 28:278–284.
- 48 Hollingsworth JS (2008) The first trilobites in Laurentia and elsewhere. *Advances in Trilobite Research, Cuadernos del Museo Geominero*, eds Rábano I, Gozalo R, García-Bellido D (Instituto Geológico y Minero de España, Madrid), Vol 9, pp 171–176.
- 49 Edgecombe GD, Ramsköld L (1999) Relationships of Cambrian Arachnata and the systematic position of Trilobita. *J Paleontol* 73:263–287.
- 50 Cotton TJ, Braddy SJ (2005) The phylogeny of arachnomorph arthropods and the origin of the Chelicerata. *Trans R Soc Edinb* 94:169–193.
- 51 Aria C, Caron J-B (2017) Mandibulate convergence in an armoured Cambrian stem chelicerate. *BMC Evol Biol* 17:261.
- 52 Rota-Stabelli O, et al. (2011) A congruent solution to arthropod phylogeny: Phylogenomics, microRNAs and morphology support monophyletic Mandibulata. *Proc Biol Sci* 278:298–306.
- 53 Peng S, Babcock LE, Cooper RA (2012) The Cambrian Period. *The Geologic Time Scale 2012*, eds Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (Elsevier, Oxford), pp 437–488.
- 54 Zhang X, et al. (2017) Challenges in defining the base of the Cambrian series 2 and stage 3. *Earth Sci Rev* 172:124–139.
- 55 Landing E, Geyer G, Brasier MD, Bowring SA (2013) Cambrian evolutionary radiation: Context, correlation, and chronostratigraphy—Overcoming deficiencies of the first appearance datum (FAD) concept. *Earth Sci Rev* 123:133–172.
- 56 Bushuev E, Goryaeva I, Pereladov V (2014) New discoveries of the oldest trilobites *Profallotaspis* and *Nevadella* in the northeastern Siberian Platform, Russia. *Bull Geosci* 89:347–364.
- 57 Liñán E, Vintaned JAG, Gozalo R (2015) The middle lower Cambrian (Ovetian) *Lunagraulos* n. gen. from Spain and the oldest trilobite records. *Geol Mag* 152:1123–1136.
- 58 Paterson JR, Brock GA (2007) Early Cambrian trilobites from Angorichina, Flinders Ranges, South Australia, with a new assemblage from the *Pararaia bunyeroensis* zone. *J Paleontol* 81:116–142.
- 59 Speyer SE, Chatterton BDE (1989) Trilobite larvae and larval ecology. *Hist Biol* 3:27–60.
- 60 Álvaro JJ, et al. (2013) Global Cambrian trilobite palaeobiogeography assessed using parsimony analysis of endemism. *Geol Soc Mem* 38:273–296.
- 61 Lieberman BS (2001) A test of whether rates of speciation were unusually high during the Cambrian radiation. *Proc Biol Sci* 268:1707–1714.
- 62 Crimes TP (1987) Trace fossils and correlation of late Precambrian and early Cambrian strata. *Geol Mag* 124:97–119.
- 63 Macnaughton RB, Narbonne GM (1999) Evolution and ecology of Neoproterozoic–Lower Cambrian trace fossils, NW Canada. *Palaios* 14:97–115.
- 64 Häntzschel W (1975) Miscellanea supplement 1 trace fossils and problematica. *Treatise on Invertebrate Palaeontology Part W*, ed Moore RC (Univ Kansas Press, Lawrence, KS), 258 p.
- 65 Osgood RG (1970) Trace fossils of the Cincinnati Area. *Palaeontogr Am* 6:277–444.
- 66 Narbonne GM, Myrow PM, Landing E, Anderson MM (1987) A candidate stratotype for the Precambrian–Cambrian boundary, Fortune Head, Burin Peninsula, southeastern Newfoundland. *Can J Earth Sci* 24:1277–1293.
- 67 McIlroy D, Brasier MD (2017) Ichhnological evidence for the Cambrian explosion in the Ediacaran to Cambrian succession of Tanafjord, Finnmark, northern Norway. *Geol Soc Spec Publ* 448:351–368.

- 68 Butterfield NJ (1995) Secular distribution of Burgess Shale-type preservation. *Lethaia* 38:1–13.
- 69 Gaines RR (2014) Burgess Shale-type preservation and its distribution in space and time. *Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Preservation*, Paleontological Society Special Papers, eds Laflamme M, Schiffbauer JD, Darroch SAF (Yale Univ Press, New Haven, CT), Vol 20, pp 123–146.
- 70 Yuan X, Chen Z, Xiao S, Zhou C, Hua H (2011) An early Ediacaran assemblage of macroscopic and morphologically differentiated eukaryotes. *Nature* 470:390–393.
- 71 Xiao S, Yuan X, Steiner M, Knoll AH (2002) Macroscopic carbonaceous compressions in a terminal Proterozoic shale: A systematic reassessment of the Miaohu Biota, South China. *J Paleontol* 76:347–376.
- 72 Luo C, Zhu M, Reitner J (2016) The Jinxian biota revisited: Taphonomy and body plan of the Neoproterozoic discoid fossils from the southern Liaodong Peninsula, North China. *Palz* 90:205–224.
- 73 Brasier MD, Perejon A, De San Jose MA (1979) Discovery of an important fossiliferous Precambrian–Cambrian sequence in Spain. *Estud Geol* 35:379–383.
- 74 Jensen S, Palacios T (2016) The Ediacaran–Cambrian trace fossil record in the Central Iberian Zone, Iberian Peninsula. *Commun Geol* 103:83–92.
- 75 Ford TD, Breed WJ (1972) The problematical Precambrian fossil Chuarina. *Proc 24th Int Geol Cong Montreal* 1:11–18.
- 76 Grazhdankin DV, Balthasar U, Nagovitsin KE, Kochnev BB (2008) Carbonate-hosted Avalon-type fossils in arctic Siberia. *Geology* 36:801–806.
- 77 Dombos SQ, Oji T, Kanayama A, Gonchigdorj S (2016) A new Burgess Shale-type deposit from the Ediacaran of western Mongolia. *Sci Rep* 6:23438.
- 78 Gaines RR, et al. (2012) Mechanism for Burgess Shale-type preservation. *Proc Natl Acad Sci USA* 109:5180–5184.
- 79 Peters SE, Gaines RR (2012) Formation of the ‘Great Unconformity’ as a trigger for the Cambrian explosion. *Nature* 484:363–366.
- 80 Gaines RR, et al. (2012) Burgess shale-type biotas were not entirely burrowed away. *Geology* 40:283–286.
- 81 Cook PJ, Shergold JH (1984) Phosphorus, phosphorites and skeletal evolution at the Precambrian–Cambrian boundary. *Nature* 308:231–236.
- 82 Xiao S, Knoll AH (1999) Fossil preservation in the Neoproterozoic Doushantuo phosphorite lagerstätte, South China. *Lethaia* 32:219–240.
- 83 Brasier MD (1992) Nutrient-enriched waters and the early skeletal fossil record. *J Geol Soc London* 149:621–629.
- 84 Signor PW, Vermeij GJ (1994) The plankton and benthos: Origins and early history of an evolving relationship. *Paleobiology* 20:297–319.
- 85 Logan GA, Hayes JM, Hieshima GB, Summons RE (1995) Terminal Proterozoic reorganization of biogeochemical cycles. *Nature* 376:53–56.
- 86 McIlroy D, Logan GA (1999) The impact of bioturbation on infaunal ecology and evolution during the Proterozoic–Cambrian transition. *Palaios* 14:58–72.
- 87 Narbonne GM (2005) The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annu Rev Earth Planet Sci* 33:421–442.
- 88 Parry LA, et al. (2017) Ichtnological evidence for meiofaunal bilaterians from the terminal Ediacaran and earliest Cambrian of Brazil. *Nat Ecol Evol* 1:1455–1464.
- 89 Antcliffe JB, Hancy AD, Brasier MD (2015) A new ecological model for the ~565 Ma Ediacaran biota of Mistaken Point, Newfoundland. *Precambrian Res* 268:227–242.
- 90 Grazhdankin D (2004) Patterns of distributions in the Ediacaran biotas: Facies versus biogeography and evolution. *Paleobiology* 30:203–221.
- 91 Grazhdankin D, Seilacher A (2002) Underground Vendobionta from Namibia. *Palaeontology* 45:57–78.
- 92 Hagadorn JW, Fedo CM, Waggoner BM (2000) Early Cambrian Ediacaran type fossils from California. *J Paleontol* 74:731–740.
- 93 Hagadorn JW, Belt ES (2008) Stranded in upstate New York: Cambrian medusa from the Potsdam Sandstone. *Palaios* 23:424–441.
- 94 Bailey JV, Corsetti FA, Bottjer DJ, Marenco KN (2006) Microbially-mediated environmental influences on metazoan colonization of matground ecosystems: Evidence from the lower Cambrian Harkless Formation. *Palaios* 21:215–226.
- 95 Bottjer DJ, Hagadorn JW, Dombos SQ (2000) The Cambrian substrate revolution. *GSA Today* 10:1–7.
- 96 Seilacher A (1992) Vendobionta and Psammocorallia: Lost constructions of Precambrian evolution. *J Geol Soc London* 149:607–613.
- 97 Grazhdankin D, Gerdes G (2007) Ediacaran microbial colonies. *Lethaia* 40:201–210.
- 98 Antcliffe JB, Brasier MD (2007) *Charnia* and sea pens are poles apart. *J Geol Soc London* 164:49–51.
- 99 Antcliffe JB, Brasier MD (2008) *Charnia* at 50: Developmental models for Ediacaran fronds. *Palaeontology* 51:11–26.
- 100 Sperling EA, Vinther J (2010) A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evol Dev* 12:201–209.
- 101 Fedonkin MA (1985) Systematic description of Vendian Metazoa. *Vendian System: Historical–Geological and Paleontological Foundation*, Paleontology, eds Sokolov BS, Iwanowski AB (Nauka, Moscow), Vol 1, pp 70–106.
- 102 Seilacher A, Grazhdankin D, Legouta A (2003) Ediacaran biota: The dawn of animal life in the shadow of giant protists. *Paleontol Res* 7:43–54.
- 103 Seilacher A (1989) Vendozoa: Organismic construction in the Proterozoic biosphere. *Lethaia* 22:229–239.
- 104 Simonetta AM, Insson E (1993) New animals from the Burgess Shale (Middle Cambrian) and their possible significance for the understanding of the Bilateria. *Boll Zool* 60:97–107.
- 105 Conway Morris S (2008) A redescription of a rare chordate, *Metaspriggina walcotti* Simonetta and Insson, from the Burgess Shale (middle Cambrian), British Columbia, Canada. *J Paleontol* 82:424–430.
- 106 Morris SC, Caron JB (2014) A primitive fish from the Cambrian of North America. *Nature* 512:419–422.
- 107 Conway Morris S (1993) Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of North America. *Palaeontology* 36:593–635.
- 108 Waggoner BM (1996) Phylogenetic hypotheses of the relationships of arthropods to Precambrian and Cambrian problematic fossil taxa. *Syst Biol* 45:190–222.
- 109 Legg DA (2015) The morphology and affinities of *Skania fragilis* (Arthropoda) from the middle Cambrian Burgess Shale. *Bull Geosci* 90:509–518.
- 110 Naimark EB, Ivantsov AY (2009) Growth variability in the late Precambrian problematic *Parvancorina* Glaessner. *Paleontol J* 43:12–18.
- 111 Paterson JR, Gehling JG, Droser ML, Bicknell RDC (2017) Rheotaxis in the Ediacaran epibenthic organism *Parvancorina* from South Australia. *Sci Rep* 7:45539.
- 112 Ivantsov AY (2001) Vendia and other Precambrian “arthropods”. *Paleontol J* 35:335–343.
- 113 Brasier MD, Antcliffe JB (2008) *Dickinsonia* from Ediacara: A new look at morphology and body construction. *Palaeogeogr Palaeoclimatol Palaeoecol* 270:311–323.
- 114 Vidal G, Moczydlowska M (1992) Patterns of phytoplankton radiation across the Precambrian–Cambrian boundary. *J Geol Soc London* 149:647–654.
- 115 Zhu M, Gehling JG, Xiao S, Zhao Y, Droser ML (2008) Eight-armed Ediacara fossil preserved in contrasting taphonomic windows from China and Australia. *Geology* 36:867–870.
- 116 Tang F, et al. (2008) Octoradiate spiral organisms in the Ediacaran of South China. *Acta Geol SINICA* 82:27–34.
- 117 Condon D, et al. (2005) U–Pb ages from the neoproterozoic Doushantuo Formation, China. *Science* 308:95–98.
- 118 Huldgren T, et al. (2011) Fossilized nuclei and germination structures identify Ediacaran “animal embryos” as encysting protists. *Science* 334:1696–1699.
- 119 Crosby CH, Bailey JV (2018) Experimental precipitation of apatite pseudofossils resembling fossil embryos. *Geobiology* 16:80–87.
- 120 Anderson RP, Macdonald FA, Jones DS, McMahon S, Briggs DEG (2017) Doushantuo-type microfossils from latest Ediacaran phosphorites of northern Mongolia. *Geology* 45:1079–1082.
- 121 Landing E, Kruse PD (2017) Integrated stratigraphic, geochemical, and paleontological late Ediacaran to early Cambrian records from southwestern Mongolia. *Geol Soc Am Bull* 129:1012–1015.
- 122 Donoghue PCJ, et al. (2006) Fossilized embryos are widespread but the record is temporally and taxonomically biased. *Evol Dev* 8:232–238.
- 123 Wray GA, Levinton JS, Shapiro LH (1996) Molecular evidence for deep Precambrian divergences among metazoan phyla. *Science* 274:568–573.
- 124 Love GD, et al. (2009) Fossil steroids record the appearance of Demospongiae during the Cryogenian period. *Nature* 457:718–721.
- 125 Antcliffe JB (2013) Questioning the evidence of organic compounds called sponge biomarkers. *Palaeontology* 56:917–925.
- 126 Wheat CW, Wahlberg N (2013) Phylogenomic insights into the Cambrian explosion, the colonization of land and the evolution of flight in Arthropoda. *Syst Biol* 62:93–109.
- 127 Wolfe JM (2017) Metamorphosis is ancestral for crown euarthropods, and evolved in the Cambrian or earlier. *Integr Comp Biol* 57:499–509.
- 128 Antcliffe JB, Callow RHT, Brasier MD (2014) Giving the early fossil record of sponges a squeeze. *Biol Rev Camb Philos Soc* 89:972–1004.
- 129 Narbonne GM, Xiao S, Shields GA (2012) The Ediacaran Period. *The Geologic Time Scale 2012*, eds Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (Elsevier, Oxford), pp 413–435.