The early fossil record of Euarthropoda, and the Cambrian Explosion

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ABSTRACT: 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 non-biomineralized 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 (*Cruziana*, *Rusophycus*, *etc.*) 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. Miaohe 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 biomineralised 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.

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Keywords: Paleontology, Paleozoic, Evolution, Arthropoda, Cambrian Radiation

Introduction

Euarthropoda (*sensu* 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 origin of bioturbation, biomineralisation, 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, biomineralised exoskeletons, microfossils (phosphatic, siliceous, and carbonaceous), and trace fossils are compared and contrasted across the Ediacaran-Cambrian boundary in order to constrain when euarthropods first evolved. In congruence with the most recent analyses from molecular paleobiology (15-17), our comprehensive fossil data set suggests an entirely Cambrian evolution for this phylum, as described below.

Cambrian Burgess Shale Type localities reveal the euarthropod stem lineage

The most renowned fossils of the Cambrian Explosion are the diverse animal assemblages found at Burgess Shale Type localities (BSTs) (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 specialised 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. 2C-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 behaviour (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 specialised 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).

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 phosphatised ‘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 non-larval crown-group fossil crustacean is *Klausmuellaria salopensis* reported from the 511 Ma *Protolenus* Limestone, Comley, Shropshire, UK. *Klausmuellaria* 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 three-dimensional microscopic carbonaceous fossils (SCFs) (Fig. 4A-D). These contain a variety of spines, setae, and setules for filter feeding (Fig. 4A-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. 2) based on the presence of derived morphological features such as biramous limbs, deutocerebral antennae (36), diverse feeding specialisations, and a heavily biomineralised calcitic exoskeleton (36, 49). Placement 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).

The oldest trilobites currently define the beginning of Cambrian Series 2 Stage 3 at c.521 Ma (53) (Fig. 1), although formal designation has yet to be finalised 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 *Profallotaspis jakutensis* and *P. tyusserica* from Siberia (48, 50, 56), *Hupetina antiqua* and fallotaspidids (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, 54, 53, 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/or 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 (20-30 thousand 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 prior to their first appearance in the fossil record at 521 Ma (*contra* 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, biomineralised skeletal elements, while stem lineage euarthropods lack biomineralised 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 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 twenty million years of the Terreneuvian for which trace fossils are abundant (9) (Fig. 1), including the euarthropod traces *Rusophycus*, *Diplichnites*, *Cruziana*, *Asaphoidichnus*, *Tasmanadia*, and *Cheiichnus*.

The general order for the first appearance of euarthropod traces has been described as *Monomorphichnus, Diplichnites, Rusophycus,* and *Cruziana* (62). Though *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" (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 for details of other Terreneuvian euarthropod traces).

During the Ediacaran period euarthropod trace fossils are "strikingly absent" (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 (see SI), 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 mouldic and chert preservation (see SI). These cover a wide variety of depositional environments, and preserve hard and soft organisms on macroscopic and microscopic scales.

BST preservation is characterised 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 Miaohe 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), 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 upwell 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 mouldic preservation is associated with Ediacaran biota fossils, where fine to course sediments preserve external moulds 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 moulding 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; see SI). In sites across the Avalonian paleogeographic terrane, such as Mistaken Point, Newfoundland, Canada and Charnwood Forest, Leicestershire, UK, the lower surfaces of organisms are moulded by smothering volcanic ash (87) and binding by microbial mats (89). Elsewhere moulds are formed from the rapid lithification of carbonates (White Sea, Russia, 90), or as infaunal whole-body three-dimensional preservation (Namibia, 91). Mouldic preservation becomes less common at the start of the Cambrian (92-94) and it 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, see SI), 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 biomineralisation 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 mouldic 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 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 an euarthropod affinity. This mode of construction is common in the Ediacaran Biota, and we emphasise that fossils should be analysed in the context of their co-occurring 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 to 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 *Praecambridium* were also suggested to have euarthropod-like guts, gonads, and intestinal caeca (112), but these are better understood as post-death 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; see SI). Numerous Precambrian BSTs (70-77) contain disc-shaped fossils of prokaryote colonies (71), such as *Beltanelloides* (73), and/or various carbonaceous ribbons and filaments interpreted as algae (14, 71). Over fifteen algal taxa are known from the Miaohe assemblage of the Doushantuo Formation of China (71) and the Lantian Formation, a basinal 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 siliclastic mouldic 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 non-metazoan, containing algal thalli, acritarch vesicles, and non-metazoan cell clusters (118). Some may even be non-biological, 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 (82, 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 phosphatised 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 faecal processing (14). As outlined earlier, euarthropods are preserved in several Cambrian phosphorites, including the 514 Ma Yu'anshan Formation, China (42, 43, 44), the 511 Ma Comley Quarry limestone, UK (10), and the Upper Cambrian Orsten limestone, Sweden (41), but none has been reported from earlier in the Cambrian (ie. Euarthropods are absent from Fortunian and Stage 2 Small Shelly Fossils; see SI) 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 ca. 640Ma or younger (124, 125; see SI). 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 1200 Ma (123) to 610-700 Ma (8, 126). More recent molecular clocks place the euarthropod split in the late Ediacaran (15, 16), 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 to 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 c537 Ma, shortly after the start of the Cambrian at c540 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. These data taken together 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 fossilisation at this time (8) or by being too small to fossilise (e.g. the meiofauna of 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. Likewise, 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 Euathropoda to younger than ~550 Ma. Even the conservative estimate of 541 Ma would then allow around twenty 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 biomineralised 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.

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Figure Captions:

Figure 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 First Appearance Datum (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.

Figure 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-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-J: Vicissicaudates. I: *Sidneyia inexpectans*, USNM 250208. J: *Emeraldella brocki,* USNM 57702. Scale bars A: 5mm; B-F, H-J: 10mm; G: 3mm.

Figure 3: A generalised phylogeny of panarthropod relationships, distinguishing the crown group Euarthropoda from the lower and upper stem lineage euarthropod taxa. Dashed lines indicates the uncertain phylogenetic placements of Megacheira and Artiopoda. Modified from refs. 1, 4, 27, 31, 34, 37.

Figure 4: Earliest fossil evidence of total group Euarthropoda, and extinct and extant crown group Euarthropoda. A-D: Small carbonaceous fossils (SCFs) of early crustaceans, images credit T. Harvey, N. Butterfield. A-B: Comparison of branchiopod filter plates from Early Cambrian Mount Cap (A) and Middle Cambrian Deadwood Formations (B, GSC 135392). C: Appendage setae from Mount Cap, GSC 34928. D: Branchiopod mandible from Mount Cap, GSC 34931. E: Oldest crustacean *Yicaris dianensis*, YKLP 10840, image credit X. Zhang. F: Earliest total group euarthropod evidence, *Rusophycus* trace fossil, GSC 85983, image credit M. Coyne. G: Fallotaspidid trilobite from Morocco, OUMNH AX.27. Scale bars A-B: 50μm; C: 70μm; D: 100μm; E: 150μm; F: 20mm; G: 10mm.

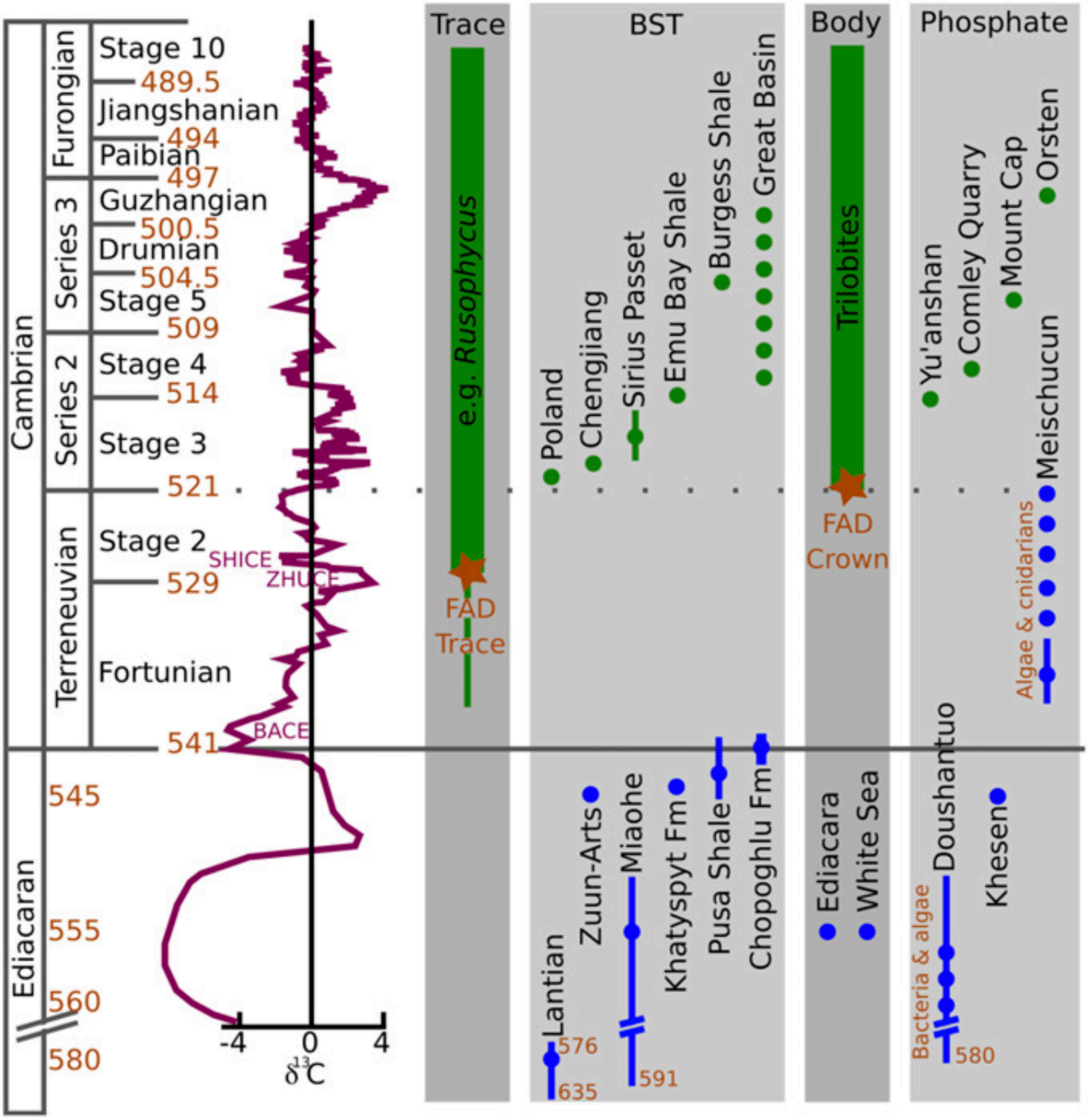
Cambrian
Furongian
Series 3
Series 2
Terreneuvian
Ediacaran
Stage 10
489.5
Jiangshanian
494
Paibian
497
Guzhangian
500.5
Drumian
504.5
Stage 5
509
Stage 4
514
Stage 3
521
Stage 2
SHICE
ZHUCE
529
Fortunian
BACE
541
545
555
560
580
-4
0
4
δ13C
Trace
e.g. Rusophycus
FAD
Trace
BST
Poland
Chengjiang
Sirius Passet
Emu Bay Shale
Burgess Shale
Great Basin
Lantian
576
635
Zuun-Arts
Miaohe
591
Khatyspyt Fm
Pusa Shale
Chopoghlu Fm
Body
Trilobites
FAD
Crown
Ediacara
White Sea
Phosphate
Yu'anshan
Comley Quarry
Mount Cap
Orsten
Meischucun
Algae & cnidarians
Doushantuo
Bacteria & algae
580
Khesen

Figure 1

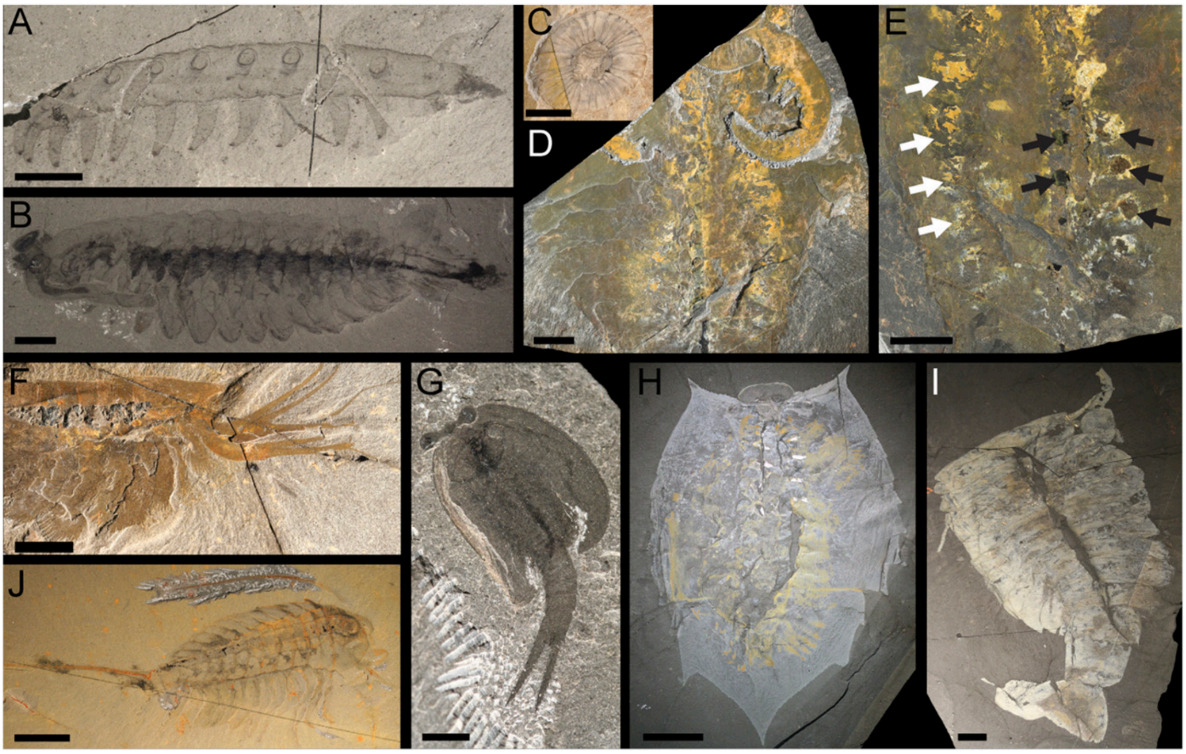

Figure 2

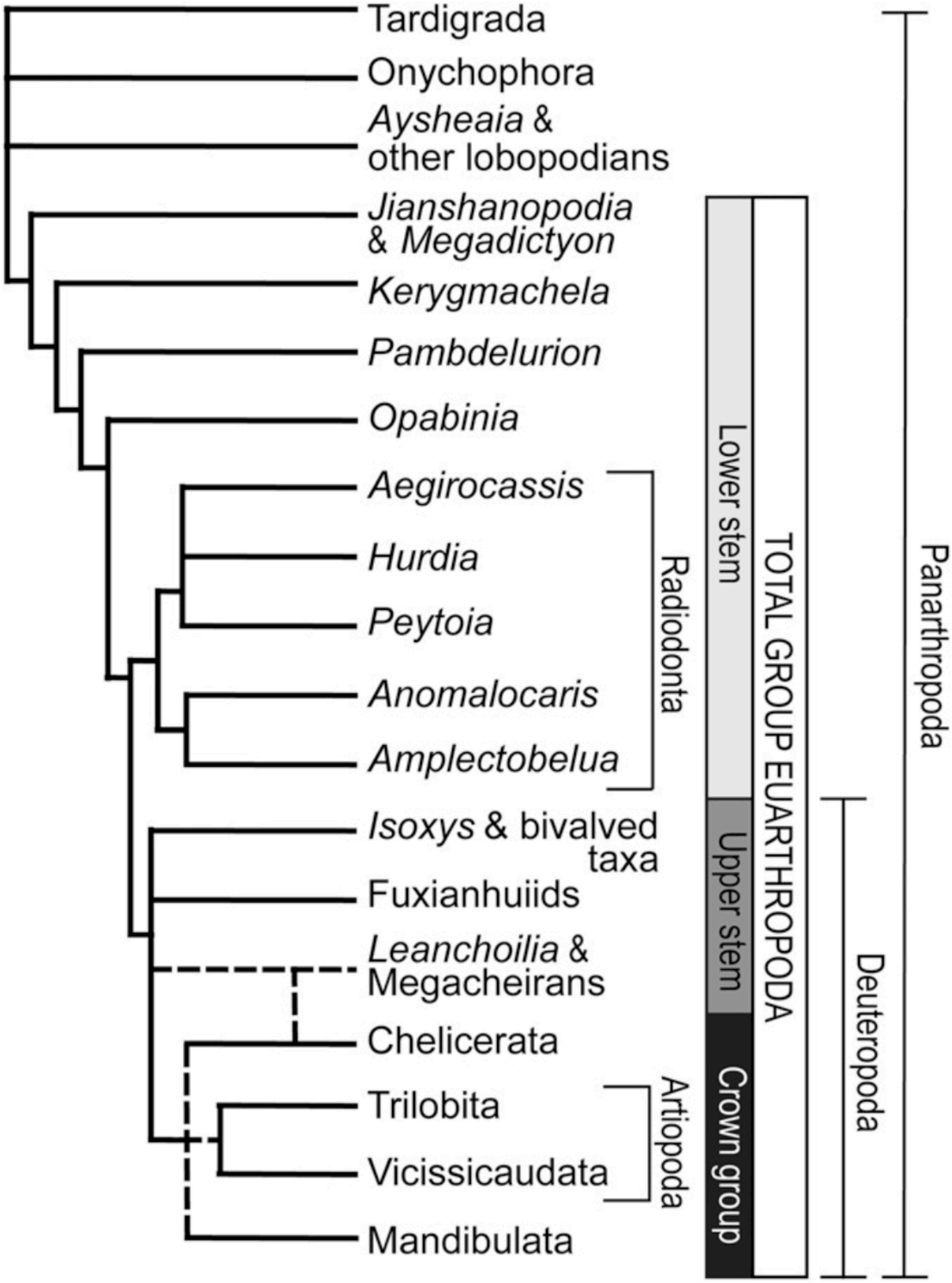
Tardigrada
Onychophora
Aysheaia & other lobopodians
Jianshanopodia & Megadictyon
Kerygmachela
Pambdelurion
Opabinia
Aegirocassis
Hurdia
Peytoia
Anomalocaris
Amplectobelua
Isoxys & bivalved taxa
Fuxianhuiids
Leanchoilia & Megacheirans
Chelicerata
Trilobita
Vicissicaudata
Mandibulata
Radiodonta
Artiopoda
Lower stem
Upper stem
Crown group
TOTAL GROUP EUARTHROPODA
Deuteropoda
Panarthropoda

Figure 3

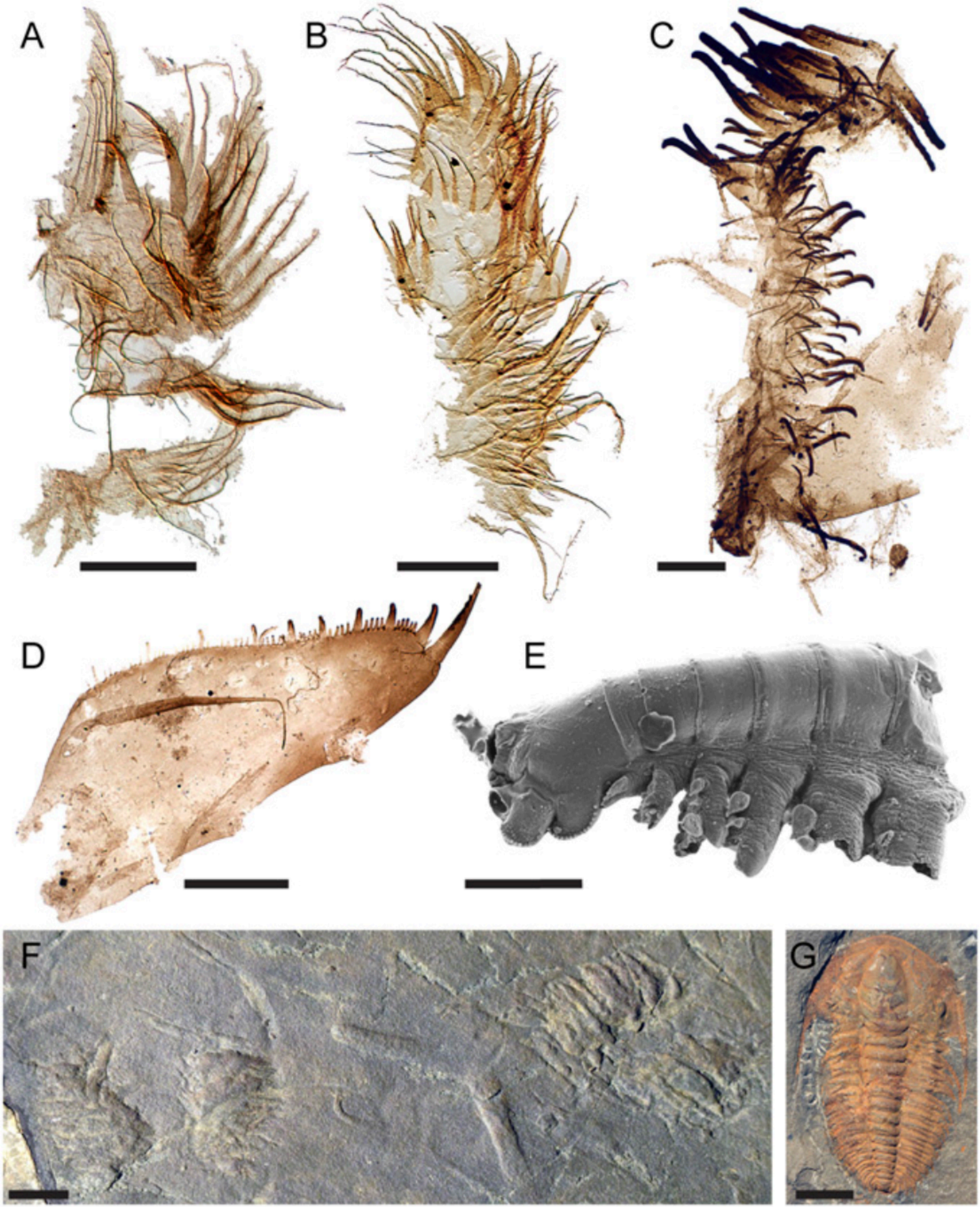

Figure 4