



# Aquatic stem group myriapods close a gap between molecular divergence dates and the terrestrial fossil record

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Identifying marine or freshwater fossils that belong to the stem groups of the major terrestrial arthropod radiations is a long-standing challenge. Molecular dating and fossils of their pancrustacean sister group predict that myriapods originated in the Cambrian, much earlier than their oldest known fossils, but uncertainty about stem group Myriapoda confounds efforts to resolve the timing of the group's terrestrialization. Among a small set of candidates for membership in the stem group of Myriapoda, the Cambrian to Triassic euthycarcinoids have repeatedly been singled out. The only known Devonian euthycarcinoid, *Heterocrania rhyiensis* from the Rhynie and Windyfield cherts hot spring complex in Scotland, reveals details of head structures that constrain the evolutionary position of euthycarcinoids. The head capsule houses an anterior cuticular tentorium, a feature uniquely shared by myriapods and hexapods. Confocal microscopy recovers myriapod-like characters of the preoral chamber, such as a prominent hypopharynx supported by tentorial bars and superlinguae between the mandibles and hypopharynx, reinforcing an alliance between euthycarcinoids and myriapods recovered in recent phylogenetic analysis. The Cambrian occurrence of the earliest euthycarcinoids supplies the oldest compelling evidence for an aquatic stem group for either Myriapoda or Hexapoda, previously a lacuna in the body fossil record of these otherwise terrestrial lineages until the Silurian and Devonian, respectively. The trace fossil record of euthycarcinoids in the Cambrian and Ordovician reveals amphibious locomotion in tidal environments and fills a gap between molecular estimates for myriapod origins in the Cambrian and a post-Ordovician crown group fossil record.

Arthropoda | Myriapoda | euthycarcinoid | terrestrialization | molecular dating

Knowledge of the early fossil record of arthropods has made enormous advances in recent years, driven largely by new discoveries in the Cambrian. Foremost among these are compression fossils from the Burgess Shale and sites of similar preservation around the world, small carbonaceous fossils that record minute details of crustacean mouthparts and other appendages, and phosphatized larval and juvenile remains (1). Taken together, these fossils have allowed the early history of some pancrustacean lineages as well as chelicerates to be traced as far back as the early Cambrian.

In contrast, Cambrian Konservat-Lagerstätten have remained silent on the stem lineages of two major arthropod lineages, the Myriapoda and Hexapoda. Fossil-calibrated molecular phylogenies predict that myriapods and hexapods both diverged from other extant arthropod lineages in the Cambrian, and there is broad agreement from dated trees that Myriapoda and Hexapoda began to diversify in the Cambrian and Ordovician, respectively

(2–5). Despite this inferred antiquity, there are no compelling fossil remains of Myriapoda until the mid-Silurian and no hexapods until the Lower Devonian. In both cases, the oldest fossils can be assigned to crown group lineages (Diplopoda in the case of Silurian myriapods and Collembola in the case of Hexapoda) and the fossils have morphological characters shared by extant species that indicate terrestrial habits. The aquatic or terrestrial stem groups of Myriapoda and Hexapoda remain unknown.

Euthycarcinoidea, a group presently known from 18 species that span the mid-Cambrian to Middle Triassic, has repeatedly been evoked as a candidate for filling this gap in knowledge about myriapod or hexapod origins. That said, a vast range of alternative affinities have been suggested for euthycarcinoids, including a relationship to branchiopod crustaceans, merostomate chelicerates, trilobitiforms, or the euarthropod stem group (reviewed in ref. 6). More recent studies have restricted their systematic position to Mandibulata (= Myriapoda and Pancrustacea), based in part on the presence of mandibles as the main mouthpart in several species (7). Some of these studies have more specifically proposed that euthycarcinoids are allied to hexapods or

## Significance

Most arthropod diversity is now found on land, with hexapods (insects), arachnids, and myriapods being major terrestrial radiations. Molecular dating consistently predicts that these groups have earlier evolutionary origins than are recorded by fossils. A reason for this difference between molecular- and fossil-based age estimates is that few candidates for marine or freshwater stem groups of these terrestrial lineages have been identified. A Devonian euthycarcinoid arthropod preserves details of the head shared by myriapods, adding support to the theory that they are each other's closest relative. The fossil record of euthycarcinoids in the Cambrian, including trackways made on tidal flats, clarifies the marine-to-terrestrial transition in the myriapod lineage and reconciles molecular and fossil-based estimates for the timing of myriapod origins.

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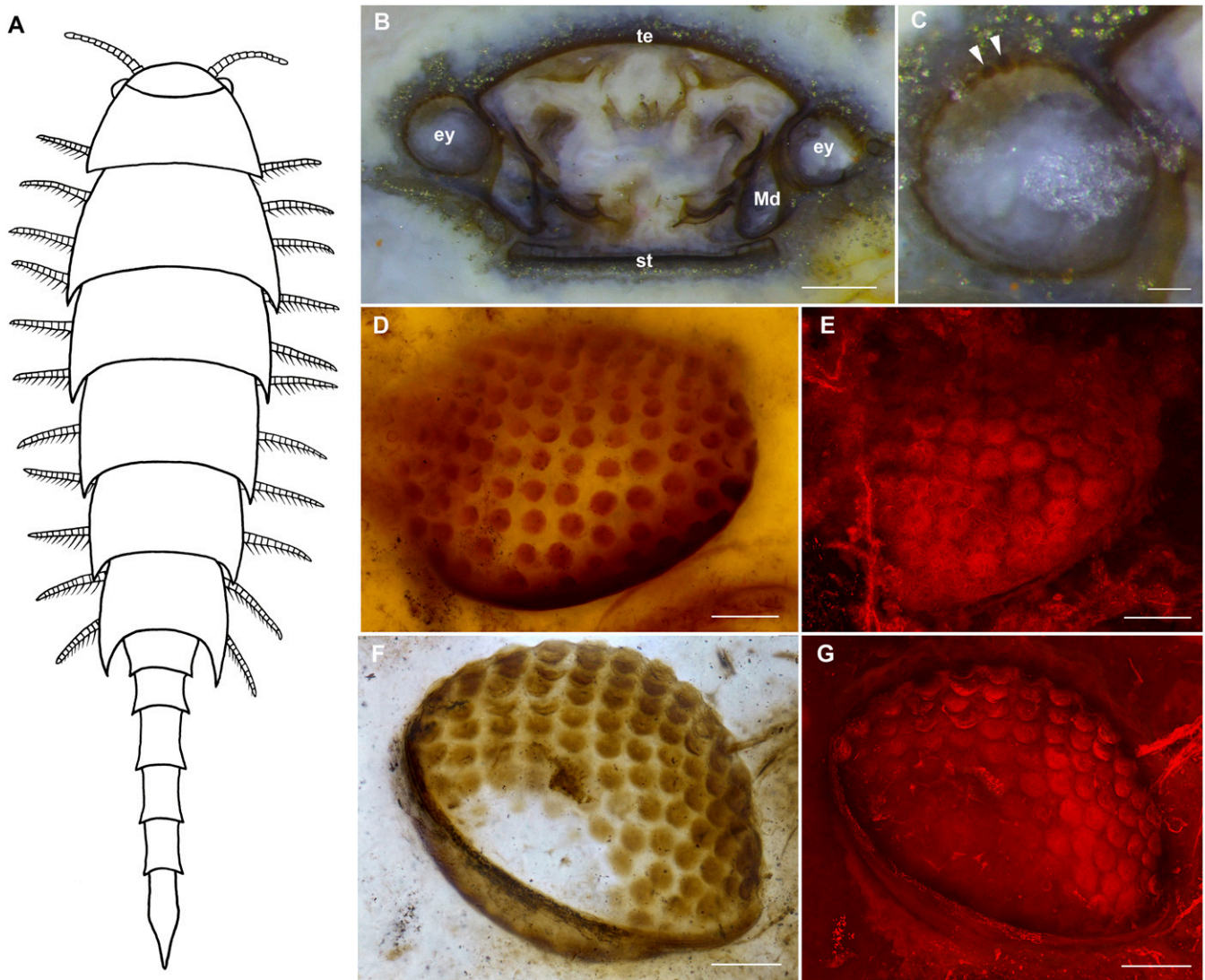
myriapods. The former option drew on comparisons between ventral cephalic plates in Carboniferous euthycarcinoids and the labrum of certain insects (8), and some phylogenetic analyses of fossil and extant Arthropoda resolved euthycarcinoids as a sister group to Hexapoda (9). More recently, however, euthycarcinoids have been allied with the Cambrian fuxianhuidi in the mandibulate stem group (10) or as a sister group of Myriapoda (11), with fuxianhuidi resolved immediately outside the mandibulate crown-group.

*Heterocrania rhyiensis* from the Early Devonian Rhyne Chert of Scotland was originally interpreted as a possible eurypterid (12), but documentation of more anatomically complete material from the overlying Windyfield Chert demonstrated that it is unquestionably a euthycarcinoid (13) (Fig. 1A). We have restudied known and new material of this species, drawing on new imaging methods, in particular confocal laser scanning microscopy, to elucidate morphological details that shed further light on the systematic position of euthycarcinoids (SI Appendix). We highlight a set of previously undocumented features of the head skeleton in particular that reinforce a euthycarcinoid-myriapod alliance.

## Results

**New Anatomic Evidence from *Heterocrania*.** Specimens of *H. rhyiensis* preserve cuticular parts of the head in clearer detail than in any other known euthycarcinoid. In what follows, we summarize previously unknown anatomic features of euthycarcinoids.

**Eyes.** The eyes of euthycarcinoids were described using a neutral terminology as “sphaeroidal processes” (14), consistently situated beneath the border of the two cephalic tergites and usually projecting beyond the margin of those tergites. An interpretation as eyes was cautiously endorsed (14) but later was implicitly rejected (e.g., coding for an absence of eyes in Euthycarcinoidea: ref. 15). New specimens of *Heterocrania* demonstrate that the “sphaeroidal processes” are compound eyes. NMS 1925.9.11.1 is an isolated eye from the Rhyne Chert with an ovoid, incomplete visual field composed of regularly patterned rows of round lenses (Fig. 1D and E). At least 90 lenses are preserved, 18 of which have diameters measured from the central part of the visual field ranging from 19.2 to 24.7  $\mu\text{m}$  (mean,  $21.9 \pm 1.7 \mu\text{m}$ ). A narrow marginal rim indicates that at least part of the outer edge of the



**Fig. 1.** *H. rhyiensis*. (A) Reconstruction in dorsal view (modified from ref. 13). (B and C) Transverse section of head, NMS G.2014.11.1.1, showing compound eyes. Left eye magnified in C; arrows point to ommatidia. (Scale bars: 250  $\mu\text{m}$  in B, 50  $\mu\text{m}$  in C.) (D and E) Light microscopy (D) and confocal microscopy (E) images of isolated eye, NMS 1925.9.11.1. (Scale bars: 50  $\mu\text{m}$ .) (F and G) Light microscopy (F) and confocal microscopy (G) images of isolated eye, GLAHM Kid2475. (Scale bar: 50  $\mu\text{m}$ .) ey, eye; Md, mandible; te, cephalic tergite; st, sternite.

visual surface is intact. The size of the eye and the diameters of its lenses correspond to the in situ “sphaeroidal processes” of *H. rhyniensis* (Fig. 1 B and C), which has clearly defined lenses, this correspondence allowing isolated eyes to be identified as belonging to this species. The position of the eye relative to the head sclerites conforms to other euthycarcinoids (8) in indicating a short stalk.

A second isolated eye from the Rhynie Chert (GLAHM Kid2475) is identified as belonging to the same species as that described above based on their correspondence in lens size and number, shape and convexity of the visual field, and marginal rim (Fig. 1 F and G). This specimen better illustrates the convexity of the visual surface, which approximates a semicircle, and shows the convexity of the corneal surface of each ommatidium. The marginal rim is preserved more completely, extending as a shallow bowl. Lenses are of similar diameter across the entire visual field, although with some slight variability between neighboring lenses, with no obvious change toward or at the margin. At least 91 lenses are countable and filling a region in which they are not preserved, and extrapolating around the circumference of the eye, we infer a total number not exceeding 150.

**Mandibles and superlinguae.** A pair of mandibles has been described as the only known gnathal appendage in a few species of euthycarcinoids, including *H. rhyniensis* (13). Both mandibles are exposed in transverse section in NMS G.2014.11.1.1, from the Windyfield Chert (Figs. 1B and 3A), with their position relative to other cephalic elements indicating that the section is across the mandibular base. A wide sternite in this section (st in Fig. 1B) would conceal these parts of the mandible in ventral view, with this sternite likely corresponding to the “labrum” of previous descriptions (8). A transverse section across hollow mandibles is likewise visible in a syntype, in which their context in the head capsule is clarified by confocal microscopy (Fig. 2 A and B). This specimen has accurately been identified as a section of the head including the buccal apparatus (ref. 13, fig. 15B).

A pair of strong projections are situated between the mandibles and hypopharynx (Fig. 2B). Their dorsal surface is arched. They correspond in position and morphology to superlinguae, which are paired outgrowths of the mandibular sternum in myriapods (Fig. 2 D and E) and most lineages of primitively flightless hexapods (16).

**Hypopharynx.** Medially in the buccal apparatus of *H. rhyniensis*, NHM PI In 24658 is a strongly sclerotized structure divided into left and right sides that abut each other medially (Figs. 2B and 3G). Its robust preservation and position are consistent with its function as the skeletal support of a medial part of the feeding apparatus, and its position and form identify it as the hypopharynx. It includes a roughly triangular proximal part, a medial bar of which continues ventrally and flares laterally into a flange on each side. The proximal part has paired sensilla on the dorsal area inferred to border the mouth, and the flaring triangular part is fenestrate, with three large perforations on each side. We infer that the soft tissue of the hypopharynx, which would be expected to have dense fields or bands of bristles, had decayed away, and only the robust skeletal support was fossilized. The hypopharynx has substantial skeletal support in myriapods (17, 18) (Fig. 3 H–J).

Sensilla are situated on each side of the hypopharynx (Fig. 2 B and F). They are set in sockets from which they only partially project, and in this respect and their conical morphology they resemble sensilla coeloconica (19). This kind of sensillum is known from the epipharynx and hypopharynx of Chilopoda, including paired clusters immediately adjacent to the mouth as in *Heterocrania* (20) (Fig. 3 E and F). A few (three?) similar sensilla are aligned on a strip of tissue lying against the outer edge of one of the mandibles.

The bipartite form of the hypopharynx, being subdivided into bell-shaped proximal and distal regions, is closely comparable to

Symphyla (Fig. 2 D and E). These two regions correspond to the hypopharynx and lingua (ref. 21, fig. 5), and their relationship to the superlinguae and mandible in Symphyla is closely approximated by *Heterocrania*. The hypopharynx is likewise divided into proximal and distal lobes in Chilopoda (Scutigermorpha) (22) (Fig. 3J), and distinctly differentiated proximal and distal fields are shared by Diplopoda (ref. 23, fig. 2.5A).

**Tentorium.** NMS G.2014.11.1.1 reveals slender but robust bilaterally symmetrical bars extending against the inner edge of the mandibles and forming an inward-curving projection with a ventromedial course (Fig. 1B; hb in Fig. 3A). In comparison with the preservation of the appendages and exoskeleton, these bars are identified as cuticular. They have a bifid medial tip, with each of the pair well separated from the other. The mandible abutting them, their position in the head capsule, and their cuticular nature identify them as parts of the tentorium. More precisely, their inferred relationship to the hypopharynx (based on comparison with Fig. 2B) suggests that they represent the hypopharyngeal bars of the tentorium (Fig. 3C). The bifid “tip” may correspond to a strengthened/thickened region of an apodeme in section, but not necessarily to its full medial extent.

The inferred hypopharyngeal bars are continuous with a similarly cuticularized pair of bars located more dorsally, projecting dorsomedially. The connection between them is marked by paler, less sclerotized cuticle (Fig. 3A). Based on its continuity, we infer that the entire cuticular structure is the tentorium and associated apodemes. The dorsomedial projections (pp in Fig. 3A) may be the posterior process of the tentorium or mandibular apodemes that display a similar connectivity to the tentorium as in extant myriapods (Fig. 3D).

We note correspondences between the inferred hypopharyngeal bars of the cephalic tentorium and cuticular bars in the trunk. The latter are similarly sclerotized, bilaterally symmetrical, and likewise have a bifid strengthening (Fig. 3B). These correspondences suggest serial homology between cephalic and trunk apodemes.

**Labrum.** Dorsal to the hypopharynx in NHM PI In 24658 is a flattened exoskeletal plate with curved margins that meet at a point (la in Fig. 2B). Based on its topological relationship in the preoral chamber and its similarity in shape to a labrum in diplopods (Fig. 2C), we interpret this structure to be part of a displaced labrum.

## Discussion

**Euthycarcinoids as Total Group Myriapoda.** Narrowing down the hypotheses for the relationships of euthycarcinoids, a sister group relationship with Myriapoda is favored in recent morphological analyses (11). Only a few homoplastic characters in the published matrix (11) unambiguously support this grouping (i.e., tergo-sternal decoupling and uniramous trunk appendages), but these are supplemented by additional characters identified in previous studies. Leg attachment via a single ventral articulation of the coxa has been cited as an autapomorphy of Myriapoda (24) and is shared by *Heterocrania*, which has a ventral condyle on the limb base (ref. 13, fig. 8A). The paired sternal pores of euthycarcinoids have been interpreted as the sites of coxal vesicles, shared by progoneate myriapods and primitively flightless hexapods (6). Slender, rod-like apodemes on each trunk segment in several species of euthycarcinoids are comparable to apodemes in Symphyla, which originate on the coxa and serve for insertion of extrinsic limb muscles and longitudinal muscles (6, 14, 25). These apodemes are readily identified in *H. rhyniensis* (13), and as in symphylans, they originate in association with the limb base (Fig. 3B).

Several previously undocumented morphological details emerged from our study as being shared by *Heterocrania* (as well as, we infer, by other euthycarcinoids) and myriapods. These include 1) a cuticular anterior tentorium connected to the preoral chamber

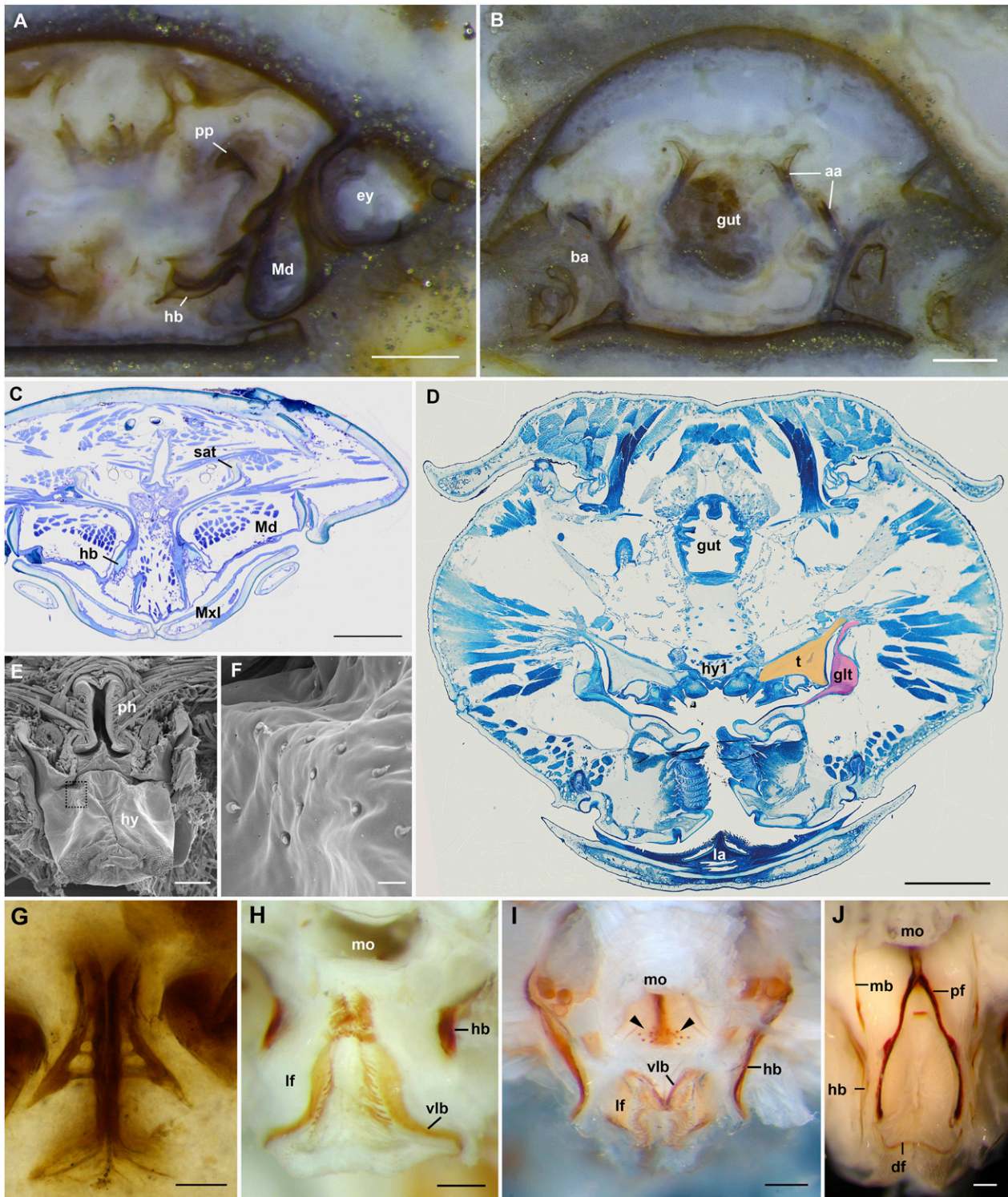


**Fig. 2.** Preoral chamber of *H. rhyhiensis* in light microscopy (A) and confocal microscopy (B and F) and scanning electron micrographs of extant Myriapoda (C–E) for comparison. (A, B, and F) *H. rhyhiensis*, NHM PI In 24658. (A) Transverse section of head, light microscopy photograph, with the buccal apparatus medially. (Inset) Corresponding to the confocal laser scan shown in B. (Scale bars: 100  $\mu\text{m}$  in A, 25  $\mu\text{m}$  in B.) (F) Confocal laser image of detail of proximal lobe of hypopharynx, showing sensilla coeloconica (arrows). (Scale bar: 10  $\mu\text{m}$ .) (C) *Polydesmus angustus* (Diplopoda). (Scale bar: 50  $\mu\text{m}$ .) (D and E) *Hanseniella agilis* (Symphyla). (D) Mouthparts, with left mandible removed to expose superlingua. (Scale bar: 25  $\mu\text{m}$ .) (E) Hypopharynx and left superlingua. (Scale bar: 25  $\mu\text{m}$ .) hy1, proximal lobe of hypopharynx; hy2, distal lobe of hypopharynx (lingua); la, labrum; Md, mandible; Mxl, first maxilla; MxII, second maxilla (labium); Sl, superlingua.

(Fig. 3 A, C, and D); 2) a prominent hypopharynx supported by hypopharyngeal bars of the tentorium (Fig. 3 A and C), and reinforced by cuticular bars (Fig. 3 G–J); 3) the bipartite form of the hypopharynx, with a distal lingua differentiated from a proximal lobe (Fig. 2 B, D, and E); 4) hypopharyngeal sensilla concentrated near the mouth (Figs. 2F and 3F and I); and 5) superlinguae flanking the hypopharynx (Fig. 2 B, D, and E).

These characters add support to an alliance between euthycarcinoids and myriapods. Anterior tentorial apodemes are more widely shared by myriapods and hexapods, but in light of the

overwhelming molecular support for Pancrustacea (a “crustacean”/hexapod clade) than for Atelocerata (a myriapod/hexapod clade), they are regarded as convergent in the two terrestrial groups. Nevertheless, the anterior tentorium is considered a shared derived character of Myriapoda, one that we now interpret as inherited from common ancestry with Euthycarcinoidea. Superlinguae are likewise shared by myriapods and primitively flightless hexapods, but likely have a broader systematic distribution, as a long-suspected homology with the paragnaths of crustaceans has found support from the recognition that the



**Fig. 3.** Cuticular skeleton of *H. rhyiniensis* and corresponding structures in extant Myriapoda in light microscopy (A–D, G, and J) and scanning electron microscopy (E and F) images. (A and B) *H. rhyiniensis*, NMS G.2014.11.1.1. (A) Transverse section of the head (Scale bar: 200  $\mu\text{m}$ .) (B) Transverse section of the trunk. (Scale bar: 250  $\mu\text{m}$ .) (C) *Dicellophilus carniolensis* (Chilopoda: Geophilomorpha), transverse section of the head. (Scale bar: 200  $\mu\text{m}$ .) The supra-mandibular arch of the tentorium (sat) continues into the posterior process (pp in A) more posteriorly. (D) *Polydesmus angustus* (Diplopoda: Polydesmida), transverse section of the head. (Scale bar: 250  $\mu\text{m}$ .) (E and F) *Orya almohadensis* (Chilopoda: Geophilomorpha), scanning electron micrographs of pharynx (ph) and hypopharynx (hy). *Inset* in E shows cluster of spear-shaped sensilla near mouth (F). (Scale bars: 100  $\mu\text{m}$  in E, 10  $\mu\text{m}$  in F.) (G) Cuticular support of the hypopharynx in *H. rhyiniensis*, NHM PI In 24658. (Scale bar: 20  $\mu\text{m}$ .) (see also Fig. 2 A, B, and F.) (H–J) Cuticular support of the hypopharynx in Chilopoda. (H) *Lithobius (Ezembius) giganteus* (Sselivanoff, 1881) (Lithobiomorpha). (Scale bar: 150  $\mu\text{m}$ .) (I) *Scolopocryptops spinicaudus* Wood, 1862 (Scolopendromorpha). Arrowheads indicate a cluster of sensilla near the mouth. (Scale bar: 150  $\mu\text{m}$ .) Reprinted with permission from ref. 17. (J) *Thereuopodina queenslandica* Verhoeff, 1925 (Scutigleromorpha). (Scale bar: 100  $\mu\text{m}$ .) aa, appendicular apodeme; ba, basal part of appendage; df, distal fork; ey, eye; glt, mandibular gnathal lobe tendon; hb, hypopharyngeal bar of tentorium; hy1, proximal lobe of hypopharynx; la, labrum; lf, lateral flap of hypopharynx; mb, marginal bar; Md, mandible; mo, mouth; Mxl, first maxilla; pf, proximal fork; pp, posterior process of tentorium; vlb, ventrolateral bar. E–F: Reprinted from ref. 20, by permission of Oxford University Press.

latter are likewise derived from the mandibular sternum rather than being appendicular (26). A general homology of at least the anlage of these outgrowths across Mandibulata is thus likely. Lack of a mandibular palp is shared by euthycarcinoids and myriapods but is convergent in allotriocaridan pancrustaceans (cephalocarids, branchiopods, remipedes, and hexapods).

Compound eyes, now confirmed for euthycarcinoids, are consistent with a position of euthycarcinoids in the myriapod stem group. They are plesiomorphic for crown group Euarthropoda, originating in stem group euarthropods such as Radiodonta (27), and are retained at the basal node of the myriapod crown group. This is indicated by their presence in Scutigermorpha within Chilopoda (28) and Penicillata within Diplopoda (29). These two lineages are sister groups of all other taxa in their respective classes, the others of which independently evolved a cluster of stemmata (simple lens eyes) as a transformation of ancestral compound eyes.

Monophyly of Euthycarcinoidea has partly been underpinned by their tagmosis, including a head with separate anterior and posterior cephalic tergites (the former much the shorter), an anterior trunk tagma (“preabdomen” in previous descriptions) in which sternites and appendages are decoupled from the tergites, and a narrow, limbless posterior trunk tagma (“postabdomen”). However, these characters, as well as antenniform trunk appendages with short articles, are shared with Cambrian fuxianhuids and may be apomorphic for a broader clade that includes both groups (10, 11). The position of the eyes at the junction between the two cephalic tergites is unique to euthycarcinoids. Euthycarcinoids have the eye stalks behind the antennal base, as in extant mandibulates, whereas the eye stalks are anterior to the antennae in fuxianhuids (30). If fuxianhuids are an immediate outgroup to euthycarcinoids and myriapods (11), then a trunk differentiated into two tagmata can be optimized as ancestral to the undifferentiated (fully limb-bearing) trunk of crown group myriapods. Other candidates for Cambrian myriapods, such as *Xanthomyria* and *Pseudoiulia* (31), have been associated based on having a homonymous, multisegmented trunk. At least some of these taxa can be assigned to other arthropod groups; for example, *Pseudoiulia* is apparently allied to jianfengiid “great appendage” arthropods (32).

Assignment of euthycarcinoids to the mandibulate stem group in earlier work (7) emphasized the absence of differentiated maxillae, and demonstrable maxillae remain undocumented in euthycarcinoids. If this apparent absence is real and the clade is allied to Myriapoda, as supported herein, then convergent transformation of a trunk-like postmandibular limb to a gnathal appendage would be forced in myriapods and pancrustaceans.

**Implications for the Timing of Myriapod Terrestrialization.** An affiliation of euthycarcinoids as total group Myriapoda has important implications for reconciling molecular divergence estimates for Myriapoda and the clade’s fossil record. Euthycarcinoids were long known only from the Upper Carboniferous to the Triassic, but their record was extended deeper in the Paleozoic by identification in the Devonian (13), Ordovician or Early Silurian (33), and Cambrian (7, 34). The Cambrian record consists of *Apankura machu*, from marine shales in Argentina (7), and *Mictomeris melochevillensis* and *Mosineia macnaughtoni*, from intertidal facies in Québec and Wisconsin, respectively (34). The latter two records are difficult to constrain biostratigraphically, the former Miaolingian to Furongian and the latter even more imprecisely constrained between the late Terreneuvian to Furongian. *Apankura*, in contrast, is precisely dated to the latest Furongian (Cambrian Stage 10) by associated trilobites of the *Neoparabolina frequens argentina* zone. *Protichnites* trackways associated with *Mosineia macnaughtoni* in the Elk Mound Group are convincingly associated with that euthycarcinoid being the

tracemaker (35). This provides an additional source of data for estimating the temporal distribution of the group, as well as its environmental range; the same *Protichnites-Diplichnites* trace fossil assemblage occurs in coastal dunes in the Miaolingian (middle Cambrian) in New York (36).

Monophyly of Euthycarcinoidea implies their divergence from any potential sister group by the time of their oldest fossil, that is, minimally by the latest Furongian (using a conservative minimum from *Apankura*). Thus, a position of euthycarcinoids on the myriapod stem lineage would extend the range of total group Myriapoda to that age. This Cambrian fossil history of the myriapod clade thus closes most of the vast gap that has until now existed between the estimated molecular dating of myriapod origins (terminal Ediacaran to Cambrian for the total group, Cambrian for the crown group; ref. 37) and the crown group’s first reliable body fossils, in the Silurian.

This gap had been thought to be partly bridged by *Diplichnites* and *Diplopodichnus* trackways from the Late Ordovician Borrowdale Volcanics of the United Kingdom. These arthropod trackways were formerly regarded as subaerial in origin (38), and the gait of the tracemaker is compatible with locomotion by penicillate millipedes (39). However, sedimentary structures in the trace-bearing strata indicate locomotion on ash deposited subaqueously (40), thereby weakening the case for a crown group millipede as the tracemaker. The inferred pre-Silurian history of the myriapod crown group has been recognized as an example of a general bias in the terrestrial fossil and rock records. Siluro-Devonian records of terrestrial arthropods and land plants are strongly facies-dependent (occurring mostly in fluvial and lacustrine sediments) and are geographically biased (being disproportionately known from Euramerica), but terrestrial sediments are rare before the latter part of the Silurian and become widespread only in the Early Devonian (41).

Euthycarcinoids record the transition of stem group myriapods from marine (*Apankura*) to freshwater environments, and their trace fossil record attests to amphibious nearshore (intertidal and coastal dune) habits by the mid-Cambrian (34–36). Our findings from *H. rhyniensis* reveal that some characters broadly associated with terrestrialization in myriapods, such as the mouthparts being encapsulated in a preoral chamber, are not innovations of the terrestrial crown group but rather evolved in aquatic environments.

## Methods

Confocal laser scans of thin sections of *H. rhyniensis* were acquired with a Nikon A1-Si laser-scanning confocal microscope. Light photographs of thin sections of *H. rhyniensis* were taken with a Nikon Eclipse LV100ND compound microscope with transmitted light. Light photographs of thick sections were taken with a Leica 250C stereomicroscope with reflected light. Histological sections of the heads of *Dicelophylus carniolensis* and *Polydesmus angustus* stained with 1% Toluidine blue were imaged using an Olympus BX 50 light microscope equipped with a Colorview II digital camera. Scanning electron microscopy of extant myriapods was performed with Fei Quanta 200 and Philips XL30 electron microscopes.

Full details are provided in *SI Appendix, Methods*.

**Data Availability.** All data discussed in the paper are present in the main text and *SI Appendix*. Figured and cited specimens of *H. rhyniensis* are accessible in the National Museums Scotland (NMS), the Hunterian, Glasgow (GLAMH), and the Natural History Museum (NHM) under registration numbers cited in the text and figure captions.

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