

ARTHROPOD EVOLUTION

The lower Cambrian lobopodian *Cardiodictyon* resolves the origin of euarthropod brains

Nicholas J. Strausfeld^{1*}, Xianguang Hou², Marcel E. Sayre^{3,4}, Frank Hirth^{5*}

For more than a century, the origin and evolution of the arthropod head and brain have eluded a unifying rationale reconciling divergent morphologies and phylogenetic relationships. Here, clarification is provided by the fossilized nervous system of the lower Cambrian lobopodian *Cardiodictyon catenulum*, which reveals an unsegmented head and brain comprising three cephalic domains, distinct from the metameric ventral nervous system serving its appendicular trunk. Each domain aligns with one of three components of the foregut and with a pair of head appendages. Morphological correspondences with stem group arthropods and alignments of homologous gene expression patterns with those of extant panarthropods demonstrate that cephalic domains of *C. catenulum* predate the evolution of the euarthropod head yet correspond to neuromeres defining brains of living chelicerates and mandibulates.

During the past decade, the discovery of fossilized brains and nervous systems in exceptionally preserved middle and lower Cambrian fossils has reopened the historic and sometimes contentious debate (1) about the composition and evolution of the arthropod head and brain and hence the early evolution of this phylum (2, 3). Two major questions arise: What comprises the head of an arthropod, and does its composition illuminate the organization of the brain (4)? A persistent assumption (5, 6) has been that exoskeletal organization of the head is an indicator of a segmental brain. Developmental and genetic studies have not supported this view.

Already in 1901, Heymons (7), in his meticulous embryological analysis of the centipede brain, showed that the rostral germ band gives rise to three nonmetameric cephalic domains. The anteriormost domain is associated with the labra, the most anterior appendages of the head. The next domain is a pair of lobes associated with the optic areas. Together, these two domains constitute the forebrain. The third pair of lobes constitutes the midbrain, which includes the antennal lobes. Heymons also documented the forward displacement of the trunk's incipient first true segment from the segmented ventral cord (7). The three cephalic domains, now identifiable by their unique gene expression patterns, are the proso-, proto-, and deutocerebrum. The rostrally displaced first trunk ganglion is the tritocerebrum. The ubiquity of these developmental

events across arthropods (8, 9) suggests an ancient origin of the developmental program patterning the brain. Nevertheless, data from developmental genetics that might clarify ambiguities of interpretation (10) have generally been absent from studies of fossils. This is made possible in this study by the fossilized remains of the nervous system in the lobopodian *Cardiodictyon catenulum*, whose cerebral domains align with expression patterns of gene homologs in extant panarthropods.

Lobopodians are an extinct group of worm-like animals that were once abundant in the lower Cambrian and were mainly constrained to the seafloor, along which they moved using tubelike, unjointed legs (11). The present species was retrieved in the late 1980s from Cambrian deposits belonging to the 518-million-year-old Chiungchussu (Yu'an-shan) Formation near Kunming, China (12, 13). Lobopodians are distantly related to today's Onychophora (velvet worms), recognized by genomics and developmental genetics as belonging to the clade Panarthropoda and the superphylum Ecdysozoa, or molting animals (3), which also includes nematode worms and priapulids. *Cardiodictyon* belongs to the "armored" lobopodians, thus named because of the sclerites and spikelike cuticular adornments on their trunks, isolated examples of which are ascribed to the oldest series of the Cambrian ~525 million years ago (14). Figure 1 provides a comprehensive description of the preserved features of *Cardiodictyon* (see also figs. S1 to S3). Central to our understanding of early nervous system evolution is the identification of neural traces, many at the micrometer scale, that resolve an expansive ventral nervous system and a brain occupying a capsule-like head.

Fossilization of nervous tissues has been ascertained for numerous Cambrian taxa, including gilled lobopodians, stem euarthropods, and annelids (15). Most traces are recognized as ventral nerve cord or brain because of their

likeness to features of extant euarthropod nervous systems. Illustrative are the optic tracts and brain of the lower Cambrian anomalocarid *Lyrarapax unguispinus*, which was imaged using digital filtering of chromatic channels to distinguish carbonaceous traces identically resolved by energy-dispersive x-ray spectroscopy (16). Chromatic filtering of high-resolution digitized images of the *Cardiodictyon* trunk and head resolves preserved neuropils and nerve cords (specimens YKLP11434 and YKLP11422; Figs. 1 and 2 and figs. S4 and S5). Unlike dark carbonaceous compressions familiar as preserved neuropil (16, 17), structures interpreted here as neural are resolved as magenta to rust-brown deposits. A recent hypothesis by Saleh *et al.* (18) explaining preservation of neural tissue proposes that authigenic tissue pyritization may be initiated by breakdown of the neuropil's native ferritin (18, 19). The absence of dark deposits indicative of overlying carbon (17) could be explained by partial decay of the carcass or recent weathering (20). In specimen YKLP11434, ganglion-like varicosities connected by ventral nerve cords beneath or lateral to the gut (Fig. 2, A to D) provide abundant collaterals extending dorsally in the trunk (Figs. 1, K and L, and 2, C and D). The head of specimen YKLP11422 is embedded in matrix showing its left half (Fig. 2, F to H). Exposed are parts of the mouth and the rostral digestive tract and its expansion into a funnel-like stomodeum at the junction of the head and trunk (Fig. 2F and fig. S6). These arrangements correspond to pharyngeal systems in the lobopodian *Onychodictyon ferox* (21) and in extant tardigrades (22) (Fig. 2, E and I). Three domains of fossilized neural tissue in the head (ce1, ce2, and ce3) reflect the sequential organization of the foregut components and the origins of the three pairs of head appendages (Figs. 1L and 2, F to H, and fig. S3). Neural traces in the head are interpreted as lying above, beneath, or lateral to pharyngeal structures. The anteriormost cephalic domain (ce1) is interpreted as lying above and partially encircling the buccal tube, as is the second domain's (ce2) reach beneath the pharyngeal bulb (Figs. 1L and 2, G and H). The third domain (ce3) is confluent with the first ventral ganglion-like varicosity (va1) at the interface of the gut and stomodeum (Figs. 1L and 2, G and H, and fig. S6).

Considerations of the early organization of the panarthropod central nervous system usually refer to extant Onychophora and Tardigrada (11, 23, 24). Both possess unarthrodized lobopodian appendages. In Onychophora, segmental ganglia are absent (24). Paired lateral nerve cords comprising continuous synaptic neuropil provide an orthogonal arrangement of collaterals (25) extending dorsally within the trunk's musculature (fig. S7). This contrasts with tardigrades (24), wherein nerves extending

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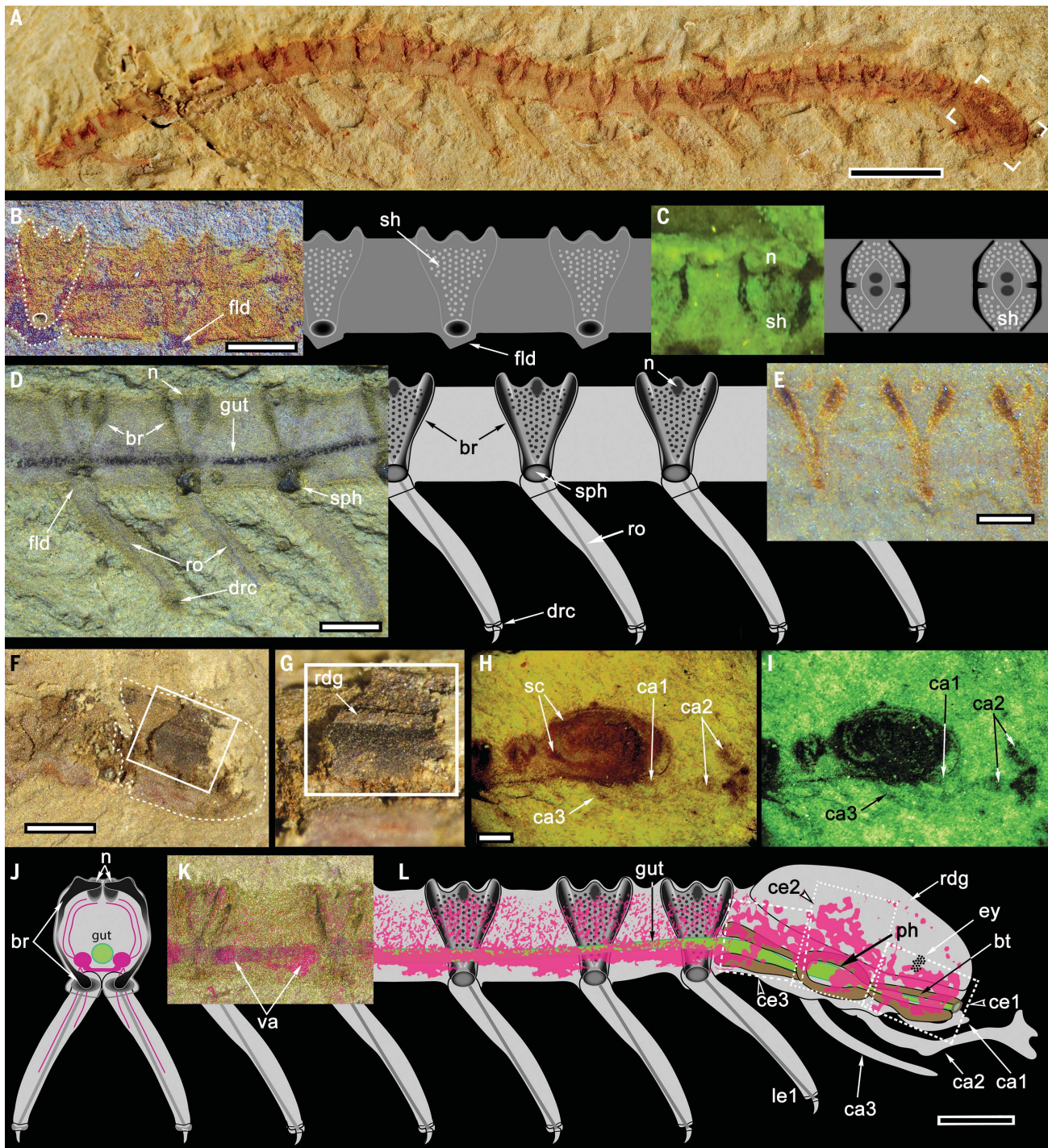


Fig. 1. External and internal organization of *C. catenulum*. (A) YKLP11426: Behind an oval head (bracketed), the trunk has 25 identical segments. (B) YKLP11425: Each segment bears bilateral shield-like sclerites (sh, outline) with punctate thickenings (fig. S2). (C) YKLP11426: Oblique top view of sclerites, following the trunk curvature, their dorsal nodules (n) meeting at the midline. (D) YKLP11423 and (E) YKLP11415: Sclerite side braces (br) converge ventrally to a spherical density (sph) at the base of each leg. A rodlike element (ro) extends from a cuticular fold (fld) beneath the density into the annulated leg and terminates at a distal ring and claw (drc; fig. S1). (F and G) YKLP11421 and (H and I) YKLP11464: An oval carapace with a sculpted midline ridge [rdg, boxed in (F) and (G)] covers the head, laterally reinforced by paired sclerites [sc, (H)]. Three pairs of appendages [ca1 to ca3; (H) and (I)] extend ventrally. The short ca1 pair projects forward from the mouth; the middle

pair (ca2) each comprise three podomere-like articles terminating as a spatula-like element (fig. S3, A to C); the ca3 pair are long and curved, tapering to a blunt end (see also fig. S3, D to F). (J) Schematic cross section of trunk: magenta, ventral cords and orthogon collaterals; green, gut. (K) YKLP11434: Segment with ganglion-like varicosities (va) and ventral nerve cord. (L) Schematic based on YKLP11422, YKLP11423, and YKLP11434: Segmentally arranged ganglion-like varicosities and connecting nerve cords project alongside the gut; collaterals extend dorsally. Three cerebral domains (ce1 to ce3), each associated with a distinct part of the foregut and an appendage pair: ce1 to buccal tube (bt) and ca1; ce2 to the pharyngeal bulb (ph) and ca2; ce3 to the stomodeum and ca3 (also fig. S6). Simple eyes (ey) comprising reflective puncta are associated with ce1. Scale bars: (A) 1 mm; (F) 500 μ m; (all others) 250 μ m.

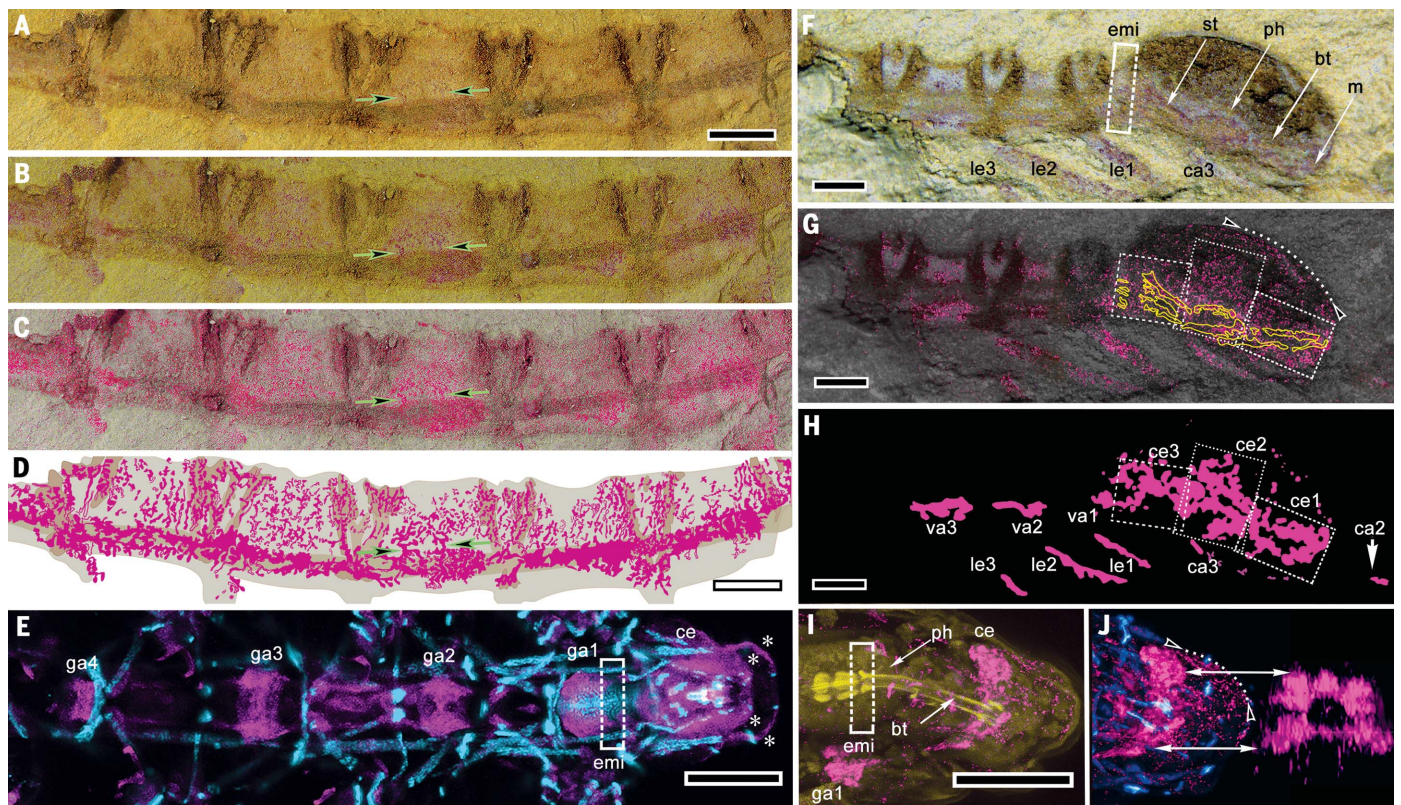


Fig. 2. Segmental nervous system and asegmental brain of *C. catenulum* and *Hypsibius exemplaris*. (A to D) YKLP11434, lateral view, white-light illumination. Arrows denote identical locations throughout chromatic filtering that resolves nerve cord and varicosities, with branches ascending within each trunk segment (fig. S4). (E) Anti-synapsin (magenta) and F-actin (cyan) immunostaining of the tardigrade *H. exemplaris* (dorsal view) resolving synaptic neuropils of the four trunk ganglia (ga1 to ga4). Boxed area rostral to ga1 indicates the endomesodermal interface (emi), the origin of the gut. (F) YKLP11422: white-light illumination of left half of split head of *Cardiodictyon*. Mouth (m) and buccal tube (bt) lead to the pharyngeal bulb (ph) connecting to the stomodeum (st); emi is boxed (fig. S6); le1 to le3 indicate the first three leg pairs of the segmented trunk. (G) Fossilized neural tissue (magenta) and structures

outlined in yellow (buccal tube, pharyngeal bulb, and stomodeum) provide comparison with arrangements in *Hypsibius* (I). (H) Maximum density rendition (fig. S5) of neural tissue resolves cerebral domains ce1, ce2, and ce3 (boxed) associated with cephalic appendages ca2 and ca3. Segmental varicosities (va1 to va3) of the ventral nerve cord relate to legs le1 to le3. (I) Lateral view of *Hypsibius* stained with anti-synapsin and F-actin, showing relationship of cerebrum (ce) and ganglion (ga1) to the autofluorescent (yellow) buccal tube (bt) and pharyngeal bulb (ph); boxed area, emi. (J) (Left) Brain [as in (I)] showing dorsal field of small dense synaptic boutons (beneath dotted line) corresponding to dorsal puncta in *Cardiodictyon* [dotted line in (G)]. (Right) Frontal view of circumesophageal brain neuropil. Scale bars: [(A) to (D) and (F) to (H)] 250 μ m; [(E) and (I)] 20 μ m.

to muscle fibers originate from discrete ganglia (Fig. 2E). In *Cardiodictyon*, numerous collaterals extend dorsally from ganglion-like varicosities and their connecting nerve cords (Fig. 2, C and D). Collaterals also ascend the sclerite braces, whose grooves and pits may suggest muscle attachment sites (fig. S2), as in crustaceans (26).

The organization in *C. catenulum* of collateral nerves from segmental varicosities and nerve cord corresponds to the fossilized trunk nervous system of the fuxianhuiid *Chengjiangocaris kunmingensis*, in which bilaterally extending nerves originate from the segmental ganglia as well as from their connecting nerve cords. This arrangement of lateral nerves looping around the inside of the trunk has been proposed as an ecdysozoan plesiomorphy owing to its occurrence in crown priapulids, nematodes, and onychophorans (27). An evolved reduction and loss of the ganglionic varicosities of *C. catenulum* would provide onychophoran-

like ventral cords linked heterolaterally by looped collaterals. Alternatively, an evolved segmental condensation of collaterals restricted to ganglion-like varicosities would provide an organization comparable to that of tardigrades, where metameric ganglia express the segmental marker *Engrailed* at their caudal margins. Notably, the absence of *Engrailed* expression at the caudal margin of the tardigrade brain suggests its asegmental organization (28). The disposition of *Cardiodictyon* neuropil at its buccal tract aligns ce1 with the most anterior part of the tardigrade brain (Fig. 2J). The absence of head appendages in tardigrades, however, obliges comparison of *C. catenulum* with Euarthropoda, which offers neuroanatomical as well as molecular and developmental genetic correspondences (Fig. 3).

All taxa, including fossils considered in this study, can be compared by aligning their specific non-neural indicator: the origin of

the gut from the stomodeum (Fig. 3 and fig. S6), which denotes the endomesodermal interface (emi). In *C. catenulum*, this occurs immediately posterior to domain ce3, at its confluence with va1, which lies beneath the gut and is associated with the first pair of trunk appendages (Fig. 2, F and H, and fig. S6). The ce3 domain and corresponding ca3 appendages align with the deutocerebrum and its appendages (the jaws) in Onychophora. They also align with the deutocerebral ganglion in stem leanchiiliids (10), which receives nerves from the grasping appendages (Fig. 3B). In extant panarthropods, this is characterized by Empty spiracles (*Emx*) and the exclusion of Homeotic (*Hox*) gene expression (Fig. 3A).

The ce2 domain and appendage pair of *C. catenulum* align with the radiodontan protocerebrum and eyestalks and the protocerebrum and lateral eyes of Leanchiiliidae (Fig. 3B). In extant panarthropods, it is characterized

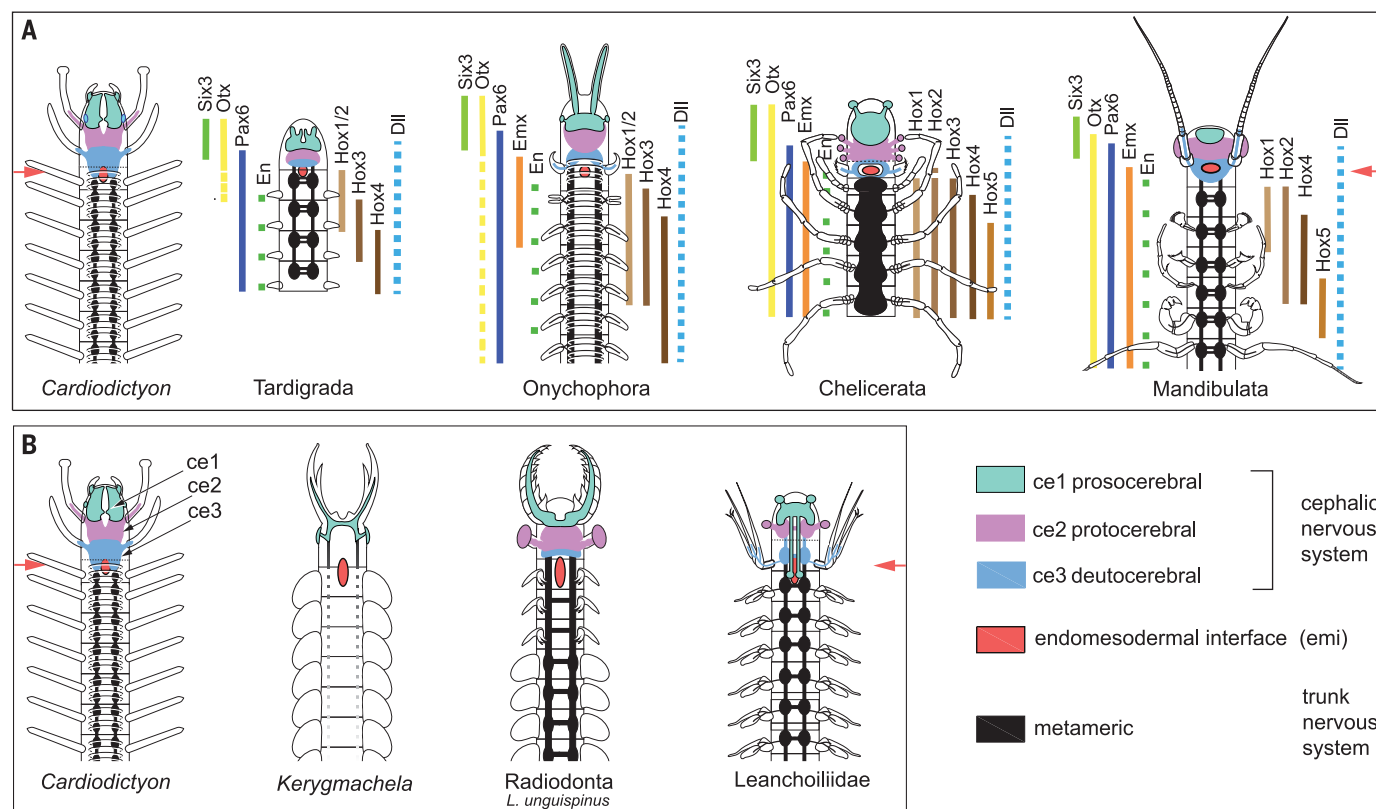


Fig. 3. Correspondence of nervous systems. Cerebral domains ce1 to ce3 in *C. catenulum* and corresponding neuromeres in fossil and extant taxa aligned (red arrows) by endomesodermal interface (emi; red ellipses). **(A)** *Cardiodictyon* aligned with tardigrade (*Hypsibius*), Onychophora, and crown euarthropods. Trunk nervous systems defined by orthogon collaterals and ganglia in *Cardiodictyon*, orthogon only in Onychophora, and ganglia in all other taxa. Expression domains of gene homologs (see table S1): *Six3* demarcating the prosocerebrum and protocerebrum (Proso +Proto); *Pax6*, the entire nervous system except the prosocerebrum; *Hox* expression

patterns align with the mesodermal domain; *Dll* expression extends rostrally to the prosocerebral labrum aligning with *Dll* expression in the tardigrade head. These relationships expressed in set theory: Anterior brain = $(Six3) \cap (Pax6) \mid$ (anterior to endomesodermal interface) $\propto$ (*Hox*-mesoderm) $\therefore$ {Proso+Proto+Deutocerebrum}. **(B)** Alignment of *Cardiodictyon* with extinct taxa shows the diminutive cerebral volume of the gilled lobopodian *Kerygmachela* as extreme rostral to the emi, indicating a prosocerebral identity contrasting with the radiodontan *L. unguispinus* (16) and upper stem Leancoiliidae (10) that reveal ce1, ce2, and ce3.

by Orthodenticle (*Otx*) and Paired box 6 (*Pax6*) gene expression (Fig. 3A). The ce1 domain and the minute frontal appendage pair of *C. catenulum* align with the preoral raptorial appendages and their neuropil in Radiodonta (16, 29) and with the prosocerebrum and its labral neuropil in Leancoiliidae (Fig. 3B) (10), characterized by *Six3* gene expression in extant panarthropods (Fig. 3A) (8). In the gilled lobopodian *Kerygmachela*, nerve cords extend from a rostral bridge of neuropil distant from the pharyngeal/buccal apparatus (30), thus aligning the brain with the ce1 domain of *C. catenulum* (Fig. 3B). The fact that benthic lobopodians possess a single pair of rostral appendages (31, 32), as does nektonic *Kerygmachela*, predicts a comparable neural organization; their phylogenetic position suggests an evolved loss of ce2 and ce3 (fig. S8).

In the tardigrade, the resolution of Distal-less (*Dll*) rostral to the endomesodermal interface (33, 34) is a cryptic correspondence with appendicular attributes of the prosocerebrum (labra) and protocerebrum [stalked eyes or their derivatives (35)] of stem and crown euarthropods, and thereby the two anterior

pairs of cephalic appendages in *C. catenulum* (Fig. 3). Although the three cephalic domains of *C. catenulum* are not morphologically identical, and thus lack the segmental attributes denoted by trunk segmentation (36, 37), they correspond to the rostral neuromeres of the brains of crown euarthropods (Fig. 3). Evidence from spiders, the beetle *Tribolium*, and *Drosophila* demonstrates that mutation of any of the several genes required for formation of the anterior gut and the cephalic appendages affects not only their development but also that of the corresponding neuromere (38–43). Hence their formation and alignment are genetically determined.

For well over a century, the euarthropod brain has been viewed as a composite of metameric neuromeres in a segmented head (44, 45). Here, the lower Cambrian lobopodian *C. catenulum* resolves the brain's ancient origin as segmental domains, the alignments of which reflect their transformation into neuromeres, as seen in upper stem euarthropods (Fig. 3 and fig. S8). Evidence that the brain evolved independently of the caudal nervous

system is validated by observations that different mechanisms underlie their formation in insects (42, 46). Only in crown Euarthropoda is there an embryonic contribution to the brain from the first metameric trunk ganglion, which migrates forward to become the tritocerebrum, contiguous with the deutocerebrum. The deutocerebral and tritocerebral interface defines the boundary between the mid- and hindbrain (47), thus marking the point of coalescence of two connected but genetically and evolutionarily distinct components of the nervous system.

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Competing interests: The authors declare that they have no competing interests. **Data and materials availability:** All data are available in the main text or the supplementary materials. **License information:** Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

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Provenance Statement

Materials and Methods

Figs. S1 to S8

Table S1

References (48–84)

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The lower Cambrian lobopodian *Cardiodictyon* resolves the origin of euarthropod brains

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Cambrian brain origin

Arthropods trace their evolutionary origins back to the Cambrian Period, and there has been continued debate about the origin of the brain in this speciose group. A prevailing view has been that the euarthropod brain was partly composed of ganglia originating from the ventral nervous system. However, Strausfield *et al.* describe the structure of the brain in a lobopodian from the Cambrian that is over 520 million years old, and found that instead the brain was already divided into three separate cerebral components even before the evolution of the head (see the Perspective by Briggs and Parry). These findings support the conclusion that the cerebral and caudal nervous system evolved differently in this group. —SNV

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