The Tully Monster is a vertebrate

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Problematic fossils, extinct taxa of enigmatic morphology that cannot be assigned to a known major group, were once a significant issue in palaeontology. A long-favoured solution to the 'problem of the problematica[1]', particularly the 'weird wonders[2]' in the Cambrian Burgess Shale, was to consider them representatives of extinct phyla. A combination of new evidence and modern approaches to phylogenetic analysis has by now resolved the affinities of most of these forms. Perhaps the most notable exception is *Tullimonstrum gregarium*[3], popularly known as the Tully Monster, a large soft bodied organism from the late Carboniferous Mazon Creek biota (~309–307 Ma) of Illinois, USA. In spite of being designated the State Fossil of Illinois in 1989, its phylogenetic position has remained uncertain and it has been compared with nemerteans[4,5], polychaetes[4],

gastropods[4], conodonts[6], and the stem arthropod *Opabinia*[4]. Here we review the morphology of *Tullimonstrum* based on an analysis of more than 1200 specimens. We find that the anterior proboscis ends in a buccal apparatus containing teeth, the eyes project laterally on a long bar, and the elongate segmented body bears a caudal fin with both dorsal and ventral lobes (Fig. 1b-d)[3-6]. We describe new evidence of a notochord, cartilaginous arcualia, gill pouches, articulations within the proboscis, and multiple tooth rows adjacent to the mouth. This combination of characters, supported by phylogenetic analysis, identifies *Tullimonstrum* as a vertebrate and places it on the stem lineage to lampreys (Petromyzontida). In addition to increasing the known morphological disparity of extinct lampreys[7-9], a chordate affinity for *Tullimonstrum gregarium* resolves the nature of a soft-bodied fossil which has been debated for more than 50 years.

Morphology

Since *Tullimonstrum gregarium* was originally described as a representative of an extinct phylum[3,5] there have been only two attempts using extensive additional specimens to resolve its affinity[4,6]. These analyses favoured its interpretation as a swimming gastropod similar to living heteropods[4,6], or as a chordate close to conodonts[6]. Distinguishing between these alternatives depends primarily on how three major morphological features are interpreted, which are generally referred to as the: (i) ‘gut trace’[4,5], a two-dimensional, light-coloured medial structure (Fig. 1c; Fig. 2a); (ii) ‘segments’[5,6], which consist of regularly spaced dark and light transverse bands (Fig. 1c,e; Fig. 2a; Extended Data Fig. 1a-g); and (iii) ‘jaw apparatus’[4-6] (Fig. 3a-b).

Our new investigation of >1200 specimens of *Tullimonstrum* counters the interpretation[4,5] of the medial structure as a ‘gut trace’. It is preserved differently to the gut in other Mazon Creek animals, which is most commonly three-dimensional and filled by a dark mineral (Fig. 2d). The medial structure is preserved in a manner that most closely resembles the notochord of the stem hagfish *Gilpichthys greenei* [7,10,11] (Fig. 1a) from Mazon creek, which is also a two-dimensional, light-coloured structure[10] (Fig. 2b). *Gilpichthys* preserves a gut trace with the typical dark, three-dimensional preservation[10] (Fig. 2d), as well as the notochord. A true gut trace is evident in a few specimens of *Tullimonstrum* (Fig. 2c) where it ends in the expected position just anterior to the tail (Fig. 2c). This feature is ventral in position in specimens of *Tullimonstrum* that afford a lateral view (Supplementary Text; Extended Data Fig. 2b), in contrast to the light-coloured linear structure which is in the expected dorsal position of a notochord and continues, unlike the gut trace, into the tail (Extended Data Fig. 1f)[9]. The notochord of *Tullimonstrum* lies immediately posterior to a three-lobed structure (in some specimens the two appear continuous) around the eyebar which is very similar to the tri-lobed chordate brain[9]. The eyebar connects the eyes to the central (optic) lobe, suggesting that the eyebar protects the optic nerves (Extended Data Fig. 3a-d). A series of ‘medial organs’[4,5] (Extended Data Fig. 1d,g) is associated with the notochord (Extended Data Fig. 2c). Their three-dimensional preservation suggests that they were decay-resistant[5,12] and we interpret them as cartilaginous arcualia. Similar (but smaller and less regular) three-dimensional, repeated structures also occur along the notochord of *Gilpichthys*[10]. Serially arranged internal structures are also present in some molluscs but they are almost always paired[14] and are unlike the structures interpreted here as arcualia in *Tullimonstrum*.

The ‘segments’[5,6] of *Tullimonstrum* (Extended Data Fig. 1a-g) are muscle blocks which have separated as a result of decay. They are preserved in the shape of a W or chevron, or they may be straight (Extended Data Fig. 1a-g), and one arcualium corresponds to each ‘segment’[5]

(Extended Data Fig. 1d,g). The different segment configurations fall within the range generated by the decay of chordate myomeres[13]. Newly observed structures in the anterior region of the body in some specimens of *Tullimonstrum,* spaced in a similar manner to the myomeres, appear to represent gill pouches (Fig. 1c, Extended Data Fig. 1h). These structures are typically wider than the myomere separations and elliptical in shape; up to five are evident (Extended Data Fig. 1h). The myomere separations show a range of shapes and are most pronounced at the edge of the body whereas the gill pouches lie close to the mid-line (Extended Data Fig. 1g,h).

The body of *Tullimonstrum* extends anteriorly into a proboscis terminating in the 'jaw apparatus'[4,5], which includes an asymmetric proximal base and a distal bifurcate projection bearing small, pointed 'stylets'[5] (Fig. 3a-b). Individual 'stylets' show a range of morphologies which reflect different cross sections through a slightly hooked hollow cone[4] (Extended Data Fig. 4d-i). Differences in preservation suggest that the 'jaw apparatus' was more decay resistant than the body, and the 'stylets' were composed of the most recalcitrant material of the three[4,5]. The 'jaw apparatus' was previously interpreted as a bifurcate buccal apparatus bearing teeth[5], or the cross section of a hollow cylindrical buccal mass containing a radula[4,6]. Our new observations resolve its nature and function.

The 'stylets', here interpreted as teeth, form at least two rows on both dorsal and ventral parts of the bifurcate structure (Extended Data Fig. 4b). Each tooth is set in a small projection of soft tissue (Fig. 3b; Extended Data Fig. 4a). The teeth curve and project posteriorly, presumably to prevent food from escaping as it was ingested. The rows of teeth extend from the anterior tip of the bifurcate structure into the base (Fig. 3b; Extended Data Fig. 4a) indicating that the mouth opening was located there. The position of the gut is evident inside the proboscis[5] (Extended Data Fig. 3c, Supplementary Text). The teeth in *Tullimonstrum* are very similar to those of lampreys and hagfish, which are often simple, posteriorly-pointed, keratinous cones, set in raised soft tissue on a cartilage-supported base[15,16]. The molluscan radula, in contrast, is a ribbon with complex, chitinous teeth[4,17] which are rarely simple cones[4] and are of the same composition as the tissue that bears them.

The proboscis is not, as commonly described, flexible[4] but is characterized by three distinct articulations (Fig. 3a, Supplementary Text): proximally at the connection to the head, about the midlength, and distally where it connects to the base of the buccal apparatus. Unlike hard mineralised tissues such as bone and shell in Mazon Creek fossils[12], these articulations are not three-dimensionally preserved, and were likely supported by unmineralised cartilage.

An elliptical to circular dark stain situated peripherally within the asymmetric base of the buccal apparatus (Fig. 3b, Extended Data Fig. 4a-b) is interpreted as decay resistant internal tissue, either cartilage or muscle, which bears some resemblance in morphology and position to the lamprey lingual organ[15].

Position within Chordata

A phylogenetic analysis of early chordates[18], together with *Tullimonstrum*, resolves it within the lamprey stem lineage (Fig. 1, Extended Data Fig. 7). A number of features align *Tullimonstrum* with lampreys (Supplementary Text): pronounced cartilaginous arcualia; a dorsal fin and asymmetric caudal fin; keratinous teeth; a single nostril; and the presence of tectal cartilages.

Unsurprisingly, given the difficulty of determining its affinities, *Tullimonstrum* displays a number of features that are not found in lampreys, but these reflect its likely mode of life. There are 20-25 myomeres in the trunk and tail of *Tullimonstrum* (Extended Data Fig. 1a-c), as opposed to the 50-70 typical of lampreys[19]. A low myomere count is often associated with a short, stout body, a tail with a high caudal fin aspect ratio, and tail-propelled rather than undulatory swimming[20] (Supplementary Text). Extant lampreys are undulatory swimmers, but the body shape of *Tullimonstrum* suggest that it may have approached tail-propelled swimming.

The eyes of *Tullimonstrum* are set on a rigid horizontal bar (Fig. 1b-d), a configuration rare in chordates but present in hammerhead sharks and larval dragon fish. The eye position is too poorly resolved to reconstruct the visual field of *Tullimonstrum*, but may reflect the position of the prey-capturing buccal apparatus at the end of a long anterior extension of the head.

The buccal apparatus of *Tullimonstrum* suggests that it grasped food with its bifurcate anterior projection, and rasped pieces off with the lingual apparatus[15] (Extended Data Fig. 5a-b). *Tullimonstrum* is one representative of a diverse fauna of Mazon Creek jawless vertebrates with a variety of feeding structures[21]: stem lampreys *Mayomyzon piekoensis*[8] and *Pipiscius zangerli*[7,10,11], and stem hagfishes *Myxinikela siroka*[22] and *Gilpichthys greenei*[7,10,11] (our phylogenetic analysis supports the assignment of *Pipiscius* and *Gilpichthys* to stem lampreys and stem hagfishes, respectively) (Fig. 1a). *Pipiscius* has a unique buccal apparatus consisting of two concentric circles of plates around an enlarged pharyngeal chamber[10] (Fig. 3c). *Gilpichthys* also has a unique buccal apparatus, consisting of an elongate pharyngeal chamber lined with muscle blocks bearing posteriorly-directed teeth[10] (Fig. 3d-e). *Tullimonstrum* significantly expands the morphological disparity known in the lamprey lineage, providing insight into a clade that is characterized by highly conserved morphologies today.

Methods

All specimens figured and discussed here are held by the Field Museum of Natural History in Chicago, Illinois, USA. They were photographed in direct and polarised light, using a Canon EOS 60D. For some images, particularly of the buccal apparatus, multiple images were z-stacked in Helicon Focus v. 4.2.8. All measurements were taken in ImageJ. Comparisons were made with specimens from the Sedgwick Museum and the University of Wisconsin-Madison Geology Museum. Specimens of *Tullimonstrum* and other taxa were analysed using EDS (energy dispersive spectroscopy) on the SEM (scanning electron microscope) at the Field Museum of Natural History. Synchrotron images were collected at beamline 8-BM-B of the Advanced Photon Source. Incident x-rays (10.7 keV) were focused to a 30 micron beam spot using Kirkpatrick-Baez mirrors. The samples were raster-scanned through this spot, in steps of 0.02 (fine scans) – 0.2 mm (coarse scans). Full x-ray fluorescence emission spectra were collected at each position using a SII Vortex ME4 4-element silicon drift detector fitted with an aluminium filter to attenuate the strong iron signal of the matrix material, at 150 ms dwell per pixel. The spectra were fitted with Gaussian models of the characteristic energy and relative intensity of the known atomic emission peaks. The data were also normalised relative to incident flux, and counts were converted to a material quantity ($\mu g/cm^2$) using relative calibration to thin film AXO standards (AXO Dresden GmbH, Heidenau, Germany), with MAPS software[23]. A modern lamprey (*Petromyzon marinus*), lancelet (*Branchiostoma* sp.) and hagfish (*Myxine glutinosa*) were dissected for anatomical comparison, with an emphasis on sectioning planes that reflect the preservation of *Tullimonstrum*. *Tullimonstrum gregarium*, *Gilpichthys greenei*, and *Pipiscius zangerli* were added to an existing phylogenetic matrix of basal vertebrates[18]. One new character, the presence of tectal cartilage, was added to the matrix. The only other changes to the matrix comprise alterations to the coding of Myxinoidea; specificially, characters 28 and 29 (‘Single confluent branchial opening' and 'Elongate branchial series') are here coded as polymorphic to represent the disparity in the clade of extant hagfishes. The resulting matrix of 117 characters and 28 taxa was analysed in TNT[24] (made available with the sponsorship of the Willi Hennig Society) using implicit enumeration with all characters unordered and of equal weight. Bootstrap[25], Jackknife[26] and Bremer[27] support values were calculated in TNT; the ensemble Consistency, Retention and Rescaled Consistency Indices were calculated in Mesquite 3.02[29]. Bootstrapping was performed with 50% character resampling for 5,000 repetitions, and jackknifing by using simple addition sequence and tree bisection-reconnection branch swapping for 5,000 repetitions with 33% character deletion. The reconstruction was created with the free program Blender.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author contributions

VEM conceived the study and wrote the initial draft. VEM, EES, LGT, JCL, and DEGB developed the project. VEM, EES, JCL, LGT, SM, SL, PM, CDW, EGC, RPA analysed and measured specimens. JCL ran the phylogenetic analysis. EES, CS, LF, SV performed the synchrotron analysis. SM created the reconstruction. HP dissected modern taxa for comparative purposes. ERL, EES and SM photographed comparative fossil taxa. All authors reviewed and edited the final manuscript.

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Figures

Figure 1: Morphology and phylogeny of *Tullimonstrum*. a, Chordate phylogeny including *Tullimonstrum gregarium*; lampreys in yellow; hagfishes in red. **b,** Reconstruction of *Tullimonstrum*. **c,** *Tullimonstrum*, FMNH PE 40113, oblique lateral view, also see Extended Data Fig. 2a: eyebar-Eyb, myomeres-My, gill pouches-GP, caudal fin-CF, notochord-No, otic lobe-OtL and optic lobe-OpL of brain, and dorsal fin-DF. **d,** Line drawing: black–teeth; grey–lingual organ; light grey–eyebar; green–gut and oesophagus; red–notochord; light green–brain; orange–tectal cartilages; pink–naris; purple–gill pouches; yellow–arcualia; dark blue–myosepta; blue with black stripes–fins with fin rays. Scale bar 10 mm.

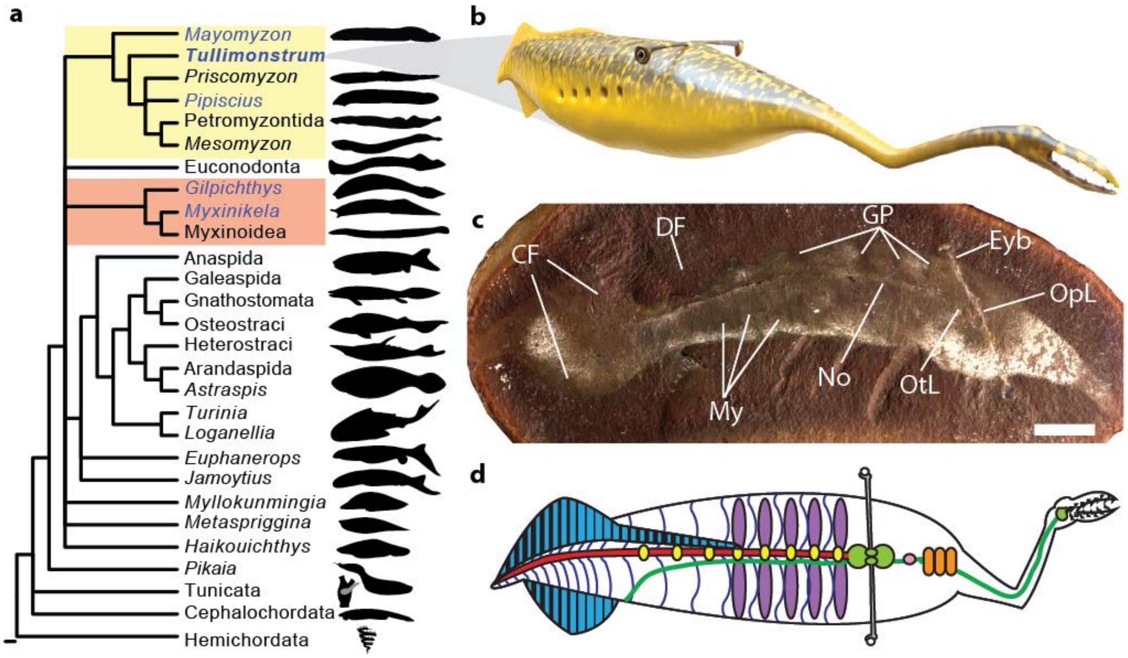


Figure 2: Notochord and gut trace of *Tullimonstrum gregarium* and *Gilpichthys greenei*. a-d, white arrows – notochord, black arrows – gut trace. Scale bars 10mm except in inset in **c**, where the scale bar is 1 mm. **a,** FMNH PE 22077, *Tullimonstrum,* dorsal view. **b,** FMNH PF8349, *Gilpichthys,* lateral view. **c,** FMNH PE9864, *Tullimonstrum,* oblique lateral view, with inset showing gut trace. Also see Extended Data Fig. 2b. **d,** FMNH PF8480, *Gilpichthys*, lateral view.

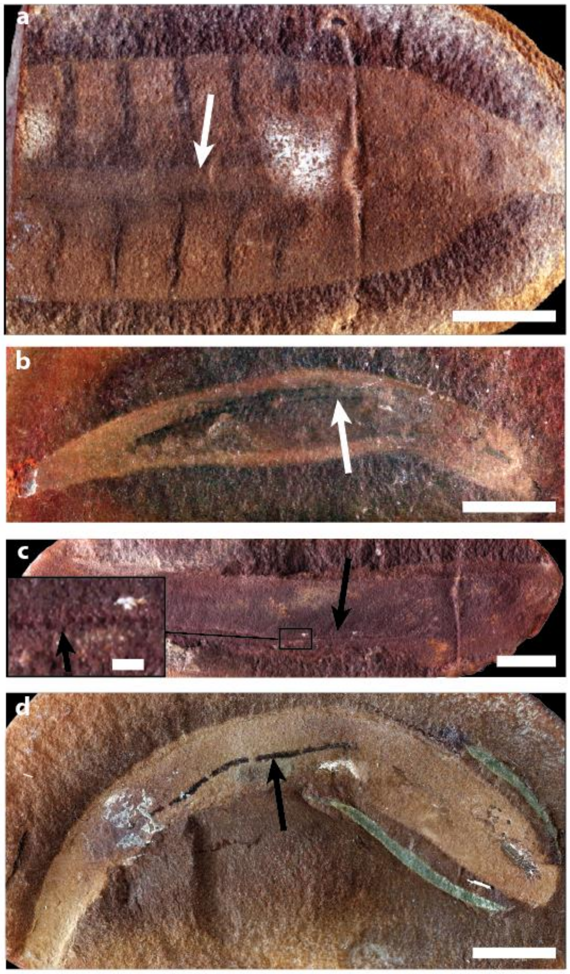
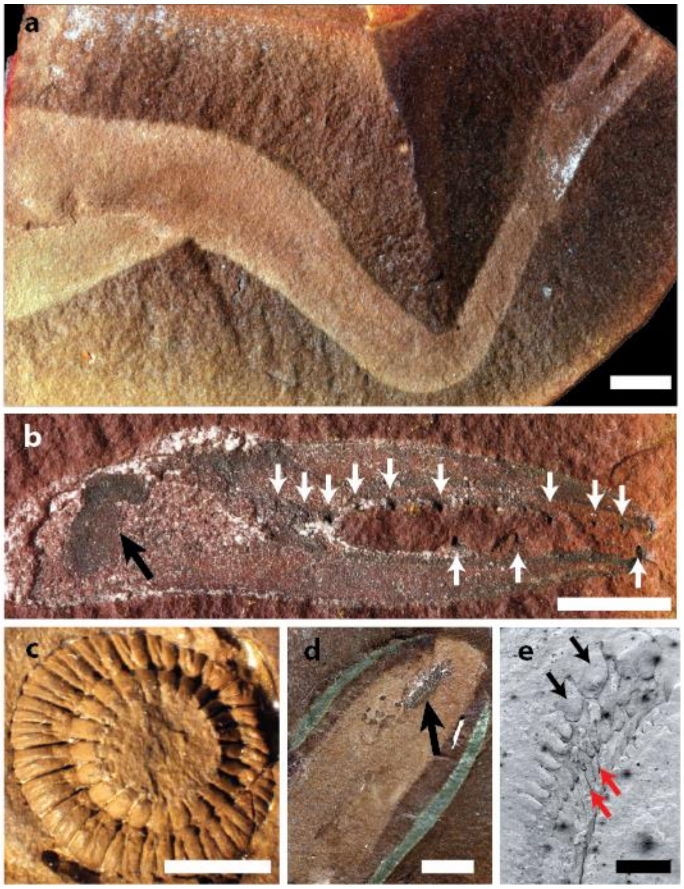


Figure 3: Buccal apparatuses of jawless vertebrates at Mazon Creek. **a, b,** *Tullimonstrum.* **a,** FMNH PE39375, jointed proboscis. Scale bar 10 mm. **b,** FMNH PE45491, buccal apparatus (bifurcate structure and base), lingual organ (arrow), and pyritised teeth (white arrows) that continue into the base. Also see Extended Data Fig. 4a. Scale bar 5 mm. **c,** *Pipiscius*, FMNH PF8344, concentric circles of plates. Scale bar 1 mm. **d, e,** *Gilpichthys*. **d,** FMNH PF8480, buccal apparatus (arrow). Scale bar 5 mm. **e,** FMNH PF8420, SEM image of buccal apparatus with muscle blocks (black arrows) and teeth (red arrows). Scale bar 1 mm.



Extended Data Figure Legends

Extended Data Figure 1: Details of myomeres, myomere separations, and gills in *Tullimonstrum*. Anterior to the right. Scale bars 10 mm. Insets are line drawings of the specimens, with colours as in Fig. 1d. **a, b,** W-shaped myomeres. **a,** FMNH PE32436, narrow myomere separations. **b,** FMNH PE32386, wider myomere separations. Note the folded tail and the dorsal fin which extends from approximately the fifth myomere (arrow). **c,** FMNH PE32423, chevron-shaped myomeres and dorsal fin extending from the fifth most posterior myomere (arrow). The tail is narrower than in a typical specimen because it is preserved in a more vertical orientation than is typical. **d,** FMNH PE7063, straight myomeres separated only at the edges and corresponding to repeated arcualia (arrows). **e,** FMNH PE32395, myomeres separated only at the margins of the body except in the tail where they are completely separated (arrows). **f,** FMNH PE10654, myomeres separated in the tail. Note the axially positioned notochord in the tail (black arrow), and the asymmetric fin with rays (white arrow). **g**, FMNH PE10601, myomere separations that resemble gill pouches but differ in their W-shape, lighter colour, and maximum width at the margin of the body. Note the arcualia (arrows) coloured white by kaolinite (arrows). **h,** FMNH PE45366, gill pouches (arrows) that are elliptical, a darker color, and widest immediately adjacent to the notochord (reddish brown in the fossil). The eyebar is indicated by a white arrow. **i, j,** Linear regressions on segmentation variables. The assumptions for linear regression were tested using the R package gvlma, and all were met. The data are presented in Supplementary Table 2. Data were included for all specimens for which segments could be counted and measured, except for one outlier, which was removed from the calculations with no change to the p-values or R^2 values of the regressions, removed. **i**, Regression between body size and average myomere size, $R^2 = 0.57$. **j,** Regression between body size and number of myomeres in the body, $R^2 = 0.05$.

Extended Data Figure 2: Dorsoventral position of axial structures in *Tullimonstrum*. Specimens preserved obliquely (as indicated by asymmetric preservation of the eyebar, its midpoint indicated by white arrow); the offset of medial structures relative to the axis of the specimen indicates their dorsoventral position. Anterior to the right. Insets are line drawings of the specimens, with colours as in Fig. 1d. Scale bars 1 cm. **a**, FMNH PE40113, displacement of the center of the eye bar, the notochord (black arrow), and the dorsal fin (red arrow)in the same direction, indicating that these are all dorsal structures. The notochord follows the curvature of the body. The tail bends ventrally at the posterior tip (blue arrow) and the dorsal lobe (DL) of the caudal fin is longer but not as deep as the ventral lobe (VL). **b,c,** Other medial features compared to the position of the center of the eyebar, which indicates the notochord position even when the notochord is not preserved. **b**, FMNH PE9864, displacement of the center bulb of the eyebar and the gut trace (black arrow), in opposite directions, indicating that the gut trace is ventral. **c**, FMNH PE24567, displacement of the central bulb of the eye bar and the arcualia (black arrow) in the same direction, indicating that the arcualia are dorsal.

Extended Data Figure 3: The tri-lobed brain of *Tullimonstrum*. Anterior to the top. Scale bars 10 mm. **a-b**, Yellow arrows, olfactory lobe; orange arrows, optic lobe; red arrows, otic lobe. **a**, FMNH PE45350, the three lobes of the brain, the large olfactory lobe anterior to the eye bar, the central optic lobe on the eye bar, and the large otic lobe posterior to it. **b**, FMNH PE22103, a faint trace of the anterior olfactory lobe, the central optic lobe as part of the eye bar, and the posterior otic lobe immediately adjacent to the notochord (black arrow). **c**, Comparison of the brain of *Tullimonstrum* (top, based on FMNH PE45350 in **a**) with the brain of a typical lamprey (bottom) showing the olfactory lobe(s) in yellow, the optic lobes and optic nerve connections in orange, the cerebellum/medulla in red, and the notochord in grey. **d** FMNH PE39890, bilobed central optic lobe (orange arrow) on the eyebar. Note the faint dark trace of the oesophagus in the proboscis (black arrow) and the crescent-shaped naris (white arrow).

Extended Data Figure 4: Buccal apparatus of *Tullimonstrum*. All scale bars 5 mm. Angled arrows indicate the lingual organ, and vertical arrows indicate teeth (not all of which are marked). **a**, FMNH PE45419, dark stain in the base of the apparatus that may represent a remnant of the lingual organ, not showing the distinctive morphology as seen in **b**. The base and bifurcate structure are both asymmetric; the thicker (presumably dorsal) element of the bifurcate structure occurs on the same side as the dorsal bulge in the base. Three teeth (indicated with arrows) lie within the base rather than along the margin of the bifurcate structure. Teeth are present as far as the distal-most (anterior-most) end of the bifurcate structure. The teeth are preserved as three dimensional moulds and casts, and occasionally as pyrite infills, and are situated on raised soft tissue areas (blue arrow in bifurcate structure). **b**, FMNH PE28739, lingual organ and two rows of teeth associated with the ventral element of the bifurcate structure. Two teeth in each row are indicated by arrows; the rows are offset and indicated by black and yellow arrows. Teeth are preserved as moulds. **c**, FMNH PE31057, teeth (one indicated) with white kaolinite infill of negative-relief moulds. Other teeth (one also indicated) are preserved as casts, beyond the distalmost preserved outline of the bifurcate structure. At the distalmost end, the teeth of each element of the bifurcate structure are offset (alternating), whereas for most of the length of the buccal apparatus they are not offset. The apparent asymmetry of the elements of the buccal apparatus is exaggerated as the kaolinite does not reveal the complete outline. **d**, A

Tullimonstrum tooth in three dimensions as a slightly hooked hollow cone with a bulbous base. **e-i**, The three dimensional tooth in **d** is ‘rotated’ and ‘sliced’ in the modeling program, to show how a two dimensional representation of a three dimensional structure may result in a variety of morphologies. These morphologies match those seen in preserved *Tullimonstrum* teeth, suggesting the three dimensional tooth in **d** might be the original shape of the teeth.

Extended Data Figure 5: Elemental maps of *Tullimonstrum*. **a-f**, Synchrotron analysis of FMNH PE10504, and **g-i**, FMNH PE45419, showing the distribution of Ca, Cu, and Zn in **a-c**, the body, **d-f**, the eye (corresponding to the box **c)**, and **g-i**, the buccal mass. Scale bars 10 mm (**a-c, g-i**) and 1 mm (**d-f, j-l)**. Zn shows a high concentration in the body and eye, but Cu is most prevalent in the buccal apparatus. Note that the imaged buccal mass bears teeth, but they are characterized by enrichments distinct from those of the bifurcate structure. **j-l,** SEM/EDS analysis of **j,l** the teeth (too small to see in **a-c**, but at the spot indicated by the black arrow in **c**, since the proboscis folds back over the body) and eye of FMNH PE10504: yellow, S and red, Fe, showing the pyrite preservation (teeth indicated by arrows), and **k**, the teeth of FMNH PE45426: green, Ca; blue, Al; and pink, Si indicating clay mineral preservation of the teeth (in purple, indicated by arrows).

Extended Data Figure 6: Elemental maps of comparative taxa. For each taxon, an icon shows the locations analysed for Zn enrichment (brighter regions) with synchrotron (**a,c,d,h,i,k**) or for general elemental composition with SEM/EDS (**b,e,f,g,j,l)**: green box, eyes; blue box, soft body tissue; red box, feeding structures. In SEM/EDS maps (**b,e,f,g,j,l)**: red, Fe; yellow, S; green, Ca; pink, Si; purple, P; blue, Al; the EDS cannot capture C, so a thin layer of carbon appears identical to the matrix, and a thick layer appears black. All scale bars 1 mm except **f** which is 0.5 mm. **a-c**, FMNH PF8719, chordate *Esconichthys apopyris*, **a**, eyes enriched in Zn, and **b**, preserved in pyrite, and **c**, body lacking Zn enrichment. **d**, FMNH PE 39321, unidentified cephalopod, radula and soft tissue lacking Zn enrichment (dark areas are due to relief). **e,f**, FMNH PF7499, chordate *Elonichthys peltigerus*, **e**, eyes lacking pyrite, and **f**, teeth preserved in Ca, S, and P interpreted to reflect the original apatite. **g,** FMNH PE12371, polychaete *Fossundecima konecniorum*, jaw apparatus (two light colored triangular areas, each with an arrow, on a darker background) preserved in a thin carbon film. **h**, FMNH PE30643, cnidarian *Essexella asherae*, oft tissue lacking Zn enrichment. **i**, FMNH PE 30643, *Etacystis communis*, unidentified soft bodied organism, possibly cnidarian, soft tissue that may be slightly enriched in Zn. **j**, FMNH PE21951, holothurian *Achistrum wheeleri*, teeth of circular jaw preserved in Ca reflecting the original (calcite) composition. **k**, FMNH PE15530, crustacean *Lobetelson mclaughlinae*, eyes lacking Zn enrichment. **l**, FMNH PE23336, horseshoe crab *Euproops danae*, telson preserved as a thick carbon film.

Extended Data Figure 7: Phylogenetic analysis. Strict consensus of 18 most parsimonious trees retrieved under equal weighting (consistency index = 0.549, retention index = 0.614, rescaled consistency index = 0.337). Jacknife support above each node in regular numbers, Bremer support bolded and in parentheses, and bootstrap values beneath each node in italics.

Extended Data Figure 8: Internal structures of *Gilpichthys* and *Tullimonstrum*. Anterior to right. **a**, FMNH PF8410, *Gilpichthys*, gut (arrow) preserved in a similar fashion to typical Mazon Creek coprolites. Scale bar 5 mm. **b**, FMNH PE10638, *Tullimonstrum* with preserved tectal cartilages (arrow). Scale bar 10 mm. **c**, FMNH PE39169, *Tullimonstrum* with liver (arrow) preserved as a diffuse dark circular structure. Inset is a line drawing: red–notochord and brown – liver. Scale bar 10 mm.

Extended Data Table 1: Tail aspect ratio for *Tullimonstrum* and extant lampreys. Lamprey measurements were obtained from pictures from www.seagrant.wisc.edu. All measurements are in mm.

Extended Data Table 2: Summary of specimen descriptions. A summary of the specimen data presented in Supplementary Table 1.