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The ‘Tully Monster’ Is Not a Vertebrate: Characters, Convergence and Taphonomy in Palaeozoic Problematic Animals.

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Abstract. The affinity of *Tullimonstrum gregarium*, a pincer-mouthed, soft bodied bilaterian, has been subject to debate since its recovery from Carboniferous coal deposits at Mazon Creek, Illinois. After decades of impasse focused on mollusc, arthropod and annelid attributes, two recent, yet conflicting, high-profile studies concluded that the ‘Tully Monster’ is a vertebrate, a relative of lampreys or jawed fishes. Here, we find that structures described as supporting vertebrate – particularly crown vertebrate – affinity face significant challenges from biological, functional and taphonomic perspectives. Problems with comparator choice, interpretation of taphonomic processes at Mazon Creek, and estimation of convergence within the bilaterian tree may have misled these recent studies, leading to conclusions which do not accommodate current understanding of the vertebrate record. For example, the absence of taphonomically-expected synapomorphies in *Tullimonstrum* (e.g. otic capsules, body pigment) calls into question vertebrate identity and implies that convergence or deeper origins are responsible for vertebrate-like traits. Further, phylogenetic placement within vertebrates is only made possible by the constraints of a chordate-only dataset with limited outgroups and use of selective characters. Long-discussed alternative placements among molluscs (e.g. heteropod gastropods), arthropods (e.g. anomalocarids), or elsewhere within non-vertebrate deuterostomes are more congruent. Indeed, many of these lineages independently evolved vertebrate-like traits, including complex eyes and ‘teeth’. Thus, given the totality of evidence, *Tullimonstrum* should be excluded from the vertebrate crown. Potential assignments for aberrant bilaterians, common throughout the

Palaeozoic fossil record, need be considered in light of the number and likelihood of required exceptions to established schemes.

Keywords. *Tullimonstrum*, Mazon Creek, lamprey, Carboniferous, taphonomy, vertebrates.

Text

Tullimonstrum gregarium Richardson 1966 is a well-known problematic bilaterian that only occurs in concretions recovered from marine Essex fauna deposits within the Carboniferous Francis Creek Shale, most notably at Mazon Creek, Illinois (307 Ma; Foster 1979; Shabica and Hay 1997; Sallan & Coates 2014). It is notable for its combination of traits uncommon in fossil and living animals, such as long-stalked eyes and an elongate proboscis with a pincer-like mouth (Richardson 1966; Johnson & Richardson 1969; Foster 1979). Like so many Palaeozoic soft-tissue fossils with divergent morphology and a single documented occurrence in time (Donoghue & Purnell 2009), the affinity of *Tullimonstrum* was immediately subject to debate. It has been serially attributed to almost every bilaterian group, including arthropods, molluscs, and ‘worms’ of all sorts (Richardson 1966; Johnson & Richardson 1969; Foster 1979; Beall 1991). Continuing uncertainty regarding *Tullimonstrum*’s classification has produced as much interest as the aberrant morphology at its source.

Despite thousands of specimens surveyed by dozens of workers over the decades, one major bilaterian clade was never linked to *Tullimonstrum*: vertebrates. Vertebrates were likely excluded from consideration by a general absence of evident synapomorphies in *Tullimonstrum*, appearance of conflicting traits such as broad superficial segments, and gross dissimilarity with the coincident crown cyclostomes and gnathostomes (jawless and jawed fishes, respectively) that have well-preserved modern morphologies (e.g. *Mayomyzon* and *Myxinikela*; Gabbott *et al.* 2016). In fact, when a single 20th century study discussed a potential connection with then-problematic conodonts, it was wholly in the context of a conodont-mollusc clade (Beall 1991). This relationship was summarily dismissed by the discoverers of the conodont animal while making a case for conodont-vertebrate affinity (Aldridge *et al.* 1993).

The recent announcements in *Nature* of a vertebrate affinity for *Tullimonstrum* was therefore unexpected (McCoy *et al.* 2016; Clements *et al.* 2016). Two simultaneous studies came to this conclusion on the basis of novel, yet distinct, interpretations of previously observed features (primarily axial structures and eye pigments respectively). However, these arguments for vertebrate attribution present major challenges in terms of taphonomy, morphology, and parsimony, and furthermore contain major inconsistencies. McCoy *et al.* (2016) used the presence of a ‘notochord’ to designate *Tullimonstrum* as a lamprey, yet noted that internal elements are not preserved in definitive Mazon Creek vertebrates. Indeed, Clements *et al.* (2016) found no such structure, but described discrete layers of melanosomes in the eye as a vertebrate synapomorphy (Bardack &

Richardson 1977; Gabbott *et al.* 2016), while acknowledging the absence of other, expected characters.

Here, we argue that a crown vertebrate – and particularly lamprey – identity for *Tullimonstrum* is unlikely. For example, the absence of taphonomically-expected vertebrate synapomorphies in *Tullimonstrum* (e.g. otic capsules, body pigment; Bardack & Richardson 1977; Janvier 1996; Sallan & Coates 2014; Clements *et al.* 2016; Gabbott *et al.* 2016; McCoy *et al.* 2016) suggests that convergence or deeper origins are responsible for vertebrate-like traits. Alternative, previously proposed, placements among molluscs (e.g. heteropod gastropods; Johnson & Richardson 1969; Foster 1979; Beall 1991), arthropods (e.g. Johnson & Richardson 1969; Foster 1979), or new attributions elsewhere within deuterostomes or chordates are more congruent for the reasons laid out below.

Anatomical Interpretations

Clements *et al.* (2016) proposed total-group vertebrate affinity for *Tullimonstrum* based on two traits: 1) a camera-like eye, 2) the presence of two organelles, cylindrical and spheroid melanosomes, in the eye. These were taken as evidence for a multilayered retinal pigmented epithelium (RPE), a vertebrate trait (although presence of the RPE was marked as equivocal in their fig. 4). With respect to the vertebrate nature of these characters, an alternative interpretation, based on three-dimensionally preserved specimens, is that the eyes are pigment cup type (Johnson & Richardson 1969), which are far more phylogenetically widespread but not found among vertebrates (Clements *et al.* 2016). Second, the distribution of pigment cell structures and melanin within the eye has not been well surveyed among other bilaterians, living or extinct (Lamb *et al.* 2007; Schoenemann *et al.* 2009; Clements *et al.* 2016). This suggests other occurrences are possible and limits the current utility of these traits in placing *Tullimonstrum*. Presence of these two melanosome types is variable even among vertebrates: the RPE — along with the lens and iris — has been lost in extant hagfish (Locket & Jørgensen 1998; Gabbott *et al.* 2016), and only spheroid melanosomes are preserved in the eyes of the chondrichthyan *Bandringa* (Clements *et al.* 2016: extended data fig. 5l). No other vertebrate traits were identified by Clements *et al.* (2016), yielding two additional possibilities beyond vertebrate affinity: 1) cylindrical melanosomes and/or the RPE evolved deeper within deuterostomes with genetic prerequisites for RPEs (see below; Lamb *et al.* 2007), or 2) *Tullimonstrum* belongs to an entirely different group of bilaterians and exhibits convergent eye structures (Foster 1979). Eye structures and characters exhibit high levels of homoplasy, convergence and parallel evolution (Ogura *et al.* 2004; Serb and Eernisse 2008; Schoenemann *et al.* 2009; Clements *et al.* 2016). While independent gain of this structure (or its loss in proximate crown vertebrate outgroups) may appear unparsimonious, this must be balanced against the absence of expected vertebrate synapomorphies in *Tullimonstrum*, not to mention its incongruous body plan.

In contrast, McCoy *et al.* (2016) identified a host of putative vertebrate traits in their description of *Tullimonstrum*, which were used to support a lamprey designation. This began with a 'notochord' represented by a mid-body light-colored stain or gap in segmentation (Johnson and Richardson, 1996; Fig. 1a, ax). 'Notochord' identity was assigned in *Tullimonstrum* only through comparison with an indented band in *Gilpichthys*, a poorly-described putative chordate mistakenly referred to as a stem-hagfish by McCoy *et al.* (2016; see Sansom *et al.* 2010; Janvier 2015; Janvier & Sansom 2015; Gabbott *et al.* 2016; Fig. 2b). Notochords are unpreserved in definitive Mazon Creek vertebrates (Bardack & Johnson 1997; Shabica & Hay 1997; Sallan & Coates 2014; Clements *et al.* 2016; Gabbott *et al.* 2016). Secondary mention of a notochord in *Mayomyzon* (Aldridge & Donoghue 1998) stems from misinterpreted pigmentation, such as an intermittent gap between dorsal stripes on dorsally preserved specimens or latero-ventral line on laterally preserved specimens, which were never interpreted as such in primary descriptions (Bardack & Zangerl 1971; Bardack & Richardson 1977; Fig. 2A). Finally, expansion of this band in *Tullimonstrum* anterior to the eye bars, used to rule out gut identity despite connection with the anterior mouth, definitively rules out notochord interpretation. Notochords terminate posterior to the optic chiasma or the hypophysis in all vertebrates (Janvier 1996; Kardong 2011; Fig. 1B, no).

Designation of a notochord was crucial to McCoy *et al.*'s (2016) description as it was used to justify choice of the vertebrate bodyplan for subsequent reconstruction of all *Tullimonstrum*'s other characters. First, it should be noted that notochords are at least a chordate, and more likely a deuterostome, synapomorphy rather than a vertebrate identifier (Holland *et al.* 2015; Annona *et al.* 2015). Second, and more importantly, this initial selection of a single comparator inflated similarities, even when many of *Tullimonstrum*'s traits do not fit a vertebrate comparison (see Donoghue & Purnell 2009 for commentary on this approach). For example, widely-spaced indentations and white lines in the anterior body were reinterpreted as vertebral arches (cartilaginous arcualia), despite the latter being identified as dorsal fin posteriorly (McCoy *et al.* 2016; Fig. 1A, wl). Arcualia are normally more numerous, closely-packed, and have paired extensions alongside the dorsal nerve cord and/or notochord (separate in lamprey, joined as arches in gnathostomes; Janvier 1996; Kardong 2011) rather than being self-contained, stout and rounded as reconstructed in *Tullimonstrum* (McCoy *et al.* 2016). Moreover, they are not readily preserved in either the jawless or jawed vertebrates of the Mazon Creek Essex fauna (Nitecki 1979; Shabica & Hay 1997; Sallan & Coates 2014; Gabbott *et al.* 2016; Table 1).

Laterally-rounded segments divided by vertical septa (Johnson & Richardson 1966), were termed gill pouches anteriorly and w-shaped muscle blocks (myomeres) posteriorly (McCoy *et al.* 2016), despite a lack of differentiation (Fig. 1A, seg, sep). These interpretations likewise present challenges. Vertebrate myomeres are relatively much thinner, posteriorly-angled and overlapping, and extend the full length of the body and pharynx (Bardack & Richardson 1977;

Janvier 1996; Donoghue & Purnell 2009; Kardong 2011; Sansom et al. 2011; Fig. 1b). Furthermore, recent decay experiments of priapulids have demonstrated that rings of circular muscles can taphonomically transform into weakly sigmoidal shapes (Sansom 2016). As such, instances of subtle curvature of serial segments (e.g. *Tullimonstrum*; *Pikaia*: Conway Morris & Caron 2012) may not be reliable evidence for the presence of W-, Z- or V-shaped chordate myomeres. Lamprey respiratory tubes, or 'gill pouches', are paired lateral extensions underlying all gill slits on each side (Fig. 1B), rather than segmented units underlying a single gill pore (McCoy et al. 2016). The reconstructed respiratory anatomy in *Tullimonstrum* (McCoy et al. 2016: fig. 1d) is also dissimilar to gnathostomes, where gill openings are situated directly off the expanded buccal cavity or connected pharynx, and are separated from each other by thin tissue, and the gill filaments themselves, attached to skeletal elements (if at all; Randall 1982; Kardong 2011; Fig. 1B). Further, lamprey respiratory tubes are buried deep within a complex gill skeleton (Fig. 1B), as is the case for the general vertebrate pharynx (not reconstructed in *Tullimonstrum*: McCoy et al. 2016; Bardack and Richardson 1977; Randall 1982; Janvier 1996; Donoghue & Purnell 2009; Kardong 2011). Finally, the faint circles described as gill slits in *Tullimonstrum* sit on septa rather than associated gill tissue or pouches (McCoy et al. 2016), preventing respiratory function, and lack expected pigmentation evident in Mazon Creek cyclostomes (Bardack & Richardson 1977; Gabbott et al. 2016; Fig. 1A).

An expanded central oval was designated as part of a naked tripartite brain otherwise preserved as stains, despite its distinct hard-tissue composition and continuity with the eye bars (Johnson & Richardson 1969). Associated skeletal (e.g. neurocrania) and nervous tissues (e.g. cranial nerves, placodes; Janvier 1996; Kardong 2011) are entirely missing. The absence of otic capsules filled with hard material (e.g. statoliths) in *Tullimonstrum* is both phylogenetically and taphonomically inconsistent with the lamprey interpretation. As decay resistant structures (Sansom et al. 2011), they are frequently preserved in demonstrable Mazon Creek vertebrates, including lampreys (Sallan & Coates 2014; Gabbott et al. 2016; Bardack & Richardson 1977; Fig. 2A, Table 1). A dark circle under the 'gills' was interpreted as the liver (McCoy et al. 2016), despite universal placement in vertebrates posterior to the pharynx (Kardong 2011; Fig. 1B, lv). Finally, a thin, ventral line shared with *Gilpichthys* was identified as the gut, yet lacks distinct units (divided intestine; Kardong 2011; Figs. 1A, dl 1B, in) and exhibits a split appearance in dorsoventral view.

Specialized traits in *Tullimonstrum* present raise additional issues. For instance, McCoy et al. (2016) reconstruct a mouth with associated 'buccal apparatus', and opposing 'tooth' rows at the anterior of the proboscis. Articulated jaws with marginal tooth rows are a trait of gnathostomes (Clements et al. 2016; Janvier 1996). They are not homologous with muscular lamprey mouth structures, which comprise extensive, multisurface 'tooth' fields and depend on internal elements (Kardong 2011; Fig. 1B). This interpretation would necessitate an exceptional

instance of convergent evolution of grasping jaws. Further, such a reconstruction is functionally improbable; most aquatic vertebrates depend on the movement of large volumes of water through the mouth into enlarged cavities for prey transport (ram and suction feeding) and/or respiration (ram ventilation) at some point (e.g. during active swimming; Roberts 1975; Randall 1982). This is particularly true for fusiform, typically pelagic and mid-water types like *Tullimonstrum* (Roberts 1975). The narrow, jointed, elongate proboscis in *Tullimonstrum* would severely limit such flow, at odds with a greatly enlarged pharyngeal region and long distance to the gut, as inferred from placement of gill slits along half the body length (McCoy *et al.* 2016). A perpendicular arrangement for the gill pouches, as reconstructed from the segments (McCoy *et al.* 2016), would likewise present an obstacle (Kardong 2011). Some fishes have circumvented these issues through the pumping of enlarged buccal cavities, spiracular openings above the gill chamber (e.g. rays), piston cartilages and velum (e.g. lampreys), and/or muscular opercula (e.g. teleosts) which suction water directly into the gills (Roberts 1975; Kardong 2011). None of these solutions are apparent in *Tullimonstrum*; the buccal cavity itself is greatly reduced and separated from the gills, a jointed proboscis would disrupt a piston cartilage, and the designated gill openings are very small and round, without any apparent cover.

Phylogenetic relationships

To reconstruct the phylogenetic relationships of *Tullimonstrum* following these anatomical interpretations, McCoy *et al.* (2016) utilised a chordate-only dataset modified from previous studies (Sansom *et al.* 2011; Conway Morris & Caron 2014). They recovered *Tullimonstrum* as a lamprey, resolved crownward of the co-occurring, anatomically-modern *Mayomyzon* (Bardack & Zangerl 1971; Bardack & Richardson 1977; Sansom *et al.* 2011; Conway Morris & Caron 2014; Gabbott *et al.* 2016; Fig. 2A), on the basis of its asymmetrical tail. The lamprey clade was defined by characters that are either missing in *Tullimonstrum* (oral hood, annular and piston cartilages, see above), or equivocal in their interpretation (tectal cartilages, for which there is no evidence in *Jamoytius*; Sansom *et al.* 2011). Furthermore, the crownward placement of *Tullimonstrum* relative to *Mayomyzon* results from incorrect interpretation of an absence of an oral disc and tail asymmetry in the latter (Gabbott *et al.* 2016; Fig. 2A). Redressing just this coding for *Mayomyzon* and removal of only the most equivocal character for *Tullimonstrum* (tectals, see above) renders the placement of *Tullimonstrum* as ambiguous in an incongruent topology (Fig. 2B); this highlights immediate issues with the lamprey interpretation of McCoy *et al.* (2016), and with a vertebrate affinity more generally. Importantly, use of an all-chordate dataset, excluding divergent non-vertebrate forms and all non-vertebrate fossils, renders a chordate and particularly vertebrate affinity as near-inevitable, irrespective of codings applied to any taxon in question. Further, cyclostome monophyly was not supported in any analysis (McCoy *et al.* 2016; Fig. 2B), at odds with mounting evidence and the majority of recent topologies (Donoghue & Purnell 2009; Sansom *et al.* 2010; Kardong 2011; Conway Morris &

Caron 2014; Janvier 2015; Gabbott *et al.* 2016). As such, the dataset employed by McCoy *et al.* (2016) does not present a test of chordate or vertebrate affinities.

Taphonomy

Taphonomy was used to explain incongruent traits in *Tullimonstrum* (McCoy *et al.* 2016; Clements *et al.* 2016), despite established preservational modes at Mazon Creek (Shabica & Hay 1997; Sallan & Coates, 2014; Table 1). The definitive vertebrates found alongside *Tullimonstrum* in the Essex fauna (Nitecki 1979; Shabica & Hay 1997; Clements *et al.* 2016) preserve a consistent subset of cyclostome and gnathostome features: pigmented body outline, jaws, oral hood, fins, superficial gill structures, tooth impressions, eyes, statolith-filled otic capsules, and lateral line traces (Bardack & Richardson 1977; Sallan & Coates 2014; Gabbott *et al.* 2016; Fig. 2A, Table 1). The last two characters are vertebrate synapomorphies and have not been identified in *Tullimonstrum*, despite detailed study of over 1200 specimens (McCoy *et al.* 2016; Clements *et al.* 2016). This indicates true absence. *Contra* the explanation by McCoy *et al.* (2016), otic capsules are found in fishes preserved in dorsoventral view at Mazon Creek (Shabica & Hay 1997; Sallan & Coates 2014), including the cyclostome *Mayomyzon* (Bardack & Zangerl 1971); as decay-resistant structures their presence is expected (Sansom *et al.* 2011). Further, no Essex vertebrate, again including *Mayomyzon* (Bardack & Richardson 1977; Sansom *et al.* 2010), preserves internal musculoskeletal structures as distinct from external, delineating melanin pigment (Sallan & Coates 2014; Gabbott *et al.* 2016). The rare 'myomeres' and guts of some dubious agnathans like *Gilpichthys* (Shabica & Hay 1997; McCoy *et al.* 2016) are therefore likely to be external features, as are those of *Tullimonstrum*. Hence, it is highly unlikely that many of the structures described by McCoy *et al.* (2016) would be preserved in *Tullimonstrum*, even if a vertebrate affinity were favoured.

Alternative Comparative Models

Considering the large number of biological and taphonomic issues presented by a lamprey or crown-vertebrate identity for *Tullimonstrum*, alternative comparisons may provide a better-fit diagnosis (e.g. multiple model comparisons for vetulicolians, Aldridge *et al.* 2007). Simply changing the interpretation of the axial band (described as a 'notochord' by McCoy *et al.* (2016) under their vertebrate interpretation) could alter downstream diagnoses enough to result in a different affiliation or suitable comparator. For example, similar axial bands, and 'muscle blocks', are widespread in exceptionally-preserved Paleozoic arthropods, representing guts with glands and exoskeletal segments (Zhang & Briggs 2007; Yang *et al.* 2016). Ventral nerve cords, pigmented, stalked eyes, brain and lateral tail-fins are widely preserved in anomalocarids (Zhang & Briggs, 2007; Yang *et al.* 2016), with an elongate, jointed proboscis with pincer present in *Opabinia* (Foster 1979; Zhang & Briggs 2007; Fig. 1D). McCoy *et al.* (2016) rejected an arthropod affinity based on a taphonomic assumption that three-dimensional preservation and cuticle carbonization was universal for Mazon Creek arthropods. This is demonstrably not the case based on available arthropod

material (Shabica & Hay 1997). It is true that arthropods do not have melanosomes under a vertebrate-based definition (Clements *et al.* 2016). However, they do have spheroid eye cells containing a related retinol-based pigment among other cell types, which may be preserved similarly to the melanosomes and melanin of vertebrates (Eakin & Westfall, 1965; Hamdorf 1979; Schoenemann *et al.* 2009).

Even positive identification of vertebrate-like differentiated melanosomes does not preclude non-vertebrate affinities. Similar structures have been identified in the eyes of other Bilateria (Clements *et al.* 2016). One example noted is molluscs, which independently evolved both melanin-containing pigment cells and complex camera eyes without the extensive extrinsic musculature required by vertebrates, and thus are a plausible alternative based on these characters alone (Hamdorf 1979; Blumer 1998). In fact, McCoy *et al.* (2016) present evidence supporting a molluscan identity for *Tullimonstrum*, in line with previous arguments for a heteropod gastropod affinity (Foster 1979). As McCoy *et al.* (2016) and previous workers such as Foster (1979) and Beall (1991) note, molluscs share many inferred features of *Tullimonstrum*, including a multi-lobed 'brain', complex eyes on hardened stalks, transverse muscle-bands, guts ending before the posterior body, asymmetrical dorsoventral tail-fin, proboscis, and bifurcate mouth with buccal mass and radular 'tooth' rows (the latter preserving like chordate teeth at Mazon Creek; Ralph 1957; Foster 1979; Fig. 1E). As noted above, since variation in eye microstructure has not been well surveyed in most non-vertebrate bilaterians, and particularly their fossil members, alternate identities cannot be ruled out on these grounds (Clements *et al.* 2016).

If the eye melanosome organisation of *Tullimonstrum* is shown to be homologous with the RPE of vertebrates, it is still likely to be better supported among non-vertebrate deuterostomes. Many invertebrate deuterostomes share, or have genetic precursors for, RPE elements (Lamb *et al.* 2007). They also lack many of the crown-vertebrate characters absent in *Tullimonstrum* (Janvier 1996; Sansom *et al.* 2010; Conway Morris & Caron 2014). These include tunicates, which have pigmented eyes and tail "fins" in larval form, as well as lancelets and hemichordate acorn worms, which have simple gill openings and a notochord extending past the "brain" (Janvier 1996, 2015; Kardong 2011). That said, the most similar, segmented forms among extinct deuterostomes are Paleozoic stem-chordate vetulicolians, themselves of problematic affinity (Janvier 1996, 2015; Aldridge *et al.* 2007; Donoghue & Purnell 2009; Fig. 1C).

Conclusion

Our review of the evidence suggests that a non-vertebrate affinity for *Tullimonstrum* would produce fewer taphonomic discrepancies and require fewer apomorphies and *Bauplan* alterations than a vertebrate assignment. It is likely that a full accounting of the evidence - morphological, taphonomic, developmental and phylogenetic - with consideration of all well-supported potential affinities, will be required to determine the most parsimonious attribution

of *Tullimonstrum* (Aldridge *et al.* 1993; Donoghue & Purnell 2009). For the time being, crown vertebrate affinity appears to be particularly weakly supported.

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TABLE 1. Comparative taphonomy among Mazon Creek vertebrates from the Essex Fauna and *Tullimonstrum* as described by McCoy *et al.* (2016) and Clements *et al.* (2016). Based on Sallan and Coates (2014), Gabbott *et al.* (2016), and Shabica and Hay (1997). “✓” indicates presence; “✗” indicates absence; “?” indicates feature not considered by authors; “?✓” indicates presence considered equivocal.

	lateral line traces	otic capsules	notochord	RPE	myomeres	arcualia	gut
<i>Tullimonstrum</i> (McCoy <i>et al.</i> 2016)	✗	✗	✓	?	✓	✓	✓
<i>Tullimonstrum</i> (Clements <i>et al.</i> 2016)	✗	✗	✗	✓	?✓	?	✗
<i>Mayomyzon</i>	✓	✓	✗	✓	✗	✗	✗
<i>Myxinikela</i>	✓	✓	✗	✓	✗	✗	✗
<i>Esconichthys</i>	✓	✓	✗	✓	✗	✗	✗
<i>Bandringa</i>	✓	✓	✗	✗	✗	✗	✗

FIG. 1 *Tullimonstrum* and potential comparators. A, A schematic of *Tullimonstrum* structures in lateral and dorsoventral views, based on figured specimens in McCoy *et al.* (2016). See McCoy *et al.* (2016) and Clements *et al.* (2016) for trait assignments by those authors. B, generalized lamprey musculoskeletal and internal anatomy; C, non-vertebrate chordate anatomies; D, Paleozoic marine arthropod anatomy based on *Opabinia*. E, Heteropod gastropod (Pterotrachiodea) mollusk anatomy; form based primarily on *Pterotrachea* and Ralph (1957). Labels: ac, annular cartilage; ad, adhesion surface; af, anal fin; an, anus; ap, atriopore; arc, arcualia; at, anterior tectal; ax, axial band; bc, buccal mass; bm, body margin; br, brain; ca, caudal appendage; cg, cerebral ganglion; cp, circular pigment; df, dorsal fin; dl, dark line; dn, dorsal nerve cord; dt, denticle; eb, eye bar; en, endostyle; eso, esophagous; es, eye stalk; fl, fin lines; fr, fin ray; gg, gut gland; gn, gonad; gf, gill filament; gs, gill slit; ht, heart; in, intestine; jj, jaw joint; jk, jaw knob; kt, keratin teeth; ln, lens; lsc, large semicircle; lv, liver; ms, myoseptum; mt, mouth; my, myomere; nh, nasohypophyseal; nc, neurocranium; no, notochord; ns, nasal capsule; og, optic ganglion; oh, oral hood; on, optic nerve; ot, otic capsule; pb, proboscis; pc, piston cartilage; pe, pericardial cartilage; ph, pharynx; pn, pincer; pt, posterior tectal; rc, raised circular patch; rd, radula; re, retina; ri, round indentation; rt, respiratory tube; sc, spinous cartilage; seg, segment; sep, septum; sk, suction disk; ssc, smaller semicircle; st, stomach; sy, statocyst; tf, tail fin; vm, visceral mass; vn, ventral nerve cord; wl, white lines; wp, white patch. [double column width]

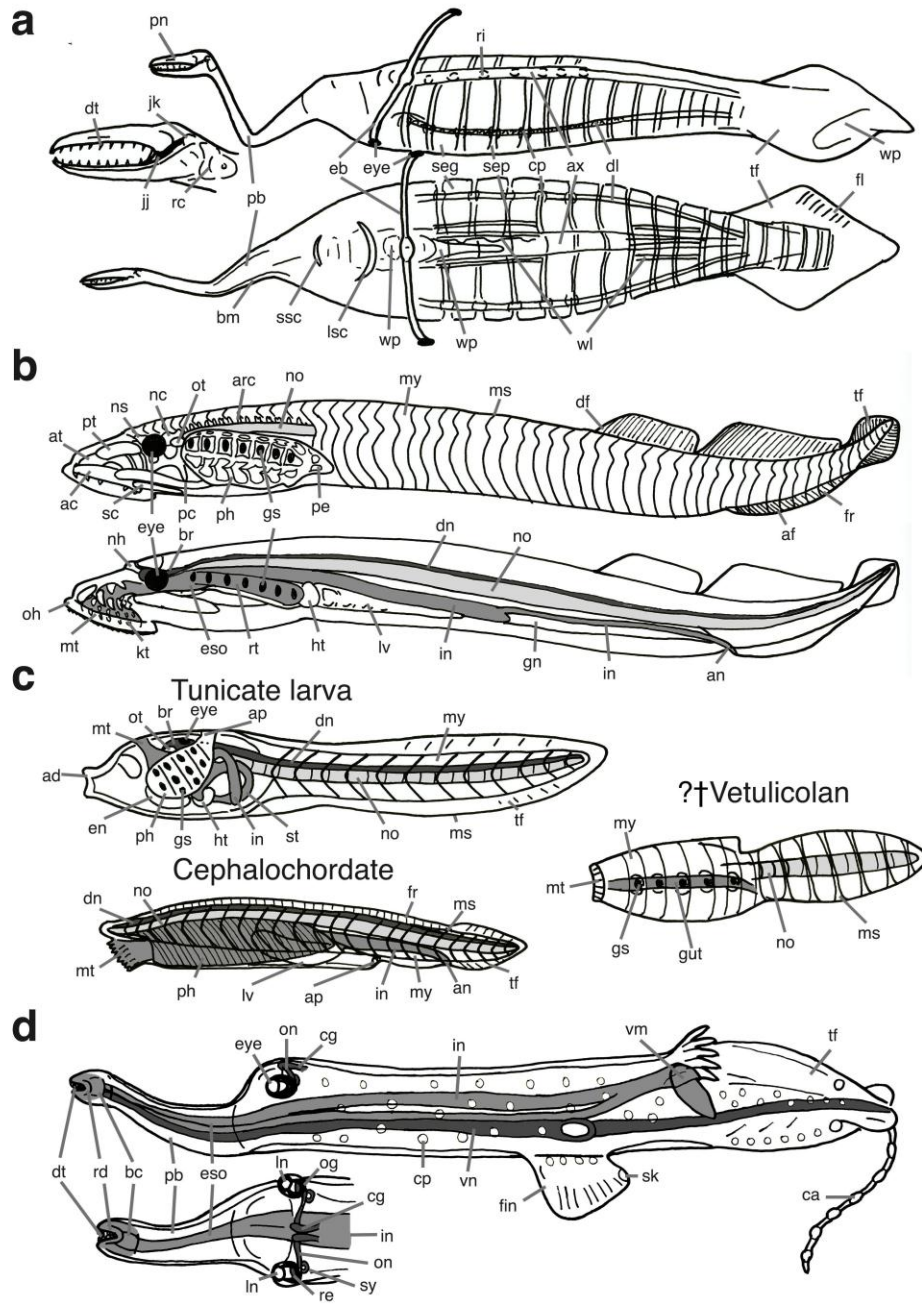


FIG. 2 Recoded phylogenetic analysis of McCoy *et al.* (2016) shows uncertainty in placement of *Tullimonstrum*. A, *Mayomyzon* showing oral disk and otic capsules (Royal Ontario Museum V56800a immersed in alcohol with rebalanced colour levels). B, Potential placements of *Tullimonstrum* in amended analysis of McCoy *et al.* (2016) performed using PAUP* and MrBayes. Amended characters: oral disc present for *Mayomyzon* (71), tail equivocal for *Mayomyzon* (52, 53) and tectal character removed (117). Blue line indicates position of *Tullimonstrum* in original analysis (nb not recovered in the amended analysis). Red lines indicate the possible placements of *Tullimonstrum* in the amended analysis (*Tullimonstrum* a-e). *Euconodonta* and *Gilpichthys* were included in the analysis but have been pruned here in order to enable visualization of the underlying signal. Labels: gp, gill pigment; od, oral disk; ot, otic capsule. [single column width]

