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## Placoderm muscles and chordate interrelationships

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## Comment

## Placoderm muscles and chordate interrelationships

Trinajstić *et al.* (2007) reported exceptionally preserved soft tissues in two placoderm fish from the Devonian of Australia. This exciting finding presents fresh morphological data with a bearing on an old phylogenetic problem: deep branching structure within the vertebrate tree. Trinajstić *et al.* (2007) show that axial muscle blocks in the placoderm *Austroptyctodus* more closely resemble those of living lampreys than those of extant gnathostomes, and argue that this is consistent with the prevailing hypothesis that placoderms are the sister group of all remaining jawed vertebrates. Unfortunately, the comparative framework that provides context for these exceptional fossils contains a number of errors that we address here.

It is stated that 'comparing muscle structure and pattern of the Gogo placoderms with extant taxa indicates that the closest extant relative to the placoderm is the lamprey (fig. 2, table 1)' (Trinajstić *et al.* 2007, p. 199). This conclusion is incorrect and contradicted by the cladogram that it references: placoderms are more closely related to living jawed vertebrates than they are to any 'agnathan'. Lampreys and placoderms share primitive characters that have no bearing on their relationships to each other. It is also stated that lampreys have seven extrinsic eye muscles, as it appears to have been the case in some placoderms. This carries with it the implication that placoderms retain a primitive condition, but lampreys have six extrinsic eye muscles (Fritzsch *et al.* 1990).

The caption of fig. 2 implies that the cladogram it depicts is derived from the matrix given in table 1, but no description of methods is provided. We reproduced this dataset and analysed it using the exhaustive search algorithm in PAUP\* v. 4.0b (Swofford 2002). We find a single shortest tree of 21 steps, but it is not the one given in fig. 2. Our analysis places acanthodians as the sister group of osteichthyans, not chondrichthyans. However, placoderms remain the sister group of all other jawed vertebrates.

A more serious matter is that more than half of the characters (9 out of 17) in the matrix contain coding mistakes, and just less than 18 per cent (18 out of 102) of all entries are wrong. We have corrected these based on the following arguments. Character 1 is re-scored '1' for chondrichthyans, acanthodians and osteichthyans because all have endoskeletal mineralization (Janvier 1996; Coates *et al.* 1998). Character 3 is re-scored as '0/1' for 'ostracoderms', some of which possess paired fins (Janvier 1996). For character 7, we take 'paired nasal sacs' to refer to broadly separated nasal capsules. This character must be re-scored as 1 for placoderms because paired nasal capsules are present in this group (Janvier 1996). Character 9 is re-scored as 1 for all taxa

The accompanying reply can be viewed on page 104 or at <http://dx.doi.org/doi:10.1098/2007.0553>.

in the analysis (thus becoming uninformative), as all of them are known to have braincases. Character 10 is re-scored as 0/1 for ostracoderms since a ring of dermal shoulder armour is found in osteostracans and pituriaspids (Janvier 1996). Character 11 should be coded as 1 for placoderms, chondrichthyans and osteichthyans, because primitive members of these groups bear dermal fin spines (Janvier 1996; Zhu *et al.* 1999). Character 14 can be scored as 1 in acanthodians based on the structures preserved in some Devonian taxa (Valiukevicius 1992, 2003). Character 16 must be scored '?' for acanthodians, however, because it is unclear if the longitudinal feature found in these specimens is a horizontal septum or the lateral line. It also seems that the same character should be coded as '?' for placoderms, because the text equivocates about the condition of the horizontal septum in this group. It is stated that 'no distinct horizontal septum is present' (Trinajstić *et al.* 2007, p. 199), but then 'the division of the myosepta at the boundary of the hypaxial and epaxial regions strongly suggests its presence' (Trinajstić *et al.* 2007, p. 200). Character 17, which regards chevron-shaped muscle blocks as present in some but not all vertebrates, is mistaken as chevron-shaped muscle blocks are classically viewed as a chordate synapomorphy (Maisey 1986).

The corrected result required fewer steps (16), but did not differ in branching order from the tree obtained from analysing the published matrix (which itself diverges from the published cladogram). So, one might wonder what the problem is, if our corrections had no effect on the topology. First, errors of this degree and frequency cannot be expected to always be so benign. Second, even though the published solution approximates the 'right answer', it still amounts to a false tree because it is supported by false character distributions.

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