biology letters

Response to Friedman and Brazeau

Kate Trinajstic, Carina Marshall, John Long and Kat Bifield

Biol. Lett. 2008 **4**, 104-105
doi: 10.1098/rsbl.2007.0553

biology letters
Palaeontology

Biol. Lett. (2008) **4**, 104–105
doi:10.1098/rsbl.2007.0553
Published online 4 December 2007

Invited reply

Response to Friedman and Brazeau

The principal objective of our paper was to describe the exceptional muscle and nerve tissues occurring in the 380 Myr old placoderms from the Gogo Formation in northern Western Australia. It was never our intention to produce an in-depth discussion on early vertebrate phylogeny, but instead to point out the possibilities of incorporating soft tissue characteristics into already published analyses and character sets (Basden *et al.* 2000; Zhu *et al.* 2001; Goujet & Young 2004). However, Friedman & Brazeau (2008) raise valid criticisms of the phylogenetic data matrix used to construct the cladogram presented in fig. 2 (Trinajstic *et al.* 2007) but note that the errors had no effect on the topology. This is because a number of transcription errors occurred when manually transcribing the data matrix from the PAUP* v. 3.0 nexus file to table 1 (Trinajstic *et al.* 2007). In addition, the character definitions were truncated for brevity and this could have led to a lack of clarity with regard to our meaning for several characters which we outline below. We thank Friedman & Brazeau (2008) for providing corrections but disagree with several of their changed character states.

Those characters which were inadequately explained comprise character 3 which should have read paired pectoral and pelvic fins, and character 17 which would have been better expressed as strong development of the anterior and dorsal arms of the myomeres. Therefore we consider the scoring was correct for both these characters. We maintain our character score also for character 10 (character 1 of Goujet & Young 2004), which in its full form stated that the rigid ring of the exoskeletal shoulder girdle articulated with the skull through a paired dermal neck-joint. This articulation always occurs between two specific dermal plates, the anterior dorsolateral and paranuchal plates, and for brevity these well-documented details were not elaborated on in our paper. It is also well established that the dermal neck-joint and the standard complement of overlapping dermal plates in the exoskeletal shoulder girdle of placoderms do not occur in osteostracans and pituriaspids. A full discussion of placoderm synapomorphies has been presented by Goujet & Young (2004).

The presence or absence of a horizontal myoseptum is of immense phylogenetic and developmental importance, as the muscles of paired fins in extant gnathostomes derive from hypaxial myotomes (Neyt *et al.* 2000). We maintain the absent score for character 16, as we could find no fossil evidence for the presence of a horizontal myoseptum. The appearance of dorsoventral patterning of myotomes is not dependent on a horizontal myoseptum with the lamprey possessing a hypobranchial muscle but not a horizontal myoseptum (Nowicki *et al.* 2003). We therefore maintain the absence of a horizontal myoseptum in placoderms but are in agreement with Kusukabe & Kuratani (2005) that some part of the hypaxial gene cascade may have originated before the evolutionary separation of epaxial and hypaxial muscles.

The statement 'comparing muscle structure and pattern in the Gogo placoderms with extant taxa…' was based solely on muscle comparison, and was meant to demonstrate that placoderms shared many primitive muscle characters with lampreys rather than as a statement of relationship. When a phylogenetic analysis, including all characters, was completed it was established, as depicted by our cladogram, that placoderms are more closely related to all jawed vertebrates but represented the most basal of the jawed vertebrate clade.

The discovery of optic capsules from placoderm fishes demonstrates the presence, in this group, of seven extrinsic eye muscles (Goujet & Young 2004). We here consider that seven eye muscles are the ancestral gnathostome condition and not the general condition for vertebrates. Friedman & Brazeau (2008) correctly state that lampreys possess six eye muscles. However, we wish to highlight that the arrangement of the extraocular muscles in placoderms more closely resembles that of jawless vertebrates including the extant lamprey rather than any known extinct or living gnathostome (Janvier 1977; Young 1986; Long & Yong 1988).

Kate Trinajstic[1,*], Carina Marshall[2], John Long[3,4], Kat Bifield[2]
[1]*School of Earth and Geographical Sciences, University of Western Australia, Perth, Western Australia 6009, Australia*
[2]*Department of Earth and Planetary Sciences, Western Australian Museum, Locked Bag 49, Welshpool, Western Australia 6896, Australia*
[3]*Museum Victoria, PO Box 666, Melbourne, Victoria 3001, Australia*
[4]*School of Earth and Marine Sciences, Australian National University, Canberra, Australian Capital Territory 0200, Australia*
**ktrinajs@bigpond.net.au*

Basden, A. M., Young, G. C., Coates, M. I. & Ritchie, A. 2000 The most primitive osteichthyan braincase? *Nature* **403**, 185–188. (doi:10.1038/35003183)

Friedman, M. & Brazeau, M. 2008 Placoderm muscles and chordate interrelationships. *Biol. Lett.* **4**, 103. (doi:10.1098/rsbl.2007.0358)

Goujet, D. & Young, G. C. 2004 Placoderm anatomy and phylogeny: new insights. In *Recent advances in the origin and early radiation of vertebrates* (eds G. Arratia, M. V. Wilson & R. Cloutier), pp. 109–126. München, Germany: Pfeil Verlag.

Janvier, P. 1977 Contribution à la connaissance de la systématique et de l'anatomie du genre Boreaspis Stensiö. *Ann. Paléontol. (Vertébrés)* **63**, 1–32.

Kusukabe, R. & Kuratani, S. 2005 Evolution and developmental patterning of the vertebrate skeletal muscles: perspective from the lamprey. *Dev. Dyn.* **234**, 824–834. (doi:10.1002/dvdy.20587)

Long, J. & Yong, G. C. 1988 Acanthothoracid remains from the Early Devonian of New South Wales, including a complete sclerotic capsule and pelvic girdle. In *Devonian*

The accompanying comment can be viewed on page 103 or at http://dx.doi.org/doi:10.1098/2007.0358.

Received 6 November 2007
Accepted 15 November 2007

and carboniferous fish studies (ed. P. Jell), pp. 65–80. Sydney, Australia: Association of Australasian Palaeontologists.

Neyt, C., Jagla, K., Thisse, C., Thisse, B., Haines, L. & Currie, P. D. 2000 Evolutionary origins of the vertebrate appendicular muscle. *Nature* **408**, 82–86. (doi:10.1038/35040549)

Nowicki, J. L., Takimoto, R. & Burke, A. C. 2003 The lateral somatic frontier: dorso-ventral aspects of anterior–posterior regionalization in avian embryos. *Mech. Dev.* **120**, 227–240. (doi:10.1016/S0925-4773(02)00415-X)

Trinajstic, K., Marshall, C., Long, J. & Bifield, K. 2007 Exceptional preservation of nerve and muscle tissue in Late Devonian placoderm fish and their evolutionary implications. *Biol. Lett.* **3**, 197–200. (doi:10.1098/rsbl.2006.0604)

Young, G. C. 1986 Relationships of the placoderm fishes. *Zool. J. Linn. Soc. Lond.* **88**, 1–57.

Zhu, M., Yu, X. & Ahlberg, P. E. 2001 A primitive sarcopterygian fish with an eyestalk. *Nature* **397**, 607–610. (doi:10.1038/17594)