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Number and arrangement of extraocular muscles in primitive gnathostomes: evidence from extinct placoderm fishes

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Exceptional braincase preservation in some Devonian placoderm fishes permits interpretation of muscles and cranial nerves controlling eye movement. Placoderms are the only jawed vertebrates with anterior/posterior obliques as in the jawless lamprey, but with the same function as the superior/inferior obliques of other gnathostomes. Evidence of up to seven extraocular muscles suggests that this may be the primitive number for jawed vertebrates. Two muscles innervated by cranial nerve 6 suggest homologies with lampreys and tetrapods. If the extra muscle acquired by gnathostomes was the internal rectus, Devonian fossils show that it had a similar insertion above and behind the eyestalk in both placoderms and basal osteichthyans.

Keywords: eye muscles; jaw evolution; gnathostome phylogeny

1. INTRODUCTION

The disposition and innervation of the extraocular (extrinsic) muscles controlling eye movement is a highly conserved and presumably ancient system among the vertebrates. Neal (1918, p. 433) stated that they 'appear in the lower vertebrates in essentially the same form as in man. Indeed their number and their nerve relations are the same in man as in the dogfish … only the superior oblique shows a function change in the course of phylogeny'.

The general pattern for gnathostome (jawed) fishes (figure 1*a*) comprises four rectus muscles inserting posteriorly in the orbit and attached around the rim of the eyeball, and two oblique muscles extending back from the anterior orbital wall to attach dorsally and ventrally. Functionally, these six muscles act as three antagonistic pairs orienting the eyeball in each of three dimensions. The 'function change' noted by Neal (1918) refers to the living lamprey, in which the muscle corresponding to the gnathostome 'superior oblique' (based on the same innervation by the fourth cranial nerve) has a posterior insertion and attachment to the eyeball ('posterior oblique', figure 1*b*).

The innervation pattern by three cranial nerves is also consistent among extant vertebrates (Fritzsch *et al*. 1990). Nerve 4 (trochlearis) innervates one

extraocular muscle (superior or posterior oblique; table 1). Nerve 6 (abducens) innervates one muscle (external rectus) in chondrichthyan and osteichthyan fishes, but two muscles in the lamprey, and in most tetrapods (in the latter assumed secondary; see below). Possible partial homologies between agnathans and gnathostomes (Fritzsch *et al*. 1990) make direct correspondence uncertain. The remaining extraocular muscles (three in the lamprey and four in gnathostomes) are innervated by nerve 3 (oculomotorius).

It is widely assumed (e.g. Dawkins 1991, p. 40) that 'eyes do not fossilize, so we do not know how long our type of eye took to evolve its present complexity and perfection from nothing'. This paper summarizes 400 Myr-old palaeontological evidence concerning the number, position and innervation of extraocular muscles in exceptionally preserved Devonian placoderm (armoured) fishes—complementing modern morphological data with evidence chronologically much closer to the presumed branching point between agnathans and gnathostomes.

Extinct placoderms, the assumed sister group to other gnathostomes (figure 1*e*; Goujet & Young 2004), represent the first major radiation of the jawed vertebrates. Primitive placoderms had a low and broad ('platybasic') braincase with thick lateral walls. The perichondrally ossified central cranial cavity and extensive canals for nerves and vessels permit a robust interpretation of intracranial morphology compared with the simple foramina piercing the narrow braincase walls typical of osteichthyans. Originally studied by serial grinding (Stensiö 1963), supplemented by mechanical preparation (Goujet 1984), the best evidence of internal structure now comes from braincases extracted by acid from Early Devonian limestones of Burrinjuck, New South Wales (genera *Buchanosteus*, *Brindabellaspis*, *Murrindalaspis* and *Ligulalepis*), and Prince of Wales Island, Arctic Canada (*Romundina*).

2. EXTRAOCULAR MUSCLE ARRANGEMENT IN PLACODERMS

(a) *Morphological evidence*

Uniquely among early vertebrates (Goujet & Young 2004), some placoderms show fusion of the ossified sclera with the dermal sclerotic ring, forming a capsule completely enclosing the eyeball (figure 1*c*,*d*), such that all its nerves and vessels are preserved as canals or foramina. Long & Young (1988) described six muscle attachments around the central eyestalk area (eys) and optic nerve foramen (2) in the acid-extracted capsule of *Murrindalaspis*; a possible additional attachment (m7) was identified by Goujet & Young (2004).

Corresponding muscle insertions in the wall of the orbit are indicated by distinct depressions (myodomes, figure 2). Associated canals, foramina and grooves contained the three cranial nerves controlling eye movement. Placoderm extraocular muscles were first interpreted to be like other jawed fishes, with the superior oblique muscle originating 'on the anterior dorsal part of the lateral face of the orbital wall above the inferior oblique eye muscle' (Stensiö 1963, p. 55), in a 'superior myodome' placed above and slightly behind the eyestalk (My3, figure 2). Stensiö's identification of a separate trochlearis
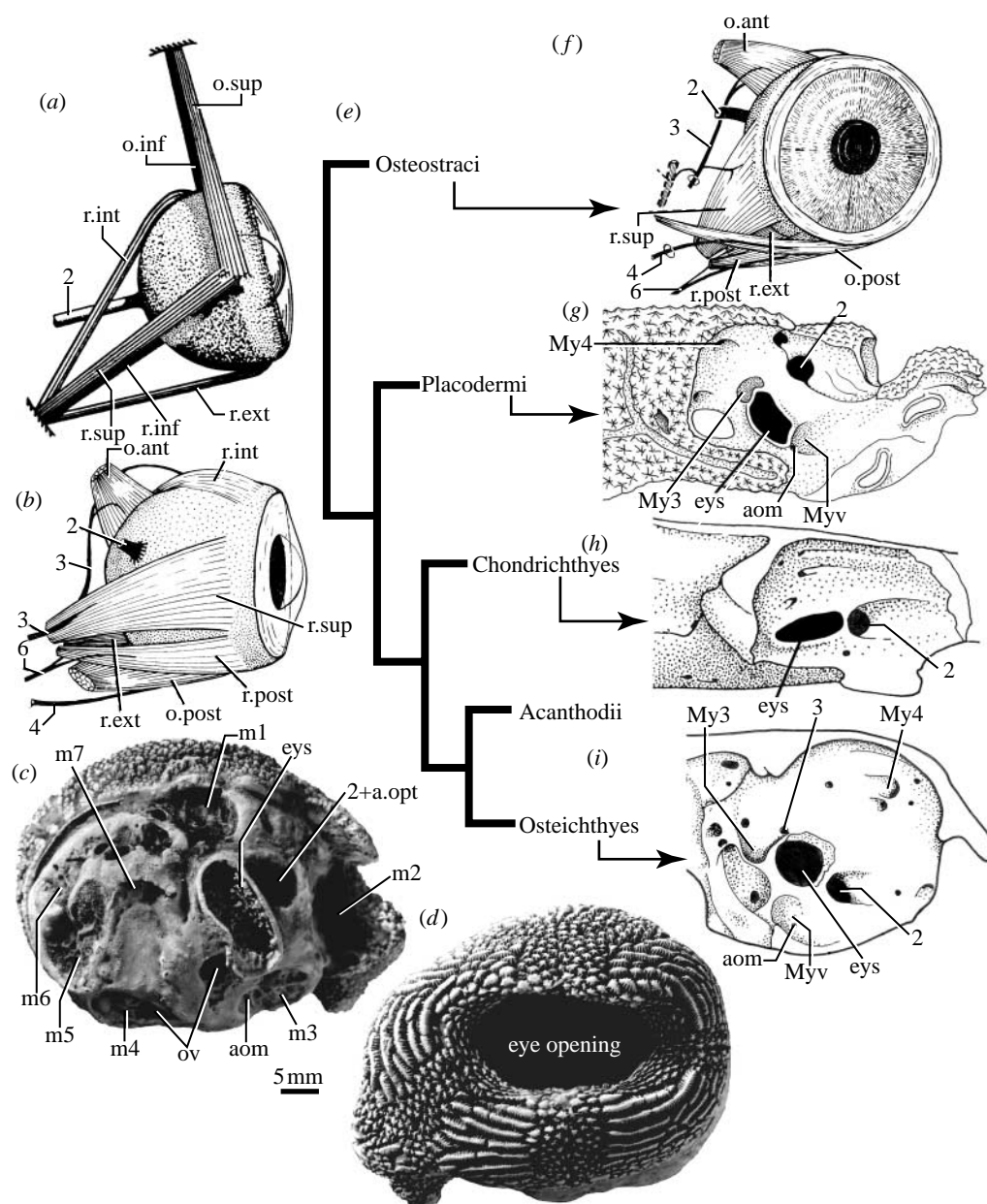
Figure 1. (*a*) 'Hypothetical primitive arrangement' of Walls (1942, fig. 165) for gnathostome extraocular muscles (right eyeball, dorsal view). (*b,f*) Right extraocular muscles in dorsal view of (*b*) the lamprey and (*f*) restored for a fossil agnathan, modified from Janvier (1975, fig. 1). (*c,d*) Acid-extracted left sclerotic capsule of *Murrindalaspis* in (*c*) internal and (*d*) external views (scale bar, 5 mm). (*e*) Relationships scheme from Goujet & Young (2004, fig. 5). Representative taxa (orbit, right lateral view) are as follows: (*g*) *Romundina* (placoderm); (*h*) *Cladodoides* (chondrichthyan); (*i*) *Ligulalepis* (osteichthyan). Illustrations not to scale. Abbreviations (labels indicate contained structures) are as follows: 2, optic nerve; 3, oculomotor nerve; 3p, posterior branch of oculomotor nerve; 4, trochlearis nerve; 5prof, profundus nerve; 5tg, trigeminal nerve; 6, abducens nerve; 7, facial nerve; aom, a.opt, ophthalmic, optic arteries; c.mes, c.met, cavities for mesencephalon and metencephalon; eys, eyestalk attachment area; gr3v, ventral groove for oculomotor nerve; m1–7, muscle scars on sclerotic cartilage; My3, myodome for insertion of oculomotor-innervated eye muscle; My4, myodome for insertion of trochlearis-innervated eye muscle; Myv, ventral myodome; n.cav, nasal cavity; o.ant, o.inf, o.post, o.sup, anterior, inferior, posterior and superior oblique extraocular muscles; ov, optic veins; r.ext, r.inf, r.int, r.post, r.sup, external, inferior, internal, posterior (caudal) and superior rectus extraocular muscles; sc, muscle scar; v.ju, v.pit, jugular and pituitary veins.

nerve canal was corroborated in *Buchanosteus* from Burrinjuck (Young 1979) and *Dicksonosteus* from Spitsbergen (Goujet 1984). However, Young (1980) noted that, in *Brindabellaspis*, the myodome was penetrated by the oculomotor nerve canal, with a clear posterior branch (3p, figure 2), and thus more likely contained an oculomotorius-innervated eye muscle. Faint grooves in *Romundina* (Goujet & Young 2004) indicate further subdivision into a ventral sub-branch (gr3v, figure 2*d*) passing to the ventral

myodome (Myv), and a posterior sub-branch directed towards a muscle scar on the floor of the orbit (sc). A well-developed posterodorsal myodome (My4), associated with the trochlearis foramen (4), demonstrates the presence of a posterior oblique eye muscle, a condition unknown in other gnathostomes. A deep posterior myodome (My6) contained the abducens nerve foramen; in *Romundina*, it is subdivided into two pockets by the groove for the trigeminal nerve, the deeper mesial pocket containing the abducens

Table 1. Terminology and suggested homology for the extraocular muscles of vertebrates (innervation in brackets).

lamprey (living agnathan)	placoderms (extinct armoured fishes)	chondrichthyans (cartilaginous fishes)	osteichthyans (bony fishes)	tetrapods (land animals)
posterior oblique (nerve 4)	posterior oblique (nerve 4)	superior oblique (nerve 4)	superior oblique (nerve 4)	superior oblique (nerve 4)
anterior oblique (nerve 3v)	anterior oblique (nerve 3v)	inferior oblique (nerve 3v)	inferior oblique (nerve 3v)	inferior oblique (nerve 3v)
superior rectus (nerve 3d)	?	superior rectus (nerve 3d)	superior rectus (nerve 3d)	superior rectus (nerve 3d)
?	?	inferior rectus (nerve 3v)	inferior rectus (nerve 3v)	inferior rectus (nerve 3v)
?internal rectus (nerve 3v)	?internal rectus (nerve 3d)	internal rectus (nerve 3d)	internal rectus (nerve 3v)	internal rectus (nerve 3v)
?inferior rectus (nerve 6)	?external rectus (nerve 6)	external rectus (nerve 6)	external rectus (nerve 6)	external rectus (nerve 6)
?posterior (caudal) rectus (nerve 6)	?extra abducens-innervated muscle (nerve 6)	?subdivided rectus (nerve 6)	?	retractor bulbi (nerve 6)

foramen. This suggests that placoderms could have had two abducens-innervated extraocular muscles, as in the living lamprey (Goujet & Young 2004, p. 121). In *Buchanosteus*, the abducens canal may be subdivided, opening through two foramina (Young 1979, figs. 7A and 8B).

In summary, six eye muscle attachments (five myodomes and one scar) are identified in the placoderm orbit, with up to seven attachments on the eyeball. A third branch of the oculomotor nerve is traceable as a groove to the ventral myodome, and in some forms a branched canal leads to two abducens foramina in a sometimes subdivided posterior myodome.

(b) Functional considerations

Unlike modern gnathostomes, there are no muscle attachments distinctly anterior to the optic nerve foramen. The large eyestalk attachment (eys) consistently has dorsal and ventral myodomes displaced slightly behind and in front of its long axis (dashed line, figure 2e). The contained dorsal muscle would abduct the eyeball if attached to its posterior surface, but turn it forward if attached anteriorly across the rotation axis (upper arrow, figure 2e). The opposite would apply to the ventral muscle.

Homology considerations make it unlikely that these myodomes contained an antagonistic muscle pair. Reasonable homologies with living taxa are that (i) an abducens-innervated muscle, posteriorly inserted in the orbit, turned the eye backwards (abduction), as does the external rectus in living gnathostomes, and one of the two abducens-innervated muscles of the lamprey, (ii) the trochlearis myodome contained a posterior oblique, attached to the posterior eyeball margin for clockwise rotation (right eye), like the posterior oblique of the lamprey and the superior oblique of gnathostomes.

Assumption (i) would imply that the antagonistic muscle to the external rectus (internal rectus) crossed the rotation axis from the dorsal myodome (My3) to insert in the deep anterior muscle pit of the eyeball (m2, figure 1c). As in the lamprey (Fritzsch *et al.* 1990), an antagonistic muscle to the posterior oblique (for anticlockwise rotation; assumption (ii)) would

extend posterolaterally from the ventral myodome (lower arrow, figure 2e); an appropriate muscle scar is preserved on the eyeball rim in *Murrindalaspis* (m4, figure 1c).

3. PRIMITIVE NUMBER OF EXTRAOCULAR MUSCLES IN GNATHOSTOMES

Early anatomists (Rondelet, Vesalius, Eustachius and Fallopius) first investigated the extraocular muscles (Cole 1949). Fabricius (1533–1619) summarized the various findings: only six eye muscles in man, ape and fishes, compared with seven in most quadrupeds. Six extraocular muscles in the lamprey indicated the primitive number for gnathostomes, with the additional seventh muscle of tetrapods ('retractor bulbi') being a new formation.

Placoderms evidently had two abducens-innervated muscles like the lamprey. Four oculomotor-innervated muscles, as in other gnathostomes, would give a total of seven, as indicated in a few living forms—in *Squalus* embryos, 'muscle E' contributing to a dual origin for the external rectus (Neal 1918), which is subdivided in the primitive shark *Chlamydoselachus* (Nishi 1938). The new placoderm evidence suggests that seven extraocular muscles may be primitive for gnathostomes.

4. EVOLUTIONARY IMPLICATIONS

Agnathan outgroups include fossil osteostracans with perichondral ossification of the endoskeleton (table 2), which are interpreted to have had anterior/posterior oblique muscles like the lamprey (figure 1f). Young (1986) proposed two special conditions of placoderm extraocular muscles (posterior oblique; anterior insertion of internal rectus), but the second no longer holds since the discovery of an eyestalk attachment and similar oculomotor myodome (figure 1i) in the basal actinopterygian *Ligulalepis* (Basden *et al.* 2000).

Nishi (1938; Fritzsch *et al.* 1990) believed the extra muscle acquired by gnathostomes was the internal rectus. Fossil evidence indicates that this muscle had a similar insertion just above and behind the eyestalk in both basal gnathostomes (placoderms)
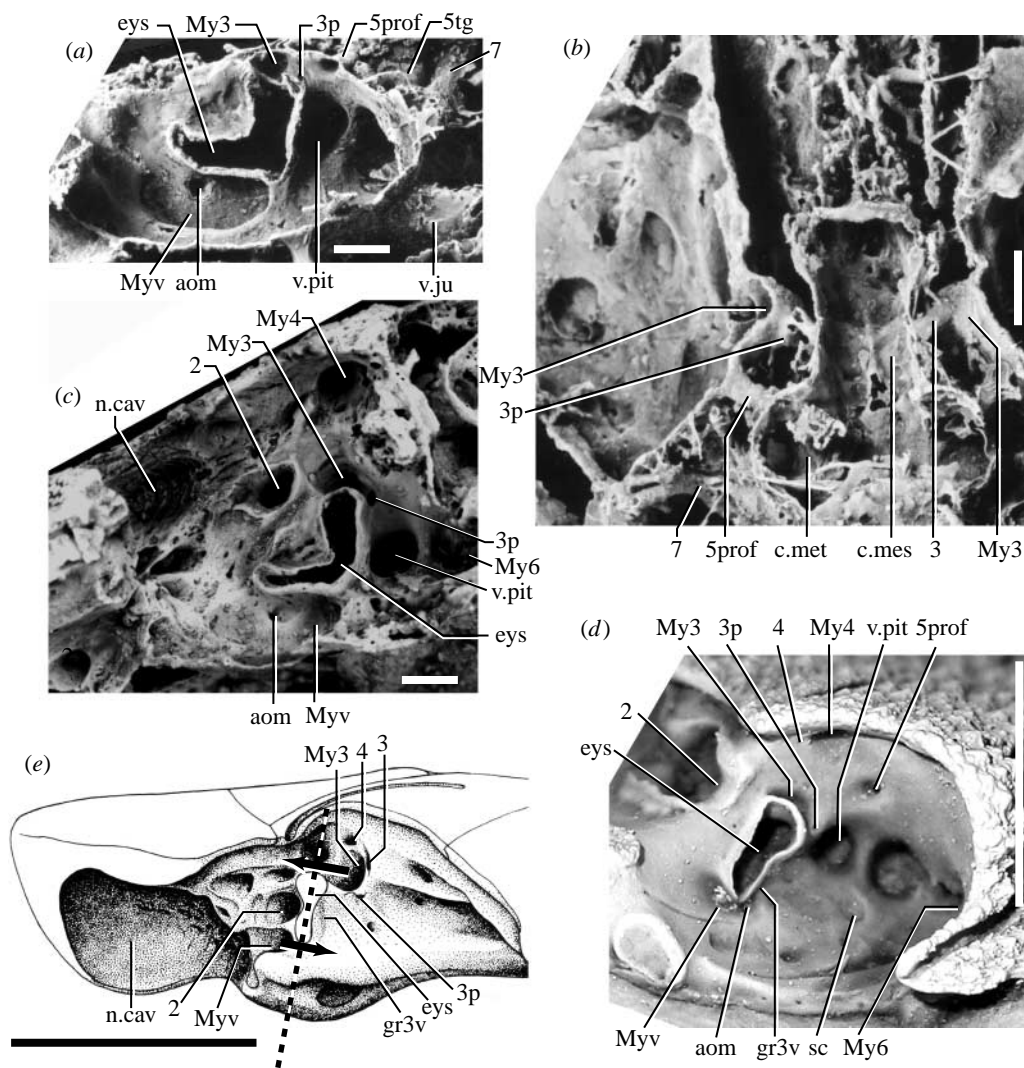
Figure 2. *Brindabellaspis*, left orbit in (*a*) lateral and (*b*) dorsal views, eroded down to expose the cranial cavity (specimen described by Young 1980). (*c*,*d*) Specimens figured by Goujet & Young (2004), showing complete left orbit of (*c*) *Brindabellaspis* and (*d*) *Romundina*. (*e*) Restoration of left orbit of *Dicksonosteus* (after Goujet 1984), showing presumed rotation axis (dashed line) and muscle orientation (arrows). Scale bars, 5 mm. Abbreviations given in figure legend 1.

Table 2. Distribution of characters relevant to extraocular muscle evolution across the agnathan–gnathostome transition (0, absent; 1, present), updated and corrected from Trinajstic *et al.* (2007, table 1). (1, perichondral ossification; 2, endochondral ossification; 3, jaws; 4, internal gill arch skeleton; 5, horizontal semicircular canal; 6, paired pectoral fins; 7, paired pelvic fins; 8, paired nasal sacs; 9, eyestalk; 10, two abducens-innervated muscles; 11, anterior/posterior oblique muscles; 12, seventh muscle (internal rectus) with anterior insertion; 13, superior/inferior oblique muscles; 14, one abducens-innervated eye muscle; 15, myomeres with horizontal septum; 16, myelinated nerve fibres.)

characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Hyperoartia	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Osteostraci	1	0	0	0	0	1	0	0	?	?	1	0	0	0	0	?
Placodermi	1	0	1	1	1	1	1	1	1	1	1	1	0	0	?	0
Chondrichthyes	0	0	1	1	1	1	1	1	1	?	0	0	1	?	1	1
Acanthodii	1	1	1	1	1	1	1	1	?	?	?	?	?	?	1	?
Osteichthyes	1	1	1	1	1	1	1	1	1	?	0	1	1	1	1	1

and basal osteichthyans (My3, figure 1*g*,*i*). Two abducens-innervated eye muscles in placoderms (as an outgroup of all extant gnathostomes) would support homology between those of the lamprey and the external rectus and retractor bulbi of tetrapods, as proposed by Nishi (1938), Fritzsch *et al.* (1990) and Bemis & Northcutt (1991).

Contrary to Trinajstic *et al.* (2007), 'seven extraocular muscles' is not a symplesiomorphy of placoderms and agnathans; a revised summary of character distributions relevant to extraocular muscle arrangement and jaw evolution is given in table 2. Further insight into this interesting question is expected from XCT scanning studies of a unique

Burrinjuck placoderm (Young *et al.* 2001) with both sclerotic capsules preserved in life position.

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