# Peripheral nervous system of the ocean sunfish *Mola mola* (Tetraodontiformes: Molidae)

Masanori Nakae[✉] and Kunio Sasaki

*Laboratory of Marine Biology, Faculty of Science, Kochi University, 2-5-1 Akebono-cho, Kochi 780-8520, Japan
(e-mail: MN, m-nakae@cc.kochi-u.ac.jp; KS, fishssk@cc.kochi-u.ac.jp)*

**Abstract**  Dissection of peripheral nerves in the ocean sunfish *Mola mola* showed the lateral line system to comprise 6 cephalic and 1 trunk lateral lines, all neuromasts being superficial. The trunk line was restricted to the anterior half of the body, the number of neuromasts (27) being fewer than those previously recorded in other tetraodontiforms. The lateral ramus of the posterior lateral line nerve did not form a "serial collector nerve" along the body. The number of foramina in the neurocranium, serving as passages for the cranial nerves, was fewer than in primitive tetraodontiforms, the reduction being related to modifications in the posterior cranium. Some muscle homologies were reinterpreted based on nerve innervation patterns. The cutaneous branch innervation pattern in the claval fin rays was clearly identical with that in the dorsal and anal fin rays, but differed significantly from that in the caudal fin rays, providing strong support for the hypothesis that the clavus comprises highly modified components of the dorsal and anal fins.

**Key words**  Molidae · Lateral line system · Peripheral nerves · Muscle innervation · Clavus

O ccurring in tropical to temperate seas worldwide, the ocean sunfish *Mola mola* is the most common species in the tetraodontiform family Molidae, reaching up to 3 m in length and more than 2000 kg in weight (Santini and Tyler, 2003). Because of its uniquely abbreviated body shape, *M. mola* has attracted the interest of many ichthyologists (see Johnson and Britz, 2005, for review), osteological and myological characteristics of the species having been well studied (e.g., Tyler, 1980; Winterbottom, 1974b), although little is known about its biology (Matsuura and Tyler, 1998; Sagara et al., 2005). In the present study, the peripheral nervous system (a formerly neglected aspect for the family) of *M. mola* was considered from a systematic point of view, because nerve studies in tetraodontiforms have been limited to those by Bal (1937) and Nakae and Sasaki (2004, 2005). Descriptions and illustrations are given here for almost all the component parts of the peripheral nervous system of *M. mola*.

Applications of nerve branching patterns for muscle homology interpretations have been attempted in very few teleost studies (Song and Boord, 1993; Parenti and Song, 1996; Nakae and Sasaki, 2004), despite the theoretical soundness of such an approach (see Parenti and Song, 1996, for review). In this article, Winterbottom's (1974b) myological interpretations for *M. mola* are reevaluated in some muscle complexes, based on neuroanatomical patterns.

Johnson and Britz (2005) concluded, from an ontogenetic perspective, that the molid clavus, a caudal finlike structure, was formed by modified elements of the dorsal and anal fins. We reached a similar conclusion, following comparisons of the innervation patterns in the dorsal, anal, and claval fin rays.

## Materials and Methods

*Mola mola* specimens examined in this study are listed below. Abbreviations in parentheses refer to the methods of examination: D, dissected; CS, cleared and stained. Measurements (in centimeters, cm) are of total length (TL). Bones and muscles were observed on specimens stained by alizarin red S, and nerves on cleared and stained specimens prepared by the Sihler technique (Fraser and Freihofer, 1971), with modifications of Nakae and Sasaki (2004). Some innervations in branchial arches were determined by treating with 1% osmium tetroxide. Descriptions are given for all peripheral nerves, except for the terminal nerve, octaval nerve (VIII), and some branches of the vagal nerve (X) (innervating visceral organs), because of some technical difficulties. Terminology generally follows Tyler (1980) for osteology, Winterbottom (1974b) for myology, Piotrowski and Northcutt (1996) and Northcutt et al. (2000) for cranial nerves, Parenti and Song (1996) for the spino-occipital nerve, and Webb (1989) for the lateral line system. Anatomical abbreviations used in the text and illustrations are listed in Table 1.

**Table 1.** Abbreviations

| | | | |
|---|---|---|---|
| I | Olfactory nerve | oinf | Obliquus inferior |
| II | Optic nerve | OPCF | Opercular cavity ramus of facial nerve |
| III | Oculomotor nerve | OPRF | Opercular ramus of facial nerve |
| IV | Trochlear nerve | OPT | Opercular ramus of trigeminal nerve |
| V | Trigeminal nerve | osup | Obliquus superior |
| VI | Abducent nerve | PIX | Pharyngeal ramus of glossopharyngeal nerve |
| VII | Facial nerve | PX | Pharyngeal ramus of vagal nerve |
| IX | Glossopharyngeal nerve | pal | Palatine |
| X | Vagal nerve | pcl | Postcleithrum |
| α | A nerve branch of glossopharyngeal nerve | PFN | Profundal nerve |
| β | A nerve branch of glossopharyngeal nerve | phce | Pharyngoclavicularis externus |
| γ | A nerve branch of vagal nerve | phci | Pharyngoclavicularis internus |
| A1-3 | Adductor mandibular subdivisions | POIX | Posttrematic ramus of glossopharyngeal nerve |
| aap | Adductor arcus palatini | POX | Posttrematic ramus of vagal nerve |
| abdp | Abductor profundus | POL | Postotic line |
| abds | Abductor superficialis | pp | Protractor pectoralis |
| ad | Adductor | PRIX | Pretrematic ramus of glossopharyngeal nerve |
| addp | Adductor profundus | PRX | Pretrematic ramus of vagal nerve |
| adop | Adductor operculi | PRF | Palatine ramus of facial nerve |
| arrv | Arrector ventralis | prhy | Protractor hyoidei |
| BX | Branchial trunk of vagal nerve | PRL | Preopercular line |
| boc | Basioccipital | prot | Prootic |
| BR | Buccal ramus of anterodorsal lateral line nerve | rcom | Rectus communis |
| cbr | Ceratobranchial | rctv | Rectus ventralis |
| cl | Cleithrum | red | Retractor dorsalis |
| cora | Coracoid | rext | Rectus externus |
| do | Dilatator operculi | rinf | Rectus inferior |
| DRX | Dorsal ramus of vagal nerve | rint | Rectus internus |
| edac | Erectores and depressores anales complex | rsup | Rectus superior |
| eddc | Erectores and depressores dorsales complex | sant | Supracarinalis anterior |
| epax | Epaxialis | sca | Scapula |
| exo | Exoccipital | scl | Supracleithrum |
| hab | Hyohyoidei abductores | SD | Dorsally oriented branches of the spinal nerves |
| had | Hyohyoidei adductores | SL | Laterally oriented branches of spinal nerves |
| HRF | Hyoid ramus of facial nerve | SO | Spino-occipital nerve |
| hyin | Hyohyoideus inferioris | SOC | Supraorbital commissure |
| IOL | Infraorbital line | SOL | Supraorbital line |
| lap | Levator arcus palatini | SOR | Superficial ophthalmic ramus of anterodorsal lateral line nerve |
| lepc | Levator pectoralis | | |
| lext | Levator externus | spo | Sphincter oesophagi |
| lint | Levator internus | stb | Sternobranchialis |
| lo | Levator operculi | sth | Sternohyoideus |
| LR | Lateral ramus of posterior lateral line nerve | STL | Supratemporal line |
| MADRF | Mandibular ramus of facial nerve | STR | Supratemporal ramus of posterior lateral line nerve |
| MANDR | Mandibular ramus of trigeminal nerve | | |
| MDR | Mandibular ramus of anteroventral lateral line nerve | SV | Ventrally oriented branches of spinal nerves |
| MXIT | Maxillary inferior ramus of trigeminal nerve | trd | Transversus dorsalis |
| MXR | Maxillary ramus of trigeminal nerve | TRL | Trunk line |
| obld | Obliquus dorsalis | trv | Transversus ventralis |
| obli | Obliquus inferioris | val | Valvulus |
| oblp | Obliquus posterior | VT | Visceral trunk of vagal nerve |
| oblv | Obliquus ventralis | | |
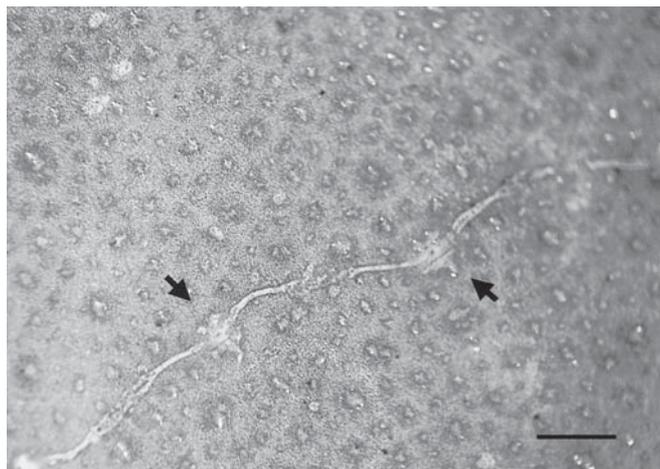
**Fig. 1.** Two lateral line scales (*arrows*) of the anterior part of the trunk line in *Mola mola*. *Bar* 1 mm

**Specimens examined.** BSKU (Laboratory of Marine Biology, Faculty of Science, Kochi University) 75496 (53 cm TL, D), BSKU 75497 (61 cm TL, D), BSKU 75498 (70 cm TL, D), BSKU 75499 (39 cm TL, CS), BSKU 75500 (40 cm TL, CS), BSKU 75162 (44 cm TL, lateral line system only observed), BSKU 76560 (69 cm TL, D, osmium tetroxide treated).

## Results

**Lateral line system** (Figs. 1, 2A). The lateral line system comprised superficial neuromasts only, each neuromast being situated on a scale encircled by 4 or 5 obtuse processes (Fig. 1). A fine white line (degenerated groove?) ran between the neuromast-bearing scales. The lateral line system (Fig. 2A) comprised the supraorbital line (SOL), supraorbital commissure (SOC), infraorbital line (IOL), preopercular line (PRL), postotic line (POL), supratemporal line (STL), and trunk line (TRL); a mandibular line was absent (see Nakae and Sasaki, 2005).

SOL coursed dorsally from the middorsal margin of the orbit and thence anteroventrally, to be terminated on the lateral surface of the snout; SOC arose from SOL and coursed posterodorsally, extending close to the dorsal midline, although a white line connecting the left and right SOC was absent; IOL connected the regions behind the orbit and immediately below the anterior nostril, dorsally being continuous with POL; PRL was U-shaped, coursing downward on the posterolateral surface of the cheek and thereafter upward below the orbit; POL connected IOL and the STL–TRL junction; STL extended upward from the POL–TRL junction; TRL initially coursed posterodorsally and thereafter posteroventrally, being terminated at the midlength of the body.

**Lateral line innervation** (Figs. 2B, 5B, 8A). The lateral line system in *M. mola* was innervated by 3 lateral line nerves: anterodorsal, anteroventral, and posterodorsal lateral line nerves, each comprising several rami (see Northcutt et al., 2000).

SOL and SOC were innervated by the superficial ophthalmic ramus (SOR) of the anterodorsal lateral line nerve; SOR emerged from a foramen in the membrane anterior to the prootic (Fig. 8A), together with the buccal ramus (BR) of the anterodorsal lateral line nerve, mandibular ramus (MDR) of the anteroventral lateral line nerve, profundal nerve, trigeminal nerve (V), and facial nerve (VII); above the posterior margin of the orbit, the 1st branch of SOR innervated all neuromasts of SOC (11 neuromasts); along the middorsal margin of the orbit, 2 branches were derived dorsally, innervating the posterior (13) and middle (7) portions of SOL, respectively; terminally, SOR innervated the anterior vertical part of SOL (10). IOL was innervated by BR that included 4 major branches: the 1st branch, after its emergence from the cranium, coursed laterally and innervated the posterodorsal portion of IOL (7); the 2nd ran obliquely downward and innervated IOL neuromasts (10) located below the posterior region of the eye; the 3rd and 4th coursed obliquely toward the snout to innervate the anterior neuromasts of IOL (7 and 5, respectively). PRL was innervated by MDR that coursed ventrally medial to the hyomandibula and thereafter approached the skin, passing between the hyomandibular and preoperculum, to be divided into 3 major branches (the posterior, middle, and anterior branches), these innervating the posterior vertical (24), ventral (13), and anterior vertical (9) portions of PRL, respectively. POL and STL were innervated by the supratemporal ramus (STR) of the posterior lateral line nerves; STR emerged from the cranium through a foramen in the prootic (Fig. 8A), together with the lateral ramus (LR) of the posterior lateral line nerves, glossopharyngeal nerve (IX), and vagal nerve (X) (Figs. 5B, 8A), coursing posteriorly and thence dorsally to innervate POL (5) and STL (7). TRL was innervated by LR that divided into dorsal and posterior branches at the dorsal end of the cleithrum; the former innervated the anterior portion of TRL (10); the latter further ramified into 2 branches, innervating 14 and 3 neuromasts of TRL, respectively; LR did not form a continuous "collector" nerve (sensu Freihofer, 1972), the dorsal and posterior branches being separated from one another along the dorsal margin of the body, although the 2 branches in the posterior were continuous.

**Olfactory nerve (I)** (Fig. 3A). The olfactory nerve emerged from the cranium passing between the left and right pterosphenoids and coursed anteriorly within the cartilage medial to the eyes; after its emergence from the cartilage near the posterior margin of the lateral ethmoid, the nerve extended anteriorly through a foramen in the bone to be connected anteriorly with the olfactory organ on the surface.

**Optic nerve (II)** (Fig. 3A). The optic nerve emerged from the cranium through a foramen in the membrane posterior to the suture of the pterosphenoid and basisphenoid, and entered the eyeball; a nerve (seemingly homologous with the radix profundus of Freihofer, 1978), emerging from the cranium and closely associated with the abducent nerve (VI) (see below), was confluent with the optic nerve before the latter reached the eye.

**Oculomotor nerve (III)** (Figs. 3B, 4A). The oculomotor nerve (Fig. 3B), together with the abducent nerve (VI) (see

**Fig. 2.** Lateral line system (**A**) and its innervation (**B**) in *Mola mola*. See Table 1 for abbreviations. *Arrowheads* (in **A**) indicate junctions of lines
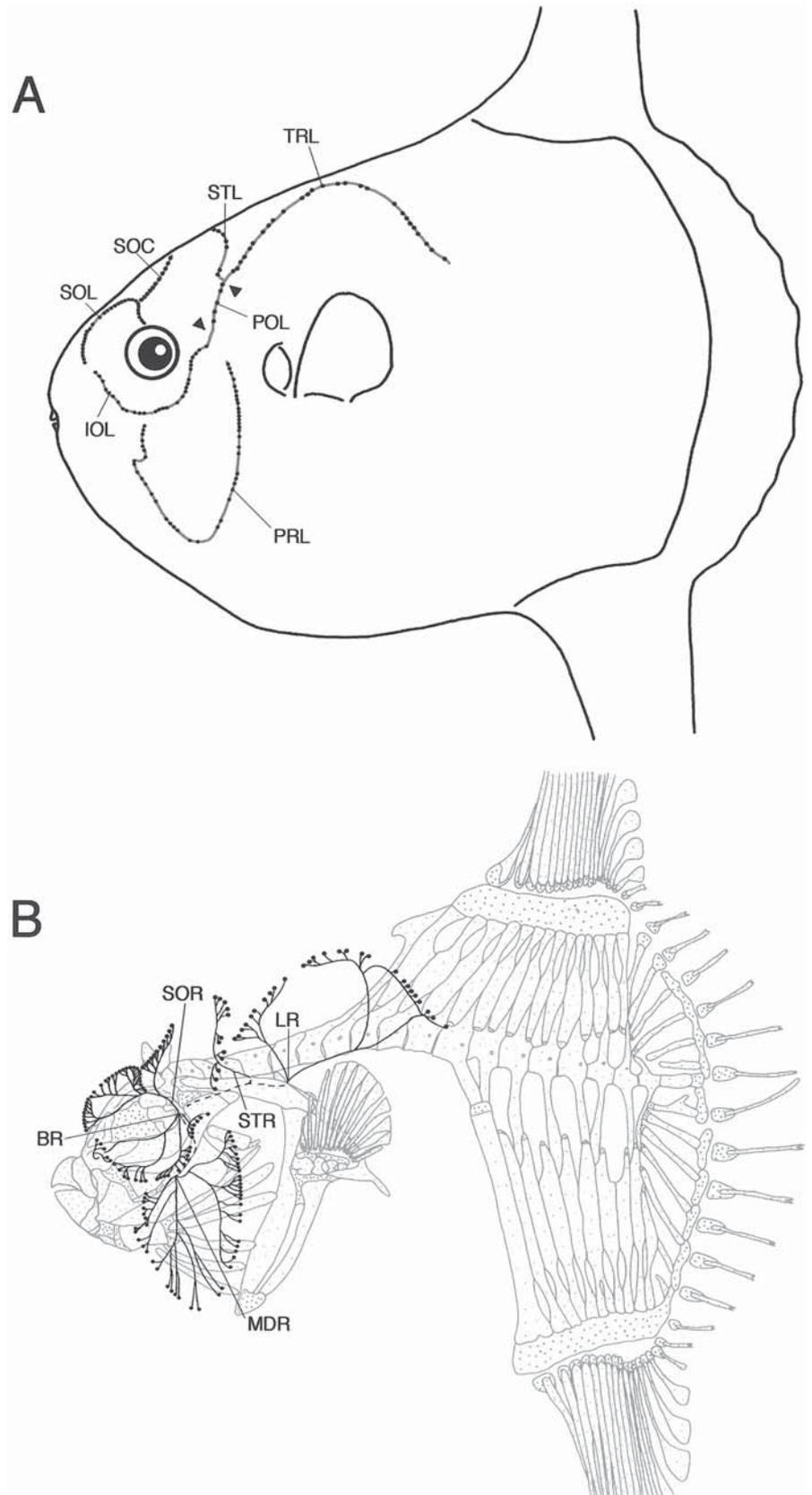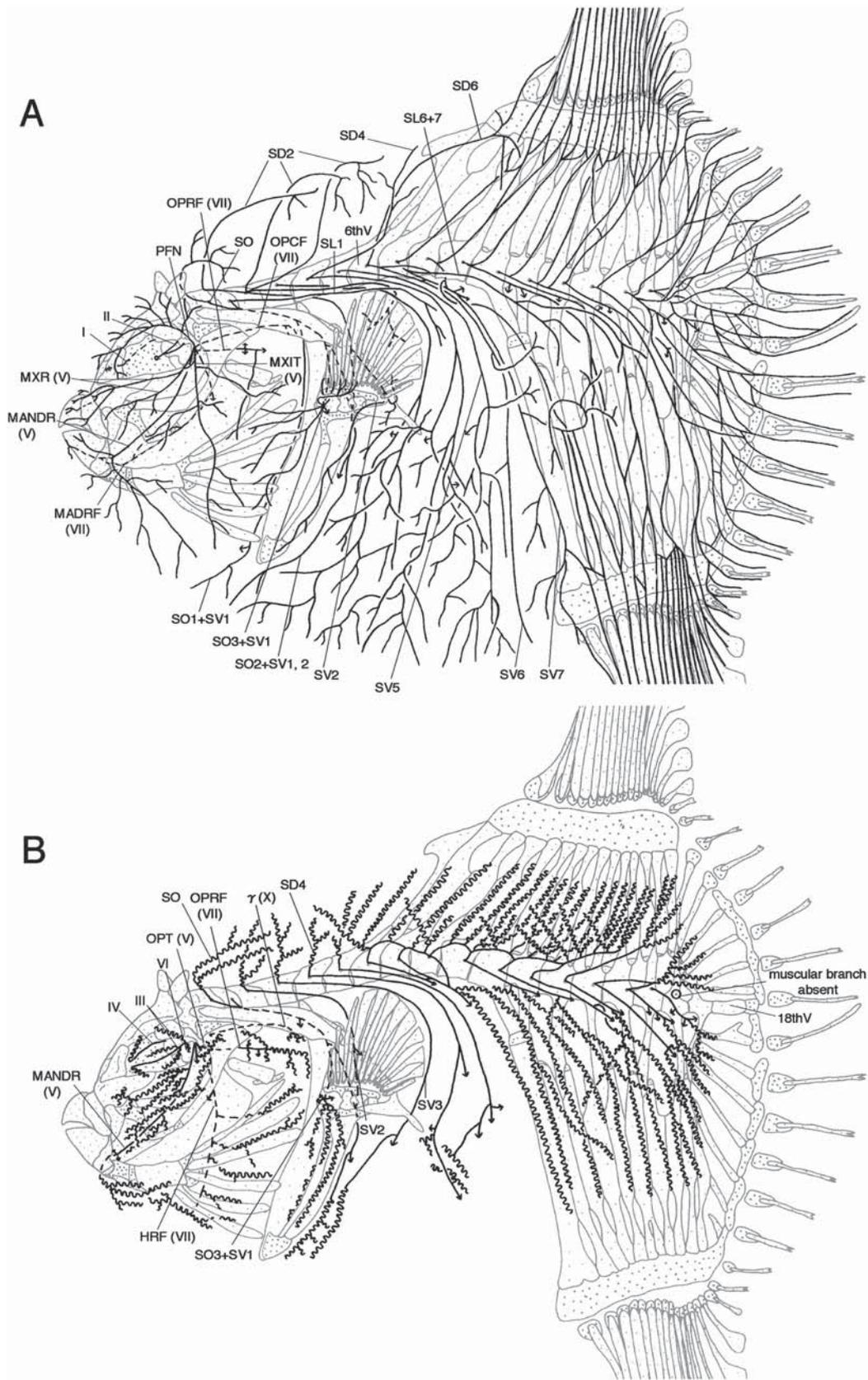
**Fig. 3.** Semischematic illustrations of the peripheral nervous system in *Mola mola*. **A** Olfactory nerve, optic nerve, and cutaneous branches; **B** muscular branches. *6thV* and *18thV*, 6th and 18th vertebrae. See Table 1 for other abbreviations. *Terminal arrows* indicate further extension as muscular branches (**A**) and cutaneous branches (**B**)
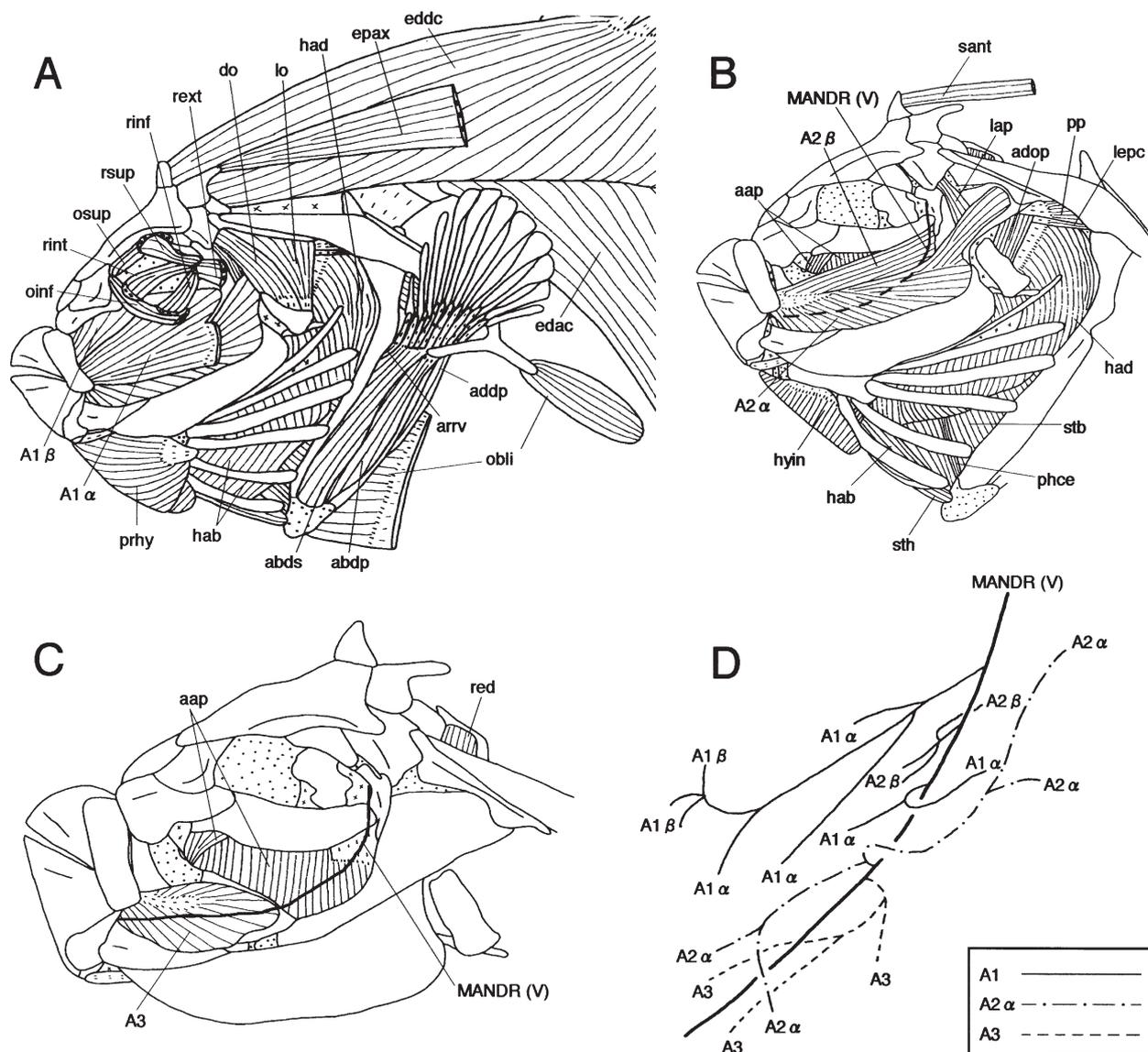
**Fig. 4.** Muscles of the anterior half of the body (**A–C**) and schematic illustration of the innervation of the adductor mandibulae muscles (**D**) in *Mola mola*. **A** Superficial anterior muscles; **B** superficial muscles removed; **C** deep muscles of the cheek; **D** branching patterns of MANDR (mandibular ramus of trigeminal nerve) (*three lines* in the *box at lower right* indicate interpretation of nerve homology). See Table 1 for other abbreviations

below), emerged from the cranium through a foramen in the membrane posterior to the dorsal part of the basisphenoid; after its emergence, the nerve immediately gave off an anterodorsal branch innervating the rectus superior (Figs. 3B, 4A); the remaining 3 anteriorly directed branches (Fig. 3B) innervated the rectus internus (by the dorsal branch), rectus inferior (ventral), and obliquus inferior (middle) (Fig. 4A).

**Abducent nerve (VI)** (Figs. 3B, 4A). After emergence from the cranium, the abducent nerve (Fig. 3B) innervated the rectus externus (Fig. 4A).

**Trochlear nerve (IV)** (Figs. 3B, 4A). The trochlear nerve (Fig. 3B) emerged from the cranium through the anterior part of the suture between the pterosphenoid

and basisphenoid, and coursed anteriorly to innervate the obliquus superior (Fig. 4A).

**Profundal nerve (PFN)** (Figs. 3A, 8A). The profundal nerve (Fig. 3A) emerged from the cranium (Fig. 8A) and coursed anterodorsally along with SOR (Fig. 2B), giving off 5 dorsally oriented branches, all extending into the skin on the anterodorsal surface of the head, including the snout.

**Trigeminal nerve (V)** (Figs. 3, 4, 5, 8A). The trigeminal nerve comprised 4 major branches: maxillary ramus (MXR; Fig. 3A), mandibular ramus (MANDR; Fig. 3A), opercular ramus (OPT; Fig. 3B), and maxillary inferior ramus (MXIT; Fig. 3A). After emergence from the cranium (Fig. 8A), a mixed branch (not illustrated) [of OPT (Fig. 3B) and MXIT (Fig. 3A)] coursed laterally (together with a branch of BR;

**Fig. 5.** Lateral view of the branchial arches and hyoid region in *Mola mola*. **A** Branchial arches and hyoid muscles; **B** nervous system of branchial arches and adjacent regions. See Table 1 for abbreviations
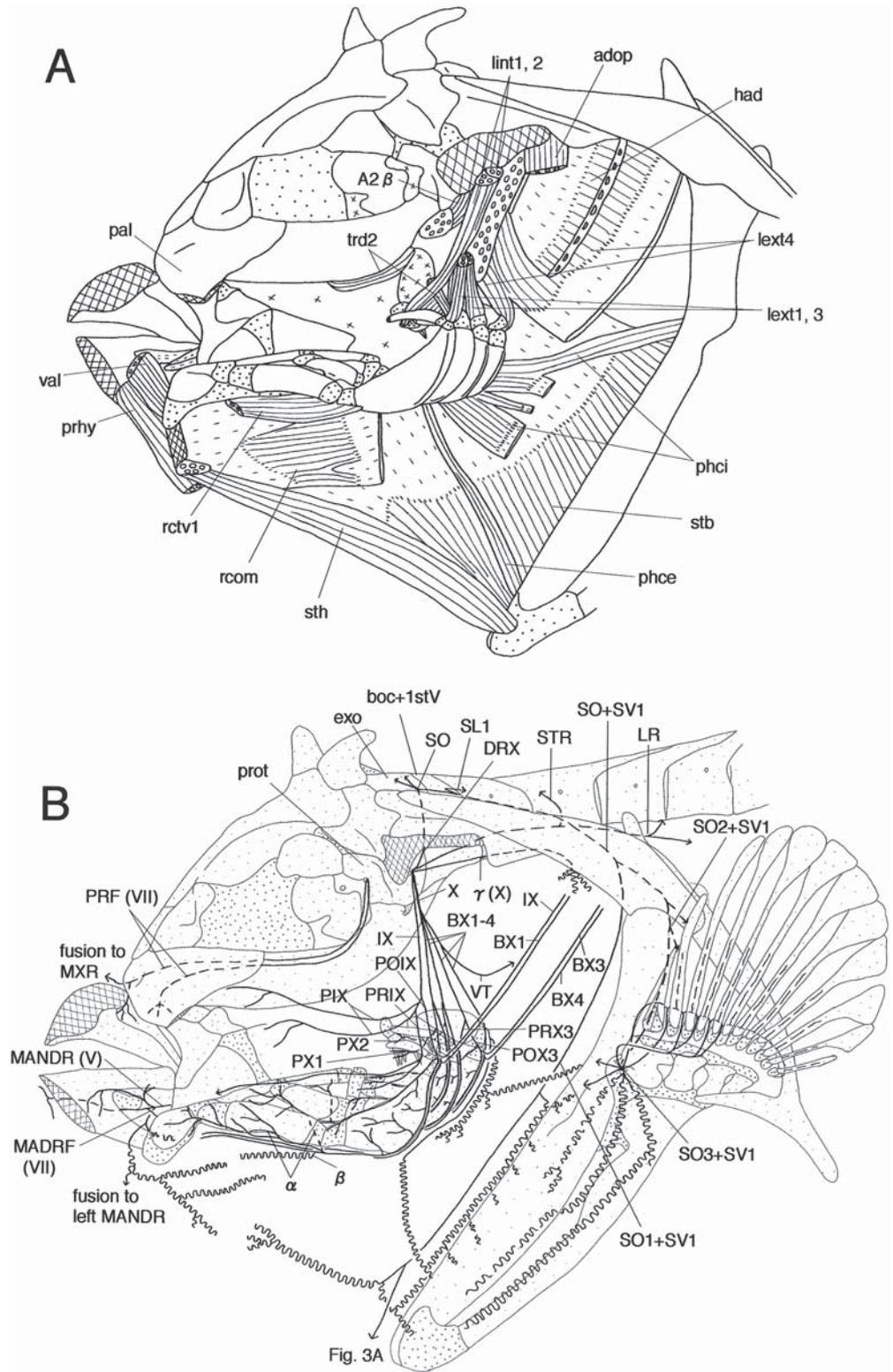


Fig. 2B); OPT and MXIT subsequently separated from one another, OPT innervating the levator arcus palatini (Fig. 4B) and dilatator operculi (Fig. 4A). MXIT (Fig. 3A) comprised 3 branches: the 1st was short and oriented anteriorly, being immediately confluent with MXR (Fig. 3A); the 2nd extended posteriorly crossing the gill cover; the 3rd ex-

tended ventrally to the skin lateral to the anterior branchiostegal rays, en route giving off 2 short branches to the preoperculum and posterior cheek, respectively.

MXR (Fig. 3A) included dorsal and ventral branches, the dorsal coursing anteriorly along the ventral eye margin to be divided into 3 branches below the lateral ethmoid, all

**Fig. 6.** Schematic illustration of the innervation of the gill arches and associated muscles in *Mola mola*. See Table 1 for abbreviations
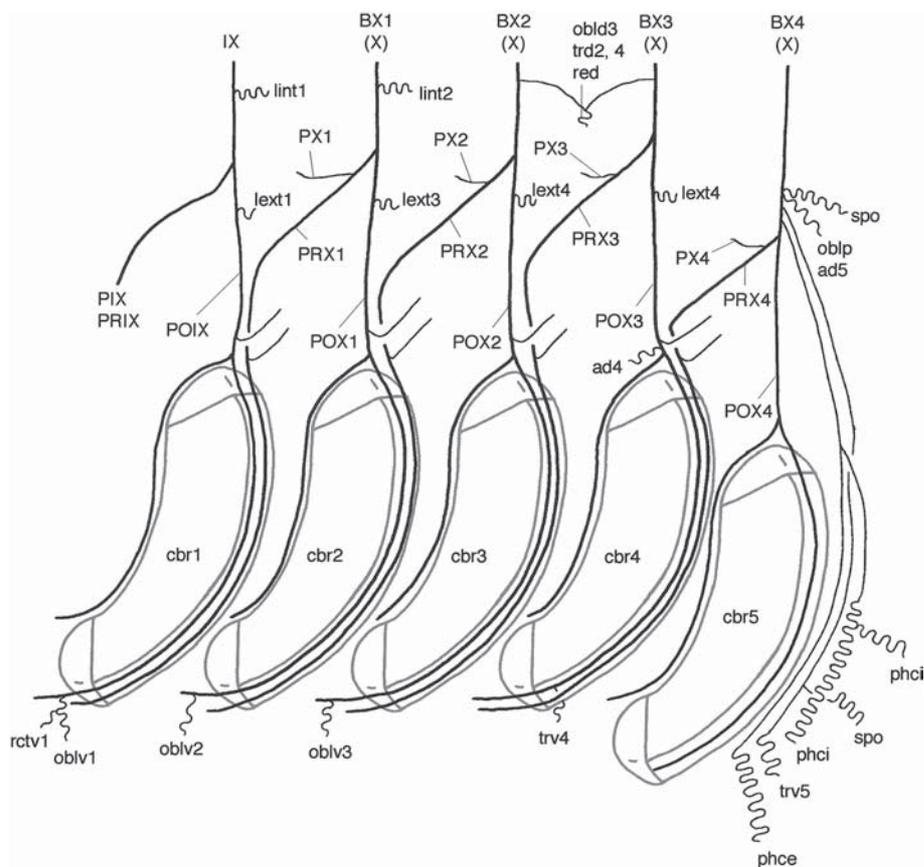


innervating the upper lip, and the ventral extending anteriorly cross the cheek.

MANDR (Fig. 3A,B) coursed obliquely downward, extending onto the medial surface of the lower jaw by passing between A2α and A3 of the adductor mandibulae subdivisions (Fig. 4B,C) [labeling of adductor mandibulae subdivisions in Fig. 4 follows Winterbottom (1974b), but nerve homology interpretations (box on lower right in Fig. 4D) are ours; see Discussion]. Along its course, MANDR (Fig. 4D) supplied 5 branches innervating the adductor mandibulae subdivisions: the 1st (dorsalmost) coursed obliquely downward, en route giving off 2 branches that innervated the posterodorsal portion of A1α (superficial subdivision; Fig. 4A), before dividing into dorsal and ventral branches, innervating A1β (superficial subdivision) and the anterior portion of A1α (Fig. 4A), respectively; the 2nd innervated A2β (posteromedial subdivision; Figs. 4B, 5A); the 3rd innervated the ventral portion of A1α; the 4th, comprising dorsally and ventrally elongated branches, innervated A2α (lateral to MANDR) (Fig. 4B); the 5th, including 3 branches, innervated A3 (medial to MANDR) (Fig. 4C). Before entering the medial surface of the lower jaw, MANDR (Fig. 3A) gave off anterior and posterior branches, innervating the lateral surface of the lower jaw and the anterior part of the hyoid region, respectively. On the medial surface of the lower jaw (Fig. 5B), MANDR divided into 3 branches: the dorsalmost terminated on the surface; the anterior branch entered the dentary through the anguloarticular–dentary suture and thence passed to the lateral surface of

the lower jaw through a foramen in the dentary to innervate the lower lip; the ventral branch further ramified into 2 branches, innervating the valvulus (Fig. 5A; val: an element unique to some tetraodontiforms; see Winterbottom, 1974b) and protractor hyoidei (Figs. 3B, 4A, 5B), respectively. In the protractor hyoidei, the left and right side branches of MANDR were connected to one another (Fig. 5B).

**Facial nerve (VII)** (Figs. 3, 4, 5B, 8A). The facial nerve comprised 6 major branches (Figs. 3, 5B): lateral palatine ramus (LPRF; not illustrated), opercular cavity ramus (OPCF; Fig. 3A), opercular ramus (OPRF; Fig. 3A,B), palatine ramus (PRF; Fig. 5B), hyoid ramus (HRF; Fig. 3B), and mandibular ramus (MADRF; Figs. 3A, 5B). After its emergence from the cranium (root not illustrated) (Fig. 8A), the nerve immediately gave off 4 branches: the 1st (PRF; Fig. 5B) was immediately divided into 2, both orientated anteriorly along the dorsal rim of the parasphenoid and thereafter the medial surface of the palatine; the dorsal element subdivided into 2 anteriorly, 1 being confluent with a branch of MXR (innervating the dorsal surface of the upper jaw; Fig. 3A) and the other ramifying on the medial surface of the upper jaw; the ventral element innervated the dorsal surface of the buccal cavity; the 2nd (OPCF; Fig. 3A) extended posteriorly to terminate at the posterodorsal part of the branchial cavity; the 3rd (LPRF; not illustrated) coursed obliquely downward to innervate the adductor arcus palatini (Fig. 4B,C); the 4th (OPRF; Fig. 3A,B) extended posteriorly, giving off (Fig. 3B) 2 dorsally and 5 ventrally oriented branches along the dorsal margin of the gill cover:

the anteriormost dorsally and ventrally oriented branches (Fig. 3B) innervated the adductor operculi (Fig. 4); the next ventrally oriented (Fig. 3A) extended downward to the lateral surface of the 5th branchiostegal ray; the posteriormost dorsally and 3rd ventrally oriented (Fig. 3B) innervated the levator operculi (Fig. 4A), and the remaining 2 ventrally oriented (Fig. 3B) innervated the dorsal element of the hyohyoidei adductores (Fig. 4A,B). After giving off the 4th branch (OPRF), the facial nerve (VII) (Fig. 3A,B) coursed ventrally along the medial surface of the hyomandibula, closely associated with MDR (anteroventral lateral line nerve; Fig. 2B), and subsequently divided into 2 branches [HRF (Fig. 3B) and MADRF (Figs. 3A, 5B)] at the hyomandibula–preoperculum suture. Passing ventrally along the medial surface of the preoperculum and branchiostegal rays, HRF (Fig. 3B) supplied 4 branches posteriorly along its course, the dorsal 3 innervating the hyohyoidei adductores (Fig. 4A,B) and the ventralmost the dorsal 2 subdivisions of the hyohyoidei abductores (Fig. 4A,B); distally, HRF divided into 2 branches, the anterior branch innervating the hyohyoideus inferioris (Fig. 4B) and the posterior the ventralmost subdivision of the hyohyoidei abductores (Fig. 4A,B). MADRF (Fig. 3A) coursed obliquely downward, emerging onto the lateral surface of the suspensorium through the hyomandibula–preoperculum suture, together with MDR (Fig. 2B); subsequently, MADRF (Fig. 3A) became separated from MDR and narrowly subdivided into dorsal and ventral branches, passing along the dorsal and ventral margins of the symplectic, respectively; the dorsal branch coursed lateral to the suspensorium posteriorly, but medial to it anteriorly, having migrated onto the latter side at the dorsal margin of the quadrate; the ventral branch also migrated immediately onto the medial side and coursed anteriorly along the anteroventral margin of the preoperculum; before entering into the medial surface of the lower jaw, the 2 branches became fused together; finally, MADRF (Fig. 5B) was confluent with a branch of MANDR on the medial surface of the lower jaw.

**Glossopharyngeal nerve (IX)** (Figs. 5, 6, 8A). The glossopharyngeal nerve (IX) (Fig. 5B) and vagal nerve (X) (see below) innervated the gill arches, IX applying to the 1st arch, BX1 (branchial trunk of X) the 1st and 2nd, BX2 the 2nd and 3rd, BX3 the 3rd and 4th, and BX4 the 4th and 5th (Fig. 6).

The glossopharyngeal nerve (Figs. 5B, 6) emerged from the cranium (Figs. 5B, 8A) and coursed ventrally (Figs. 5B, 6). It gave off a short posterior branch (Fig. 6) that innervated levator internus 1 (Fig. 5A), and was subsequently divided into anterior and posterior (posttrematic ramus, POIX) branches. The anterior branch (Figs. 5B, 6) comprised the pharyngeal (PIX) and pretrematic (PRIX) rami: PIX (Fig. 5B) immediately divided into the dorsal and ventral branches, extending into the epithelium of dorsal and dorsolateral portions of the buccal cavity, respectively; PRIX (Fig. 5B) ramified into a long dorsal and short ventral branch, the dorsal confluent with MNDRF (Fig. 5B) at the medial surface of the quadrate, en route supplying some branches (not illustrated) innervating the pseudobranch,

and the shorter also innervating the pseudobranch. POIX (Fig. 5B), passing down the anterior surface of levator externus 1 (Fig. 5A), extended a branch (Fig. 6) to that muscle, and thereafter gave off a long posterodorsal branch (Figs. 5B, 6) that reached close to the supracleithrum (Fig. 5B), extending along the basal parts of the gill filaments of the 1st gill arch [note that gill filaments do not occur on the dorsal parts of the gill arches in *M. mola*, the 4 series of filaments (of the 4 gill arches) instead extending posterodorsally to the supracleithrum]; slightly more ventrally, POIX divided into anteroventral and posteroventral branches (Figs. 5B, 6): the anteroventral innervated the gill rakers and epithelium of ceratobranchial 1; the posteroventral extended obliquely downward along the ventrolateral margin of the bone to the anterior cartilage of hypobranchial 1 (passing along the gill filament bases of the 1st gill arch); in addition to a number of short branches supplying ceratobranchial 1, the posteroventral gave off 2 branches (α and β in Fig. 5B) below the ceratobranchial–hypobranchial articulation: α was immediately subdivided into lateral and medial branches, innervating the epithelium of the anterior and anteromedial portions of the ventral buccal cavity, respectively; β innervated rectus ventralis 1 (Figs. 5A, 6) and obliquus ventralis 1 (Fig. 6).

**Vagal nerve (X)** (Figs. 3B, 4, 5, 6, 8A). The vagal nerve (X) (Figs. 5B, 6), after its emergence from the cranium (Fig. 8A), immediately gave off a posteriorly oriented branch (γ in Figs. 3B, 5B) to innervate the protractor pectoralis and levator pectoralis (Fig. 4B). Otherwise, the nerve comprised 5 major branches (Fig. 5B) directed ventrally: the 1st to 4th vagal branchial trunks (BX1–BX4) and visceral trunk (VT; not described), BX1–BX4 being serially homologous and similarly branched (Fig. 6).

BX1 (Figs. 5B, 6) passed between levatores interni 1 and 2 (Fig. 5A), giving off a branch innervating the latter muscle (Fig. 6), and thereafter divided into anterior (pretrematic ramus, PRX1) and posterior (posttrematic ramus, POX1) branches (Fig. 6). Dorsally, PRX1 (Fig. 6) supplied 1 cutaneous [pharyngeal ramus (PX1)] branch at the medial surface of levator externus 1 (Fig. 5A), innervating the oropharyngeal roof (anterior to epibranchial 1); dorsally, POX1 (Fig. 6) supplied a short muscular branch to levator externus 3 (Fig. 5A); PRX1 and POX1 continued ventrolaterally between levatores externi 1 and 3 (Fig. 5A) (note: levator externus 2 absent in *M. mola*), and thereafter extended to the lateral cartilages of ceratobranchials 1 and 2, respectively; immediately before reaching the cartilages, each gave off a posterodorsal branch as in POIX (Figs. 5B, 6; in Fig. 5B, a branch from PRX1, POX3, and PRX4 only illustrated; homologous branches in POX1, BX2, and PRX3 not illustrated) that passed along the basal parts of the gill filaments of the 1st and 2nd gill arches, respectively; subsequently, PRX1, supplying a number of branches innervating the epithelium of the medial surface of ceratobranchial 1, coursed anteroventrally along the ventromedial margin of that bone, distally reaching below the medial cartilage of hypobranchial 1; POX1 (Fig. 6) however, was divided into anterior and posterior branches, the subsequent array following the pattern of POIX, except for innervation of the epithelium
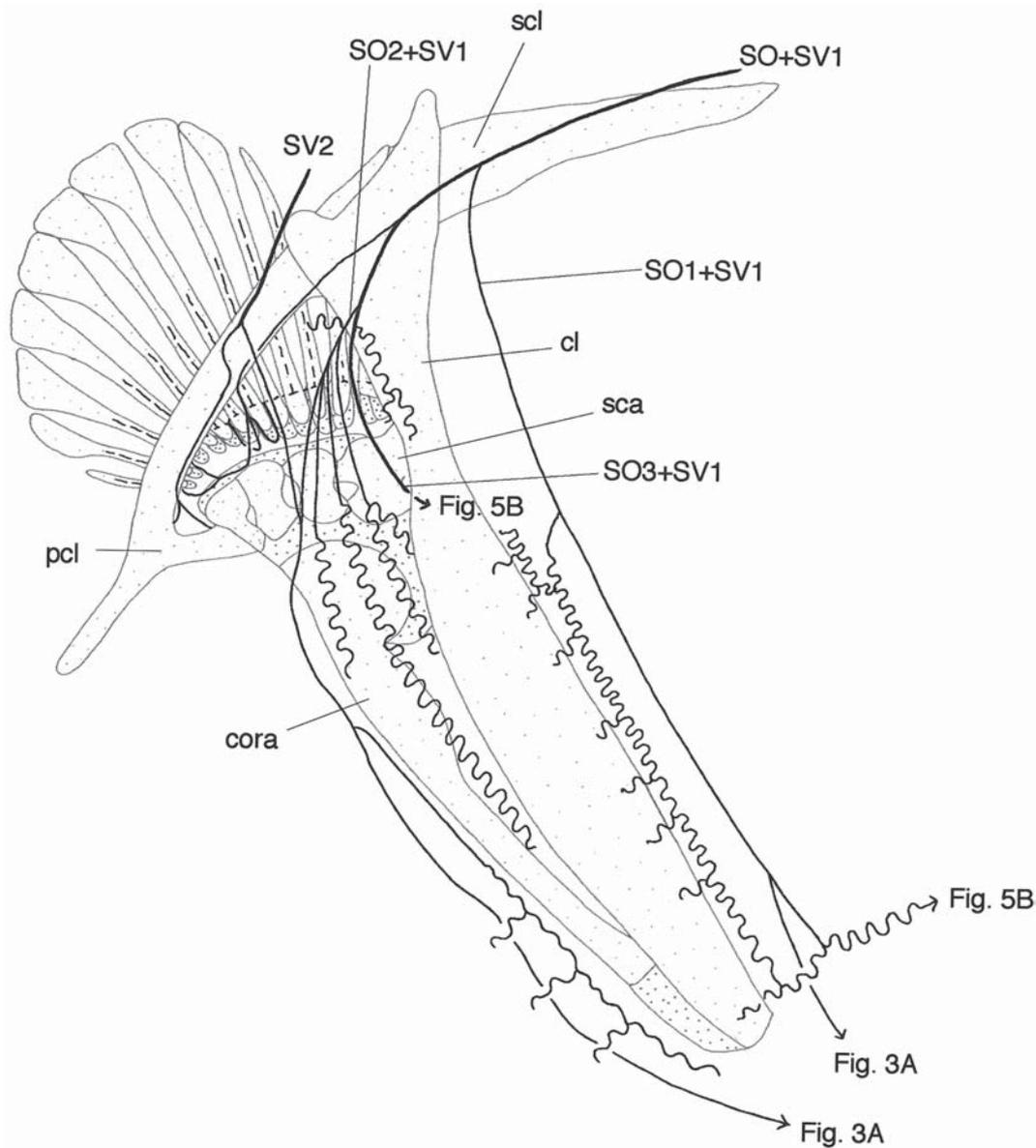
**Fig. 7.** Medial view of the pectoral girdle in *Mola mola*. See Table 1 for abbreviations

covering the posterior portion of the ventral buccal cavity and obliquus ventralis 2 (Fig. 6) by the posterior branch.

BX2 (Figs. 5B, 6) gave off a posteriorly oriented muscular branch at the anteromedial surface of levator externus 4 (Fig. 5A), being confluent with an anteriorly oriented muscular branch of BX3; subbranches of the muscular branch innervated the anterior bundle of transversus dorsalis 2, obliquus dorsalis 3, transversus dorsalis 4, and retractor dorsalis (Figs. 5A, 6). Subsequently, BX2 divided into PRX2 and POX2 posterolateral to the surface of levator internus 2 (Fig. 5A), PRX2 supplying PX2 (Figs. 5B, 6) to the oropharyngeal roof between epibranchial 2 and 3; PRX2 and POX2, both passing between levatores externi 3 and 4 (Fig. 5A), extended to the lateral cartilages of ceratobranchials 2 and 3, respectively; POX2 innervated the anterior bundle of levator externus 4 dorsally (Figs. 5A, 6) and obliquus ventra-

lis 3 ventrally. BX3 (Figs. 5B, 6) gave off an anteriorly oriented muscular branch (see above); more ventrally, BX3 comprised PRX3 and POX3, extending to the 3rd and 4th branchial arches, respectively, by passing along the anteromedial surface of levator externus 4 (Fig. 5A); POX3 innervated the posterior sheetlike bundle of levator externus 4 dorsally (Figs. 5A, 6), adductor 4 at midlength (Fig. 6), and anterior and posterior bundles of transversus ventralis 4 ventrally (Fig. 6). BX4 (Fig. 5B) was closely associated with VT; after separating from VT, BX4 gave off 4 branches at the anteromedial surface of levator externus 4 (Fig. 5A), innervating the sphincter oesophagi (Fig. 6), obliquus posterior (Fig. 6) and adductor 5 (Fig. 6), ventral portion of sphincter oesophagi and transversus ventralis 5 (Fig. 6), and pharyngoclaviculares externus and internus (Figs. 5, 6), respectively; subsequently, BX4 divided into
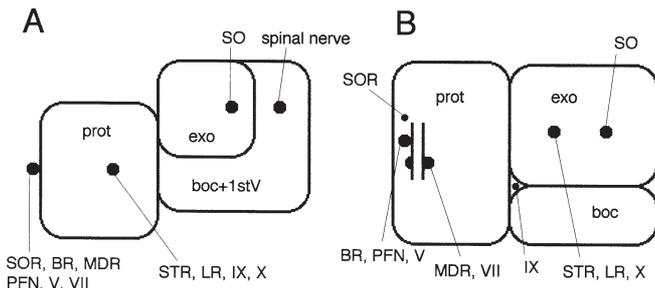
**Fig. 8.** Schematic illustrations of foramina for nerve emergence in the posterior cranium of *Mola mola* (**A**) and *Triacanthodes anomalus* (**B**). *boc + 1stV*, fused basioccipital and 1st vertebra. See Table 1 for other abbreviations

PRX4 and POX4; PRX4 gave off a long posterodorsally oriented branch along the basal parts of the gill filaments of the 4th gill arch (Fig. 5B).

*Remarks.*—Innervations of the rectus communis and posterior bundle of transversus dorsalis 2 could not be determined.

Although a nerve (dorsal ramus of the vagal nerve: DRX; Fig. 5B) extending between the posterior foramen in the prootic and the foramen in the exoccipital (for the spino-occipital nerve; see below) was recognized (Fig. 5B), it could not be traced distally.

**Spino-occipital nerve (SO)** (Figs. 3, 5B, 7, 8A). The spino-occipital nerve (SO) (Fig. 5B) emerged from the cranium through a foramen in the exoccipital (Fig. 8A). It comprised 3 (excluding DRX; see above) branches; 2 dorsal branches (1 each in Fig. 3A and Fig. 3B) innervated the skin covering the occipital region (anterior branch) (Fig. 3A) and the supracarinalis anterior, anterior portions of the epaxialis, and the erectores and depressores dorsales complex (posterior branch) (Fig. 3B); the remaining posteriorly directed branch (Fig. 5B) was confluent with the ventrally oriented branch that emerged from a foramen in the 1st vertebral part of the fused basioccipital and 1st vertebra bone (see Britz and Johnson, 2005), constituting SO + SV1 branch (SV1, the 1st ventrally oriented branch of spinal nerve; see below) posteriorly.

SO + SV1 (Figs. 5B, 7) coursed posteriorly along the medial surface of the supracleithrum, giving off a single (1st) branch (SO1 + SV1; Figs. 5B, 7) before reaching the anterior margin of the cleithrum. SO1 + SV1 (Fig. 5B) coursed ventrally, detaching a ventrally oriented branch at its midpoint to innervate the sternobranchialis (Figs. 5, 7); more ventrally, SO1 + SV1 (Fig. 5B) forked into anterior and ventral branches; the former comprised 2 muscular branches [the posterior being confluent with the ventrally oriented branch (above)] innervating the sternohyoideus (Fig. 5A); the latter innervated the skin (Fig. 3A) ventral to the branchiostegal rays.

After giving off SO1 + SV1 (Fig. 7), SO + SV1 was divided into posterior and ventral branches at the dorsomedial surface of the cleithrum. The posterior branch turned ventrally at the medial surface of the postcleithrum, subdividing into 3 branches, the anterior applying to the

5th and 6th pectoral fin ray bases, the middle to the 7th and 8th bases, and the posterior (as 2 branches) to the 10th and posteriormost bases, respectively; these 3 branches (and some branches of SO3 + SV1; see below) were transversely connected to one another at the basal part of the fin (Figs. 5B, 7) to radiate a nerve to each fin ray, the nerve being sandwiched by the left and right halves of the ray. The ventral branch of SO + SV1 was further divided into SO2 + SV1 and SO3 + SV1.

SO2 + SV1 (Fig. 7), after detaching from SO3 + SV1, immediately gave off a short posterior branch innervating the posterior portion of the adductor superficialis. Otherwise, SO2 + SV1 comprised 4 major branches: the anterior 3 branches innervated the arrector dorsalis and anterior portion of the adductor profundus, middle portion of the latter, and posterior portion of the latter, respectively; the posteriormost branch, being confluent with a branch of the 2nd spinal nerve (SV2), innervated the anteroventral bundle of the obliquus inferioris (the muscle comprising anteroventral and posteroventral bundles; Fig. 4A) and the skin ventral to the pectoral girdle (Fig. 3A).

SO3 + SV1 (Figs. 5B, 7), after giving off a short anteroventral branch (Fig. 7) innervating the anterior portion of the adductor superficialis, emerged to the lateral surface of the pectoral girdle (Fig. 5B), passing through a foramen anterior to the scapula. After emergence (Fig. 5B), SO3 + SV1 was divided into 8 major branches; 3 dorsally directed branches were applied to the anterior pectoral fin rays (see also SO1 + SV1 above); 2 anteriorly directed branches (Fig. 3A) innervated the skin lateral to the branchiostegal rays; 3 ventrally directed muscular branches (Fig. 5B) innervated the arrector ventralis (Fig. 4A) and anterior portion of the abductor superficialis, posterior portion of the latter muscle, and abductor profundus (Fig. 4A), respectively.

**Spinal nerves** (Figs. 3, 7). The spinal nerves (Fig. 3), emerging from a foramen at each vertebra, comprised 3 series: the dorsally (SDX) (X being the number of the vertebra), laterally (SLX), and ventrally (SVX) oriented branches. Generally, cutaneous branches of the nerves (Fig. 3A) reached the skin, passing through a plane between the dorsal (erectores and depressores dorsales complex, eddc; Fig. 4A) and ventral (erectores and depressores anales complex, edac; Fig. 4A) body muscle masses, whereas the muscular branches (Fig. 3B) were distributed below or within the masses. The cutaneous branches of SD2, SD4, and SD6 (Fig. 3A) were exceptional in reaching to the skin by passing through the medial surface of eddc.

The cutaneous branches of SD (Fig. 3A) innervated the dorsal half of the body; SD2 and SD4 innervated the skin of the predorsal region; SD6–SD15 innervated both the skin of the posterior trunk (small branches innervating the skin not illustrated) and fin rays; of these, SD6–SD13 (being confluent with adjacent SD branches dorsally) innervated the dorsal fin rays, SD13–SD15 (being confluent with adjacent SD and SV branches) innervating the dorsal claval fin rays; SD branches extended between the rays on the fins (not sandwiched by the halves of each ray), the condition being identical in all vertical fins; SD3, SD5, and SD16 were absent.

The muscular branches of SD (Fig. 3B) innervated the epaxialis and eddc (Fig. 4A): SD2 and SD3 innervated both anterior portions of the epaxialis and eddc, innervation of the posterior portion of the former muscle being unclear; SD4–SD14 innervated eddc; SD6–SD10 and SD13 were confluent with SD branches of the next vertebrae before ramifying into the eddc; the muscular branch was absent in SD15.

SL (Fig. 3A), supplying cutaneous branches only, comprised SL1, SL2, SL6, and SL7 (the latter 2 being fused), innervating the skin medial to the pectoral fin and that covering the lateral surface of the anterior edac, respectively.

The cutaneous branches of SV (Figs. 3A, 7), all being confluent with adjacent SV branches, innervated the ventral half of the body, and the anal and ventral claval fin rays; SV1 was confluent with SO (described above); SV2 (Fig. 7) coursed posteroventrally, to be divided into 2 on the medial surface of the postcleithrum; the ventral branch was confluent with the posteriormost branch of SO2 + SV1; the posterior branch, ramifying into 2, migrated to the lateral surface of the girdle passing between the bone and 3rd actinost to innervate the skin (Fig. 3A) immediately posterior to the pectoral fin and lateral to the pectoral girdle, respectively; SV3–SV13 (small branches innervating the skin illustrated only in SV5–SV7; Fig. 3A) innervated the skin covering the ventral half of the body; SV6–SV12 also innervated the anal fin rays; SV12–SV16 innervated the ventral claval fin rays.

In the clavus, SD and SV branches gave off many fine branches to the skin between the rays (not illustrated).

The muscular branches of SV (Figs. 3B, 7) innervated the anterior (by SV2–SV3; Figs. 3B, 7) and posterior (by SV4–SV5; Fig. 3B) bundles (Fig. 4A) of the obliquus inferior and edac (Fig. 4A) (by SV6–SV15; Fig. 3B); muscular branches were totally absent in the 16th vertebra (Fig. 3B), the vertebra having a cutaneous branch only (Fig. 3A).

## Discussion

The peripheral nervous system of *Mola mola* observed in this study is discussed in four sections: the lateral line system and its innervation, other cranial and spinal nerves, some muscle innervation, and homology of the clavus.

**Lateral line system and its innervation.**   The lateral line system in tetraodontiforms was summarized and illustrated by Tyler (1980), although the Molidae was exceptional because the lateral line was "not discernible" to him. Recently, Nakae and Sasaki (2005) described the lateral line system and its innervation in detail in the triacanthodid *Triacanthodes anomalus* and ostraciid *Ostracion immaculatus*, tetraodontiform and perciform conditions being compared.

The lateral line system in *M. mola* comprised 6 cephalic and 1 trunk lateral line (Fig. 1A), the lines including only superficial neuromasts (Figs. 1, 2) as in other tetraodontiforms (Nakae and Sasaki, 2005). The number of neuromasts in TRL (27) was fewer than those previously reported in tetraodontiforms (47 in *T. anomalus*, 35 in *O.*

*immaculatus*; Nakae and Sasaki, 2005). Apparently, the fewer TRL neuromasts resulted from the relatively shorter TRL, being restricted to the anterior half of the body (Fig. 1A). Neuromast distribution indicated that *M. mola* senses mechanical stimuli in the anterior half of the body, especially in the head.

Compared with *T. anomalus* and *O. immaculatus* (Nakae and Sasaki, 2005), the lateral line system in *M. mola* differed in the following: presence of SOC, absence of the otic line (OTL), higher number of neuromasts in SOL (30 in *M. mola*, 18 in *T. anomalus*, 17 in *O. immaculatus*), and lower number of neuromasts in TRL (27, 47, 35; see above). Owing to the disjunction of SOL–IOL and PRL–POL, respectively, OTL (connecting the 2 junctions) was absent in *M. mola*, the otic ramus innervating OTL also being absent. On the other hand, the above three species are similar to one another in the absence of the mandibular line (MDL), and in the numbers of neuromasts in PRL (46, 41, 42) and on the whole body (155, 138, 145).

Although LR emerged from the cranium by passing through the foramen in the prootic (Fig. 5B) in *M. mola*, the foramen utilized in *T. anomalus* was the exoccipital (personal observation; see below for more discussion). In *M. mola*, LR did not form a "serial collector" nerve (sensu Freihofer, 1972) on the trunk (Fig. 1B), as in *O. immaculatus* (Nakae and Sasaki, 2005), although it gave off 2 dorsally oriented "collector" nerves during its course, to supply short branches to the neuromasts. Because a "serial" condition is primitively present in tetraodontiforms (Nakae and Sasaki, 2005), the *Mola* condition is considered as secondary.

**Other cranial and spinal nerves.**   Innervations of the eye (Fig. 3A) and eye muscles (Fig. 3B) in *M. mola* were basically identical with those in *Polypterus senegalus* (see Piotrowski and Northcutt, 1996), *Menidia beryllina* (see Herrick, 1899), *Polycentrus schomburgkii* (see Freihofer, 1978), and *Takifugu oblongus* (see Bal, 1937), the innervation pattern apparently being highly conservative, although the foramina through which the nerves passed were variably positioned (e.g., the oculomotor nerve passed through a foramen in the orbitosphenoid in *Polypterus senegalus*, through a membrane below the sphenotic in *M. beryllina*, and through a membrane posterior to the basisphenoid in *M. mola*).

The reduced number of foramina for emergence of the nerves from the cranium is a distinct feature of *M. mola* (Fig. 8A). In that species (Fig. 8A), SOR, BR, MDR, PFN, V, and VII all emerged from a foramen immediately anterior to the prootic (Fig. 8A), whereas in *T. anomalus* (Fig. 8B), 3 foramina were present on that bone, being utilized by SOR, BR + PFN + V, and MDR + VII, respectively. Moreover, the independent foramen for IX in *T. anomalus* (Fig. 8B) was absent in *M. mola* (Fig. 8A), the nerve sharing a prootic foramen with STR, LR, and X in *M. mola*. The location of the foramen at the prootic appeared to be unusual, an equivalent foramen perforating the exoccipital primitively in tetraodontiforms (Fig. 8B). In *M. mola*, the "basioccipital [is] greatly prolonged dorsally behind the exoccipitals to border the foramen magnum to the exclusion of the exoccipitals" [Tyler (1980), but see also Britz and Johnson

(2005) for the occipito–vertebral fusion]. Because modification of the bone also involved the dorsal relocation of the exoccipital (thus the ventral surface of the bone became barely exposed) (Tyler, 1980: fig. 308), the exoccipital–nerve foramen relationship seems to have been altered so as to allow ventral passage of nerves accommodated IX and X, although a reason for the inclusion of STR and LR (both passing posteriorly; Fig. 5B) within the same foramen is not obvious.

Descriptions of whole spinal nerves have not been published in any teleosts, and innervations of the fins remain unknown. Branches innervating the dorsal and anal fins in *M. mola* extended along the anterior or posterior margins of the rays (i.e., between the rays). However, in the pectoral fin, SO branches, supplying the fin ray bases laterally (Fig. 5B) and medially (Fig. 7), formed a transverse nerve along the fin base from which 11 rami (1 for each ray) were derived, each ramus being sandwiched by the left and right halves. The innervation patterns of the claval fin rays in *M. mola* were identical with those of the dorsal and anal fin rays (Fig. 3A; see below for more discussion).

**Innervations of some muscles.** The adductor mandibulae in *M. mola* comprised 5 subdivisions (Fig. 4): A1α, A1β, A2α, A2β, and A3 (sensu Winterbottom, 1974b). All subdivisions of the muscle were innervated by MANDR (Figs. 3B, 4). Nakae and Sasaki (2005) hypothesized homologies of the subdivisions in eight tetraodontiform families (excluding Triodontidae and Molidae) from the branching patters of MANDR (RMT in that study), showing that the insertion points are not reliable criteria for homology. In the present study, the innervating pattern of the adductor mandibulae in *M. mola* was examined (Fig. 4D) and homologies of the subdivisions analyzed following the methods of Nakae and Sasaki (2005). We found difficulty with Winterbottom's (1974b) identification of A2β, that element appearing to be an A1 subdivision. Although A2β is ventral to A2α primitively in tetraodontiforms, A2β was entirely dorsal to A2α in *M. mola*. Because the homology of A2α in *M. mola* is presumed by its position (lateral to MANDR), "A2β" is most likely a medial subdivision of A1, the 2nd branch innervating "A2β" budding off between the 1st and 3rd branches, both innervating the A1 subdivisions. Therefore, A2β is judged to have been lost, the remaining subdivisions comprising A1α, A1α'(2), A1β, A2α, and A3 (see Nakae and Sasaki, 2004). This pattern is identical with that of *Diodon holocanthus* in the presence of A1α'(2) and absence of A2β.

Although Winterbottom (1974b) described the hyohyoidei adductores in *M. mola*, the dorsomedial portion of his "hyohyoidei adductores" was identified as a well-developed levator externus 4 (Figs. 4A, 4B, 5A) in our material: "the hyohyoidei adductores" comprised sheetlike lateral and medial elements dorsally, being innervated by OPRF (VII) (Fig. 3B) and BX3 (X) (i.e., by a posteriorly directed muscular branch innervating "lest 4" in Fig. 6), respectively; the medial element (Fig. 5A) was anteriorly continuous with the bundle of levator externus 4, innervated by BX2 (Fig. 6). In *Polycentrus schomburgkii* (see Freihofer, 1978), the dorsal part of the hyohyoidei adductores and levator externus 4 are innervated by OPRF and BX2, respectively. Although inclusion of BX3 for innervation raises the question of the identity of the element, we suggest that the enormous posterior extension of the muscle requires innervation by the posterior BX branch (i.e., BX3). Winterbottom (1974b) recognized a *M. mola*-like levator externus 4 in tetraodontids and diodontids.

In addition to the pharyngoclavicularis internus (phci in Fig. 5A), *M. mola* possessed a well-developed sheetlike muscle (stb in Fig. 5A) arising from the anteroventral surface of the cleithrum, the insertion being an aponeurotic sheet forming the inner wall of the opercular cavity. Although Winterbottom (1974b) identified the sheetlike muscle, including the "narrow long subdivision," as the pharyngoclavicularis externus (phce in Fig. 5A), the innervations clearly indicated that only the "subdivision" represents the pharyngoclavicularis externus. In *M. mola*, the sheetlike division and narrow long subdivision were innervated by SO1 + SV1 and BX4 (Fig. 5B), respectively, their homologies being determined as elements derived from the sternohyoideus and pharyngoclavicularis externus, respectively, based on the perciform condition (i.e., *Polycentrus schomburgkii*; Freihofer, 1978). In this study, the sheetlike division is labeled as "sternobranchialis (stb)," based on its position (see Winterbottom, 1974a).

Parenti and Song (1996) defined SO1 as "ramus 1 of the SO: innervates muscle of . . . such as the sternohyoideus and pharyngoclavicularis,. . . ." However, the pharyngoclaviculares externus and internus in *M. mola* were clearly innervated by the branches of BX4, as in *P. schomburgkii* (see figs. 18–19 and description of Freihofer, 1978). Therefore, their definition of SO1 is questionable.

**Homology of the clavus.** Molids are characteristic in having an aborted caudal finlike structure, termed "clavus" by Fraser-Brunner (1951). Homology of the clavus was unclear, being recognized either as the highly modified caudal fin or highly modified components of the dorsal and anal fins that have replaced the caudal fin (see Johnson and Britz, 2005, for review). Johnson and Britz (2005) concluded that the clavus is formed by dorsal and anal fin elements, based on the ontogeny of the median fins and axial skeleton in the molid *Ranzania laevis*.

As Johnson and Britz (2005) stated, innervation of the muscles related to the clavus is irrelevant in determining claval homology, muscles of the 3 fins being innervated by spinal (muscular) nerves (Fig. 3B). However, the innervation pattern of the cutaneous branch (Fig. 3A) is significant in the homology assessment. In *M. mola*, the fin rays constituting the clavus are innervated in the same manner as the dorsal and anal fin rays. More specifically, the branches that innervate the dorsal, anal, and claval fin rays are confluent with adjacent branches before reaching the fin ray bases, each extending between the fin rays without passing a branch into the suture between the left and right halves of each ray (i.e., branch not sandwiched) (Fig. 3A). In the tetraodontiforms *Triacanthodes anomalus*, *Ostracion immaculatus*, and *Diodon holocanthus*, the caudal fin rays are innervated as follows (personal observation): the main dorsal branch entered the uppermost fin ray base and

coursed ventrally, passing through the upper fin ray bases; the main ventral branch entered the ventralmost fin ray base and coursed dorsally, passing through the lower fin ray bases; the 2 main branches, forming a continuous transverse nerve along the fin base, supply branches posteriorly into the rays (1 for each), each branch being sandwiched by the ray halves. In forming a transverse nerve supplying a number of branches to the rays, the caudal and pectoral (Fig. 5B) fins are identical. Thus, the innervation pattern of the claval fin rays is clearly identical with those in the dorsal and anal fin rays, but differs from that of the caudal fin rays, thereby providing a strong support for the hypothesis that the clavus is formed by elements of the dorsal and anal fin (Johnson and Britz, 2005).

## Literature Cited

Bal DW (1937) Studies in Indian puffers or globe fishes. III. The nervous system of *Tetraodon oblongus*, Bloch. J Bombay Univ 5(pt V):44–57

Britz R, Johnson GD (2005) Occipito-vertebral fusion in ocean sunfishes (Teleostei: Tetraodontiformes: Molidae) and its phylogenetic implications. J Morphol 266:74–79

Fraser-Brunner A (1951) The ocean sunfishes (Family Molidae). Bull Br Mus (Nat Hist) Zool 1:89–121

Fraser TH, Freihofer WC (1971) Trypsin modification for Sihler technique of staining nerves for systematic studies of fishes. Copeia 1971:574–576

Freihofer WC (1972) Trunk lateral line nerves, hyoid arch gill rakers, and olfactory bulb location in atheriniform, mugilid, and percoid fishes. Occas Pap Calif Acad Sci 95:1–31

Freihofer WC (1978) Cranial nerves of a percoid fish, *Polycentrus schomburgkii* (Family Nandidae), a contribution to the morphology and classification of the order Perciformes. Occas Pap Calif Acad Sci 128:1–78

Herrick CJ (1899) The cranial and first spinal nerves of *Menidia*; a contribution upon the nerve components of the bony fishes. J Comp Neurol 9:153–455, pls 14–20

Johnson GD, Britz R (2005) Leis's conundrum: homology of the clavus of the ocean sunfishes. 2. Ontogeny of the median fins and axial skeleton of *Ranzania laevis* (Teleostei, Tetraodontiformes, Molidae). J Morphol 266:11–21

Matsuura K, Tyler JC (1998) Triggerfishes and their allies In: Paxton JR, Eschmeyer WN (eds) Encyclopedia of fishes. Academic Press, San Diego, pp 227–231

Nakae M, Sasaki K (2004) Homologies of the adductor mandibulae muscles in Tetraodontiformes as indicated by nerve branching patterns. Ichthyol Res 51:327–336

Nakae M, Sasaki K (2005) The lateral line system and its innervation in the boxfish *Ostracion immaculatus* (Tetraodontiformes: Ostraciidae): description and comparisons with other tetraodontiform and perciform conditions. Ichthyol Res 52:343–353

Northcutt RG, Holmes PH, Albert JS (2000) Distribution and innervation of lateral line organs in the channel catfish. J Comp Neurol 421:570–592

Parenti LR, Song J (1996) Phylogenetic significance of the pectoral–pelvic fin association in acanthomorph fishes: a reassessment using comparative neuroanatomy. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes. Academic Press, San Diego, pp 427–444

Piotrowski T, Northcutt RG (1996) The cranial nerves of the Senegal bichir, *Polypterus senegalus* (Osteichthyes: Actinopterygii: Cladistia). Brain Behav Evol 47:55–102

Sagara K, Yoshita Y, Nishibori M, Kuniyoshi H, Umino T, Sakai Y, Hashimoto H, Gushima K (2005) Coexistence of two clades of the ocean sunfish *Mola mola* (Molidae) around the Japan coast (in Japanese with English abstract). Jpn J Ichthyol 52:35–39

Santini F, Tyler JC (2003) A phylogeny of families of fossil and extant tetraodontiform fishes (Acanthomorpha, Tetraodontiformes), Upper Cretaceous to Recent. Zool J Linn Soc 139:565–617

Song J, Boord RL (1993) Motor components of the trigeminal nerve and organization of the mandibular arch muscles in vertebrates. Acta Anat 1993:139–149

Tyler JC (1980) Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). NOAA Tech Rep NMFS Circular 434:1–422

Webb JF (1989) Gross morphology and evolution of the mechanoreceptive lateral line system in teleost fishes. Brain Behav Evol 33:34–53

Winterbottom R (1974a) A descriptive synonymy of the striated muscles of the Teleostei. Proc Acad Nat Sci Phila 125:225–317

Winterbottom R (1974b) The familial phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as evidenced by their comparative myology. Smithson Contrib Zool 155:1–201