**Review of spino-occipital and spinal nerves in Tetraodontiformes, with special
reference to pectoral and pelvic fin muscle innervation**

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Abstract Spino-occipital nerve (SO) and ventral rami of spinal nerves (SV) in 10 tetraodontiform families and 5 outgroup taxa were examined, with special reference to pectoral and pelvic fin muscle innervation. Compared with the outgroup taxa, tetraodontiforms were characteristic in having SO3 + SV1 (SO3 in tetraodontids) that gave off several lateral sub-branches to the pectoral fin base and SO participation in infracarinalis anterior innervation. SO and SV1 were connected with one another (6 patterns) before entering the pectoral fin muscles in most species, including the outgroup taxa, resulting in the participation of SV1 in the innervation of almost all of the pectoral fin muscles. SO3 + SV1 was present in all tetraodontiforms (except in 2 tetraodontids having only SO3) and the outgroup taxa, an upper dorsal branch uniformly extending dorsally into the pectoral fin base. The pectoral fin base also received a branch ventrally, but its identity differed (participation or non-participation of SV2). SV1 alone constituting the branch was a derived condition occurring in Aracanidae, Ostraciidae, Tetraodontidae, Diodontidae, and Molidae. No strong characters supporting a tetraodontiform sister group were recognized among the spino-occipital nerve and ventral rami of spinal nerves.

Key words Tetraodontiformes • Spino-occipital nerve • Spinal nerves • Muscle innervation

The great diversity of tetraodontiform body forms and unique life characteristics have attracted the interest of many ichthyologists since the 18th century (see Tyler, 1980, for review), Santini and Tyler (2003) being the latest morphology-based phylogenetic study on the order. Although molecular phylogenetic approaches have also been attempted (Bass et al., 2005; Holcroft, 2005), the relationships obtained were more or less ambiguous, except for strong support for the sister relationship of Tetraodontidae + Diodontidae to the Molidae (Bass et al., 2005) and monophyly of the Balistidae + Monacanthidae and the Tetraodontidae + Diodontidae, respectively (Holcroft, 2005). Overall, interfamilial relationships have at no time been satisfactorily resolved, tree topologies differing significantly between authors (see Holcroft, 2005: fig. 1). Furthermore, the sister group of Tetraodontiformes has also remained unresolved, although several putative groups have been proposed (see Tyler et al., 2003; Holcroft, 2005; for review). Clearly, additional studies on the order are required, including searches for new characters. In this article, innervation patterns of the spino-occipital nerve and ventral rami of the anterior spinal nerves in tetraodontiforms are reviewed in an attempt to provide new insights into the phylogeny of the group. Moreover, five non-tetraodontiform species are also studied, being the first step in a sister group search based on nerve characters.

Parenti and Song (1996) reviewed the spino-occipital nerve and ventral rami of spinal nerves in acanthomorph fishes, providing definitions of main nerve branches and new interpretations of pelvic fin muscle homologies. Although 26 families were considered in that review, tetraodontiforms were omitted. Nakae and Sasaki (2006)

described and illustrated the spino-occipital and spinal nerves in *Mola mola* in their review of the peripheral nervous system of that species. However, comparable conditions in other tetraodontiforms remained unknown. These nerves in all families of Tetraodontiformes are therefore described herein and their systematic significance discussed for the first time.

Materials and Methods

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 millimeters, mm) are of standard (SL) and total length (TL). Bones and muscles were observed on specimens stained by Alizarin red S (D), 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 were determined by treatment with 1% osmium tetroxide. Dorsal rami of spinal nerves are not described herein, because they are not involved in pectoral and pelvic fin muscle innervation. Terminology generally follows Tyler (1980) for osteology, Winterbottom (1974) for myology, Parenti and Song (1996) for the spino-occipital nerve, and Nakae and Sasaki (2006) for the spinal nerve. Detailed descriptions of both nerve branching patterns and innervation are given first for *Triacanthodes anomalus*, followed by notes on characteristics of other species.

Specimens examined. Triacanthodidae: *Triacanthodes anomalus*, BSKU (Laboratory of Marine Biology, Faculty of Science, Kochi University) 70467 (62.7 mm SL, D), BSKU 70470 (3 specimens; 79.2—80.3 mm SL, CS), BSKU 79387 (67.4 mm SL, D), BSKU 79388 (73.8 mm SL, D). Triacanthidae: *Triacanthus biaculeatus*, BSUK 79390 (150.6 mm SL, D), BSKU 79391 (137.3 mm SL, D), BSKU 79457 (8 specimens; 133.4—182.0 mm SL, CS). Balistidae: *Sufflamen chrysopterum*, BSKU 79392 (92.8 mm SL, D), BSKU 79393 (100.1 mm SL, D), BSKU 79459 (6 specimens; 72.2—152.4 mm SL, CS). Monacanthidae: *Stephanolepis cirrhifer*, BSKU 79394 (81.9 mm SL, D), BSKU 79395 (78.9 mm SL, D), BSKU 79460 (10 specimens; 48.7—128.7 mm SL, CS). Aracanidae: *Kentrocapros aculeatus*, BSKU 79396 (88.4 mm SL, D), BSKU 79397 (100.8 mm SL, D), BSKU 79463 (3 specimens; 62.2—114.7 mm SL, CS). Ostraciidae: *Ostracion immaculatus*, BSKU 60471 (2 specimens; 110.3 and 115.6 mm SL, CS), BSKU 70468 (122.8 mm SL, D), BSKU 79398 (106.7 mm SL, D), BSKU 79463 (4 specimens; 82.4—128.4 mm SL, CS). Triodontidae: *Triodon macropterus*, BSKU 79403 (355 mm SL, D), BSKU 79404 (410 mm SL, D), BSKU 79464 (335 mm SL, CS), BSKU 79465 (371 mm SL, CS), BSKU 79466 (2 specimens; 310 and 371 mm SL, CS). Tetraodontidae: *Takifugu poecilonotus*, BSKU 79399 (64.1 mm SL, D), BSKU 79400 (94.3 mm SL, D), BSKU 79467 (9 specimens; 61.6—121.4 mm SL, CS); *Canthigaster rivulata*: BSKU 79401 (75.5 mm SL, D), BSKU 79402 (74.2 mm SL, D), BSKU 79468 (8 specimens; 51.8—99.7 mm SL, CS). Diodontidae: *Diodon holocanthus*, BSKU 79405 (86.3 mm SL, D), BSKU 79406 (84.1 mm SL, D),

BSKU 79469 (8 specimens; 89.8—125.1 mm SL, CS). Molidae: *Mola mola*, BSKU 75496 (530 mm TL, D), BSKU 75497 (610 mm TL, D), BSKU 75498 (700 mm TL, D), BSKU 75499 (390 mm TL, CS), BSKU 75500 (400 mm TL, CS). Lophiidae (Lophiiformes): *Lophiomus setigerus*, BSKU 79428 (86.0 mm SL, D), BSKU 79429 (94.4 mm SL, D), BSKU 79470 (5 specimens; 46.0—129.6 mm SL, CS). Zeidae (Zeiformes): *Zeus faber*, BSKU 79430 (83.3 mm SL, D), BSKU 79431 (83.3 mm SL, D), BSKU 79471 (3 specimens; 94.2—110.0 mm SL, CS). Acropomatidae (Perciformes): *Malakichthys wakiyae*, BSKU 70466 (86.0 mm SL, D), BSKU 70469 (3 specimens; 95.2—107.4 mm SL, CS), BSKU 79435 (90.3 mm SL, D), BSKU 79473 (87.0 mm SL, CS). Caproidae (Perciformes; see Nelson, 2006): *Antigonia capros*, BSKU 79433 (161.0 mm SL, D), BSKU 79434 (156.3 mm SL, D), BSKU 79472 (2 specimens; 158.4 and 162.9 mm SL, CS). Siganidae (Perciformes): *Siganus spinus*, BSKU 79436 (89.6 mm SL, D), BSKU 79437 (88.4 mm SL, D), BSKU 79474 (6 specimens; 77.7—83.4 mm SL, CS).

Results

***Triacanthodes anomalus* (Triacanthodidae)** (Figs. 1, 2). The pectoral and pelvic fin muscles and surrounding skin were innervated by the spino-occipital nerve (SO) and the ventral rami of the anterior spinal nerves (SV) emerging from the 1st (SV1) to 7th (SV7) vertebrae (1st and 2nd innervating the pectoral fin and 1st to 7th the

pelvic fin) (Figs. 1, 2).

Pectoral fin (Figs. 1, 2A). — SO emerged from the cranium through a foramen [posterior to that for the vagal nerve (X)] in the exoccipital, shortly thereafter combined with SV1, and subsequently ramified into 4 branches: SO1 + SV1, SO2 + SV1, SO3 + SV1, and SOc +SV1 (SOc: spino-occipital connecting branch; newly-proposed in this study; Fig. 2A).

SO1 + SV1 (Fig. 1) coursed ventrally along the anteromedial margin of the cleithrum and divided into external and internal branches; the former innervated the skin ventral to the pectoral and pelvic girdles; the latter passed medially to the pharyngoclavicularis externus (phce) to innervate the sternohyoideus (sth) and sternobranchialis (stb).

SO2 + SV1 (Fig. 2A) innervated the adductor superficialis (adds), adductor profundus (addp), arrector dorsalis (arrd), adductor radialis (addr) (the muscle originating from the medial surfaces of the actinosts and lying laterally to the adductor profundus), and coracoradialis (corr).

SO3 + SV1 (Fig. 1) emerged to the lateral surface of the pectoral girdle, passing through a foramen in the scapula. After emergence, it gave off 3 major branches (α , β , and γ). The 1st (α) divided into a dorsal branch extending to the dorsalmost vestigial fin ray and a posterior branch coalescing with a posterodorsally-directed branch derived from the posterior branch (β 2), one of the two branches (β 1 and β 2) split immediately from β . The branch β 1 comprised 2 branches, one supplying the skin laterally to the abductor profundus (abdp), the other being confluent with a vertical branch of β 2 (and

more posteriorly with a branch of SOc + SV1—2); β 2 comprised 4 posterodorsally-directed branches (to the pectoral fin rays) and 2 ventrally-directed branches [one confluent with a branch of β 1 (see above) and the other innervating the skin laterally to the posteroventral portion of the abductor superficialis (abds)]. Branch γ comprised many sub-branches innervating the arrector ventralis (arrv), abductor superficialis (abds), and abductor profundus (abdp). The nerve branches associated with the pectoral fin base (branches of α , β 2, and SV2; see below) were transversely connected to one another along the base and radiated a nerve (sandwiched by the respective ray components) to each fin ray.

SOc + SV1 (Fig. 2A) fused with SV2, forming SOc + SV1—2 ventrally (see below).

SV2 (Fig. 1) coursed ventrally, initially giving off a branch posteroventrally (Fig. 2A) that included 5 sub-branches (all supplied the pectoral fin base), and thereafter quickly coalescing with SOc + SV1 to form SOc + SV1—2. This branch subsequently divided into anterior and posterior branches: the former (Fig. 2A) further subdivided into 2, innervating the infracarinalis anterior (infa; Fig. 2B) and skin ventral to that muscle, and the skin laterally to the pelvis (Fig. 1), respectively; the posterior branch (Fig. 2A) divided into dorsally and ventrally-oriented branches (Fig. 2A); the former extended to the pectoral fin base from the ventralmost ray, being confluent with branches (α and β) of SO3 + SV1 (Fig. 1), and the latter (Fig. 1) innervated the skin dorsolaterally to the pelvic girdle.

Pelvic fin (Figs. 1, 2).—The pelvic fin muscles, including the infracarinales

anterior (infa) and medius (infm), and skin were innervated by SO and SV1—7 (Figs. 1, 2B).

See above for anterior branch of SOc + SV1—2 (Figs. 1, 2B).

SV3 (Fig. 1) coursed ventrally along the medial surface of the hypaxialis (i.e., obliques superioris and inferioris) to reach the pelvic girdle. Ventrally, it gave off 5 branches: the 1st (1 in Fig. 1) extended posteriorly onto the anterolateral surface of the pelvic fin spine; the 2nd (2 in Fig. 1) innervated the arrector dorsalis pelvici (ardp); the 3rd (3 in Fig. 1) coalesced posteriorly with a branch of SV4; the 4th (4 in Fig. 1) innervated the adductores superficialis pelvici (adsp) and profundus pelvici (adpp; tendon only illustrated in Fig. 1); the 5th (5 in Figs. 1, 2B) extended to the midventral surface of the pelvic girdle (Fig. 2B), passing through the medial foramen of the consolidated pelvic girdle, and subdivided into anterior and posterolateral branches, these innervating the arrector ventralis pelvici (arvp; Fig. 2B) and the ventral surface of the pelvic fin spine (Fig. 2B), respectively.

SV4 (Fig. 1) comprised 4 branches ventrally, the 1st coalescing with the 3rd branch of SV3 (see above), the 2nd coursing along the dorsal surface of the pelvic fin spine, the 3rd innervating 2 pelvic fin rays (of 2 rays; see Fig. 2B), and the 4th extending posteriorly along the dorsal surface of the pelvic girdle.

SV5 (Fig. 1) was terminated ventrally at the posterior portion of the pelvic girdle. SV5, SV6, and SV7 comprised sub-branches, each innervating the infracarinalis medius (infm).

***Triacanthus biaculeatus* (Triacanthidae)** (Fig. 3). The pelvic fin muscles and

skin were innervated by SO and SV1—6 (Fig. 3; SV6 not illustrated). SOc + SV1—2 fused with SV3, and the latter with SV4. SOc + SV1-3 innervated the arrector dorsalis pelvici (ardp), adductor superficialis pelvici (adsp), and arrector ventralis pelvici. SV3 did not innervate the adductor profundus pelvici, that muscle being absent in this species.

Remarks.—Although SV3 in *Triacanthodes anomalus* innervated the arrector dorsalis pelvici (ardp), arrector ventralis pelvici (arvp), and adductor superficialis pelvici (adsp), SOc + SV1—3 also extended to those elements in *Triacanthus biaculeatus*. Despite the likelihood that only SV3 is functional for innervation in *Triacanthus biaculeatus*, as in *Triacanthodes anomalus*, the coalescence of SV3 with SOc + SV1—2 before reaching the above muscles in *Triacanthus biaculeatus* prevents conclusive determination, the latter therefore being considered as functional in this study.

***Sufflamen chrysopterum* (Balistidae)** (Fig. 4). A dorsal branch of SO3 + SV1 (homologous with the dorsal branch of α in *Triacanthodes anomalus*; Fig. 1) entered the pectoral fin base between the 1st (vestigial) and 2nd rays. The adductor radialis was absent.

The pelvic fin muscles and skin were innervated by SO and SV1—5. SV3—5 innervated the infracarinalis medius (infm), and SV4 the pelvic fin rudiment extending from the posterior tip of the pelvis (note: the pelvic fin rudiment was encircled by several elongated scales, the latter only being illustrated in Fig. 4). Other pelvic fin muscles were absent.

***Stephanolepis cirrhifer* (Monacanthidae)** (Fig. 5). SO2 coalesced with SOc along most of its length [SO (2 + c) + SV1; Fig. 5B]. A dorsal branch of SO3 + SV1 (homologous with the dorsal branch of α in *Triacanthodes anomalus*; Fig. 1) entered the pectoral fin base between the 1st (vestigial) and 2nd rays (Fig. 5A). The adductor radialis was absent.

The pelvic fin muscles and skin were innervated by SO and SV1—5 (Fig. 5A; SV5 not illustrated). SOc + SV1—2 (Fig. 5A; see also *Remarks* below) innervated the infracarinalis anterior (infa), SOc + SV1—3 (Fig. 5A) the arrector ventralis pelvici (arvp) and adductor superficialis pelvici (adsp), and SV3—5 (Fig. 5A) the infracarinalis medius (infm). The pelvic fin rudiment (Fig. 5A) was innervated by SV3 (note: the pelvic fin rudiment was encircled by several elongated scales, the latter only being illustrated in Fig. 5A). Other pelvic fin muscles were absent.

Remarks.—In the medial surface of the pectoral girdle (Fig. 5B), SO (2 + c) + SV1 gave off several branches (homologous with sub-branches of SO2 + SV1 in *Triacanthodes anomalus*; Fig. 2A) innervating the pectoral fin muscles. Accordingly, the most posterior branch was identified as SOc + SV1.

***Kentrocapros aculeatus* (Aracanidae)** (Fig. 6). Coursing ventrally, SO was confluent with a short branch of SV1 (differing from all other species described above in the separation of SO from the main branch of SV1); it thence gave off 3 branches (SO1 + SV1, SO2 + SV1, and SO3 + SV1); innervation by these 3 branches was essentially identical with that in *Triacanthodes anomalus*, except for the dorsal separation (into 2) and subsequent ventral fusion of SO2 + SV1 and absence of SOc.

SV1 provided several sub-branches medially to the pectoral fin base. A branch of SV1 + 2, formed by anastomosis between an SV2 and two SV1 branches immediately below the pectoral fin base, entered the pectoral fin base from the ventralmost ray. The adductor radialis was absent.

The pelvic fin and girdle, and associated muscles were all absent in this species.

***Ostracion immaculatus* (Ostraciidae)** (Fig. 7). The pectoral fin muscles and skin were innervated by SO and SV1. The innervation patterns were essentially identical to those in *Triacanthodes anomalus*, except for the following: SV1 separated from SO1 dorsally (as in *Kentrocapros aculeatus*; see above); SV1 gave off a short branch anteriorly, the fusion of the latter with SO occurring below SO1 detachment [SO1 passed anteroventrally along the lateral surface of the pharyngoclavicularis externus (vs. the medial surface of the muscle in *T. anomalus*)]; on the medial surface of the pectoral girdle, some SO branches innervated the anterior portion of the adductor superficialis dorsally to the separation into SO2 + SV1 and SO3 + SV1; SOc was absent; SV2 did not extend ventrally to the pectoral fin base. The adductor radialis was absent.

The pelvic fin and girdle, and associated muscles were all absent in this species.

***Triodon macropterus* (Triodontidae)** (Fig. 8). Coursing ventrally, SO gave off a short branch posteriorly that fused with SV1, and thence forked into SO1 and SO2 + 3. Ventrally, SO1 innervated 2 subdivisions of the sternohyoideus (sth) and skin laterally to the infracarinalis anterior (infa). SO2 + 3 (Fig. 8B) was immediately confluent with the anteriormost branch (of 3 branches) of SO + SV1, forming SO (2 + 3) + SV1, and

thence divided into SO2 + SV1 and SO3 + SV1. SO2 + SV1 combined with the middle branch of SO + SV1 posteriorly (Fig. 8B), en route quickly giving off 3 branches; 2 innervated the adductor superficialis (adds) dorsally, and the other the arrector dorsalis (arrd) and anterodorsal portion of the adductor superficialis (adds) ventrally. After fusion with the branch of SO + SV1, SO2 + SV1 distally innervated the adductor radialis (addr), adductor profundus (addp), and coracoradialis (corr). SV2 (Fig. 8B) divided into 3 branches at the medial surface of the pectoral girdle: the 1st (anteriormost) coalesced with the posteriormost branch of SO + SV1 (i.e., SOc + SV1); the 2nd (middle) comprised 3 branches, of which 2 were distributed on the skin between the pectoral and pelvic girdles (Fig. 8A), and the other, looping dorsally, extended to the ventralmost pectoral fin ray (Fig. 8A, B). The sternobranchialis and adductor radialis were absent.

The pelvic fin muscles and skin (Fig. 8A) were innervated by SO and SV1—7 (Fig. 8A; SV5—7 not illustrated). SOc + SV1—2 (Fig. 8A) combined with SV3 beneath the anteroventral margin of the coracoid; before fusion (Fig. 8B), it gave off short branches into the obliquus inferioris (obli). SOc + SV1—3 (Fig. 8A) and SV3—7 (Fig. 8A) innervated the infracarinales anterior (infa) and medius (infm), respectively. Other pelvic fin muscles were absent.

Remarks.—Although Winterbottom (1974) stated that the adductor radialis (addr; Fig. 8B) was absent in *Triodon macropterus*, it was present in our specimens. Insertion of the muscle was the 5 ventralmost rays of the pectoral fin.

***Takifugu poecilonotus* (Tetraodontidae)** (Fig. 9). The pectoral fin muscles and

skin were innervated by SO and SV1. SO comprised 6 branches: SO1—3, SOc?, SO α , and SO β (Fig. 9); SO1 extended anteroventrally passing laterally to the pharyngoclaviculares internus and externus, and innervated the sternohyoideus (sth); most of the terminal branches of SO2 innervated the muscles of the medial side of the pectoral girdle; SOc? detached from SO2 and was fused with SV1 posteriorly; SO3 innervation was basically identical to that in *Triacanthodes anomalus*, except in its entering the pectoral fin base between the 1st (vestigial) and 2nd rays (not illustrated); SO α coursed anteroventrally and innervated the obliquus inferioris (obli), infracarinalis anterior (infa), cutaneous muscles (cuta), and skin; SO β passed ventrally and innervated the obliquus inferioris (obli) together with a branch of SO (c? + β) + SV1. SV1, widely separated from SO, coursed ventrally and combined with SOc? at the ventral margin of the postcleithrum. Thereafter, SOc? + SV1 forked into 3 branches, the anteriormost going to the skin ventral to the fin, the middle branch innervating the obliquus inferioris (obli), and the posteriormost, comprising many sub-branches, entering between the fin ray bases. The sternobranchialis and adductor radialis were absent.

Although the pelvic fin and its girdle were absent, the infracarinales anterior (infa; Fig. 9) (innervated by SO) and medius (by SV2, 5, and 6; not illustrated) were present.

Remarks.—Although SOc (+ SV1) coalesced with SV2 in all of the other species described above (if SOc present), SOc? coalesced with SV1 in *Takifugu poecilonotus* (and *Canthigaster rivulata*; see blow). Despite of the positional similarity (i.e., at the medial surface of the pectoral fin) and its connection with SV, homology between SOc and SOc? is highly questionable.

***Canthigaster rivulata* (Tetraodontidae).** The pectoral fin muscles and skin were innervated by SO and SV1. The innervation pattern was basically identical to that in *Takifugu poecilonotus*, except that SOc? detached from SO dorsal to the subdivision of the latter into SO1—3 and SO1 passed medially to the pharyngoclavicularis internus.

Although the pelvic fin and its girdle were absent, the infracarinales anterior and medius were present, being innervated by SO and SV4—5, respectively.

***Diodon holocanthus* (Diodontidae)** (Fig. 10). The pectoral fin muscles and skin were innervated by SO and SV1. Coursing posteroventrally, SO was interconnected with SV1 by a short branch, and divided into 4 branches [SO1 + SV1, SO2 + SV1, SO3 + SV1, and SO ($\alpha + \beta$?) + SV1], the last-mentioned innervating the obliquus inferioris (obli), cutaneous muscles (cuta), and skin. SO and SV1 innervation was basically identical to that in *Triacanthodes anomalus*, except that SO1 coursed laterally to the pharyngoclavicularis externus. The sternobranchialis and adductor radials were absent.

Although the pelvic fin and its girdle were absent in this species, the infracarinalis medius was present (not illustrated), being innervated by SV4—7.

Remarks.—Because the anterior border of the infracarinalis medius was obscure, anterior innervation of that muscle (by SV4) was somewhat arbitrary.

***Mola mola* (Molidae).** The SO and SV were described and illustrated in detail by Nakae and Sasaki (2006). The pectoral fin muscles and skin were innervated by SO and SV1, which fused into one immediately after emergence from the cranium. The branch innervating the adductor superficialis was detached from the dorsal portion of

SO3 + SV1. Other conditions were basically identical to those in *Triacanthodes anomalus*. The adductor radials and coracoradialis were absent.

The pelvic fin, and its girdle and muscles were all absent.

***Lophiomus setigerus* (Lophiiformes: Lophiidae)** (Figs. 11, 12). The pectoral fin muscles and skin were innervated by SO and SV1—2 (Fig. 11A). Coursing ventrolaterally, SO gave off SO1 anteriorly to innervate the sternohyoideus (sth). Posteriorly, SO coalesced with SV1, thereafter forking into SO2 + SV1 and SO3 + SV1. SO2 + SV1 was ventrally confluent with a branch of SV2 to form SO2 + SV1—2, and innervated the skin covering the posterodorsal surface of the fin (not illustrated). En route (Fig. 11A), SO2 + SV1 gave off sub-branches innervating the coracoradialis (corr), muscle α ($m\alpha$; subdivision of the coracoradialis?; Fig. 11B), arrector dorsalis (arrd), adductor superficialis (adds), and adductor profundus (addp). SO3 + SV1 (Fig. 11A) innervated the skin covering the anterodorsal and anteroventral surfaces of the fin, muscle β ($m\beta$; subdivision of the abductor superficialis or abductor profundus?; Fig. 11B), arrector ventralis (arrv), abductor superficialis (abds), and abductor profundus (abdp); SO3 + SV1 (Fig. 11A) distally entered the base of the 1st fin ray, and passed posteriorly through the upper and lower halves of all rays whilst radiating a sub-branch between each pair of adjacent rays (last 3 sub-branches only illustrated in Fig. 11A). SV2 (Fig. 11A) forked widely into anterior and posterior branches: the anterior branch coalesced with SV3, SV2 + 3 innervating the pelvic fin (see below); the posterior branch subdivided further into a dorsalmost branch distributed on the skin surrounding the gill opening, an anteroventral branch entering the last fin ray and fusing with SO3 +

SV1 along the basal part of the fin, and a posteroventral branch which coalesced with SO2 + SV1. Lateral and medial association of the SO3 + SV1 and SV1 (or SO, SV2) sub-branches, respectively, with the pectoral fin rays was absent (vs. both conditions present in all tetraodontiforms examined). The sternobranchialis and adductor radialis were absent.

The pelvic fin muscles and skin were innervated by SV2—7 (Figs. 11A, 12; SV5—7 not illustrated). Coursing obliquely downward, SV2 + 3 (Figs. 11A, 12) divided into anterior and medial branches (Fig. 12). The former innervated the infracarinalis anterior (infa), en route giving off some branches (not illustrated) innervating the obliquus inferioris. The latter comprised 3 major branches (α , β , and γ in Fig. 12): the 1st (α) innervated the arrector ventralis pelvici (arvp), abductor superficialis pelvici (absp), and abductor profundus pelvici (abpp); the 2nd (β) comprised 3 branches (β 1—3), β 1 innervating the arrector dorsalis pelvici after coalescing with a branch of SV4 (not illustrated), β 2 the adductores superficialis pelvici and profundus pelvici after coalescing with another branch of SV4 (not illustrated), and β 3 the anterior portion of the infracarinalis medius (infm); the 3rd (γ) comprised 2 branches, one entering the basal parts of the pelvic fin rays from the 1st ray to be connected with a branch of SV4, and the other innervating the skin posterior to the pelvic girdle. SV4 (Fig. 12) gave off 3 branches: the 1st (posteriormost) directed anteriorly and forked into 2 branches, being fused with β 1 and β 2 of SV2 + 3, respectively (not illustrated); the 2nd (anteromedial) innervated the skin posterior to the girdle; the 3rd (anterolateral) entered the fin base from the innermost fin ray and

connected to a branch of SV3 (i.e., γ). Some branches of SV5—7 (not illustrated) innervated the middle and posterior portions of the infracarinalis medius (infm).

***Zeus faber* (Zeiformes: Zeidae)** (Fig. 13). The pectoral fin muscles and skin were innervated by SO and SV1—2 (Fig. 13A, B). SO joined SV1 before giving off SO1—3. SO2 + SV1 innervated a muscle ($m\gamma$, see *Remarks*; Fig. 13B) that developed ventromedial to the adductor superficialis (adds) and was inserted onto the posteroventral surface of the 4th actinost. A branch of SV2 (Fig. 13B) looped dorsally to enter the fin base from the ventralmost fin ray. SO3 + SV1 (Fig. 13A) emerged to the lateral surface of the pectoral girdle, passing between the cleithrum and scapula; subsequently, it forked into dorsal and ventral branches; the former entered the fin base from the uppermost fin ray to be connected with the branch of SV2 coming from the medial surface (see above); the latter comprised sub-branches innervating the abductor superficialis (abds), abductor profundus (abdp), and arrector ventralis (arrv). SO3 + SV1 and SV2 sub-branches associated laterally and medially with the pectoral fin rays, respectively, were absent. The sternobranchialis was absent.

The pelvic fin muscles and skin (Fig. 13A) were innervated by SV3—8 (SV8 not illustrated). Coursing ventrally, SV3 divided into 2 branches below the pectoral fin base; the anterior branch innervated the dorsal and ventral subdivisions of the infracarinalis anterior (infa); the other, comprising 2 finer branches, supplied the skin laterally to the pelvic girdle and coalesced with a branch of SV4, respectively. SV3 + 4 innervated the arrector ventralis pelvici (by α in Fig. 13A), adductor superficialis pelvici (adsp), and arrector dorsalis pelvici (ardp). SV4 + 5 ramified anterior and

ventral branches at the junction of SV4 and SV5; the anterior branch innervated the abductor superficialis pelvici (adsp) (by β ; Fig. 13A), abductor profundus pelvici (by β), and adductor profundus pelvici (adpp); the ventral branch divided into 2 finer branches and entered the pelvic fin spine and 1st fin ray, respectively. SV5 (Fig. 13A) comprised 3 branches ventrally, the most anterior branch coalescing with SV4 (see above), and the most posterior with SV6, en route giving off a branch innervating the extensor proprius (extp). The ventralmost branch comprised 2 sub-branches, entering the 2nd and 3rd pelvic fin rays, respectively. SV5 + 6 + 7 entered the pelvic fin base from the innermost ray; SV7 and SV8 innervated the infracarinalis medius (not illustrated).

Remarks.—Muscle *my* could be recognized as a subdivision of the adductor superficialis, based on its innervation (by SO2 + SV1) and position.

***Malakichthys wakiyae* (Perciformes: Acropomatidae)** (Fig. 14). The pectoral fin muscles and skin were innervated by SO and SV1—2 (Fig. 14A). SO and SV1 unified before giving off SO1—3. SO (1—3) + SV1 innervation was basically identical to that in *Triacanthodes anomalus*, except in the innervation of the anterior portion of the adductor superficialis (adds) by a sub-branch detached from SO3 + SV1 (Fig. 14A). Coursing ventrally, SV2 (Fig. 14A) divided into anterior and posterior branches. The anterior branch further divided into 3 branches: the 1st (anterior) comprised 2 major branches, innervating the pelvic fin (see below) and obliquus inferioris (obli), respectively; the 2nd (middle) emerged to the lateral surface of the coracoid via a foramen and united with a branch of SO3 + SV1; the 3rd (posterior)

comprised 2 branches, entering the pectoral fin base from the ventralmost ray and innervating the skin ventrally to the girdle, respectively. The posterior branch comprised many sub-branches that supplied the fin base medially. The sternobranchialis and coracoradialis were absent.

The pelvic fin muscles and skin (Fig. 14B) were innervated by SV2—9 (SV6—9 not illustrated). The branch of SV2 (described above) innervated the infracarinalis anterior (infa) ventrally. SV3 divided into 2 branches immediately above the pelvic girdle, the anterior branch innervating the arrector dorsalis pelvici (ardp), and the posterior, uniting with a branch of SV4, the adductor superficialis pelvici (adsp), adductor profundus pelvici (adpp), and extensor proprius (extp). SV4 forked into 4 major branches near the base of the pelvic fin spine: the 1st (outermost) subdivided into 2 branches, one coursing posteriorly along the dorsomedial surface of the pelvic spine and the other entering the 1st soft fin ray; the 2nd and 3rd (both middle) were confluent with a branch of SV3 and SV5, respectively; the 4th (innermost) extended to the ventral surface of the pelvic girdle, passing between the left and right halves of the girdle, and innervated the arrector ventralis pelvici, abductor superficialis pelvici, and abductor profundus pelvici. SV5 comprised 3 branches: the 1st (outermost) innervated the anterior part of the infracarinalis medius (infa); the 2nd (middle) was confluent with a branch of SV4; the 3rd (innermost) entered the fin base from the innermost ray. Some branches of SV6—9 (not illustrated) innervated the middle and posterior portions of the infracarinalis medius (infa).

***Antigonia capros* (Perciformes: Caproidae)** (Fig. 15). The pectoral fin muscles

and skin were innervated by SO and SV1—3 (Fig. 15A, B). SO emerged from the cranium as 2 parallel branches (Fig. 15A, B); the anterior branch, at mid-course, detached a short branch that fused with the posterior branch; more ventrally, the former supplied the skin on the hyoid region and innervated the sternohyoideus (sth) and sternobranchialis (stb); the posterior branch (Fig. 15B) combined with the anterior branch of SV1 and soon gave off anterior (SO3 + SV1) and posterior (SO2 + SV1) branches. The innervation pattern was basically identical to that in *Triacanthodes anomalus*. The posterior branch of SV1 (Fig. 15B) was confluent with the anterior branch of SV2 and innervated the skin covering the medial surface of the fin. The posterior branch of SV2 (Fig. 15B) comprised 3 major branches: the 1st (dorsalmost) extended to the pectoral fin base with several sub-branches; the 2nd, directed posteriorly, forked into 2 branches, both innervating the skin laterally to the pectoral girdle; the 3rd (ventralmost) innervated the pelvic fin (see below). SV3 (Fig. 15B) divided into dorsal and ventral branches at the medial surface of the postcleithrum: the former entered the pectoral fin base from the ventralmost ray, while the latter innervated the pelvic fin (see below).

The pelvic fin muscles and skin (Fig. 15A) were innervated by SV2—6. SV2 innervated the infracarinalis anterior (infa), partly joining with a branch of SV3. SV3 innervated the arrector dorsalis pelvici (ardp) and adductor profundus pelvici (adpp), the latter being innervated by SV3 after its fusion with a short, anterior branch of SV4. SV4 forked into 3 major branches slightly above the pelvic girdle: the 1st combined with a branch of SV3 (see above); the 2nd extended to the ventral surface of the pelvic

girdle, passing between the left and right halves of the girdle, and entered the pelvic fin base, en route giving off a branch innervating the arrector ventralis pelvici (arvp); the 3rd coursed posteriorly and forked into 2 sub-branches, one extending onto the dorsal surface of the pelvic spine and the other innervating the adductor superficialis pelvici (adsp), together with a branch of SV5. SV5 entered the pelvic fin base distally (from the inner 3 soft rays). SV6 innervated the infracarinalis medius (infm). The abductores superficialis pelvici and profundus pelvici were absent.

Remarks.—Although the adductor radialis was present in *A. capros*, its innervation could not be determined. It is most likely, however, that SO2 + SV1 innervates the muscle as in the other species examined in this study.

***Siganus spinus* (Perciformes; Siganidae)** (Fig. 16). The pectoral fin muscles and skin (Fig. 16A) were innervated by SO and SV1—2. SO was unified with the anterior branch of SV1 before giving off SO1—3. SO (1—3) + SV1 innervation was basically identical to that in *Triacanthodes anomalus*, except for the innervation of the anterior portion of the adductor superficialis (adds) by sub-branches derived from SO + SV1 dorsally to the subdivision of SO2 + SV1 and SO3 + SV1 (Fig. 16A). The posterior branch of SV1 joined with SV2; SV1 + 2 comprised 3 major branches: the dorsalmost, comprising several sub-branches, entered the pectoral fin base; the 2 ventral branches innervated the skin ventral to the girdle (after giving off a branch that extended into the fin base from the ventralmost ray) and the pelvic fin (see below), respectively.

The pelvic fin muscles and skin (Fig. 16B) were innervated by SV1—4. SV1 + 2 comprised 4 branches ventrally: the 1st (dorsalmost) coalesced with a branch of SV3,

forming SV1 + 2 + 3 ventrally; the 2nd coalesced with an anterior branch of SV1 + 2 + 3, forming a mixed branch; the mixed branch comprised external and internal sub-branches; the external sub-branch innervated the arrector dorsalis pelvici (ardp), adductor superficialis pelvici (adsp), and adductor profundus pelvici (adpp); the internal sub-branch innervated the arrector ventralis pelvici (arvp) and abductor superficialis pelvici (absp); the 3rd branch innervated the skin laterally to the pelvic girdle; the 4th branch innervated the infracarinalis anterior (infa). SV3 divided into anterior and posterior branches slightly above the pelvic girdle; the former subdivided into 2 branches after combining with SV 1 + 2 (see above), one coalescing with the 2nd branch of SV1 + 2 (see above) and the other coursing along the anterior surface of the outer pelvic fin spine (note: outer and inner pelvic fin spines present in this species); the latter coursed along the posterior surface of the outer pelvic fin spine. SV4 innervated the infracarinalis medius (infm), and the inner pelvic fin spine and soft rays. The abductor profundus pelvici was absent.

Discussion

The spino-occipital nerve and ventral rami of the anterior spinal nerves in Tetraodontiformes were herein reviewed for the first time (see Tables 1—3), providing new insights into tetraodontiform monophyly and the interrelationships within the group. Osteologically (Tyler, 1980; Santini and Tyler, 2003) and myologically (Winterbottom,

1974), the monophyly of the order has been well established, although molecular data did not necessarily support it (Holcroft, 2005). Two putative neuroanatomical synapomorphies of the order are newly presented here, in addition to 2 lateral line system characteristics previously suggested (i.e., absence of canal neuromasts and the mandibular line; Nakae and Sasaki, 2005, 2006), but because anatomy of the peripheral nervous system is still very poorly known in teleosts (see Parenti and Song, 1996), further evaluation is necessary, with more information needed on strategic taxa.

In all of the tetraodontiforms examined, SO3 + SV1 (SO3 in two tetraodontids; see Fig. 18F) extended several sub-branches laterally to the pectoral fin base (Table 2), in addition to a branch entering the base dorsally. On the other hand, in all of the outgroup taxa examined, such sub-branches were absent, despite the presence of SO3 + SV1. Furthermore, in the tetraodontiforms, SO was involved in the innervation of the infracarinale anterior (if present) (Table 3), SV2 being the anteriormost nerve innervating the pelvic fin muscles in advanced acanthomorphs according to Parenti and Song (1996; note, however, that their consideration of nerves was limited). SV1—3 innervated the pelvic fin muscles in the outgroup taxa examined here (Table 3). SO participation occurred owing to the connection of SV2 with SO + SV1 due to the presence of SOc, such a condition being primitively common in tetraodontiforms (Table 2), but absent in the outgroup taxa. Therefore, SO participation (i.e., presence of SOc) can be recognized as a synapomorphy of the order. The innervation of the pelvic fin muscles by SO alone in 2 tetraodontids (Table 3; see below) appears to be a derived condition within the group.

SO and SV1 combined with one another before entering the pectoral fin muscles in most of the species examined in this study, including the outgroup taxa (Table 2), although Parenti and Song (1996) neither mentioned nor illustrated (i.e., *Apogon maculatus*: fig. 3) such a condition in their review, based on 30 genera in 26 families. However, we confirmed in *Apogon carinatus* that SO, after giving off SO1, combined with SV1 before entering the pectoral fin muscles. Moreover, similar fusion also occurs in the atherinid *Menidia beryllina* (Herrick, 1899: pl. 15). If this condition is widespread in teleosts, as now suggested, Parenti and Song's simple definition of SO and SV1, presumably based on the assumption that they were separated, seems to be unsatisfactory. Although SV1 was defined as innervating a limited number of pectoral fin muscles, the fusion with SO resulted in the participation of SV1 in the innervation of almost all of the pectoral fin muscles (Table 1). Parenti and Song's definition of S2 (SV2 in this study) also appears to be questionable in its inclusion of the arrectores dorsalis and ventralis of the pectoral fin as target elements, none of the pectoral fin muscles being innervated by SV2 according to our observations (Table 1).

Six combination patterns between SO and SV1 were recognized in the tetraodontiforms and outgroup taxa examined (Fig. 17; Table 2). In 5 tetraodontiforms (*Triacanthodes anomalus*, *Triacanthus biaculeatus*, *Sufflamen chrysopteron*, *Stephanolepis cirrifer*, and *Mola mola*) and 3 outgroup taxa (*Zeus faber*, *Malakichthys wakiyae*, and *Siganus spinus*) (Fig. 17A), SO and SV1 were unified into a common branch and subsequently divided into SO1+SV1, SO2+SV1, and SO3+SV1, "pure" SV1 therefore being absent ventrally; in *Kentrocapros aculeatus* and *Diodon*

holocanthus (Fig. 17B), combination occurred owing to an SV1 sub-branch that was fused with SO1 (i.e., “pure” SV1 present ventrally); in *Ostracion immaculatus* (Fig. 17C), SO, after giving off SO1, was connected with a SV1 sub-branch (i.e., “pure” SO1 and SV1 present ventrally); in *Triodon macropterus* and *Lophiomus setigerus* (Fig. 17D), SO gave off a short sub-branch subsequently fused with SV1 (i.e., “pure” SO1 present ventrally); in *Takifugu poecilonotus* and *Canthigaster rivulata* (Fig. 17E), SO2 branched into two, the dorsal branch (SOc?) being fused with SV1 (i.e., “pure” SO1—3 present ventrally) and “SOc?” being either a mixed branch of SO and SV or entirely SV; in *Antigonia capros* (Fig. 17F), SV1 combined with the posterior SO branch (i.e., “pure” SO1 remained anteriorly). The presence of “pure” SO1 ventrally resulted in the non-participation of SV1 from innervation of the sternohyoideus in 6 species (and the sternobranchialis in 2 species) (Table 1). The various combination patterns of SO and SV1, plus the overall dominance of SV1 participation, suggested that SO and SV1 collectively innervate the pectoral fin muscles, there being no unique definition possible solely for SV1.

As discussed above, SO3 + SV1 was present in all species examined (except in 2 tetraodontids), being consistent in having a raised branch (α in Fig. 1) that entered the pectoral fin base dorsally (a branch of SO3 in 2 tetraodontids; Fig. 18F). The pectoral fin base also received a branch ventrally in all species, although the identity of the branch varied in the participation or non-participation of SV2 (Table 2), the former being classified into 4 types (Fig. 18A—D) and the latter into 3 types (Fig. 18E—H). In *Triacanthodes anomalus* and *Triacanthus biaculeatus* (Fig. 18A), the branch was

SOc + SV1—2, owing to the confluence of SOc + SV1 and SV2 before entering the pectoral fin base; in *Sufflamen chrysopterum*, *Stephanolepis cirrhifer*, *Triodon macropterus*, and 3 outgroup taxa (*Lophiomus setigerus*, *Zeus faber*, and *Malakichthys wakiyae*) (Fig. 18B), SV2 only constituted the branch; in *Kentrocapros aculeatus* (Fig. 18C), two SV1 and one SV2 branches were crossed, the branch extension to the pectoral fin base (presumably SV1 + 2, but see below) arising off from the anterior crossing; in *Siganus spinus* (Fig. 18D), the branch was SV1 + 2. Conversely, in *Ostracion immaculatus* and *Diodon holocanthus* (Fig. 18E), SV1 simply entered the fin base; in *Takifugu poecilonotus*, *Canthigaster rivulata* (Fig. 18F), and *Mola mola* (Fig. 18G), SO + SV1 constituted the branch, but the dorsal branch was SO3 in the former 2 species (Fig. 18F); in *Antigonia capros* (Fig. 18H), SV 3 only was included.

In all tetraodontiforms and 3 outgroup taxa (*Malakichthys wakiyae*, *Antigonia capros*, and *Siganus spinus*), the pectoral fin base received several sub-branches medially (see Fig. 2; Table 2). Generally, in those species in which the pectoral fin base ventrally received a branch including SV2 (see above; Table 2), the sub-branches were SV2, whereas in the species in which the fin base received SV1 (or SO + SV1), the sub-branches were SV1 (or SO + SV1). However, *Kentrocapros aculeatus* and *Antigonia capros* were exceptional in having SV1 (instead of SV2) and SV2 sub-branches (the fin base receiving SV3), respectively. The fact suggests that nerve supply to the fin base in *K. aculeatus* is actually only by SV1 branch despite of SV1 + 2 appearance. SV2 branch might be just “crossing” with SV1 without giving fibers to the fin base. The *Antigonia capros* condition appears to be neomorphic.

In summary, tetraodontiforms can be divided into 2 groups, based on the nerve branches extending ventrally into the pectoral fin base: the SV1 (6 species, including *K. aculeatus*) and SV2 (5 species) groups. Because the SV2 group occurs primitively in perciforms (i.e., *Malakichthys wakiyae*) and tetraodontiforms (i.e., *Triacanthodes anomalus*), the SV1 group appears to be advanced, therefore being informative for phylogenetic considerations. The SV1 group (Aracanidae + Ostraciidae + Tetraodontidae + Diodontidae + Molidae) is generally consistent with Rosen's (1984) hypothesis and one of two equally parsimonious trees of extant tetraodontiform species (Santini and Tyler, 2003: fig. 3A) in its forming of a monophyletic group, although the exclusion of Triodontidae (i.e., SV2 group) in the nerve character is inconsistent.

Two species of tetraodontids, *Takifugu poecilonotus* (Fig. 9) and *Canthigaster rivulata*, were unique in the absolute non-participation of SV1 from pectoral fin muscle innervation (Table 1; but note reservations regarding the nature of SOc?; see above) owing to the absence of fusion between SO and SV1 dorsally (Fig. 17E). The two branches were widely separated and parallel in their downward extension, thereby giving a sharp contrast to the close approximation or fusion of downward extensions in other species, although the structural and functional background for the former condition remains unclear.

In all outgroup taxa examined, SO1 passed medially to the pharyngoclaviculares internus and externus (Table 2), and an SO3 + SV1 branch entered the pectoral fin base from the dorsalmost ray (Table 2). However, in tetraodontiforms, three SO1 and two SO3 + SV1 conditions were recognized. Because the conditions in the outgroup taxa

were common to those in primitive tetraodontiforms (i.e., *Triacanthodes anomalus*), “SO1 passing medially to the pharyngoclavicularis internus and laterally to the pharyngoclavicularis externus” (in *Ostracion immaculatus*, *Canthigaster rivulata*, and *Diodon holocanthus*), “SO1 passing laterally to the pharyngoclavicularis internus and externus” (in *Takifugu poecilonotus*), and “SO3 (+ SV1) extending into the pectoral fin base from the second dorsalmost ray” (in *Sufflamen chrysopterum*, *Stephanolepis cirrifer*, *Takifugu poecilonotus*, *Canthigaster rivulata*, and *Diodon holocanthus*) could all be recognized as derived conditions, being informative for phylogenetic considerations.

Five outgroup taxa were examined as possible candidates for the tetraodontiform sister group. However, no strong indicators for such a relationship could be found in the spino-occipital nerve and ventral rami of the anterior spinal nerves. In having the infracarinalis anterior innervated by SV1 and SV2, tetraodontiforms primitively resembled *Siganus spinus* (Table 3), owing to the SV1—2 connection. However, it was not certain if the branch linking SO + SV1 and SV2 (i.e., SOc + SV1) in the former and that between SV1 and SV2 in the latter (Fig. 16A) were homologous. Various connection patterns between SO and SV1 within a single order, as shown in Fig. 17, suggest that nerve characters in general should be evaluated very carefully when considering higher level phylogenies.

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Table 1. Pectoral fin muscle innervation in 11 tetraodontiforms (*upper*) and 5 outgroup taxa (*lower*) by spino-occipital nerve (SO) and ventral rami of spinal nerves (SV)

Species	sth	stb	adds	addp	arrd	addr	corr	arrv	abds	abdp
<i>Triacanthodes anomalus</i>	SO1+SV1	SO1+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Triacanthus biaculeatus</i>	SO1+SV1	SO1+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Sufflamen chrysopteron</i>	SO1+SV1	SO1+SV1	SO2+SV1	SO2+SV1	SO2+SV1	-	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Stephanolepis cirrhiifer</i>	SO1+SV1	SO1+SV1	SO2+SV1	SO2+SV1	SO2+SV1	-	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Kentrocapros aculeatus</i>	SO1+SV1	SO1+SV1	SO2+SV1	SO2+SV1	SO2+SV1	-	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Ostracion immaculatus</i>	SO1	SO1	SO2+3+SV1	SO2+SV1	SO2+SV1	-	-	SO3+SV1	SO3+SV1	SO3+SV1
<i>Triodon macropterus</i>	SO1	-	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Takifugu poecilonotus</i>	SO1	-	SO2	SO2	SO2	-	SO2	SO3	SO3	SO3
<i>Canthigaster rivulata</i>	SO1	-	SO2	SO2	SO2	-	SO2	SO3	SO3	SO3
<i>Diodon holocanthus</i>	SO1+SV1	-	SO2+SV1	SO2+SV1	SO2+SV1	-	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Mola mola</i>	SO1+SV1	SO1+SV1	SO2+3+SV1	SO2+SV1	SO2+SV1	-	-	SO3+SV1	SO3+SV1	SO3+SV1
<i>Lophiomus setigerus</i>	SO1	-	SO2+SV1	SO2+SV1	SO2+SV1	-	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Zeus faber</i>	SO1+SV1	-	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Malakichthys wakiyae</i>	SO1+SV1	-	SO2+3+SV1	SO2+SV1	SO2+SV1	SO2+SV1	-	SO3+SV1	SO3+SV1	SO3+SV1
<i>Antigonia capros</i>	SO1	SO1	SO2+3+SV1	SO2+3+SV1	SO2+3+SV1	(SO2+SV1)?	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1
<i>Siganus spinus</i>	SO1+SV1	-	SO2+3+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO2+SV1	SO3+SV1	SO3+SV1	SO3+SV1

-, absent

See figure legends for abbreviations

Table 2. Conditions of spino-occipital nerve (SO) and ventral rami of spinal nerves (SV) in 11 tetraodontiforms (*upper*) and 5 outgroup taxa (*lower*)

Species	SO-SV1 association	SO-SV2 connection	SO1 passage	SOc	SV1 pectoral fin muscle innervation	SO3 (+ SV1) branch entering pectoral fin base
<i>Triacanthodes anomalus</i>	unified	+	medial to phci and phce	+	all muscles	from dorsalmost ray
<i>Triacanthus biaculeatus</i>	unified	+	medial to phci and phce	+	all muscles	from dorsalmost ray
<i>Sufflamen chrysopteron</i>	unified	+	medial to phci and phce	+	all muscles	from 2nd ray
<i>Stephanolepis cirrhifer</i>	unified	+	medial to phci and phce	+	all muscles	from 2nd ray
<i>Kentrocapros aculeatus</i>	branch connection	-	medial to phci and phce	-	all muscles	from dorsalmost ray
<i>Ostracion immaculatus</i>	branch connection	-	medial to phci, lateral to phce	-	except sth and stb	from dorsalmost ray
<i>Triodon macropterus</i>	branch connection	+	medial to phci and phce	+	except sth	from dorsalmost ray
<i>Takifugu poecilonotus</i>	branch connection	-	lateral to phci and phce	+?	no muscles	from 2nd ray
<i>Canthigaster rivulata</i>	branch connection	-	medial to phci, lateral to phce	+?	no muscles	from 2nd ray
<i>Diodon holocanthus</i>	branch connection	-	medial to phci, lateral to phce	-	all muscles	from 2nd ray
<i>Mola mola</i>	unified	+	medial to phci and phce	+	all muscles	from dorsalmost ray
<i>Lophiomus setigerus</i>	branch connection	-	medial to phci and phce	-	except sth	from dorsalmost ray
<i>Zeus faber</i>	unified	-	medial to phci and phce	-	all muscles	from dorsalmost ray
<i>Malakichthys wakiyae</i>	unified	-	medial to phci and phce	-	all muscles	from dorsalmost ray
<i>Antigonia capros</i>	branch connection	-	medial to phci and phce	-	except sth and stb	from dorsalmost ray
<i>Siganus spinus</i>	unified	-	medial to phci and phce	-	all muscles	from dorsalmost ray

+, present; -, absent

See figure legends for abbreviations

Table 2. Continued

Species	Lateral SO3 (+ SV1) sub-branches extending to pectoral fin base	Medial sub-branches extending to pectoral fin base	Nerve elements entering pectoral fin base ventrally	Nerve elements constituting medial sub-branches
<i>Triacanthodes anomalus</i>	+	+	SO,SV1,2	SV2
<i>Triacanthus biaculeatus</i>	+	+	SO,SV1,2	SV2
<i>Sufflamen chrysopterum</i>	+	+	SV2	SV2
<i>Stephanolepis cirrhifer</i>	+	+	SV2	SV2
<i>Kentrocapros aculeatus</i>	+	+	SV1,2	SV1
<i>Ostracion immaculatus</i>	+	+	SV1	SV1
<i>Triodon macropterus</i>	+	+	SV2	SV2
<i>Takifugu poecilonotus</i>	+	+	SO,SV1	SO,SV1
<i>Canthigaster rivulata</i>	+	+	SO,SV1 ¹⁾	SO,SV1
<i>Diodon holocanthus</i>	+	+	SV1 ¹⁾	SV1
<i>Mola mola</i>	+	+	SO,SV1	SO,SV1
<i>Lophiomus setigerus</i>	-	-	SV2	-
<i>Zeus faber</i>	-	-	SV2	-
<i>Malakichthys wakiyae</i>	-	+	SV2	SV2
<i>Antigonia capros</i>	-	+	SV3	SV2
<i>Siganus spinus</i>	-	+	SV1,2	SV1,2

1) ventral 2nd ray; +, present; -, absent

See figure legends for abbreviations

Table 3. Pelvic fin (P2) muscle innervation in 11 tetraodontiforms (*upper*) and 5 outgroup taxa (*lower*) by spino-occipital nerve (SO) and ventral rami of spinal nerves (SV) (the latter indicated only by number)

Species	P2 girdle	P2 spine	P2 rays	infa	infm	ardp	arvp	adsp	adpp	absp	abpp	extp
<i>Triacanthodes anomalus</i>	+	3,4	4	SO,1,2	5--7	3	3	3	3	-	-	-
<i>Triacanthus biaculeatus</i>	+	3,4	-	SO,1,2	5,6	SO,1--3	SO,1--3	SO,1--3	-	-	-	-
<i>Sufflamen chrysopterygum</i>	+	-	4	SO,1,2	3--5	-	3	3	-	-	-	-
<i>Stephanolepis cirrhifer</i>	+	-	SO,1--3	SO,1,2	3--5	-	SO,1--3	SO,1--3	-	-	-	-
<i>Kentrocapros aculeatus</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ostracion immaculatus</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Triodon macropterus</i>	+	-	-	SO,1--3	3--7	-	-	-	-	-	-	-
<i>Takifugu poecilonotus</i>	-	-	-	SO	3,5,6	-	-	-	-	-	-	-
<i>Canthigaster rivulata</i>	-	-	-	SO	4,5	-	-	-	-	-	-	-
<i>Diodon holocanthus</i>	-	-	-	-	4--8	-	-	-	-	-	-	-
<i>Mola mola</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lophiomus setigerus</i>	+	-	2--4	2,3	4--7	2--4	2,3	3,4	3,4	2,3	2,3	-
<i>Zeus faber</i>	+	4,5	4--7	3	7,8	3,4	3,4	3,4	4,5	4,5	4,5	5
<i>Malakichthys wakiyae</i>	+	4(5?)	4,5	2	5-9	3	4	3,4	3,4	4	4	3,4
<i>Antigonia capros</i>	+	4(5?)	4,5	2,3	6	3	4	4,5	3,4	-	-	-
<i>Siganus spinus</i>	+	1--3*	4	1,2	4	1--3	1--3	1--3	1--3	1--3	-	-

+, present; -, absent; *, outer pelvic fin spine

See figure legends for abbreviations

Fig. 1. Spino-occipital nerve and ventral rami of anterior spinal nerves in *Triacanthodes anomalus*. 1—5, branches of spinal nerve from the 3rd vertebra; X, vagal nerve; α , β and γ , branches of ramus 2 of spino-occipital nerve (SO2) + spinal nerve from the 1st vertebra (SV1); *abdp*, abductor profundus; *abds*, abductor superficialis; *adpp*, adductor profundus pelvici; *addr*, adductor radialis; *adsp*, adductor superficialis pelvici; *ardp*, arrector dorsalis pelvici; *arrv*, arrector ventralis; *arvp*, arrector ventralis pelvici; *corr*, coracoradialis; *infa*, infracarinalis anterior; *infm*, infracarinalis medius; *phce*, pharyngoclavicularis externus; *phci*, pharyngoclavicularis internus; *SO*, spino-occipital nerve; *SOc*, spino-occipital connecting branch; *sth*, sternobranchialis; *sth*, sternohyoideus; *SV*, ventrally rami of spinal nerves. *Terminal arrows* indicate continuing extensions (not shown). *Bar* 5 mm

Fig. 2. Pectoral (A) and pelvic (B) girdles in *Triacanthodes anomalus*. A Medial view; B ventral view. *addp*, adductor profundus; *adds*, adductor superficialis; *arrd*, arrector dorsalis. Other abbreviations and *terminal arrows* as in Fig. 1. *Bars* 5 mm

Fig. 3. Dorsal view of the pelvic girdle in *Triacanthus biaculeatus*. Abbreviations and *terminal arrows* as in Fig. 1. *Bar* 5 mm

Fig. 4. Lateral view of the pectoral and pelvic girdles in *Sufflamen chrysopteron*. Sub-branches innervating the pectoral fin rays not illustrated. Abbreviations as in Fig. 1. *Bar* 5 mm

Fig. 5. Pectoral and pelvic girdles in *Stephanolepis cirrifer*. A Lateral view of the pectoral and pelvic girdles; B medial view of the pectoral girdle. Abbreviations and *terminal arrows* as in Figs. 1, 2. *Bars* 5 mm

Fig. 6. Medial view of the pectoral girdle in *Kentrocapros aculeatus*. Abbreviations and *terminal arrows* as in Figs. 1, 2. *Bar* 5 mm

Fig. 7. Lateral view of the pectoral girdle in *Ostracion immaculatus*. Sub-branches innervating the pectoral fin rays not illustrated. Abbreviations and *terminal arrows* as in Fig. 1. *Bar* 5 mm

Fig. 8. Pectoral and pelvic girdles in *Triodon macropterus*. **A** Lateral view of the pectoral and pelvic girdles; **B** medial view of the pectoral girdle. *obli*, obliquus inferioris. Other abbreviations and *terminal arrows* as in Figs. 1, 2. *Bars* 5 mm

Fig. 9. Medial view of the pectoral girdle in *Takifugu poecilonotus*. *cuta*, cutaneous muscles; *obli*, obliquus inferioris. Other abbreviations and *terminal arrows* as in Figs. 1, 2. *Bar* 5 mm

Fig. 10. Medial view of the pectoral girdle in *Diodon holocanthus*. *cuta*, cutaneous muscles; *obli*, obliquus inferioris. Other abbreviations and *terminal arrows* as in Figs. 1, 2. *Bar* 5 mm

Fig. 11. Ventromedial (**A**) and dorsomedial (**B**) views of the pectoral girdle in *Lophiomus setigerus*. Sub-branches innervating the pectoral fin rays illustrated only for the last 3 rays. *mα* and *mβ*, muscle subdivisions of questionable identity (see text). Other abbreviations and *terminal arrows* as in Figs. 1, 2. *Bars* 5 mm

Fig. 12. Ventral view of the pectoral girdle and occipital region in *Lophiomus setigerus*. Sub-branches innervating the pelvic fin rays not illustrated. *α*, *β*, and *γ*, sub-branches of SV2 + 3; *abpp*, abductor profundus pelvici; *absp*, abductor superficialis pelvici. Other abbreviations and *terminal arrows* as in Fig. 1. *Bar* 5

mm

Fig. 13. Pectoral and pelvic girdles in *Zeus faber*. **A** Lateral view of the pectoral and pelvic girdles; **B** medial view of the pectoral girdle. α and β , branches of SV3 + 4 and SV4 + 5, respectively; *extp*, extensor proprius; *my*, muscle subdivision of questionable identity (see text). Other abbreviations and *terminal arrows* as in Figs. 1, 2. Bars 5 mm

Fig. 14. Pectoral (**A**) and pelvic (**B**) girdles in *Malakichthys wakiyae*. **A** Medial view; **B** dorsal view. *extp*, extensor proprius; *obli*, obliquus inferioris. Other abbreviations and *terminal arrows* as in Figs. 1, 2. Bars 5 mm

Fig. 15. Pectoral and pelvic girdles in *Antigonia capros*. **A** Lateral view of the pectoral and pelvic girdles; **B** medial view of the pectoral girdle. Abbreviations and *terminal arrows* as in Figs. 1, 2. Bars 5 mm

Fig. 16. Pectoral (**A**) and pelvic (**B**) girdles in *Siganus spinus*. **A** Medial view; **B** lateral view. *absp*, abductor superficialis pelvici. Other abbreviations and *terminal arrows* as in Figs. 1, 2. Bars 5 mm

Fig. 17. Connection patterns between spino-occipital nerve and ventral ramus of spinal nerve from the 1st vertebra in 11 tetraodontiforms and 5 outgroup taxa. **A** *Triacanthodes anomalus*, *Triacanthus biaculeatus*, *Sufflamen chrysopterum*, *Stephanolepis cirrifer*, *Mola mola*, *Zeus faber*, *Malakichthys wakiyae* and *Siganus spinus*; **B** *Kentrocapros aculeatus* and *Diodon holocanthus*; **C** *Ostracion immaculatus*; **D** *Triodon macropterus* and *Lophiomus setigerus*; **E** *Takifugu poecilonotus* and *Canthigaster rivulata*; **F** *Antigonia capros*. Abbreviations as in Fig. 1. Arrows

indicate nerve fiber direction

Fig. 18. Nerve element pattern entering pectoral fin base dorsally and ventrally in 11 tetraodontiforms and 5 outgroup taxa. **A** *Triacanthodes anomalus* and *Triacanthus biaculeatus*; **B** *Sufflamen chrysopterum*, *Stephanolepis cirrhifer*, *Triodon macropterus*, *Lophiomus setigerus*, *Zeus faber* and *Malakichthys wakiyae*; **C** *Kentrocapros aculeatus*; **D** *Siganus spinus*; **E** *Ostracion immaculatus* and *Diodon holocanthus*; **F** *Takifugu poecilonotus* and *Canthigaster rivulata*; **G** *Mola mola*; **H** *Antigonia capros*.

Abbreviations as in Fig. 1

Fig. 1

Fig. 2

Fig. 3

Fig. 6

Fig. 7

Fig. 8

Fig. 9

Fig. 10

Fig. 11

Fig. 12

Fig. 13

Fig. 14

A

B

Fig. 16

Fig. 17

Fig. 18

フグ目魚類における後頭神経と脊髄神経腹側枝—特に胸鰭と腹鰭に関与する筋肉の神経支配について—

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本論文 00 (0):00-00

フグ目魚類 10 科 11 種と外群 5 科 5 種の後頭神経と脊髄神経腹側枝を観察し、胸鰭と腹鰭に関わる筋肉要素の神経支配を明らかにした。フグ目は外群と比較し、後頭神経第 3 枝と第 1 脊髄神経腹側枝の複合枝が胸鰭基底に数本の分枝を伸ばす点および後頭神経が *infracarinalis anterior* の支配に関与する点で特徴的であった。外群を含む多くの種では後頭神経と第 1 脊髄神経腹側枝が合流（6 パターン）し、この合流によって胸鰭に関わるほぼすべての筋肉要素は後者の支配を受けていた。フグ科 2 種を除く 9 種では、後頭神経第 3 枝と第 1 脊髄神経腹側枝が合流し、合流後に発する神経小枝が胸鰭基底に上方から進入していた。胸鰭基底は下方からも神経小枝の進入を受ける。その枝に第 2 脊髄神経腹側枝が含まれる種と含まれない種があった。後者の状態が派生的と考えられ、イトマキフグ科、ハコフグ科、フグ科、ハリセンボン科、およびマンボウ科の状態がこれに該当した。後頭神経と脊髄神経腹側枝では、フグ目魚類の姉妹群を特定する強力な形質は発見されなかった。

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