

Review of the Teleostean Adductor Mandibulae and Its Significance to the Systematic Positions of the Polymixiiformes, Lampridiformes, and Triacanthoidei

Kao-yi Wu* and Shih-chieh Shen

Department of Zoology, National Taiwan University, Taipei, Taiwan 106, R.O.C.

(Accepted August 2, 2004)

Kao-yi Wu and Shih-chieh Shen (2004) Review of the teleostean adductor mandibulae and its significance to the systematic positions of the Polymixiiformes, Lampridiformes, and Triacanthoidei. *Zoological Studies* 43(4): 712-736. Divisions of the adductor mandibulae among a wide spectrum of teleostei were surveyed. Feeding habits do not generally dominate the number or nature of divisions of the adductor mandibulae. This muscle is innervated by the ramus mandibularis V, which is a reliable character for identifying divisions, which were redefined on this basis. Section A2 β of the adductor mandibulae inserts into the Meckelian fossa, and connects with section Aw. The ramus mandibularis V always lies lateral to section A2 β , and enters the Meckelian fossa together with it. Sections named A1 β vary among teleosteans and are not always homologous. In the Clupeomorpha, Cyprinidae, Mugilomorpha, Atherinomorpha, and Percomorpha, the adductor mandibulae shows consistent and stable subdivisions. Divisions of the adductor mandibulae also support the Mugilomorpha and Atherinomorpha being sister groups. An A1+A2 α division is found in the Percomorpha, Lampridiformes, and Polymixiiformes. Another particular configuration of A1 and A2 α is found in the Triacanthoidei and Percoidei. The synapomorphic characters in the past literature for supporting Acanthomorpha and Percomorpha were revised, and these show large amounts of homoplasy.
<http://www.sinica.edu.tw/zool/zoolstud/43.4/712.pdf>

Key words: Teleostei, Adductor Mandibulae, Systematics, Percomorpha, Triacanthoidei.

The adductor mandibulae is the largest superficial muscle of the cheek in teleosteans, and is responsible for closing the jaws. It originates primarily from the hyoid arch (hyomandibular, symplectic) or palatal arch (metapterygoid, mesopterygoid, ectopterygoid, and preopercle), and inserts on the maxilla, angular, or on the angular and dentary.

This muscle is usually divided into sections A1, A2, A3, and Aw. Section A1 is defined by its dorsal position and its insertion on the maxilla, and apparently develops from dorsal encroachment of fibres of A2 along the ligamentum primordium (maxilla-mandibular ligament, passing from the posterolateral region of the angular to the posterodorsal part of the maxilla) (Winterbottom 1974a). Winterbottom (1974a) also described a medially situated division, the A1 β division: "The muscle originates from the metapterygoid and hyomandibular medial to the levator arcus

palatine". In addition to the dorsally situated section A1 and the more-medial section A1 β , a more-superficial section A1 originates from the ethmoid and prefrontal in the Monacanthidae (e.g., section A1 α in Winterbottom 1974b), from the symplectic, quadrate, and articular in *Cyprinus* (e.g., section A1 in Takahasi 1925, the external part of the external division in Gosline 1989, and section A0 in Diogo and Chardon 2000), and from the lateral ethmoid and infraorbital ligament in the Acanthuridae (e.g., section A1 in Borden 1998). This superficial section A1 is not developed along the ligamentum primordium, but directly inserts on the maxilla. Because the sites of origin of section A1 are not consistent within the Teleostei, there are doubts concerning the homology of these A1 divisions.

Section A2, occupying the ventrolateral region of the cheek, originates from the hyomandibular, quadrate, symplectic, mesopterygoid,

or preopercle (Winterbottom 1974a). Many insertion sites of section A2 have been found: (1) it may have a tendinous insertion on the posterior face of the coronoid process of the dentary; (2) it may share a myocomma anteriorly with the posterior fibres of Aw; (3) it may insert directly into the Meckelian fossa; or (4) it may insert in some combination of the above (Winterbottom 1974a). Winterbottom (1974a b) used sections A2 α and A2 β to respectively represent the dorsolateral and ventromedial subdivisions of A2.

Section A3 is the most-medial section, which lies on the lateral face of the palatal arch medial to section A2. It originates from the lateral face of the quadrate, symplectic, metapterygoid, and sometimes the hyomandibular, and inserts on the medial face of the dentary or into the Meckelian fossa (Winterbottom 1974a).

Section Aw fills the Meckelian fossa on the medial face of the dentary (Winterbottom 1974a).

The number and nature of the divisions exhibit noticeable variety: (1) the number may be anything from 2 sections (neopterygians, sections A2 and Aw) to 10 sections distinguishable in certain monacanthins (Winterbottom 1974a) and (2) the section which inserts on the maxilla has a normal site of origin that includes the hyomandibular, preopercle, quadrate, symplectic (Winterbottom 1974a), articular (e.g., *Cyprinus*; Takahasi 1925), infraorbitals (Borden 1998), palatal arch (e.g., Paracanthopterygii; Rosen and Patterson 1969), prefrontal, ethmoid, and parasphenoid (e.g., some Tetraodontiformes; Winterbottom 1974a b).

Winterbottom (1974a) expressly stated that subdivisions of the adductor mandibulae which had been identified were not, in many cases, homologous, and therefore homology was not to be inferred from the name of the section. However, some ambiguities occur in the definitions of Winterbottom on the divisions of the adductor mandibulae. Sections A2, A2 α , and A2 β all may insert on the dentary, while sections A2, A2 α , A2 β , and A3 all may insert into the Meckelian fossa of the dentary. Complications arise in practice when a division with an insertion site related to the mandible is being identified. If there are 2 divisions, one inserting on the dentary and the other into the Meckelian fossa of the dentary, these 2 sections identified by the combination of relative position and inserting site may be A2 and A3, or A2 α and A2 β , or A2 β and A3, respectively (e.g., figs. 1 and 8 in Gill and Mooi 1993). Diogo and Chardon (2000) also discussed misinterpretations of divisions in the ostariophysins followed by most

authors. The A0 of their work is usually called A1, and A1-OST, A2, A3, and A3' are often respectively called A2, A3, A3" and A3" -P.

The adductor mandibulae is innervated by the ramus mandibularis V (RMV), a motor branch of the 5th cranial nerve (trigeminal nerve) (Kent 1983). Gill and Mooi (1993) used the RMV to demonstrate that sections A1 β of the Grammatidae and Opistognathidae are not homologous. It is contentious as to whether the path of the RMV is a reliable indicator of subdivisions of the adductor mandibulae. Edgeworth (1935) pointed out that the path of the RMV is quite variable, and is therefore an unreliable character. However, in our opinion, the different paths of the RMV might be caused by (1) comparisons of the RMV with different (= non-homologous) subdivisions, which are superficial A1 and A1 β or (2) confusion and indistinctness of the divisions related to the mandible, e.g., sections A2, A2 α , A2 β , and A3 as described above. Gosline (1989) believed that the variability in the course of the RMV is due to non-homology between divisions of ostariophysin fishes and acanthopterygians. It seems reasonable to suggest that the RMV is a reliable character for identifying the division of the adductor mandibulae, especially divisions related to the mandible. But unfortunately, most of the literature, even the most recent, fails to describe the RMV (Devaere et al. 2001, Van Tassel 2001).

Gosline (1989) considered that the basic adductor mandibulae pattern in higher teleosts had been adequately treated (Gosline 1986). This basic pattern is present in the Beryciformes, Zeiformes, Perciformes, Scopaeniformes, Tetraodontiformes, and among lower teleosts, in the genus *Aulopus*. Gosline (1989) described this basic pattern as follows: "It has upper cheek section (A1) with a maxillary attachment, and a lower section (A2,3) that passes into Aw on the inside of mandible", and "The N. ramus mandibularis extends anteroventrally between the two cheek sections and thence to the mandible". Gosline believed that sections of the adductor mandibulae in ostariophysin fishes were not homologous to those of the acanthopterygians described above. Because both sections in *Salminus* (a characin) have mandibular attachments, he called the lower external section the "external division" and the upper internal section the "internal division", and the main branch of the ramus mandibularis V "passed to the inside of mandible between external and internal divisions of the cheek muscle" (p. 652, Gosline 1989). Gosline (1989) also showed

that the small-mouthed characins of *Curimata*, *Hemiodus*, *Bivibranchia*, and *Leporinus* have an adductor mandibulae attachment to the upper jaw.

We attempted to examine whether feeding habits influence divisions of the adductor mandibulae. To do this, it is necessary to examine species with different feeding habits among the same higher taxon.

The adductor mandibulae in ostariophysin fishes displays a wide range of differentiation, and has received considerable attention by numerous authors (Gosline 1989, Adrianes and Verraes 1997, Cabuy et al. 1999, Diogo and Chardon 2000, Devaere et al. 2001). Diogo and Chardon (2000) examined the adductor mandibulae of numerous catfishes in detail, and compared their results with those of several other teleosts described in the literature. They interpreted the internal division of Gosline (1989) as section A2 and the median section lying medial to the internal division as section A3 (homologous to A3 of the acanthopterygians). They also proposed new terms for the divisions in ostariophysin fishes: A1-OST for the external division of Gosline (1989) (or the internal part of the external division, if the external division subdivided into internal and external parts), and A0 for the external part of the external division of Gosline (1989). The insertion site of A1-OST is angulo-articular or coronomeckelian, and the insertion site of A0 is on the maxilla.

Winterbottom (1974b) described this muscle in the order Tetraodontiformes in detail. The adductor mandibulae of triacanthoids greatly differs from those of monacanthids and other tetraodontiforms. In the triacanthoids, section A2 α inserts on section A1 instead of the dentary, and section A1 originates from section A2 α instead of the hyomandibular. Further research is needed to reveal the particular pattern of the adductor mandibulae found in triacanthoids.

The purposes of this research were to survey divisions of the adductor mandibulae among a wide spectrum of Teleostei, to clarify the misleading nomenclature of these divisions, and to discuss significant systematic applications of the diversity of these divisions.

MATERIALS AND METHODS

Anatomical descriptions were made after dissection of alcohol-preserved specimens. Specimens examined for this study were dissected on the right side of cheek under a Wild M5 stereomi-

croscope equipped with a camera lucida. Three species of cyprinids, *Carassius auratus*, *Varicorhinus tamusuiensis*, and *Zacco platypus*, which respectively feed by sucking, scraping, and predation were chosen to explore whether feeding habits influence the number and nature of the division of the adductor mandibulae. All specimens are deposited in the Museum of the Department of Zoology, National Taiwan University (NTUM).

Materials examined

Albulidae, *Albula vulpes*, NTUM06653, 1, 250 mm SL.

Antennariidae, *Antennarius striatus*, NTUM-08631, 1, 72 mm SL.

Apogonidae, *Apogon aureus*, NTUM08677, 1, 95 mm SL.

Aulopodidae, *Hime* sp., NTUM08652, 1, 180 mm SL.

Bagridae, *Pseudobagrus taiwanensis*, NTUM05270, 1, 108 mm SL.

Bembridae, *Bembras japonicus*, NTUM07968, 1, 136 mm SL.

Blenniidae, *Istiblennius lineatus*, NTUM-08565, 1.

Carangidae: *Alectis ciliaris*, NTUM08674, 1, 98 mm SL; *Seriolina nigrofasciata*, NTUM08679, 1, 102 mm SL.

Chaetodontidae: *Chaetodon vagabundus*, NTUM08664, 1, 68 mm SL; *Chaetodon xanthurus*, NTUM08647, 1, 87 mm SL.

Chlorophthalmidae, *Chlorophthalmus acutifrons nigromarginatus*, uncatalogued, 1, 150 mm SL.

Citharinidae, *Citharinus citharus*, uncatalogued, 1, 86 mm SL.

Clupeidae: *Amblygaster sirm*, NTUM06970, 1, 140 mm SL; *Ilisha melastoma*, NTUM08689, 1, 81 mm SL; *Nematalosa japonica*, NTUM08651, 1, 130 mm SL.

Cyprinidae: *Carassius auratus*, NTUM00440, 1, 97 mm SL; *Varicorhinus tamusuiensis*, NTUM04994, 1, 110 mm SL; *Zacco platypus*, NTUM04942, 1, 90 mm SL.

Ehippiidae: *Platax teira*, NTUM08649, 1, 92 mm SL.

Exocoetidae: *Cypselurus cyanopterus*, NTUM06161, 1, 270 mm SL; *Parexocoetus mento mento*, NTUM07745, 1, 133 mm SL.

Fundulidae, *Fundulus diaphanus*, NTUM-04167, 1, 53 mm SL.

Gadidae, *Lota lota*, NTUM04182, 1, 80 mm SL.

- Gasterosteidae, *Culaea inconstans*, NTUM-04159, 1, 31 mm SL.
- Gerreidae, *Gerres filamentosus*, NTUM-08667, 1, 133 mm SL.
- Glaucosomatidae, *Glaucosoma hebraicum*, NTUM08609, 1, 144 mm SL.
- Gobiidae: *Cryptocentrus filifer*, NTUM08659, 1, 75 mm SL; *Rhinogobius giurinus*, NTUM07098, 1, 50 mm SL.
- Haemulidae, *Plectorhinchus pictus*, NTUM-08672, 1, 88 mm SL.
- Hemiodontidae, *Potamorhina latior*, NTUM-02057, 1, 77 mm SL.
- Holocentridae, *Sargocentron ittodai*, NTUM-03695, 1.
- Kuhliidae, *Kuhlia mugil*, NTUM08678, 1, 115 mm SL.
- Kyphosidae: *Kyphosus cinerascens*, NTUM-08668, 1, 91 mm SL; *Microcanthus strigatus*, NTUM08663, 1, 65 mm SL.
- Labridae, *Anampses caeruleopunctatus*, NTUM03881, 1.
- Lutjanidae, *Lutjanus kasmira*, NTUM08673, 1, 115 mm SL.
- Moridae, *Physiculus japonicus*, NTUM08656, 1, 150 mm SL.
- Mugilidae: *Chelon macrolepis*, NTUM08655, 1, 70 mm SL; *Crenimugil crenilabis*, NTUM06949, 1, 112 mm SL.
- Mullidae, *Parupeneus ciliatus*, NTUM03163, 1, 92 mm SL.
- Muraenidae, *Echidna nebulosa*, uncatalogued, 1, 350 mm TL.
- Myctophidae, *Diaphus diadematus*, NTUM-04294, 1, 126 mm SL.
- Nemipteridae, *Scolopsis bilineatus*, NTUM-08671, 1, 112 mm SL.
- Neoscopelidae, *Neoscopelus microchir*, NTUM 07595, 1, 128 mm SL.
- Ophidiidae, *Neobythites sivicola*, NTUM-06102, 1, 158 mm SL.
- Osmeridae, *Plecoglossus altivelis*, NTUM-01667, 1, 103 mm SL.
- Pempheridae, *Pempheris oualensis*, NTUM-08661, 1, 117 mm SL.
- Pinguipedidae, *Parapercis sexfasciata*, NTUM-01646, 1.
- Platycephalidae, *Onigocia spinosa*, NTUM-08201, 1, 83 mm SL.
- Polymixiidae, *Polymixia japonica*, NTUM-07593, 1, 95 mm SL.
- Pomacanthidae, *Genicanthus semifasciatus*, NTUM08636, 1, 75 mm SL.
- Pomacentridae, *Stegastes altus*, NTUM-08666, 1, 75 mm SL.
- Priacanthidae, *Priacanthus cruentatus*, NTUM08676, 1, 97 mm SL.
- Pseudochromidae, *Labracinus melanotaenia*, NTUM08683, 1, 115 mm SL.
- Salmonidae, *Oncorhynchus masou*, NTUM-00204, 1, 170 mm SL.
- Scaridae, *Scarus* sp., NTUM08660, 1, 115 mm SL.
- Scatophagidae, *Scatophagus argus*, NTUM-08662, 1, 92 mm SL.
- Sciaenidae, *Johnius belengerii*, NTUM08669, 1, 115 mm SL.
- Scombridae: *Scomber japonicus*, NTUM-06850, 1; *Scomberomorus commerson*, uncatalogued, 1, 114 mm SL.
- Scorpaenidae: *Minous pictus*, NTUM08405, 1, 82 mm SL; *Sebastiscus marmoratus*, NTUM-08657, 1, 119 mm SL.
- Serranidae: *Anthias squamipinnis*, NTUM-07488, 1, 70 mm SL; *Chelidoperca pleurospilus*, NTUM08686, 1, 142 mm SL; *Epinephelus coioides*, NTUM08684, 1, 102 mm SL; *Grammistes sexlineatus*, NTUM08685, 1, 130 mm SL.
- Sillaginidae, *Sillago sihama*, NTUM08675, 1, 160 mm SL.
- Siluridae, *Parasilurus asotus*, NTUM05275, 1, 125 mm SL.
- Sparidae, *Dentex tumifrons*, NTUM08670, 1, 104 mm SL.
- Stomiidae, *Astronesthes lucifer*, uncatalogued, 1, 75 mm SL.
- Synodontidae: *Trachinocephalus myops*, NTUM07636, 1, 165 mm SL; *Saurida undosquamis*, NTUM06511, 1, 115 mm SL.
- Teraponidae: *Pelates quadrilineatus*, NTUM-08682, 1, 114 mm SL; *Terapon jarbua*, NTUM-08680, 1, 100 mm SL; *Terapon theraps*, NTUM-08681, 1, 160 mm SL.
- Trachichthyidae, *Paratrachichthys prosthemi*, uncatalogued, 1.
- Trichiuridae, *Trichiurus lepturus lepturus*, NTUM00688, 1, 280 mm SL.
- Triglidae, *Lepidotrigla alata*, NTUM01563, 1, 96 mm SL.
- Veliferidae, *Velifer hypselopterus*, NTUM-08654, 1, 107 mm SL.
- Zeidae, *Zenopsis nebulosa*, NTUM08687, 1, 70 mm SL.

RESULTS

After surveying divisions of the adductor mandibulae among a wide spectrum of the Teleostei (sampling was confined to elopoccephalans; osteoglossomorphs were not included), a universal division existing in all specimens was found. This division contains the following characteristics: (1) insertion into the Meckelian fossa; (2) connection with section Aw in the Meckelian fossa; and (3) the ramus mandibularis V lying lateral to and entering the Meckelian fossa together with this division. In all divisions described by Winterbottom (1974a b), only his section A2 β has the characteristics described above; therefore, the universal division and section A2 β are identical. This universal section A2 β is an important division for distinguishing other divisions related to the mandible. A stricter definition of section A2 β is proposed for displacing the loose definition by the relative position (e.g., the ventromedial subdivision of section A2).

Redefinitions of divisions of the adductor mandibulae

Divisions of the adductor mandibulae found among the Teleostei in this study are listed below.

Section A1 – This dorsal subdivision originates from the hyomandibular, and inserts on the lateral or medial face of the maxilla. Because “this division is apparently developed from the dorsal encroachment of the fibres of the section A2 α along the ligamentum primordium” (Winterbottom 1974a), it occurs alone, fuses with section A2 α , or is slightly separated from section A2 α . The RMV passes medial to this section (Fig. 1).

Section A1 α – This dorsal and the most-superficial subdivision inserts on the maxilla. It originates from the ethmoid, prefrontal, hyomandibular, and infraorbital ligament. This division is not developed along the ligamentum primordium, but inserts directly on the maxilla. The RMV passes medial to this division.

Section A1 β – This deeply medial subdivision lies on the palatal arch, and inserts on the maxilla. It originates from the hyomandibular or palatal arch, always lies medial to section A2 β , and may be lateral or medial to the LAP (lavator arcus palatini) posteriorly (Fig. 2).

Ventrolateral section A1 (A1-VL) – A ventral and the most-superficial subdivision insert on the maxilla. It originates from the hyomandibular, symplectic, quadrate, or articular. This section does

not coalesce with the ligamentum primordium, but inserts directly on the maxilla. The RMV passes medial to this section (Fig. 3A).

Section A2 α – This dorsolateral subdivision originates from the hyomandibular, and inserts either on the coronoid process of the dentary, on the ligamentum primordium, or on the hind margin of the angular, but seldom inserts directly into the Meckelian fossa. It never connects with section Aw when it does insert into the Meckelian fossa, and always lies dorsolateral to section A2 β . The RMV must pass medial to A2 α (Figs. 1, 3A, B).

A1+A2 α division – As described previously, section A1 is sometimes continuous with A2 α . This division can never be completely separated into sections A1 and A2 α , but it may be slightly separated at the lateral face by a groove in the muscle mass which serves as a boundary between the 2 sections. It originates from the hyomandibular, and inserts on the ligamentum primordium, the coronoid process of the dentary, and the maxilla. In general, the muscle fibres in the dorsolateral portion (e.g., section A1) of this division consolidate as a tendon which extends along the ligamentum primordium and inserts on the maxilla (or the fibres insert on the ligamentum primordium along the maxilla), while muscle fibres in the medial and ventrolateral portions (e.g., section A2 α) insert on the coronoid process of the dentary or the ligamentum primordium at the region of the dentary. This division always lies dorsolateral to section A2 β , and the RMV passes medial to it (Figs. 1, 10).

Section A2 β – This subdivision originates from the hyomandibular, or sometimes from the palatal arch, and inserts into the Meckelian fossa by a tendon, to which section Aw connects, or directly inserts into the Meckelian fossa and shares a myocomma anteriorly with the posterior fibres of section Aw. The RMV is lateral to this section, and enters the Meckelian fossa with it. This subdivision always lies ventromedial to A2 α . It is a constant subdivision and exists universally in all taxa we examined (Figs. 1-3).

Section A2 – This subdivision originates from the skull, hyomandibular, or palatal arch. The main mass of fibres of this section inserts into the Meckelian fossa by a tendon, or directly inserts into the Meckelian fossa and shares a myocomma anteriorly with the posterior fibres of section Aw (as in section A2 β). The most-superficial or dorsal fibres of this section insert on the posterior margin of the angular or on the coronoid process of the dentary (as in section A2 α). These 2 parts of the

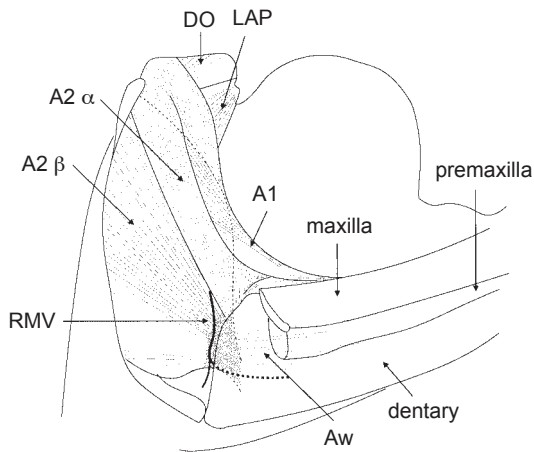


Fig. 1. Right lateral view of the cheek musculature of *Polymixia japonica* (NTUM07593, 95 mm SL), after removal of the head of the maxilla and premaxilla.

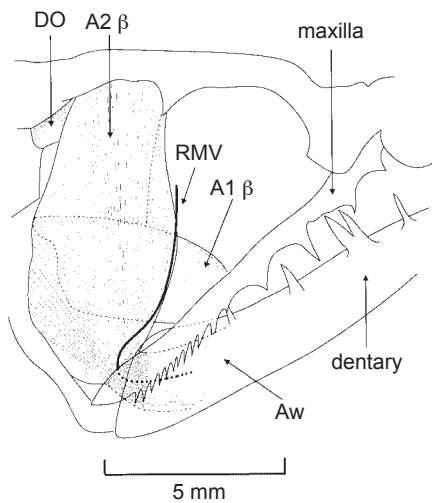


Fig. 2. Right lateral view of the cheek musculature of *Astronesthes lucifer* (uncatalogued, 75 mm SL).

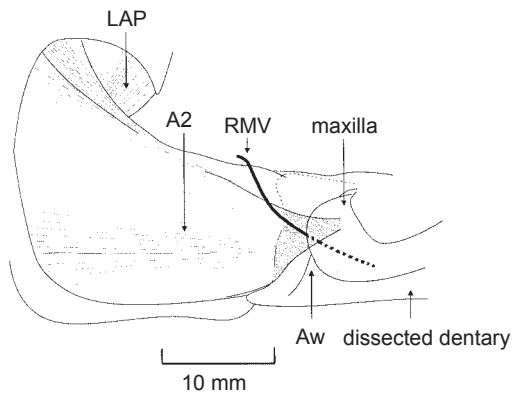
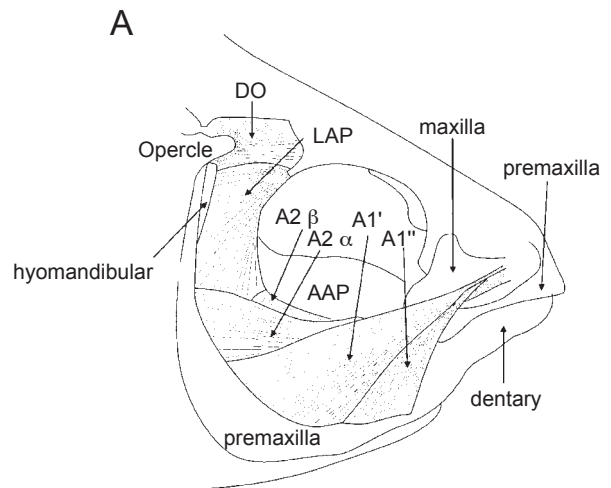
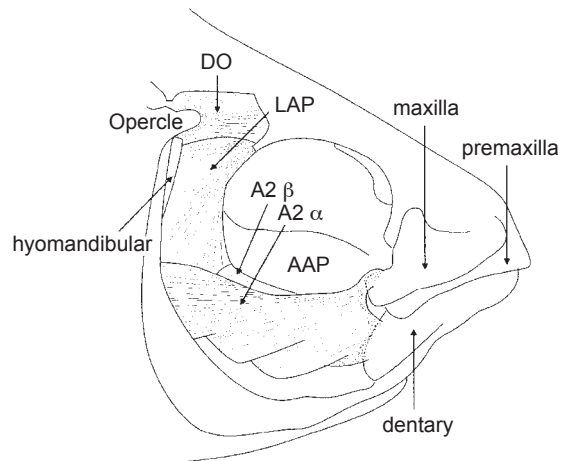


Fig. 4. Right lateral view of the cheek musculature of *Albulula vulpes* (NTUM06653, 250 mm SL).



B



C

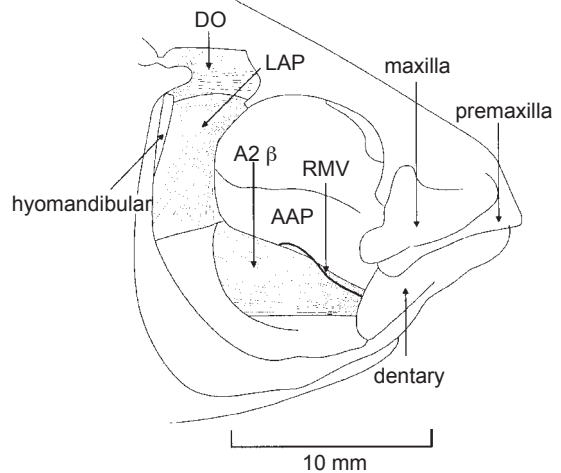


Fig. 3. Right lateral view of the cheek musculature of *Carassius auratus* (NTUM00440, 97 mm SL). A: Superficial view. B: Medial view, after removal of A1. C: Medial view, after removal of A1 and A2 α .

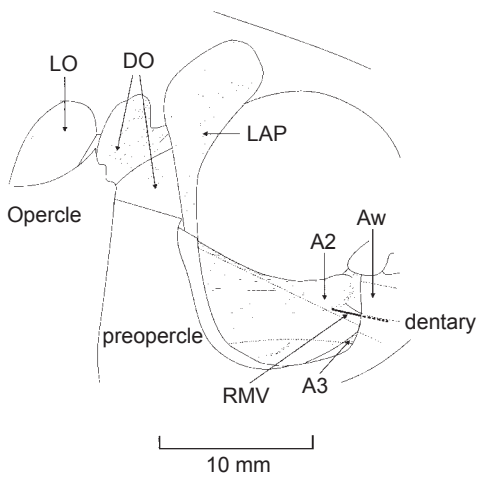


Fig. 5. Right lateral view of the cheek musculature of *Nematalosa japonica* (NTUM08651, 130 mm SL).

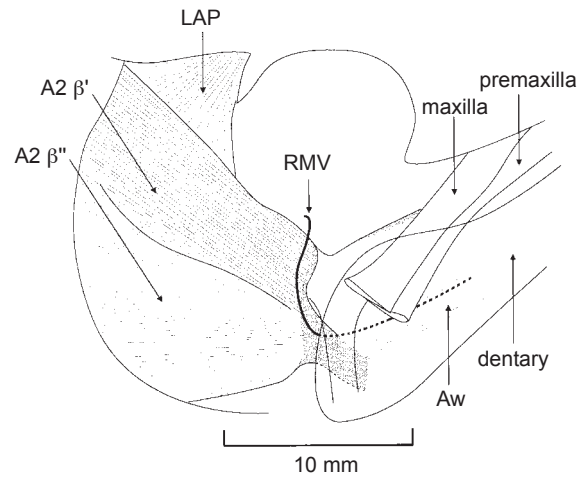


Fig. 8. Right lateral view of the cheek musculature of *Neoscopelus microchir* (NTUM07595, 128 mm SL), after removal of the head of the maxilla and premaxilla.

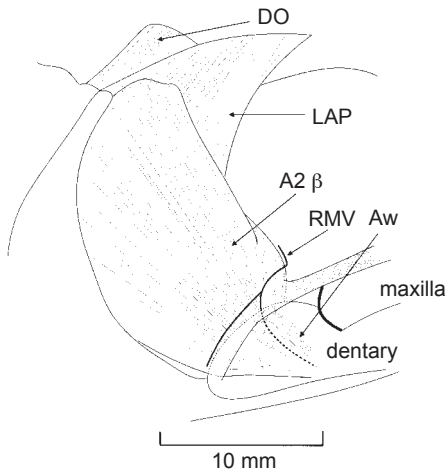


Fig. 6. Right lateral view of the cheek musculature of *Oncorhynchus masou* (NTUM00204, 170 mm SL).

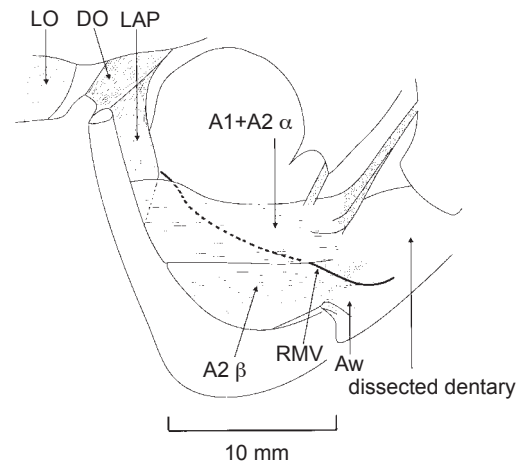


Fig. 9. Right lateral view of the cheek musculature of *Velifer hypselopterus* (NTUM08654, 1, 107 mm SL).

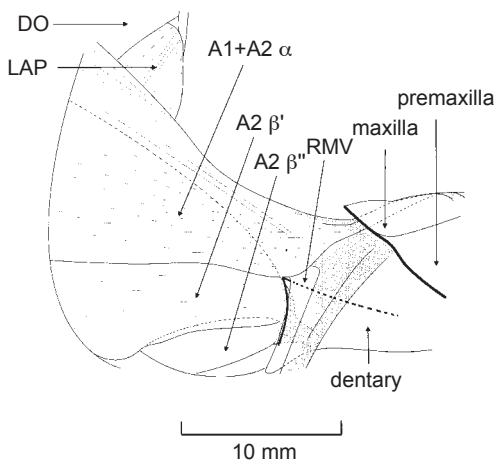


Fig. 7. Right lateral view of the cheek musculature of *Hime* sp. (NTUM08652, 180 mm SL), after removal of the head of the maxilla.

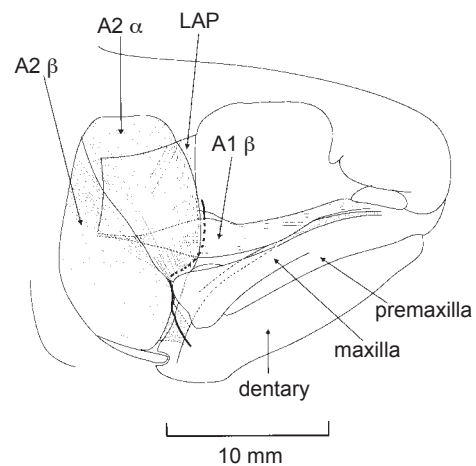


Fig. 10. Right lateral view of the cheek musculature of *Neobythites sivicola* (NTUM06102, 158 mm SL).

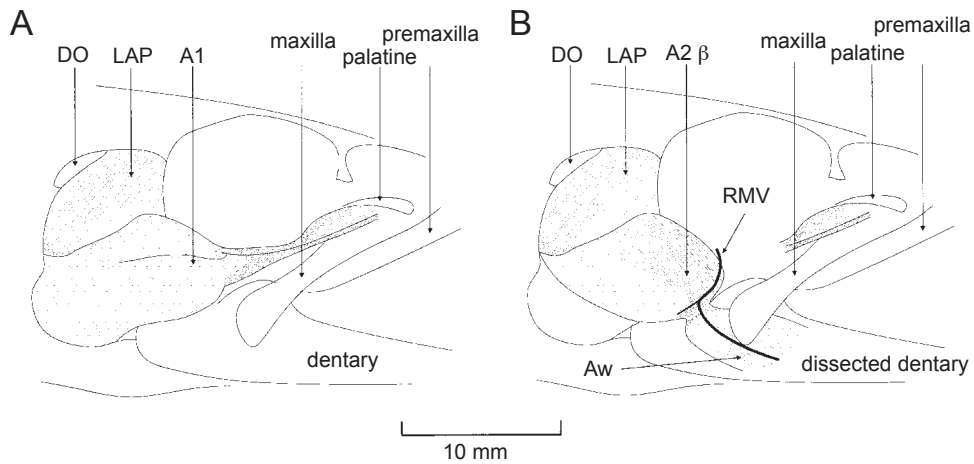


Fig. 11. Right lateral view of the cheek musculature of *Physiculus japonicus* (NTUM08656, 150 mm SL). A: Superficial view. B: Medial view, after removal of A1.

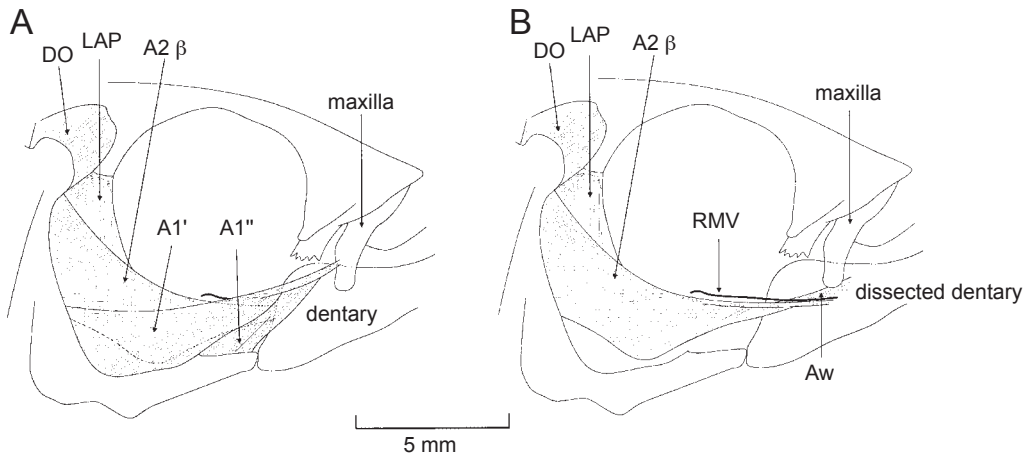


Fig. 12. Right lateral view of the cheek musculature of *Chelon macrolepis* (NTUM08655, 70 mm SL). A: Superficial view. B: Medial view, after removal of A1.

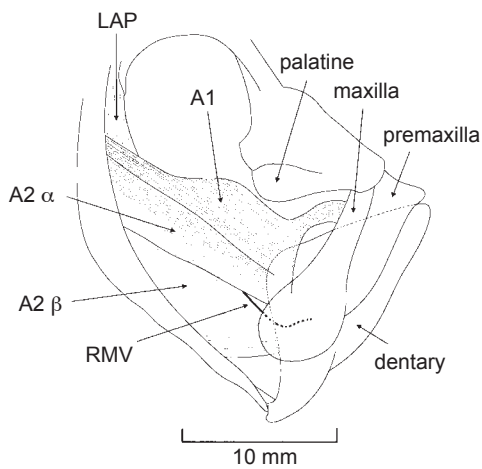


Fig. 13. Right lateral view of the cheek musculature of *Zenopsis nebulosa* (NTUM08687, 70 mm SL).

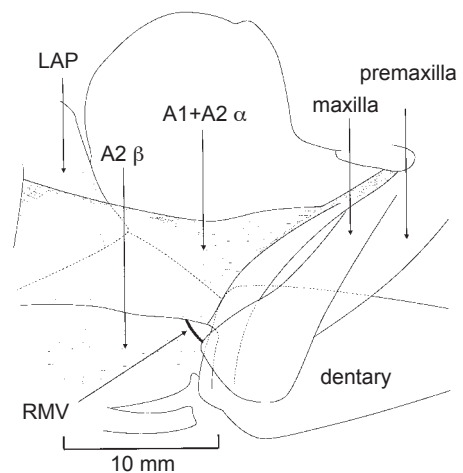


Fig. 14. Right lateral view of the cheek musculature of *Sebastiscus marmoratus* (NTUM08657, 119 mm SL).

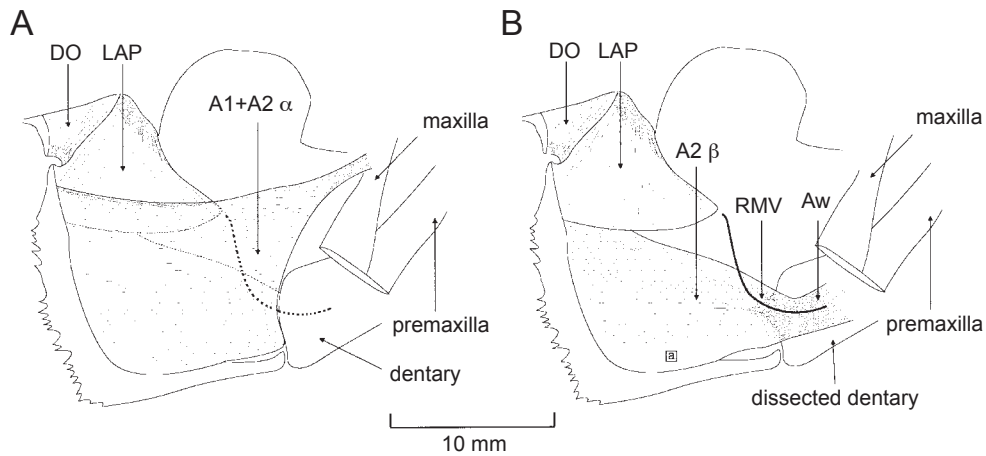


Fig. 15. Right lateral view of the cheek musculature of *Epinephelus coioides* (NTUM08684, 1, 102 mm SL). A: Superficial view, after removal of the head of the maxilla and premaxilla. B: Medial view, after removal of A1+A2 α . The letter [a] indicates the region that fuses with A2 α .

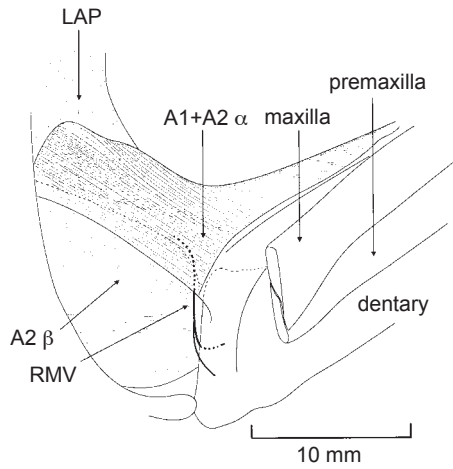


Fig. 16. Right lateral view of the cheek musculature of *Glaucosoma hebraicum* (NTUM08609, 144 mm SL), after removal of the head of the maxilla and premaxilla. The dashed area indicates the thin tendinous sheath.

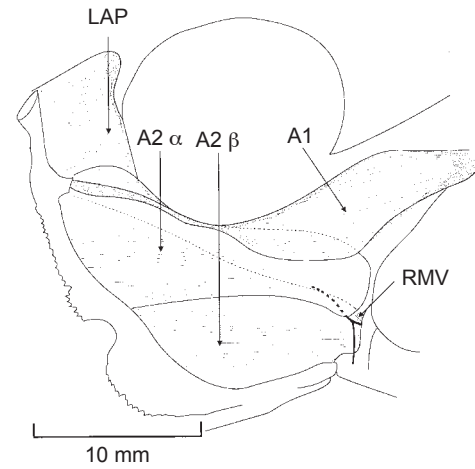


Fig. 18. Right lateral view of the cheek musculature of *Lutjanus kasmira* (NTUM08673, 115 mm SL).

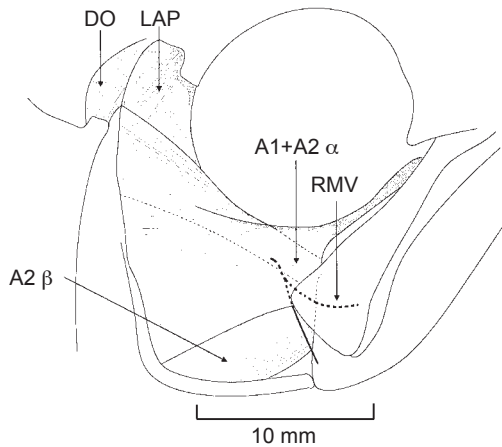


Fig. 17. Right lateral view of the cheek musculature of *Apogon aureus* (NTUM08677, 95 mm SL).

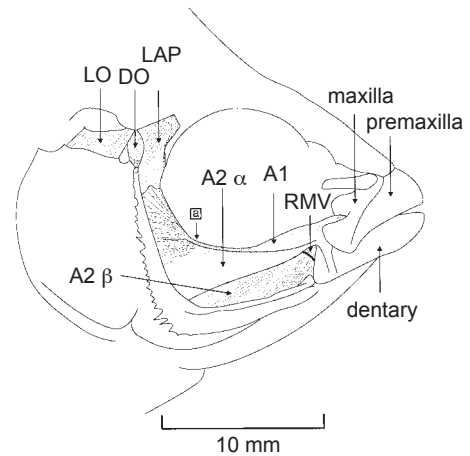


Fig. 19. Right lateral view of the cheek musculature of *Microcanthus strigatus* (NTUM08663, 65 mm SL). The letter [a] indicates the strong tendinous sheath.

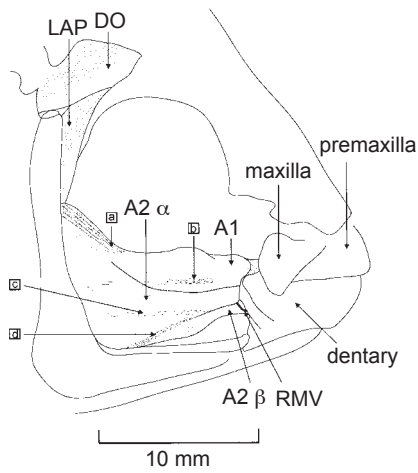


Fig. 20. Right lateral view of the cheek musculature of *Scatophagus argus* (NTUM08662, 92 mm SL). The letter [a] indicates the strong tendinous sheath; the letter [b] indicates a ligament on the medial face of A1 for insertion of A2 α ; the letter [c] indicates a ligament on the medial face of A2 α for insertion of A2 β ; and the letter [d] indicates the tendinous sheath of A2 α .

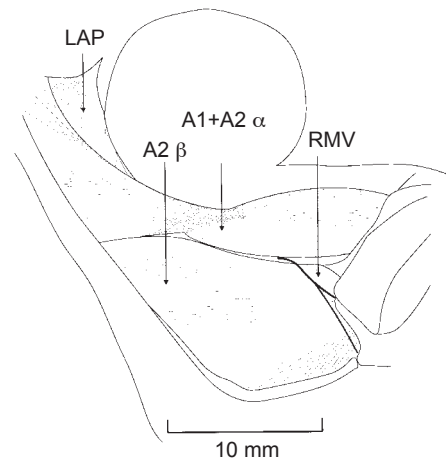


Fig. 22. Right lateral view of the cheek musculature of *Dentex tumifrons* (NTUM08670, 104 mm SL).

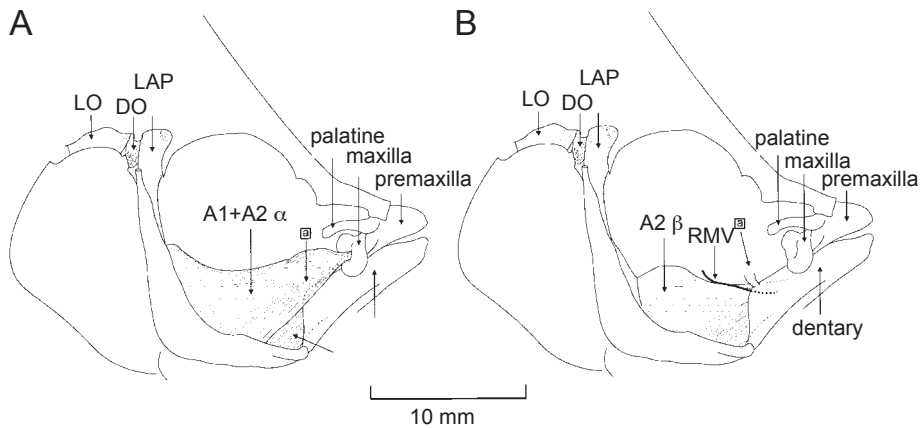


Fig. 21. Right lateral view of the cheek musculature of *Chaetodon vagabundus* (NTUM08664, 68 mm SL). A: Superficial view. B: Medial view, after removal of A1+A2 α . The letter [a] indicates the connecting site for the tendon between the medial face of A1+A2 α and the coronoid process of the dentary.

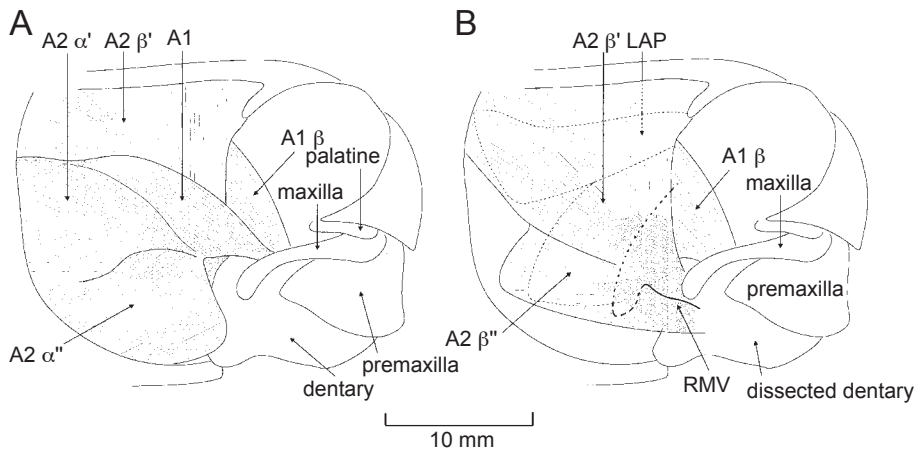


Fig. 23. Right lateral view of the cheek musculature of *Istiblennius lineatus* (NTUM08565). A: Superficial view. B: Medial view, after removal of A1+A2 α .

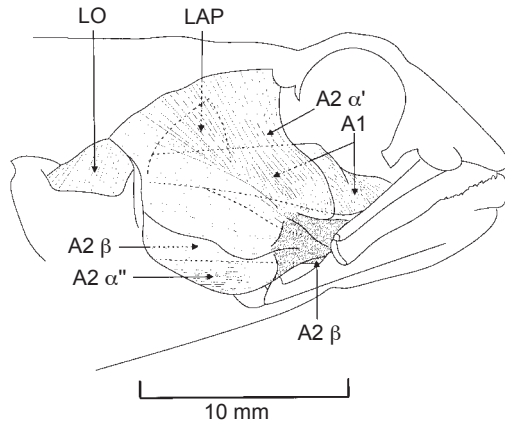


Fig. 24. Right lateral view of the cheek musculature of *Cryptocentrus filifer* (NTUM08659, 75 mm SL), after removal of the head of the maxilla and premaxilla.

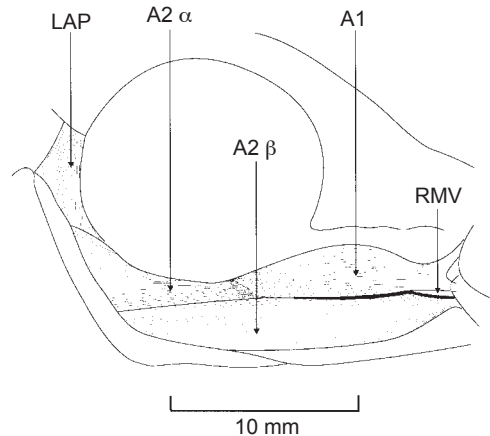


Fig. 25. Right lateral view of the cheek musculature of *Triacanthoides anomalus* (NTUM07514).

fibres cannot be separated. The RMV lies lateral to section A2, and enters the Meckelian fossa with it, or penetrates the muscle mass from the medial face, and enters the Meckelian fossa with the fibres. (Fig. 4).

Section A3 – The most-medial division (if existing) lies upon the palatal arch, and inserts into the Meckelian fossa, but never connects with section Aw. This subdivision lies medial to section A2 β (Fig. 5).

Section Aw – This section fills the Meckelian fossa, and connects with the tendon of section A2 β (Figs. 1-5).

Divisions of the adductor mandibulae in Teleostei

The following descriptions present the distributions of divisions of the adductor mandibulae in the Teleostei (except osteoglossomorphs). The systematic scheme is based on Nelson (1994). The distributions of the divisions are summarized in table 1.

Subdivision Elopomorpha

In *Echidna nebulosa* (Muraenidae), only section A2 is found. It originates from the hyomandibular, symplectic, and skull. The superficial muscle fibres insert on the coronoid process of the dentary and the hind margin of the angular. The inner fibres insert into the Meckelian fossa, and consolidate as a tendon extending throughout the Meckelian fossa. The RMV penetrates the muscle mass of A2 from the medial face, and enters the

Meckelian fossa with the fibres, but it lies lateral to the muscle fibres in the Meckelian fossa.

In *Albula vulpes* (Albulidae), the adductor mandibulae splits into 2 divisions, sections A2 and Aw (Fig. 4). Section A2 originates from the hyomandibular, and inserts into the Meckelian fossa by a tendon. The uppermost fibres are slightly separated from the main mass, and insert on the coronoid process of the dentary and ligamentum primordium. Section Aw fills all of the Meckelian fossa, and connects with the tendon of A2 in it.

Subdivision Clupeomorpha

In *Ilisha melastoma*, *Amblygaster sirm*, and *Nematalosa japonica* (Clupeidae), the adductor mandibulae is divided into 3 sections, sections A2, A3, and Aw (Fig. 5). Section A2, originating from the hyomandibular, inserts into the Meckelian fossa and connects with Aw. It also connects with the ligamentum primordium at the coronoid process of the dentary. Below the levator arcus palatini (LAP, a muscle occupying the area at the rear of the orbit between the skull and the palatal arch) and medial to A2, section A3 lies on the lateral face of the palatal arch. In *Ilisha melastoma* and *Amblygaster sirm*, the RMV lies lateral to A2. In *Nematalosa japonica*, the RMV penetrates A2 from the medial side to emerge on the lateral side.

Superorder Ostariophysi

In cyprinids, the adductor mandibulae greatly differs from the condition described above. This

Table 1. Distributions of the divisions of the adductor mandibulae (F: A1 fusing with A2 α ; double symbol presenting additional subdivisions)

	A1	A1 β	A1 α	A1-VL	U.A1	A2 α	A1+A2 α	A2 β	A2	A3	Aw
Elopomorpha											
<i>Echidna</i>	-	-	-	-	-	-	-	-	+	-	-
<i>Albula</i>	-	-	-	-	-	-	-	-	+	-	+
Clupeomorpha											
<i>Ilisha</i>	-	-	-	-	-	-	-	-	+	+	+
<i>Amblygaster</i>	-	-	-	-	-	-	-	-	+	+	+
<i>Nematalosa</i>	-	-	-	-	-	-	-	-	+	+	+
Ostariophysi											
<i>Carassius</i>	-	-	-	++	-	+	-	+	-	-	+
<i>Varicorhinus</i>	-	-	-	++	-	+	-	+	-	-	+
<i>Zacco</i>	-	-	-	+	-	+	-	+	-	-	+
<i>Pseudobagrus</i>	-	-	-	-	-	+	-	+	-	+	+
<i>Parasilurus</i>	-	-	-	-	-	-	-	+	-	+	+
<i>Potamorhina</i>	-	-	-	-	-	+	-	+	-	+	+
<i>Citharinus</i>	-	-	-	-	-	+	-	+	-	+	+
Protacanthopterygii											
<i>Plecoglossus</i>	-	-	-	-	-	-	-	+	-	+	-
<i>Oncorhynchus</i>	-	-	-	-	-	-	-	+	-	-	+
Stemopterygii											
<i>Astronesthes</i>	-	+	-	-	-	-	-	+	-	-	+
Cyclosquamata											
<i>Hime</i>	F	-	-	-	-	+	+	++	-	-	+
<i>Trachinocephalus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Saurida</i>	-	-	+	-	-	+	-	+	-	-	+
<i>Chlorophthalmus</i>	-	-	-	-	-	-	-	-	?	-	+
Mytophiformes											
<i>Diaphus</i>	-	+	-	-	-	-	-	+	-	-	+
<i>Neoscopelus</i>	-	-	-	-	-	-	-	+	-	-	+
Lampridiomorpha											
<i>Velifer</i>	F	-	-	-	-	+	+	+	-	-	+
Polymixiomorpha											
<i>Polymixia</i>	F	-	-	-	-	+	+	+	-	-	+
Paracanthopterygii											
<i>Neobythites</i>	-	++	-	-	-	+	-	+	-	-	+
<i>Physiculus</i>	-	-	-	+	-	-	-	+	-	-	+
<i>Lota</i>	-	+	-	+	-	-	-	+	-	+	+
<i>Antennarius</i>	-	-	-	-	+	+	-	+	-	-	+
Mugilomorpha											
<i>Chelon</i>	-	-	-	++	-	-	-	+	-	-	+
<i>Crenimugil</i>	-	-	-	++	-	-	-	+	-	-	+
Atherinomorpha											
<i>Fundulus</i>	-	-	-	+	-	-	-	++	-	-	+
<i>Parexocoetus</i>	-	-	-	+	-	-	-	++	-	-	+
<i>Cypselurus</i>	-	-	-	+	-	-	-	++	-	-	+
Percomorpha											
<i>Zeus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Zenopsis</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Paratrachichthys</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Sargocentron</i>	F	+	-	-	-	+	+	+	-	-	+
<i>Culaea</i>	-	-	-	F	-	+	+	+	-	-	+
<i>Sebastiscus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Minous</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Bembras</i>	F	-	-	-	-	+	+	+	-	-	+

muscle is divided into the ventrolateral section A1, and sections A2 α , A2 β , and Aw. Ventrolateral section A1 occupies the ventrolateral region of the cheek (Fig. 3) and is usually subdivided (*Carassius auratus* and *Varicorhinus tamsuiensis*). Section A2 α lies medial to ventrolateral section A1 and inserts on the coronoid process of the dentary, the hind margin of angular, and the ligamentum primordium at the angular region. Section A2 α of

cyprinids was named A2 (Edgeworth 1935, Winterbottom 1974a) and A1-OST (Diogo and Chardon 2000). Section A2 β is the most-medial division in the cyprinids. It lies on the palatal arch, medial to A2 α . Section A2 β of cyprinids was named A3 (Edgeworth 1935) and A2 (Diogo and Chardon 2000). The RMV lies between A2 α and A2 β and enters the Meckelian fossa with A2 β . No true A3 section was found in the cyprinids. In the

Table 1. (Cont.)

	A1	A1 β	A1 α	A1-VL	U.A1	A2 α	A1+A2 α	A2 β	A2	A3	Aw
<i>Onigocia</i>	S	-	-	-	-	+	+	+	-	-	+
<i>Lepidotrigla</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Anthias</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Chelidoperca</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Terapon</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Pelates</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Plectorhinchus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Glaucosoma</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Priacanthus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Apogon</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Pempheris</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Labracinus</i>	S	-	-	-	-	+	+	+	-	-	+
<i>Seriolina</i>	S	-	-	-	-	+	+	+	-	-	+
<i>Alectis</i>	S	-	-	-	-	+	+	+	-	-	+
<i>Lutjanus</i>	S	-	-	-	-	+	+	+	-	-	+
<i>Microcanthus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Kyphosus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Scatophagus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Chaetodon</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Dentex</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Acanthopagrus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Genicanthus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Centropyge</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Drepane</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Polynemus</i>	-	-	+	-	-	+	-	+	-	-	+
<i>Johnius</i>	-	++	-	-	-	+	-	+	-	-	+
<i>Scolopsis</i>	-	-	-	+	-	-	-	+	-	-	+
<i>Kuhlia</i>	-	-	-	+	-	-	-	+	-	-	+
<i>Anampses</i>	-	-	-	-	+	++	+	+	-	-	+
<i>Scarus</i>	-	-	-	-	+	++	+	+	-	-	+
<i>Stegastes</i>	S	-	-	-	-	++	+	+	-	-	+
<i>Amphiprion</i>	S	-	-	-	-	++	+	+	-	-	+
<i>Tilapia</i>	S	-	-	-	-	+	+	+	-	-	+
<i>Pterophyllum</i>	S	-	-	-	-	+	+	+	-	-	+
<i>Parapercis</i>	F	-	-	-	-	++	+	+	-	-	+
<i>Istiblennius</i>	F	+	-	-	-	++	+	+	-	-	+
<i>Praealticus</i>	F	+	-	-	-	++	+	+	-	-	+
<i>Rhinogobius</i>	F	-	-	-	-	++	+	+	-	-	+
<i>Cryptocentrus</i>	-	-	-	-	+	++	-	+	-	-	+
<i>Scomberomorus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Scomber</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Trichiurus</i>	F	-	-	-	-	+	+	+	-	-	+
<i>Sphyaena</i>	F	-	-	-	-	+	+	+	-	-	+

3 cyprinids examined (*C. auratus*, *V. tamusuiensis*, and *Zacco platypus*), the adductor mandibulae has the same divisions. These 3 species have different feeding habits (sucker, scraper, and predator, respectively). This implies that the feeding habits have not influenced the number or nature of the subdivision of the adductor mandibulae in these fishes.

No section A1 was found in the siluriforms in this study (and none in the works of Diogo and Chardon 2000 either). In *Pseudobagrus taiwanensis*, the adductor mandibulae is divided into sections A2 α , A2 β , A3, and Aw. Section A2 α occupies the ventrolateral region of the cheek, and inserts on the coronoid process of the dentary and the hind margin of the angular. Section A2 β , originating from the lateral face of skull and hyomandibular, lies medial to A2 α . The RMV lies between A2 α and A2 β . No section A2 α is present in *Parasilurus asotus*. The main mass of the adductor mandibulae occupying the superficial lateral region of the cheek is A2 β . Section A3 is the most-medial division among all of the siluriform species examined here.

No section A1 was found in the characiforms in this study. In *Potamorhina latior* and *Cirrhinus citharus* (Characiformes), the adductor mandibulae is divided into sections A2 α , A2 β , A3, and Aw. Section A2 α occupies the ventrolateral region of the cheek. It originates from the symplectic and quadrate, and inserts on the coronoid process of the dentary, the hind margin of the angular, and the ligamentum primordium. Section A2 β lies medial to A2 α . It originates from the hyomandibular and consolidates into a tendon before inserting into the Meckelian fossa. Section Aw extends out of the Meckelian fossa to the palatal arch, and connects with the tendon of A2 β . The RMV lies lateral to A2 β and Aw. Section A3 lies lateral to the palatal arch and medial to A2 β , but its tendon fuses with the consolidated tendon of A2 β . Gosline (1989) demonstrated that in *Curimanta*, *Hemiodus*, and *Bivibranchia*, the outer part of the external division (A1-VL here) passes forward to the maxilla, and thus an A1 component of the adductor mandibulae is not universally absent from the characiforms.

Superorder Protacanthopterygii

The adductor mandibulae of *Plecoglossus altivelis* (Osmeriformes) is divided into sections A2 β and A3. Section A2 β inserts into the Meckelian fossa by a consolidated tendon.

Section A3 lies lateral to the palatal arch and medial to A2 β and LAP. There is no Aw filling the Meckelian fossa. The adductor mandibulae of *Oncorhynchus masou* (Salmoniformes) is divided into sections A2 β and Aw (Fig. 6). A3 is absent. A2 β inserts directly into the Meckelian fossa, and shares a myocomma anteriorly with the posterior fibres of Aw.

Superorder Sternopterygii

In *Astronesthes lucifer* (Stomiidae), the adductor mandibulae is divided into sections A1 β , A2 β , and Aw. A2 β originates from the sphenotic and hyomandibular. The medial A1 β lies on the palatal arch between A2 β and LAP. It originates from the hyomandibular and partially from the palatal arch, and inserts on the dorsomedial face of the maxilla (Fig. 2).

Superorder Cyclosquamata

In the Aulopiformes, divisions of the adductor mandibulae are quite variable. In *Hime* sp. (Aulopidae), the adductor mandibulae is divided into sections A2 β , Aw, and the A1+A2 α division (Fig. 7). The most-superficial A1+A2 α division originates from the hyomandibular, and inserts on the ligamentum primordium. The ligamentum primordium is a curved, tendinous ligament, arising from the posterolateral region of the angular and passing beneath the posterior head of the maxilla to the posterodorsal part of that bone. The muscle fibres of the dorsolateral portion of the A1+A2 α division consolidate as a tendon, which extends along the ligamentum primordium and inserts on the maxilla. Most of the fibres on the medial face of this division insert on the coronoid process of the dentary by a ligament. A2 β lies medial to A1+A2 α , is subdivided into the 2 sections A2 β ' and A2 β ", but these insert by the same tendon into the Meckelian fossa. In *Trachinocephalus myops* (Syndodontidae), the adductor mandibulae is also divided into sections A2 β and Aw, and the A1+A2 α division. The A1+A2 α division is very large, occupying the entire lateral face of the cheek. The superficial fibres of the lower portion of the A1+A2 α division insert on the coronoid process of the dentary and the hind margin of the angular. The lower medial fibres insert onto the angular, but do not connect with the tendon of A2 β . In *Saurida undosquamis* (Syndodontidae), the adductor mandibulae is divided into sections A1 α , A2 α , A2 β , and Aw. Section A1 α originates from

the hyomandibular. Sections $A2\alpha$ and $A2\beta$ fuse together. In *Chlophthalmus acutifrons nigromarginatus* (Chlorophthalmidae), the adductor mandibulae is not divided. The RMV penetrates the muscle on the medial side.

Superorder Scopelomorpha

The adductor mandibulae of the *Diaphus diadematus* (Myctophidae) is divided into sections $A1\beta$, $A2\beta$, and Aw. Divisions of the adductor mandibulae are identical to those in *Astronesthes*. Section $A1\beta$ lies on the palatal arch between $A2\beta$ and LAP. It originates from the hyomandibular and palatal arch, and inserts on the dorsomedial face of the maxilla.

In *Neoscopelus microchir* (Neoscopelidae), the adductor mandibulae is divided into sections $A2\beta'$, $A2\beta''$, and Aw (Fig. 8). Winterbottom (1974a) described how the $A1$ subdivision of *Neoscopelus* apparently develops from the dorsal encroachment of the fibres of section $A2$ along the ligamentum primordium between the lower jaw and the head of the maxilla. But this description differs from the situation found in the species of *Neoscopelus* examined here. In our specimen, section $A2\beta$ is subdivided into the 2 subdivisions, $A2\beta'$ and $A2\beta''$. These 2 subdivisions of $A2\beta$ consolidate as a single tendon which inserts into the Meckelian fossa, and to which section Aw connects. The RMV lies lateral to these 2 subdivisions as it enters the Meckelian fossa. None of the sections we named $A1$, $A2\alpha$, and $A1\beta$ is found in *Neoscopelus*.

Superorder Lampridiomorpha

In *Velifer hypselopterus* (Veliferidae), the adductor mandibulae splits into the $A1+A2\alpha$ division and sections $A2\beta$ and Aw (Fig. 9). Fibres of the dorsal portion of the $A1+A2\alpha$ division (section $A1$) consolidate as a tendon which extends along the ligamentum primordium and inserts on the maxilla. Lateral fibres of the ventral portion of the $A1+A2\alpha$ division (section $A2\alpha$) insert on the ligamentum primordium and the coronoid process of the dentary. Some medial fibres of the $A1+A2\alpha$ division connect with the tendon of $A2\beta$, which lies on the ventromedial region of the cheek. The RMV lies between $A2\beta$ and $A1+A2\alpha$.

Superorder Polymixiomorpha

In *Polymixia japonica* (Polymixiidae), the adductor mandibulae splits into the $A1+A2\alpha$ divi-

sion and sections $A2\beta$ and Aw (Fig. 1). Fibres of section $A1$ (the dorsolateral portion of $A1+A2\alpha$) insert on the medial face of the maxilla, and are slightly separated from the ventral fibres of $A1+A2\alpha$. Fibres of section $A2\alpha$ insert mainly on the coronoid process of the dentary. A few medial fibres of section $A2\alpha$ consolidate as a tendon, and insert into the Meckelian fossa.

Superorder Paracanthopterygii

The adductor mandibulae exhibits great variety in the Paracanthopterygii.

Ophidiiformes – In *Neobythites sivicola* (Ophidiidae), the adductor mandibulae is divided into sections $A2\alpha$, $A2\beta$, $A1\beta$, and Aw (Fig. 10). Section $A2\alpha$ originates from the sphenotic, and inserts on the coronoid process of the dentary. Medially situated section $A1\beta$ has 2 origins. One branch of $A1\beta$ originates from the hyomandibular and lies medial to $A2\alpha$ and $A2\beta$ and lateral to the LAP. The other branch originates from the palatal arch medial to the LAP. These 2 branches of $A1\beta$ fuse in front of the LAP and insert into the dorso-medial face of the anterior maxilla below the palatine. The RMV passes through the 2 branches of $A1\beta$ in front of the LAP and lies lateral to $A2\beta$ as it enters the Meckelian fossa.

Gadiformes – In *Physiculus japonicus* (Moridae), the adductor mandibulae is divided into sections $A2\beta$ and Aw, and ventrolateral section $A1$ (Fig. 11). The large and slightly subdivided ventrolateral section $A1$ originates from the hyomandibular and symplectic, and inserts on the lateral face of the anterior maxilla below the palatine. In *Lota lota* (Gadidae), the adductor mandibulae is divided into sections $A2\beta$, $A3$, $A1\beta$, and Aw, and ventrolateral section $A1$. Ventrolateral section $A1$ is also slightly subdivided. Section $A1\beta$ originates from the hyomandibular, lies between $A2\beta$ and $A3$, and fuses with ventrolateral section $A1$ at the site of insertion. The RMV passes medially to $A1\beta$, and lies lateral to $A2\beta$ as it enters the Meckelian fossa.

Lophiiformes – In *Antennarius striatus* (Antennariidae), the adductor mandibulae is divided into sections $A2\alpha$, $A2\beta$, and Aw, and an undefined section $A1$. Section $A2\alpha$ occupies the entire lateral surface of the cheek, and inserts onto the ligamentum primordium and the coronoid process of the dentary. The undefined section $A1$ lies between $A2\alpha$ and $A2\beta$, and consolidates as a tendon, which inserts on the lateral face of the anterior maxilla below the palatine. The RMV lies lateral to $A2\beta$ and medial to $A2\alpha$ and the undefined sec-

tion A1.

Series Mugilomorpha and Series Atherinomorpha

The adductor mandibulae of the Mugilomorpha and Atherinomorpha are identical and are characterized by (1) ventrolateral section A1, (2) the upper margin of A2 β which consolidates as a tendon, and (3) the absence of A2 α and A3.

Mugilomorpha – In *Chelon macrolepis* and *Crenimugil crenilabis* (Mugilidae), the adductor mandibulae is divided into ventrolateral section A1 and sections A2 β and Aw (Fig. 12). The ventrosuperficial section A1 occupies the ventrolateral region of the cheek. It originates from the symplectic, quadrate, and part of the hyomandibular, and is subdivided into A1' and A1''.

Atherinomorpha – In *Fundulus diaphanus* (Cyprinodontiformes), *Parexocoetus mento mento*, and *Cypselurus cyanopterus* (Beloniformes), the adductor mandibulae is also divided into ventrolateral section A1 and sections A2 β and Aw. Ventrolateral section A1 occupies the ventrolateral region of the cheek. It originates from the symplectic and quadrate. Section A2 β originates from the hyomandibular, symplectic, and quadrate, and lies lateral to the palatal arch and medial to the ventrolateral section A1. The posterior portion of A2 β splits into lateral and medial subdivisions. The RMV passes between the lateral and medial subdivisions of A2 β to emerge on the lateral side of anterior A2 β , and enters the Meckelian fossa with it.

Series Percomorpha

In all taxa of the Percomorpha examined, divisions of the adductor mandibulae generally include the A1+A2 α division and sections A2 β and Aw.

Zeiformes – In *Zeus* and *Zenopsis nebulosa* (Zeidae), the adductor mandibulae splits into the A1+A2 α division and sections A2 β and Aw (Fig. 13). Fibres of section A1 are slightly separated from A2 α on the lateral face, but not on the medial face. Some medial fibres of A2 α connect with the ligament of A2 β .

Beryciformes – In *Paratrachichthys prosthemi* (Trachichthyidae), the adductor mandibulae splits into the A1+A2 α division and sections A2 β and Aw. The A1+A2 α division inserts on a consolidated tendon along the ligamentum primordium. The upper part of this tendon inserts on

the dorsomedial face of the maxilla; the lower part receives fibres of A2 α and some fibres of A2 β , and enters the Meckelian fossa. In *Sargocentron ittodai* (Holocentridae), the adductor mandibulae splits into the A1+A2 α division and sections A2 β , Aw, and A1 β . The large A1+A2 α division occupies the entire lateral surface of the cheek. Fibres of A1 consolidate as a tendon which inserts on the anterolateral face of the maxilla. Fibres of A2 α insert on the angular and dentary. Section A1 β originates from the palatal arch in front of the LAP and inserts on the tendon of A1.

Gasterosteiformes – In *Culaea inconstans* (Gasterosteidae), the adductor mandibulae is divided into ventrolateral section A1 and sections A2 α , A2 β , and Aw. Ventrolateral section A1 originates from the lower limb of the hyomandibular and symplectic, and inserts on the dorsomedial face of the maxilla. However, medial fibres of section A1 fuse with A2 α .

Scorpaeniformes – The adductor mandibulae splits into the A1+A2 α division and sections A2 β and Aw in scorpaeniforms. Fibres of A1 and A2 α cannot be separated in *Sebastes marmoratus* (Fig. 14), *Minous pictus* (Scorpaenidae), or *Bembras japonicus* (Bembridae), but are fully separated in *Onigocia spinosa* (Platycephalidae). The A1+A2 α division, which has shifted anteriorly to under the infraorbitals, is slightly separated in *Lepidotrigla alata* (Triglidae). It originates from the tendon under the infraorbitals instead of the hyomandibular.

Perciformes – The adductor mandibulae generally splits into the A1+A2 α division and sections A2 β and Aw in the Perciformes.

In *Anthias squamipinnis* and *Chelidoperca pleurospilus* (Serranidae), the A1+A2 α division occupies the dorsolateral region of the cheek. Fibres of A1 originate directly from the hyomandibular. A large A1+A2 α division, which overlies all of A2 β , is not separated as A1 and A2 α in *Epinephelus* (Serranidae) (Fig. 15). The ventrolateral portion of A2 β fuses with the ventromedial portion of A2 α . The A1+A2 α divisions in *Terapon* and *Pelates quadrilineatus* (Teraponidae) are identical with that of *Epinephelus* in that (1) the A1+A2 α division overlies all of A2 β and (2) the ventrolateral portion of A2 β fuses with the ventromedial portion of A2 α . However, in the Teraponidae, fibres of A1 originate indirectly from the hyomandibular by a thin tendinous sheath and are slightly separated from A2 α . In *Grammistes* (Serranidae), *Plectorhinchus* (Haemulidae), *Glaucosoma* (Glaucosomatidae), and *Platax*

(Ephippidae), the A1+A2 α division occupies the dorsolateral region of the cheek. Fibres of A1 originate indirectly from the hyomandibular by a thin tendinous sheath (Fig. 16). In *Priacanthus* (Priacanthidae) and *Apogon* (Apogonidae), fibres of A1 originate directly from the hyomandibular, and an upper-tendinous border of A2 can be found on the medial side of the A1+A2 α division (Fig. 17). *Pempheris* (Pempheridae) has a slightly separated A1+A2 α division, of which A1 and A2 α are fully separated on the lateral side. Fibres of A1 originate directly from the hyomandibular. The A1+A2 α division is fully separated in *Labracinus* (Pseudochromidae), *Seriolina*, *Alectis* (Caragidae), and *Lutjanus* (Lutuanidae). Section A1, which lies dorsolateral to A2 α , originates indirectly from the hyomandibular by a strong tendon (Fig. 18).

In *Microcanthus* (Kyphosidae), there is another type of unseparated A1+A2 α division, for which almost all fibres of A2 α insert on the muscle mass of A1 (Fig. 19). Fibres of A1 originate indirectly from the hyomandibular by a strong tendinous sheath. Almost all fibres of A2 α insert on this sheath and the muscle mass of A1, instead of on the ligamentum primordium at the coronoid process of the dentary. Only a few fibres of the lower portion of A2 α insert on the ligamentum primordium at the coronoid process of the dentary. *Kyphosus* (Kyphosidae) has the same insertion as A2 α of *Microcanthus*. In addition, section A2 α of *Kyphosus* connects with A2 β at the posterior and anterior regions. In *Scatophagus* (Scatophagidae), the insertion sites of A2 α include A1 as well. In addition to the tendinous sheath of A1, most fibres of section A2 α insert on a tendon at the belly of A1. Sections A2 α and A2 β fuse at their posterior regions (Fig. 20). In *Chaetodon* (Chaetodontidae), almost all fibres of A2 α insert on the tendinous sheath and the tendon at the belly of A1. A strong, short tendon from the coronoid process of the dentary connects with A2 α on the medial side of the A1+A2 α division (Fig. 21). In the taxa described above (Kyphosidae, Scatophagidae, and Chaetodontidae), regardless of whether fibres of the lower part of A2 α insert on A1, some fibers of the lower part of A2 α extend and terminate at the region of the coronoid process of the dentary. Another type, slightly differing from the Kyphosidae, Scatophagidae, and Chaetodontidae, can be found in the Sparidae. In *Dentex* and *Acanthopagrus* (Sparidae), all fibres of A2 α insert on section A1 at the middle of the A1+A2 α division. Section A1 originates from the end of A2 α at the midpoint of the A1+A2 α division, instead of

from the hyomandibular (Fig. 22). This pattern differs from the Kyphosidae, etc. in that (1) the insertion site of A2 α is totally free from the region of dentary and (2) the origin site of A1 is free from the hyomandibular.

In *Genicanthus* and *Centropyge* (Pomacentridae), there is a short ligament between A1 and A2 α which serves as the insertion site of some fibres of both sections at the insertion region of the A1+A2 α division. In *Drepane* (Drapanidae), the large, fan-like A1+A2 α division occupies the entire lateral surface of the cheek. There is a long, strong, tendinous ligament between A1 and A2 α on which some fibres of both sections insert.

The A1+A2 α division was not found in some taxa of the suborder Percoidei examined herein. In *Polynemus* (Polynemidae), section A1 α lies lateral to and crosses A2 α and A2 β . In *Johnius* (Sciaenidae), section A1 is absent. However, section A1 β , inserting on the medial face of the maxilla, lies on the palatal arch, medial to the LAP. Section A2 α is absent from *Scolopsis* (Nemipteridae) and *Kuhlia* (Kuhliidae).

In *Anampses* and *Scarus* (Labroidei), a large, subdivided section A2 α overlies all of A2 β . A large unnamed section A1 lies medial to A2 α in *Anampses*. In *Scarus*, an unnamed section A1 connects with A2 α by a tendinous sheath and lies on the dorsomedial face of A2 α . Kaufman and Liem (1982), Liem (1986), and Stiassny and Jensen (1987) included Pomacentridae and Cichlidae, previously considered to be percoids, as members of the Labroidei. In *Stegastes*, *Amphiprion* (Pomacentridae), *Tilapia*, and *Pterophyllum* (Cichlidae), the large section A2 α also lies lateral to all of A2 β , but the separated section A1 lies on the dorsolateral face of A2 α , instead of on the medial face.

In *Parapercis* (Pinguipedidae), the A1+A2 α division with a large A2 α overlies all of A2 β . Fibres of the posteroventral A2 β fuse with A2 α .

In *Istiblennius* and *Praealticus* (Blennidae), the A1+A2 α division is like that of *Parapercis*. Section A2 β originates from the sphenotic and hyomandibular. Section A1 β lies on the palatal arch, and inserts on the dorsomedial face of the maxilla. The path of the RMV greatly differs from that in all of the taxa described above. The RMV passes between the palatal arch and A1 β to the medial face of the tendon of A2 β , and exits the tendon to the lateral face of A2 β before entering into the Meckelian fossa (Fig. 23).

A large A1+A2 α division lying lateral to A2 β is also found in the Gobiidae. Section A2 α is always

subdivided into 2 sections. Section A1 is not separate from A2 α in *Rhinogobius*. An unnamed section A1 separates from A2 α and lies between A2 α and A2 β in *Cryptocentrus* (Fig. 24).

In *Scomberomorus*, *Scomber*, *Trichiurus*, and *Sphyraena* (Scombroidei), all fibres of A1+A2 α and A2 β originate from the preopercle, so that the preopercle lies medial to the adductor mandibulae.

Tetraodontiformes and Acanthuridae – In the Acanthuridae, the adductor mandibulae is divided into a superficial section A1 α , and sections A2 α , A2 β , A3, A1 β , and Aw. The superficial section A1 α is separated into 2 to 3 subdivisions, and A1 β and A3 fuse together. Divisions in the Acanthuridae are morphologically identical with those reported for the Balistoidea (Winterbottom 1974b). The superficial section A1 α of the Acanthuridae originates from the infraorbital ligament, instead of the ethmoid and prefrontal in the Balistoidea, and A1 γ of the Monacanthidae is not found in the Acanthuridae. We particularly want to point out here that the adductor mandibulae splits into the A1+A2 α division and sections A2 β and Aw in the Triacanthodidae (Fig. 25), and that the A1+A2 α division is identical with that of *Dendex*. In the Triacanthodidae, fibres of section A1 originate from the end of A2 α , instead of the hyomandibular, and fibres of A2 α insert on A1 instead of the dentary.

DISCUSSION

In the “Introduction”, we pointed out the ambiguities of the past definitions that cause complications in practice. For example, Gill and Mooi (1993) described the large muscle in *Notograptus*, which occupies the entire lateral surface of the cheek as “perhaps of A1+2, because inserts anteriorly onto the maxilla via tendon and anteroventrally onto the coronoid process of dentary”, and described the medial section “lying medial to the ramus mandibularis V is interpreted as A3”. Furthermore, they described the ventromedial section lying medial to the ramus mandibularis V (RMV) as A2 in *Grama*, *Lipogramma*, and *Lonchopisthus*. In the meantime, they used the RMV to demonstrate that section A1 β of the Grammatidae and Opistognathidae are non-homologous. It is conflicting that they used this nerve to judge A1 β , but ignored the value of this nerve when interpreting the medial subdivision lying medial to the RMV. They interpreted the median section in *Notograptus* as A3, because

section A2 was used for nominating the division inserting on the coronoid process of the dentary. In addition, they interpreted the median section in the Grammatidae and Opistognathidae as A2, because none of the divisions inserted onto the coronoid process of the dentary in their study. According to the present definitions, their large A1+2 in *Notograptus* is an enlarged division A1+A2 α , and their A1 α in the Grammatidae and Opistognathidae is also the A1+A2 α division, while all of the median sections are A2 β .

The enlarged division A1+A2 α is very common in non-percoid perciforms (e.g., Labroidei, *Parapercis*, Blennidae, and Gobiidae). Van Tassell (2001) described the adductor mandibulae of *Chromogobius* (Gobiidae) that splits into sections A1 α , A1 β , A2 and A3. This differs from our observations of *Rhinogobius* (Gobiidae), where an enlarged A1+A2 α is present. Section A1 separates from A2 α in *Cryptocentrus* (Gobiidae), and A2 α subdivides into A2 α' and A2 α'' . Van Tassell described A1 α of *Chromogobius* as inserting on the lateral surface of the coronoid process of the dentary. This is incorrect, because A1 is related to the maxilla, not the mandible. Sections A1 α , A2, and A3 as named by Van Tassell are respectively corrected as sections A2 α' , A2 α'' , and A2 β herein. Van Tassell described A1 β of *Chromogobius* as originating on the medial posterior surface of A1 α (corrected as A2 α' here). This is not a real section A1 β , because it does not originate from the palatal arch. This unnamed section A1 can also be found in *Cryptocentrus*, *Anampses*, and *Scarus*, and lies between A2 α and A2 β . The unnamed A1 of *Anampses* is very large and fully separated from A2 α . A1 of *Scarus* is smaller than that of *Anampses*, and fuses to A2 α . This unnamed section A1 is interpreted here as being derived from A1, and may develop from the “dorsomedial” encroachment of fibres of A2 α , because it lies medial to A2 α .

Section A1 α was used to describe the dorso-lateral division in the Monacanthidae (Winterbottom 1974b) and Acanthuridae (Winterbottom 1993, Borden 1998). We believe this section A1 α is also derived from section A1, because in 13 species of *Naso*, the intergradation of fibres of A1 α and A2 α is extensive, and A1 α and A2 α do not intergrade in *N. lituratus*, *N. unicornis*, or other acanthurids and zancids (Borden 1998). The intergradation of A1 α and A2 α is the same as division A1+A2 α .

The adductor mandibulae of *Trachurus japonicus* (Carangidae), divided into sections A1, A2 α ,

A2 β , and Aw (Suda, 1996), is identical with our observations of *Seriolina* and *Alectis*.

Gosline (1989) noticed that the internal division of the basic pattern of ostariophysin fishes inserts into the Meckelian fossa and connects with section Aw, that the external division inserts on the coronoid process of the dentary, and that the RMV passes into the mandible between these 2 sections. It is obvious that the internal and external divisions (Gosline 1989) and A2 and A1-OST (Diogo and Chardon 2000) are sections A2 β and A2 α , respectively, here. Because A1-OST inserts on the mandible, we are unsure why they named it A1 (related to the maxillary)-OST (in ostariophysines). A2 α (A1-OST in Diogo and Chardon 2000) is distributed in many taxa of teleosts (Table 1).

Gill and Mooi (1993) used the RMV to demonstrate that section A1 β of the Grammatidae and Opistognathidae is non-homologous. This section A1 β was used as a synapomorphy to link the Grammatidae and the Opistognathidae by Mok et al. (1990). Whether the RMV is a reliable character is an interesting topic. Winterbottom (1974a) quoted from Edgeworth (1935) that the ramus mandibularis V may pass (1) external to the adductor mandibulae (e.g., *Salmo* and *Clupea*), (2) external to section A2 (e.g., *Pleuronectes*), (3) between sections A2 and A3 (e.g., *Scomber*, *Cyprinus*, and *Esox*), (4) external to section A1 and then internal to section A2 or sections A2 and A3 (e.g., *Ktalurus* and *Galeichthys*), or (5) internal to section A3 (e.g., *Zoarces*). In the Salmoniformes and Clupeiformes described previously, section A2 is identical with A2 β on which the RMV lies. Sections A2 and A3 of *Scomber* and *Cyprinus* in Edgeworth (1935) are identical with A2 α and A2 β in this study, and the specimen of *Scomber* examined has the A1+A2 α division. Neither *Ktalurus* nor *Galeichthys* were examined in this study, but in specimens of Siluriformes we examined, the RMV lies lateral to A2 β and to the retractor tentaculi, which develops from section A1 (Edgeworth 1935). The retractor tentaculi is medially situated, lying medial to the LAP. In *Pleuronichthys cornutus*, we found A2 α and A2 β . These 2 divisions share a common tendon which inserts into the Meckelian fossa, and the RMV lies between them. All of the specimens examined in this study exhibit the RMV which lies lateral to A2 β , and enters the Meckelian fossa together with it. It is therefore concluded that the RMV is a reliable character for identifying divisions of the adductor mandibulae, as are sections A2 β , A2 α ,

and A3 (but not A1 β).

The configurations of section A1 β and the RMV exhibit great variety. It is currently difficult to decide if sections A1 β of the Grammatidae and Opistognathidae are homologous. In this study, 2 types of A1 β were found. They all lie medial to A2 β , but one lies lateral to the LAP and the other lies medial to that muscle. Section A1 β in *Astronesthes* (Stomidae) originates from the hyomandibular, and lies lateral to the LAP. This muscle is free from the palatal arch, and there is space medial to A1 β for passage of the RMV; however, the path of the RMV lies on A1 β itself. Two taxa of the Mytophiformes were examined in this study, and we found that (1) *Neoscopelus* lacks section A1 β and (2) section A1 β and the path of RMV in *Diaphus* are identical to those in *Astronesthes*. Section A1 β is also found in the Paracanthopterygii (Table 1). *Antennarius* (Lophiiformes) and *Physiculus* (Gadiformes) lack section A1 β . In *Neobythites* (Ophidiiformes), this section A1 β contains 2 branches which fuse in the front of the LAP. One originates from the hyomandibular lateral to the LAP, while the other originates from the palatal arch medial to the LAP. The RMV passes along the anterior margin of the LAP and passes between the 2 branches of A1 β . In *Lota* (Gadiformes), A1 β originates from the hyomandibular between A2 β and A3. The RMV passes medially to A1 β . In *Lota* and *Astronesthes*, all fibres of A1 β originate from the hyomandibular, not directly from the palatal arch. However, here the path of the RMV differs, but in *Johnius* (Sciaenidae), fibres of A1 β originate from the palatal arch itself, and the RMV passes laterally of it. The widespread and unstable nature of section A1 β among members of the Acanthomorpha suggests that this muscle is not homologous among them. It is worthy mentioning that no section A1 β was found in basal percoids in this study, except in the Grammatidae and Opistognathidae as described above.

In the taxa described above, i.e., the Clupeomorpha, Cyprinidae, Mugilomorpha, Atherinomorpha, and Percomorpha, subdivisions of the adductor mandibulae are stable. This is not the case in the Aluopiformes, Mytophiformes, and Paracanthopterygii. The Mugilidae was removed from the Percomorpha and placed as the sister group of the atherinomorph assemblage (Stiassny 1990). According to this scheme, the Percoromorpha is the sister group of a monophyletic Mugilomorpha plus a monophyletic Atherinomorpha. Mugilids share 7 characters relating them to

the Atherinomorpha, and 3 pelvic characters suggesting a percomorph (holocentrids + higher percomorphs) relationship (Stiassny 1993). Parenti (1993) proposed that atherinomorphs, excluding the Mugilomorpha, are the sister group of some or all paracanthopterygian fishes. Johnson and Patterson (1993) advocated a new taxon, Smegmamorpha, a grouping of Atherinomorpha, Mugiloidei, Gasterosteiformes, Elasmobranchiiformes, and Synbranchiiformes, because of the configuration of the 1st vertebra and its intermuscular bone. The Percomorpha comprises Smegmamorpha with Dactylopteriformes, Scopaeiniformes, Perciformes, Pleuronectiformes, and Tetraodontiformes. Although several characters provide evidence that Atherinomorpha and Mugilomorpha are a monophyletic group, they are still considered of uncertain affinity to the other group. According to this study, the Atherinomorpha shares the same nature of divisions of the adductor mandibulae as the Mugilomorpha (i.e., with ventrolateral section A1, the upper margin of section A2 β consolidated as a tendon, and the absence of sections A2 α and A3). No evidence demonstrating the above relationship of these 2 groups to the Percomorpha or to the Paracanthopterygii, was found in the adductor mandibulae.

Baldwin and Johnson (1996) identified four of the 7 derived features proposed by Rosen (1973) plus the fusion of the medial process of the pelvic girdle by cartilage in support of the monophyly of the Aulopiformes. Stiassny (1996) reviewed 6 derived features and 5 possible characters for supporting the monophyly of the Ctenosquamata (Scopelomorpha + Acanthomorpha), and excluded the Aulopiformes from the Ctenosquamata, and also documented that some of the aulopiform lineages have lost the supraorbital bones of the circumorbital series. The loss of the supraorbital bones is a derived feature of the Ctenosquamata, but the presence of supraorbitals in the most-basal aulopiform lineage suggests that these losses are best interpreted as having occurred independently of that in ctenosquamates (Stiassny 1996). Another 2 derived features for the Aulopiformes can be found in the intermusculars. In non-acanthomorphs, a series of epicentral ligaments extends anterior to the 1st centrum, but in most aulopiforms, the epicentral series begins above the last epipleurals (Patterson and Johnson 1995). This posterior displacement of the epicentrals to the mid-body is only found in higher percomorphs (if the epicentrals are present). In addition, aulopiforms are uniquely characterized by having epi-

pleural bones extending anterior to the 1st or 2nd vertebra (Patterson and Johnson 1995, Baldwin and Johnson 1996). As described in the "Introduction", a basic adductor mandibulae pattern in higher teleosts (Gosline 1989) of an upper section (A1) with a maxillary attachment and a lower section (A2, 3) grading into Aw is present in the Beryciformes, Zeiformes, Perciformes, Scopaeiniformes, and Tetraodontiformes, and among lower teleosts, in the genus *Aulopus*. These patterns are termed A1+A2 α and A2 β in this study. Division A1+A2 α appears first in some aulopiforms, and is also in lampridiforms, polymixiiforms, and percomorphs. There are 3 interpretations for describing the distributions of division A1+A2 α : (1) division A1+A2 α is randomly distributed in the Teleostei; (2) division A1+A2 α is commonly distributed in the Eurypterygii (Cyclosquamata + Ctenosquamata, a taxon elected by Rosen 1973); and (3) the presence of division A1+A2 α in some aulopiforms is the result of convergence. We argue against the 1st interpretation, because this division is commonly distributed in percomorphs. We also do not intend to emphasize that the presence of division A1+A2 α in aulopiforms is due to convergence or that this division is a synapomorphy for the Eurypterygii. However, loss of the supraorbitals and the posterior displacement of the epicentrals in aulopiforms are interpreted as having occurred independently of that in ctenosquamates and higher percomorphs, respectively. If division A1+A2 α is a synapomorphy for the Eurypterygii, it will produce a large amount of homoplasy, because of secondary losses of A1+A2 α in the Scopelomorpha, Paracanthopterygii, Atherinomorpha, and Mugilomorpha.

Rosen (1973) recognized the Percomorpha, a grouping of Lampridiformes, Polymixiiformes, Beryciformes, Perciformes, and groups placed between and beyond those in Greenwood et al. (1966). Although lampridiforms share an apparent synapomorphy with percomorphs (i.e., a pelvic girdle dorsally inclined to the pectoral girdle, Stiassny and Moore 1992) and a synapomorphy of higher percomorphs (i.e., loss of autogenous lateral radials in adults, Stiassny and Moore 1992), Olney et al. (1993) showed that the percomorph synapomorphy described by Stiassny (1990) and Stiassny and Moore (1992) is equivocal for lampridiforms, and concluded that lampridiforms are the basal acanthomorph. However, Olney et al. (1993) described lampridiforms as having 2 other synapomorphic characters of percomorphs: (1) the cartilaginous tip of the central process of each 1/2 of

the pelvic girdle attached by a strong ligament to the medial face of the cleithrum and (2) the posterior processes tightly applied along the midline of the pelvic girdle. Stiassny and Moore (1992) showed that in non-acanthomorphs with pelvic plates, the plates are frequently loosely bound together by connective tissue for most of their length (by cartilage at median processes in aulopiiforms, Baldwin and Johnson 1996, Johnson et al. 1996), and that the acanthomorph girdle differs from this basic plan in that the bony expansions of the median process form an overlapping connection between contralateral pelvic elements. These bony expansions occur in *Polymixia*, "percopsiform" paracanthopterygians, and atherinomorphs (but with a loss of overlap in other paracanthopterygians). Moreover, Stiassny and Moore (1992) also documented that the pelvic girdle of acanthomorphs is attached to the distal postcleithrum by the postcleithrum ligament. This attachment occurs in *Polymixia*, paracanthopterygians (but is absent from *Percopsis*), and percomorphs, but in atherinomorphs, the attachment of pelvic girdle is displaced to the posterior-most proximal pleural rib. They interpreted this as a secondary posterior migration into an abdominal position. Parenti and Song (1996) showed that ontogeny (indicated by the innervation pattern) allows the use of the pelvic-fin position as a character in phylogenetic analyses. Without this information, "jugular" pelvis in 2 teleost taxa might erroneously be considered homologies. They also demonstrated that atherinomorph monophyly has the posterior spinal nerve innervation of the pelvic fin muscle. We were interested in determining whether the abdominal position of atherinomorphs is primitive or a secondary migration, although Stiassny and Moore (1992) interpreted this abdominal position as a secondary migration. Because (1) the posterior spinal nerve innervation of the pelvic fin is also found in other lower teleosts and (2) the secondary migration of the pelvis together with the nerve innervation becomes more difficult than migration of bone and ligament only for ontogenetic reasons, it is more reasonable to postulate that the abdominal position of the pelvis in atherinomorphs is primitive, not a secondary migration. If this pelvic migration in atherinomorphs is a plesiomorphy, the attachment of the pelvic girdle to the distal postcleithrum in *Polymixia* should receive more attention. Stiassny and Moore (1992) presented 2 views of interrelationships of lampridiforms and acanthomorphs: (1) lampridiforms as an unresolved polychotomy with trachichthyiforms,

berycids, and higher percomorphs and (2) lampridiforms being a basal acanthomorph. Both views result in a large amount of homoplasy.

As described above, one of the 6 synapomorphies for supporting the monophyly of ctenosquamates is 2 (or fewer) posterior ceratohyal branchiostegal rays, but the single branchiostegal ray articulated with the posterior ceratohyal in *Polymixia* is interpreted as an autapomorphy (Stiassny 1996). A list of distributions of branchiostegal rays summarized from the data of McAllister (1968) and Tyler (1980) is presented here (Tables 2-4). The 2 (or fewer) posterior ceratohyal branchiostegal rays cannot support the monophyly of the Ctenosquamata, since many taxa have more than 2 branchiostegals on the posterior ceratohyal (especially in beloniforms and stephanoberyciforms). Furthermore, many ctenosquamate taxa have fewer than 2 branchiostegals on the posterior ceratohyal. Lampridiforms have 0-3 rays, and Polymixiiforms have 1.5 rays (Table 2). Besides these 2 taxa, in general, the non-percomorph acanthomorphs with fewer than 2 branchiostegals on the posterior ceratohyal comprise the Percopsiformes, Gadiformes, Lophiiformes, and Cyprinodontiformes. Percomorphs with fewer than 2 branchiostegals on the posterior ceratohyal include the Zeiformes, Gasterosteiformes, Synbranchiformes, Scopaeniformes, Perciformes, and Tetraodontiformes. Distributions with fewer than 2 branchiostegals on the posterior ceratohyal seem to be mosaics, but in the Percomorpha, apart from the Stephanoberyciformes and Beryciformes, the trend is of reduction to fewer than 2 branchiostegals. This implies that lampridiforms and polymixiiforms also have the advanced affinity.

We reviewed several characters that demonstrate the large amount of homoplasy in the Acanthomorpha. Johnson and Patterson (1993) considered the Lampridiformes and Polymixiiformes as basal groups of the Acanthomorpha, with the Polymixiiformes as the basal group of the Euacanthomorpha (Polymixiiformes, Paracanthopterygii, Atherinomorpha, and Percomorpha) based on evidence of intermuscular bone (Patterson and Johnson 1995). All non-acanthomorphs have 3 series of intermusculars: epineurals, epicentrals, and epipleurals. The epineurals are primitively fused with the neural arches and dorsolaterally directed. A series of epicentral ligaments lie anterior to the 1st centrum (except in the Aulopiiformes). The intermusculars of the Lampridiformes retain all features of the non-acanthomorphs. The

Table 2. Distributions (rearranged under the systematic scheme of Nelson 1994) of branchiostegal rays summarized from McAllister (1968). (AC, anterior ceretohyal; PC, posterior ceretohyal; HH2, ventral hypohyal)

Taxa	Total	AC	PC	HH2	Taxa	Total	AC	PC	HH2
Aulopiformes					Mugiliformes				
Aulopodidae	13~16	7~8	6~8		Mugilidae	6	2	4	
Chlorophthalmidae	7~10	3~4	5~5		Atheriniformes				
Ipnopidae	10~17	3~5	7~8		Melanotaeniidae	6	2	4	
Scopelarchidae	9~10	3~4	5~6		Atherinidae	6	2	4	
Notosudidae	6~8	4	4		Phallostethidae	5	1	4	
Synodontidae	11~26	6~14	9~10		Beloniformes				
Paralepididae	6~9	3~4	4~5		Adrianichthyidae	5~6	1	4~5	
Anopteridae	7~9	3~4	4~5		Belonidae	9~15	3	8	0~1
Evertmannellidae	8	4	4		Scomberesocidae	14~15	3~4	8~9	2~3
Omosudidae	8	4	4		Exocoetidae	10~13	2	7~8	0~3
Alepisauridae	7~8	4	3~4		Hemiramphidae	10~14	3	9	1
Myctophiformes					Cyprinodontiformes				
Neoscopelidae	8~10	2	6~8		Anablepidae	6	1	5	
Myctophidae	8~10	2	5~6	1-2	Poeciliidae	6	1	5	
Lampridiformes					Goodeidae	5	1	4	
Veliferidae	6				Cyprinodontidae	6	1	5	
Lamprididae	6~7				Stephanoberyciformes				
Stylephoridae	6	3	3		Melarnphaidae	8	2	6	
Trachipteridae	6	1	5		Gibberichthyidae	9	4	5	
Regalecidae	5	0	5		Rondeletidae	7~8	3~4	4	
Polymixiiformes					Barbourisiidae	8	3	5	
Polymixiidae	7	1.5	2.5	3 (rudiments)	Cetomimidae	8~10	4	4	
Percopsiformes					Mirapinnidae	7~9	3~5	4	
Percopsidae	6	1	5		Beryciformes				
Aphredoderidae	6	1	5		Anoplogastridae	8	3	5	
Amblyopsidae	6	1	5		Monocentridae	8	2	6	
Ophidiiformes					Trachichthyidae	8	2	6	
Carapidae	7	2	5		Berycidae	7~9	2	5	
Ophidiidae	7~9	2	5		Holocentridae	8	2	6	
Gadiformes					Zeiformes				
Macrouridae	6~7	1	6		Zeidae	7	0	7	
Moridae	7	1	6		Gasterosteiformes				
Bregmacerotidae	7	1	6		Aulorhynchidae	4	1	3	
Gadidae	7	0~1	6~7		Gasterosteidae	3	1	2	
Batrachoidiformes					Pegasidae	5	2~3	2~3	
Batrachoididae	6	2	4		Solenostomidae	1	1		
Lophiiformes					Syngnathidae	1~3	0	1~3	
Lophiidae	6	1	5		Indostomidae	5~6			
Antennariidae	6	0	6		Aulostomidae	4	4	0	
Chaunacidae	6	0	6		Fistulariidae	5	2~3	2~3	
Ogcocephalidae	5~6	0	5~6		Macrorhamphosidae	4~5	0	4	
Caulophrynidae	6	0	6		Synbranchiformes				
Melanocetidae	6	0			Synbranchidae	6	2~2.5	3.5~4	
Himantolophidae	6	0	6		Chaudhuriidae	6	1	5	
Diceratiidae	6	0~1	5~6		Mastacembelidae	6	1.5	4.5	
Oneirodidae	6	0	6		Scorpaeniformes	5~7	1~2	4~6	
Centrophrynidae	6	0	6		Dactylopteridae	6	3	3	
Ceratiidae	6	0	6		Pleuronectiformes				
Gigantactinidae	6	0~1	5~6		Bothidae	6~7	2	5	
Linophtynidae	5	0	5						

intermusculars of *Polymixia* differ from the non-acanthomorphs in having (1) the distal part of the 1st epineural displaced ventrally into the horizontal septum (in the acanthomorphs, the distal part of the 2nd and several succeeding epineurals are displaced ventrally into the horizontal septum); (2) the points of origin of the 3rd to 10th epineurals are displaced ventrally from the neural arch to the parapophysis or centrum (in the acanthomorphs, the points of origin of the 3rd and several succeeding epineurals are displaced onto the ribs, except in *Holocentrus*); and (3) the epicentral ligaments extend anterior to the 2nd centrum (in the acanthomorphs, the epicentral ligaments, if present, lie posterior to the ventrally displaced epineurals). *Polymixia* and *Holocentrus* are the only living acanthomorphs with a series of epipleurals.

In our study, all percomorphs were found to have the same divisions of the adductor mandibulae (A1+A2 α), which can be found in all members of this taxon; so it seems that this configuration can be treated as a synapomorphic character supporting the monophyly of the Percomorpha.

However, an A1+A2 α division is also present in the Lampridifonnes and Polymixiiformes. The presence of A1+A2 α may support the Lampridiformes and Polymixiiformes having close affinities to the Percomorpha, or may be synapomorphic at a higher level. Further evidence pertaining to this issue is needed.

Many studies have concluded the some or all of the tetraodontiforms are most closely related to the acanthuroids (Tyler 1970a b c 1980, Mok and Shen 1983), as well as being related to zeiform fishes (Rosen 1984, Tyler et al. 2003). The evidence presented in this study also suggests that acanthuroids show an affinity to the Balistoidea. In the study of Winterbottom (1974b), the major difference between the Triacanthoidei and Tetraodontoidei was in the divisions of the adductor mandibulae. It is worth noting here that the pattern of the Triacanthoidei can only be found in the Percoidei, but neither in acanthuroids nor in zeiforms. In some basal Percoidei, there is a free section of A1 separated from the hyomandibular plus an insertion site of section A2 α free from the

Table 3. Distributions of branchiostegal rays in the Perciformes summarized from McAllister (1968). (AC, anterior ceretohyal; PC, posterior ceretohyal; HH2, ventral hypohyal)

Taxa	Total	AC	PC	HH2	Taxa	Total	AC	PC	HH2
Percoidei	5~7	0.5~2	4~5		Ammodytoidei	7	2	5	
Scombroidei	7	2~3	4~5		Callionymoidei	5~7	3~4	2~3	
Carangoidei	5~8	2~3	3~6		Blennioidei	4~7	1~2	3~5	
Kurtoidei	7	2	5		Schindlerioidei	5	2	3	
Polynemoidei	7	1	6		Labroidei	5~6	1	4	
Trachinoidei	6~7	1~2	4~6		Gobioidei	4~7	1~2	4~5.5	
Uranoscoipoidei	6	1	5		Siganoidei	5	1.5	3.5	
Stromatiodei	5~7	2	4~5		Icosteidae	6~7	1~2	4~5	
Chaetodontoidei	4~7	1~3	3~5		Echeneidae	8~11	2	6~9	
Embiotocoidei	6	2~2.5	3.5~4		Gobiesocidae	6	2	4	
Pomacentroidei	4~6	1~3	3~4		Anabantoidei	5~6	0~2	4~5	
Nototherniodei	5~7	2	4~5						

Table 4. Distributions of branchiostegal rays in the Tetraodontiformes summarized from Tyler (1980). (AC, anterior ceretohyal; PC, posterior ceretohyal; HH2, ventral hypohyal)

Taxa	Total	AC	PC	HH2	Taxa	Total	AC	PC	H2
Triacanthodidae	6	0	6		Triodontidae	6	2.5	3.5	
Triacanthidae	6	1.5	4.5		Tetraodontidae	6	0	6	
Balistidae	6	1~4	2~5		Diodontidae	6	0	6	
Monacanthidae	5	1~2	3~4		Molidae	6	2	4	
Ostraciidae	6	0	6						

dentary. In *Grammistes*, *Plectorhinchus*, *Glaucosoma*, and *Platax*, fibres of A1 originate indirectly from the hyomandibular by a thin tendinous sheath. In *Labracinus*, *Seriolina*, *Alectis*, and *Luiyanus*, section A1 originates indirectly from the hyomandibular by a strong tendon. In *Microcanthus*, *Kyphosus*, *Scatophagus*, and *Chaetodon*, fibres of A1 originate indirectly from the hyomandibular by a strong tendinous sheath, and most fibres of A2 α insert on the tendinous sheath and the ventral part of A1. In *Dentex* and *Acanthopagrus*, the insertion site of section A2 α is on A1, and the origin of A1 is A2 α . Although all percomorphs have the typical A1 +A2 α division, the special configuration of A2 α on A1 is only found in the Percoidei (especially the Sparidae and lineages of the Chaetodontidae, Scatophagidae, and Kyphosidae) and Triacanthoidei.

Winterbottom (1974a) described 3 muscles, the flexor dorsalis superior, flexor ventralis inferior and levator arcus palatini, that suggest an affinity between acanthurids and non-triacanthoid tetraodontiforms. In these fishes, (1) the flexor dorsalis superior is extensively developed and originates from the centra (or neural arches in acanthurids), (2) the flexor ventralis inferior is also extensively developed, and originates from the centra (or haemal arches in acanthurids), and (3) the levator arcus palatini is reduced. In triacanthoids, (1) the flexor dorsalis superior originates from tips of the neural spine, (2) the flexor ventralis inferior originates from tips of the haemal spine, and (3) the levator arcus palatini is well developed and conical in shape. However, these conditions in triacanthoids are plesiomorphic at this level of analysis. These muscles suggest an affinity between acanthurids and non-triacanthoid tetraodontiforms, but not between triacanthoids and percoids. However, acanthurids have been very firmly placed within the acanthuroids (Tyler et al. 1989, Winterbottom 1993) to the complete exclusion of any group of tetraodontiforms.

Acknowledgments: We thank Dr. H. K. Mok (National Sun Yat-sen University, Kaohsiung, Taiwan), Dr. K. C. Shao (Academia Sinica, Taipei, Taiwan) and Dr. R. Winterbottom (Royal Ontario Museum, Toronto, Ontario, Canada) for reading and commenting on the manuscript.

ADDREVIATIONS

A1 Adductor mandibulae A1;

A2 Adductor mandibulae A2;
 A3 Adductor mandibulae A3;
 Aw Adductor mandibulae Aw;
 AAP Adductor arcus palatini;
 DO Dialator operculi;
 LAP levator arcus palatini;
 LO levator operculi;
 RAP Retractor arcus palatini;
 RMV Ramus mandibularis V.

REFERENCES

- Adriaens D, W Verraes. 1997. Ontogeny of the maxillary barbel muscles in *Clarias gariepinus* (Siluroidei: Clariidae), with some notes on the palatine-maxillary mechanism. *J. Zool. Lond.* **241**: 117-133.
- Baldwin CC, GD Johnson. 1996. Interrelationships of Aulopiformes. In MLJ Stiassny, LR Parenti, GD Johnson, eds. *Interrelationships of fishes*. New York: Academic Press, pp. 355-404.
- Borden WC. 1998. Phylogeny of the unicornfishes (*Naso*, Acanthuridae) based on the soft anatomy. *Copeia* **1998**: 104-113.
- Cabuy E, D Adriaens, W Verraes, GG Teugels. 1999. Comparative study on the cranial morphology of *Gymnallabes typus* (Siluriformes: Clariidae) and their less anguilliform relatives, *Clariallabes melas* and *Clarias gariepinus*. *J. Morphol.* **240**: 169-194.
- Devaere S, D Adriaens, W Verraes, GG Teugels. 2001. Cranial morphology of the anguilliform clariid *Chanallabes apus* (Günther, 1873) (Teleostei: Siluriformes): Are adaptations related to powerful biting? *J. Zool. Lond.* **255**: 235-250.
- Diogo R, M Chardon. 2000. Homologies among different adductor mandibulae sections of teleostean fishes, with special regard to catfishes (Teleostei: Siluriformes). *J. Morphol.* **243**: 193-208.
- Edgeworth FH. 1935. *The cranial muscles of the vertebrates*. Cambridge, UK: Cambridge Univ. Press, 493 pp.
- Gill AC, RD Mooi. 1993. Monophyly of the Grammatidae and the Notograptidae, with evidence for their phylogenetic positions among perciforms. *Bull. Mar. Sci.* **51**: 327-350.
- Gosline WA. 1986. Jaw muscle configuration in some teleostean fishes. *Copeia* **1986**: 705-713.
- Gosline WA. 1989. Two patterns of differentiation in the jaw musculature of teleostean fishes. *J. Zool. Lond.* **218**: 649-661.
- Greenwood PH, DE Rosen, SH Weitzman, GS Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. *Bull. Am. Mus. Nat. Hist.* **131**: 339-456.
- Johnson GD, CC Baldwin, M Okiyama, Y Tominaga. 1996. Osteology and relationships of *Pseudotriconotus altivelis* (Teleostei: Aulopiformes: Pseudotriconotidae). *Ichthyol. Res.* **43**: 17-45.
- Johnson GD, C Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bull. Mar. Sci.* **52**: 554-626.
- Kaufman LS, KF Liem. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): phylogeny, ecology, and evolutionary significance. *Breviora* **472**: 1-19.

- Kent GC. 1983. Comparative anatomy of the vertebrates. 2nd ed. St. Louis, MO: CV Mosby, 604 pp.
- Liem KF. 1986. The pharyngeal jaw apparatus of the Embiotocidae (Teleostei): a functional and evolutionary perspective. *Copeia* **1986**: 311-323.
- McAllister DE. 1968. The evolution of branchiostegals and associated gular, opercular and hyoid bones and the classification of teleostome fishes, living and fossil. *Bull. Natl. Mus. Can.* **221**: 1-239.
- Mok HK, HJ Chang, CY Lee. 1990. Phylogenetic interrelationships of the perciform Acanthoclinidae, Grammidae, Plesiopidae, Pseudochromidae and Opistognathidae. *Bull. Inst. Zool. Acad. Sin. (Taipei)* **29**: 29-39.
- Mok HK, SC Shen. 1983. Osteology and phylogeny of Squamipinnes. Taipei, Taiwan: Taiwan Mus. Spec. Publ. Ser. Zool. 1. 87 pp.
- Nelson JS. 1994. *Fishes of the world*. 3rd ed. New York: J Wiley, 600 pp.
- Olney JE, GD Johnson, CC Baldwin 1993. Phylogeny of lampridiform fishes. *Bull. Mar. Sci* **52**: 137-169.
- Parenti LR. 1993. Relationships of atherinomorph fishes (Teleostei). *Bull. Mar. Sci.* **52**: 170-196.
- Parenti LR, J Song. 1996. Phylogenetic significance of the pectoral-pelvic fin association in acanthomorph fishes: a reassessment using comparative neuroanatomy. In MLJ Stiassny, LR Parenti, GD Johnson, eds. *Interrelationships of fishes*. New York: Academic Press, pp. 427-444.
- Patterson C, GD Johnson. 1995. The intermuscular bones and ligaments of teleostean fishes. Washington, DC: Smithsonian. *Contrib. Zool.* no. 559, 83 pp.
- Rosen DE. 1973. Interrelationships of higher euteleostean fishes. In PH Greenwood, RS Miles, C Patterson, eds. *Interrelationships of fishes*. *J. Linn. Soc. (Zool.)* **53**: 397-513. **Supplement 1**. New York: Academic Press.
- Rosen DE. 1984. Zeiformes as primitive plectognath fishes. *Am. Mus. Novit.* **2782**: 1-45.
- Rosen DE, C Patterson. 1969. The structure and relationships of the paracanthopterygian fishes. *Bull. Am. Mus. Nat. Hist.* **141**: 357-474.
- Stiassny MLJ. 1990. Notes on the anatomy and relationships of the bedotiid fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotiidae). *Am. Mus. Novit.* **2979**: 1-33.
- Stiassny MLJ. 1993. What are grey mullets? *Bull. Mar. Sci.* **52**: 197-219.
- Stiassny MLJ. 1996. Basal ctenosquamate relationships and the interrelationship of the mytophiform (scopelomorph) fishes. In MLJ Stiassny, LR Parenti, GD Johnson, eds. *Interrelationships of fishes*. New York: Academic Press, pp. 405-426.
- Stiassny MLJ, JS Jensen. 1987. Labroid intrarelations revisited: morphological complexity, key innovations, and the study of comparative diversity. *Bull. Mus. Comp. Zool.* **151**: 269-319.
- Stiassny MLJ, J Moore. 1992. A review of the pelvic girdle of acanthomorph fishes, with a provisional hypothesis of acanthomorph intrarelations. *J. Zool. Lond.* **104**: 209-242.
- Suda Y. 1996. Osteology and muscular attachments of the Japanese jack mackerel, *Trachurus japonicus*. *Bull. Mar. Sci.* **58**: 438-493.
- Takahasi N. 1925. On the homology of the cranial muscles of the cypriniform fishes. *J. Morphol.* **40**: 1-103.
- Tyler JC. 1970a. The dorsal and anal spine-locking apparatus of surgeon fishes (Acanthuridae). *Proc. Calif. Acad. Sci.* **38**: 391-409.
- Tyler JC. 1970b. The progressive reduction in the number of elements supporting the caudal fin of fishes of the order Plectognathi. *Proc. Acad. Nat. Sci. Phil.* **122**: 1-85.
- Tyler JC. 1970c. Osteological aspects of interrelationships of surgeon fish general (Acanthuridae). *Proc. Acad. Nat. Sci. Phil.* **122**: 87-124.
- Tyler JC. 1980. Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). NOAA Tech. Rept. NMFS Circular **434**: 1-422.
- Van Dobben WH. 1935. Über den Kiefermechanismus der Knochenfische. *Arch. néerlandaises Zool.* **2**: 1-72.
- Van Tassel JL. 2001. *Chromogobius* (Teleostei: Gobiidae): a new species from the Eastern Atlantic. *Copeia* **2001**: 1073-1080.
- Winterbottom R. 1974a. A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Phil.* **125**: 225-317.
- Winterbottom R. 1974b. The familial phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as evidenced by their comparative myology. Washington, DC: Smithsonian. *Contrib. Zool.* 155, 201 pp.
- Winterbottom R. 1993. Myological evidence for the phylogeny of recent genera of surgeonfishes (Percomorpha, Acanthuridae), with comments on the Acanthoidei. *Copeia* **1993**: 21-39.