

Comparative morphology of the adductor mandibulae musculature of notothenioid fishes (Pisces, Perciformes)

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Abstract: The jaw musculature of notothenioid fishes is described and compared based on a total of 38 species referred to eight families of the suborder Notothenioidei. In the Notothenioidei, the adductor mandibulae, the largest and most conspicuous of the cranial muscles, is generally composed of sections A1, A2, A3 and Aw as in the generalized percoids. The morphology of the adductor mandibulae is similar in most notothenioid families except the Nototheniidae and Bathydraconidae. *Notothenia*, *Paranotothenia* and *Dissostichus* are clearly distinguished from the other nototheniid genera in having A3. *Gymnodraco* of the Bathydraconidae has a fused A1-A2 complex and the anterior element is segmented by a tendinous intersection from the A1-A2 complex. These features are unique to *Gymnodraco* and not seen in other bathydraconids. The Harpagiferidae and Artedidraconidae share the same apomorphy, the presence of A1 β , with the Nototheniidae and have no synapomorphies with the Bathydraconidae and Channichthyidae. The character distribution, however, shows some inconsistencies with the previous classifications. Based on the limited evidence obtained in this study, the Notothenioidei can be divided into six groups and it seems reasonable to suggest a review of the current classification of the Nototheniidae.

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Introduction

The suborder Notothenioidei is the most abundant in terms of biomass and species diversity in the Antarctic Ocean and comprises the important element of the Antarctic marine ecosystems. This suborder is composed of eight families, the Pseudaphritidae, Bovichtidae, Eleginopidae, Nototheniidae, Harpagiferidae, Artedidraconidae, Bathydraconidae and Channichthyidae and underwent a distinctive diversification in morphology (Eastman 1993, Eastman & Eakin 2000, Balushkin 2000). Phylogenetic reconstructions of the Notothenioidei have been carried out using both morphological and molecular data (Iwami 1985, Bargelloni *et al.* 1994, 2000, Bargelloni & Lecointre 1998, Balushkin 2000). However, the results are partly inconsistent and phylogenetic relationships among the notothenioid genera and families are still controversial.

To shed light on these controversial issues of notothenioid relationships, the morphology of the adductor mandibulae musculature was analysed. According to Winterbottom (1974) and Gosline (1986), muscle architecture is a reliable and easily accessible character for the phylogenetic analyses. However there has never been a study of the comparative myology of the Notothenioidei. This paper illustrates the detailed morphology of the adductor mandibulae, and uses these data as systematic characters in hypothesizing interrelationships within the Notothenioidei.

Material and methods

Specimens for myological examinations were partially stained with Lugol's solution and/or cyanin blue solution prepared according to Bock & Shear (1972) and Saruwatari *et al.* (1997) respectively. Muscle nomenclature is taken from Winterbottom (1974). The terminology follows Johnson *et al.* (1996) for osteology, and Freihofer (1978) for nerves. The species examined in this study are listed in Table I.

Myology

The adductor mandibulae of notothenioid fishes is composed of sections A1, A2, A3 and Aw (Figs 1 & 2). A1 is a superficial muscle originating on the lateral face of the preopercle and inserting via a tendon on the medial surface of the maxillary head. The anteroventral corner of this section converges on the ligamentum primordium inserting in the lateral surface of the maxillary. In the Nototheniidae, Harpagiferidae and Artedidraconidae, this muscle is further subdivided into two subsections (Fig. 1d & f). The anteromedial expansion of A1, tentatively named A1 β , is separated from the original A1 (A1 α) by fascia and is clearly identified as an isolated muscle element. This subsection, A1 β , lies completely medial to A1 α and does not originate from any bony elements. Since A1 is defined by its insertion on the maxillary (Winterbottom, 1974), the fact that the anterior margin of A1 β fuses with a tendon

Table I. Character conditions of the adductor mandibulae in the Notothenioidei.

| Family/Species | Characters | | | | |
|-----------------------------------|------------|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| Pseudaphritidae | | | | | |
| <i>Pseudaphritis urvillii</i> | 0 | 0 | 0 | 0 | 0 |
| Bovichtidae | | | | | |
| <i>Bovichtus angustifrons</i> | 0 | 0 | 0 | 0 | 0 |
| <i>Bovichtus argentinus</i> | 0 | 0 | 0 | 0 | 0 |
| <i>Cottopecter trigloides</i> | 0 | 0 | 0 | 0 | 0 |
| Eleginopsidae | | | | | |
| <i>Eleginops maclovinus</i> | 0 | 0 | 0 | 0 | 0 |
| Nototheniidae | | | | | |
| <i>Dissositchus eleginoides</i> | 0 | 1 | 0 | 0 | 0 |
| <i>Dissositchus mawsoni</i> | 0 | 1 | 0 | 0 | 0 |
| <i>Gobionotothen gibberifrons</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Lepidonotothen kempfi</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Lepidonotothen larseni</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Lepidonotothen nudifrons</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Notothenia coriiceps</i> | 0 | 1 | 0 | 0 | 0 |
| <i>Notothenia rossii</i> | 0 | 1 | 0 | 0 | 0 |
| <i>Pagothenia borchgrevinkii</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Paranotothenia magellanica</i> | 0 | 1 | 0 | 0 | 0 |
| <i>Patagonotothen ramsayi</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Patagonotothen tessellata</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Pleuragramma antarcticum</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Trematomus bernacchii</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Trematomus eulepidotus</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Trematomus hansonii</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Trematomus loennbergii</i> | 0 | 1 | 0 | 1 | 0 |
| <i>Trematomus scotti</i> | 0 | 1 | 0 | 1 | 0 |
| Harpagiferidae | | | | | |
| <i>Harpagifer antarcticus</i> | 0 | 1 | 0 | 0 | 0 |
| Artedidraconidae | | | | | |
| <i>Histiadraco velifer</i> | 0 | 1 | 0 | 0 | 0 |
| <i>Pogonophryne marmorata</i> | 0 | 1 | 0 | 0 | 0 |
| <i>Pogonophryne scotti</i> | 0 | 1 | 0 | 0 | 0 |
| Bathydraconidae | | | | | |
| <i>Bathydraco macrolepis</i> | 0 | 0 | 0 | 0 | 1 |
| <i>Gerlachea australis</i> | 0 | 0 | 0 | 0 | 1 |
| <i>Gymnodraco acuticeps</i> | 1 | 0 | 1 | 0 | 1 |
| <i>Parachaenichthys charcoti</i> | 0 | 0 | 0 | 0 | 1 |
| Channichthyidae | | | | | |
| <i>Chaenocephalus aceratus</i> | 0 | 0 | 0 | 0 | 1 |
| <i>Chaenodraco wilsoni</i> | 0 | 0 | 0 | 0 | 1 |
| <i>Champscephalus gunnari</i> | 0 | 0 | 0 | 0 | 1 |
| <i>Channichthys rhinoceratus</i> | 0 | 0 | 0 | 0 | 1 |
| <i>Chionodraco rastrospinosus</i> | 0 | 0 | 0 | 0 | 1 |
| <i>Cryodraco antarcticus</i> | 0 | 0 | 0 | 0 | 1 |
| <i>Neopagetopsis ionah</i> | 0 | 0 | 0 | 0 | 1 |

Characters: 1 = fused A1-A2 complex present, 2 = A1 β present, 3 = "anterior section" present, 4 = A3 absent, 5 = A3 well developed.
States: 0 = primitive state (plesiomorphic), 1 = derived state (apomorphic).

connecting with A2 and Aw suggests uncertainty in its classification. The homology for A1 β found in the Nototheniidae, Harpagiferidae and Artedidraconidae with that described in other fishes is therefore questionable, and the appropriate terminology for this small element is left for future study.

A2 is a superficial muscle occupying the ventrolateral region of the cheek, and originates on the lateral surface of the preopercle, metapterygoid, symplectic and quadrate. It inserts on the medial surface of the retroarticular and on Aw by a tendon. Sometimes in the bathydraconids, A2 is not clearly divided from A1 superficially, but the boundary between the two elements can be confirmed in cross section of the muscles. In *Gymnodraco*, A2 fuses with A1 α completely and to form A1-A2 complex. The anterior part of this A1-A2 complex is segmented by a tendinous intersection and could be recognized as a different element from the rest part of A1-A2 complex (Fig. 2c). Since the origin and the process of formation of this element is obscure, it is tentatively called "the anterior section".

A3, the most medial section of the adductor mandibulae, is found in all nototheniid fishes examined except for the nototheniid genera, *Gobionotothen*, *Lepidonotothen*, *Pagothenia*, *Patagonotothen*, *Pleuragramma* and *Trematomus*. It lies on the dorsolateral surface of the palatal arch and connects with the posterior border of Aw by an aponeurosis. In the Channichthyidae and Bathydraconidae, A3 is well developed and originates from the lateral faces of the hyomandibular, symplectic, metapterygoid and quadrate (Fig. 2e). External to A3 the ramus mandibularis trigeminus runs downward and innervates the lower jaw components (Figs 1 & 2).

Aw is situated on the medial surface of the lower jaw. This section connects with the anterior border of A2 and A3 via a strong tendon. There is no remarkable difference in the morphology of Aw among nototheniid fishes.

Results and discussion

Since there is little information on the occurrence and homology of muscles of the Notothenioidei within the teleostean fishes, the condition of the cheek musculature of generalized perciform fishes is used for examining trends in the notothenioids (Winterbottom 1974, Yabe 1985, Gosline 1986).

Among nototheniid families, A1 β is found only in the Nototheniidae, Harpagiferidae and Artedidraconidae. The fact that the generalized percoids have no such small subsection suggests that the presence of A1 β is apomorphic. The condition found in the rest of nototheniid groups, the Pseudaphritidae, Bovichtidae, Eleginopidae, Bathydraconidae and Channichthyidae, is thus considered plesiomorphic.

In the Bathydraconidae, partial or total fusion between A1 and A2 may occur. Among bathydraconid genera examined, only A1 of *Gymnodraco* fuses with A2 completely and forms A1-A2 complex. According to Yabe (1985), the cheek muscles of generalized percoid fishes are not well separated. However Gosline (1986) showed that A1 and A2 of generalized percoids are distinct from one another and are not subdivided. The condition found in *Gymnodraco* is

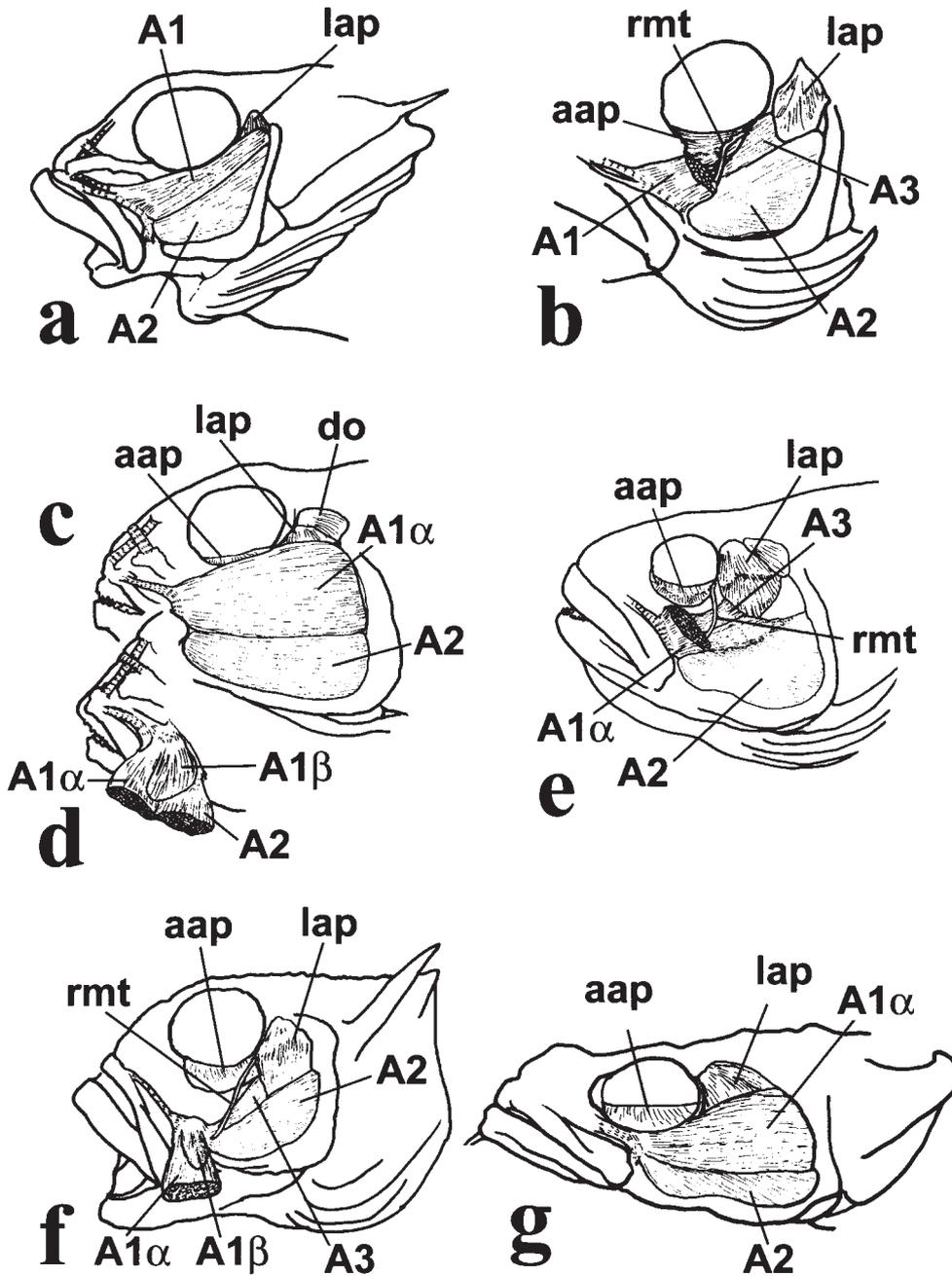


Fig. 1. Left lateral view of the cheek muscles. **a.** *Bovichtus argentinus* (superficial view), **b.** *B. argentinus* (lateral view after removing A1), **c.** *Gobionotothen gibberifrons* (superficial view), **d.** *G. gibberifrons* (medial view of A1 and A2), **e.** *Notothenia coriiceps* (lateral view after removing A1), **f.** *Harpagifer antarcticus* (superficial view), **g.** *Pogonophryne marmorata* (superficial view). A = adductor mandibulae, aap = adductor arcus palatine, do = dilatator operculi, lap = levator arcus palatine, rmt = ramus mandibularis trigeminus. Aw is not visible in this view.

regarded here as apomorphic according to Gosline (1986). The fact that all but the Bathydraconidae have A1 clearly separated from A2 may provide additional support for this character analysis. *Gymnodraco* is further characterized by having the small anterior section of the A1-A2 complex isolated by a tendinous intersection. Since the element is

absent in generalized percoids and other notothenioids, this condition is considered an autapomorphy of *Gymnodraco*.

Except for some nototheniid genera, all of the nototheniid fishes have A3. Since A3 is present in the generalized percoids as the most medial section of the adductor mandibulae, the loss of A3 in most nototheniids is

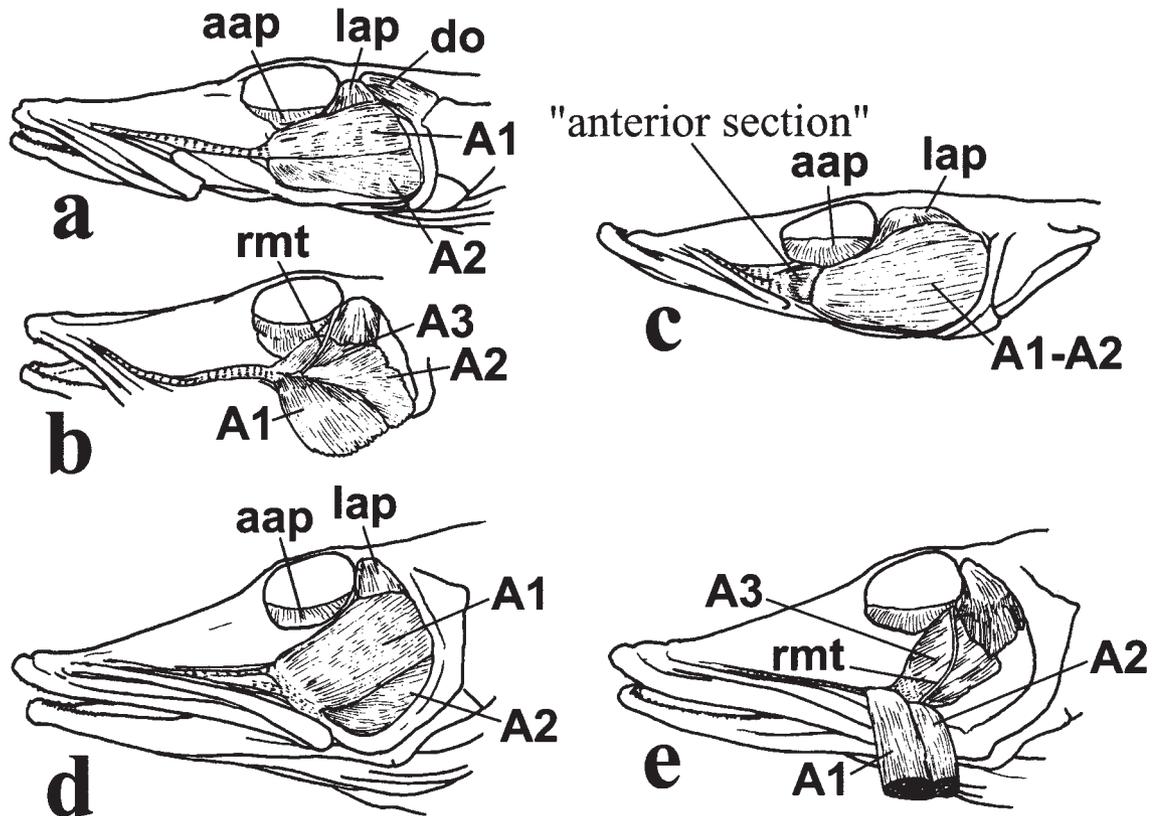


Fig. 2. Left lateral view of the cheek muscles. **a.** *Parachaenichthys charcoti* (superficial view), **b.** *P. charcoti* (medial view of A1 and A2), **c.** *Gymnodraco acuticeps* (superficial view), **d.** *Chaenocephalus aceratus* (superficial view), **e.** *C. aceratus* (medial view of A1 and A2). A = adductor mandibulae, aap = adductor arcus palatini, do = dilatator operculi, lap = levator arcus palatini, rmt = ramus mandibularis trigeminus. Aw is not visible in this view.

considered apomorphic. In contrast with A3 of most notothenioids, that of the Bathydraconidae and Channichthyidae is well developed and the separation between A2 and A3 is distinct. It is clear that the condition found in the Bathydraconidae and Channichthyidae shows a different character state from that of other notothenioids with A3. The developed A3 is regarded here as apomorphic.

The conditions of the characters discussed above in the notothenioid fishes are summarized in Table I. Based on the patterns of the adductor mandibulae, six groups are recognized:

- 1) the Pseudaphritidae - Bovichtidae - Eleginopidae,
- 2) the Nototheniidae (*Notothenia* / *Paranotothenia* / *Dissostichus*) - Harpagiferidae - Artedidraconidae,
- 3) Nototheniidae (*Gobionotothen* - *Lepidonotothen* - *Pagothenia* - *Patagonotothen* - *Pleuragramma* - *Trematomus*),
- 4) Bathydraconidae (*Bathydraco* - *Gerlachea* - *Parachaenichthys*),
- 5) Bathydraconidae (*Gymnodraco*), and

6) Channichthyidae.

Close relationships among the members of the group (3) are supported by the presence of A1 β . This indicates that the Harpagiferidae and Artedidraconidae have a sister group relationship with the Nototheniidae, rather than with the Bathydraconidae and Channichthyidae. This taxonomic position of the Harpagiferidae and Artedidraconidae is inconsistent with that of the previous studies (Iwami 1985, Bargelloni *et al.* 1994, Ritchie *et al.* 1997, Balushkin 2000, Bargelloni *et al.* 2000), and can be attributed to a small number of useful characters. In addition, even though the present findings are based on limited evidence, the Nototheniidae could be clearly divided into two groups by the presence or absence of A3. The monophyly of the Nototheniidae has been controversial (Bargelloni *et al.* 1994, Ritchie *et al.* 1997, Bargelloni *et al.* 2000, Tokita *et al.* 2002) and the present result is consistent with these molecular studies. Therefore it seems reasonable to revise the current classification of the Nototheniidae. Since the number of characters found in the adductor mandibulae is too small to construct a reliable phylogeny, a detailed cladistic analysis will be left for future study.

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