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ON THE FUNCTIONAL SIGNIFICANCE OF THE DORSAL PART OF THE Aω MUSCLE IN *POMATOSCHISTUS LOZANOI* (TELEOSTEI : GOBIIDAE)

by

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SUMMARY

In *Pomatoschistus* the dorsal fibres of the A_ω section of the musculus adductor mandibulae-complex insert on the tendon of the A_3 section. Three hypotheses are postulated concerning the mechanical implication of this construction during co-contraction of both muscle parts. These are tested for *P. lozanoi* by means of a mathematical statical bite model. Most likely, this adductor configuration enhances the overall bite performance whithin the spatial constraints of the gobiid head.

Key words : Biomechanics, muscle function.

INTRODUCTION

In *Pomatoschistus* the cheek muscles (musculus adductor mandibulae-complex) are very well developed (Fig. 1, A and B). Broadly, the division of these muscles follows the general percomorph pattern as discribed by WINTERBOTTOM (1974). Remarkable, however, is the insertion of the dorsal fibres of the A_ω section (A_ωd) on the tendon of the A_3 portion (Fig. 1B). This paper deals with the functional relevance of such a construction.

MATERIALS AND METHODS

Pomatoschistus specimens were obtained from the Marine Section of the Institute of Zoology (Universty of Ghent). Dissections and observations were done on 10 *P. lozanoi* specimens of several length classes. One series of transverse sections (glycol-metacrylate; 5µm) of *Pomatoschistus lozanoi* (SL 48.1 mm;

TL 56.7 mm) was used to calculate the physiological cross sections of the muscles and the coordinates of the points in Fig. 1C. They where measured with the aid a Hewlett Packard 9826A microcomputer extended with a Summagraphics digitiser (type ID). The mathematical model was implemented on an IBM AT computer (see discussion).

RESULTS

MESTERMANN and ZANDER (1984) gave a detailed description of the cranial osteology of the *Pomatoschistus* genus. A general description was already given by REGAN (1911) and GREGORY (1933). The typically fenestrated suspensorium in this family can be related to the extensive development of the cheek muscles (DECLEYRE *et al.*, 1990).

The A_3 muscle fibres originate on the caudal rim of the fenestra (Fig. 1B). They insert as two distinct bundles on a tendinous connective tissue sheet. This sheet tapers rostrally into a tendon (A_3t ; see Fig. 1B) that passes to the medial side of the mandible at the level of the mandibulo-suspensorial articulation (called further on « the articulation *s.s.* »). A_3t inserts via the sesamoid coronomeckelium on the cartilago meckeli.

On the lateral surface of the suspensorium the A_1 section is situated dorsally from the A_3 part. They are both covered by the well developed A_2 portion of the cheek muscle which in turn is divided in a dorsal α and a ventral β part (Fig. 1A).

The A_ω section inserts on the medial surface of the mandible. Most of its fibres originate from a tendinous sheet, connected to the medial side of the suspensorium. A small portion of this muscle, the dorsalmost fibres (A_ωd), however, do not attach to the tendon sheet but originate on A_3t (Fig. 1B). This description refers to *Pomatoschistus lozanoi.* The same muscle configuration has also been found in *P. minutus* and *P. norvegicus.*

The presence of a connection between the A_3 and the A_ω sections is not unique among Teleosts (see WINTERBOTTOM, 1974). For instance, a comparable configuration of A_3 and A_ω to that of *Pomatoschistus lozanoi* also exists in the carp (*Cyprinius carpio* ; SCAPALO, 1989), where all fibres of A_ω are connected to A_3t.

DISCUSSION

The contraction of A_3 will cause a moment on the lower jaw about the articulation. Contraction of A_ωd, (1) can result in the lifting of A_3t (thereby increasing its angle of insertion) which will affect the moment component of the A_3 force on the lower jaw and (2) can cause an additional moment on the lower jaw (see Fig. 1C). As a functional explanation for the presence of A_ωd on A_3t three hypotheses can be proposed :

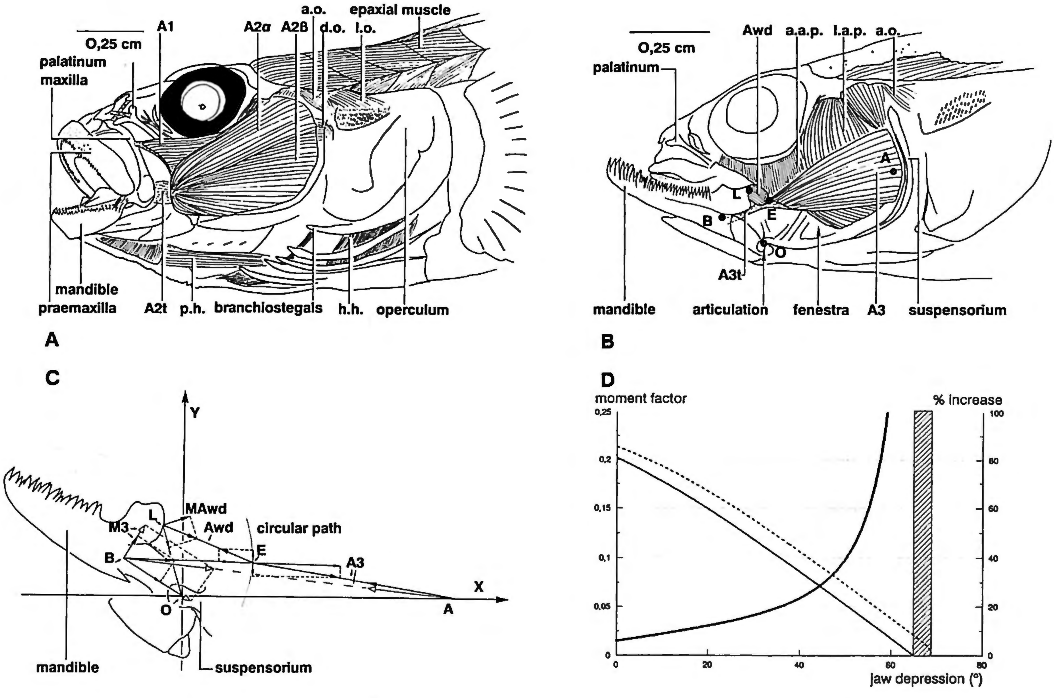

Fig. 1. — A : *Pomatoschistus lozanoi*, SL 50.55 mm ; TL 60.65 mm, dissection of the musculus adductor mandibulae-complex, skin removed. B : *Pomatoschistus lozanoi*, SL 54.2 mm ; TL 65.0 mm, dissection of the musculus adductor mandibulae-complex : A_1, $A_2\alpha$, $A_2\beta$ and upper jaw removed. C : Force diagram. The forces resulting in a moment on the lower jaw are shown. Fully black arrows are used in the case of co-contracting of A_3 and $A_\omega d$; sole contraction of A_3 is is represented by white arrow-heads. $A_\omega d$ and A_3 here refer to the line of action of these muscles ; M_3 : moment component of A_3 on the lower jaw ; $MA_\omega d$: moment component of $A_\omega d$. D : Graph of the moment factor (left Y-axis) on the lower jaw without (full line) and with the co-contraction of $A_\omega d$ (dashed line). The bold line gives the percental increase of the moment factor as the result of the co-contraction referred to the sole A3 activity (right Y-axis). The hatched zone represents the shift of DP (see text).

Abbreviations : A : caudal insertion of A_3 ; a.a.p : adductor arcus palatini ; a.o. : adductor operculi ; $A_{1,2,3}$: parts of the adductor mandibulae-complex ; A_2t : tendon of A_2 ; A_3t : tendon of A_3 ; $A_\omega d$: dorsal part of A_ω ; B rostral insertion of A_3 ; d.o. : dilatator operculi ; E : insertion of $A_\omega d$ on A_3t ; h.h. : hyohyoideus ; L : insertion of $A_\omega d$ on the coronoid process ; l.a.p. : levator arcus palatini ; l.o. : levator operculi ; M_3 : moment component of A_3 on the lower jaw ; $MA_\omega d$: moment component of $A_\omega d$; O : mandibulo-suspensorial articulation ; p.h. : protractor hyoidei.

Hypothesis 1 : From a certain degree of mouth opening onwards, A_3t will lie on the articulation. In these circumstances A_3 is no longer functional because the force exerted by the muscle passes almost through the fulcrum of the lever. The lower jaw position in which this initially occurs is called the 'dead point' (DP). Lifting of A_3t can thus postpone the DP of A_3 to a larger angle of jaw depression.

Hypothesis 2: $A_\omega d$ can trigger the fast closure of the mouth. If the lower jaw has passed the DP, the A_3 can be active without influencing that jaw position. Hence, if A_3t could be lifted from the articulation, this would provide a trigger for the sudden release of the A_3 power. $A_\omega d$ might function as a trigger in two ways: (1) by direct elevation of A_3t and (2) indirectly by elevation of the lower jaw, which will also lift A_3t (Fig. 1C).

Hypothesis 3: For any given jaw position $A_\omega d$ contraction can lift A_3t. This can, together with the moment component of $A_\omega d$ ($MA_\omega d$ in Fig. 1C) enlarge the total moment on the lower jaw and produce a stronger bite (Fig 1C and D).

These hypotheses are tested by means of a mathematical static bite model for *Pomatoschistus lozanoi* (Fig. 1C). This calculates the moment exerted on the lower jaw by A_ω with and without the co-contraction of $A_\omega d$. All involved lengths are standardized, taking the distance OA (Fig. 1B and C) as unit length. As a simplification the muscles were considered always to contract maximally. The maximal muscle force is directly proportional to the physiological cross section (= section perpendicular to the fibre direction, see a.o. (GANS, 1982). This was used as a measure for the muscle force. The force of A_3 is arbitrary set to 1 and the ratio of the force of $A_\omega d$ to A_3 is 0.14. Consequently, the model output is given as dimensionless moment factors (Fig. 1D). In the model a fixed length for A_3t (BE in Fig. 1B and C) has been assumed. Therefore, activity of $A_\omega d$ tends to move the point E upwards along a circular path around the point B (Fig. 1C). For each position of jaw depression, there will exist only one point on this path coinciding with static force equilibrium.

The predicted shift of DP is depicted as the hatched area in Fig. 1D. It can be questioned whether an increase of only 4° adequately explains the extraordinary positioning of $A_\omega d$ muscle fibres. Moreover, measurements indicate that the angle of maximal jaw depression immediately precedes or just coincides with the hatched area in the graph (± 65°). This obviates the need for a shift in DP. Therefore hypothesis 1 is rejected. However, it must be noticed that for the maximally opened mouth the co-contracting $A_\omega d$ and A_3 exert a moment on the jaw, contrary to the sole activity of A_3 (hatched area in Fig. 1D).

$A_\omega d$ will only be able to lift the tendon, to act as the trigger for the pre-stressed A_3, for jaw positions just under the DP (hatched area in Fig. 1D). This will demand a very precise regulation of the jaw opening: if the jaw is depressed too far (beyond the hatched area) the trigger will not work. If it is not depressed far enough (before the hatched area) there will exist no pre-stressed situation. As mentioned above maximal gape might coincide with the hatched area. Thus, in these circumstances triggering will be possible. On the other hand elevation of the lower jaw (second aspect of triggering, see above) can also be done by the other sections of the musculus adductor mandibulae. Electromyography of the involved muscles may further help to falsify or to consolidate hypothesis 2.

From Fig. 1D, hypothesis 3 seems to be the most plausible one. The moment on the lower jaw is considerably enhanced for all possible opening angles of the lower jaw. For an intermediate jaw position an increase of about 20 % is calculated (see Fig. 1D). An equally forceful A_3 muscle *without the aid of* A_ω*d* would be more voluminous as its physiological cross section would increase to the same extent. Since the well developed $A_2\alpha$ and $A_2\beta$ sections strongly limit the expansion of A_3, the presence of the (small) A_ωd can considerably optimize the bite force.

CONCLUSION

A functional explanation for the insertion of the dorsal fibres of the A_ω section on the tendon of the A_3 portion can be found in the fact that this substantially enhances the overall biting force of the individual within the spatial constraints of the gobiid fish head.

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