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A NOVEL BITING MECHANISM IN DAMSELFISHES (POMACENTRIDAE): THE PUSHING UP OF THE LOWER PHARYNGEAL JAW BY THE PECTORAL GIRDLE

by

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ABSTRACT

This study presents a novel mechanism for biting with the pharyngeal jaws in the labroid family Pomacentridae (damselfishes). Results of experiments in which 9 branchial and hyoid muscles were electrically stimulated are presented. Upon contraction of the m. protractor pectoralis the pectoral girdle is protracted and makes contact with the lower pharyngeal jaw resulting in the elevation of the lower pharyngeal jaw. The force of the m. protractor pectoralis contributes to the biting force of the m. levator externus 4 and m. levator posterior during biting and in this way increases the total biting force that can be exerted on prey.

KEY WORDS: Pomacentridae, Cichlidae, Labroidei, pharyngeal jaw apparatus, pectoral girdle, biting.

INTRODUCTION

The pharyngeal jaw apparatus of labroid fishes is of strong evolutionary significance: 7 out of the 8 characters that distinguish this suborder from other perciforms are found in the pharyngeal jaw apparatus (STIASSNY & JENSEN, 1987). Furthermore, the functioning of the pharyngeal jaw apparatus is supposed to have played an important role in the speciation and diversification of cichlids and other labroids (LIEM, 1973; LIEM & SANDERSON, 1986; GALIS & DRUCKER, 1996). The pharyngeal biting in labroids is characterized by a powerful upward movement of the lower pharyngeal jaw against the prey and the upper pharyngeal jaw. The upper pharyngeal jaw is pressed against the neurocranium so that the neurocranial reaction force contributes to the biting force (fig. 1; GALIS, 1993; GALIS & DRUCKER, 1996). At the place of contact there are large articulation facets, both on the neurocranium and on the upper pharyngeal jaw (a diarthrosis). These

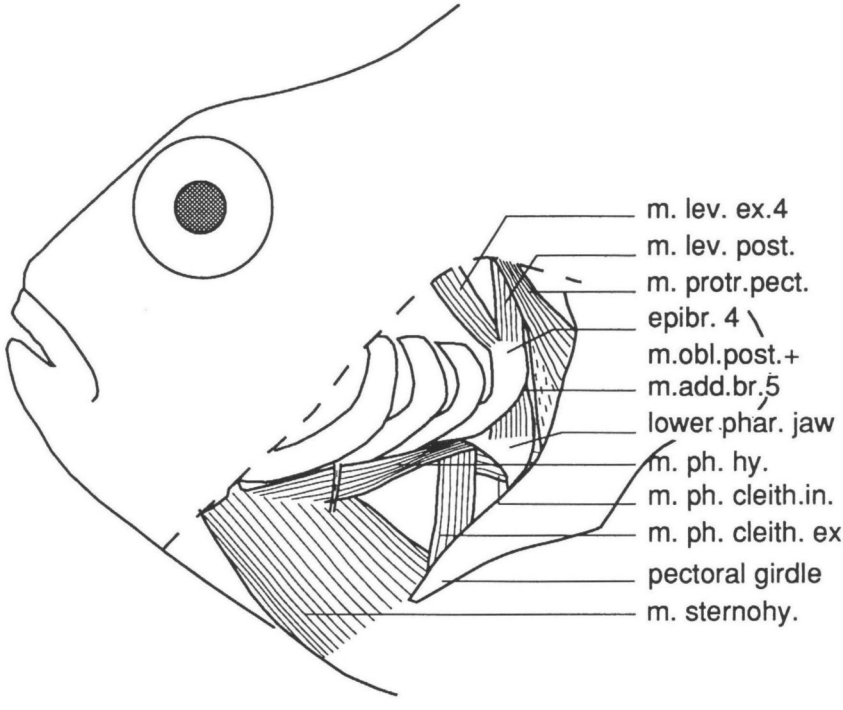

Fig. 1. Lateral view of the pharyngeal jaw musculature in *Amphiprion ocellaris*. Note the large tendinous extension of the m. protractor pectoralis which connects to a large part of the pectoral girdle.

articulation facets are derived characters of the labroids (KAUFMAN & LIEM, 1982; STIASSNY & JENSEN, 1987). Generalized perciforms have a different biting mechanism in which not only the lower pharyngeal jaws are pulled up, but the upper pharyngeal jaws are pressed down at the same time upon contraction of the same levator muscles (coupled biting mechanism, GALIS & DRUCKER, 1995).

Pomacentrids alone lack the key innovation which characterizes the other labroid families (Cichlidae, Labridae and Embiotocidae): the shift of insertion of the m. levator externus 4 from the epibranchial 4 to the lower pharyngeal jaw (figs 1, 2; KAUFMAN & LIEM, 1982; STIASSNY & JENSEN, 1987). The importance of this shift lies in the increased mobility of the lower pharyngeal jaw (LIEM, 1973; GALIS & DRUCKER, 1996). The m. levator posterior, which in some labroids has also shifted from the epibranchial 4 to the lower pharyngeal jaw, is in pomacentrids in the primitive position inserting on the epibranchial 4 (figs 1, 2). These levatores can only indirectly lift the lower pharyngeal jaw via the connection between

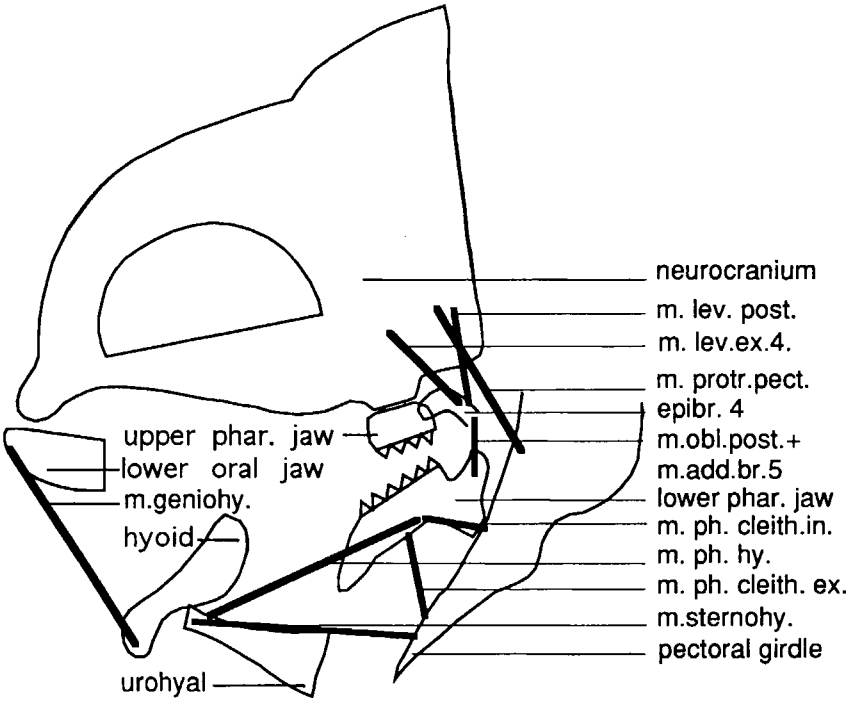

Fig. 2. Schematic illustration of head muscles effecting movements of the lower pharyngeal jaw and the pectoral girdle.

epibranchial 4 and the lower pharyngeal jaw (m. obliquus posterior and m. add. branch. 5, figs 1, 2). A correlated primitive character of the pomacentrids is the presence of strong ligamentous connections between the lower pharyngeal jaw and the fourth gill arches (pers. observation) which couple the movements of these bones as in the generalized perciform centrarchids (GALIS & DRUCKER, 1996). In cichlids these ligaments are absent, adding to the flexibility of the pharyngeal jaw apparatus (probably at a loss of strength, GALIS & DRUCKER, 1996).

A specialized character of the Pomacentridae and the Labridae is the articulation of the lower pharyngeal jaw with the pectoral girdle. It is assumed that this articulation evolved independently in the two families (LIEM & GREENWOOD, 1981; KAUFMAN & LIEM, 1982; STIASSNY & JENSEN, 1987). In cichlids and embiotocids there is no articulation between lower pharyngeal jaw and pectoral girdle. The function of the articulation between pectoral girdle and lower pharyngeal jaw has thusfar not been investigated in pomacentrids. In labrids the pectoral girdle is supposed to support the

lower pharyngeal jaw during biting, because the two bones are continuously in contact during the masticatory cycle (LIEM & SANDERSON, 1986).

We electrically stimulated muscles of the branchial apparatus and of the pectoral girdle in three *Amphiprion* species to investigate the functioning of the lower pharyngeal jaw and the pectoral girdle in pharyngeal biting.

MATERIAL AND TECHNIQUES

Amphiprion specimens for experimentation were obtained from local commercial suppliers. Stimulation experiments were carried out on four specimens: two *Amphiprion ocellaris* Cuvier (7.0 and 5.6 cm SL), one *A. sebae* Bleeker (6.6 cm SL) and one *A. clarkii* (Bennet) (6.8 cm SL). Fishes were anaesthetized with a solution of Hypnodil metomidaat (50 mg/l). The operculum was removed to ensure an unobstructed lateral view of the pharyngeal jaw apparatus. Bipolar fine-wire electrodes (0.05 mm diam.) were inserted via a syringe. A muscle stimulator was used to deliver tetanic stimuli (40 Hz, 1-6 V). Movements of the pharyngeal jaws during muscle stimulation were observed through a stereomicroscope and were confirmed by two observers.

The following muscles were stimulated (see figs 1, 2): m. protractor pectoralis, m.m. pharyngocleithralis internus and externus, m. levator externus 4, m. levator posterior, m. obliquus posterior, m. adductor branchialis 5 (we did not distinguish between the latter two muscles), m. geniohyoideus, m. sternohyoideus and m. pharyngohyoideus.

RESULTS

Contraction of the m. levator posterior and m. levator externus 4 resulted in elevation of the lower pharyngeal jaw as in cichlids, centrarchids and haemulids (GALIS & DRUCKER, 1996; WAINWRIGHT, 1989). Unexpectedly, contraction of the m. protractor pectoralis did not only protract and elevate the pectoral girdle, but in doing so caused elevation of the lower pharyngeal jaw: the pectoral girdle made contact with the lower pharyngeal jaw and actually lifted the lower pharyngeal jaw. Contraction of the m. pharyngocleithralis internus resulted in retraction of the lower pharyngeal jaw against the pectoral girdle. This muscle will therefore aid the functioning of the m. protractor pectoralis in lifting the lower pharyngeal jaw via the pectoral girdle. Contraction of the m. obliquus posterior will also contribute to the lifting of the lower pharyngeal jaw by maintaining a connection between epibranchials 4 and the lower pharyngeal jaw, thereby allowing the force

of the m. levator posterior and m. levator externus 4 to be transmitted to the lower pharyngeal jaw (figs 1, 2). Contraction of the m. sternohyoideus resulted in a backward movement of the lower pharyngeal jaw and a forward movement of the pectoral girdle. It is likely that this muscle is also involved in the lifting of the lower pharyngeal jaw via the pectoral girdle. The simultaneous action of the muscles will need to be studied further in electromyography experiments. Contraction of the m. pharyngohyoideus and m. geniohyoideus resulted in protraction of the lower pharyngeal jaw. Contraction of the m. pharyngocleithralis externus resulted in a downward and slightly backward movement of the lower pharyngeal jaw.

DISCUSSION

These results show a novel biting mechanism for the pharyngeal jaws. The pectoral girdle appears to lift the lower pharyngeal jaw upon contraction of the m. protractor pectoralis. Therefore, the force of the strong m. protractor pectoralis is added to that of the other big levator muscles, m. levator posterior and m. levator externus 4. The advantage must be a considerable increase in biting force. Interestingly, in haemulid fishes the m. protractor pectoralis also contributes to the biting force of the lower pharyngeal jaw, however, in this family the insertion of the muscle has shifted from the pectoral girdle to the lower pharyngeal jaw and the muscle force is directly applied to the lower pharyngeal jaw (WAINWRIGHT, 1989). It is quite possible that the articulation between lower pharyngeal jaw and pectoral girdle in labrids serves the same function so that the m. protractor pectoralis also contributes to the biting force in these fishes. Detailed comparisons of the biting mechanisms are necessary to throw light on whether the articulations evolved independently in the two families or are homologous. More information on the pharyngeal biting is crucial for the establishment of the phylogeny of the labroids as a whole, which is at present controversial (compare KAUFMAN & LIEM, 1982 versus STIASSNY & JENSEN, 1987).

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