

Morphofunctional analysis of the feeding apparatus in four Pomacentridae species: *Dascyllus aruanus*, *Chromis retrofasciata*, *Chrysiptera biocellata* and *C. unimaculata*

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KEYWORDS: Pisces - Pomacentridae - Feeding apparatus - Osteology

ABSTRACT

Pomacentrids display a significant biodiversity through a variety of sympatric species with various feeding habits. The use of eco-morphological methods, based on the study of skeletal and muscular structures of the feeding apparatus could result in a better understanding of the adaptive radiation of this family. Significant differences in teeth and in the shape and thickened areas of the different bones were observed. The strongest structures occur in species which had teeth characteristic of suction feeding, and the weakest structures in species with biting teeth.

ACKNOWLEDGEMENTS

We thank S. Houbart and C. Michel (Aquarium Dubuisson, Liège, Belgium), J-M Ouin and G. Seghers (Laing Island Biological Station, Papua New-Guinea), Dr J.-C. Bussers and Dr M. Poulicek (Institut de Zoologie, University of Liege, Belgium) for help obtaining specimens. This work is supported by Grant n° 2. 4560. 96 from the Belgian 'Fonds National de la Recherche Scientifique'.

INTRODUCTION

The Pomacentridae family comprised a great number of species mostly from tropical and sub-tropical waters. Pomacentrids are typically inshore or coral reef dwellers and can be extremely abundant at some locations. Brightly coloured and similar in external morphology, they exhibit a wide diversity of living modes that include the symbiotic *Amphiprion* spp., schooling species of *Chromis*, and bottom-dwelling *Chrysiptera* spp. This diversity is expressed also by the many different ways of feeding (Randall, 1967; Coates, 1980; Montgomery, 1980; Allen, 1991).

There have been many studies on the damselfishes, especially on their ecology (Ciardelli, 1967; Fishelson, 1970; Emery, 1973; Sikkil, 1995), reproductive behaviour (Myrberg *et al.*, 1967), development (Potthoff *et al.*, 1987) and larval recruitment (Sweatman, 1983). The food habits of these fishes have been studied for many pomacentrids. Some of species were found to be omnivorous, while for others the principal food was algae, benthic crustaceans or worms (Allen, 1991).

According to Kotrschal (1988), diet differences between these pomacentrid species are due to varying ability to capture prey, mostly bound to morphological modification of the feeding

apparatus and/or locomotion. An ecomorphological approach, which involves a search for relationships between structures and diet to understand distribution, evolution and trophic relationships, has already been used in studies of some fish families: Cichlidae (Liem & Osse, 1975; Barel *et al.*, 1977; Liem, 1978; Barel, 1983), Chaetodontidae (Motta, 1982, 1988), Labridae (Stiassny & Jensen, 1987; Wainwright, 1987, 1988), and Blennidae (Kotrschal, 1989).

This study focused on pomacentrids, and begins with a comparison of four species from two sub-families. This paper deals with skeletal morphology of the jaws and suspensorium. The species examined were *Dascyllus aruanus* (Linnaeus, 1758) and *Cbromis retrofasciata* (Weber, 1913), from the sub-family Chrominae, and *Chrysiptera unimaculata* (Cuvier, 1830) and *Chrysiptera biocellata* (Quoy & Gaimard, 1824), from the sub-family Pomacentrinae. *D. aruanus* is omnivorous, feeding essentially on small pelagic animals; *C. retrofasciata* is planktivorous (copepods); *C. unimaculata* herbivorous; and *C. biocellata* omnivorous feeding essentially on pelagic algae (Allen, 1991).

MATERIALS AND METHODS

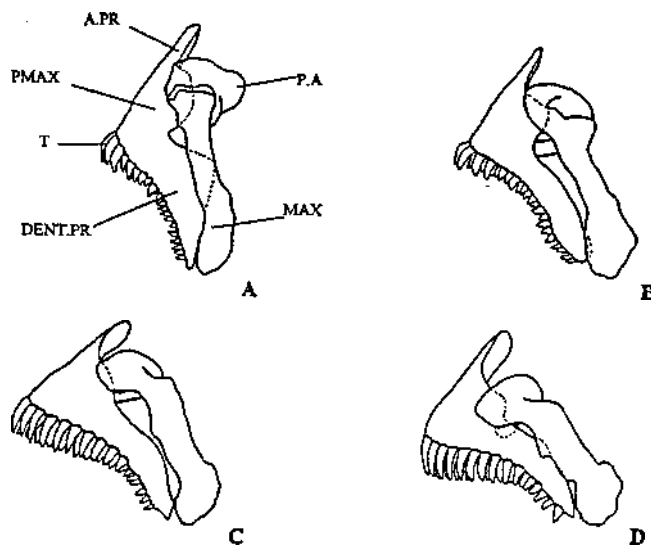
Specimens of the each species were collected on a part of the coral reef at Laing Island (Bismarck Sea, Papua New Guinea), in October 1996. Anatomical descriptions were based on dissected specimens, originally fixed in alcohol and trypsin-cleared and alizarin-stained specimens following Taylor & Van Dyke (1985). Dissected specimens consisted of three *D. aruanus* (32 to 42 mm SL), two *C. retrofasciata* (32 and 33 mm SL), two *C. biocellata* (36 and 38 mm SL), and one *C. unimaculata* (47 mm SL). Cleared and stained specimens consisted of two *D. aruanus* (21 and 31 mm SL), two *C. retrofasciata* (29 and 32 mm SL), two *C. biocellata* (29 and 30 mm SL) and one *C. unimaculata* (45 mm SL). Drawings were made with the aid of a camera lucida. The osteological nomenclature follows the description of Barel *et al.* (1976) and Emery (1973).

RESULTS

In all four species, the maxilla (Fig. 1) is elongate, with an enlarged anterior pivotal area, ventrally overlapping the premaxillary and in contact dorsally with the palatine. In *C. retrofasciata*, the maxilla is narrow with an expanded posterior blade. The maxilla is more massive and better developed posteriorly in *C. biocellata* and *C. unimaculata*. In *D. aruanus*, the maxillary is narrow, except the large pivotal area, and the posterior part is not as an enlarged blade as in the others species (Fig. 1).

The premaxilla bears an ascending process slightly shorter than the dentigerous process. It is thin in *D. aruanus* and *C. retrofasciata* and broader in *C. biocellata* and *C. unimaculata*. In all species, the joint area between the ascending process and the dentigerous process is enlarged and extends as a rounded flange on which the maxillary articulates. This flange is more developed in *D. aruanus* and *C. retrofasciata*. The dentigerous process is dorsally extended in a postmaxillary process in *D. aruanus*. The angle between the ascending process and the dentigerous process is less than 90° in *C. biocellata* and *C. unimaculata*, almost right angle in *C. retrofasciata* and more than 90° in *D. aruanus* (Fig. 1).

Figure 1 - Lateral view of the left premaxillary and the maxillary bones. **A**, *Dascyllus aruanus*-. **B**, *Cbromis retrofasciata*-, **C**, *Chrysiptera biocellata*; **D**, *Chrysiptera unimaculata*. A. PR, ascending process; DENT. PR, dentigerous process; MAX, maxillary; P. A, pivotal area; PMAX, premaxillary; T, teeth.



The lower jaw (Fig. 2) is a strong structure with a dentary proportionally shorter than the angulo-articular bone and stoutly curved in the Chrominae. The coronoid process of the dentary and its teeth are recovered by the distal part of the upper jaw when the mouth is closed. In the Pomacentrinae, the lower jaw is also thick, but the dentary is proportionally longer and less curved. The retroarticular bone is longer in *D. aruanus* and *C. biocellata* (Fig. 2).

Teeth are present on the entire length of the premaxillary and dentary. In *D. aruanus* and *C. retrofasciata*, there are two rows of caniniform teeth anteriorly. The anterior teeth in the first row are clearly bigger. Posteriorly, there is a single row of small conical teeth. In *C. biocellata* and *C. unimaculata*, there are two closely-spaced rows of incisiform teeth - mobile in their insertion. The extremity of the structures bears only one row. In the four species, teeth are erect. The neck of the teeth perpendicularly implanted on the tooth-bearing area. In the Chrominae, the lower jaw is sloped upwards when the mouth is closed. When the mouth is open, the lower jaw is pulled down and the premaxillary protrudes, so that the teeth are well arranged facing the prey. In the Pomacentrinae, the lower jaw is nearly horizontal when the mouth is closed and the premaxillary slightly overlaps it so that the mouth opening is turned downwards. The protrusion of the upper jaw is more significant in this sub-family.

The palatine (Fig. 3) is strong with a long anterior process dorso-ventrally flattened. This process lies in a dorsal concavity of the maxillary. It is movable in relation to the ecto- and entopterygoid, with which it has ligamentous connections. In *D. aruanus* and *C. retrofasciata*, the dorsal side bears a concave surface which lies in the horizontal plane and articulates ventrally with the lateral ethmoid. In *C. biocellata* and *C. unimaculata*, such a prominent lateral projection is not developed.

Figure 2 - Lateral view of the left lower jaw. **A**, *Dascyllus aruanus*, **B**, *Cbromis retrofasciata*; **C**, *Chrysiptera biocellata*; **D**, *Chrysiptera unimaculata*. ANG, angulo-articular; COR. PR, coronoid process;

DENT, dentary; RAR, retroarticular; T, teeth.

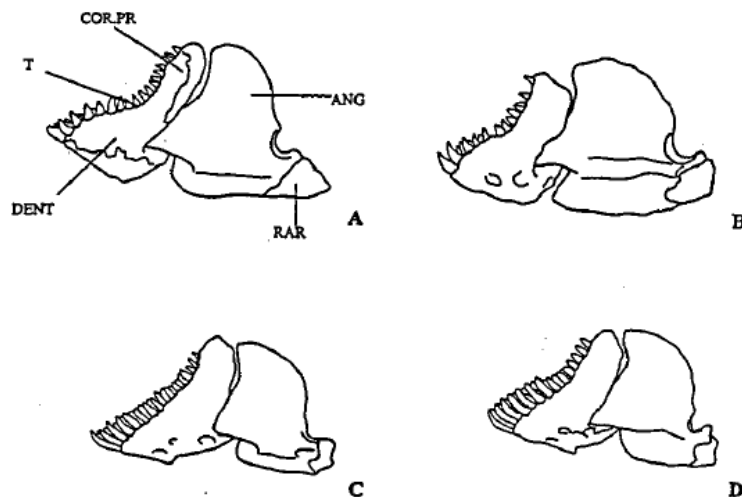


Figure 3 - Lateral view of the left suspensorium and the left preopercular bone. **A**, *Dascyllus aruanus*-, **B**, *Cbromis retrofasciata*-, **C**, *Chrysiptera biocellata*-, **D**, *Chrysiptera unimaculata*. ECPT, ectopterygoid; ENPT, entopterygoid; HM, hyomandibular; MEPT, metapterygoid; PAL, palatine; PO, preopercular; Q, quadrate; SY, symplectic. The thickened areas are stippled.

The quadrate (Fig. 3) is a flattened structure with a prominent condyle of articulation with the articular. A lateral flange covers the rostral part of a strong symplectic. In *D. aruanus* and *C. unimaculata*, the posterior part of the quadrate is strengthened where it connects with the pterygoid bones. In these two species, this flange is especially thickened in the area of the quadrate-articular articulation. In *C. retrofasciata*, the quadrate is thin but has two thickened areas, one close to the ectopterygoid, and the other at the joint with the metapterygoid. In *C. biocellata*, the quadrate is uniformly thickened (Fig. 3). In the four species, the symplectic is thickened at its joint with the hyomandibular process and bears a dorsal extension recovering the ventral part of the metapterygoid. This extension is more developed in *C. biocellata* and moreover in *C. unimaculata* (Fig. 3).

The metapterygoid is a flattened bone connected to the ventral shaft of the hyomandibular. Its connection with the quadrate is thickened in *C. retrofasciata* and *C. unimaculata* (Fig. 3).

The hyomandibular (Fig. 3) is elongate and slightly arched anteriorly. Its dorsal end has two thickened articular heads. The anterior head articulates with the sphenotic, the posterior one with the pterotic. In *C. retrofasciata*, these two heads are more rounded and strengthened than in the other species. In *C. biocellata* and *C. unimaculata*, the two condyles are nearly flat and less thickened than the others are. A third head on the caudal side articulates with the opercular bone. The hyomandibular bears a wide lateral flange, more developed in *C. biocellata* and *C. unimaculata*, that covers the dorsal part of the metapterygoid. This flange is more lateral in *D. aruanus* and *C. retrofasciata*.

The sensory canal going through the preopercular is completely enclosed in *D. aruanus* and *C. retrofasciata*, but open over its whole length in *C. biocellata* and *C. unimaculata* (Fig. 3).

DISCUSSION

The jaw and suspensorium morphology of the four species examined in this study is typical of

perciform fishes (Kotrschal, 1988). However, in these four pomacentrid species, there are some unique characteristics. The palatine bone principally articulates on the vomer and its anterior process is located higher than the parasphenoid-vomer axis. This makes possible an inside rocking during the adduction of the suspensorium. For example, in Cichlidae and Serranidae, the palatine articulates on the lateral ethmoid (Vandewalle, 1975; Barel, 1983). Its ligamentary relationship with the ecto- and entopterygoid makes it possible for the palatine to shift independently from the rest of the suspensorium.

The two species of each sub-family present common characters. The two Chrominae, that are planktivorous fishes, bear caniniform teeth that characterise suction feeding in Cichlidae and Blenniidae. This way of feeding is typical of a planktivorous diet (Barel, 1983; Kotrschal, 1989). *Chrysiptera biocellata* and *C. unimaculata*, the two species in Pomacentrinae, have incisiform teeth. The dentition that is typical of biters (Barel, 1983) or browsers (Kotrschal, 1989) is according to their presumed food ration.

The low protrusion of the mouth is bound to a short ascending process of the premaxillary bone, but the difference in protrusibility between Pomacentrinae and Chrominae would be explained by the different angles between the ascending process and the dentigerous process of the premaxillary. In Serranidae, Benmouna *et al.* (1983) estimated that a smaller angle allows a greater protrusion. The importance of the development of the dentigerous process of the premaxillary, and the pivotal area of the maxillary would also have, according to Gosline (1987), an impact on protrusion. A bigger development would involve a smaller protrusion, which has been confirmed by our observations. The Pomacentrinae are characterised by a greater protrusion than that in *C. retrofasciata* and especially that in *D. aruanus*.

In the two species of Chrominae, the palatine bears on its inner middle face an extension that leans against the ventral face of the lateral ethmoid. This extension probably limits possibilities of palatine movements. It is not developed in the two species of Pomacentrinae examined here.

The articulation heads of the hyomandibular on the neurocranium are stoutly marked and enlarged in the two species of Chrominae, and even more in *C. retrofasciata*. According to Vandewalle (1978) and Parmentier (in preparation), thickness and orientation of articular heads account for the importance of the mandibula adductor musculature. These muscles should be better developed in Chrominae than in Pomacentrinae.

These few considerations are apparently contradictory. The strongest structures are described here in fishes whose teeth indicate suction feeding, and the weakest structures in fishes with biter teeth.

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