

Morphological Adaptations of Pearlfish (Carapidae) to their various Habitats

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INTRODUCTION

One of the most stunning aspects of the living world is the diversity of organism adaptations to a multitude of situations, often unexpected. Coral environments present a remarkable biodiversity in which there are numerous examples of associations among animals. Among those involving a fish and an invertebrate host, the anemonefish (*Amphiprion* sp., Pomacentridae) is doubtless the most well known (e.g., Mader, 1987; Bauchot, 1992; Elliott and Mariscal, 1996) although some Hexagrammidae can also have the same kind of association (Elliott, 1992). These fish are capable of seeking refuge between the sea anemone's tentacles without being attacked by nematocysts. Depending on the species involved, these relationships can be of commensal (Elliott, 1992; Mariscal, 1996), mutual (Fautin, 1991; Godwin, 1992) or parasitic (Allen, 1972). Other fish use the mantle of certain bivalves as a shelter: Cyclopteridae *Liparis inquilinus* and Gadidae *Urophyciss chuss* in the scallop *Planopecten magellanicus*, Apogonidae *Astrapogon alutus* in the mesogasteropod *Strombus pugilis* (Able, 1973; Markle *et al.* 1982; Reed, 1992). Other fishes like Gobiidae live intimately in massive sponges (Tyler and Böhlke, 1972) whereas certain Gobiesocidae live in association with sea urchins (Dix, 1969; Schoppe and Werding, 1996; Patzner, 1999).

Another remarkable example is that of a Carapidae fish (Paracanthopterygians, Ophidiiformes) known as the pearlfish. The origin of this name was the discovery of dead carapid fish, paralysed and completely covered in mother-of-pearl in the inner face of the bivalves of certain oysters (Ballard, 1991). The phyletic relationships among various Carapidae species and their natural environment have been described by

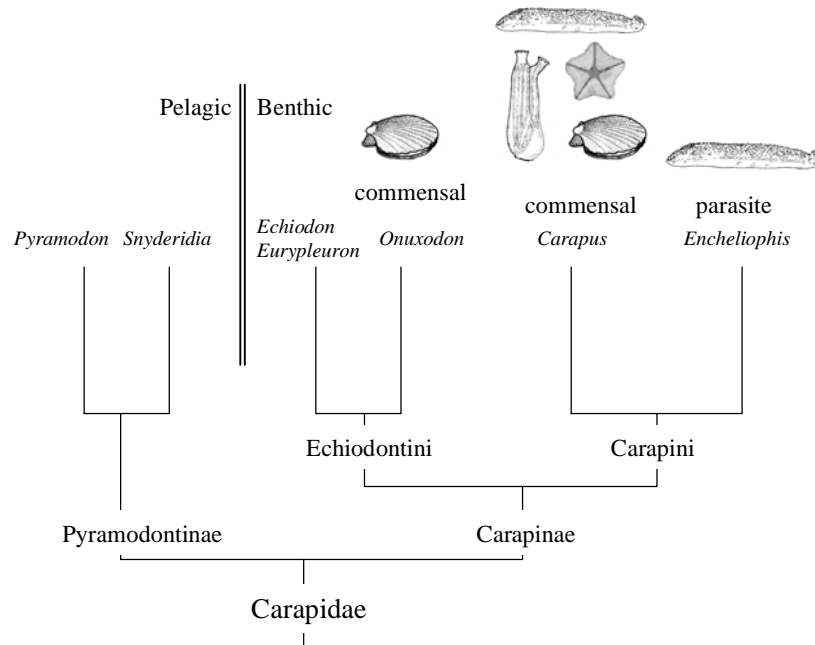


Fig. 11.1 Cladogram of generic relationships between Carapidae and main hosts.

Williams (1983, 1984b), Markle and Olney (1990) and Parmentier and co-authors (2000a) and are summarised in Figure 11.1. Genus *Eurypleuron* is distinguishable from genus *Echiodon* only in the presence of greatly expanded plate-like parapophyse on centra 5 to approximately 22 in the male and the presence of an exterilium gut in the larvae (Markle and Olney, 1990). In the present chapter, comments concerning the genus *Echiodon* are also applicable to the genus *Eurypleuron*. Fish belonging to genera *Onuxodon*, *Carapus* and *Encheliophis* are capable of penetrating and residing inside various invertebrates (Fig. 11.1) such as sea-cucumbers (Emery, 1880; Smith, 1964; Smith and Tyler, 1969; Trott and Chan, 1972; Trott and Trott, 1972; Shen and Yeh, 1987; Van Den Spiegel and Jangoux, 1989; Jangoux, 1990), sea-stars (Meyer-Rochow, 1977, 1979), bivalve molluscs (Tyler 1970; Trott and Trott, 1972; Machida, 1989; Castro-Aguirre *et al.*, 1996; Paredes-Rios and Balart, 1999) and ascidians (Weber, 1913). On the other hand, species of genera *Snyderidia*, *Pyramodon* and *Echiodon* are free-living. Their distribution in the water column is deduced principally by their captures. Species of genera *Pyramodon* and *Snyderidia* are considered pelagic since they are usually found by mid-water trawling (Trott, 1970). Species of *Echiodon* are supposedly benthic (or demersal) because fished on continental shelves and slope waters (Williams, 1984a; Nielsen *et al.*, 1999). Nevertheless, Ayling and Cox (1982) mention the

presence of *Echiodon exsilium* in sponges. The benthic (or demersal) way of life of certain species of *Echiodon* has been proven by their feeding regimen, comprising benthic preys for *Echiodon exsilium* (Trott, 1970) and observation of several specimens of *Echiodon dentatus* lying on the sand in natural conditions (Fries *et al.*, 1893).

According to the hypothesis proposed by Trott (1970), Carapidae must have passed from a pelagic to a benthic state from which certain species were capable of seeking refuge in different hosts (commensalism) and then parasitising them (Fig 11.1). In this chapter a morphological approach to the various genera has been adopted for investigating their adaptations to various ecological niches.

The adaptive radiation of an animal group in unoccupied niches (or recently vacated) implies the absence of competition between ancestral and new forms, which leads to the coexistence of different morphotypes (Mayr, 1989; Ridley, 1989; Allano and Clamens, 2000). Among the Carapidae, the existence of several original ecological niches implies this coexistence among forms, whose comparison allows testing the evolutionary history of the family proposed by Trott (1970).

BEHAVIOUR AND EXTERNAL MORPHOLOGY

The behaviour of penetration in holothurian hosts has been closely observed and described in species of genera *Carapus* and *Encheliophis* (Fig. 11.2). A fish trying to enter a sea cucumber swims with its head towards the bottom and explores objects. Once a host is found, the fish identifies the posterior end by swimming along the tegument of the sea cucumber (Trott, 1970; Gustato, 1976; Kloss and Pfeiffer, 2000). The cloaca is located by the current of water exhaled from the respiratory trees of the selected host (Arnold 1957; Gustato, 1976). Two strategies have then been observed: (1) either the fish penetrates the host head first, propelling itself by violent strokes of the tail or (2) places its head at the entry to the host anus and brings its thin caudal extremity forwards, alongside the fish body, at the level of the lateral line (Fig. 11.2). This position allows the fish to use its body as a guide to rapidly bring its tail towards the cloaca and penetrate it when the host exits an exhalant respiratory current. Once the caudal extremity of the fish is inside the sea cucumber, the Carapidae redresses itself and enters the host with backward movements. This second strategy is more frequently observed (Arnold, 1953; Trott, 1970). Once inside host, the Carapidae fish first lodge themselves in the respiratory tree. Penetration of *Carapus mourlani* in the asteroid *Culcita novaeguinae* is done through the host mouth (Meyer-Rochow, 1977). The fish searches for an ambulacral groove to introduce its caudal extremity and follows it backwards to the peristome and then the stomach (Trott, 1970, pers. obsv.). Individuals have often been found in the general cavity

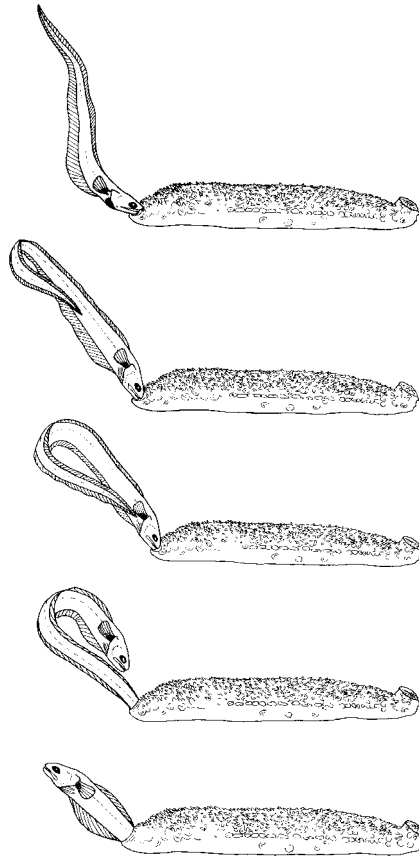


Fig. 11.2 Schematic view of the tail-first penetration in a Carapini.

of echinoderms, implying a perforation of the respiratory tree or the stomach. *Carapus dubius* slips headmost between the mantle and shell of bivalve molluscs (Castro-Aguirre, pers comm.). The entry of species of genus *Onuxodon* into bivalves has not been described.

Even if Smith (1981) think that the eel-like shape of Carapidae (Fig. 11.3) is not necessary for penetration of a host, comparing them to the stolid Gobiidae that penetrate sponges, their elongated shape facilitates penetration of hosts which have a sphinctered anus. If entry is done head first, the elongated eel-like form (Fig. 11.3), laterally compressed, allows for violent movements of the body, which force passage of the head. When entry is done tail first, the thin caudal extremity introduced into the cloaca avoids complete obstruction of the entryway. Large oscillatory lateral movements then facilitate advance into the cloaca. These penetration strategies are possible not only because of the general morphology of the Carapinae body, but also through reduction of friction

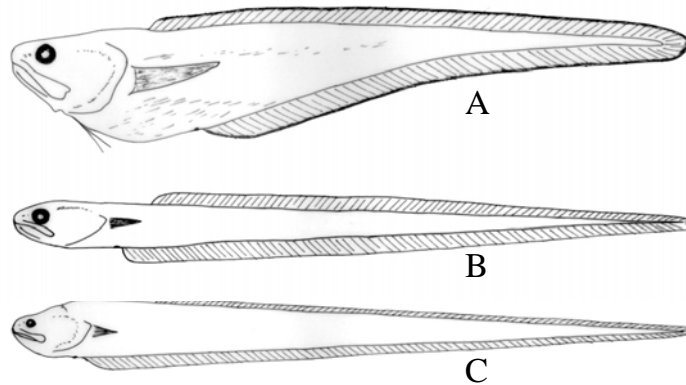


Fig. 11.3 Lateral view of *Pyramodon lindas* A, *Echiodon exsilium* B and *Carapus boraborensis* C (modified from Markle and Olney, 1990).

surfaces: absence of scales and pelvic fins, reduced pectoral fins (absent in *Encheliophis vermicularis*), and long ventral and dorsal fins consisting only of soft rays. Also, the opercular and subopercular needles are flexible and bordered by a dense, flexible mesenchyma (Parmentier *et al.*, 1998). These characteristics were already present in the *Echiodon* (Fig 11.3.), and can be interpreted as preadaptations (in the sense of Hildebrand, 1989, p.14) and not as characteristics specially adapted to life within a host. The Pyramodontinae (Fig. 11.3) have small pelvic fins (except *Snyderidia canina*), a body proportionally higher and larger, longer pectoral fins with a greater number of rays, and longer dorsal and anal fin pterygiophores (Markle and Olney, 1990; Nielsen *et al.*, 1999). These characteristics could be better related to a pelagic life that requires better swimming capacities. According to the meristic data of Markle and Olney (1990), the *Encheliophis* are species that present the smallest length of pectoral fins.

Another characteristic distinguishing the Pyramodontinae from the Carapinae (Fig. 11.1) concerns the position of the anus. It is quite forward, at the level of the pectoral fins in Carapinae, but further back in Pyramodontinae (Fig. 11.3). This specialisation could have evolved to minimise exposure to predators if the fish has to emerge to avoid intestinal waste (Trott, 1981; Ballard, 1991).

CEPHALIC ECOMORPHOLOGY

Very little data exist on the feeding regimen of free-living forms: that of *Echiodon exsilium* is composed of shrimps and crabs (Trott, 1970) and shrimps have been found in the stomachs of two *Snyderidia canina* (unpubl. data). Among the forms that live in invertebrates, *Onuxodon fowleri* feeds on Ostracoda, Amphipoda and Annelida (Parmentier *et al.*, 2000b); spe-

cies of genus *Carapus* eat decapods, amphipods, isopods, annelids and fish including Carapidae; *Encheliophis* feed on the gonads or respiratory tree of their holothurian host (see Parmentier *et al.*, 2000a). The carnivorous character of *Pyramodon*, *Snyderidia* and *Echiodon* can be deduced from the structures of their mouths, which present similarities principally with those of *Onuxodon* and *Carapus*. In all genera except *Encheliophis*, the mouth is widely split, the lower jaws are robust with high coronoid processes and numerous teeth are present on the jaws, palate and vomer. Also, the hyomandibular is reinforced by areas of thickness (Fig. 11.4) necessary to resist contraction of the powerful adductor mandibulae A2 and A3 (Fig. 11.5). These are set not only on the suspensorium as in most teleosts, but also on the neurocranium as in certain biting fish (Vandewalle *et al.*, 1982; Parmentier *et al.*, 1998, 2000b). The presence of more or less well-developed teeth in front of pre-maxillaries and dentaries in Pyramodontinae and Echiodontini (Figs. 11.1 and 11.4) reinforces the carnivorous character of these fish. On the other hand, in *Encheliophis* the jaws are frailer and present a reduced denture (Figure 11.4). Also, the amplitude of the opening of mouth is limited by the presence of short collagen fibres between the premaxillary and the dentary by the special insertion of the adductor mandibular A₁α muscle directly on the maxillary (Parmentier *et al.*, 1998) while it is attached to the same bone in other species by the intermediary of the maxillo-mandibular ligament (Fig. 11.5). These differences should be viewed in relation to two aspects of their food: *Encheliophis* feed on soft, immobile food located in a limited space while the feeding regimen of species of other genera comprises harder and more vagile prey in an open environment. An ecomorphological comparison, based on feeding regimen and buccopharyngeal morphology, reinforces the assumptions of a parasitic life of adult *Encheliophis*.

Certain teeth held by the Carapini (Fig. 11.1) could also play another role in the relationship with their hosts. Carapinae have one to several rows of small conical teeth all along their jaws, except for genus *Encheliophis* in which these teeth are limited to the forward half of the premaxillaries (Fig. 11.4); conical teeth are absent in *Encheliophis gracilis*. Carapini on the other hand lack fangs at the front end of their jaw. They are the only fish that have, in addition to possible conical teeth, cardiform teeth arranged in a short row on the frontal, external side of the premaxillaries (Arnold, 1956; Nielsen *et al.*, 1999, Parmentier *et al.*, 2000a, b). Parmentier *et al.* (1998) suggested that these cardiform teeth could be used in the manner of a saw to cut internal tissues of their hosts. *Onuxodon*, found in bivalves, do not possess these cardiform teeth (Tyler, 1970; Parmentier *et al.*, 2000b) but their penetration between the mantle and the shell does not require perforation of tissues. Such is not true for *Carapus*

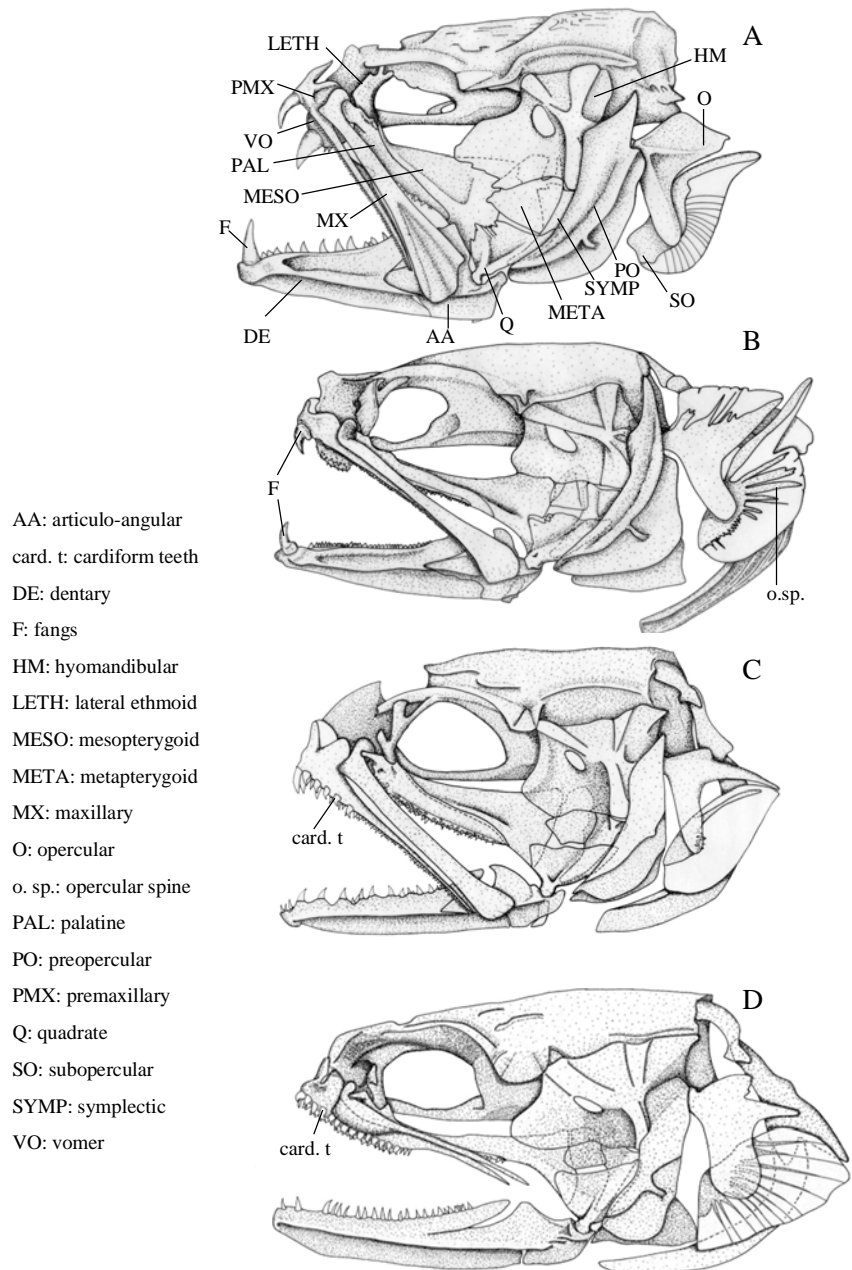


Fig. 11.4 Lateral view of the head skull in *Pyramodon lindas* A, *Echiodon exsilium* B, *Carapus boraborensis* C and *Encheliophis vermicularis* D.

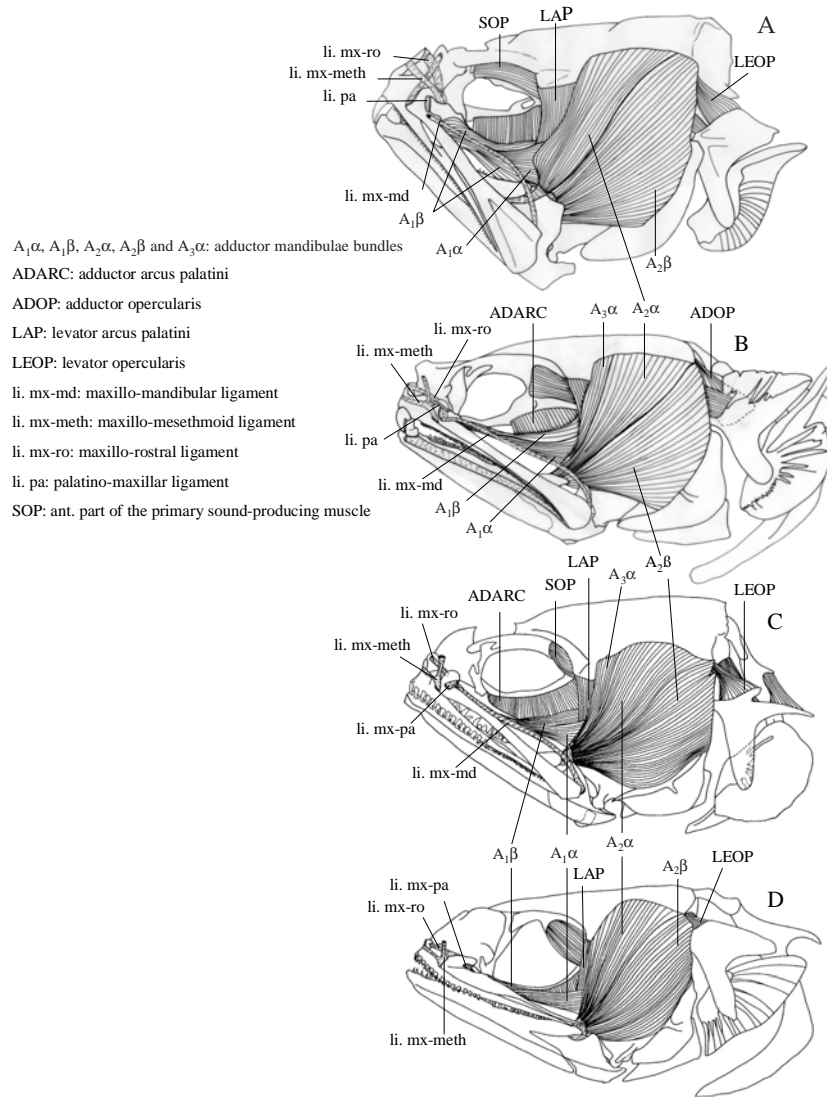


Fig. 11.5 Lateral view of the head musculature in *Pyramodon lindas* A, *Echiodon exsilium* B, *Carapus bermudensis* C and *Encheliophis sagamianus* D.

dubius, which also lives in bivalve molluscs but possesses cardiform teeth as do other fish of this genus (Trott, 1981; Castro-Aguirre *et al.*, 1996; Paredes-Rios and Balart, 1999; Parmentier *et al.*, 2000b). The closest species phylogenetically to *Carapus dubius* is *Carapus homei*, which usually lives in sea cucumbers. The presence of *Carapus dubius* in this host, so unusual for the *Carapus* genus, could be explained by a change of host during mass

extinction of the species in the coral reef environment of the Eastern Pacific (Markle and Olney, 1990). The cardiform teeth of *Carapus dubius* would therefore be part of the common heritage of Carapini.

OTOLITHS

The distribution of various habitats and different morphotypes of Carapidae can be confirmed by an ecomorphological study of their otoliths (Parmentier *et al.*, 2001). When comparing several species of Carapidae, it would appear that the thinnest sagittae (sacculus otolith) held in the proportionally smallest otic cavities are those of Pyramodontinae. Their otoliths resemble those of the fast-swimming Paracanthopterygians, such as Gadidae (Dale, 1976), Merluccidae (Lombarte and Fortuno, 1992) and Macrouridae (Lombarte and Morales-Nin, 1995). *Echiodon drummondi* possesses a much thicker sagitta in an otic cavity whose proportions are pretty much identical to those of Pyramodontinae (Parmentier *et al.*, 2001). Proportionally thicker otoliths can also be found in recognised benthic species such as Congridae or certain Ophidiiformes (Nolf, 1985). The sagittae of species of *Carapus* and *Encheliophis*, with a more pronounced sedentary mode of living, appear proportionally thicker and heavier and are located in otic cavities proportionally much larger (Parmentier *et al.*, 2001). It would also appear that the most developed otoliths are present in fish with more developed sound-producing structures. These are mainly composed of two 'sonic' muscles, inserted in the roof of the orbit and the forward end of the swim bladder covered by expansions of the third ribs (Courtenay and McKittrick, 1970). These last are particularly well developed in commensal or parasitic species (Markle and Olney, 1990). The structures involved in sound-producing and hearing are possibly adapted to match the loss of energy by the sonic vibrations when travelling through the host tissues (Parmentier *et al.* 2002).

EVOLUTION OF MORPHOTYPES

The various morphological characters examined (body shape, buccal shape, otoliths, etc.) are evidence of the adaptations of different genera. Each genus therefore constitutes a morphotype tied to an ecological niche. We have still to verify whether the character variations correspond to an evolutionary tendency. If affirmative, the direction of this tendency could help to reconstruct the evolutionary history of the group. This evolutionary tendency appears in at least a few characters in Carapidae. Otoliths seem to become thicker as the fish tends to become less mobile. The forward teeth of the premaxillary also seem to have evolved. The large teeth present in *Pyramodon* and *Snyderidia* become smaller in *Echiodon*. For

Carapus, these conical teeth are barely larger than those that follow, and in *Encheliophis* cannot be distinguished from the other teeth in the premaxillary (Fig. 11.4). This tendency also appears in a character not previously mentioned here, as its adaptive aspect has yet to be proven: Pyramodontinae possess an interarcual cartilaginous element (Fig. 11.6) between epibranchial 1 and the pharyngobranchial 2 (Markle and Olney, 1990; Parmentier *et al.*, 2000a). The order of the character modifications presented here tends to reinforce the hypothesis expounded by Trott.

The monophyly of Carapidae is accepted (Markle and Olney, 1990). Nevertheless, a search can be made among modern forms for that which presents the closest morphology to the ancestral form. The presence of well-developed pelvic and pectoral fins allows us to consider the genus *Pyramodon* as close to the primitive state. Pyramodontinae are morphologically close to other Ophidiiforme fish due to the rather posterior position of the anus and the forward insertion of the dorsal fin in respect to the ventral (Nielsen *et al.*, 1999). Also, as in Pyramodontinae, Ophidiidae possess a cartilaginous interarcual element between epibranchial 1 and pharyngobranchial 2 (Markle and Olney, 1990). The intermediate position of the interarcual element on the epibranchial 1 and the presence of large teeth in front of the premaxillaries and dentaries in Echiodontini would allow us to consider them the closest group to Pyramodontinae. Passage from pelagic to benthic (or demersal) life would have then been accompanied by reduction of structures favouring swimming, such as size of pectoral fins, disappearance of pelvic fins, lesser height of body and proportionally thicker and heavier otoliths. This change of habitat would also have been accompanied by modification of the buccal structures with a less pronounced carnivorous character: lower and upper jaws less robust, vomer no longer carries large conical teeth and the size of the teeth is reduced. Among Echiodontini, morphotype of genus *Echiodon* seems to be closest to the primitive shape, while genus *Onuxodon* presents an ensemble of very specialised characters (Williams, 1984a; Markle and Olney, 1990), such as position of upper buccal jaws, sharp buccal teeth (Parmentier *et al.*, 2000b) or original shape of the otic capsule (Tyler, 1970; Parmentier *et al.*, 2001).

The morphotype which presents the most affinity with the genus *Echiodon* is that of the *Carapus*. Their general forms (body proportions, size of pectoral fins, position of anus) are similar and, from this point of view, the morphotype of genus *Echiodon* appears preadapted (*sensu* Hildebrand, 1988, p.14) for the commensal behaviour developed by *Carapus*. Their buccal anatomies present several points in common except for the teeth (Figures, 11. 4 and 11.5). The morphological passage from a benthic to a commensal life seems only to be justified by the appearance of cardiform teeth in the *Carapus* genus.

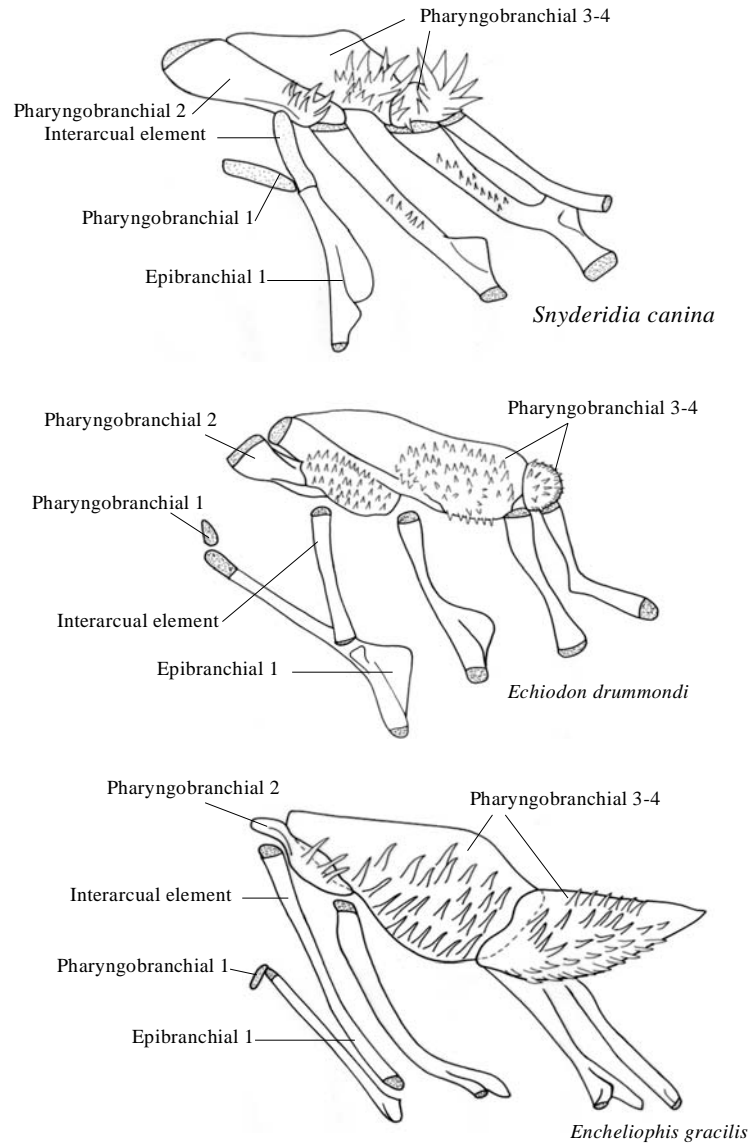


Fig.11.6 Ventral view of the left half of upper jaw in *Snyderidia canina* (modified from Parmentier *et al.*, 2000a), *Echiodon drummondi* and *Encheliophis gracilis* (both modified from Markle and Olney, 1990).

Parasitism would imply occupancy of a more specialised ecological niche. Various *Encheliophis* species are found only in sea cucumbers whereas *Carapus* species have colonised different invertebrate hosts (Weber, 1913; Trott, 1970; Meyer-Rochow, 1979; Castro-Aguirre, 1986).

The parasitic form derived from commensalism can be displayed in two ways: reduction in the *Carapus* form of pre-existent features (reduction of teeth number and lighter buccal structures) and the presence of unique characters (absence of maxillo-mandibular ligament, adnate superior jaws) whose specialised aspect allow us to place them at the end of the evolutionary chain.

CONCLUSIONS

In Carapidae, species of the same genus present an identical morphotype tied to a particular ecological niche. In this group, what appears as the passage from one morphotype to another (a macroevolutionary process) is accompanied by the discovery of a new ecological environment that would allow the morphotypes to avoid competition with each other, while remaining sympatric. On the other hand, the minor morphological modifications within the species of the genus lead to a specific diversity and occupancy of more specialised niches (Mayr, 1989). Therefore, if the primitive ecological niche of the commensal in sea cucumbers is associated with the morphotype of the genus *Carapus*, occupancy of sea-stars by *C. mourlani*, ascidians by *C. sluiteri* and bivalves by *C. dubius* could be the result of an ensemble of specialisation not yet identified.

Various environmental constraints have occupied an important place in bearing evolutionary theories since the concept of adaptation was developed by Darwin; they can in certain cases favour morphological modifications of a structure facilitating occupancy of new ecological niches. The ecomorphological approach attempts to prove the eventual interactions between environmental factors of an organism and its phenotype (Sanderson, 1990; Block *et al.*, 1991; Motta and Kotrschal, 1992; Motta *et al.*, 1995; Norton, 1995; Norton *et al.*, 1995; Westneat, 1995). Adaptative traits alone do not permit retracing the evolutionary history of a group; they only show the evolutionary stages. In Carapidae, the otoliths or body morphology for example, can be tied to the occupancy by the fish of a specific ecological niche. An overall view of adaptative stages can nevertheless reveal the existence of an evolutionary axis. Orientation of evolutionary history needs the presence of characters apparently independent of a niche and existing in 'pivotal' morphotypes (*Echiodon*, *Carapus*) and features whose strong specialisation places the morphotypes involved at the extremes of an evolutionary process (*Onuxodon*, *Encheliophis*). This strategy as applied to Carapidae allows us to confirm Trott's hypothesis (1970).

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