

FORAGING TACTICS IN MOLLUSCA: A REVIEW OF THE FEEDING BEHAVIOR OF THEIR MOST OBSCURE CLASSES (APLACOPHORA, POLYPLACOPHORA, MONOPLACOPHORA, SCAPHOPODA AND CEPHALOPODA)

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ABSTRACT

Mollusca is regarded as the second most diverse phylum of invertebrate animals. It presents a wide range of geographic distribution patterns, feeding habits and life standards. Despite the impressive fossil record, its evolutionary history is still uncertain. Ancestors adopted a simple way of acquiring food, being called deposit-feeders. Amongst its current representatives, Gastropoda and Bivalvia are two most diversely distributed and scientifically well-known classes. The other classes are restricted to the marine environment and show other limitations that hamper possible researches and make them less frequent. The upcoming article aims at examining the feeding habits of the most obscure classes of Mollusca (Aplacophora, Polyplacophora, Monoplacophora, Scaphoda and Cephalopoda), based on an extense literary research in books, journals of malacology and digital data bases. The review will also discuss the gaps concerning the study of these classes and the perspectives for future analysis.

Key words: diet, feeding habits, mollusks

RESUMO

TÁTICAS DE FORRAGEAMENTO EM MOLLUSCA: UMA REVISÃO SOBRE O COMPORTAMENTO ALIMENTAR DAS SUAS CLASSES MAIS OBSCURAS (APLACOPHORA, MONOPLACOPHORA, POLYPLACOPHORA, SCAPHOPODA E CEPHALOPODA).

O filo Mollusca é o segundo mais diverso e, portanto, apresenta os mais variados hábitos de vida, padrões de distribuição geográfica, comportamentos alimentares, dentre outros aspectos. Apesar de seu rico registro fóssil, a história evolutiva do grupo ainda é incerta. Os táxons tidos como ancestrais do filo alimentavam-se de forma simples, sendo considerados depositívoros. Dentre os representantes atuais, as classes Gastropoda e Bivalvia são as mais diversas e amplamente distribuídas, sendo as mais conhecidas cientificamente. As demais classes, por outro lado, estão restritas ao ambiente marinho e exibem outras limitações que dificultam o seu estudo e o tornam menos freqüente. Aqui será apresentada uma síntese dos hábitos alimentares das classes mais obscuras do filo Mollusca (Aplacophora, Polyplacophora, Monoplacophora, Scaphoda e Cephalopoda) com base em uma extensa busca em livros, principais periódicos de Malacologia e bases de dados digitais. Além disso, realiza-se uma discussão acerca das lacunas de conhecimento e das perspectivas para estudos futuros.

Palavras-chave: dieta, hábitos alimentares, moluscos

INTRODUCTION

Amongst all the activities performed by an animal, perhaps the most important is finding and consuming food. Besides being an individual necessity, feeding is crucial for various levels of ecosystem processes (O'Brien *et al.* 1990). Different phenotypes have different abilities to acquire food, which are distributed in patches around the environment (Mac Arthur and Pianka 1966). Aiming to predict the foraging behavior patterns of the animals which actively look for feeding resources, Mac Arthur and Pianka (1966) developed the Optimal Foraging Theory. The study has received several contributions over the years

regarding the consumers preferences, habitat selection and territories dimensions. These studies also investigated if they are going to hunt in groups, the ideal size of such groups, the foraging period choice and, at last, the level of specialization and generalism (Belosvsky 1978, Pyke and Pullian 1977, Schoener 1971, 1973, 1983, 1987, Stephens and Krebs 1986). The Optimal Foraging Theory or behavioral ecology can be defined as the maximum return of energy obtained under foraging and habitat conditions (Townsend *et al.* 2010, Odum and Barrett 2011). The behavior pattern of an individual subjected to natural selection is the sum of the decisions that determine its diet and its food chain structure (Petchey *et al.* 2008).

Different species detain different foraging strategies to minimize energy expenditure and maximize their gains, selecting the potential feeding items and the areas or spots to be hunted (Odum and Barrett 2011).

True predators and grazers typically forage. Amongst the mobile prey predators, the most renowned foraging strategies are: the Sit-and-wait Hunter, in which they set up ambushes to catch their preys (therefore, the method is based on the evasive behavior of the latter); and the Active Hunters, in which the predators move around their own habitat looking for preys - their contact is, consequently, determined by the behavior of the predators (Greene 1986, Townsend *et al.* 2010). The sit-and-wait strategy is less studied, but recent researches have shown that it is more changeable than what had been predicted in the past, depending on the internal state of the individuals and their interactions with the environment (Hugie 2003, Scharf *et al.* 2011). Lima and Dill (1990) indicate, in their review, that the protection against predation may deeply influence the choices made by a determined species during the foraging process.

Feeding is regarded as one of the main pillars of the taxonomic diversity. By influencing population dynamics and the organization of communities, trophic interactions, alongside with competition, it molds ecological niches, which, in an evolutionary time scale, lead to radiation (Hughes, 2009). Given this thought, the mollusks are the second most diverse phylum in the world, with 100.000 Recent species described, therefore, they present the most diverse life styles, geographic distribution patterns, feeding habits, amongst other aspects (Haszprunar 2001, Caetano *et al.* 2007). Within the classes of the phylum Mollusca, Gastropoda and Bivalvia are the most analyzed in the scientific field. Since they are the two most diversified and well-distributed groups, they become more accessible to studies and researches. Gastropods can be found in all environments (marine, terrestrial and freshwater) and bivalves can be spotted everywhere, but in terrestrial areas (Caetano *et al.* 2007). The remaining classes, on the other hand, are limited to marine environment, with most of the representatives of Aplacophora and Monoplacophora being found below depths of 200m (Martins 2008, Wilson *et al.* 2009).

The present article proposes a knowledge synthesis on the foraging strategies of the less examined classes of the phylum Mollusca (Aplacophora, Polyplacophora, Monoplacophora,

Scaphopoda and Cephalopoda) showing the gaps of knowledge and discussing the perspectives of future studies.

MATERIAL AND METHOD

An extensive research was held from October to November 2012 and went through books of malacology and the main journals in this same subject (American Malacological Bulletin, Malacologia, Journal of Molluscan Studies, Journal of Shellfish Research, Molluscan Research, The Nautillus, The Veliger), as well as the following bases of digital data: "Periódicos CAPES", Web of Science, Google Scholar using the keywords: "foraging" + "scaphopoda or aplacophora or monoplacophora or cephalopoda or polyplacophora", "feeding behavior" + "scaphopoda or aplacophora or monoplacophora or cephalopoda or polyplacophora", "feeding habits" + "scaphopoda or aplacophora or monoplacophora or cephalopoda or polyplacophora" and "diet" + "scaphopoda or aplacophora or monoplacophora or cephalopoda or polyplacophora". After the research effort, only published articles and final papers (monographs and thesis) were considered.

HISTORY OF RESEARCHES ABOUT FORAGING IN MOLLUSCA

The phylum Mollusca comprises several feeding habits, having the radula as the fundamental organ of food capture and disposing of a wide range of foraging tactics (Caetano *et al.* 2007). In some groups, the radula is not related to food capture, but to post-ingestion processes. This will be detailed further.

Despite the huge diversity of the group and its rich shelly fossil record, their early evolutionary history remains uncertain. Two taxa from the Middle Cambrian, *Wiwaxia corrugata* and *Odontogriphus omalus*, have been considered as the ancient members that might have originated the mollusks, exhibiting a radula-like organ very similar to the one found in the genus *Helicoradomenia*, an extant solenogaster. Their radular function was probably limited to sweeping food from a surface, abrading soft tissues and excavating sediments, thus being classified as grazing deposit-feeders (Scheltema *et al.* 2003, Smith 2012).

In this review, we found a total of 79 references related to the subject discussed here (Figure 1). The foraging tactics within the classes Monoplacophora and

Aplacophora (Solenogastres and Caudofoveata) are less known. This can be explained by the fact that most of their species live in deep water and, consequently, are difficult to be reached (Okusu and Giribet 2003).

In the last 20 years, the study on the classes behavior has faced a considerable increase (Figure 1) due to the new filming and photography technologies that enabled researchers to have a deeper look into areas that were once unknown. Until 1952, the class Monoplacophora was regarded only as a fossil group, and then was found in the abyssal waters of the Pacific Ocean, in Costa Rica (Lemche and Wingstrand 1959). Not only until 1978 was the first species of Monoplacophora studied in laboratory and had a few of its ecological aspects analyzed. However, the animal was kept alive for 25 days and not many conclusions were taken from the experience (Lowenstam 1978, Wilson *et al.* 2009). Also, most species of Scaphopoda and Aplacophora have small size and live in great depths always digging in the sediment, which complicates the conduction of

researches. Cephalopoda, on the other hand, are much more studied, due to development of industrial fishing and to their economic importance (Figure 1).

APLACOPHORA FORAGING BEHAVIOR

The Aplacophora are divided in two larger taxa: Solenogastres and Caudofoveata. The separation of the two groups, both discovered in Scandinavia in 1844 and 1875 (respectively), is related to the existence of a little foot inside the ventral furrow of the Solenogastres and its absence in the Caudofoveata (Glaubrecht *et al.* 2005).

The representatives of this class are exclusively marine, have vermiform bodies, covered with a cuticle or calcareous spicules, among other plesiomorphic aspects of the phylum Mollusca (Scheltema and Schander 2000). They are more numerous and present a greater diversity in depths of more than 200 meters (Martins 2008). Most researches on the class comprise their anatomy and phylogenetic and very little is known about their life story, behavior and physiology (Lamprell and Scheltema 2001). As well as the other mollusks,

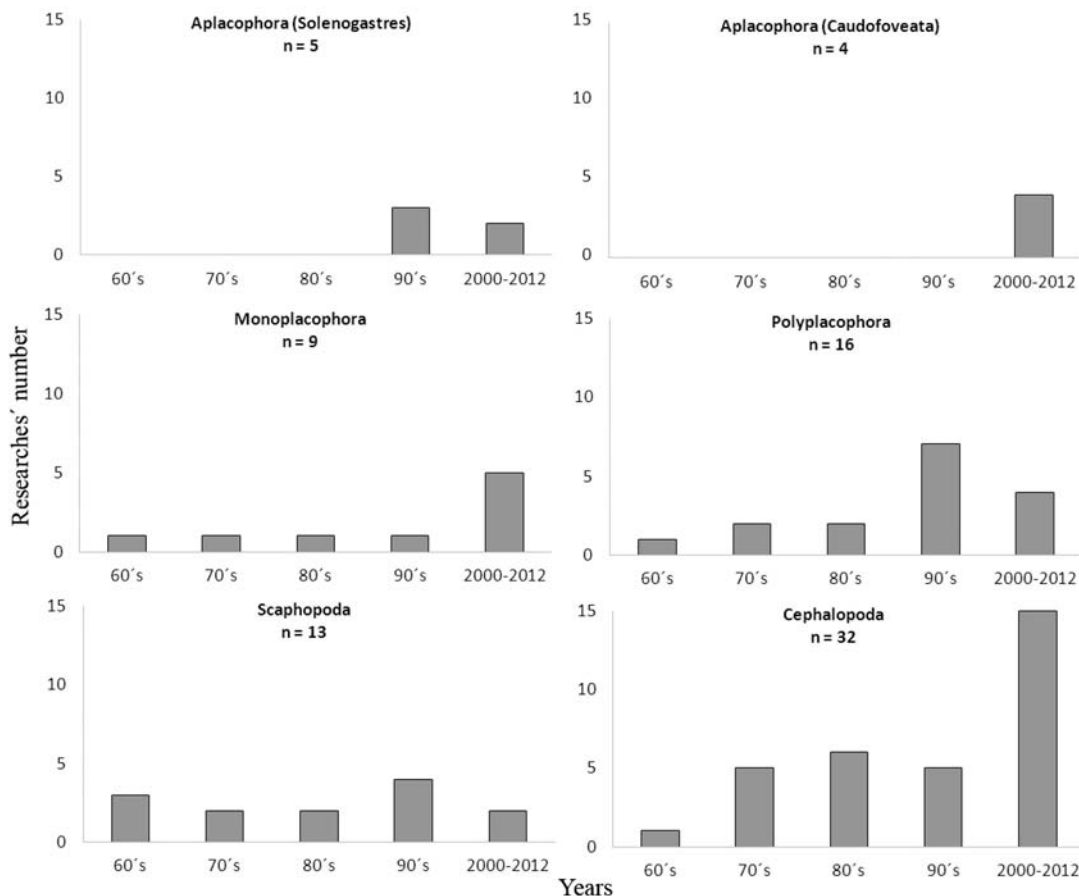


Figure 1. Studies of foraging habits of Aplacophora, Monoplacophora, Polyplacophora, Scaphopoda and Cephalopoda over the years.

Solenogastres and Caudofoveata have a discrete buccal mass with a radula, radular sac, and paired or fused bolsters with their protractor and retractor muscles. Radulae vary morphologically and several Solenogastres have none (Beesley *et al.* 1998).

SOLENOGASTRES

The diet of the Solenogastres is determined through the observation of their stomach content or, in some cases, due to the fact that the species are found fixed to their preys (Scheltema 1992). The radula of Solenogastres is considered not to be used for rasping the food, because it is formed of a weak cuticle and the distal teeth are not worn (Scheltema and Jebb 1994).

As regards the foraging tactics adopted by the Solenogastres, it is known that they have, in their ventral furrow, a narrow and ciliated delta, with which they creep on soft and hard substrates or on colonies of cnidarians which serve them as food (Ponder and Lindberg 2008). The strategy is well described for the genera *Epimania*, which hooks the teeth into the soft coral prey, holding the head in place, while the pharynx sucks in the polyps. It is believed that the species *Epimania australis* may detect their soft coral preys through chemical sense (Scheltema and Jebb 1994).

According to other studies, the group also consumes bacteria and not only cnidarians (Scheltema *et al.* 2003, Morse and Norenburg 1992, Okusu and Giribet 2003).

CAUDOFOVEATA

The Caudofoveata have infaunal habits and move through hydrostatic action, feeding themselves with detritus or with selected foraminifera, burying their suboral or perioral shield, located in the upper oral region, in the mud (Glaubrecht *et al.* 2005, Ponder and Lindberg 2008).

The family Prochaetodermatidae is numerous and ecologically important in the macrobenthos of deep waters, which prompts the researches on the subject. The individuals of this family are the only ones that present, in their feeding apparatus, a pair of cuticular jaws that hold the food as two plucks while it is scraped by a little radula (Scheltema and Ivanov 2000).

POLYPLACOPHORA FORAGING BEHAVIOR

The individuals of this class, also named chitons, are one of the oldest representatives of the phylum

Mollusca, with a fossil record that extends from as early as the Upper Cambrian (Ponder and Lindberg 2008). Living on hard sediments, these slow-moving animals may appear in the bathyal zone or in the intertidal zone. Their feeding habits have also been understudied (Boyle 1977, Latyshev *et al.* 2004).

The chitons leave their small depressions or holes to forage usually in nights of low tide, aiming to avoid possible predators and the dissection caused by sun exposure. In their feeding process, they usually stretch their radula and a sensorial subradular tongue-like organ (Eernisse and Reynolds 1994); since they have lateral teeth hardened by the incorporation of minerals such as iron and calcium to an organic mold, they manage to scrape hard surfaces to obtain food, generally algal cover (Shaw *et al.* 2002). After eating, they return to their small depressions or holes and remain there during the day, when the excretion process starts (Hulings 1991, Barbosa *et al.* 2008). Some chitons may also graze in low tide mornings, as long as the foraging zone is not exposed to the sun (Cretchley *et al.* 1997).

According to Sirenko (1998, 2000), the Polyplacophora can be divided in six different feeding habits: herbivores, detritivores, omnivores, carnivores, epizoophagous and true predators. Most chitons are generalist grazers of hard substrata, feeding mainly on microflora, algae and small encrusting animals (Eernisse and Reynolds 1994). However, there are some species that feed on detritus such as skeletons of diatoms, foraminiferans, radiolarians, spicules of calcareous sponges and even sunken wood, which was observed in some species of *Lepidopleurina* that inhabit regions up to 8000 meters deep (Beesley *et al.* 1998). Barnes (1972) studied the species *Tonicella lineata* feeding on coralline algae and was overwhelmed when he realized that the animal did not scrape the rock until the algae layer was completely destroyed, as it would occur with the patelid gastropods, but ingested only the layers above the meristem. The experiment underlined Putman's (1990) results, which had identified a selective foraging behavior in the species *Stenoplax heathiana*. Langer (1983), on the other hand, while studying the feeding habits of three chiton species in the Atlantic, realized that they scraped the epibenthic film of algal-covered substrates, being common the accidental intake of the sediment. Piercy (1987) highlighted the same behavior pattern in his researches.

When it comes to carnivorous chitons, the

majority feed on sedentary animals, as well as, sponges, bryozoans, coelenterates and young barnacles (Beesley *et al.* 1998). The carnivorous chiton of the genus *Placiphorella* had its foraging habits observed by McLean (1962), who described the process as follows: the animal lifts the head-flap, which is a variation of the mantle margin, and keeps the oral tentacles adhered to the surface that it is found on. Any stimulus in the area prompts a quick reflex of lowering the flap, to catch the potential prey. The tentacles are then slowly raised and retracted so that the mouth can be expanded towards the prey and the ingestion happens. In some cases, the tentacles also help manipulating the prey. Another interesting observation on the genera *Placiphorella* is that the inferior face of the head-flap exhibits strong staining, which may serve as a distraction for preys with average visual capability (Clark 1994). A similar predatory behavior was described for *Loricella angasi* and two species of *Craspedochiton* (Eernisse 2007).

MONOPLACOPHORA FORAGING BEHAVIOR

The Monoplacophora dispose of only one valve, shaped as a convex dorsal shield with its apex facing towards the upper region and length from 1.5 to 3.7 millimeters (Caetano *et al.* 2007). The Monoplacophora is, undoubtedly, the less studied class of the phylum Mollusca. There is a considerable gap concerning its ecological and ultrastructural aspects, immunocytochemistry and ontogenetic (including the evo-devo) (Ponder and Lindberg 2008). A deeper knowledge of the representatives of this class, which was believed to be extinct, is seen as an important key to the study of the evolution of the phylum (Schwabe 2008).

Laevipilina hyalina is the most accessible species of the group in terms of habitat, since it lives in depthless waters (174-388 meters deep). It was the first one to be photographed live and cultivated in aquarium, which made it become rather well-known (Wilson *et al.* 2009). In one of the few researches on the species, no feeding activity was registered; however another three studies suggest that the Monoplacophora might be generalists, feeding on detritus and foraminifera, as well as specialists in protozoans of the class Xenophyophorea (Lemche and Wingstrand 1959, Tendal 1985, Warén and Hain 1992).

Little is known about the foraging tactics adopted by the group, but it is fairly accepted that their cusps

are used as pallets to scrape the organo-mineral surface layer of ferromanganese nodules. They feed on protozoans, radiolarians, diatoms, foraminifera and sponges (Urgorri *et al.* 2005, Lindberg 2009).

SCAPHOPODA FORAGING BEHAVIOR

The Scaphopoda are a class of exclusively marine and infaunal mollusks, well-known for the muscular foot used for digging, univalve tusk shaped shell with two apertures, and for tactile organs named captacula, which are used in the feeding process (Reynolds and Okusu 1999). The researches regarding their feeding behavior are very limited, but the few species studied in this respect suggest the existence of a pattern.

Among the members of the order Dentaliida, the foraging process begins with the opening of muscle sheath of the mantle cavity, allowing the exit of the foot and the captacula. With the tapered part of the foot, the scaphopod creates a spacious and almost spherical cavity, and begins, with the aid of the captacula, to probe the sediment by fumbling the particles with their bulbous tips and capturing them through long cilia situated in the alveoli of these structures (Morton 1959, Dinamani 1964a, 1964b, Gainey 1972).

The particles are transported to the mouth in three possible ways: by being captured or trapped by the tip of captacula by simple adhesion or wrapping (Morton 1959, Poon 1987, Shimek 1988); one group of captacula can be used together to capture larger prey (Dinamani 1964b), or the particles may be carried from the bulb to the base of the captacula by ciliary action - in this case the existence of a ciliary band at the filaments of the captacula is needed (Gainey 1972). The particles are gathered into a furrow on the dorsal surface of the foot, behind the podal lobes. Repeated upthrows are carried out in order to bring the set of collected particles nearer the labial palps which, on the other hand, evert and select the material to be intaken. After some time, the mantle cavity is opened, allowing the expulsion of rejected material (Gainey 1972, Bilyard 1974, Byrum and Ruppert 1994, Reynolds 2002).

In the order Gadilida, the behavior pattern is a little different. After excavation, the animal expands and retracts its discoid foot edge, creating a feeding cavity similar to the one constructed by dentaliids, but of smaller size. Still within the shell, the proboscis

are extended to the previous opening, from where captacula emerge and, while penetrating in the sediment, are followed by more captacula, which go down and pass their cilia along the filaments that are probing the substrate. Finally, the captacula are then taken towards the oral cavity with or without adhering particles; the selection occurs through the labial palps and the ingestion process is completed (Davis 1968, Poon 1987).

According to Gainey (1972), once the feeding cavity has been sufficiently used, the animal must seek a new foraging area. Therefore, it occurs with the extension of the mantle cavity followed by expansion of its epipodial and central lobes; muscle contraction generates circular upthrows which cause rearward movements; foot lobes get less swollen and the shell becomes responsible for the anchoring function. This process repeats itself over and over again, with small angle variations, but always taking the scaphopod to a new foraging area. There are some evidences that the Scaphopoda prefer eating foraminifera and small heterotrophic animals (Bilyard 1974, Shimek 1990, Glover *et al.* 2003, Gudmundsson *et al.* 2003). Apparently, once the scaphopod eats the foraminifera, it preferentially breaks the chambers of the last part of its shell, but the reason is not well known (Langer *et al.* 1995).

CEPHALOPODA FORAGING BEHAVIOR

Cephalopoda is a very diverse and successful group that occupies a variety of niches in the marine environment. Its members belong to one of two subclasses: Nautiloidea, which includes only two remaining genera with external shell, and Coleoidea, comprising shellless or internally shelled mollusks, such as octopuses, cuttlefishes and squids (Teichert 1988).

The Coleoidea are active predators that capture their preys in many different ways. Among the octopus (Octopodiformes), the most used senses during foraging are touch and sight, therefore there are two main tactics inherent to any individuals in this group and known by groping and pouncing (Hartwick *et al.* 1981, Huffard 2007). Groping is the tactile detection without a specific object, when the animal passes the tentacles on the sediment, algae banks, inside cracks and other substrates until prey is eventually found. On the other hand, pouncing is an aimed tactic, in which the individual removes a

specific object from its place, completely stretching its arms. The animal involves the object and uses the tips of the tentacles to hunt around and underneath it (Forsythe and Hanlon 1997).

When the detection is purely visual, the swimming direction (back to front) is changed. Arms are pointed out in the direction of the prey and the swimming speed is slightly reduced near the same (Villanueva *et al.* 1996). Finally, the prey is subdued and eaten or if they have rigid bodies and protection structures, as in bivalves, gastropods and crustaceans, the animal needs to play two more complementary tactics. Shell and carapace perforation may happen by the action of the beak and the inoculation of toxins present in saliva, which relax the muscle attachments of the prey, allowing the extraction and ingestion of its body. The prey may also be removed by force (Grisley *et al.* 1996, Cortez *et al.* 1998, Fiorito and Gherardi 1999, Šifner and Vrgoè 2009). It often happens with females of the species *Octopus vulgaris*, that, during spawning or nesting do not produce toxins (Wodinsky 1978).

With this prospect, it is worth mentioning a few exceptions, such as a species of the Pacific *Wunderpus photogenicus*, which probe the muddy sediment with its arms, capturing the preys using the suckers at its tips. Another strategy adopted by this animal is the extension of the arms and the membrane between them over an area of sediment, building a “net” to capture any hidden prey in the substrates (Hochberg *et al.* 2006). While studying larvae of *Octopus dofleini*, Marliave (1981) noticed a predatory behavior pattern, in which the contact between the larval mantle and the krill prompted reflex movements and the larvae would start spinning their bodies and adhering their tentacles to the water surface film, keeping a backward posture; the siphon was then used to create lateral movements, in order to bring the krill down to the bottom, where the ingestion occurred. Another exception was observed by Voight (2008), where, using submersible vehicles, deep sea octopods were seen using specifically the middle portion of their arms in search of infaunal prey, while their dorsal arms were extended in the water column, probably in search of smaller animals. Furthermore, Scheel and Anderson (2012) observed that the species *Enteroctopus dofleini* learned to forage on fishing nets.

Squids and cuttlefishes (Decapodiformes) show a more aggressive behavior, being considered great hunters. The squid have nocturnal habits and hunts in shallow waters (Markaida and Sosa-Nishizaki 2003). Their attack happens as follows: they approach the prey, extending their arms sideways and eventually emitting a flash of bioluminescence of their tips. The animal is captured with the suckers of their two tentacles, that are used to bring the prey into their arms, holding it so that the intake occurs. On the other hand, when the prey is bigger and faster, the squid chases until they can catch it with their arms and without using the tentacles (Squires and Barragan 1979, Kubodera *et al.* 2007).

An exception is the pygmy squid, *Idiosepius paradoxus*, that uses its arms to capture and paralyze the prey by its posterior portion, extending its buccal mass toward the preys and releasing enzymes for external digestion. Finally, the intake of semi-digested meat occurs, in a process that does not involve biting (Kasugai *et al.* 2004). Another special case is the jumbo squid (*Dosidicus gigas*), that is considered to have no fixed foraging strategy, changing its tactics according to modifications on the environment (Lorrain *et al.* 2011).

The cuttlefish is a diurnal hunter (Aitken *et al.* 2005) and has its attacking behavior divided into three phases: observation, positioning and seizure (Adamo *et al.* 2006). In the first phase, the animal undergoes color changes, elevation of the first and second pair of arms, head and eye movement and change of direction until the prey is ahead. In the second stage, the animal approaches or moves away from the prey slowly, so that the “striking distance” is achieved. In the third and final phase, the two tentacles are ejected in a split second, capturing the prey by suction terminals and bringing it to its mouth. Shrimps and crabs are poisoned and die within a maximum of 9 seconds (Messenger 1968, 1973, Tang and Khoo 1974, Cole and Adamo 2005). In their study, Darmaillacq *et al.* (2004) discovered that once the cuttlefish experience inedible prey, they learn to recognize and avoid it for a long time.

Unlike the representatives of the subclass Coleoidea, the Nautiloidea are not big predators but scavengers of nocturnal habits (Ward and Wicksten 1980, Westermann and Schipp 1998). The detection of food can occur randomly during a behavior called Cat’s Whiskers Pose, in which 3 or 4 pairs of tentacles are extended radially, while the animal swims upwards

to the water column and descends towards the bottom, maintaining the tentacles’ position, which allows the perception of any food items around it (Haven 1972). They also locate their food through a combination of touch and smell, following a boost from some distant source of odor. In this case, after leaving the position, they swim towards the possible source of food and extend its tentacles to form the so-called “cone of search”. The increase of the breathing movements and the swimming rhythm allows a greater flow of water passing through the ocular tentacles and rhinophore. While swimming forward, backward and making pendular movements, the digital tentacles grope random substrates to find food. Then, the nautilus goes deeper in the water until it is possible to lean over one medium digital tentacle and grab the prey with another one, passing over to the oral tentacle and, finally, to the beak (Wells 1989, Ruth *et al.* 2002, Westermann and Beuerlein 2005).

CONCLUSIONS, GAPS IN KNOWLEDGE AND FUTURE PERSPECTIVES

Main hypothesis on interrelationships of basal molluscan groups, Testaria (Taylor 1996, Haszprunar, 2000) and Aculifera (Scheltema 1993), postulated that Solenogastres and Caudofoveata (=Aplacophora) constitute the most basal taxa. In this sense, we can assume that primitive mollusks were wormlike, epifaunal, true predators and/or deposit-feeders. Both hypothesis display Polyplacophora as a result of a new lineage after Aplacophora. Despite the fact that most chitons (=Polyplacophora) are generalist grazers of hard substrata, in this class we observed a variety of feeding habits. Conchifera constitutes the next step (according to Testaria and Aculifera hypothesis) and are represented in this study by Monoplacophora, Scaphopoda and Cephalopoda. Monoplacophora is a basal taxon that presents deposit-feeding habits. Scaphopoda is also a deposit-feeder but presents a specialized organ to detect and capture organic matter on the substratum. Cephalopoda could be treated as sister group of either Gastropoda or Scaphopoda and shows two feeding habits: scavengers and true predators. In general, feeding habits cannot be used to phylogenetic inference, since they are easily influenced by external factors. Furthermore, the degree of variability in feeding habits found within the group could be a direct consequence of huge radiation (see Tables 1-2 for a detailed description).

Table 1. List of taxa with its respective sources, feeding habits and habitats (Aculifera/Amphineura). ^aReviews of Solenogastres: Scheltema, 1992, Beesley *et al.* 1998, Ponder and Lindberg, 2008; ^bReviews of Caudofoveata: Beesley *et al.* 1998, Glaubrecht, 2005; ^cReviews of Polyplacophora: Boyle, 1977, Eerisse and Reynolds, 1994, Sirenko, 2000.

TAXA	SOURCES	FEEDING HABIT	HABITAT
SOLENOGASTRES^a			
Cavibelonia			
Epimeniidae			
<i>Epimenia australis</i> (Thiele, 1897)	Scheltema and Jebb 1994	True predators / Active hunters	Continental shelf
<i>Epimenia babai</i> Salvini-Plawen, 1997	Okuso and Giribet 2003	True predators / Active hunters	Continental shelf
Simrothiellidae			
<i>Helicoradomenia</i> spp.	Scheltema <i>et al.</i> 2003	True predators / Active hunters	Hydrothermal vent
<i>Helicoradomenia</i> sp.	Okuso and Giribet 2003	True predators / Active hunters	Hydrothermal vent
Pholidoskepia			
Meiomeniidae			
<i>Meioherpia stygalis</i> Salvini-Plawen and Sterrer, 1985	Okuso and Giribet 2003	True predators / Active hunters	Littoral
<i>Meiomenia arenicola</i> Salvini-Plawen and Sterrer, 1985	Morse and Norenburg 1992	True predators / Active hunters	Littoral
CAUDOFOVEATA^b			
Chaetodermatida			
Chaetodermatidae			
<i>Chaetoderma nitidulum</i> Lovén, 1844	Ponder and Lindberg 2008	Deposit-feeder	Littoral - Bathyal
Prochaetodermatidae			
<i>Prochaetoderma boucheti</i> Scheltema and Ivanov, 2000	Scheltema and Ivanov 2000	Deposit-feeder	Mesopelagic
<i>Prochaetoderma raduliferum</i> (Kowalewsky, 1901)	Scheltema and Ivanov 2000	Deposit-feeder	Littoral - Continental shelf
<i>Spathoderma alleni</i> Scheltema and Ivanov, 2000	Scheltema and Ivanov 2000	Deposit-feeder	Littoral - Bathyal
POLYPLACOPHORA^c			
Chitonida			
Acanthochitonidae			
<i>Acanthochitona garnoti</i> (Blainville, 1825)	Cretchley <i>et al.</i> 1997	True predators / Active hunters	Littoral
<i>Acanthopleura gemmata</i> (Blainville, 1825)	Hulings 1991, Barbosa <i>et al.</i> 2008	True predators / Active hunters	Littoral

Continued

TAXA	SOURCES	FEEDING HABIT	HABITAT
<i>Acanthopleura hirtosa</i> (Blainville, 1825)	Shaw <i>et al.</i> 2002	True predators / Active hunters	Littoral
<i>Notoplax speciosa</i> (H. Adams, 1861)	Beesley <i>et al.</i> 1998	True predators / Active hunters	Littoral
<i>Craspedochiton</i> spp.	Eernisse 2007	True predators / Sit-and-wait	Littoral
Ischnochitonidae			
<i>Lepidochitona dentiens</i> (Gould, 1846)	Piercy 1987	True predators / Active hunters	Littoral
<i>Stenoplax heathiana</i> Berry, 1946	Putman 1990	True predators / Active hunters	Littoral
<i>Ischnochiton albus</i> (Linnaeus, 1767)	Langer 1983		Littoral
Loricidae			
<i>Loricella angasi</i>	Eernisse 2007	True predators / Sit-and-wait	Continental shelf
Mopaliidae			
<i>Mopalia ciliata</i> (Soweby, 1840)	Piercy 1987	True predators / Active hunters	Littoral
<i>Mopalia hindsi</i> (Soweby MS, Reeve, 1847)	Piercy 1987, Beesley <i>et al.</i> 1998	True predators / Active hunters	Littoral
<i>Mopalia muscosa</i> (Gould, 1846)	Piercy 1987	True predators / Active hunters	Littoral
<i>Placiphorella</i> sp.	Clark 1994	True predators / Sit-and-wait	Littoral
<i>Placiphorella velata</i> (Carpenter MS, Dall, 1879)	McLean 1962	True predators / Sit-and-wait	Littoral
<i>Tonicella lineata</i> (Wood, 1815)	Barnes 1972, Piercy 1987	True predators / Active hunters	Littoral
<i>Tonicella marmorea</i> (O. Fabricius, 1780)	Langer 1983	True predators / Active hunters	Littoral
<i>Tonicella rubra</i> (Linnaeus, 1767)	Langer 1983	True predators / Active hunters	Littoral
<i>Katharina tunicata</i> (Wood, 1815)	Piercy 1987	True predators / Active hunters	Littoral
Lepidopleurida			
Leptochitonidae			
<i>Leptochiton vietnamensis</i> Sirenko, 1998	Sirenko 1998	True predators / Active hunters	Continental shelf - Bathyal
<i>Leptochiton vijazae</i> (Sirenko, 1977)	Beesley <i>et al.</i> 1998	Deposit-feeder	Abyssal
Abyssochitonidae			
<i>Xylochiton xylophagus</i> Gowlett-Holmes and Jones, 1992	Beesley <i>et al.</i> 1998	Deposit-feeder	Abyssal

Table 2. List of taxa with its respective sources, feeding habits and habitats (Conchifera). ^aReviews of Monoplacophora: Lindberg, 2009; ^bReviews of Scaphopoda: Shimek 1988, Reynolds 2002.

TAXA	SOURCES	FEEDING HABIT	HABITAT
MONOPLACOPHORA^a			
Tryblidiida			
Neopilinidae			
<i>Laevipilina antarctica</i> Warén and Hain, 1992	Warén and Hain 1992	Deposit-feeder	Bathyal - Abyssal
<i>Laevipilina cachuchensis</i> Urgorri, García-Álvarez and Luque, 2005	Urgorri <i>et al.</i> 2005	Deposit-feeder	Bathyal
<i>Micropilina arntzi</i> Warén and Hain, 1992	Warén and Hain 1992	Deposit-feeder	Continental shelf - Bathyal
<i>Neopilina galathea</i> Lemche, 1957	Lemche and Wingstrand 1959, Tendal 1985	Deposit-feeder	Abyssal
SCAPHOPODA^b			
Dentaliida			
Dentaliidae			
<i>Dentalium conspicuum</i> Melvill, 1897	Dinamani 1964a, 1964b	Deposit-feeder	Littoral
<i>Dentalium eboreum</i> Conrad, 1846	Gainey 1972	Deposit-feeder	Littoral
<i>Dentalium entale stimpsoni</i> Henderson, 1920	Bilyard 1974	Deposit-feeder	Continental shelf - Bathyal
<i>Dentalium entalis</i> Linnaeus, 1758	Morton 1959	Deposit-feeder	Littoral
<i>Dentalium pseudo-hexagonum</i> Henderson, 1920	Gainey 1972	Deposit-feeder	Littoral
<i>Dentalium rectius</i> Carpenter, 1864	Shimek 1990	Deposit-feeder	Continental shelf - Bathyal
<i>Fissidentalium megathyris</i> (Dall, 1890)	Langer <i>et al.</i> 1995	Deposit-feeder	Bathyal
<i>Graptacme calamus</i> (Dall, 1889)	Byrum and Ruppert 1994	Deposit-feeder	Littoral
Laevidentaliidae			
<i>Laevidentalium lubricatum</i> (Sowerby, 1860)	Glover <i>et al.</i> 2003	Deposit-feeder	Littoral
Gadilida			
Gadilidae			
<i>Cadulus aberrans</i> Whiteaves, 1887	Shimek 1990	Deposit-feeder	Continental shelf
<i>Cadulus quadridentatus</i> Dall, 1881	Davis 1968	Deposit-feeder	Continental shelf
<i>Cadulus tomiei</i> (Dall, 1897)	Poon 1987	Deposit-feeder	Continental shelf - Bathyal

Continued

TAXA	SOURCES	FEEDING HABIT	HABITAT
<i>Polyschides olivi</i> (Scacchi, 1835)	Gudmundsson <i>et al.</i> 2003	Deposit-feeder	Bathyal
<i>Siphonodentalium lobatum</i> (G.B. Sowerby II, 1860)	Gudmundsson <i>et al.</i> 2003	Deposit-feeder	Bathyal
Pulsellidae			
<i>Pulsellum affine</i> (M. Sars, 1865)	Gudmundsson <i>et al.</i> 2003	Deposit-feeder	Bathyal
<i>Pulsellum salishorum</i> Marshall, 1980	Shimek 1990	Deposit-feeder	Continental shelf
<i>Pulsellum teres</i> (Jeffreys, 1883)	Gudmundsson <i>et al.</i> 2003	Deposit-feeder	Bathyal
CEPHALOPODA			
Octopoda			
Octopodidae			
<i>Abdopus aculeatus</i> (d'Orbigny, 1834)	Huffard 2007	True predators / Active hunters	Littoral
<i>Benthoctopus</i> sp.	Voight 2008	True predators / Active hunters	Continental shelf - Bathyal
<i>Eledone cirrhosa</i> (Lamarck, 1798)	Grisley <i>et al.</i> 1996	True predators / Active hunters	Continental shelf - Bathyal
<i>Eledone moschata</i> (Lamarck, 1798)	Šifner and Vrgoč 2009	True predators / Active hunters	Continental shelf - Bathyal
<i>Enteroctopus dofleini</i> (Wülker, 1910)	Hartwick <i>et al.</i> 1981, Marliave 1981, Scheel and Anderson 2012	True predators / Active hunters	Littoral - Continental shelf
<i>Graneledone</i> sp.	Voight 2008	True predators / Active hunters	Bathyal - Abyssal
<i>Octopus cyanea</i> Gray, 1849	Forsythe and Hanlon 1997	True predators / Active hunters	Littoral
<i>Octopus mimus</i> Gould, 1852	Cortez <i>et al.</i> 1998	True predators / Active hunters	Littoral
<i>Octopus vulgaris</i> Cuvier, 1797	Wodinsky 1978, Villanueva <i>et al.</i> 1996, Fiorito and Gherardi 1999	True predators / Active and Sit-and-wait	Littoral - Continental shelf
<i>Vulcanoctopus hydrothermalis</i> Gonzalez and Guerra in Gonzalez <i>et al.</i> 1998	Voight 2008	True predators / Active hunters	Hydrothermal vent
<i>Wunderpus photogenicus</i> Hochberg, Norman and Finn, 2006	Hochberg <i>et al.</i> 2006	True predators / Active and Sit-and-wait	Continental shelf
Oegopsida			
Ommastrephidae			
<i>Dosidicus gigas</i> (d'Orbigny, 1835)	Markaida and Sosa-Nishizaki 2003, Lorrain <i>et al.</i> 2011	True predators**	Epipelagic - Mesopelagic
Octopoteuthidae			
<i>Taningia danae</i> Joubin, 1931	Kubodera <i>et al.</i> 2007	True predators / Active hunters	Mesopelagic

Continued

Conclusion

TAXA	SOURCES	FEEDING HABIT	HABITAT
Idiosepiida			
Idiosepiidae			
<i>Idiosepius paradoxus</i> (Ortmann, 1888)	Kasugai <i>et al.</i> 2004	True predators / Active hunters	Littoral
Myopsida			
Loliginidae			
<i>Lolliguncula panamensis</i> Berry, 1911	Squires and Barragan 1979	True predators / Active hunters	Littoral
Sepiida			
Sepiidae			
<i>Sepia apama</i> Gray, 1849	Aitken <i>et al.</i> 2005	True predators / Sit-and-wait	Littoral - Continental shelf
<i>Sepia officinalis</i> Linnaeus, 1758	Messenger 1968, Messenger 1973, Darmaillacq <i>et al.</i> 2004, Cole and Adamo 2005, Adamo <i>et al.</i> 2006	True predators / Sit-and-wait	Continental shelf
<i>Sepiella inermis</i> (Van Hasselt, 1835)	Tang and Khoo 1974	True predators / Sit-and-wait	Continental shelf
Nautiloidea			
Nautilidae			
<i>Nautilus macromphalus</i> Sowerby, 1848	Ward and Wicksten 1980, Westermann and Schipp 1998	Scavengers	Mesopelagic
<i>Nautilus pompilius</i> Linnaeus, 1758	Haven 1972, Westermann and Schipp 1998, Ruth <i>et al.</i> 2002, Westermann and Beuerlein 2005	Scavengers	Mesopelagic
<i>Nautilus</i> sp.	Wells 1989	Scavengers	Mesopelagic

The non-selective deposit-feeding is the simplest feeding strategy within the benthic invertebrates, although it is absent in Mollusca. The second simplest feeding method is the selective deposit-feeding, which is found between the representatives of Caudofoveata, Monoplacophora and Scaphopoda. More complex strategies were developed by true predators, such as solenogasters, cephalopods and polyplacophorans, and suspension-feeders, such as bivalves (not included in this study). Amongst true predators, it is possible to highlight the ones that (1) creep on substrata searching for specific prey, not eating the entire individual and (2) the ones that actively subdue and eat the entire prey. It is possible to observe active hunters in both types of true predators, but only the second group comprises sit-and-wait hunters. Nautiloids are exceptions amongst cephalopods because of their scavenger feeding habit; therefore, they fit in the deposit-feeders category.

The highest percentage (*ca.* 58%, *n*=50) of the study was conducted in shallow waters/continental shelf taxa while 26% (*n*=26) were conducted in deep waters taxa. Nearly 15% (*n*=13) of the studied taxa presented wide bathymetric range, occurring from shallow to great depths. Solenogastres, in spite of their high diversity at great depths, have been mostly studied at shallow waters. Additionally, we observed almost none studies about Polyplacophora from deep waters. These results showed that scarce knowledge about deep waters represents an important paradigm.

Within the studied classes, Aplacophora and Monoplacophora were the ones with less detailed descriptions of their feeding behavior. Polyplacophora and Scaphopoda seemed to be relatively well studied as a result of the effort of a few expert researchers. Although Cephalopoda was the class with the highest number of studies, most of the covered taxa was repeatedly investigated and presents economic value (*e.g.* Fisheries species). We showed that the major gaps in the knowledge of feeding habits are concentrated to basal taxa of the phylum Mollusca and from deep water habitats.

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