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Diet preferences of the Aglajidae: a family of cephalaspidean gastropod predators on tropical and temperate shores

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Aglajidae is a family of tropical and temperate marine Cephalaspidea gastropod slugs regarded as active predators. In order to better understand their food habits and trophic interactions, we have studied the diet of all genera through the examination of gut contents. Specimens were dissected for the digestive tract and gut contents were removed and identified by optical and scanning electron microscopy. Our results confirmed that carnivory is the only feeding mode in aglajids and showed a sharp preference for vagile prey (94% of food items). We suggest that the interaction between crawling speed, presence of sensorial structures capable of detecting chemical signals from prey, and unique features of the digestive system (e.g. lack of radula, eversion of the buccal bulb, thickening of gizzard walls) led aglajid slugs to occupy a unique trophic niche among cephalaspideans, supporting the hypothesis that dietary specialization played a major role in the adaptive radiation of Cephalaspidea gastropods.

Keywords: aglajids, Cephalaspidea, Mollusca, predation, trophic ecology

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INTRODUCTION

Aglajidae is a diverse group of predominantly shallow-water cephalaspidean gastropods with an extensive degree of morphological and colour variation (Rudman, 1971, 1972a, b, c, 1974, 1978; Gosliner, 1980, 2008). The family contains seven recognized genera and approximately 80 species worldwide distributed in tropical, sub-tropical and temperate shores. They are mostly found in soft bottom habitats and alga tufts around rocky shores, coral reefs and seagrass meadows (Thompson, 1977; Martínez *et al.*, 1993; Nakano, 2004; Valdés *et al.*, 2006; Gosliner *et al.*, 2008; Camacho-García *et al.*, 2013; Costello *et al.*, 2013; Bouchet, 2014; Malaquias, 2014).

A recent phylogenetic hypothesis of the Aglajidae confirmed the monophyly of the genera *Aglaja, Melanochlamys, Nakamigawaia, Navanax, Odontoglaja* and *Philinopsis* but suggested the paraphyly of *Chelidonura* which branched in three subclades (Camacho-García *et al.*, 2013). The general morphology and anatomy of several species in these three subclades are well known and they all depict similar body plans (Rudman, 1974; Gosliner, 1980; Yonow, 1992, 1994; Ornelas-Gatdula *et al.*, 2012). As a consequence, the taxonomic status of *Chelidonura* is presently not clear and thus, for the purpose of this research, we adopted its traditional definition (*sensu* Burn & Thompson, 1998).

In addition to these seven genera, there has been some debate about the validity and inclusion in the family Aglajidae of three other lineages, namely *Noalda, Pseudophiline* and *Spinoaglaja*. The genus *Spinoaglaja* was proposed for western Atlantic species with a spine-like extension on the anterior part of the shell (Ortea *et al.*, 2007), but Camacho-García *et al.* (2013) have regarded it as a synonym of *Philinopsis*; the latter authors did not consider *Noalda* as part of the Aglajidae, but this remains to be tested in a molecular phylogenetic framework. *Pseudophiline* has morphological similarities with *Philine* (Gosliner, 1980; Kitao & Habe, 1982) and the genus was recently ascribed to the family Philinidae based on the presence of philinid-like gizzard plates and radula (Chaban, 2011). More recently, the new genus *Migaya* was proposed by Ortea *et al.* (2014) for the western Atlantic species *Aglaja felis*, but the validity of this genus remains to be tested in a phylogenetic framework.

Herbivory is considered the plesiomorphic feeding condition in the Cephalaspidea (Jensen, 1994; Mikkelsen, 1996; Göbbeler & Klussmann-Kolb, 2009; Malaquias *et al.*, 2009), and carnivory was suggested by Malaquias *et al.* (2009) to have arisen independently two or three times in different lineages. The latter authors have hypothesized that dietary specialization played a major role in the adaptive radiation of Cephalaspidea gastropods and that relations between prey structure, habitat and anatomy were important in the diversification within each lineage, allowing the development of more specific predator–prey interactions.

Aglajids show several unique evolutionary traits with potential relevance for feeding strategies and diversification, such as the reduction and posterior internalization of the shell, simplification of the digestive system (e.g. loss of hard mastication

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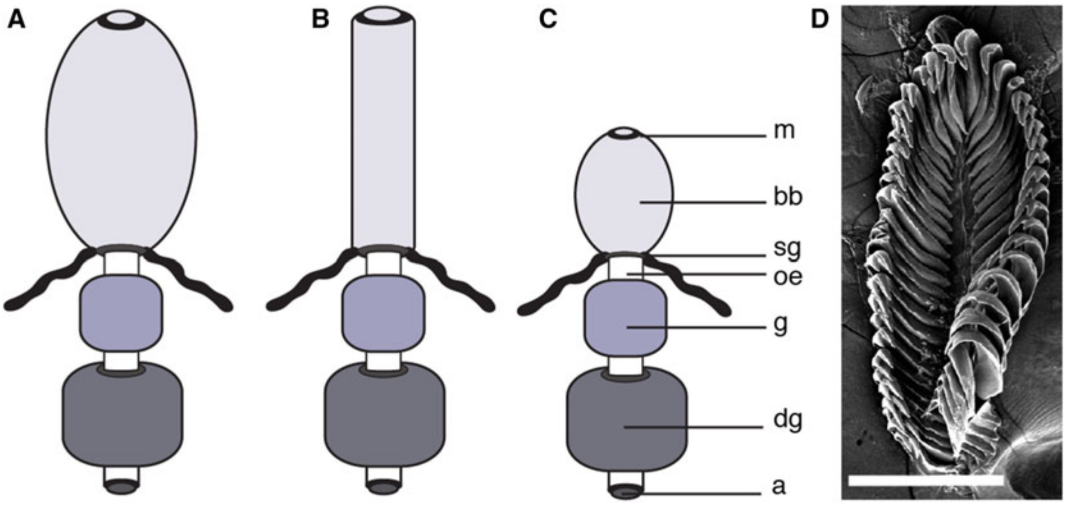

Fig. 1. Diagrammatic representation of the digestive system in Aglajidae and SEM image of the radula of *Odontoglaja guamensis*: (A) massive buccal bulb of *Aglaja, Melanochlamys, Navanax* and *Philinopsis*; (B) tubular buccal bulb variation of *Philinopsis*; (C) reduced buccal bulb in *Chelidonura, Nakamigawaia* and *Odontoglaja*; (D) radula of *O. guamensis*. (m) mouth; (bb) buccal bulb; (sg) salivary glands; (oe) oesophagus; (g) gut; (dg) digestive gland; (a) anus. Scale bar: 100 μm.

structures like the radula and gastric plates in the large majority of species), development and thickening of the buccal bulb and gizzard, secretion of deterrent chemicals, and cephalization of sensorial organs (Rudman, 1972a, b, c, 1978; Gosliner, 1980; Sleeper *et al.*, 1980; Leonard & Lukowiak, 1984; Wägele & Klussmann-Kolb, 2005; Cruz-Rivera, 2011).

Several sensory structures in gastropods (e.g. eyes, anterior lateral folds, Hancock's organs, cephalic bristles, labial palps) are known to aid in tracking mucous trails (Kohn, 1983) and for example, Paine (1963, 1965) and Leonard & Lukowiak (1984) have demonstrated that active predation in *Navanax* involves mucous trail and chemoreception. The few empirical data available on the crawling speed of aglajids suggests that they are among the fastest moving sea slugs (Turner, 1978).

The size of the buccal bulb and its ability of eversion are also important features in feeding: in *Aglaja, Melanochlamys, Navanax* and *Philinopsis*, the buccal bulb occupies almost half of the body length; while in *Chelidonura, Nakamigawaia* and *Odontoglaja* it is reduced to one-fifth of the body (Rudman, 1971). Two different forms of the buccal bulb prevail in *Philinopsis*: the typical bulbous shape (e.g. *P. taronga, P. orientalis*) that is also present in *Aglaja, Melanochlamys* and *Navanax*; and a tubular variation (e.g. *P. depicta, P. pilsbryi*) (Rudman, 1971, 1972a, b, c, 1974, 1978) (Figure 1A–C). The buccal bulb in *Aglaja* and *Navanax* can evert completely, whereas this ability is absent in *Chelidonura, Nakamigawaia, Melanochlamys* and *Philinopsis* (Rudman, 1971, 1974; Gosliner, 1980, 1994).

The genus *Navanax* feed upon other cephalaspideans including conspecifics, sacoglosans, anaspideans, nudibranchs, caenogastropods, polychaetes, crustaceans and small fish (Paine, 1963, 1965; Blair & Seapy, 1972; Gosliner, 1980; Leonard & Lukowiak, 1984; Pennings, 1990; Pennings *et al.*, 2001; Korb, 2003); *Philinopsis* and *Melanochlamys* feed upon cephalaspideans and polychaetes (Rudman, 1972a, b, Göbbeler & Klussmann-Kolb, 2009); *Chelidonura* upon flatworms (Gosliner, 1987, 1994; Yonow, 1992; Mangubhai, 2007); while *Odontoglaja* feeds on polychaetes and bivalves (Rudman, 1978; Wägele & Klussmann-Kolb, 2005; Lobo-da-Cunha *et al.*, 2009). No data are available on the diet of *Aglaja* and *Nakamigawaia*.

In this study we provide the first assessment of the dietary habits of Aglajidae sea slugs based on a comprehensive review of the literature and examination of gut contents of specimens representing the generic diversity of the family. We discuss our findings in relation to the distinctive anatomical, ecological and behavioural adaptations of these slugs.

MATERIALS AND METHODS

Ninety-two specimens belonging to 32 species of Aglajidae were dissected and their gut contents removed and examined (Table 1). Buccal bulb, oesophagus, intestine, and digestive gland were extracted and opened and the contents spread in Petri dishes filled with 70% ethanol and identified to the lowest possible taxonomic level using stereo, compound and scanning electron microscopy (SEM). Food items were mounted on SEM metallic stubs and coated with gold-palladium. Macrophotography was also used when convenient (Figures 2–4). In addition to gut content analyses, we revised the literature for records of Aglajidae food preferences in the wild (Table 2).

Food items were classified in 'sessile' and 'vagile' according to their mobility capacities (Menge *et al.*, 1994; Wägele, 2004; Madden *et al.*, 2008) and an estimate of food preference (vagile *vs* sessile) was inferred based on the total diversity of food items recognized during this study and from literature records presented in Table 2.

RESULTS

Food items were found in the gut of 11 out of the 32 species studied and in 24 of the 92 specimens dissected, corresponding to 26% of the specimens analysed (Table 1): one specimen of *Aglaja* and *Nakamigawaia*, three specimens of *Navanax*, four specimens of *Chelidonura, Philinopsis* and *Odontoglaja*, and seven of *Melanochlamys*.

Based on literature records and our own results, 70 different food items were recognized belonging to 20 major taxonomic groups, with vagile organisms accounting for 94% (=66 food items) of the diet composition. Carnivory is

Table 1. List of Aglajidae species dissected for gut contents. Numbers in brackets are the total number of specimens dissected. (ZMBN – Natural History Collections, University Museum of Bergen, Norway; WAM – Western Australian Museum; USNM – United States National Museum, Smithsonian; CNMO – Colección Nacional de Moluscos, National Autonomous University of México; NMVF – Museum Victoria, Australia).

Species dissected [no. of specimens dissected]	Species with gut content	No. of specimens with gut content	Voucher No	Food item	No. of food items in the gut
Aglaja Renier, 1807					
A. felis Er. Marcus & Ev. Marcus, 1970 [11]	*A. felis*	1 of 11	ZMBN 84913	Foraminiferans	4
A. tricolorata Renier, 1807 [1]					
Aglaja sp. [3]					
Chelidonura A. Adams, 1850					
C. africana Pruvot–Fol, 1953 [1]	*C. fulvipunctata*	1 of 6	WAM S80134	Nuculidae (Bivalvia)	1
C. amoena Bergh, 1905 [2]	*C. inornata*	1 of 4	ZMBM 94027	*Chelidonura inornata*	1
C. berolina Er. Marcus & Ev. Marcus, 1970 [2]				(Cephalaspidea gastropods)	
C. cubana Ortea & Martínez, 1997 [2]				*Stylocheilus longicaudus*	1
C. electra Rudman, 1970 [1]				(Anaspidea gastropods)	
C. fulvipunctata Baba, 1938 [6]					
C. hirundinina (Quoy & Gaimard, 1833) [1]	*C. sandrana*	2 of 4	ZMBM 94028	*Philinopsis* sp.	1
C. inornata Baba, 1949 [4]				(Cephalaspidea gastropods)	
C. pallida Risbec, 1951 [1]				*Retusa* sp.	1
C. sandrana Rudman, 1973 [4]				(Cephalaspidea gastropods)	
C. tsurugensis Baba & Abe, 1964 [1]					
C. varians Eliot, 1903 [1]					
Chelidonura sp. [2]					
Melanochlamys Cheeseman, 1881					
M. cylindrica Cheeseman, 1881 [1]	*M. diomedea*	7 of 8	USNM	Enoploidea (Nematoda)	5
M. diomedea (Bergh, 1893) [8]			771859	Kinorhyncha	2
				Aciculata (Polychaeta)	2
Nakamigawaia Kuroda & Habe, 1961					
N. spiralis Kuroda & Habe, 1961 [7]	*N. spiralis*	1 of 7	ZMBM 94029	Foraminiferans	3
Nakamigawaia sp. [2]					
Navanax Pilsbry, 1895					
N. aenigmaticus (Bergh, 1893) [3]	*N. aenigmaticus*	2 of 3	USNM 734396	*Bulla punctulata*	3
				(Cephalaspidea gastropods)	
N. inermis (J.G. Cooper, 1863) [4]	*N. inermis*	1 of 4	CNMO 1818	Gobiidae (Pisces)	1
N. orbygnianus (Rochebrune, 1881) [2]					
Noalda Iredale, 1936					
N. exigua (Hedley, 1912) [1]	–	–	–	–	–
Odontoglaja Rudman, 1978					
O. guamensis Rudman, 1978 [4]	*O. guamensis*	4 of 4	ZMBM 94030	*Philine* sp.	2
				(Cephalaspidea gastropods)	
				Isopoda	1
				(Crustacea, Eumalacostraca)	
				Holothuroidea	1
				(Echinodermata)	
Philinopsis Pease, 1860					
P. depicta Pease, 1860 [3]	*P. depicta*	2 of 3	ZMBM 94031	Facelinidae	1
P. falciphallus Gosliner, 2011 [5]				(Nudibranchia gastropods)	

Continued

Table 1. Continued

Species dissected [no. of specimens dissected]	Species with gut content	No. of specimens with gut content	Voucher No	Food item	No. of food items in the gut
P. gardineri (Eliot, 1903) [1]				*Rissoina* sp. (Caenogastropoda)	1
P. gigliolii (Tapparone–Canefri, 1874) [1]					
P. orientalis (Baba, 1949) [1]	*P. taronga*	2 of 3	NMVF K02	*Haminoea* sp. (Cephalaspidea gastropods)	1
P. reticulata (Eliot, 1903) [1]					
P. speciosa Pease, 1860 [3]				*Melanochlamys cylindrica* (Cephalaspidea gastropods)	1
P. taronga (Allan, 1933) [3]					

confirmed as the only feeding strategy in Aglajidae. The sessile organisms recognized in the gut of aglajids were bivalves, foraminiferans and sponge spicules (Table 2).

Foraminiferans were the only food item found in the gut contents of *Aglaja* and *Nakamigawaia*, whereas *Navanax* yielded the most diverse assemblage of food items, namely sponges, cephalaspidean gastropods, nudibranch gastropods, sacoglossan gastropods, caenogastropods, annelids, crustaceans and fish.

Field observations showed that *Chelidonura inornata* feed upon conspecifics and *Navanax inermis* was observed sucking in juveniles of *Aplysia* sp. (A. Zamora, personal observation).

DISCUSSION

With the exception of the studies by Paine (1963, 1965) on the diet of the genus *Navanax*, knowledge about dietary preferences of aglajid slugs is based on sparse records included in general works about the diversity or morphological aspects of the Aglajidae (e.g. Tchang-Si, 1934; Marcus, 1961; Marcus & Marcus, 1966; Blair & Seapy, 1972; Rudman, 1972a, b, 1978; Pennings, 1990; Pennings *et al.*, 2001; Padilla *et al.*, 2010; Gosliner, 2011; Camacho-García *et al.*, 2013; see Table 2). This study is the first comprehensive account dedicated to understand the trophic interactions of Aglajidae slugs as a whole.

The rather low percentage of slugs found with food remains in the gut (26%) may be partly explained by the fact that some aglajids regurgitate the hard parts of prey items after digestion when those seem to be above a certain threshold size. This behaviour was documented by Rudman (1971, 1972a) for the species *Philinopsis speciosa*, which he observed regurgitating several empty shells of the gastropod *Bulla ampulla* after 2–3 h of capture. Aglajids do not have a crushing gizzard with plates and in some cases large shells are likely too difficult to be carried along the digestive tract and end up, therefore, being regurgitated. However, Paine (1963) and Pennings (1990) have demonstrated that in the large sized-body aglajid species *Navanax inermis* (average adult size *c.* 40 mm; Leonard & Lukowiak, 1984), complete shells of small 'prosobranchs' and 'opisthobranchs' (e.g. *Aplysia*, *Bulla*) and hard-parts of sea slugs (e.g. radulae, jaws, shells) can be defecated unaltered.

A striking result of this research is the recognition that aglajids feed nearly exclusively upon vagile prey (94% of food items; Table 2). Motile organisms secrete mucus to aid in crawling or as a protective mechanism (e.g. opisthobranchs, nematodes, platyhelminths, annelids, gastropods) (Brusca & Brusca, 2003; Hickman *et al.*, 1993), leaving behind mucous trails that can be located and traced by aglajids using their sensorial organs (Paine, 1965; Kohn, 1983; Davies & Blackwell, 2007; Terrence *et al.*, 2013).

The genera *Navanax* and *Philinopsis* include relatively large animals (adult size over 10 mm in most cases) with a massive buccal bulb that occupies about half of the body cavity (Rudman, 1972a, 1974) (Figure 1). These slugs are active crawlers and can feed upon larger prey (e.g. fish, bulloid gastropods, polychaetes, flatworms, crustaceans, ctenophores and other sea slugs; Table 3) by a rapid, partial or complete eversion of the buccal bulb. Paine (1963) documented cannibalism in *Navanax* (*N. inermis*) but only between animals of dissimilar size and when those attempted to

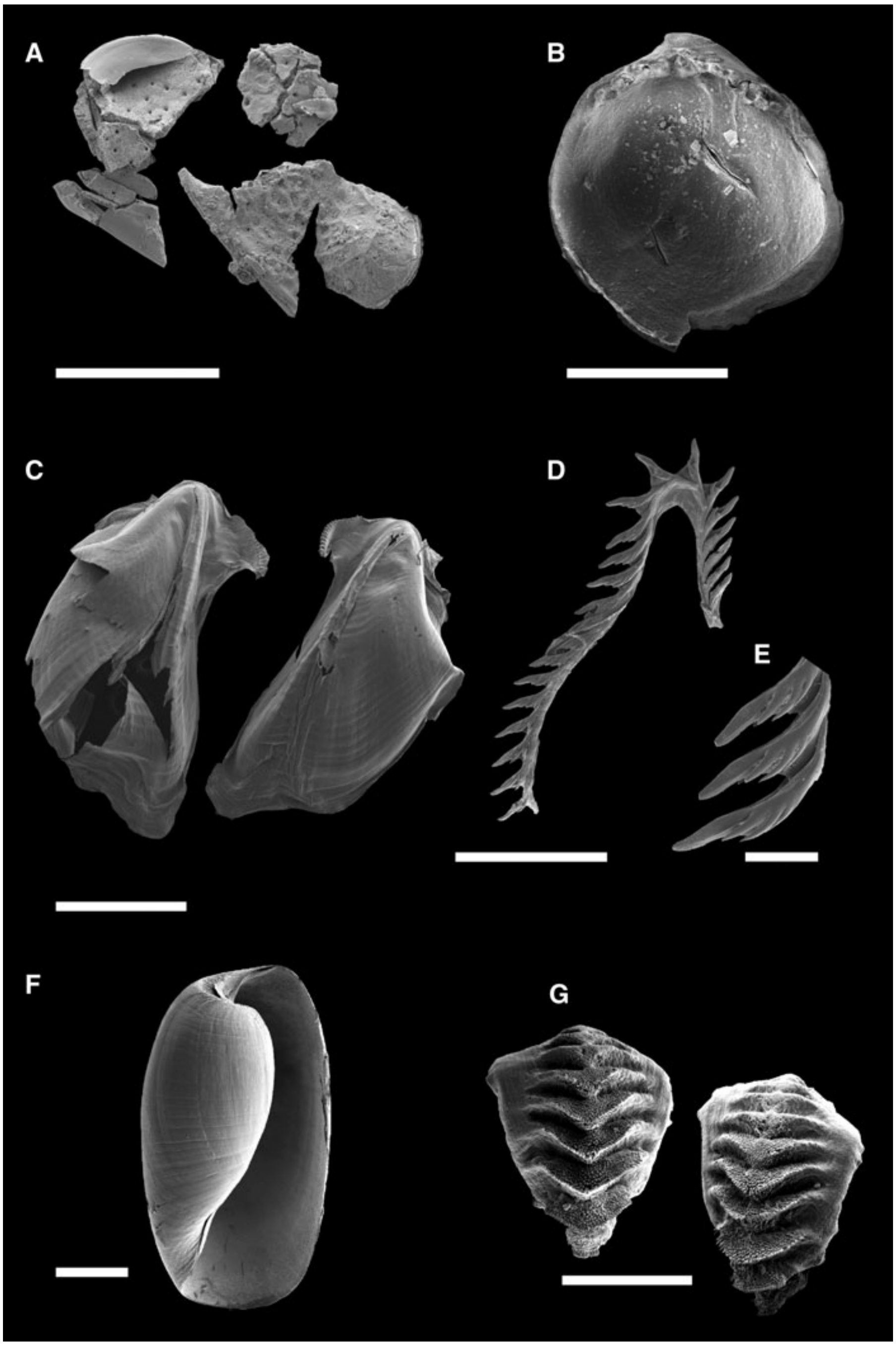

Fig. 2. Scanning electron micrographs of food items found in the digestive tract of Aglajidae specimens: (A) residues of foraminiferans in *Aglaja felis* ZMBN 84913; (B) valve of Nuculidae bivalve in *Chelidonura fulvipunctata* WAM S80134; (C) jaws of Facelinidae nudibranch in *Philinopsis depicta* ZMBM 94031; (D) radula of Facelinidae nudibranch in *Philinopsis depicta* ZMBM 94031; (E) detail of radula of Facelinidae nudibranch in *Philinopsis depicta* ZMBM 94031; (F) shell of *Haminoea* sp. in *Philinopsis taronga* NMVF K02; (G) gizzard plates of *Haminoea* sp. in *Philinopsis taronga* NMVF K02. Scale bars A and E: 200 μm; B and F: 100 μm; C, D, and G: 20 μm.

mate. The diet of *N. inermis* is by far the best known among aglajids as a result of the long-term and dedicated studies by Paine (1963, 1965; see Table 2). These studies seem to indicate that the genus *Navanax* is the most generalist among the Aglajidae, but of course this can be the result of the uneven amount of data collected for this genus when compared with the others. The presence of sponge spicules found by us in the gut of *Navanax* is likely the result of random ingestion.

On the other hand, *Chelidonura, Melanochlamys* and *Odontoglaja* species are on average smaller slugs (adult size less than 10 mm in most cases; exceptions are common in *Chelidonura*) that have comparatively a reduced and non-eversible buccal bulb (the latter is partially eversible in *Odontoglaja*) (Rudman, 1972b, 1974; Figure 1; Table 3). *Chelidonura* seems to have a preference for epifaunal organisms (e.g. flatworms, slugs, shelled gastropods), whereas *Melanochlamys* feed predominantly upon infaunal prey such

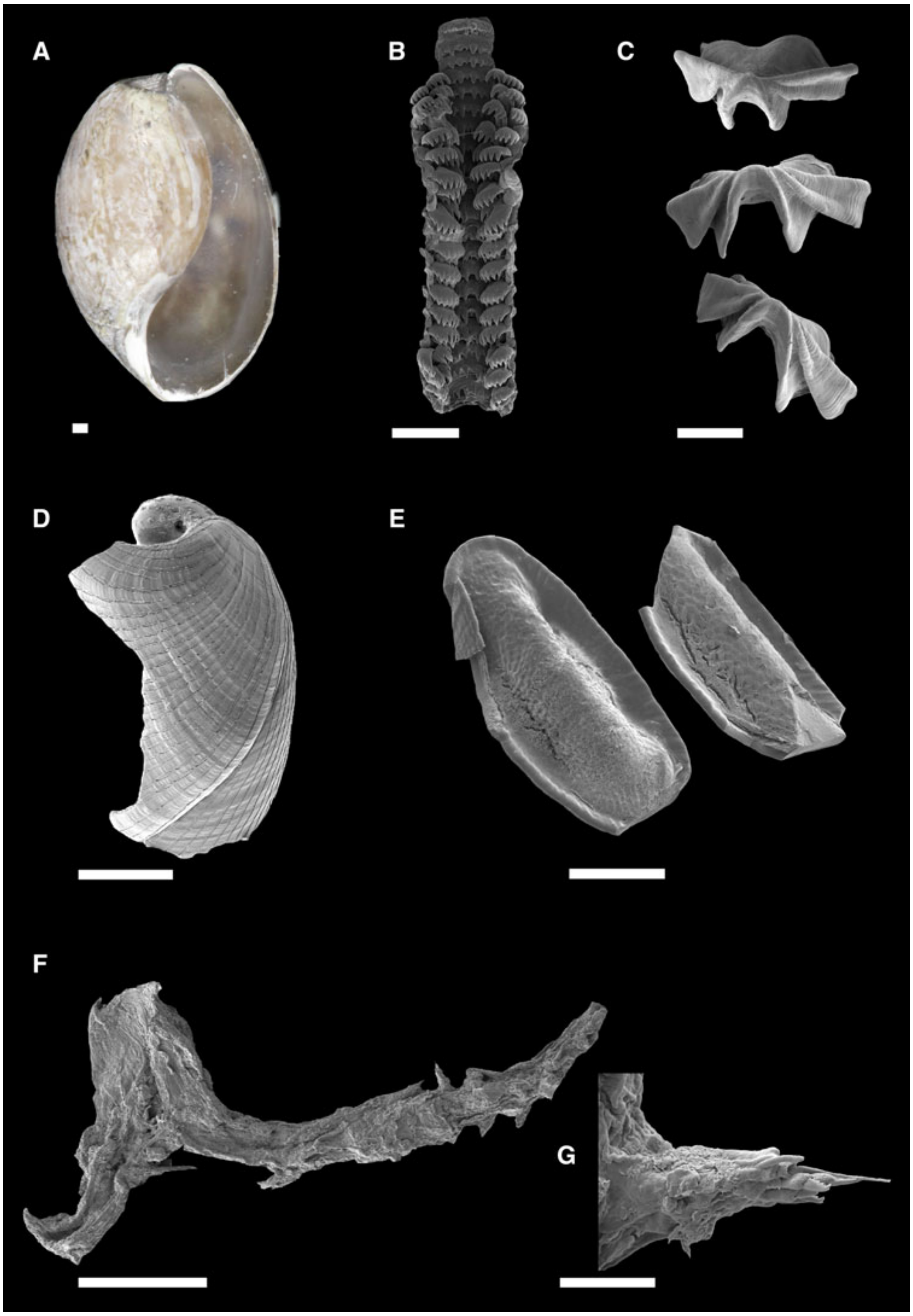

Fig. 3. Scanning electron micrographs of food items found in the digestive tract of Aglajidae specimens: (A) shell of *Bulla punctulata* in *Navanax inermis* CNMO 1818; (B) radula of *B. punctulata* in *Navanax inermis* CNMO 1818; (C) gizzard plates of *B. punctulata* in *Navanax inermis* CNMO 1818; (D) shell of *Philine* sp. in *Odontoglaja guamensis* ZMBM 94030; (E) gizzard plates of *Philine* sp. in *Odontoglaja guamensis* ZMBM 94030; (F) Aciculata polychaete in *Melanochlamys diomedea* USNM 771859; (G) detail of the parapodia of Aciculata polychaetes in *Melanochlamys diomedea* USNM 771859. Scale bars A: 1 mm; B, C and D: 200 μm; E and G: 20 μm; F: 100 μm.

as polychaetes, nemerteans, nematodes and kinorhynchs (Table 3).

Odontoglaja, the only confirmed genus with radula (Gosliner *et al.*, 2008; Figure 1; referred to a possible *Chelidonura* with a vestigial radula), which is well developed with strong bicuspid lateral teeth (Gosliner *et al.*, 2008; Figure 1), has apparently a preference for organisms with thicker dermis such as crustaceans, ?holothurians, and polychaetes (Hickman *et al.*, 1993; Table 3).

Aglaja and *Nakamigawaia* are genera for which nothing was previously known about their diet. Most species have an average adult size over 10 mm (Rudman, 1972c; Baba, 1985), but based on our results it is not possible to ascertain where the sole presence of foraminiferans found in the gut reflects a dietary preference or results from accidental ingestion. Because of average size, anatomical configuration of the digestive tract, and crawling capacities of these snails (Rudman, 1972c; Baba, 1985; Gosliner *et al.*, 2008; Figure 1;

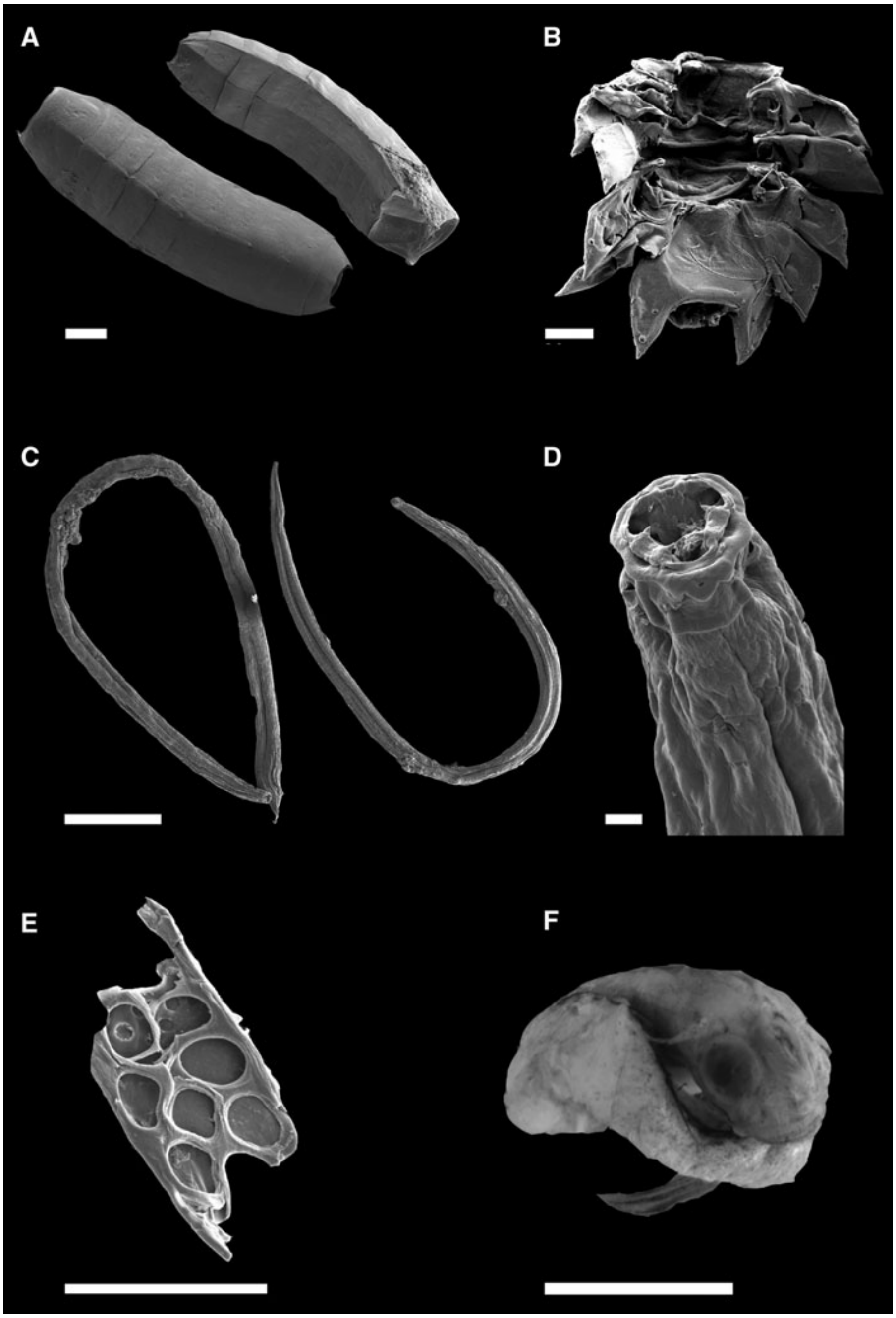

Fig. 4. Scanning electron micrographs of food items found in the digestive tract of Aglajidae specimens: (A) Kynorhyncha sp. in *Melanochlamys diomedea* USNM 771859; (B) ?exoskeleton of Isopoda in *Odontoglaja guamensis* ZMBM 94030; (C) Enoploidea nematodes in *Melanochlamys diomedea* USNM 771859; (D) detail of the mouth of the nematodes in *Melanochlamys diomedea* USNM 771859; (E) ?fragment of a spicule of Holothuria in *Odontoglaja guamensis* ZMBM 94030; (F) complete specimen of Gobiidae fish in *Navanax inermis* CNMO 1818. Scale bars A: 20 μm; B: 30 μm: C and E: 100 μm; D: 10 μm, F: 5 mm.

Tables 2 & 3), our expectation was to find a diet composed by several motile invertebrates.

Malaquias *et al.* (2009) mapped the diet of most lineages of cephaslaspids onto a molecular phylogeny of the group and have suggested that dietary specialization played a major role in the adaptive radiation of these gastropods. Our results reinforced the view that Aglajidae slugs are the only active hunter group of cephalaspids and the only one to be specialized on motile prey (Malaquias *et al.*, 2009; Göbbeler & Klussmann-Kolb, 2009).

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Table 2. Review of the diet of Aglajidae based on literature records and novel data (based on animals collected in the wild).

Species	Food item	Prey ecology	References
Aglaja Renier, 1807			
A. felis Er. Marcus & Ev. Marcus, 1970	- Foraminiferans	Sessile	Present study
Chelidonura A. Adams, 1850			
C. alisonae Gosliner, 2011	- *Convoluta* acoels flatworms (Acoelomorpha)	Vagile	Gosliner (2011)
C. fulvipunctata Baba, 1938	- Nuculidae (Bivalvia)	Sessile	Present study
C. hirudinina (Quoy & Gaimard, 1833)	- Free living flatworms (?Acoelomorpha/Platyhelminthes)	Vagile	Gosliner (1987)
			Cruz-Rivera (2011)
			Kohn (1983)
C. inornata Baba, 1949	- *Chelidonura inornata* (Cephalaspidea gastropods)	All vagile	Rudman, 1974
	- *Stylocheilus longicaudus* (Anaspidea gastropods)		Present study
C. punctata Eliot, 1903	- Acoels flatworms	Vagile	Mangubhai (2007)
C. sandrana Rudman, 1973	- *Philinopsis* sp.	All vagile	Present study
	- *Retusa* sp. (Cephalaspidea gastropods)		
C. varians Eliot, 1903	- Acoels flatworms (Acoelomorpha)	Vagile	Yonow (1992, 1994)
Melanochlamys Cheeseman, 1881			
M. cylindrica Cheeseman, 1881	- Polychaeta	All vagile	Rudman (1971, 1972b, c)
	- Nemertea		
M. diomedea (Bergh, 1893)	- Enoploidea (Nematoda)	All vagile	Present study
	- Kinorhyncha		
	- Aciculata (Polychaeta)		
Nakamigawaia Kuroda & Habe, 1961			
N. spiralis Kuroda & Habe, 1961	- Foraminiferans	Sessile	Present study
Navanax Pilsbry, 1895			
N. aenigmaticus (Bergh, 1893)	- *Haliclona* sp. (Porifera)	Sessile	Ev. Marcus & Er Marcus (1966)
	- *Tethya* sp. (Porifera)		Padilla *et al.* (2010)
	- *Bulla* sp.		Present study
	- *Bulla punctulata* (Cephalaspidea gastropods)	Vagile	
N. gemmatus (Mörch, 1863)	- Platyhelminthes	All vagile	Thompson (1976, 1977)
	- *Elysia crispata* (Sacoglossa gastropods)		Gosliner, 1980
N. inermis (J. G. Cooper, 1863)	- *Aplysia californica* (Anaspidea gastropods)	All vagile	Paine (1963, 1965)
	- *Bulla punctulata*		Emlen (1966)
	- *B. gouldiana*		Blair & Seapy (1972)
	- *Haminoea virescens*		Gosliner (1980; 1994)
	- *Navanax inermis* (Cephalaspidea gastropods)		Sleeper, *et al.* (1980)
	- *Elysia* sp. (Sacoglossa gastropods)		Leonard & Lukowiak (1984)
	- *Barleeia* sp. (Caenogastropoda)		Pennings (1990)
	- *Cystiscus* sp. (Neogastropoda)		Pennings *et al.* (2001)
	- Gobiidae (Pisces)		Korb (2003)
			Present study
N. polyalphos (Gosliner & Williams, 1972)	- *Haminoea* sp. (Cephalaspidea gastropods)	Vagile	Gosliner & Williams (1972)

Odontoglaja Rudman, 1978			
O. guamensis Rudman, 1978	- Polychaeta	Vagile	Rudman (1978)
	- *Philine* sp. (Cephalaspidea gastropods)		Present study
	- Isopoda (Crustacea)		
	- Holothuroidea (Echinodermata)		
O. mosaica Gosliner, 2011	- Benthic copepods (Crustacea)	Vagile	Gosliner (2011)
Philinopsis Pease, 1860			
P. ctenophoraphaga Gosliner, 2011	- *Coeloplana (Benthoplana) meteoris* (Benthic ctenophores)	Vagile	Gosliner (2011)
P. depicta Pease, 1860	- Polychaeta	All vagile	Marcus (1961)
	- *Philine quadripartita*		Gosliner (1980)
	- *P. scabra* (Cephalaspidea gastropods)		Chiu, 1990
	- Facelinidae (Nudibranchia gastropods)		Lobo-da-Cunha *et al.* (2009)
	- *Rissoina* sp. (Caenogastropoda)		Lobo-da-Cunha *et al.* (2011)
			Present study
P. falciphallus Gosliner 2011	- Polyclad flatworms (Platyhelminthes)	Vagile	Gosliner (2011)
P. pilsbryi (Eliot, 1900)	- Small opisthobranchs (Opisthobranchia gastropods)	Vagile	Göbbeler & Klussmann–Kolb (2009)
P. minor (Tchang-Si, 1934)	- Small molluscs	Vagile	Tchang-Si (1934)
P. speciosa Pease, 1860	- *Aliculastrum cylindricum*	All vagile	Rudman (1972a)
	- *Bulla ampulla*		Gosliner (1980)
	- *Chelidonura sandrana*		Yonow (1992)
	- *Haminoea* sp. (Cephalaspidea gastropods)		
	- *Aplysia parvula* (Anaspidea gastropods)		
	- *Ringicula* sp. (Heterobranchia gastropods)		
P. taronga (Allan, 1933)	- *Amalda* sp. (Caenogastropoda)	All vagile	Rudman (1972a)
	- *Haminoea* sp.		Present study
	- *Haminoea zelandiae*		
	- *Melanochlamys cylindrica*		
	- *Philine auriformis* (Cephalaspidea gastropods)		

Table 3. Synoptic table of the diet preferences and buccal bulb features in the Aglajidae genera.

Genus	Buccal bulb features	Diet preferences
Aglaja	Massive, eversible	Foraminiferans
Chelidonura	Reduced, non-eversible	Flatworms, slugs, shelled gastropods, 'Bivalves'
Melanochlamys	Massive, non-eversible	Polychaetes, Nemerteans, Nematodes, Kinorhynchs
Nakamigawaia	Reduced, non-eversible	Foraminiferans
Navanax	Massive, eversible	Shelled gastropods, flatworms, slugs, fish, 'Sponges'
Odontoglaja	Reduced, non-eversible	Polychaetes, shelled gastropods, Crustaceans, Holothurians
Philinopsis	Massive/Tubular, non-eversible	Benthic ctenophorans, Polychaetes, Shelled gastropods, Flat worms, Slugs

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