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ORIGINAL PAPER

Sympatry in grapsoid crabs (genera *Planes* and *Plagusia*) from olive ridley sea turtles (*Lepidochelys olivacea*), with descriptions of crab diets and masticatory structures

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Abstract Grapsoid crabs of the genera *Planes* and *Plagusia* are commonly referred to as "rafting crabs" due to their propensity to live on flotsam and pelagic marine animals. *Planes minutus* and *Planes major* (=*Planes cyaneus*) are epibionts of sea turtles. Occurrences of grapsoid crabs in the genera *Planes* and *Plagusia* were evaluated on a total of 27 olive ridley sea turtles, *Lepidochelys olivacea*, from the eastern tropic Pacific (1998–2001) and the Hawaiian Islands (2002) captured in July–December each year. This is the first report of *Planes marinus* and *Plagusia squamosa* on sea turtles, and of *P. major*, *P. marinus*, and *P. squamosa* in sympatry on a confined substrate. Stomach content analyses showed *P. major* and *P. marinus* consumed a variety of neuston and marine vegetation, with the former consuming considerably more animal material. Epibiotic *P. squamosa* consumed mostly plant material. The three *Planes* species had distinctive differences in gastric mill tooth morphology. The versatile mouthparts of *P. marinus* are described and resemble those of their congeners. Most female *P. major* and *P. marinus* collected were ovigerous and present in all survey months.

Introduction

Grapsoid crabs of the genus *Planes* (Brachyura: Grapsidae) are relatively small and live upon most objects that float in the open ocean—including pelagic marine animals such as sea turtles, jellyfish, siphonophores, and gastropods (Davenport 1994; Frick et al. 2004). Currently, three species are recognized: *Planes major* (MacLeay), *Planes marinus* (Rathbun 1914), and *Planes minutus* (Linnaeus 1758). To date, much of the recorded life history and ecology of the *Planes* species has come from specimens of *P. major* and *P. minutus* collected as epibionts of loggerhead sea turtles, *Caretta caretta* (Davenport 1994; Dellinger et al. 1997; Frick et al. 2000, 2004, 2006; Carranza et al. 2003). When hosted by loggerheads, both species often occur on individual turtles as heterosexual pairs (Dellinger et al. 1997; Carranza et al. 2003). Dietary analyses indicate that *P. minutus* feed upon the sessile epibiota of host turtles and they hunt neustonic organisms that swim near the host turtle (Frick et al. 2004). *Planes minutus* probably scavenge food particles drifting away from host turtles that are masticating prey items (Frick et al. 2004).

Little is known of the life history of the third species *P. marinus* (Spivak and Bas 1999; Carranza et al. 2003). It is almost always found in association with flotsam in oceanic drifts and items washed ashore onto continental beaches (Chace 1951; Spivak and Bas 1999). This study is the first report of *P. marinus* as an epibiont of sea turtles or from any marine vertebrate. Nothing is known of the life history of *P. marinus* as an epibiont of marine turtles, but it

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may well be similar to that of its congeners that occur on sea turtles.

Another grapsoid species often associated with flotsam in the Pacific Ocean is *Plagusia squamosa* (Herbst 1790) (Brachyura: Plagusiidae). It occupies both oceanic and rocky-intertidal habitats throughout the Pacific region (Schubart and Ng 2000). Our study represents the first report of *P. squamosa* as an epibiont of sea turtles. The morphology, development, phylogenetics, and distribution of *P. squamosa* have been extensively documented, but there is a paucity of information concerning the life history and occurrence of *P. squamosa* as a commensal of other marine organisms.

The present study reports the occurrence of *P. major*, *P. marinus*, and *P. squamosa* as epibionts of olive ridley sea turtles, *Lepidochelys olivacea* from the oceanic waters surrounding the Hawaiian Islands to the eastern tropical Pacific Ocean from northern Baja California to northern South America. To our knowledge, ours is the first report of two or more grapsoid crab species living in sympatry upon a relatively confined substrate. We provide the first dietary analyses of *P. marinus* and *P. squamosa*, and we present the results of similar analyses of *P. major*. We also provide the first descriptions of the mouthparts of *P. marinus*. During the analysis of the stomach contents of *Planes* spp., the major teeth of the gastric mill were examined. These structures are illustrated and described herein.

Materials and methods

The nomenclature of the species here follows Ng and Ahyong (2001) who noted that *P. major* (MacLeay, 1838) is the senior synonym for the better known *P. cyaneus* (Dana, 1852). Grapsoid crabs were opportunistically sampled from immature and adult olive ridley turtles from the eastern tropical Pacific Ocean from northern Baja California, Mexico to northern South America from 1998 to 2001 (25°N to 15°S, from the west coast of the Americas to 155°W), and the oceanic waters surrounding the Hawaiian Islands in 2002 (32°N/182°W southeast to 25°N/152°W, south to 16°N/156°W and northwest to 26°N/182°W) (Fig. 1). Each research cruise was conducted from July to December.

Turtle maturity class was determined by carapace length (Márquez-M 1990). For adult turtles (individuals $\geq$60 cm), the secondary sexual characteristics were noted to determine gender. Crab specimens were placed in 95% ethanol. The gastric mills of crabs were removed and examined under light microscopy (up to 1,000×)—using a computer-interfaced microscope with a digital imager to construct figures of the internal masticatory structures (gastric teeth). *Planes minutus* were collected from flotsam and immature loggerhead turtles near the Azores (see Frick et al. 2004 for ecological and technical information regarding *P. minutus* specimens), and the gastric teeth were removed from these crabs for comparison with the gastric teeth of crabs collected from olive ridleys.

Dietary data were collected and analyzed following Frick et al. (2004) utilizing a “points system” developed by Hynes (1950) and Hartnoll (1963) in which 20 points are assigned to a full stomach, 10 points to a half full stomach, etc. These points are then allocated among the diet items in the digestive tract according to their volume. The points allocated to each type of food are summed and then expressed as a percentage of the overall diet for each crab category. Salps were identified from crab diets by the presence of tunic cells, and cnidarians were identified via nematocysts viewed under squash preparations of crab digesta mixed with water (see Frick et al. 2001, 2009 for methods).

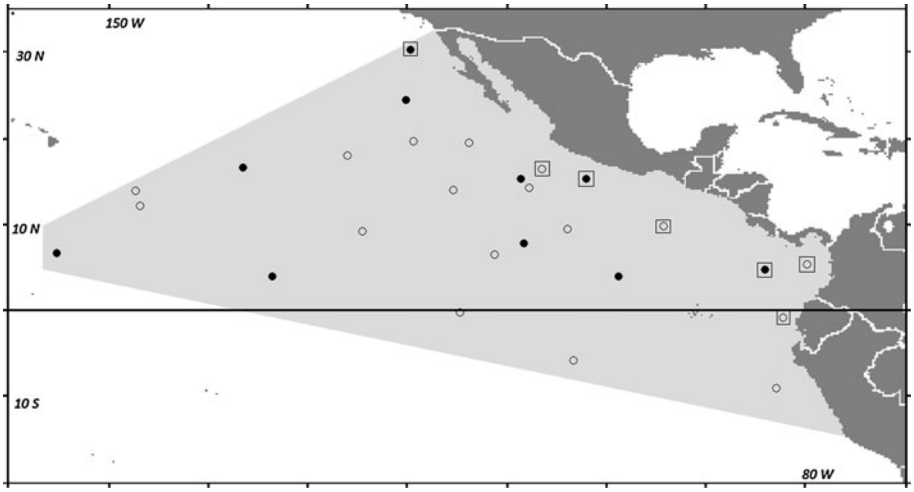

Fig. 1 Survey area in *gray*. *Open circles* denote turtles hosting only *Planes major*, *closed circles* denote turtles hosting both *P. major* and *Planes marinus*, and *boxed circles* denote turtles also hosting *Plagusia squamosa*

Results

Population structure and diets of grapsoid crabs

Host turtle size ranged from 50 to 69 cm curved carapace length (average = 61 cm). The gender of immature turtles (individuals $\leq$59 cm) was not ascertained. Crabs were collected from 10 adult and 17 immature *L. olivacea* (Table 1). Gender of adult host turtles had no effect on crab data reported here, so turtle gender is not discussed. *Planes major* heterosexual pairs and megalopae occurred on 100% of the turtles examined. Four adult turtles hosted juvenile *P. major* singletons and one adult turtle hosted five juvenile *P. major*. *Planes marinus* heterosexual pairs occurred on all turtles except two immature turtles that hosted adult female singletons. No *P. marinus* megalopae were encountered. A large proportion of female crabs was ovigerous; the proportions of ovigerous females were not significantly different between *P. major* and *P. marinus* (chi-square test, $\chi^2 = 1.21$, $df = 1$, $p = 0.271$). A single *P. squamosa* heterosexual pair was found on an immature olive ridley. The remainder of *P. squamosa* specimens (four females, one male) occurred as singletons on adult and immature olive ridleys. A single *P. squamosa* megalopa was collected from an immature turtle.

The carapace widths of the grapsoid crabs collected with respect to sex, reproductive condition, and life stage are presented in Table 2. Agonistic interactions between grapsoid species occupying the same host turtle were evident through the loss of walking legs on some specimens. Ten male and seven female *P. marinus* were missing one walking leg. Three male and one female *P. major* were missing one walking leg. The occurrence of missing legs was significantly greater in *P. marinus* than in *P. major*

Table 1 Occurrence of each grapsoid crab species, sex, and stage from olive ridley turtles

Host data		*Planes major*				*Planes marinus*		*Plagusia squamosa*		
Turtle #	Turtle CCL (cm)	Male	Female	Juv	Meg	Male	Female	Male	Female	Meg
1[a]	69.0	1	1[b]	1	×	1	1	0	0	0
2[a]	64.5	1	1[b]	0	×	1	1	0	0	0
3[a]	69.0	1	1	0	×	1	1[b]	0	0	0
4[a]	67.6	1	1[b]	1	×	1	1[b]	0	0	0
5[a]	68.4	1	1	1	×	1	1[b]	0	1[b]	0
6[a]	65.5	1	1[b]	0	×	1	1[b]	0	1	0
7[a]	63.2	1	1[b]	0	×	1	1	0	0	0
8[a]	65.4	1	1	1	×	1	1	0	0	0
9[a]	67.1	1	1[b]	0	×	1	1	0	1[b]	0
10[a]	68.7	1	1[b]	5	×	1	1	0	0	0
11	59.0	1	1[b]	0	×	1	1[b]	0	0	0
12	57.2	1	1	0	×	1	1[b]	0	0	0
13	59.0	1	1[b]	0	×	1	1	0	0	0
14	59.0	1	1	0	×	1	1[b]	0	0	0
15	56.7	1	1[b]	0	×	1	1[b]	0	0	0
16	59.0	1	1[b]	0	×	1	1	0	0	0
17	57.8	1	1	0	×	1	1[b]	0	0	0
18	58.9	1	1[b]	0	×	1	1	1	0	0
19	59.0	1	1[b]	0	×	1	1[b]	0	0	0
20	50.0	1	1[b]	0	×	1	1[b]	0	0	0
21	55.8	1	1[b]	0	×	1	1[b]	0	0	0
22	58.6	1	1	0	×	1	1	0	1	0
23	59.0	1	1[b]	0	×	1	1	0	0	0
24	58.3	1	1[b]	0	×	1	1	0	0	0
25	59.0	1	1	0	×	1	1[b]	0	0	0
26	58.5	1	1[b]	0	×	0	1	1	1[b]	0
27	58.8	1	1	0	×	0	1	0	0	×

CCL curved carapace length, *Juv* juvenile, *Meg* megalopa, × denotes presence

[a] Adult turtle, [b] Ovigerous female

Table 2 Carapace widths (CW, mm) of adult and juvenile grapsoid crabs and carapace lengths (CL, mm) of megalopae

	Planes major					*Planes marinus*			*Plagusia squamosa*			
	Female CW	Ovig CW	Male CW	Juv CW	Meg CL	Female CW	Ovig CW	Male CW	Female CW	Ovig CW	Male CW	Meg CL
Mean	16.3	16.1	14.8	5.2	4.0	15.1	15.4	14.1	14.2	15.7	13.5	5.2
Min	10.1	10.1	11.2	4.3	3.3	11.7	12.1	10.0	10.8	11.9	13.4	–
Max	25.6	25.6	18.9	7.4	4.5	21.5	21.5	16.9	19.4	19.4	13.6	–
n	27	18	27	9	75	27	13	25	5	3	2	1

Female and male crabs are all adults

Ovig ovigerous females, *juv* juvenile, *meg* megalopa, *min* minimum value, *max* maximum value, *n* sample size

Table 3 Diets of adult grapsoid crabs collected from olive ridley turtles

Diet	*Planes major*		*Planes marinus*		*Plagusia squamosa*	
	Male	Female	Male	Female	Male	Female
Crab-stage congener	24 (5.8)	32 (9.1)	17 (5)	19 (5)	–	–
P. major megalopae	34 (8.3)	20 (5.7)	30 (9)	42 (11.8)	–	–
P. squamosa megalopae	1 (0.2)	–	–	–	–	–
Unidentified megalopae	–	1 (0.3)	2 (0.6)	–	–	–
Pleuroncodes	21 (5.1)	10 (2.8)	10 (3)	7 (1.3)	–	–
Cirriped	52 (12.6)	41 (11.6)	1 (0.3)	4 (1.1)	–	–
Cnidarian	12 (2.9)	17 (4.8)	8 (2.3)	5 (1)	–	–
Salpidae	33 (8.0)	35 (9.9)	21 (6)	28 (7.9)	–	–
Unidentified animal material	212 (51.5)	186 (52.8)	54 (15.8)	67 (18.9)	–	5 (15.2)
Unidentified plant material	23 (5.6)	10 (2.8)	198 (58.1)	187 (52.1)	14 (100)	28 (84.8)
Total number of points	412	352	341	354	14	33
Total number of crabs	27	27	25	27	2	5

Twenty points are assigned to a full stomach, 10 points to a half full stomach, etc. These points are then allocated among diet items in the digestive tract according to their volume. Points allocated to each type of food are summed and then expressed as a percentage of the overall diet for each crab category in parentheses

(chi-square test, $\chi^2 = 9.13$, $df = 1$, $p = 0.003$). A single *P. squamosa* male was missing a single walking leg. All juvenile *P. major* were missing at least one walking leg. Three juvenile *P. major* were missing two walking legs.

Table 3 summarizes the diets of adult grapsoid crabs collected from olive ridley turtles. Male and female crabs of all species contained similar amounts and similar types of food. Adult and juvenile congeners were represented in diets as walking leg pieces and setae. Megalopae were represented in diets by walking leg and cheliped pieces, and setae. Pelagic galatheid crabs, *Pleuroncodes planipes* (squat lobsters; Anomura: Galatheoidea), were represented by larval pieces, particularly uropods and legs, and adult leg fragments. Nematocyst analyses yielded identifiable cnidarian genera from some of the stomach contents of *P. marinus* and *P. major*: *Chrysaora* sp., *Aurelia* sp., *Physalia* sp., *Porpita* sp., and *Mitrocoma* sp. Barnacles (cirripeds) were represented in the diet as cyprid larvae and cirri. Ten *P. major* were documented carrying identifiable and partially consumed prey items. These items were large pieces of *Pleuroncodes planipes* adults (four crabs), small lepadomorph barnacles *Conchoderma virgatum,* and *Lepas anserifera* (one crab each), conspecific megalopae (three crabs) and an engraulid fish *Anchoa* sp. (one crab). Unidentified animal material contained masticated tissue and keratinized scales.

Planes major and *P. marinus* adults had similar amounts of digesta in their digestive tracts and both were omnivorous. *Planes major* consumed significantly more animal material and less plant material than did *P. marinus* (chi-square test, $\chi^2 = 457.5$, $df = 1$, $p < 0.0001$). *Plagusia squamosa* contained relatively full digestive tracts comprised primarily of plant material. Cannibalism appears common among *P. major* and, likely in *P. marinus*—given the comparable number of *P. major* megalopae and crab-stage congeners consumed by *P. marinus*. One unidentified

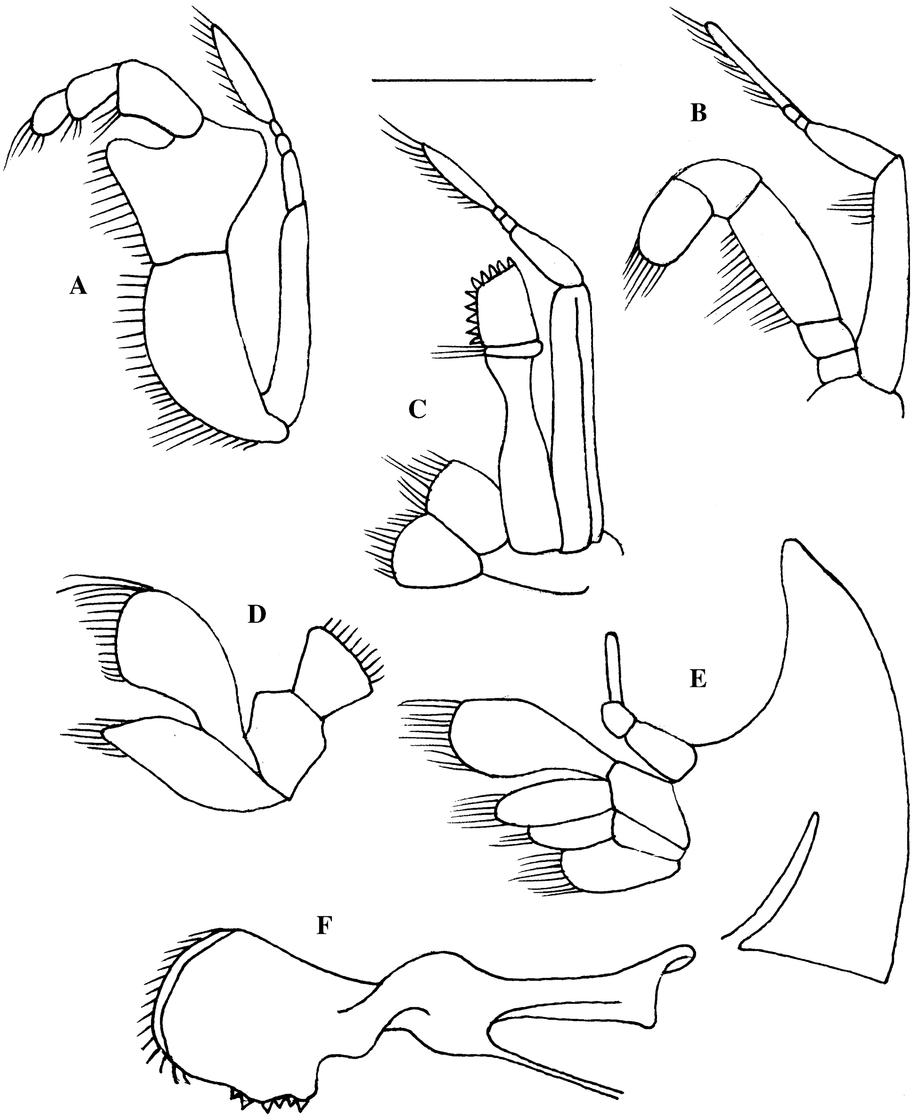

Fig. 2 *Left-side* mouthparts of *Planes marinus*. **a** Third maxilliped, **b** second maxilliped, **c** first maxilliped, **d** second maxilla, **e** first maxilla, **f** mandible. *Scale bar* for **a**–**e** is 5 mm, **f** is 2 mm

megalopa was consumed by *P. major*; one *P. major* also fed upon a *P. squamosa* megalopa.

Morphology of grapsoid masticatory structures

The morphology of the external (mouthparts) and internal (gastric teeth) masticatory structures of the genus *Planes* are illustrated in Figs. 2 and 3. The morphology of the mouthparts and major gastric teeth of the gastric mill were similar between juvenile and adult specimens. The morphology of the maxillipeds and maxillae of all three *Planes* spp. are virtually identical; thus, illustrations of these structures in the present study are limited to those of *P. marinus*.

Maxillipeds. The third maxilliped (Fig. 2a) bears numerous long setae along the inner edges of the ischium and merus. The terminal segment of the exopod (five total segments) bears numerous long setae along the inner margin. The endopod (palp) of the third maxilliped consists of three segments (carpus, propodus and dactylus), each bearing simple setae in tufts along the inner apical margin of each segment.

The five-segmented exopod of the second maxilliped (Fig. 2b) bears a small fringe of setae along the inner margin of the first segment, and long setae line most of the inner surface of the terminal segment. The endopod consists of five segments. The first three segments emanating from the coxa bear short to long, brush-like setae along much of the inner margin. The next carpal segment bends inwardly and perpendicular to the base of the endopod and bears little or no setation. The dactylus of the endopod is rounded at its terminus and fringed with long brush-like setae.

The exopod of the first maxilliped (Fig. 2c) is five-segmented and long. It bears long setae that line the inner margin of the long, finger-like terminal segment.

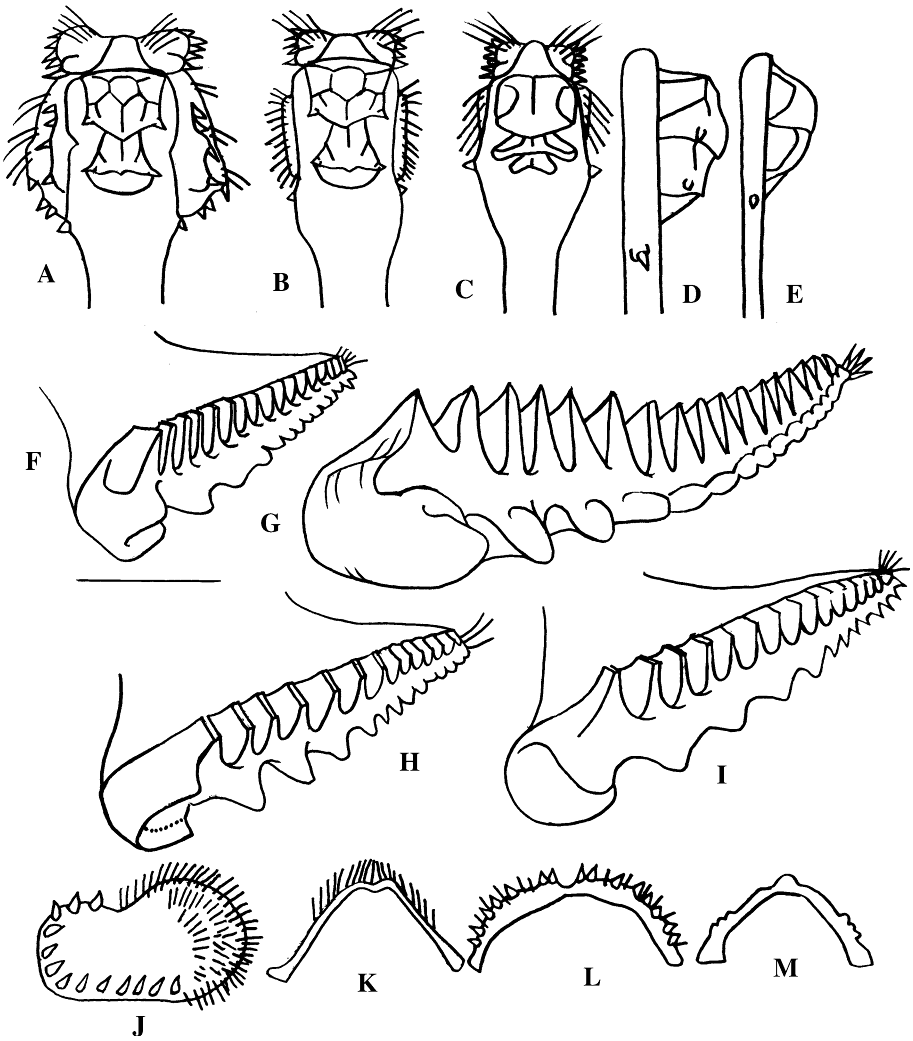

Fig. 3 Masticatory structures of the gastric mill of the *Planes* spp. **a–e** Median tooth and associated urocardiac ossicle of **a** *Planes major*, **b** *Planes marinus*, **c** *Planes minutus* (all in *ventral* view), **d** *Planes major*, and **e** *Planes minutus* (both in *lateral* view), **f–i** right-side lateral tooth of **f** *Planes major*, **g** *Planes major* (*oblique* view with zygocardiac ossicle removed), **h** *Planes marinus*, and **i** *Planes minutus*, **j** accessory lateral tooth of *Planes*, **k–m** cardiac-pyloric valve of **k** *Planes major*, **l** *Planes marinus*, and **m** *Planes minutus*. *Scale bar* for all = 1 mm

The endopod is three-segmented and spatula-shaped. The second segment is narrow and bears three to four long setae that line the inner margin. The distal segment is rectangular and bears numerous conical tubercles along the top and inner margins. Situated more inwardly along the coxa of the first maxilliped are two small endites (basipodite and coxopodite), both of which bear long setae extending from the distal end.

Maxillae. The second maxilla (Fig. 2d) consists of a large, wing-like scaphognathite bearing a short, three-segmented and finger-like endopod without setae. The basipodite is Y-shaped—containing two distal segments, both with distal ends bearing numerous long brush-like setae. The neighboring coxopodite is similarly-structured.

The first maxilla (Fig. 2e) consists of a rudimentary endopod, basipodite and coxopodite, each bearing setae along the distal margin. The setae of the endopod are very short and sparse. The basipodite and coxopodite setation is longest at the tip of the structure.

Mandibles. The mandibles (Fig. 2f) are robust, club-shaped and fully-calcified. They are symmetrically arranged with the two cutting edges meeting medially. The cutting edges bear no cusp-like convolutions but are sharp-edged. Along the top of the cutting edge are numerous, regularly-spaced, short setae. The basal margin of the distal end bears 4–6 conical teeth.

Proventriculus (foregut). This structure in *Planes* spp. is as for the Brachyura in general, as described by Woods (1995) and Abrunhosa and Melo (2008). The proventriculus is a triangular sac and it is divided into two chambers (the cardiac and pyloric stomachs). The cardiac chamber (gastric mill) is large and extends more laterally than posteriorly. The masticatory ossicles of the proventriculus are symmetrically arranged where two laterally-situated zygocardiac ossicles and a single, dorsal urocardiac ossicle meet at the median of the proventriculus to triturate food items. Each of these ossicles bears a heavily calcified tooth with a number of cusps and/or sharp serrations that crush and rasp food items into smaller pieces for digestion (Fig. 3).

The teeth of the paired zygocardiac ossicles are referred to here as "lateral teeth" and the single tooth of the urocardiac ossicle is referred to as the "median tooth." The median tooth of all *Planes* species has three distinct parts that form (Fig. 3d, f). The median teeth of *P. major* and *P. marinus* are virtually identical, but the shape and setation of the urocardiac ossicle behind and surrounding the median tooth differ markedly between the two species (Fig. 3a, b). The ventral surfaces of the urocardiac ossicles of *Planes* species are somewhat inflated and bear spines and/or setae that are visible ventrally—surrounding the median tooth. This feature in *P. major* is well-developed and bears numerous long setae and distinct spines, the same structure in *P. marinus* is also setose, but less developed and it only bears spines on either side of the distal region of the urocardiac ossicle. The median tooth of *P. minutus* is smaller than and not as angular as those of its congeners, and it bears distinct concavities (on either side of the major cusp) that are not present in other *Planes* species (Fig. 3c, e). The setation surrounding the median tooth of *P. minutus* and *P. marinus* is virtually identical. In all *Planes* species, the edge of the urocardiac ossicle just posterior to the median tooth bears a single lateral-backward projecting spine.

The paired lateral teeth of the zygocardiac ossicles vary markedly among the three *Planes* spp. (Fig. 3f–i). All lateral teeth examined were composed of a prominent anterior protuberance followed posteriorly by a series of sharp-edged, evenly-spaced cusps and serrations. The cusps and serrations are larger anteriorly and decrease in size posteriorly. The cusps along the ventral interior margin of the lateral teeth in *Planes* spp. generally number from 13 to 16, are the largest and most prominent in *P. marinus* and less-prominent and sinusoidal in *P. major*. These cusps in *P. marinus* are widely-separated and sinusoidal anteriorly and more prominent and pointed posteriorly. The posterior tips of the lateral teeth in *Planes* bear 3–5 setae. The anterior protuberances of the lateral teeth differ markedly among the three species. This structure is tiered in *P. major*, flat with risen edges in *P. marinus* and rounded in *P. minutus*.

The accessory lateral teeth (ALT) (Fig. 3j) of *Planes* spp. are located just posterior to each lateral tooth and they are identical among the three species. It is kidney-shaped, and the anterior portion is edged by 11–14 large, stout spines. The remaining edge surrounding the posterior-dorsal region of the ALT is fringed in long setae that extend onto a third of the adjacent dorsal surface.

The cardio-pyloric valves (CPV) are unique among the different *Planes* spp. (Fig. 3k–m). *Planes marinus* contains the most complex CPV. It is broadly-fringed with stout, sharp spines and long setae. The CPV of *P. major* is fringed only in setae, and in *P. minutus* it lacks both spines and setae.

Discussion

Olive ridley turtles in the eastern tropical Pacific Ocean (ETP) host the most diverse grapsoid crab aggregations of any sea turtle population examined to date. The three species examined here (*P. major*, *P. marinus* and *P. squamosa*) are well-documented inhabitants of the eastern and central Pacific regions (Chace 1951; Kepel et al. 2002; Zaouali et al. 2007). All turtles hosting *P. squamosa* were captured within 24 km of the shore for reasons that are not understood.

The relationship between Pacific *L. olivacea* and grapsoid crabs is undoubtedly facilitated by the host turtle's propensity to frequent pelagic and oceanic waters (Bolten 2003). Scant dietary analyses of *L. olivacea* from this region indicate that turtles feed largely on pelagic invertebrates, but also consume shallow-water benthic prey items when close to the continental shelf (Bjorndal 1997). Numerous prey items in the diets of *P. marinus* and *P. major* reflect the reported prey items consumed by *L. olivacea* in the ETP. For instance, both host turtles and crabs consume pelagic galatheid crabs *Pleuroncodes planipes*, cnidarians and salps (Marquez-M. et al. 1976; Silva et al. 1986; Bjorndal 1997). Like epibiotic *P. minutus* in the Atlantic Ocean, it is possible that *Planes* spp. on *L. olivacea* consume food particles drifting away from prey being torn apart and masticated by host turtles (Frick et al. 2004). It is also possible that *P. major* and *P. marinus* can swim short distances, catch prey, and return to their floating substrate (Davenport 1992). If a host turtle is feeding within an aggregation of neustonic organisms, *Planes* spp. may also hunt the same items and, as a result, consume similar prey (Frick et al. 2004).

Additionally, hunting from host turtles seems likely given the occurrence of fish-like scales within the unidentified animal material and the fact that an individual *P. major* was collected holding an anchovy (*Anchoa* sp.). Olive ridleys are not known to feed upon anchovies and it is unlikely that these small fish directly attract foraging turtles as potential prey items. Instead, turtles forage within areas also frequented by anchovy schools (i.e., up-wellings and convergence zones; Lehodey et al. 1998; Polovina et al. 2004) and *Planes* spp. may utilize such opportunities to hunt *Anchoa* species, or they may scavenge anchovies that were originally captured and killed by the cnidarians consumed by host turtles. Fish-like scales in the diets of *Planes* spp. may also represent large fish consumed by host turtles (Silva et al. 1986).

If *Planes* spp. are consuming particles of items masticated by host turtles, the occurrence of identifiable cnidarians *Chrysaora* sp., *Aurelia* sp., *Physalia* sp., *Porpita* sp. and *Mitrocoma* sp. in the diets of *Planes* spp. suggests that these genera are also being consumed by olive ridleys.

Numerous studies summarized by Bjorndal (1997) report unidentified cnidarians and pelagic scyphozoan medusae (*Pelagia* sp.) from Pacific olive ridleys. Future studies on the diets of *L. olivacea* may encounter the aforementioned cnidarian genera.

Cirripeds and congeners consumed by *Planes* spp. were likely gleaned from host turtles as epibionts. Both barnacle species observed from *Planes* spp., *L. anserifera* and *C. virgatum*, are reported as epibionts from olive ridleys in Mexico (Angulo-Lozano et al. 2007). Similarly, plant material (and animal material) was likely removed from host turtles by epibiotic *P. squamosa*. Olive ridleys are documented to host marine algae in addition to invertebrate species (Cheung and Wan 2006).

Although there appears to be a great deal of dietary overlap between *Planes* spp. and *Plagusia squamosa* when occurring together on olive ridleys, the amounts of each food type consumed by each species suggests that there is some degree of resource partitioning. *Planes major* and *P. marinus* are more carnivorous than *P. squamosa*, and *P. major* ingests a significantly more carnivorous diet than does *P. marinus*. Whether *P. marinus* prefers an herbivorous diet or consumes a higher proportion of plants due to the presence of *P. major* cannot be determined. The dominance of *P. major* is supported by the significantly higher leg loss in *P. marinus*, although from observed instances of agonistic interactions in both *Planes* spp. it is clear that neither species is passive. Laboratory studies or observations on the diet of *P. marinus* in the absence of *P. major* would help determine diet preferences in *P. marinus*.

The diet of epibiotic *P. squamosa* consists primarily of soft-celled plant material resembling, and likely representing, chlorophycean algae. Its congener *Plagusia dentipes* is documented to consume a large amount of coralline algae and, to a lesser extent, chlorophycean algae and amphipods (Samson et al. 2007). We were unable to determine the type of animal material consumed by *P. squamosa*, but it is possible that this material represents amphipods. Turtle amphipods, *Podocerus chelonophilus*, are documented as epibionts of *L. olivacea* (Angulo-Lozano et al. 2007).

The external masticatory structures of *Planes* species (maxillipeds, maxillae, and mandibles) are somewhat generalized and stereotypical of brachyuran crabs (Caine 1974). That is, the third maxillipeds clearly serve a dual purpose as pre-masticatory and grooming appendages. The toothed median margin (cristae dentatae) of the third maxillipeds hold items that are then manipulated by the inner mouthparts or chelae. Setae rasp away particles of large pieces but also serve to clean eyestalks and antennae after feeding. The second maxillipeds have three functions: setae along the medial edge of the dactylus in concert with the setose medial edge of the first maxillped basipodite transfer food to the mandibles, and these same setae also aid in grooming while the longer setae of the exopod and endopod prevent sand from entering the mouth and branchial chamber during feeding. These latter structures also likely generate water currents into the branchial chamber (Skilleter and Anderson 1986; Hereen and Mitchell 1997). The second maxillae and first maxillae of *Planes* spp. appear to serve only in the transference of food backwards where the medially projecting endites of the first maxillae hold food close to the mandibles and then push it into the esophagus (Salindeho and Johnston 2003).

The internal masticatory structures of the *Planes* spp., particularly the heavily calcified teeth of the gastric mill, are similar in their general shape and form to those described for other brachyuran crabs (see Huespe et al. 2008; Brösing 2010). The lateral teeth of the Brachyura consist of an anterior portion bearing a large cusp followed by secondary teeth along the outer edge. Vertical ridges are positioned posterior to the anterior cusp. Thus, the teeth of the gastric mill in *Planes* spp, like other brachyuran crabs, appear suited for masticating both soft and hard plant and animal material (Martin et al. 1998; Huespe et al. 2008). Similarly, the accessory lateral teeth and cardiac-pyloric valves of *Planes* species resemble those of other brachyuran crabs and serve to further triturate prey items as they are moved from the cardiac chamber (gastric mill) to the pyloric chamber (Salindeho and Johnston 2003)—excepting the cardio-pyloric valve of *P. minutus*, which appears only to limit the passage of particular-sized fragments into the pyloric chamber.

Studies on the morphology of the gastric teeth of brachyuran crabs have debated whether these structures reflect decapod ancestry, adaptation to habitat/feeding, or some combination of the two (Martin et al. 1998). A synoptic examination of these studies reveals that the teeth of the brachyuran gastric mill follow a basic morphological plan to triturate a diverse repertoire of items—including coral mucous (Kropp 1986), coralline algae (Huespe et al. 2008), and conspecifics (present study). Yet, subtle differences in these structures are useful indicators of phylogenetic relationships (Brösing 2010).

A study by Huang et al. (1998) clearly demonstrates the distinctiveness of two closely related ghost crab species, *Ocypode sinensis* and *Ocypode cordimanus*, through comparisons of external morphological characters and the teeth of the gastric mill. A similar comparison by Huespe et al. (2008), combined with molecular data (Spivak and Schubart 2003), indicates that the grapsoid crabs *Cyrtograpsus altimanus* and *Cyrtograpsus affinis* represent a single species. Our data, along with the diagnoses of external characteristics by Chace (1951) and Spivak and

Bas (1999), emphasize the distinctiveness of the three species that comprise the genus *Planes*.

Although the general shapes of the teeth of the gastric mill in *Planes* spp. are similar, certain features on these structures are quite different. The anterior protuberances and the number of lateral ridges and associated cusps of the lateral teeth differ among the species, and there are also subtle differences in the median teeth.

Our observations supplement those of Brösing (2010) by providing the first morphological descriptions of the masticatory structures of the *Planes* spp. The overall shape of the gastric mill in *Planes* species is identical to those presented by Brösing (2010) for other grapsoid species: *Cardisoma armatum*, *Pseudosesarma moeschi*, and *Eriocheir sinensis*. But, the fine details in the shape and form of the teeth of the gastric mill are remarkably different between each family, genus, and species. Describing and illustrating these structures creates an important resource for those seeking to identify crustaceans in animal diets or from the fossil record (Huespe et al. 2008).

In conclusion, *P. major*, *P. marinus*, and *P. squamosa* are common epibionts of olive ridley sea turtles in the Pacific Ocean—sometimes all three occurring in sympatry upon the same host turtle. Megalopae of all three species recruit to host turtles and reproductive adults of all three species are also present. Adults commonly occur as heterosexual pairs and females are often ovigerous. While epibiotic with *L. olivacea*, *Planes* spp. consume a variety of neustonic organisms that may be captured from the water column or consumed as particulate debris drifting away from foraging turtles. Morphological differences in the teeth of the gastric mill of *P. major*, *P. marinus*, and *P. minutus* support the distinctiveness of all three species in this genus.

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