

***Glottidia audebarti* (Broderip), (Brachiopoda, Lingulidae)
from the Gulf of Nicoya, Costa Rica**

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Abstract: Specimens of the burrowing brachiopod *Glottidia audebarti* (Broderip) were collected by coring at the Punta Morales intertidal mud flat (65% sand, 32% silt + clay) in the upper Gulf of Nicoya (10°N, 85°W), an estuary on the Pacific coast of Costa Rica. This collection extends the present distribution of the species from the Pacific coasts of Mexico to Ecuador. A detailed description of the shell is provided. The internal muscle arrangement, not observed previously except on dry specimens, appears as intermediate between those of *G. pyramidata* Stimpson and *G. palmeri* Dall. Deposit feeders dominate the associated fauna, and lists of the ten most important species of the macrofauna and meiofaunal groups are included. *G. audebarti* is an important food item for two species of shore birds: *Catoptrophorus semipalmatus* and *Limnodromus griseus*. In the Gulf of Nicoya *G. audebarti* co-occurs with *G. albi-da* Hinds.

Key words: systematics, redescription, morphology.

The Brachiopoda, or lamp shells, are lophophorate benthic invertebrates that are enclosed in a bivalve shell attached directly or by means of a pedicle to or in the substrate (Hyman 1959). In the Class Inarticulata the valves are held together by muscles only, and its family Lingulidae includes two genera, *Lingula* and *Glottidia*. Dall (1870) created the genus *Glottidia* which stands out from the genus *Lingula* by the presence of septa inside the shell, two in the ventral valve diverging from the beak and a median septum in the dorsal valve, and gill ampullae in the mantle (Figs., 2A, and 3). There are no species of *Lingula* known to occur in the coasts of the Americas.

Specimens of a burrowing brachiopod were collected by H. Cummings in an extensive intertidal coarse sand environment (twenty kilometers long and 3 km wide) at Puna Island,

Bay of Guayaquil (Ecuador). The specimens had been originally described by Broderip (1835) under the name *Lingula audebardii* while dedicated to the Baron J. d'Audebart de Férussac: thus, the species name had to be corrected as did Deshayes in Lamarck's edition (1836) into *audebarti*. The short description by Broderip (1835, p.144) concerned mainly the greenish colour in transverse lines "produced by progressive increase of the shell". From the complementary information given in the same journal by Owen (1835), only figures 14 and 15 are useful, being similar to our figure 2.

Davidson (1888) in a comparison of *G. audebarti* and *G. pyramidata* Stimpson was convinced by their synonymy. Dall (1870), however, kept both species separated and later stated (Dall 1921, p. 268) "the extraordinary confusion introduced by the synonymy with *G. pyramidata*". He also pointed out that the differences between both species are mainly because they come from "a different

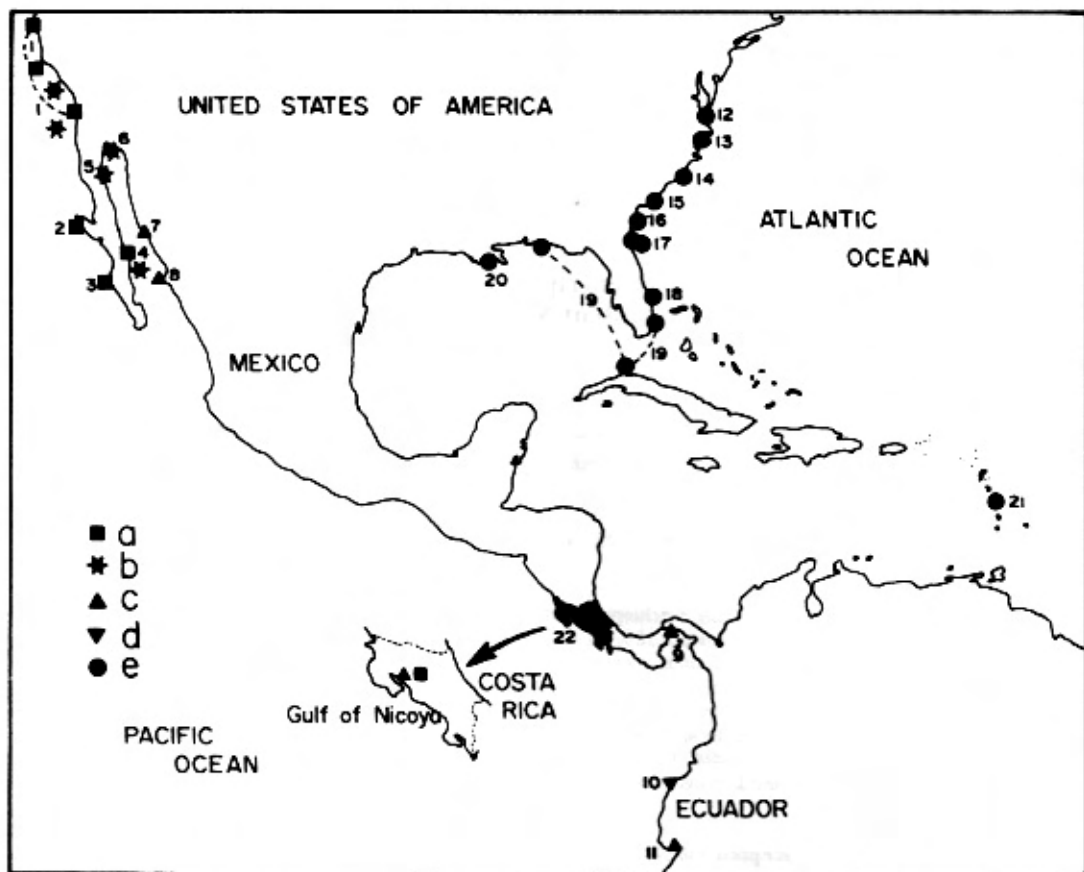


Fig. 1. Geographic distribution of the species of *Glottidia*: a. *G. albida*; b. *G. palmeri*; c. *G. audebarti*; d. *G. semen*; e. *G. pyramidata*. 1. Monterey; San Diego; 2. San Bartolomé; 3. Magdalena Baja; 4. Concepción Baja; 5. San Felipe; 6. Mouth of Colorado river; 7. Guaymas; 8. Topolobampo; 9. Fort Amador; 10. La Plata; 11. Guayaquil; 12. Hampton; 13. Beaufort; 14. Wilmington; 15. Charleston; 16. Sapelo Island; 17. Jacksonville; 18. Fort Pierce; 19. Miami, Pensacola; 20. Grand Isle; 21. Martinique; 22. Gulf of Nicoya. (Modified from Emig 1983, Fig.1).

zoological province" (*G. pyramidata* from the North Atlantic coast of America). Dall (1921) also remarked that "*Glottidia audebarti* is a large species with the umbonal half mostly white, the distal half of the valves painted with a brilliant blue green, unlike any other species in the genus".

Since Dall's paper, the only work on the systematics of *Glottidia* is by Emig (1983) and all the few specimens available of *G. audebarti* were dry, thus precluding a close examination of the soft parts. The recent finding of this species on the Gulf of Nicoya, Costa Rica (Fig. 1) by one of us (J.A. Vargas), is the opportunity to get a detailed description of *G. audebarti* and to compare it with the three other species of the genus.

MATERIAL AND METHODS

Glottidia audebarti was collected by coring (to a depth of 15 cm in the sediment) during a two year survey of the macrofauna (organisms > 500 μ m) of the Punta Morales intertidal mud flat (tidal range is 2.3 m) in the Gulf of Nicoya, an estuary on the Pacific coast of Costa Rica. Specimens were originally preserved in 10% buffered formalin in sea water, and later transferred to vials filled with 70% ethanol. On the average sediments at the site were made of 65% sand, 32% silt + clay, and about 2% organic matter content (by combustion). The very fine sand (62 to 125 μ m) and fine sand (125 to 250 μ m) were the most important (by weight) sand fractions. Sediments were also

characterized by a thin (< 1 cm deep) oxidized layer. Salinity oscillated seasonally from 24 ‰ (rainy season) to 36 ‰ (dry season), Vargas (1987, 1988).

RESULTS & DISCUSSION

Systematics.

Broderip 1835 (p. 143-144, Fig. 17); Owen 1835 (p.157, Figs. 14-16); Dall 1870 (p.159); Dall 1921 (p.268); Davidson 1888 (p. 223-227); Cooper 1977 (p. 51); Emig 1983 (p.484, Fig.8).

Geographic distribution (see Fig. 1).

7. Guaymas (Emig 1983);
8. Topolobampo (Dall 1921, Emig 1983);
9. Fort Amador (Emig 1983); Bridge of the Americas, Balboa Harbor (Cooper 1977).
11. Type-locality: Isla de Puna (Broderip 1835; Davidson 1888);
22. Gulf of Nicoya (Vargas 1987, 1988).

The present distribution of *G. audebarti* extends from the Pacific coasts of Mexico to Ecuador. In the Gulf of Nicoya this species co-occurs with *G. albida* Hinds: 102 specimens of *G. audebarti* reported by Vargas (1987) may include, however, individuals of both species. Most of the specimens collected during that first year survey were very small. The second year only five large individuals of *G. audebarti* were found (Vargas 1988). The known distribution of *G. albida* is thus extended southward from Monterey (see Emig 1983). The last species occurring on the Pacific American coasts is *G. palmeri* Dall, found near San Diego and San Pedro (California), and in the Gulf of California (Emig 1983). *G. pyramidata* mentioned earlier, is the only species of the genus for the American Atlantic coasts (Figs. 1). The status of *G. semen* (Broderip), Fig. 1, is uncertain at present.

Taxonomic characteristics

Shell (Fig. 2 A & 3; Tables 1 & 2).

General shape: oblong-elongate; subparallel to parallel lateral margins; anterior edge slightly rounded up to nearly straight with a

small median angular projection in large individuals; external surface smooth but growth lines little marked (Fig. 3).

The measurements and ratios of some shell characteristics of *G. audebarti* are included in Table 1. The comparison with data for the other *Glottidia* species (Table 2) shows similar variability of ratios within *G. albida*, *G. pyramidata* and *G. audebarti*, while more data are needed on *G. palmeri*. On *Lingula* shells the W/L ratio varies between 0.381 and 0.552 in *L. anatina*, and from 0.543 to 0.698 in *L. adamsi*.

Colour: creamy white on the posterior half of the shell and lateral margins; bright green to turquoise in horizontal lines on the anterior half with two oblique posterior tips (Fig. 4). This shell colour is specific of *G. audebarti* (Dall 1921).

Deltidial regions: acute; dorsal valve with a beak profile oblique and less concave than the ventral valve; the pedicle groove (ventral valve) with growth lines and discontinuous with the internal side of the valve, and concave beak profile (Fig. 2A). The deltidial region of both valves shows smaller but sharper beaks than in the other species. The dorsal beak profile is rather similar to that of *G. palmeri*; and the ventral one is similar to that of *G. albida*, as well as the discontinuous pedicle groove.

Septa of the ventral valve: oblique straight to slightly curved as in *G. pyramidata* and *G. palmeri*; the left septum is a little longer than the right one, as in *G. palmeri* (Fig. 2A, and 3b). The septa in the ventral valve extend forward over about 25 to 32% shell's length, and the septum in the dorsal valve over about 38% (Table 1). Such data are similar to those in the other *Glottidia* species as reported in Table 2.

Muscle disposition: The muscle disposition has not been observed previously, except on a dry specimen by Emig (1983). The general disposition is elongate (Fig. 2B). On the dorsal side the two anterior oblique muscles have an oval shape. On the ventral side the oblique internal muscles, anterior and posterior, are well separated and both, together with the median one, are similarly elongate. The anterior oblique muscles are near the anterior adductors. The insertion of the posterior adductor is minutely shifted on the right septum (Fig. 2A). The general muscle disposition of *G. audebarti* appears as intermediate between those of *G. pyramidata* and *G. palmeri*.

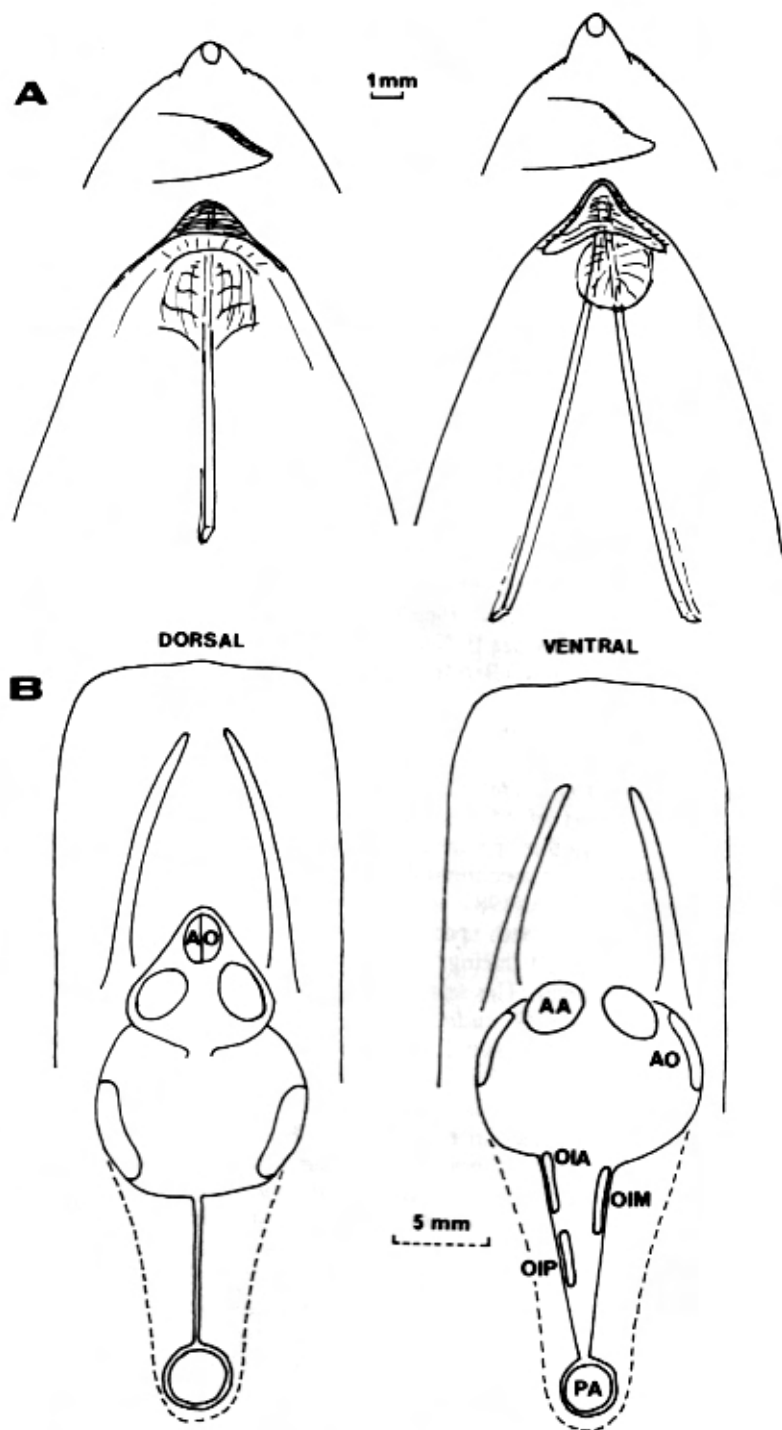


Fig. 2. *Glottidia audebarti* from Gulf of Nicoya. A. Deltidial regions of the dorsal and ventral valve (external view, lateral profile, and internal view). B. Disposition of the body muscles and of the two main anterior canals of the mantle. Muscles: AA: anterior adductor; AO: anterior oblique; OIA: oblique internal anterior; OIM: oblique internal median; OIP: oblique internal posterior; PA: posterior adductor.

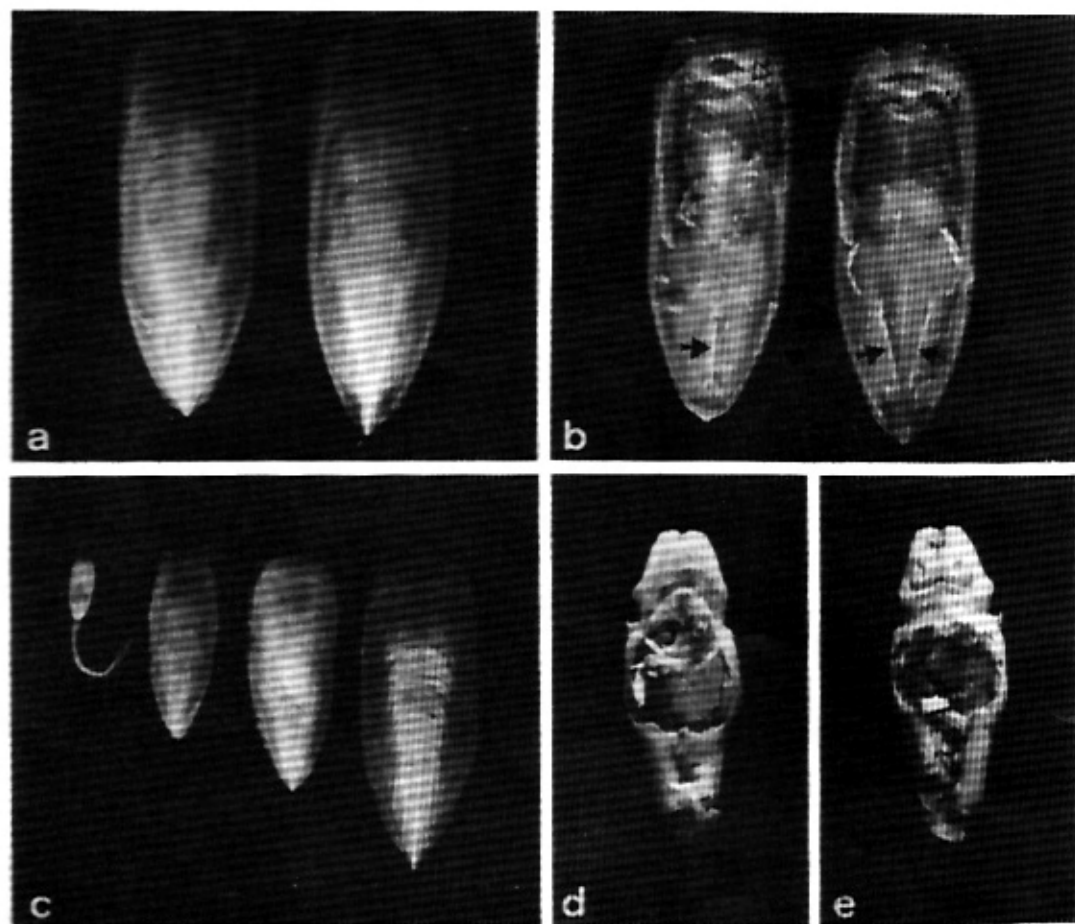


Fig. 3. *Glottidia audebarti* from the Gulf of Nicoya: a. External view of a dorsal and ventral valve; b. Internal view of a dorsal and ventral valve, showing the septa (black arrows) and the gill ampullae in the mantle (white arrows); c. Shell of some of the studied specimens; d. Muscle disposition on the dorsal body side; e. Muscle disposition on the ventral body side; the lophophore is spirolophous like in all living Lingulidae.

Mantle canal disposition: the two main anterior canals are oblique subrectilinear to slightly convex, rather similar to those of *G. pyramidata* (Fig. 2B).

Ecology.

The Gulf of Nicoya region is characterized by a dry season, usually extending from December through April, and a rainy season from May through November. Thus, as it is characteristic of the Lingulidae (Emig 1983, 1986), *G. audebarti* (and *G. albida*) seem to tolerate the minimum salinities found in this

upper region of the Gulf of Nicoya during the rainy season. This is also the season when very small individuals (less than 1 cm shell length) were collected more frequently (Vargas 1987). A rough estimate of *G. audebarti* abundance is 17 individuals per m². This density is relatively low, but within the range reported by Jones and Barnard (1963 Fig. 6) for *G. albida*.

The associated fauna of *Glottidia* is composed mainly of deposit feeders. A list of the 10 most abundant (as % of the total number of individuals) species of the macrofauna and the meiofaunal groups is included in Table 3. Other conspicuous species found at the mud flat were the snails, *Nassarius luteostoma* (Broderip &

TABLE 1

Measurements (in mm) on the ventral valve of 6 specimens of *G. audebarti* from the Gulf of Nicoya, and two data from Emig (1983). L: valve length; W: width; I: median septum of the dorsal valve; V: oblique septa of the ventral valve (Fig. 2 A); length: septum length; %: percentage of the extension of the septa in relation to the ventral valve length; --- no data.

L	W	W/L	I length	%	V length	V %
39.5	14.5	0.367	10.0	25.3	14.5	36.7
30.8	11.8	0.383	8.6	27.9	11.7	38.0
26.9	9.6	0.357	8.5	31.6	10.0	37.2
23.2	8.8	0.379	7.1	30.6	8.9	38.4
18.1	6.5	0.359	---	---	---	---
6.5	2.7	0.415	---	---	---	---
29.0	11.0	0.379	---	---	---	---
27.0	9.0	0.333	8.5	31.5	10.5	38.9

TABLE 2

Variability within the *Glottidia* species of the ratio Width/Length of the ventral valve and the percentage of the septum length (I: median septum of the dorsal valve; V: oblique septa of the ventral valve) in relation to the valve length (data from Table 1 and Emig 1983). Between brackets the mean value; N: number of measured specimens; L max: maximum ventral valve length in mm.

Species	N	L max	W/L	N	I %	V %
<i>pyramidata</i>	13	26	0.37-0.44 (0.40)	13	25-30 (27)	30-38 (34)
<i>albida</i>	10	24	0.38-0.42 (0.39)	10	24-29 (26)	29-41 (36)
<i>audebarti</i>	8	39.5	0.33-0.42 (0.37)	5	25-32 (29)	37-39 (38)
<i>palmeri</i>	3	49	0.32-0.33 (0.33)	1	37	44

N. chemnitzii Pfeiffer (these two naticid species are potential predators of *Glottidia*; see Emig 1983); the portunid crab, *Callinectes arcuatus* Ordway; the alpheid shrimp, *Alpheus mazatlanicus* Wicksten; several species of penaeid shrimp, stomatopods, and hermit crabs; the ophiuroid, *Amphipholis geminata* (Le Comte) and the echinoid, *Encope stokessi* Agassiz. An unidentified species of hemichordate (Enteropneusta) was also collected throughout the survey. The Punta Morales mud flat is not rich in suspension feeding invertebrates; *Tellina rubescens*, a bivalve (Table 3), acts as a deposit feeder. The filter-feeding brachiopods, however, appear to survive in the turbid waters overlying the sediments. A plausible explanation for this observation is that the bivalve gill (mesh like structure) is more susceptible to clogging in turbid waters than the open filamental structure of the lophophore (Steele-Petrovic 1975).

The mud flat is visited seasonally by migratory birds, and at least 13 species were observed foraging at low tide (Vargas 1988). At a

similar site in Chomes (SW of Punta Morales), Pereira (1989) collected *G. audebarti* during a study of the feeding habits of three species of shore birds. Stomach contents of *Catoptrophorus semipalmatus* (Gmelin), but more frequently of *Limnodromus griseus* (Gmelin), revealed utilization of the brachiopod as an important food item. *C. semipalmatus* and *Symphurus plagiatus* are known predators of *Glottidia* (Paine 1963, Cooper 1973). This wide assemblage of predators is perhaps an important source of mortality for species of *Glottidia* and it may explain why only five large *G. audebarti* were collected during the second year, as cited earlier. Other sources of mortality, however, may be important as evidenced by the unexpected results of predator-exclusion experiments conducted at the Punta Morales mud flat (see Vargas 1988). Voucher specimens of *G. audebarti* and *G. albida* are deposited at the Museo de Zoología, Universidad de Costa Rica (UCR-PM-057A and UCR-PM-057B, respectively).



Fig. 4. *Glottidia audebarti* from the Gulf of Nicoya. View of complete specimens. Note diagnostic colour of the valves under shiny periostracum. Fourth specimen from the left has remains of encasement of the free end of pedicle by agglomerated sand grains and mud. Numbers indicate cm.

TABLE 3

Percentage of the total number of organisms of the macrofauna and the meiofauna found at the Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica. C: Cumacea; D: Decapoda; M: Mollusca; O: Ostracoda; P: Polychaeta

Macrofauna*			Meiofauna**	
		%		%
<i>Coricuma nicoyensis</i> Watling & Breedy	C	19.32	Nematoda	88.10
<i>Mediomastus californiensis</i> Hartman	P	13.90	Foraminifera	5.90
<i>Cyprideis pacifica</i> Hartmann	O	13.14	Ostracoda	2.90
<i>Polydora citrona</i> Hartman	P	10.94	Copepoda	1.10
<i>Paraprionospio pinnata</i> (Ehlers)	P	3.59	Nauplii	0.60
<i>Pinnixa valerii</i> Rathbun	D	3.00	Mollusca	0.30
<i>Lumbrineris tetraura</i> Schmarda	P	2.30	Polychaeta	0.30
<i>Tellina rubescens</i> Hanley	M	1.82	Cumacea (manca)	0.16
<i>Glycinde armigera</i> Moore	P	1.48	Kinorhyncha	0.09
<i>Tagelus bourgeoisae</i> Hertlein	M	1.24	Others	0.50

* Data from Vargas (1988, Table 1); a total of 78 species was collected.

** Data from De la Cruz & Vargas (1987); organisms within a size range of 62 to 500 μ m were considered as meiofauna.

RESUMEN

Ejemplares del braquiópodo excavador *Glottidia audebarti* (Broderip) fueron colectados con un barreno en la planicie fangosa (65% arena, 32% limo + arcilla) de Punta Morales, en la región superior del Golfo de Nicoya, un estuario en la costa Pacífica de Costa Rica. Este hallazgo extiende la distribución actual de esta especie desde las costas del Pacífico de México hasta Ecuador. Se incluye una descripción detallada de la concha. La disposición de la musculatura interna, no observada anteriormente excepto en ejemplares secos, aparece como intermedia entre las de *G. pyramidata* Stimpson y *G. palmeri* Dall. La fauna asociada está dominada por especies que se alimentan de materia depositada, y se incluye listas de las diez especies más importantes de la macrofauna y de los grupos de la meiofauna. *G. audebarti* es una fuente importante de alimento para dos especies de aves costeras: *Catoptrophorus semipalmatus* y *Limnodromus griseus*. En el Golfo de Nicoya *G. audebarti* coexiste con *G. albida* Hinds.

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