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A NEW GENUS OF INTERTIDAL SALDIDAE FROM THE EASTERN TROPICAL PACIFIC WITH NOTES ON ITS BIOLOGY (Hemiptera)[1]

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Abstract: Paralosalda innova n. gen., n. sp. is described from the intertidal zone of the Pacific coast of Central America. This genus is placed in the subfamily Chiloxanthinae, and is the first known member of this group to possess 4 cells in the hemelytral membrane. A key to the chiloxanthine genera is included, as is a summary of the intertidal saldid genera of the world, with a discussion of their relationship to *Paralosalda*. *P. innova* inhabits the mid- to upper littoral zone of protected rocky shores extending from northern Colombia to northern Costa Rica and, like other intertidal saldids, the adults spend periods of submergence by high tides in rock crevices and emerge at low tide. The nymphs, however, remain in the crevices most of the time.

Until the discovery of the species described herein, only one saldid was known to exclusively inhabit the intertidal zone in the New World: *Pentacora mexicanum* (Van Duzee). This insect, which evidently does not belong in *Pentacora*, is locally common on intertidal rocks in the northern part of the Gulf of California though the species was described from one specimen found under kelp on a beach (Van Duzee 1923).

Other species of New World Saldidae are known to inhabit salt marshes and mud flats where they apparently survive submersion (for instance, *Saldula notalis* Drake, and *Saldula palustris* Douglas), but there is no evidence that they complete their life cycle in the intertidal zone or that they inhabit this zone exclusively; hence, for the present they are not considered to be intertidal in the true sense.

Four genera of intertidal saldids inhabit the Pacific Region and the Old World; *Aepophilus*, *Omania*, *Orthophrys* and *Salduncula*. These genera, along with the New World genera, have little in common except habitat: *Aepophilus* is in a subfamily by itself; *Omania* is considered by Cobben (1959) to be a separate family; *Orthophrys* and *Salduncula* are divergent, but both belong to the subfamily Saldinae. The two New World genera are also quite different from each other, and belong to the subfamily Chiloxanthinae. Hence it would appear that independent evolutionary paths have been followed by these various bugs in successfully invading the intertidal zone.

The biology and ecology of *Omania* have been studied in much more detail than the other genera, as is evident in the papers of Kellen (1960), Woodward (1958) and Herring & Chapman (1967). Some brief ecological data for *Salduncula* have been given by Brown

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(1959) and Miyamoto (1963). Several accounts have been given of the marine bug *Aepophilus*, summarized briefly by China (1927), and brief ecological notes on *Orthophrys* were given by Drake (1958). The only ecological data given for the New World intertidal saldids are those of Evans (1968) and Polhemus (in preparation).

Due to their small size and propensity to dart into rock crevices when disturbed, these insects are usually collected only by specialists and are poorly represented in collections. Undoubtedly many more species, and perhaps more genera, remain to be discovered along the sea shores of the World, especially in the warmer climates.

Specimens of the saldid species described here were collected by Evans during Cruise 18 of Stanford Oceanographic Expeditions on R. V. "Te Vega" and the unpublished report resulting from that cruise has been invaluable in the preparation of this paper. The expedition was planned to survey the biota of the "Panamic Province" and its bordering regions, comprising the coastline extending from Magdalena Bay, Baja California to Paita, Peru. Recent proposals to construct one or more sea level canals either across the Isthmus of Panama or in adjacent regions made it imperative to survey the marine littoral organisms before they have a chance to mix with Caribbean forms which have been isolated from their Pacific counterparts since the last closure of the Panama seaway during the late Tertiary. In addition, the southern part of the Eastern Tropical Pacific comprising the coasts of Colombia and Ecuador is a region where knowledge of the distribution and biology of these marine littoral organisms, especially the invertebrates and algae, is extremely fragmentary. The finding, therefore, of this saldid as well as other marine littoral insects should contribute much toward the understanding of the zoogeography of this poorly known group which inhabit the intertidal zones of most of the world's coastlines.

Genus **Paralosalda** Polhemus and Evans, new genus

(Paralos. Cr., Gr., by or near the sea+*Salda*)

Membrane of hemelytra with 4 closed cells. Ovipositor of ♀ with 8 well developed teeth. Tube leading from spermatheca bulb with tapering walls, thinned toward apex, without flange. Larval organ present in nymphs. Ocelli separated by 2 × the width of an ocellus, closer to margins of eyes than to each other. Preocellar spots absent. Caudal margin of ♀ subgenital plate strongly indented. Fracture of hemelytra very long. All other generic characters typical of the Chiloxanthinae (sensu Cobben 1959) *i. e.* base of filum gonopori forming 1 closed ring; median sclerotized structure of aedeagus paired; apicolateral structure of aedeagus absent; ♀ subgenital plate truncate; head without postclypeus [of Cobben (1960), not Parsons (1962)].

Type species: *Paralosalda innova* n. sp.

Paralosalda innova Polhemus and Evans, new species Fig. 1-2.

Small, black, slender, macropterous. (For all measurements, 60 units=1 mm).

Head: Black, moderately shining, finely rugulose, covered with very short black decumbent pubescence, preocellar spot absent; with 3 pairs of long erect black hairs on frons and vertex; ocelli raised slightly and separated by 2× the width of an ocellus; lateral margin of frons, clypeus, labrum yellowish; anteclypeus well defined, brown; no indication of postclypeus; rostrum brown, reaching between hind coxae; labrum narrowly triangular, long, sharply pointed

apically. *Thorax*: Pronotum black, faintly shining, finely rugulose, pubescence as on head; lateral margins straight, anteriorly convergent (humeral width: anterior width; 62:43); callus slightly raised, marked off from posterior lobe by a narrow sulcus, with deep oval depression in center; anterior lobe longer than posterior lobe (9: 5, not including collar); collar width 2. Shape and yellow markings as shown in fig. 1. Underparts brown to black; lateral margin of pronotum with leucine stripe wider than hind tibia; anterior and middle coxae margined with leucine; clothed with moderately long silvery pubescence. Scutellum black, with vestiture as on head, width subequal to length (42: 44), transversely depressed at center. *Wings*: Hemelytra fully developed, covered with short decumbent black pubescence; ground color deep brown-black, with yellowish markings as shown in fig. 1; irregular area in middle of outer corium shining, remainder dull ; membrane fumose, with 4 cells, veins not salient; vein on inner corium forked apically, reaching membrane. Flight wings well developed, reaching apex of hemelytra. *Abdomen*: Brown, covered with short decumbent silvery pubescence; caudal margins of 1st 5 segments margined with ochroleucus; ♀ subgenital plate as shown in fig. 2G; parandria as shown in fig. 2 A. *Extremities*: Antenna black; dorsal 2/3 of segment 1 yellowish, whole apex lighter ; apex of segment 2 yellowish in some specimens; shape of segments as shown in fig. 1; antennal proportions: holotype ♂, 13:37:20: 22; allotype ♀, 13: 40:20:22. Legs brown; knees, apices of tibia, trochanters, anterior faces of fore femora, 1st and 2nd tarsal segments light brown to yellowish; with usual dark spines.

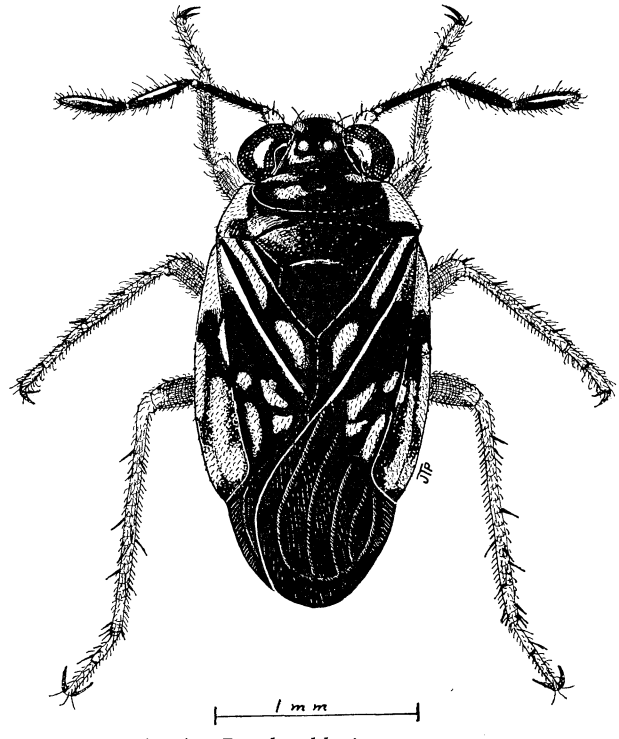

Fig. 1. *Paralosalda innova* new gen., n. sp. (holotype).

Genitalia: ♂ paramere and aedeagus as shown in fig. 2B-E. Spermatheca and ovipositor of ♀ as shown in fig. 2F and 2H respectively.

Measurements: Holotype (♂), length 2.45 mm, width 1.13 mm; allotype (♀), length 2.74 mm, width 1.30 mm. Length of 10 ♂♂; mean 2.44 mm, min. 2.34 mm, max. 2.71 mm. Width of 10 ♂♂; mean 1.11 mm, min. 1.05 mm, max. 1.28 mm. Length of 3 ♀♀; mean 2.68 mm, min. 2.62 mm, max. 2.74 mm. Width of 3♀♀; mean 1.30 mm, min. 1.23 mm, max. 1.37 mm.

Holotype ♂, allotype ♀, (Calif. Acad. Sci.) 9 ♂♂, 1 ♀ paratypes, 21 nymphs, Colombia, Punta Cotuda, Bahia de Solano, 1. V. 1968, W. G. Evans. Additional paratypes and nymphs : 2 ♂♂, 3 nymphs, Colombia, Punta San Francisco Solano, Bahia de Solano, 30. IV. 1968, Evans; 11 ♂♂, 1 ♀, 3 nymphs, Colombia, Punta Cruces, Cupica Bay, 2. V. 1968, Evans; 1 nymph, Panama, Culebra I., 5. V. 1968, Evans; 2 ♂♂, 2 ♀♀, 4 nymphs, Panama, Punta Paitilla, Panama City, 6. V. 1968, Evans ; 1 ♀, 1 ♂, 2 nymphs, Panama, Isla Montuosa, 9. V. 1968, Evans; 2 ♂♂, Costa Rica, Bahia de Brasilito (10°25′ N, 85°49′ W)

13. V. 1968, Evans.

Some of the paratypes will be deposited in the California Academy of Sciences and the University of Alberta Strickland Museum and some will be retained in the collections of both authors.

Paralosalda innova does not resemble any of the known New World saldids but is superficially rather similar to species of the intertidal genus *Salduncula*. The latter is presently known from a region extending from the mid-Pacific to Madagascar. In both genera the bugs are small, slender, lack preocellar spots and have no postclypeus. (*Salduncula swezeyi* Usinger has a weak transverse swelling, but this cannot be considered a postclypeus as defined by Cobben (1960). Also, Brown (1956) pointed out the lack of "transverse ridges on the front of the face at the level of the lower margin of the eyes" in *Salduncula seychellensis* Brown, a characteristic shared by *Salduncula woodwardi* Drake. So while Cobben (1959) used the presence of a postclypeus as a subfamily character for the Saldinae, and stated that he had studied all genera except *Oiosalda* Drake & Hoberlandt, it appears that he missed *Salduncula*, and that perhaps this character should be discarded.)

The genus *Paralosalda*, however, does not stand close to any described genus. It falls in the subfamily Chiloxanthinae as characterized by Cobben (1959), in spite of its superficial alliance to the Saldinae, i. e. the membrane with 4 cells. That a member of the Chiloxanthinae could evolve to the condition of having 4 cells in the membrane was hypothesized by Cobben (1961), and in that paper his figure 1C closely resembles *P. innova*, including the long fracture which is also a subfamily characteristic. In the same paper, Cobben also stated the secondary importance of membrane venation.

The "connecting piece", at the base of the female ovipositor, is not free in this species; and while the phylogenetic importance of this structure has not been established, the study

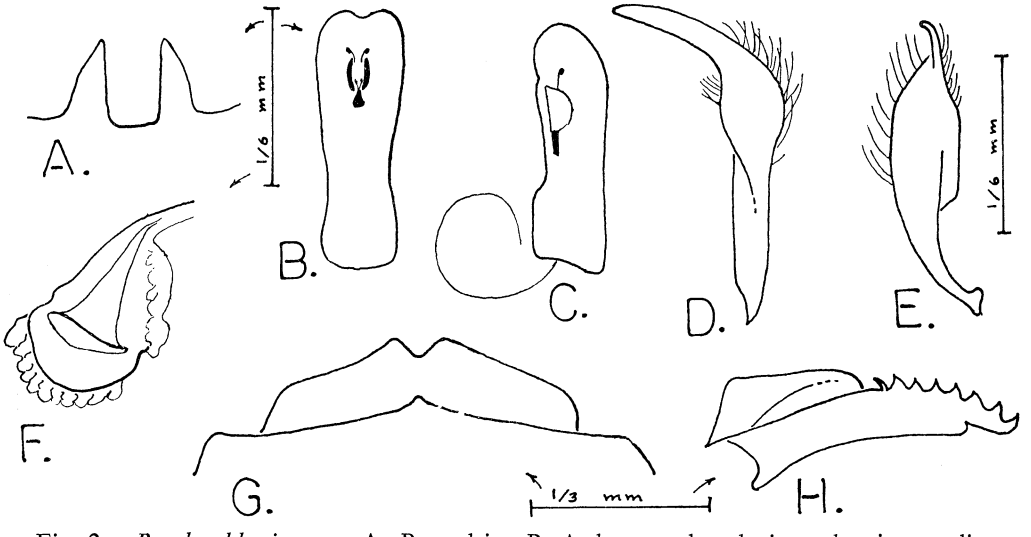

Fig. 2. *Paralosalda innova*: A, Parandria; B, Aedeagus, dorsal view, showing median sclerotized structures; C, Aedeagus, side view, and filum gonopori; D and E, ♂ paramere, 2 views; F, Spermatheca; G, ♀ subgenital plate; H, ♀ ovipositor.

of a few species showed it attached in the Saldinae and free in the Chiloxanthinae. (See discussion in Polhemus (loc. cit.).

The spermatheca of *innova* does not have a discernible pump flange (fig. 2F), whereas most species of Saldidae possess it. The other New World intertidal saldid genus also lacks a pump flange.

The following key will serve to separate the 5 genera of the subfamily Chiloxanthinae.

1. ♀ subgenital plate with no, or very slight, median notch on caudal margin 2
   ♀ subgenital plate with deep median notch on caudal margin 3
2. Sublateral cell of membrane approximately 1/2 the length of the lateral cell; ♀ hemelytral margin not or weakly modified to accept ♂ coupling plate (Holarctic) ..... **Chiloxanthus** Reuter
   Sublateral cell of membrane subequal in length to lateral cell; ♀ hemelytral margin strongly modified to accept ♂ coupling plate (Cosmopolitan) ..... **Pentacora** Reuter
3. Membrane with 4 well developed cells; preocellar spot absent (Eastern Tropical Pacific, intertidal) ..... **Paralosalda** Polhemus & Evans
   Membrane with 5 well developed cells, or with cell pattern confused, indistinct and membrane subcoriaceus; preocellar spot present 4
4. Body long, slender; eyes prominent, separated by less than width of an eye; membrane well developed, with five cells (Australia) ..... **Pelachoris** Drake
   Body short, stout; eyes small, separated by more than the width of an eye; membrane thickened, reduced, cell pattern confused or indistinct (Mexico, Gulf of California, intertidal) ..... **Enalosalda**, n. gen.[4]

Biology. As indicated in Table 1 specimens of *P. innova* were collected in the rocky marine littoral extending from Punta San Francisco Solano, Colombia to Bahia de Brasilito, Costa Rica, a distance of approximately 1440 km (900 mi). It is unlikely that its distribution extends much further than this because it was not seen at more southerly rocky shore collecting points, i. e. Gorgona I., Colombia; Punta Galera, Ecuador or more northerly points such as Golfo de Fonseca, El Salvador and Salina Cruz, Mexico. The distribution of this insect then falls well within the boundaries of the marine littoral zoogeographic region designated by Ekman (1953) as "tropical" where the water temperature at the coldest time of the year does not fall below 20°. Maximum air temperatures above intertidal rocks at the times when specimens of *P. innova* were collected ranged from 26.5° to 32.0°, while sea water temperatures ranged from 27.4° to 29.1°.

P. innova could conceivably be found on the Atlantic side of the Isthmus of Panama, which is approximately 64 km (40 mi.) from the Punta Paitilla collecting site. *Trochopus salinus* Champion, a marine water strider is widely distributed on the Atlantic side of Central and tropical South America and also in the Eastern Tropical Pacific though in a much more restricted area. A similar amphi-American distribution of *P. innova* is conceivable. Its establishment on Isla Montuosa, a small, (1.6 km diameter) forested island indicates that it flew or drifted there on natural rafts or was carried by storms the 32 km (20 mi.) from adjacent, larger Isla Coiba, or from the more distant mainland. Hurricane dispersal of semi-aquatic Hemiptera has been discussed by Herring (1958) in

4. This monotypic genus is erected (Polhemus, loc. cit.) to hold *Orthophrys mexicanum* Van Duzee which has recently been transferred to *Pentacora* by Lattin & Cobben (1968). A more extensive discussion will be given elsewhere (Polhemus, loc. cit.).

the Tropical West Atlantic. Although it is possible that *innova* could disperse through flight, as the hind wings are well developed, the usual mode of locomotion that was observed was walking and short leaps particularly when disturbed.

P. innova inhabits the mid to high intertidal zone of rocky shores. The nymphs were found in crevices and were collected by splitting open these crevices with a geological hammer. The adults, on the other hand, were found in crevices as well as in the open among barnacles, littorines and other high littoral animals. The adults take refuge in crevices when the tide is high and emerge again when the tide recedes. The cuticle of *P. innova* is unwettable and individuals placed on the surface of small pools appeared to be helpless and struggled until they could crawl out. Herring & Chapman (1967) reported a similar behaviour for *Omania nauruensis* Herring and Chapman.

Other intertidal saldids also inhabit crevices and probably subsist on air trapped in interstices of the rocks during low tide. Woodward (1958) states that *Omania marksae* Woodward probably utilizes trapped air in this manner but also states that a bubble of

Table 1. The habitats of *Paralosalda innova* at various localities with estimates of abundance.

Date, Station Number Locality	Habitat	Relative abundance
30. IV. 1968, 18-12a, Punta San Francisco Solano, Bahia de Solano, Colombia.	upper littoral; crevices of massive, weathered igneous rocks of exposed rocky peninsula.	scarce
1. V. 1968, 18-12b, Punta Cotuda, Bahia de Solano, Colombia.	upper littoral; on surface and in crevices of weathered metamorphic rocks of protected promontory.	scarce
2. V. 1968, 18-13 Punta Cruces, Bahia Cupica, Colombia	mid-littoral; in crevices and on surface of rocky outcrops of stria protected by offshore island.	very abundant
5. V. 1968, 18-14a Culebra Island, Panama.	mid-littoral; in crevices and on surface of volcanic rocks of a wide reef exposed to heavy surge.	scarce
6. V. 1968, 18-14b Punta Paitilla, Panama City, Panama.	mid- to upper littoral; in crevices and on surface of volcanic and pyro clastic rocks of extended protected reef.	abundant
9. V. 1968, 18-16 Isla Montuosa, Panama.	upper littoral; in crevices of highly fissured sandstone of extensive exposed reef.	scarce
13. V. 1968, 18-18 Bahia de Brasilito, Costa Rica.	mid-littoral; in crevices of basaltic rock of protected reef.	very scarce

air is held beneath the elytron-like fore-wings. Kellen (1960) also considers that trapped air in rock crevices enables *Omania samoensis* Kellen to survive periods of immersion during high tide.

Like many other intertidal insects (Evans 1968), *P. innova* probably is a scavenger-predator feeding on copepods and other small organisms stranded on rock surfaces and trapped in crevices as the tide recedes. The small size of *P. innova*, 2 to 3 mm, another characteristic of intertidal insects, excludes it from feeding on anything much larger than zooplankton unless intertidal collembolans and mites are also present; but the large intertidal collembolan *Anurida maritima* (Guérin-Méneville), though abundant in other marine littoral areas of the Eastern Tropical Pacific, was only rarely found in precisely the same localities as *P. innova* and then only in very low numbers. Mites were not always found with this bug. Table 2 shows that other tracheate arthropods such as bdellid mites, geophilomorphan centipedes, staphylinid adults and pseudoscorpions were generally present with *P. innova* in upper littoral crevices. These representatives of terrestrial forms which have adapted to the intertidal habitat also are scavenger-predators and in this respect are indicators along with *P. innova* of a particular combination of environmental factors, the most important of which is a constant replenishment through tidal cycles of suitable food

Table 2. Organisms associated with *Paralosalda innova* at various localities.

Locality	in crevices	on rock surfaces
Punta San Francisco Solano, Bahia de Solano, Colombia.	centipedes, isopods, *Onchidella*, pseudoscorpions.	*Siphonaria, Planaxis*, littorines, *Nerita funiculata, Acmaea.*
Punta Cotuda, Bahia de Solano, Colombia.	centipedes, pholadids, isopods, *Onchidella*, pseudoscorpions.	Littorines, chitons, neritids, grapsid crabs, *Siphonaria*, keyhole limpets
Punta Cruces, Bahia Cupica, Colombia.	polychaetes, centipedes, isopods, sipunculids, bivalves, snapping shrimps.	*Siphonaria gigas, Nerita scabracosta, N. funiculata, Lottia, Tetraclita*, littorines.
Culebra Island, Panama.	isopods, sipunculids, bdellid mites, pseudoscorpions, *Onchidella, Anurida maritima*, nemerteans.	*Nerita scabracosta*, littorines, oysters, *Siphonaria gigas, Tetraclita*, chitons.
Punta Paitilla, Panama City, Panama.	sipunculids, centipedes, mites, polychaetes, pseudoscorpions, isopods, *Onchidella.*	*Nerita funiculata, N. scabracosta, Siphonaria gigas*, barnacles, *Cerithium.*
Isla Montuosa, Panama.	isopods, pseudoscorpions, polychaetes, sipunculids.	*Nerita scabracosta, N. funiculata, Tetraclita, Chthamalus*, littorines, *Siphonaria gigas.*
Bahia de Brasilito, Costa Rica.	centipedes, *Onchidella*, isopods, polychaetes, sipunculids.	*Nerita scabracosta, N. funiculata, Siphonaria gigas, Tetraclita, Chthamalus*, littorines.

that is trapped in crevices and on the surfaces of rocks. The rock surface fauna listed in Table 2 is given to show those conspicuous animals, such as large barnacles (*Tetraclita*) and various gastropods, that can be used as indicators of the type of habitat which harbors *P. innova*.

The largest number of specimens of *P. innova* were found in those areas most protected from heavy surf or spray. Large numbers were seen at Punta Cruces, Bahia Cupica, Colombia on a rocky outcrop protected from the open sea by an island (Table 1). Even though heavy breakers pounded the seaward point and high surf rolled onto beaches in the bay itself, the area where the saldids were found was so calm that boats could tie up to the rocks themselves. Similarly in Punta Paitilla, Panama, where large numbers of *P. innova* were seen the area is characterized by calm waters. So calm in fact that extensive mud flats are found east of the collecting site. From these observations we conclude that these saldids prefer more potected areas of the littoral zone with little surf and spray.

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