

A review of the Oedemeridae (Coleoptera) of the Galápagos Islands, Ecuador

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Abstract

Extensive new collections contribute new information on the identity and distribution of the oedemerid beetles of the Galápagos Islands. Specimens previously recorded as near *Oxaxis pilosa* CHAMPION are described as *Oxycopsis galapagoensis* sp. n. *Oxaxis pilosa* CHAMPION of Guatemala and Nicaragua is transferred to the genus *Oxycopsis*. *Hypasclera collenettei* (BLAIR) is the most common and widespread species in the islands, and is variable in that it shows significant differences in aedeagus morphology between separate islands. *Alloxaxis hoodi* VAN DYKE is found to be a synonym of *H. collenettei*. *H. seymourensis* (MUTCHLER) is known only from the central islands. *Paroxaxis galapagoensis* (LINELL) is also widespread. All four Galápagos species are presently considered to be endemic, and each represents a separate ancestral colonization of the archipelago.

Keywords: *Hypasclera*, *Oxycopsis*, *Paroxaxis*, island insects, endemic species, colonization.

Introduction

Members of the beetle family Oedemeridae are commonly called the false blister beetles. Adults are found frequently at lights or by sweeping vegetation, and they are obligate pollen feeders (ARNETT, 1984). Larvae may feed on plant roots or may be inhabitants of moist decaying wood and some may live in salt-soaked driftwood (ARNETT, 1984, KRISKA, 2002). Oedemerids have been described and reported from the Galápagos by several workers: BLAIR (1928; 1933); FRANZ (1985); LINELL (1898); MUTCHLER (1938); and VAN DYKE (1953). As part of a long-term study on the entire beetle fauna of the Galápagos Islands (PECK, 1996; PECK & KUKALOVA-PECK, 1990), we have examined large series of newly collected specimens taken in the past 15 years from all islands in the archipelago (PECK, 2001). These beetles were most

commonly taken in large numbers at lights in the coastal arid vegetation zones of the islands. With this new material we have clarified the identity of specimens reported as near to *Oxacis pilosa* CHAMPION, found *Oxacis pilosa* itself to belong in the genus *Oxycopis*, found *Hypasclera hoodi* VAN DYKE to be a synonym of variable *H. collettei* BLAIR, and added to knowledge of the distributions of the species throughout the islands.

Material and methods

The genera of New World Oedemeridae were revised by ARNETT (1951, 1961) and these generic concepts are used here. We used standard entomological techniques in the study of series of dry mounted specimens from each island (Fig. 1). Dissections were made of males and the median lobe and parameres of the aedeagus were mounted on microslides in Euparal mounting medium. Drawings were made of these structures from digital photographs. Our specimens were compared with the historically important Galápagos material in the American Museum of Natural History (AMNH), New York, NY, USA; California Academy of Sciences (CAS), San Francisco, CA, USA; The Natural History Museum (BMNH), London, England; the National Museum of Natural History (USNM), Washington, D. C., USA;

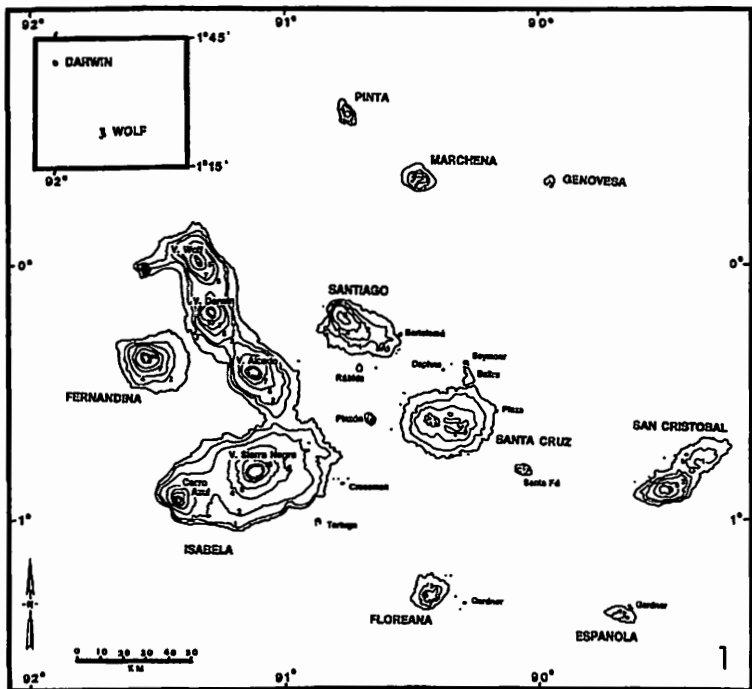


Fig. 1. Map of islands of the Galápagos Archipelago

Royal Institute of Natural Sciences (KBIN), Brussels, Belgium; the H. FRANZ collection in the Naturhistorisches Museum Wien (NHMW), Vienna, Austria; and the extensive material in the collections of the late Ross H. ARNETT, Jr., now in the Florida State Collection of Arthropods (FSCA), Florida Department of Agriculture, Gainesville, Florida, USA. Our voucher specimens are deposited in the Canadian Museum of Nature (CMNC), Ottawa, Ontario, Canada.

Taxonomic results

The Galápagos genera of Oedemeridae can be separated with the use of the following key (adapted from KRISKA, 2002).

- 1a. Both mandibles bifid (divided) at their tips; female front tibia with two movable apical spurs; male front tibia with single broad fixed apical spur, without slender movable spurs; tarsal claws with basal bulge but not basally conspicuously toothed *Oxycopsis* ARNETT
- 1b. Both mandibles not bifid at tips; male and female front tibia with two slender movable apical spurs; tarsal claws basally conspicuously toothed 2
- 2a. Right mandible with small dorsal preapical tooth, left mandible entire (without tooth); body usually of uniformly darker colour and usually lighter along elytral suture; elytra with pronounced longitudinal costae ..
..... *Hypasclera* KIRSCH
- 2b. Both mandibles entire; body usually with longitudinal lighter and darker stripes; without longitudinal elytral costae *Paroxacis* ARNETT

Subfamily Oedemerinae

Tribe Asclerini

Genus *Oxycopsis* ARNETT, 1951

Oxycopsis was described by ARNETT (1951) as a subgenus of *Oxacis*, and was elevated to genus rank in ARNETT (1961). *Oxycopsis* has 34 recognised species in North and Central America, and the West Indies. The numbers in South America have not been revised or catalogued (ARNETT, 1983). Many of the species listed in BLACKWELDER (1944) in the genera *Sessina* PASCOE and most of those in *Copidita* LECONTE belong here (ARNETT, 1961) and some have been transferred (ARNETT, 1983). The following species has diagnostic characters of *Oxycopsis* as given by ARNETT (1951: 318) and in his key (ARNETT, 1961) except for the following.

The description and key state that in *Oxycopsis* there should be two apical tibial spurs and a tibial spur formula of 2-2-2. This is so in females, but males of some species have no protibial spurs, but instead have an apical projection from the inner margin of the protibia. We have seen this previously unreported condition also in males of *Oxycopsis vittata* (FABR.), *O. dietrichi* (ARNETT), *O.*

suturalis (HORN), and *O. tenella* (WATERHOUSE); all species which occur in the southeastern USA or the West Indies and Central America. Males of *Oxycopsis* thus have a tibial spur formula of either 2-2-2 or 0-2-2. This feature may have been previously overlooked because males seem to be collected far less often than females. In our review of the extensive holdings of Neotropical genera and species in the ARNETT collection at FSCA no other genus or species was seen to have the 0-2-2 tibial spur condition.

Male *Oxycopsis* can be correctly keyed to genus if the second part of couplet 3 in the generic key of KRISKA (2002) is changed to read: "Prothoracic tibiae each with two apical spurs, or without apical spurs and with an apical thumb-like projection".

BLAIR (1928) associated one Galápagos specimen from James (=Santiago) Island with *Oxaxis pilosa* CHAMPION from Guatemala. FRANZ (1985) reported additional Galápagos material as specimens of *O. pilosa* CHAMPION, but our study of his material finds it to be misidentified specimens of *Hypasclera*. Study of CHAMPION's syntype material shows it to have the characters of *Oxycopsis*. This necessitates the following new combination.

Oxycopsis pilosa (CHAMPION), new combination

Oxaxis pilosa CHAMPION, 1890: 156. Syntype material seen, BMNH. Type locality: Guatemala.

ARNETT (1961) started the process of reassigning described Neotropical species to his revised generic categories and continued this for some Central American species in ARNETT (1983). In this he adds Nicaragua (with no other data) to the distribution of *Oxaxis pilosa*. That he did not place the species in *Oxycopsis* shows that he was not then aware of its correct placement.

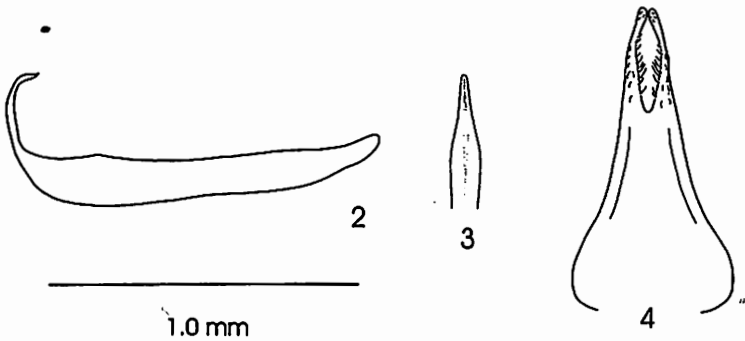
Our examination of available material confirms the external differences noted by BLAIR (1928: 673) which separate syntype material of *O. pilosa* from the Galápagos specimens. We note, in addition, that the abdomen is very pale, rather than dark ventrally and especially posteriorly; the pilosity of the elytra is subappressed and with several longitudinal rows of semi-erect setae, rather than less appressed and with less distinct rows of semi-erect setae; the pronotum is narrower anteriorly rather than more robust and wider anteriorly. Consequently the Galápagos material is considered to be a new species and is described below.

Oxycopsis galapagoensis new species

Figs 2-4

Oxaxis pilosa CHAMPION, BLAIR, 1928: 673; VAN DYKE, 1953: 42; FRANZ, 1985: 91 (misidentification of specimens of *Hypasclera*).

Holotype male in CMNC. Type data. Ecuador. Galápagos Islands. Isabela Island, 1 km W Villamil, 6.IV.1996, 1 m elev., backdune uv [light], upper littoral zone, on sand, S. Peck, 96-91.



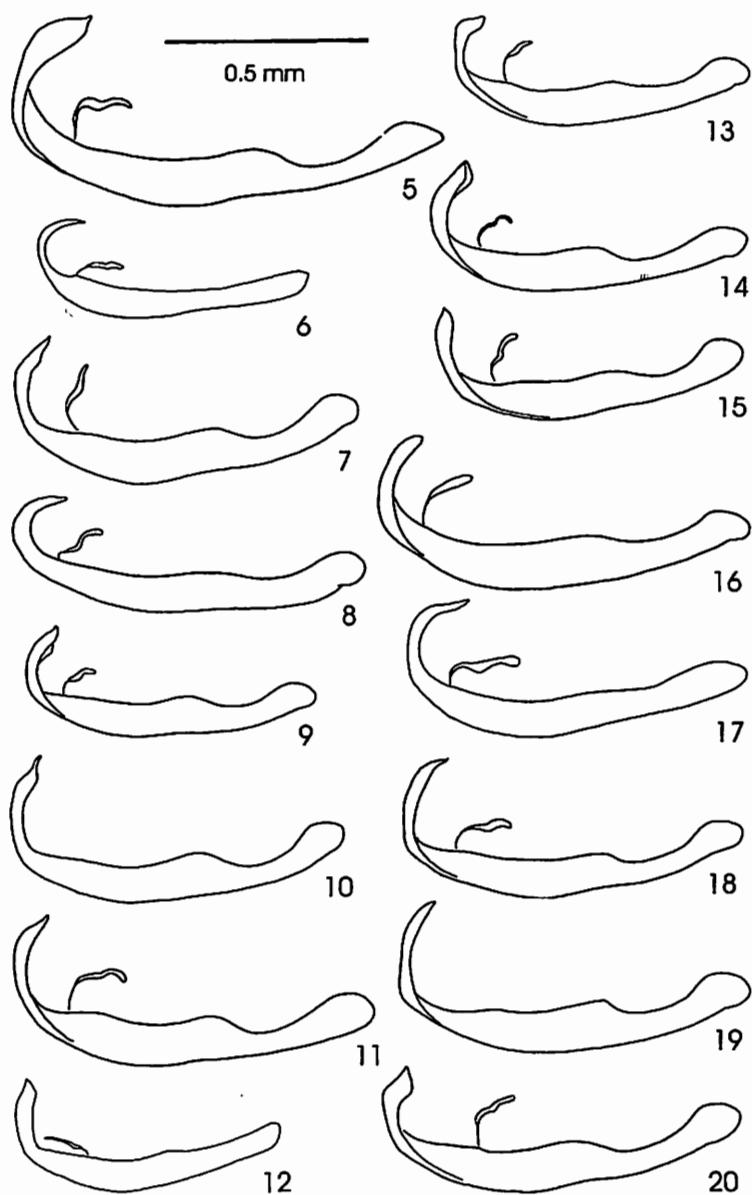
Figs 2-4. Genital structures of *Oxycopsis galapagoensis* n. sp. 2: medial lobe, lateral; 3: apex of median lobe, ventral; 4: parameres, ventral.

Paratypes: eight with same data, in CMNC. Galápagos. Fernandina Island, Punta Espinosa, arid zone, 12.V.1992, mv and uv lights, mangrove on sand and lava, J. Cook and S. Peck, 92-174, one in CMNC. Galápagos, James [Santiago] Island, July 1924, St. George Expedition, C.L. Collenette; British Museum 1925-488; [in pencil] near *O. pilosa* Ch.; one in BMNH (the specimen mentioned in BLAIR (1928) and VAN DYKE (1953)).

Description and diagnosis. With the generic characters in the key above and in ARNETT (1951: 318) and in the key in ARNETT (1961). Additional characters are the following. Body length 9-10 mm. Body colour uniformly light brown, somewhat more pale brown on appendages and along elytral suture. Uniformly covered with sparse, long, pale setae. Dorsum of head and prothorax punctured. Elytral surfaces very finely granular, each elytron with two distinct low costae. Last joint of maxillary palpus widest near apex. Median lobe of aedeagus elongate (Fig 2), without sub-basal apodeme; apex thin, narrowly rounded at tip (Fig 3). Paramere (Fig 4) with basal plates projecting posterior-dorsally, apical lobes elongate, blunt at tips, with setae on inner faces.

Distribution. The species is endemic to the Galápagos Islands and is relatively scarce. It is now known from 11 specimens from the islands of Fernandina, Isabela, and Santiago.

Discussion of endemism. Because the first records of specimens of the species in the Galápagos date to the 1924 St. George Expedition (BLAIR, 1928) we think that they represent a naturally occurring species, and that it has not been recently introduced from the Ecuador mainland (PECK et al., 1998). In the absence of any records from coastal Ecuador, we presently consider the species to be endemic to the Galápagos. We accept the possibility that further collecting of the poorly known insects of coastal mainland Ecuador might find it there. The large numbers of described species placed in the genera *Copidita* LECONTE, *Sessinia* PASCOE, and *Oxycopsis* ARNETT in north-western South America prevent us from reviewing them all to determine if one is conspecific with the Galápagos specimens. The only oedemerid species which are



Figs 5-20. *Hyasclera collenettei*, median lobe, lateral, variation between different islands. 5: Bartolomé; 6: Española; 7: Fernandina; 8: Floreana; 9: Genovesa; 10: Isabela, Tagus Cove; 11: Isabela, Villamil; 12: Isla Darwin; 13: Isla Wolf; 14: Marchena; 15: Pinta; 16: Rábida; 17: San Cristobal; 18: Santa Cruz; 19: Santa Fe; 20: Santiago.

recorded from mainland Ecuador are *Ananca debilis* SHARP (1891) and *A. costulata* KIRSCH (1886) (both listed in the genus *Sessinia* in BLACKWELDER, 1944), but we exclude these because they were collected in habitats of 2800 m elevation and higher.

Bionomics. Larvae are possibly scavengers in rotted wood and adults are probably herbivores on pollen; arid zone; May-July; at lights.

Genus *Hypasclera* KIRSCH, 1866

The genus contains eight species in the USA (KRISKA, 2002; ARNETT, 1951), and eight others in the West Indies and Mexico (listed as *Alloxaxis* ARNETT, 1951). None are listed from Central or South America (ARNETT, 1983) except for the Galápagos species. This suggests Mexico as the source of the colonists of the Galápagos. The two Galápagos species are highly similar and variable and can be separated with confidence only by the characters of the male genitalia.

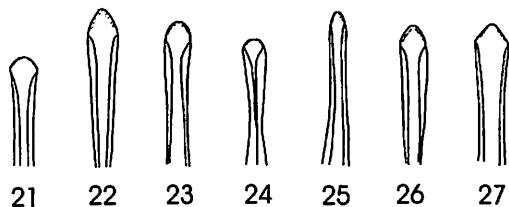
Key to the species of Galápagos *Hypasclera*

- 1a. Lateral lobes of parameres elongate, length greater than one-third length of basal piece (Figs 28-40); lateral margins of median lobe with longitudinal folds (Figs 21-27); dorsal margin of median lobe usually sinuate (Figs 5-20) (exceptions are populations on Española, San Cristóbal and Floreana where *H. seymourensis* is not known to occur) . . .
 *H. collenettei* (BLAIR)
- 1b. Lateral lobes of parameres short, length about one-third length of basal piece (Fig 43); lateral margins of median lobe without longitudinal folds (Fig 42); dorsal margin of median lobe never sinuate (Fig 41)
 *H. seymourensis* (MUTCHLER)

Hypasclera collenettei (BLAIR), new combination

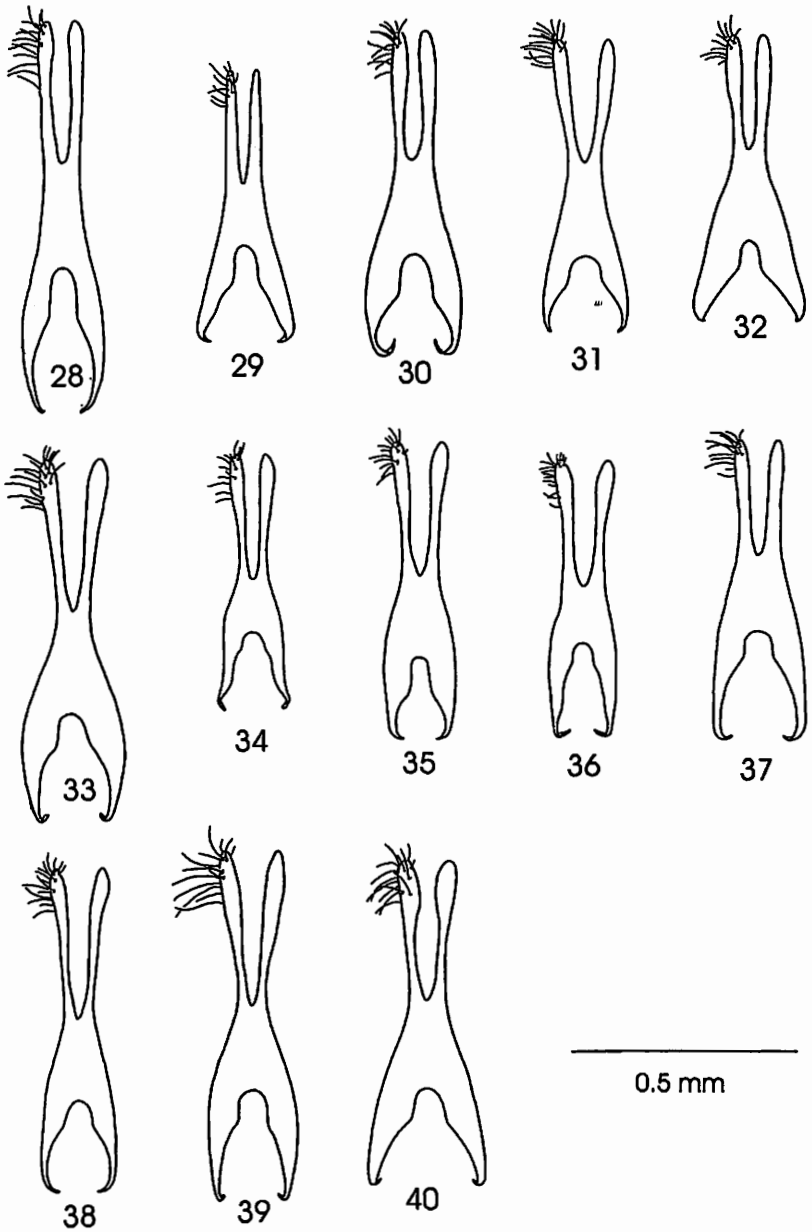
Figs 5-40

Alloxaxis collenettei BLAIR, 1928: 673; BLAIR, 1933: 480; MUTCHLER, 1938: 3; VAN DYKE, 1953; FRANZ, 1985: 91; 43. Syntype specimens in BMNH,



0.5 mm

Figs 21-27. *Hypasclera collenettei*, apex of median lobe, ventral, variation between different islands. 21: Española; 22: Fernandina; 23: Floreana; 24: Isla Wolf; 25: Pinta; 26: San Cristóbal; 27: Santiago.



Figs 28-40. *Hypasclera collenettei*, parameres, ventral, variation between different islands. 28: Bartolomé; 29: Española; 30: Fernandina; 31: Floreana; 32: Genovesa; 33: Isabela, Villamil; 34: Isla Wolf; 35: Marchena; 36: Pinta; 37: San Cristóbal; 38: Santa Cruz; 39: Santa Fé; 40: Santiago.

seen. Type locality: James [=Santiago] Island.

Alloxaxis hoodi VAN DYKE, 1953: 43. Type specimen in CAS, seen. Type locality: Hood [=Española] Island. **New synonymy.**

Diagnosis. With characters of the genus and species in the keys above.

Discussion of synonymy. This species shows minimal variation in the median lobe of the aedeagus within populations on a single island, but considerable variation between separate islands (Figs 5-40). The original description of *Alloxaxis hoodi* was based on a single specimen (VAN DYKE, 1953). We have seen an additional 78 new specimens from Española [=Hood] Island (Figs 6, 21, 29) and find these populations to fall within the range of variation of *H. collenettei*. We thus consider *Alloxaxis hoodi* VAN DYKE to be a synonym of *Hypasclera collenettei* (BLAIR).

Distribution. The species is endemic to and distributed throughout the Galápagos Islands. It was the most commonly collected species and we have seen 701 new specimens from the islands of Baltra, Bartolomé, Darwin, Fernandina, Floreana, Genovesa, Isabela, Marchena, Pinta, Rábida, San Cristóbal, Santiago, Santa Cruz, Santa Fé, and Wolf.

There is the possibility that the species is not endemic to the Galápagos, and that it will be found on the mainland of Pacific coastal Ecuador or other neighbouring countries. In the several collections we have seen there are no specimens of *Hypasclera* from coastal mainland Ecuador.

Bionomics. The larvae are probably scavengers in rotted wood (maybe driftwood), and the adults are probably herbivores. We have seen them feeding on the pollen in flowers of *Opuntia* cactus and *Cordia lutea* trees at night. The collections are all from the littoral and arid zones from the months of January-June and October-November. The species is often very abundant at lights but has also been taken in sweeping samples and in flight intercept and malaise traps.

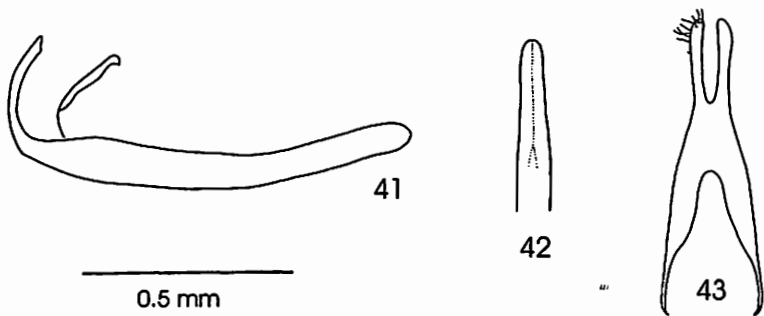
***Hypasclera seymourensis* (MUTCHLER), new combination**
(Figs 41-43)

Alloxaxis seymourensis MUTCHLER, 1925: 226; VAN DYKE, 1953: 43. Type specimen in AMNH; seen; a female, but otherwise matching male specimens. Type locality: Seymour [=Baltra] Island.

Diagnosis. With characters of the genus and species in the keys above.

Distribution. This species is endemic to and distributed in the central and younger western islands of the Galápagos Archipelago. We have seen 161 new specimens from the islands of Baltra (= South Seymour), Bartolomé, Isabela, Rábida, Santa Cruz, Santa Fé, and Santiago.

Bionomics. The larvae are probable scavengers in rotted wood (maybe driftwood), and the adults are probably herbivores but we have no host plant records. The collections are all from the littoral and arid zones in the months of January and March-June. The species is often taken at lights.



Figs 41-43. Genital structures of *Hyposclera seymourensis*. 41: median lobe, lateral; 42: apex of median lobe, ventral; 43: parameres, ventral.

Genus *Paroxacis* ARNETT, 1951

Paroxacis contains 16 species in North and Central America and the West Indies (ARNETT, 1983). Many described species in South America (listed in BLACKWELDER (1944) in various genera) belong here (ARNETT, 1961) but have not been revised or catalogued.

Paroxacis galapagoensis (LINELL)

Oxaxis galapagoensis LINELL, 1898: 266; BLAIR, 1928: 673; VAN DYKE, 1953: 42. FRANZ, 1985: 91. Type specimen in USNM, seen. Type locality: Chatham [=San Cristobal] Island.

Paroxacis galapagoensis (LINELL); ARNETT, 1961; 60

Diagnosis. With characters of the genus as in the key above. Body length 8-13 mm. Body colour light to dark brownish, appendages uniform light brown; thorax sides and midline usually darker; elytra usually darker along sides and with a narrow short longitudinal dark stripe in middle of each elytron. Uniformly covered with dense, short, pale setae. Dorsum of head and thorax punctured, with granular microsculpture between punctures. Elytron surface granular; each elytron with vague traces of two longitudinal costae. Last joint of maxillary palp widest before apex.

Distribution. This species is considered to be endemic to the Galápagos Islands and is widespread in them. We have seen 139 new specimens from the islands of Bartolomé, Española, Floreana, Isabela, Marchena, Pinta, Santiago, San Cristóbal, Santa Cruz, Santa Fé, and Seymour.

BLAIR (1928) notes the species to be close to or synonymous with *Paroxacis litoralis* (CHAMPION) of Guatemala and Panama. This species was described in *Oxaxis* and placed in *Paroxacis* by ARNETT (1961: 59). Additional mainland collecting and specimen study may thus find that it is not endemic.

Bionomics. The larvae are probably scavengers in rotted wood, and the adults are probably herbivores but we have no host plant records. The

collections are all from the littoral and arid zones from the months of January-June, and October. The species is often very abundant at lights.

Discussion

The above species and records are additional examples of several of the common patterns in Galápagos organisms. Many of these have been previously documented in Galápagos insects (PECK, 2001).

Endemic species. Species limited to the archipelago (as are the four oedemerid species) is a common and well known pattern in insects and other organisms. Endemic species with functional flight wings, as in the four species of Oedemeridae, are usually widespread in the archipelago. This is not at all surprising for flying insects which live in the littoral and lowland arid zones, the zones most likely to provide propagules for inter-island dispersal (PECK, 1994a). But the hypothesis of endemism should be used with some caution. Many insect groups are much better known and studied in the Galápagos than on the Ecuadorian mainland. Additional study of the mainland fauna is still needed to test the hypotheses of endemism of many Galápagos species.

Differential colonization. The two *Hypasclera* species are interpreted to represent two separate colonization events: (a) an earlier colonization by the ancestor of *H. collenettei* on the older islands and its subsequent spread throughout the archipelago; and (b) a later colonization by the ancestor of *H. seymourensis* after the emergence of the younger central islands (some 0.7 - 1.5 million years ago). The earlier colonization by *H. collenettei* allows for its greater distribution and the development of variation in island aedeagal characters. A later colonization by *H. seymourensis* accounts for the lack of such significant variation between island populations, and its geographic distribution is less extensive. It is not unusual for species to be present on the younger central islands and not the older eastern and southern islands.

It is interesting to note that on all islands where *H. collenettei* and *H. seymourensis* occur sympatrically, the antennal segments of *H. collenettei* have a dark band at their base and/or apex. This can be interpreted as an instance of character displacement (BROWN & WILSON, 1956) and this may function as a pre-mating isolating mechanism. We have observed the condition on the islands of Baltra, Bartolomé, Isabela, Rábida, Santa Cruz, Santa Fé and Santiago. On the islands of Darwin, Wolf, Marchena, Genovesa and Pinta this character is present in some individuals but is not consistently expressed. This suggests that these islands may have been colonized by populations occurring on islands also populated by *H. seymourensis*, but in the absence of *H. seymourensis* the character is not consistently maintained.

Inter-island variation. There is appreciable variation in the male genital structures of *H. collenettei* from island to island (Figs 5-40). The taxonomic meaning of this is not clear. We think it unlikely that these island populations are genetically isolated because the beetles are good fliers, and live in the coastal zone where they are exposed to inter-island transport opportunity by flight or rafting (PECK, 1994a, 1994b). We suspect that earlier taxonomists

would probably have given subspecific recognition to each island's population, as has been done in groups such as cerambycid beetles (LINSLEY & CHEMSAK, 1966) and the Galápagos tortoises. We think that it is not necessary to give formal names because each island population can be informally identified by its individual island name. The evolutionary meaning of this variation might be resolved by the application of molecular genetics techniques. Such contributions to resolving the evolutionary dynamics of Galápagos animals have been CACCONE *et al.* (2002) for the giant tortoises, SATO *et al.* (2001) for Darwin's finches, SEQUEIRA *et al.* (2000) for *Galapaganus* weevils, DHUYVETTER *et al.* (2002a) for *Calosoma* carabids and DHUYVETTER *et al.* (2002b) for *Gerstaeckeria* weevils.

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References

- ARNETT R. H., Jr. 1951. - A revision of the Nearctic Oedemeridae (Coleoptera). *American Midland Naturalist* 45: 257-391.
- ARNETT R. H., Jr. 1961. - Contributions toward a monograph of the Oedemeridae 14. A key to and notes on the New World genera. *Coleopterists Bulletin* 15: 49-64.
- ARNETT R. H., Jr. 1983. - Family 119. Oedemeridae (first series), *In*: Arnett, R. H., Jr., Checklist of the beetles of North and Central America and the West Indies, vol. 6. The darkling beetles, Strepsiptera, and related groups. Flora and Fauna Publishing, Gainesville. 6 pp.
- ARNETT R. H., Jr. 1984. - The false blister beetles of Florida (Coleoptera: Oedemeridae). *Florida Department of Agriculture and Consumer Services, Entomology Circular* no. 259: 1-4.
- BLACKWELDER R.E. - 1944. Checklist of the coleopterous insects of México, Central America, the West Indies, and South America. *United States National Museum Bulletin* 185(1-5) I-XII, 1-925. Reprinted in 1982.
- BLAIR K. G. 1928. - Coleoptera (Heteromera, Terebrantia, Malacodermata and

- Bruchidae) from the Galápagos Islands, collected on the St. George Expedition, 1924. *The Annals and Magazine of Natural History*, ser. 10, vol. 1: 671-680.
- BLAIR K. G. 1933. - Further Coleoptera from the Galápagos Archipelago. *The Annals and Magazine of Natural History*, ser. 10, vol. 11: 471-487.
- BROWN W.L., JR. & WILSON E.O. - 1956. Character displacement. *Systematic Zoology* 5: 49-64.
- CACCONE A., GENTILE G, GIBBS J. P., FRITS T. H., SNELL H. H., BETTS J. & POWELL J. R.. 2002. - Phylogeography and history of giant Galápagos tortoises. *Evolution* 56: 2052-2066.
- CHAMPION G. 1890. - *Biologia Centrali-Americana, Insecta, Coleoptera (Oedemeridae, Xylophilidae, Anthicidae, Mordellidae)*, vo. 4, part 2, pp. 121-256.
- DHUYVETTER H., GAUBLOMME E, VERDYCK P., DESENDER K., MONDOR-GENSON G, & RASPLUS J.-Y. 2002. - Isolation and characterization of microsatellite loci in Galápagos caterpillar hunters (Coleoptera, Carabidae, *Calosoma*). *Molecular Ecology Notes* 2: 284-286.
- DHUYVETTER H., VERDYCK P., GAUBLOMME E, DESENDER K., MONDOR-GENSON G, & RASPLUS J.-Y. 2002. - Isolation and characterization of microsatellite loci in the Galápagos *Opuntia* weevil *Gerstaeckeria galapagoensis* (Coleoptera, Curculionidae). *Molecular Ecology Notes* 2: 475-477.
- FRANZ H. 1985. - Beitrag zur Kenntnis der Koleopteren fauna der Galápagos-Inseln. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abteilung I*, 194 Band, 1 bis 5 Heft.
- KIRSCH Th. 1886. - Neue südamerikanische Käfer. *Berliner Entomologische Zeitschrift* 30: 331-340.
- KRISKA N. L. 2002. - 109. Oedemereidae Latreille 1810. In: Arnett, R. H., Jr., M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles*, vol. 2. 514-519. CRC Press. Boca Raton, FL.
- LINELL M. L. 1898. - On the coleopterous insects of the Galápagos Islands. *Proceedings of the United States National Museum*, 21 (1143): 249-268.
- LINSLEY E. G. & CHEMSAK J. A.. - 1966a. Cerambycidae of the Galápagos Islands. *Occasional Papers of the California Academy of Sciences*, ser. 4, 33: 197-236, Figs 1-28, tables 1-5.
- MUTCHLER A. J. 1925. - Coleoptera of the Williams Galápagos Expedition. *Zoologica* 5: 219-240.
- MUTCHLER A. J. 1938. - Coleoptera of the Galápagos Islands. *American Museum Novitates* no. 981: 1-19.
- PECK S. B. 1994a. - Aerial dispersal of insects between and to islands in the Galápagos Archipelago, Ecuador. *Annals of the Entomological Society of America* 87: 218-224.
- PECK S. B. 1994b. - Sea-surface (pleuston) transport of insects between islands in the Galápagos Archipelago, Ecuador. *Annals of the Entomological Society of America* 87: 576-582.
- PECK S. B. 1996. - Origin and development of an insect fauna on a remote archipelago: The Galápagos Islands, Ecuador. In A. Keast and S. Miller (eds). *The Origin and Evolution of Pacific Island Biotas, New Guinea to eastern Polynesia: Patterns and Processes*, pp. 91-122, SPB Academic Press, The Netherlands, 531 pp.

- PECK S. B. 2001. - Smaller orders of insects of the Galápagos Islands, Ecuador: evolution, ecology, and diversity. NRC Research Press, Ottawa, Ontario, Canada. 278 pp. .
- PECK S.B. & KUKALOVA-PECK J. - 1990. Origin and biogeography of the beetles (Coleoptera) of the Galápagos Archipelago, Ecuador. *Canadian Journal of Zoology* 68: 1617-1638.
- PECK S. B., HERATY J., LANDRY B., & SINCLAIR, B. J. 1998. - The introduced insect fauna of an oceanic archipelago: The Galápagos Islands, Ecuador. *American Entomologist* 44: 218-237.
- SHARP D. 1891. - Coleoptera. *In*: Supplementary appendix to travels amongst the great Andes of Ecuador by Edward Whymper. Pp. 40-44. John Murray, London.
- SATO A., TICHY H., O'HUIGIN C., GRANT P. R., GRANT R., & KLEIN J. 2001. - On the origin of Darwin's finches. *Molecular Biology and Evolution* 18: 299-311.
- SEQUEIRA A. S., LANTERI A. A., SCATAGLINI M. A., CONFALONIERI V. A., & FARRELL B. D. 2000. - Are flightless *Galapaganus* weevils older than the Galápagos Islands they inhabit? *Heredity* 85: 20-29.
- VAN DYKE E. C. 1953. - The Coleoptera of the Galápagos Islands. *Occasional Papers of the California Academy of Sciences* no. 22: 1-181.