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THE SALDIDAE OF THE HAWAIIAN ARCHIPELAGO (HEMIPTERA: HETEROPTERA)[1]

By **R. H. Cobben**[2]

Abstract. The following *Saldula* species are described from the Hawaiian Is: *S. intermedia* from Oahu, Maui and Hawaii; *S. usingeri* from Molokai and Maui; *S. kauaiensis* from Kauai and Oahu; and *S. longicornis* from Oahu. *S. nubigena* is known only from Maui. The remaining 3 *Saldula* species (*exulans, oahuensis* and *procellaris*) are widely distributed over most or all islands. Lectotypes are selected for *S. exulans, S. oahuensis, S. procellaris,* and *S. nubigena.* A revised key to all species is presented. The terminology of wing-morphs is discussed. Distributional patterns and extent of wing reduction, in addition to morphological differences, are used to reconstruct the probable relationships of the Hawaiian species in relation to evolutionary time. The 8 species known, all endemic, presumably arose from 3 independent invasions. *S. exulans* is supposed to represent the most recent introduction and *S. nubigena* the oldest. The latter species may be considered as the ancestor of 5 Hawaiian species.

The Saldidae constitute a worldwide, although moderate-sized, family of predatory bugs living in moist habitats. The 5 species known from the Hawaiian Is were keyed by Zimmerman (1951, 1957). This key was an important improvement on the one given by the same author in 1948, which was based partly on misidentified material from the Hawaiian collections; nevertheless, the correct identification of many individuals remained in doubt, as is demonstrated by the many question marks on the labels in various collections.

In 1960, I received some 150 specimens of Hawaiian material from the late Dr Usinger (University of California, Berkeley), and in recent years, abundant additions were forwarded to me by Dr Gagné from the Bishop Museum, Honolulu (BISHOP). I also studied the Hawaiian material of the American Museum of Natural History in New York, the Drake Collection in the Smithsonian Institution in Washington in 1973, and the British Museum of Natural History (BMNH), London. At that time, I was not yet familiar with the taxonomic problems of the group of small-sized Hawaiian species. Since the material in the Drake Collection may not be loaned, I have had no opportunity to determine these specimens in light of my present conceptions and, unfortunately, they had to be omitted from the present revision.

The 5 known species were described in 1878, 1888 and 1908, without holotype designations, and with mostly insufficient locality indications. Specimens of 4 of the

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[1] Material examined from Bishop Museum resulted from fieldwork supported by grants to the Museum from the U.S. National Science Foundation (BMS-70-00697, GB-3105, GB-3721).

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5 species, located in the British Museum, are labeled as B.M. types and were recently studied, so that a revision based on the more than 600 specimens at hand seemed to promise a profitable enterprise.

THE TAXONOMIC PUZZLE

The saldid fauna of the Hawaiian Archipelago belongs to *Saldula,* the largest and most cosmopolitan genus of the family, and falls into 2 size classes. One is represented by only the species *S. exulans,* which ranges from 3.4–5.3 mm. Its size and its wing and pronotum design with pale margin (FIG. 1, 17) distinguish this species generally from all remaining species which make up the smaller size class (2.8–3.7 mm).

Saldula kauaiensis, n. sp. is easily recognizable on the basis of its shiny wings and the clavus design (FIG. 6). *S. nubigena,* represented so far by only 2 specimens, has a unique antennal formula. *S. longicornis,* n. sp. is characterized by proportionally long antennae. However, the remaining populations, recognized here as 4 valid species, offer great problems taxonomically. Often when I thought I had found a minor specific character, additional material proved it not to apply to all individuals of one population.

As in other insect groups in the Hawaiian biota [e.g., Drosophilidae (Carson et al. 1970), Lygaeidae, Orsillinae (Usinger 1942)[3]], I had hoped to find greater morphological diversification among the saldid species by adaptive radiation than is exhibited by continental Saldidae. Support for this belief was the fact that some Hawaiian species were collected (by beating) from moss on shrubs and trees, a quite unusual habitat. However, intraspecific variation of Hawaiian saldids appears to be considerable, and reliable genitalic differences among species is absent. Statistical treatment of detailed morphometric data was predominantly disappointing for species separation. Therefore, I refrain from giving long tables of measurements which are not relevant for species delimitation, in spite of the intensive work devoted to this subject.

The only way to discriminate between species is to use a set of characters, among which a eunomic series of wing pigmentation is essential (as in continental species; see Wagner 1950, Cobben 1960).[4] The German term "Eunomie," introduced by Voigt & Voigt (1938), refers to the phenomenon of continuous variation of a character. Most Saldidae have a highly variable wing pattern. When such color morphs are arranged in a logical sequence from light to dark specimens, the total spectrum of

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3. Of interest in this connection is the introduction to the important paper of Usinger (1942): "Hawaiian species of the tribe Orsillini are attractive subjects for study from at least three entirely different points of view. To the resident of Hawaii they are among the least known though commonest insects from sea level to the tops of the mountains on introduced and native plants. To the hemipterist they present a fascinating array of primitive and modern forms comprising half of the known orsilline fauna of the world. To the evolutionist they represent the first case of tremendous proliferation of species in insular areas which presents a possibility of experimental analysis."
4. Although I applied in 1960 Latin names to the most light and most dark extremes of one eunomic series of a species, I abstain here from this habit. One can better refer to accurate drawings in order to stress intraspecific variation, rather than burdening the taxonomic literature with still more Latin epithets.

pigment distribution follows a more or less continuous pattern, mostly specific by species (cf FIG. 3b–f with FIG. 7b–f). Environmental factors exert influence on the proportion of different morphs in a population. High temperatures and/or lower humidity shift the preponderance of the eunomic series toward the light segment of the color spectrum. The reverse generally occurs under cooler and more humid conditions. Small fluctuating deviations from the hypothetical ideal eunomy always occur, but discontinuities in the pigmentation trend are suggestive of genetic divergence. For example, the series drawn in FIG. 10a–c does not fit within the series in FIG. 7b–f because the area bordering the clavus in the specimens shown in FIG. 10 tends to remain unpigmented, whereas the same area in the series of FIG. 7 is subject to blackening. The decision made in the present paper, to consider the series of FIG. 10a–c and the series of FIG. 11a–e as each belonging to a new species mainly on the basis of this deviant wing pattern, may sound questionable to taxonomists not familiar with Saldidae. But this decision is consistent with my experience with the European and Caribbean saldid fauna. Sibling species, morphologically hardly identifiable on the basis of small museum samples and sometimes exhibiting nearly the same wing pigment eunomies, are more readily recognized in the field, not in the least by slightly different microhabitat preferences. I presume that this is also true of the 3 new species described in this paper; more evidence must come from on-the-spot observation.

Other insect groups characterized by pronounced variability of wing picturation are Chrysomelidae (Cassidinae) and Coccinellidae among Coleoptera (survey in Simon Thomas 1964) and Cercopidae (the genus *Philaenus*) among Homoptera (Halkka 1964; Wagner 1968). The intraspecific variation in these groups often consists of a hodge-podge of numerous phenotypes determined by different genes. Such polymorphism does not allow one to arrange all different morphs into 1 smoothly running eunomic series. However, the great regularity of pigment extension in Saldidae, where the genome of a species is responsible for one characteristic type of eunomy, is entirely different. It seems therefore justified to attribute 2 populations of saldids exhibiting basically different eunomies to different species.

I will not give lengthy descriptions of the species, but stress only the differences among species, supplemented with ample illustrations. All species of the Hawaiian Is have in the adult stage rudiments of the larval organ (Cobben 1957, 1976), pregenital glands with a crescent-shaped sclerite (Cobben 1961), and mostly similar parameres, phallic sclerites, length of penis-filum, parandria, subgenital plates, and spermathecae. Such characters are omitted from the species descriptions and are only used in the key below when relevant for the recognition of species.

THE TAXONOMIC REVISION

KEY TO SPECIES OF *Saldula* IN THE HAWAIIAN IS

1. Preocellar spots projecting anteriorly of the level of ocelli (FIG. 4a–c). Lateral margin of pronotum usually pale. Clavus often with anterior pale spot, bordering the interior edge (FIG. 1b,

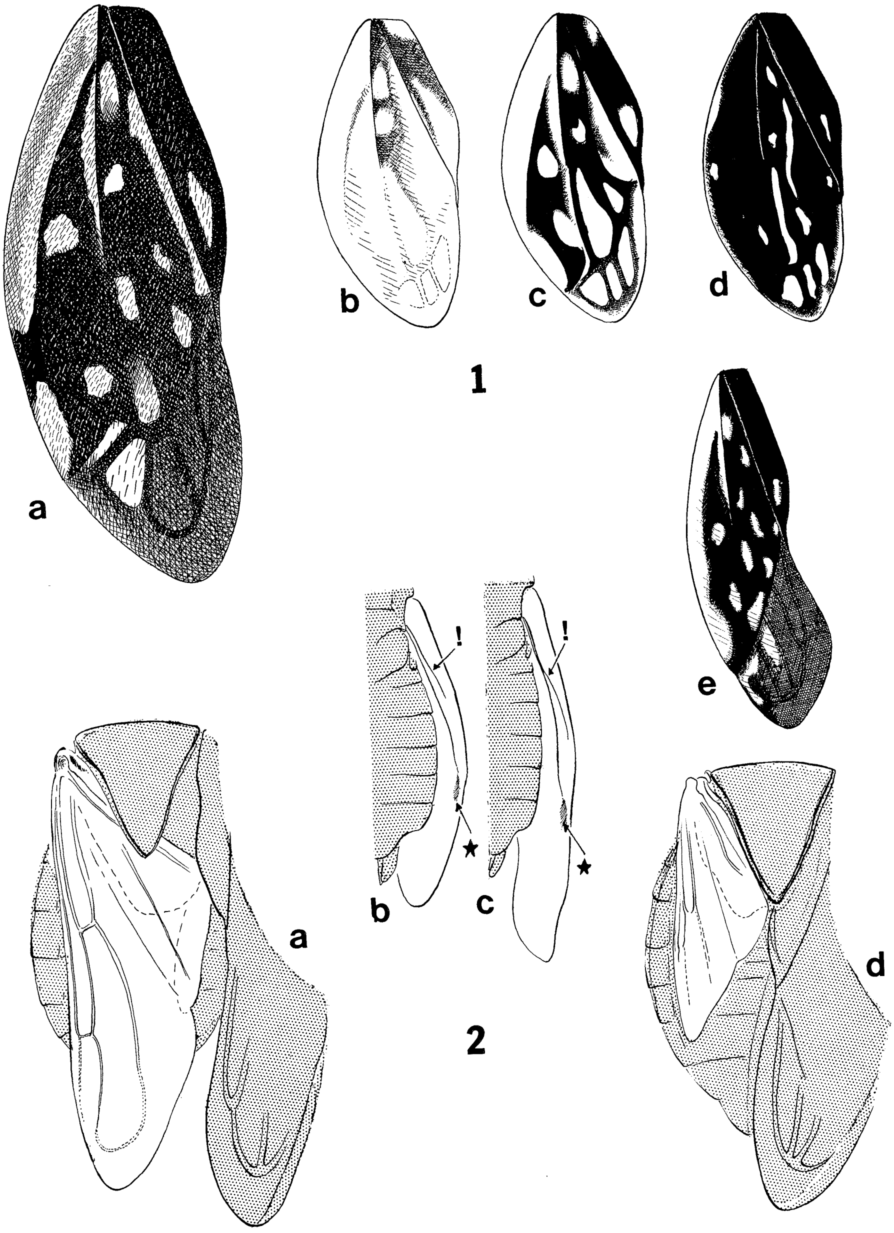


FIG. 1–2. *Saldula exulans*. **1.** Left fore wing: a, detailed presentation of submacropterous ♀; b–d, showing only the eunomic pattern, semibrachypterous: (b) F_2 ♀ from Oahu, reared by the late Prof. Usinger, (c) ♀ from Waialua, Maui, (d) ♀ from Waikamoi, Maui, (e) macropterous ♂ from Kamoki Flat, Molokai. **2.** Extent of development of fore and hind wing in the submacropterous ♀ (a, c) and the semibrachypterous ♀ (b, d); the star marks the depression in the lateroventral site of the fore wing, preadapted to fit the grasping plate of the ♂ during copulation (note the difference in length of the lateral ridge in b and c, indicated by "!").

c). Eunomy of fore wings as depicted in FIG. 1a–e, without pruinose areas. Ratio: width of head/minimum width of frons, below 3. Rather stout species, usually above 3.8 mm (rarely 3.4–3.7 mm) .... **exulans**

Preocellar spots about at the same level as ocelli (FIG. 5a, b). Pronotum entirely black. Fore wings mostly with pruinose areas. Ratio: width of head/minimum width of frons, over 3. Small species, under 3.8 mm 2

2 (1). Fore wing with overall distinct shininess; clavus with subanterior pale spot, confluent with distal spot in light-colored specimens (FIG. 6a–d) .... **kauaiensis, n. sp.**

Fore wing predominantly dull; clavus without anterior pale spot 3

3 (2). Second and 4th antennal segments nearly subequal in length; ratio segment 2/4 about 1.05 .... **nubigena**

Second antennal segment distinctly longer than 4th segment; ratio segment 2/4 more than 1.28 4

4 (3). Ratio: Length of antennae/median length of pronotum (without pronotal collar) more than 5. Pruinose area surpassing midpoint of clavus (FIG. 8) .... **longicornis, n. sp.**

Ratio: length of antennae/median length of pronotum (without pronotal collar) less than 5. Pruinose area not surpassing midpoint of clavus 5

5 (4). Central area of clavus without hairs (FIG. 3e, 11b) 6

Clavus with uniformly distributed pubescense (FIG. 7b, 10a) 7

6 (5). Eunomic pattern of fore wing as depicted in FIG. 3b–h; the dark pigment in the light spectrum of this eunomic series starts in the midposterior part of the corium. Femora mostly with a wide dark median band (lacking in the lightest-colored specimens) .... **oahuensis**

Eunomic pattern of fore wings as depicted in FIG. 11a–e; the dark pigment in the light spectrum of this eunomic series starts in the distal exocorial part. Femora unicolorless pale; only in the darker specimens sometimes with fuscous median band .... **intermedia, n. sp.**

7 (5). Eunomic pattern of fore wing as depicted in FIG. 7b–f. Corium with a dark band along clavus; anterior pruinose area of clavus narrow and short .... **procellaris**

Eunomic pattern of fore wing as depicted in FIG. 10a–c. Corium broadly pale along clavus; pruinose area covering anterior ⅓ of clavus .... **usingeri, n. sp.**

Saldula exulans (White) FIG. 1, 2, 4a–c, 12, 17, 19b, 21, 23, 24, 25, 29b, 30, 38

Salda exulans White, 1878, Ann. Mag. Nat. Hist. **1:** 373.

Acanthia exulans (White): Kirkaldy, 1908, Proc. Hawaii. Entomol. Soc. **1:** 198.

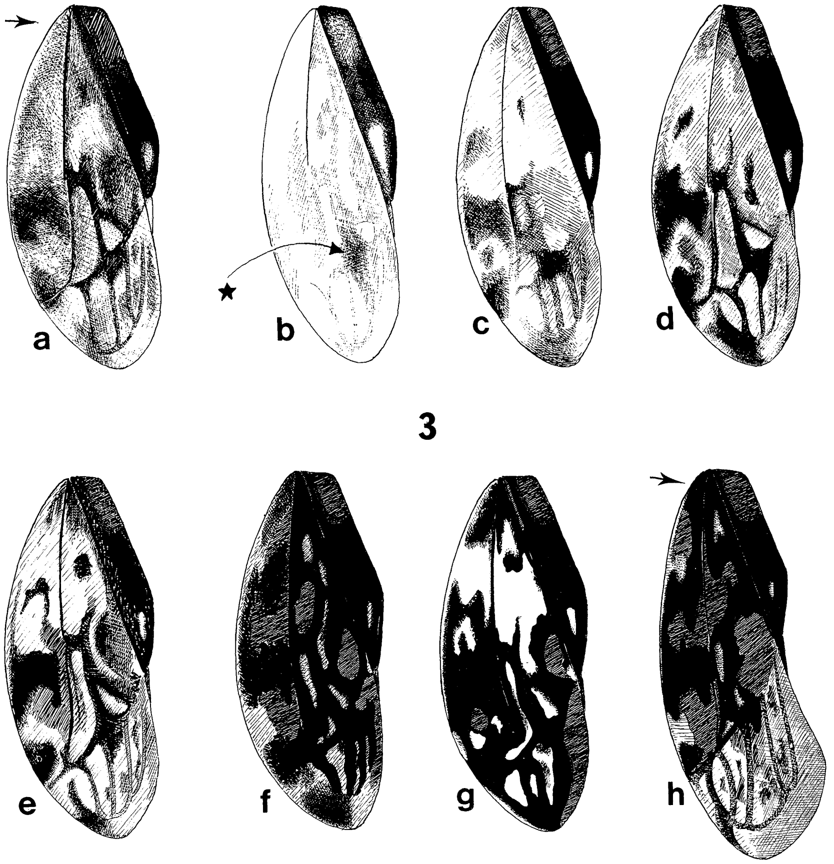
Saldula exulans: Zimmerman, 1948b, Insects of Hawaii, Vol. 3: 222; 1951, Proc. Hawaiian Entomol. Soc. **14:** 335; 1957, Insects of Hawaii, Vol. 6: 191.—Drake & Hoberlandt, 1951, Acta Entomol. Mus. Natl. Pragae **26:** 8 (Kirkaldy erroneously cited as author of species).

Lectotype ♂. Yellow type label numbered 25, Honolulu. In BMNH (label: presented by Perth Museum, B.M. 1953-629). Left fore wing lacking; right fore wing without membrane, glued on card, abdomen separate from thorax.

Description

General characteristics. Moderately large with proportionally long antennae, mostly semibrachypterous (terminology in Cobben 1960), variable wing pattern (FIG. 1a–e), shining, with short, sparse brown pubescence.

Head. Range of light and dark pattern as shown in FIG. 4a–c; shining, vertex punctate. Rostrum brown, reaching apex of hind coxae. Antennae unicolorous brown, 2nd segment with only short hairs. *Thorax.* Pronotum (FIG. 17) black, shiny, with straight or weakly concave sides, often with submarginal pale stripe dorsally and ventrally (especially in ♀). Scutellum black, smooth and shiny. Thorax ventrally black, apex of acetabulae and coxae pale (rarely entirely light). *Wings.* Hemelytra mostly semibrachypterous (FIG. 1a–



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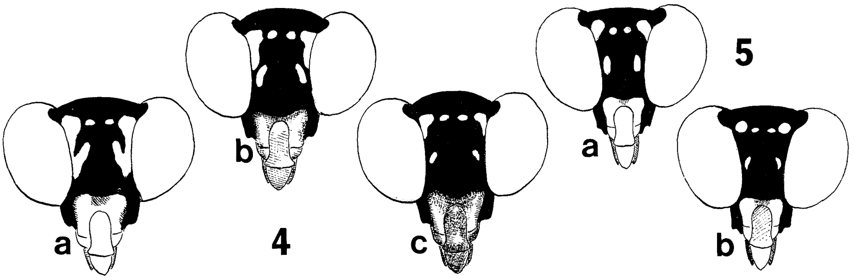

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Fig. 3–5. **3.** Left fore wing of *Saldula oahuensis*: a, ♀ in BMNH coll. (NW Koolau, V.1901, Perkins); b–f, eunomic series, from the light (b) towards the dark extreme (f), reconstructed from all the semibrachypterous material seen by the author (pruinose areas are indicated with oblique hatching; note that the area of the exocorium indicated in 3b with a star remains marked with dark pigment even in the lightest extreme of wing pigmentation; g, color morph deviating from the normal eunomy; h, macropterous ♀. **4–5.** Frontal aspects of heads: 4, *S. exulans*; (a), light-colored specimen, (c) dark-colored specimen; 5a, *S. oahuensis*, light-colored specimen; 5b, *S. procellaris* (conditions are similar in normally pigmented *S. oahuensis*, *S. intermedia*, *S. usingeri*, *S. nubigena*, *S. longicornis*, and *S. kauaiensis*).

d); only 3 ♂ and 4 ♀ of the total number of 270 specimens seen by me are macropterous. Variation of pigment distribution as in FIG. 1a–e, exocorium shining. Clavus with a subapical and, in light-colored specimens also with a proximal, pale spot. Apex of hind wing reaching about the base of the internal cell of the membrane of fore wing (FIG. 2d). Macropterous hemelytron as in FIG. 1e, accompanied by fully developed hind wing (FIG. 2a). The submarginal central area of the fore wing, to which the grasping plate of the ♂ is attached during copulation, is not markedly differentiated (star in FIG. 2b, c). *Legs.* Unicolorous brown, with only very short brown hairs, spines not longer than diameter of tibia; 2nd segment of hind tarsus slightly longer than 3rd segment. *Abdomen.* Entirely dark brown, rarely uniformly pale; subgenital plate brown with truncate hind margin. Grasping plate, paramere, phallic structures, and spermatheca as depicted in FIG. 24, 30, 21, 23 and 25, respectively.

Measurements. Mean length of 90 semibrachypterous ♂, 3.76 mm (min 3.40, max 4.20), width, 1.87 mm (1.70, 2.05); length of 111 semibrachypterous ♀, 4.37 mm (3.60, 5.30), width 2.27 mm (1.85, 2.65). Two macropterous ♂ vary from 4.80–5.00 mm in length and 2.05–2.25 in width; 3 macropterous ♀ measure 5.20–5.50 mm in length and 2.45–2.60 mm in width.

Specimens examined. HAWAIIAN IS. HAWAII I: Alakahi Gorge, XI.1961, 1♀, F.A. Bianchi; Hilo, Wailuku Riv, 2♂,1♀, 875 m, M.S. Polhemus; Kohala Ditch Trail, Honokane Nui Stream, VIII.1956, 2♂,1♀, D.E. Hardy; Kohala Mts, Honopue Val, 9.VI.1970, 1♂,2♀, 666 m, W.C. Gagné; Upper Hamakua, Ditch Trail, 15.VIII.1935, 1♂, R.L. Usinger; Waimea, Waikoloa Stream, 2.XII.1968, 1♂,1♀, 1066 m, along streams, W.C. Gagné. MAUI I: Haipuaena, 29.VI.1920, 1♂,1♀, C.N. Forbes; Haleakala, 1972, 7♂,7♀, 666 m, J.T. Polhemus; Haleakala Natl. Park, Kipahulu Val, 2.VII.1975, 1♂,6♀, 690 m, on rocks in stream, W.C. Gagné; Honomanu, 23.VI.1920, 1♂, E.H. Bryan, Jr.; Kipahulu Val, 18-20.VIII.1967, 1♀, 1250 m, Camp Z, N. Wilson; Upper Hana For. Res. Mid Camp, 4.VIII.1973, 4♂,2♀, 1700 m, Greensword, leaf-litter, F.G. Howarth; T.B.L., 1♂,1♀, Blackburn; Waiakamoi Stream, 24.VII.1968, 1♂, rocks in stream, W.C. Gagné; Waikamoi, VIII.1958, 1♀, 333 m, banana bait, D.E. Hardy; Wailua, III.1901, 1♀, VI.1953, 1♂,4♀, C.R. Joyce, VII.1953, 1♂, Hardy. MOLOKAI I: Honoulimaloo Crk, 2.XII.1933, 1♀, 333 m, F.X. Williams; Kainalu Gulch, 9.IV.1963, 1♀, Hardy; Kamoku, 14.VII.1963, 1♂, D.E. Hardy; Kamoku Flats, 8.10.VII.1968, 9.VII.1968, 2♂,5♀, 1183 m, streams, D.M. Tsuda; Kawela Gulch, 8.10.VII.1968, 2♂,4♀, 1068–1144 m, along streams, W.C. Gagné; Manawainui Val, VIII.1953, 5♂,4♀, D.E. Hardy & M. Tamashiro; Mapulehu, 14.VIII.1936, 15.VIII.1936, 2♂,3♀, R.L. Usinger; Molokai Mts, VI.1896, 1♀, 1333 m, Perkins; MTS, 5.VI.1893, 1♀, R.C.L. Perkins; Pupaakai Stream, 27.VI.1967, 6♂,4♀, ex stream, J. Tenorio; Waikolu, 18.VI.1928, 1♀, A.M. Adamson. OAHU I: Ahuimanu, 24.VII.1929, 1♀, O.H. Swezey; Haleanau, 8.XII.1935, 1♀, along stream, R.L. Usinger, 8.III.1936, 3♀, Usinger; Hauula, 20.IX.1924, 1♂, Swezey; Kahaluu, 4.VII.1935, 2♂, R.L. Usinger; Kalihi Val, 13.III.1937, 1♂, E.C. Zimmerman; Kamiloiki Val, 2.IV.1933, 1♀, under stone, O.H. Swezey; Koolau Mts, SE, X.1917, 1♀, J.C. Bridwell, 12.I.1974, 1♂, in debris at stream, 490 m, F.G. Howarth & E.L. Bousfield; Koolau, NW, 2♀, R.C.L. Perkins; Lanihuli, 3.IX.1917, 1♂,2♀, J.C. Bridwell; Lulumahu streamside, 4.V.1937, 2♀, F.X. Williams; Manoa Falls, 8.IX.1944, 3♀, Y. Tanada; Mt Kaala, 19.I.1945, 2♂, summit 1333 m, Parsons & Werner, VI.1952, same locality, 1♂, M. Adachi, same locality, 3.X.1975, 17♂,17♀, 1200 m under alga mat, F.G.

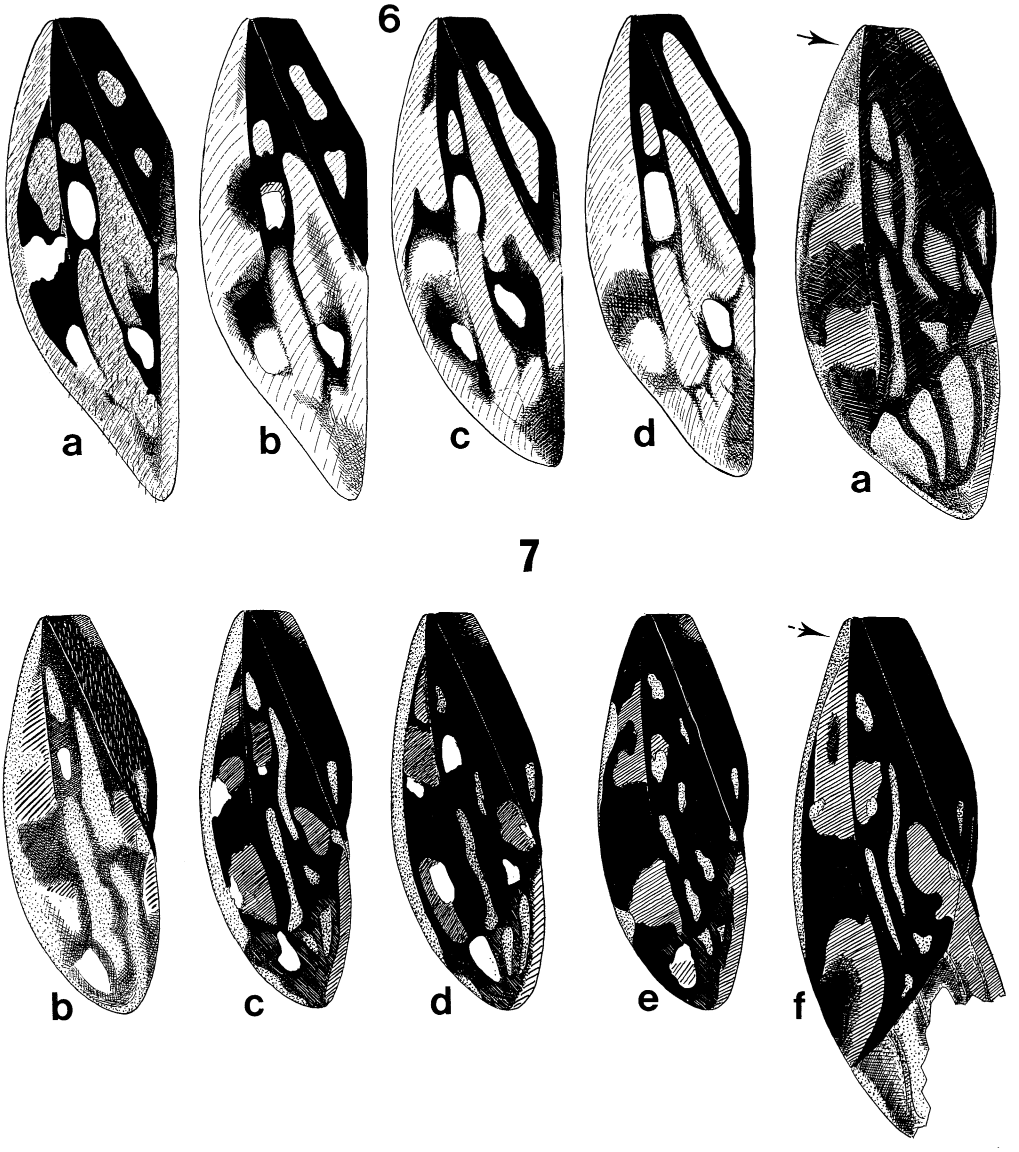


FIG. 6–7. **6.** Left fore wing (strongly semibrachypterous) of *Saldula kauaiensis* arranged in a sequence (a–d) of decreasing dark pigment; the sparse pubescence is only shown in a. **7.** Left fore wing of *Saldula procellaris*: a, lectotype ♀; b–e, eunomy from light to dark of semibrachypterous specimens; f, macropterous wing (membrane broken off).

Howarth; Nuuanu Pali, 28.VI.1917, 12♂,22♀, J.C. Bridwell; Palolo, 29.VI.1917, 1♀, J.C. Bridwell; Punaluu, 1.III.1936, 1♀, R.L. Usinger, 18.X.1936, 1♂,3♀; 2♂, T. Blackburn; Waianae Mts, Palikea Peak, 12.X.1975, 2♀, jumping on trail, F.G. Howarth; Waianae Mts, N side, 29.I.1970, 1♂, below culvert, 1166 m, W.C. Gagné; Waihi

Falls, 29.VI.1935, 1♀, R.L. Usinger; Waihi Nui Falls, 26.I.1936, 6♂,2♀, Life Hist. F_1,F_2, R.L. Usinger; Waiomao, 17.I.1915, 4♂,4♀, H.T. Osborn. KAUAI I: Alakai Swamp: 3.I.1936, 1♀, R.L. Usinger, VIII.1953, 3♂,1♀, 1333 m, D.E. Hardy, 13–17.IX.1965, 2♂,1♀, C.M. Yoshimoto; Alakai Swamp trail, 16.XI.1965, 5♀, 3rd bog, P.D. Ashlock; Alakai Swamp trail C1 1355, 6.III.1973, 3♂,5♀, 1230 m, M.S. Polhemus; Kawaikoi Stream, VIII.1953, 1♀?, 1233 m, D.E. Hardy; Koaie Waialeale Trail, 25.V.1973, 1♂, on rock, A.D. Hart; Kaholuamanu, IV.1895, 1♂, 1333 m, Perkins; Kokee, 24.VIII.1959, 1♀, light trap, J.W. Beardsley; Kokee, Kauaikinana Stream, 9.VI.1919, 4♂,7♀, H.T. Osborn, 10–18.VI.1919, 2♂, H.T. Osborn; Lihue, 11.VIII.1936, 1♀; N Alakai Swamp, 21.VII.1968, 1♀, W.C. Gagné; Wainiha, 20.VIII.1949, 1♂,1♀?, L. Tuthill; Waipoo Falls, VIII.1953, 2♀, D.E. Hardy.

Additional material BMNH. 1♀, no. 25 Haw. Is. (cotype BM label); 1♂ Sandw. Is. 80-13 (cotype BM label).

General remarks. To judge from the many records, *S. exulans* is the most common saldid species occurring on the 5 larger islands of the Hawaiian Archipelago. The localities given above indicate that the species lives in a variety of habitats (sandy or stony shores along rivers, waterfalls, open or protected places), both at low and high elevations. The type-material occurred "sparingly in wet moss in one place on the mountains" (White 1878). Specimens, in particular females, of Oahu and Molokai tend to be somewhat larger (mean 4.4 mm, n=88) than those of Maui and Kauai (mean 4.2 mm, n=42). The species only rarely appears in the full-winged form. Of the about 270 specimens seen, only 2 ♂ from Maui, 1 ♂, 1 ♀ from Molokai, and 3 ♀ from Oahu were macropterous. The predominant state of fore wing reduction is weakly semibrachypterous (membrane ½ reduced), sometimes submacropterous (membrane only slightly reduced, FIG. 1a). These forms are most probably not capable of flight, at least not for long distances. The hind wing is shortened by ⅓ its maximum length and there is no difference in this ratio between populations of the 5 larger islands. Although there is quite a bit of variation in the extent of pale markings on pronotum and hemelytra, this variation occurs alike on all islands; specimens from high elevations, however, are usually darker. A series of specimens from Oahu, Waihi Nui Falls (26.I.1936), are very pale; some are teneral, but others have a solidified cuticle with hardly any dark markings on the fore wing (FIG. 1b). This material is labeled "Life Hist. F1 or F2," from which I conclude that the late Dr Usinger reared these specimens to 2 generations under indoor conditions (possibly lower humidity and higher temperatures than outdoors). The potential eunomic variation of this species may thus be wider than exhibited under natural conditions.

Saldula oahuensis (Blackburn) FIG. 3, 5a, 13, 18, 26, 27d–g, 29a, 31, 39

Acanthia oahuensis Blackburn, 1888, Proc. Linn. Soc. N.S.W. **3** (1): 353, 354.

Acanthia humifera Kirkaldy, 1908, Proc. Hawaii. Entomol. Soc. **1:** 199. **New synonymy.**

Saldula oahuensis: Zimmerman, 1948, Insects of Hawaii, Vol. 3: 223.—Drake & Hoberlandt, 1951, Acta Entomol. Mus. Natl. Pragae **26:** 9.

Saldula humifera: Zimmerman, 1951, Proc. Hawaii. Entomol. Soc. **14:** 336; 1957, Insects of Hawaii, Vol. 6: 191.

Lectotype ♂ (BISHOP 1465), Hawaiian Is, coll. Blackburn (type label with code of 2 black lines meaning Oahu). This species is generally referred to as *S. humifera*. Kirkaldy (1908) described *Acanthia humifera* from Oahu, NW Koolau Range; date and collector name are not indicated. He did not fix a holotype, nor did he mention whether the original material of that locality contained more than 1 specimen. The fact, however, that Kirkaldy gave a variable length of 3–3¼ mm suggests that there was a type-series. I have seen 2 females collected from the type-locality. One is from the Fauna Hawaiiensis Collection (BISHOP), NW Koolau, no date, no collector, antennae missing, with a handwritten label which might be deciphered as "ind. type." The 2nd specimen from the BMNH collection bears the data "NW Koolau, V.1901, Perkins (Sandw. Isl. 193-323)"; it has a British Museum (BMNH) type label. These 2 specimens agree with the lectotype of *S. oahuensis*. The shape and pigmentation of the left fore wing of the female in the BMNH is shown in FIG. 3a.

Description

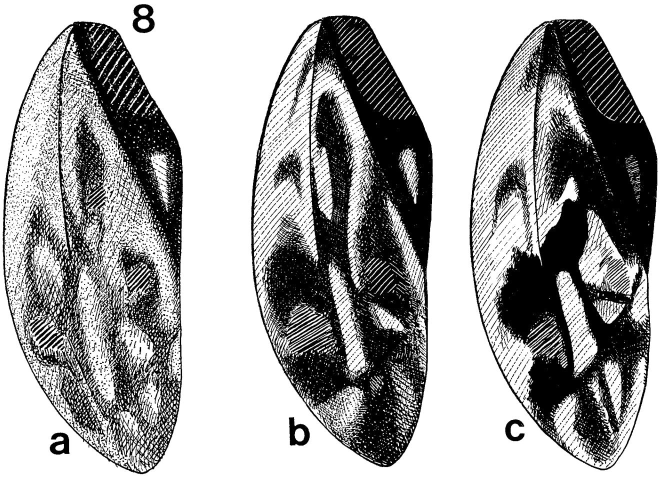
General characteristics. Small, mostly semibrachypterous, not shiny, dense pubescence on pronotum, highly variable wing design (FIG. 3a–h), with extensive indistinct pruinose areas in dark individuals (hatched in FIG. 3f–h).

Head. Dark brownish or black with location of pale areas as indicated in FIG. 5a (the drawing is of a very pale specimen; extent of light spots may be less in other specimens), buccula black or with pale front margins, vertex coarsely punctate, with dense golden pubescence. Rostrum brown, extending beyond hind coxae. Antennae unicolorous pale or dark brown, hairs of 2nd segment not longer than diameter of segment. *Thorax.* Pronotum entirely black, punctate, with golden pubescence, lateral margin inflexed in anterior part (FIG. 18a). Ventral side of thorax inclusive of acetabulae black, shiny, with silver hairs. *Wings.* Central area of clavus without hairs. Hemelytra in the great majority of specimens semibrachypterous, variation of brown pigment distribution as in FIG. 3a–g. The lightest extreme (FIG. 3b) has not only the apical light spot on the clavus but also a pale proximal area; the corium of this specimen is completely pale with a vaguely darker part in the middle of the boundary between corium and membrane (indicated with a star). The always dark condition of this area characterizes the eunomy of this species. The internal proximal edge of the clavus with indistinct leaden hue. Four specimens of the total of about 150 have a wing design with more contrasting transverse light fasciae (FIG. 3g). This picture deviates from the regular eunomic series, but the 4 individuals belong to syntopic populations with more usual wing pattern. Length of hind wing in semibrachypterous individuals is variable (FIG. 20d). The hemelytra of the only 3 macropterous specimens (2♀,1♂) fit the dark extreme of the eunomy (FIG. 3h). *Legs.* Apical part of coxae and trochanter white; femora with a wide dark median band, very clear in dark specimens, indistinct or even absent in the palest animals; in the latter specimens the proximal part is always lighter than the remainder of the femur; tibiae more or less brownish, proximal and distal part light; 2nd tarsal segment light, 3rd segment brownish. *Abdomen.* Black or light brownish, subgenital plate broadly truncate caudally (FIG. 14). Parandria, paramere, spermatheca and ovipositor as depicted in FIG. 27d–g, 31, 26, 29a, respectively.

Measurements. Mean length of 20 semibrachypterous ♂, 3.02 mm (min 2.80, max 3.20); width, 1.52 mm (1.41, 1.65); length of 20 semibrachypterous ♀, 3.46 mm (3.25, 3.70); width, 1.81 mm (1.64, 2.00). Two macropterous ♀ vary from 4.3–4.4 mm in length and 2.0–2.1 mm in width; the single macropterous ♂ measures 4 by 1.9 mm.

Specimens examined. HAWAIIAN IS. HAWAII I: Akaka Falls, 28.XI.1968, 1♀, ex stream, J.M. Tenorio, 15.III.1973, 3♂,3♀, 335 m, M.S. Polhemus; Hilo, Wailuku

Riv, 11.III.1973, 2♀, M.S. Polhemus; Hualalai, 31.VII.1929, 1♀, 1333 m, F.X. Williams; Kaiholena Ridge, VIII.1952, 1♀, 766 m, W.C. Mitchell; Kalopa State Park, 15.III.1973, 3♂, M.S. Polhemus; Kil. (?), VII.1906, 2♂,2♀, caught running high on the wet barks of tree trunks, R.C.L. Perkins; Kipuka on Saddle Rd, 30.XI.1968, 1♂, W.C. Gagné; Kohala Mts, 31.VII.1958, 1♂, 633 m, L.W. Quate; Kohala Mts, Hamakua Ditch Trail, 3.XI.1919, 1♀, O.H. Swezey; Kohala Mts, Honopue Val, 9.VI.1970, 1♂, rotting *Cheirodendron trigynum,* W.C. Gagné; Olaa, 7.VII.1918, 2♀, 766 m, W.M. Giffard; Upper Hamakua Ditch Trail, 14.VIII.1935, 2♂,1♀, beating from fern, fronds etc., 15.VIII.1935, 5♂,3♀, R.L. Usinger, 16.VIII.1935, 1♀, R.L. Usinger; Waikoloa Stream above Waimea, 2.XII.1968, 1♂, 1066 m along stream, W.C. Gagné. MAUI I: Haeleau, 18.XII.1928, 1♂, 1000 m, N.M. Walker; Haipuaena, 30.VI.1920, 1♂, E.H. Bryan; Haleakala, 3.II.?, 1♀, 1000 m, Fauna Hawaiiensis Coll., 1♂; Kaulalewelewe-Puukukui Trail, 18.II.1970, 1♀, 900 m, on mossy trunk, W.C. Gagné. LANAI I: Haalelepaakai, VII.1894, 1♂, Perkins; 29.XI–3.XII.1935, 1♂,1♀, R.L. Usinger. MOLOKAI I: Kamiloloa, 22.VI.1928, 2♂, 1000–1166 m, A.M. Adamson; Kamoku, 14.VII.1963, 1♀, D.E. Hardy; Kawela, 23.XII.1925, 1♀, 1233 m, E.H. Bryan; Makakupaia, 21.VI.1928, 1♂,2♀, 1000–1166 m, A.M. Adamson; Manawainui, VIII.1953, 1♀, D.E. Hardy; nr Waikolu, XI.1902, 2♀, 1333 m, wet forest, R.C.L. Perkins, 1909, 1♀, D.T. Fullaway. OAHU I: Hauula, 2.IX.1914, 1♂, 20.IX.1924, 1♂, O.H. Swezey; Kaala Mts, I.1893, 1♀, 333 m, R.C.L. Perkins, III.1893, 1♀, 666 m, Perkins, 6.II.1935, 1♀, beating, E.C. Zimmerman, 6.III.1938, 1♂, beating, Zimmerman, 14.I.1945, 3♀, 1333 m, C.T. Parsons, 25.III.1945, 1♀, 833 m, Parsons, VI.1951, 2♀, on mossy rocks, Ford, IV.1952, 6♂,3♀, D.E. Hardy, IV.1952, 2♂,1♀, M.S. Adachi; Kaluanui Val, 22.II.1931, 1♂, 666 m, F.X. Williams, 1950, 1♂,3♀, on rocks in stream, W.C. Gagné; Kawaihapai, 29.IV.1951, 1♂, M. Tamashiro; Kawailoa Ridge, 2.X.1934, 1♂, Swezey; Koolau Mts, 12.I.1974, 1♂, 490 m, in debris at stream margin, F.G. Howarth & E.L. Bousfield; Lanihuli, 18.VII.1920, 1♀, Bryan; Mokuleia, Kapuna Val, 11.IV.1936, 5♂,4♀, R.L. Usinger; Mt Tantalus, V. 1953, 1♂, D.E. Hardy, 1.VI.1955, 7♂,2♀, J.L. Herring, 1.VIII.1968, 1♀, forested area, W.C. Gagné; NW Koolau, 1♀; Poamoho Stream, 12.I.1974, 1♂, 490 m, wet meadow, W.C. Gagné & S.L. Montgomery; Poamoho Trail, 15.IX.1974, 2♀, 333 m, on muddy trail, W.C. Gagné; Punaluu, 1.III.1936, 1♀, R.L. Usinger; Schofield-Waikane Trail, 28.IV.1938, 1♂, 833 m, E.C. Zimmerman; Puu Kanehoa, 10.VIII.1959, 1♀, beating shrubbery, J.W. Beardsley; Mt Tantalus, 8.III.1931, 1♂, on rocks, etc., F.X. Williams; Waialae Iki, 19.IX.1920, 1♂,1♀, O.H. Swezey; Waianae Mts, 1♀, J.F. Illingworth; Waianae Mts, N side Kaala Mt, 29.I.1970, 1♂, below culvert 1066–1166 m, W.C. Gagné; Waianae Mts, Palikea, 11.XI.1936, 1♀, beating, E.C. Zimmerman, 11.XI.1936, 3♀, 1000 m, F.X. Williams. KAUAI I: Alakai Swamp, 3.7 km E of Waialeale, 3.I.1974, 2♂,7♀, 1500 m, open areas of bog, W.C. Gagné; Alakai Swamp trail, 6.III.1973, 3♀, M.S. Polhemus; Kokee, Alakai Swamp trail, Kawaikoi Ridge, 18.VIII.1961, 1♂,1♀, tree ferns, R.L. Usinger; Alakai Swamp trail, 15.IX.1965, 1♂, J.W. Beardsley; Alakai Swamp trail, Waineke Swamp, 22–25.VII.1968, 1♀, in moss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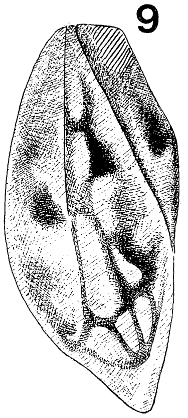
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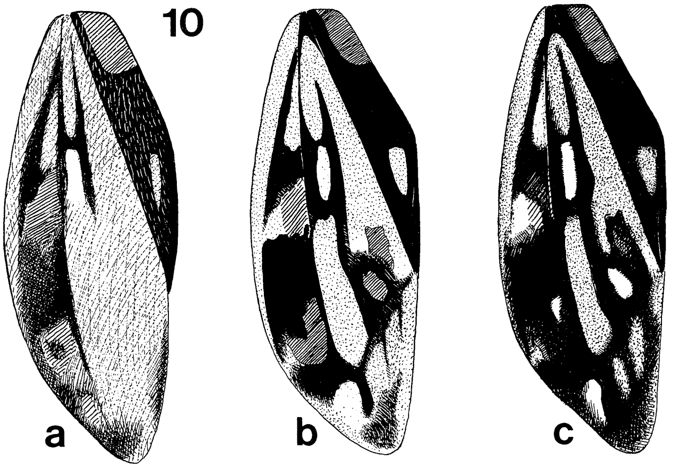
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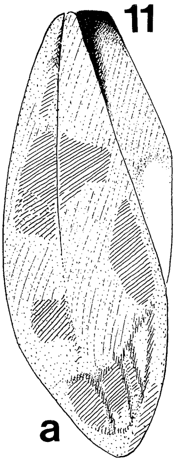
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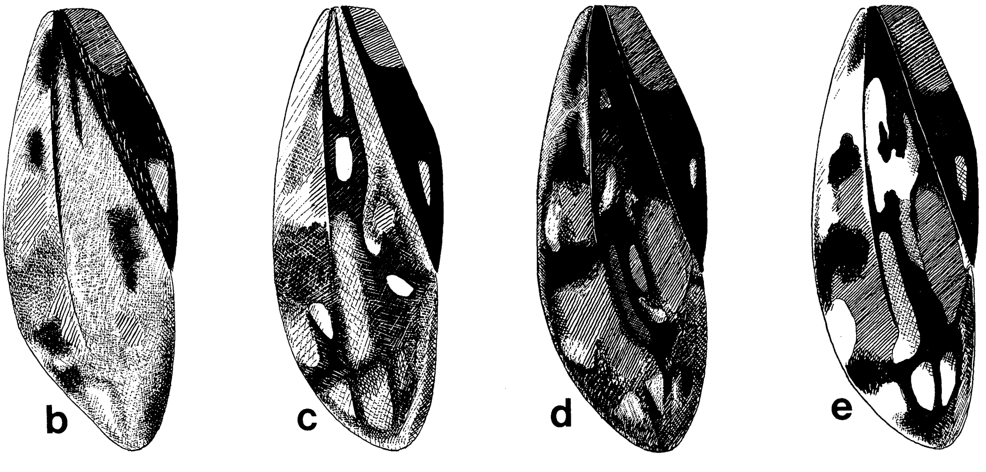
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on trees, W.C. Gagné; Kaunuohua Ridge, 21.VII.1937, 1♀, under logs, E.C. Zimmerman, 22.VII.1937, 1♀, beating, Zimmerman; Koaie-Waialeale Trail, 25.VIII.1970, 1♂, 1166 m, in moss on trees, W.C. Gagné; Kokee, 15.II.1934, 1♀, E.C. Zimmerman, 23.VII.1937, 1♂,1♀, Zimmerman; nr Halemanu, 10.VIII.1937, 1♂, ex reservoir, E.C. Zimmerman; Pole Line Trail, nr Kualapa, 28.VIII.1970, 2♂,2♀, 620 m, on mossy trunk, W.C. Gagné; Wainiha Val, VIII.1953, 1♀, D.E. Hardy.

General remarks. Saldula oahuensis is the second species in sequence of abundance as shown by the 160 specimens before me from more than 50 localities on all 6 major islands. The large measure of eunomic variation bears no apparent relation to different islands or single localities. Samples of a certain size harbor generally light and dark specimens. Populations on the island of Hawaii tend to be generally darker than populations on other islands. Three specimens (1♂,2♀ from Hawaii I, Kohala Mts, Kohala Ditch Trail, on mossy embankment, 660 m, 9–13.IV.1970, W.C. Gagné) offered some difficulties to me. The 3 specimens do not have a typical *oahuensis* facies; they have a similar wing design, resembling somewhat *S. longicornis*; the antennae superficially seem longer, but the ratio of antennal length to pronotum length definitely falls outside the range of *S. longicornis* and within that of *S. oahuensis.* Provisionally I consider the 3 specimens to be *S. oahuensis*; additional material is needed to decide whether we deal here with an isolated population.

The species is nearly always flightless. The total of 3 macropters originate from Molokai I (Kamoku, 14.VII.1963); Hawaii I (Hualalai, 1333 m, 31.VII.1929); and Lanai I (Haalelepaakai, VII.1894).

S. oahuensis seems to have a wide ecological tolerance and occurs at elevations between 300 and 1500 m. It was sampled from a variety of habitats on soil level, such as along streams, on rocks in streams, debris, muddy trail, forest litter, moss and open areas of bog (1500 m). There are also 17 records from above soil level (moss on trees, beatings from shrubbery).

Saldula procellaris (Kirkaldy) FIG. 5b, 7a–f, 15, 20c, 32, 36

Acanthia procellaris Kirkaldy, 1908, Proc. Hawaii. Entomol. Soc. **1:** 200.

Saldula procellaris: Zimmerman, 1948, Insects of Hawaii, Vol. 3: 224; 1951, Proc. Hawaii. Entomol. Soc. **14:** 336; 1957, Insects of Hawaii, Vol. 6: 192.—Drake & Hoberlandt, 1951, Acta Entomol. Mus. Natl. Pragae **26:** 10.

Lectotype ♀. Kirkaldy (1908) described the species from Molokai, 4000 ft (1333 m); sex, data and collector were not indicated. He did not fix a holotype nor did he mention whether the original material contained more than 1 specimen. He mentioned 3.5 mm for the length of the species. I studied 1 ♀ from the Molokai Mts, 1333 m, VI.1896, which might represent the original insect or one of the original

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←
FIG. 8–11. Left fore wings: **8,** *Saldula longicornis* (a, holotype ♂); **9,** *Saldula nubigena,* lectotype ♂; **10,** *Saldula usingeri*; **11,** *Saldula intermedia.*

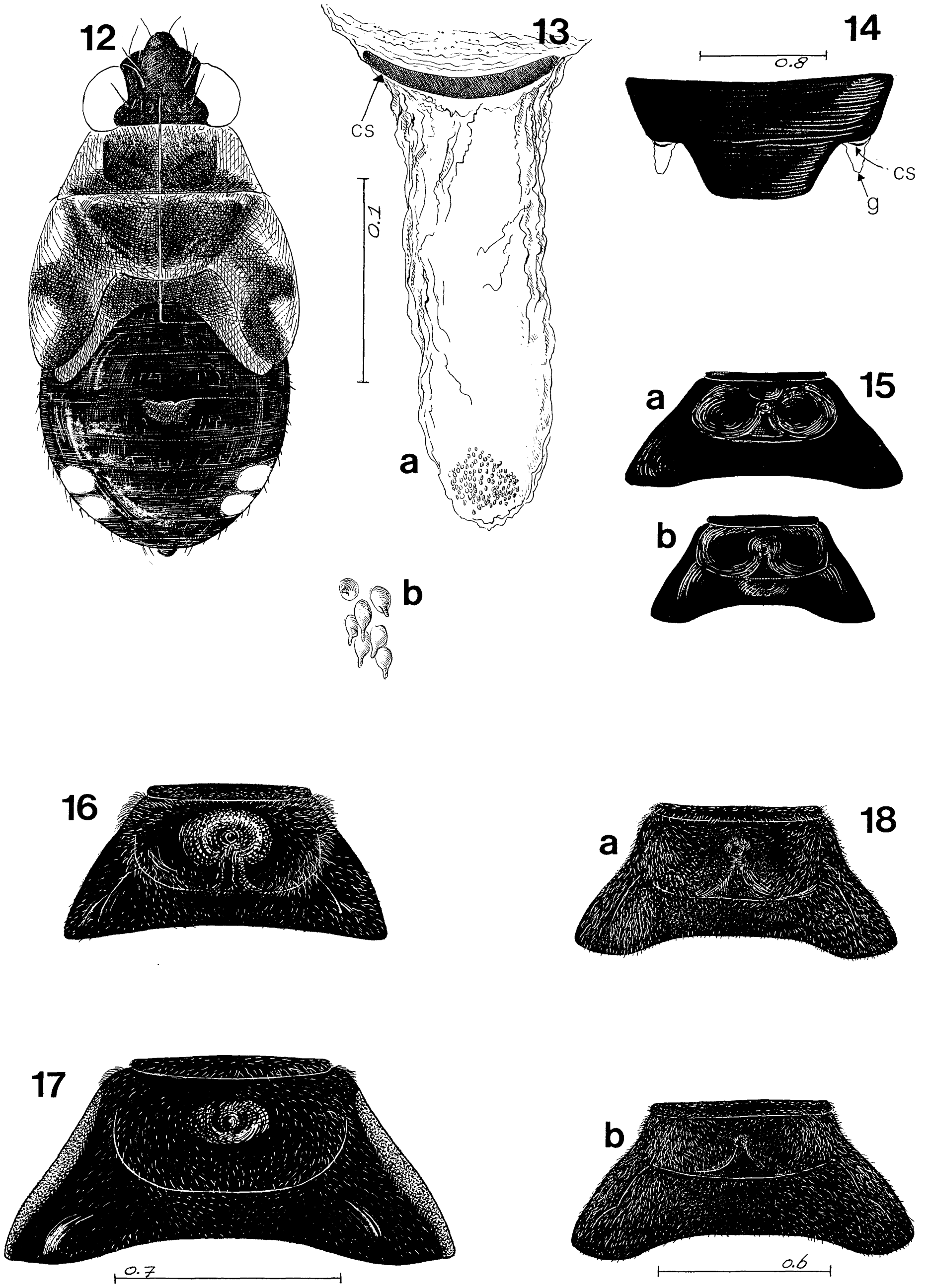


FIG. 12–18. **12.** Last larval instar of *Saldula exulans*. **13.** *S. oahuensis*, ♀: a, extruded pregenital gland, fixed in alcohol 70% (cs = crescent-shaped sclerite); b, some excretory gland-cells. **14.** *S. oahuensis*, subgenital plate of ♀ with extended glands (cs = crescent-shaped sclerite, g = gland). **15.** Pronotum of *S. procellaris*: a, macropterous; b, semibrachypterous. **16.** Pronotum of semibrachypterous *S. longicornis*. **17.** Pronotum of semibrachypterous *S. exulans*. **18.** Pronotum of *S. oahuensis*: a, semibrachypterous; b, macropterous.

series. It bears a BMNH type label and I selected it as lectotype, having added a label to that effect under the specimen. The lectotype is deposited in the British Museum. Its wing shape and picturation are shown in FIG. 7a.

Description

General characteristics. Small, mostly semibrachypterous, head and pronotum shiny, more sparsely pubescent and generally with darker wing pigment than the previous species; pruinose areas of wing often strikingly bluish.

Head. Black with pale areas as in FIG. 5b, vertex finely punctate, buccula pale with brown anterior margin, rarely entirely dark brown. Rostrum light brownish, reaching apex of hind coxae or extending beyond it. Antennae unicolorous brown, 1st segment often more pale, last segment sometimes with light apex. *Thorax.* Pronotum entirely black, shiny and smooth, with only sparse adpressed pubescence; lateral margin straight or slightly convex, anteriorly only weakly concave: note the pronotal differences between the rare macropterous (FIG. 15a) and the common semibrachypterous form (FIG. 15b). Acetabula black, apex sometimes with light margin. *Wings.* Clavus uniformly covered with fine, short hairs without a bare central area. Hemelytra in all but 1 specimen with strongly reduced membrane (slightly more than in *S. oahuensis*); some pigment variations are depicted in FIG. 7a–e. Length of hind wing in semibrachypterous individuals reaching level of scutellum apex or slightly beyond that level. The only macropterous specimen, a female with damaged membrane, is from Molokai (Kamoku Flats, 9.VII.1968); its left fore wing is drawn in FIG. 7f. Proximal part of exocorium generally narrow, both in short-winged and long-winged forms (arrow in FIG. 7a, f; in majority of specimens of *S. oahuensis,* anterior edge of exocorium wider than adjacent part of endocorium, compare with FIG. 3a, h). *Legs.* Coxae black with light apex. Legs light brown, apex of tibiae white; sometimes midpart of femur infuscate and proximal part white. *Abdomen.* Black, sometimes light brownish. Subgenital plate broadly truncate distally, dark with apical ½ white. Parandria almost as in previous species (FIG. 27d, e), paramere somewhat variable (FIG. 36a–c).

Measurements. Mean length of 16 semibrachypterous ♂, 3.02 mm (min 2.85, max 3.20); width, 1.49 mm (1.40, 1.58). Length of 12 ♀: 3.41 mm (3.15, 3.60); width, 1.76 mm (1.63, 1.90).

Specimens examined. HAWAIIAN IS. HAWAII I: Humuula Trail, Mauna Kea, 13.XI.1936, 2♂, E.Y. Hosaka; Kohala Mts, Honopue Val, 9.VI.1970, 1♂, 666 m, W.C. Gagné; Nauhi Gulch, X.1931, 2♀, 1666–2000 m, creek pool, O.H. Swezey & F.X. Williams; 34 km from Olaa, 4.VII.1918, 1♂, 1666 m, W.M. Giffard. MAUI I: Haleakala Natl. Park, Kipahulu Val, 2.VII.1975, 3♂,3♀, 690 m, on rocks in stream, W.C. Gagné; Kula Pipe Line, VII.1956, 1♂,2♀, 1400 m, D.E. Hardy; VII.1956, 1♀, 1300 m, R. Namba; Waikapu Val, 23.III.1924, 1♀, O.H. Swezey. LANAI I: Lanai, XII.1893, 1♀, 666 m, R.C.L. Perkins, 3.XII.1935, 2♀, in stream, R.L. Usinger, MOLOKAI I: above Waikolu Val, 28.IV.1955, 1♂, 1400 m, C.R. Joyce, 1.V.1955, 1♂,2♀, Joyce, 2.V.1955, 2♂, 1400 m, Joyce; Kainalu Gulch, 9.IV.1963, 1♂,1♀, D.E. Hardy; Kamoku, 19.VII.1963, 2♀, D.E. Hardy; Kamoku Flats, 9.VII.1968, 2♂,7♀, stream, D.M. Tsuda; Manawainui Val, VIII.1953, 1♂,2♀, D.E. Hardy, VIII.1953, 1♀, M. Tamashiro; Mapulehu, 14.VIII.1936, 3♂, R.L. Usinger, 15.VIII.1936, 6♂, Usinger, 5.XI.1947, 1♀, on rocks, nr stream, N.L.H. Krauss; Pepeopae, 30.VII.1959, 3♂, 1333 m, D.H. Habeck; Puu Kolekole, VII.1953, 1♀, 1200 m, D.E. Hardy, 30.VII.1959, 1♂,1♀, Hardy, 19.VII.1963, 1♀, 1333 m, Hardy. OAHU I: Konahuanui, 9.V.1943, 1♂, 866–1000 m, beating shrubbery; Lulumahu Canyon, 11.X.1936, 1♂,1♀, banana grove, 466 m, F.X. Williams; Lulumahu streamside, 9.V.1937, 1♀, F.X. Williams; Manoa Falls, VIII.1955, 2♀, D.E. Hardy; Manoa Val, I.1952, 2♂, M.S. Adachi; Mt

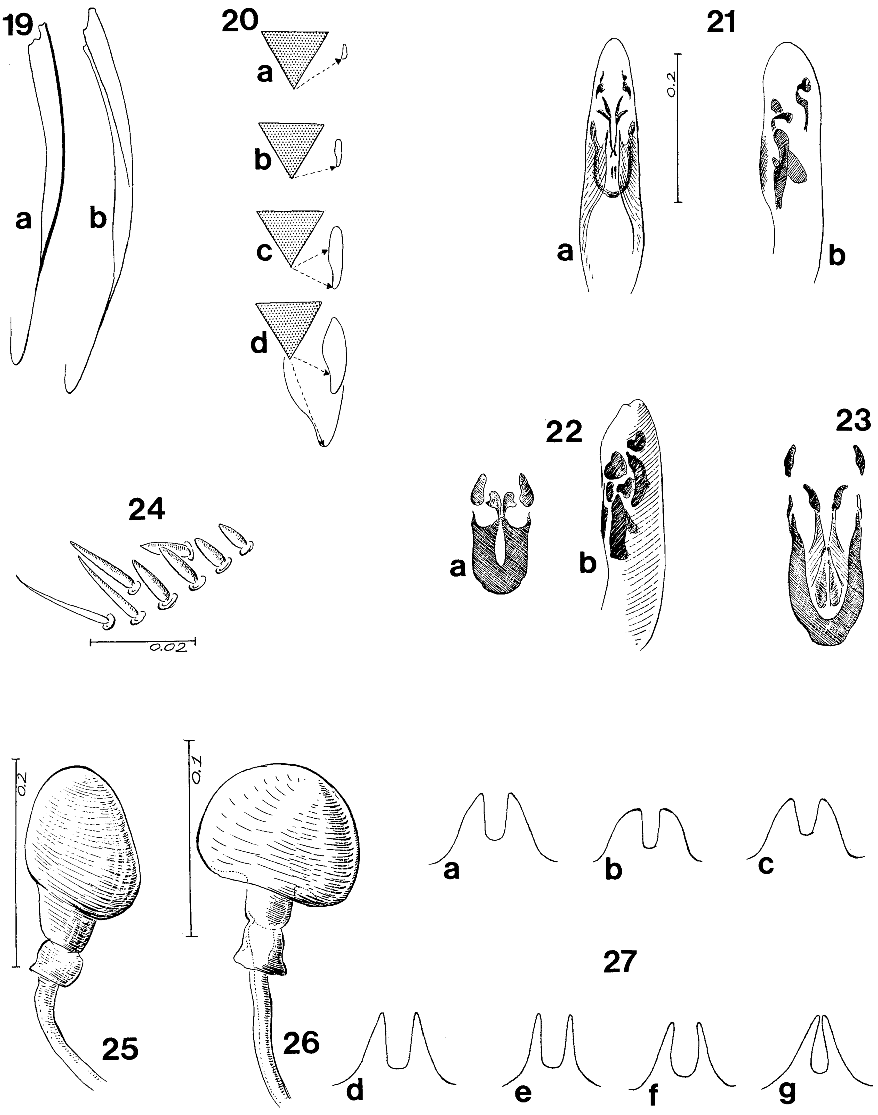


Fig. 19–27. **19.** Lateral view of fore wing with subcostal fold: a, all Hawaiian species except *S. exulans*; b, *S. exulans* (note that only *S. exulans* possesses an oblique ridge; compare also semibrachypterous with macropterous forms, Fig. 2b, c). **20.** Scutellum (shaded) and rudiment of hind wing (right) of semibrachypterous specimens (see text) (arrows indicate variations of wing length in relation to the apex of the scutellum): a, *S. nubigena*; b, *S. longicornis* and *S. usingeri*; c, *S. kauaiensis* and *S. procellaris*; d, *S. oahuensis* and *S. intermedia*. **21.** Phallotheca and endosomal sclerites of *S. exulans*: a, front view; b, left lateral view. **22.** Endosomal sclerites of *S. kauaiensis*: a, front view of median sclerite; b, left lateral view through phallotheca. **23.** Median sclerite of *S. exulans*, a specimen other than that in Fig. 21. **24.** Part of the ♂ grasping plate of *S. exulans* (the plate contains about 18 spines of which only those facing the abdominal tergites are shown). **25.** Spermatheca of *S. exulans* (potash treatment). **26.** Spermatheca of *S. oahuensis*. **27.** Variations in parandria: a–c, *S. longicornis*; d–g, *S. oahuensis*.

Olympus, 26.VII.1936, 1♀, 666–800 m, no water, F.X. Williams; Mt Tantalus, 12.V.1955, 1♂,1♀, J.L. Herring, 24.V.1955, 7♂,7♀, Herring, 1.VI.1955, 1♂,2♀, Herring, VI.1955, 3♂, nut ridge, R. Namba; Nuuanu Pali, 28.VI.1917, 1♀, J.C. Bridwell; Palolo, 29.VI.1917, 3♂,5♀, J.C. Bridwell, 26.II.1922, 2♂,1♀, O.H. Swezey; Schofield-Waikane Trail, 28.VI.1938, 1♂, 833 m, under stones, E.C. Zimmerman; Waianae Mts, V.1939, 1♀, T. Yoshida; Waihi Falls, 29.VI.1935, 2♀, R.L. Usinger; Honolulu, Manoa, Waihiki Val, 17.IX.1933, 1♂,1♀, F.X. Williams; Waihi Nui Falls, 26.I.1936, 1♂,1♀, R.L. Usinger.

General remarks. This species is rather widely distributed (more than 100 specimens from some 30 different places), although apparently less common than the previous 2 species. It has not yet been found on Kauai. The few locality descriptions refer to such habitats as streams, on or under stones, and on shrubs, between 466–1400 m. *S. procellaris* is of the same size as *S. oahuensis,* but the male is slightly more slender [ratio mean length/mean width is 1.99 in *S. oahuensis* (n=20) and 2.03 in *S. procellaris* (n=16)]. Specimens from the same locality are rather uniform, contrasting with the more variable *S. oahuensis.* Individuals from Molokai, Pepeopae, 1333 m, have a very contrasting dark wing picturation with 5 ivory-white spots (FIG. 7d). The parameres of this population (FIG. 36c) are also slightly different from others (FIG. 36a, b), but it seems useless to subdivide this species into intraspecific taxonomic categories.

Saldula intermedia Cobben, **new species** FIG. 11a–e

In size and general facies, this taxon is so close to *S. oahuensis, S. procellaris* and the species described hereafter, that I refrain from giving a formal lengthy diagnosis. Only the specific differences are stressed here. *S. intermedia* exhibits more or less a mosaic of the characters of *S. oahuensis* and *S. procellaris* with respect to cuticular sculpturing of pronotum and scutellum, pubescence, and hemelytral eunomy. Pronotum shape (straight lateral margins), shininess, and sparse pubescence of thorax are more like those of *S. procellaris.* The hair-covering of the clavus (lacking in the central field, FIG. 11b) and the variation of fore wing design and its eunomy (FIG. 11a–e) are more like that of *S. oahuensis.* However, the dark pigmentation in the lightest extremes starts from the distal exocorial part in *S. intermedia* (FIG. 11a, b), and from the distal part between mesocorium and membrane in *S. oahuensis* (FIG. 3b, c). In 7 of the 22 specimens of *S. intermedia,* the anterior ½ of the corium has a more or less transverse light pattern of varying extent (FIG. 11e), which occurs sometimes also in *S. oahuensis* (FIG. 3g). The strip of the corium bordering the clavus tends to remain lightish in *S. intermedia* to a greater extent than in *S. procellaris* (compare FIG. 11c with FIG. 7b). The pruinose areas on the fore wing of dark specimens of the new species are bluish as in *S. procellaris,* whereas they are lead-colored in *S. oahuensis.* The coloration of femur 1 of *S. intermedia* is more like that of *S. procellaris,* namely, unicolorous pale and only in a few specimens fuscous in the midregion (conditions in *S. oahuensis* are

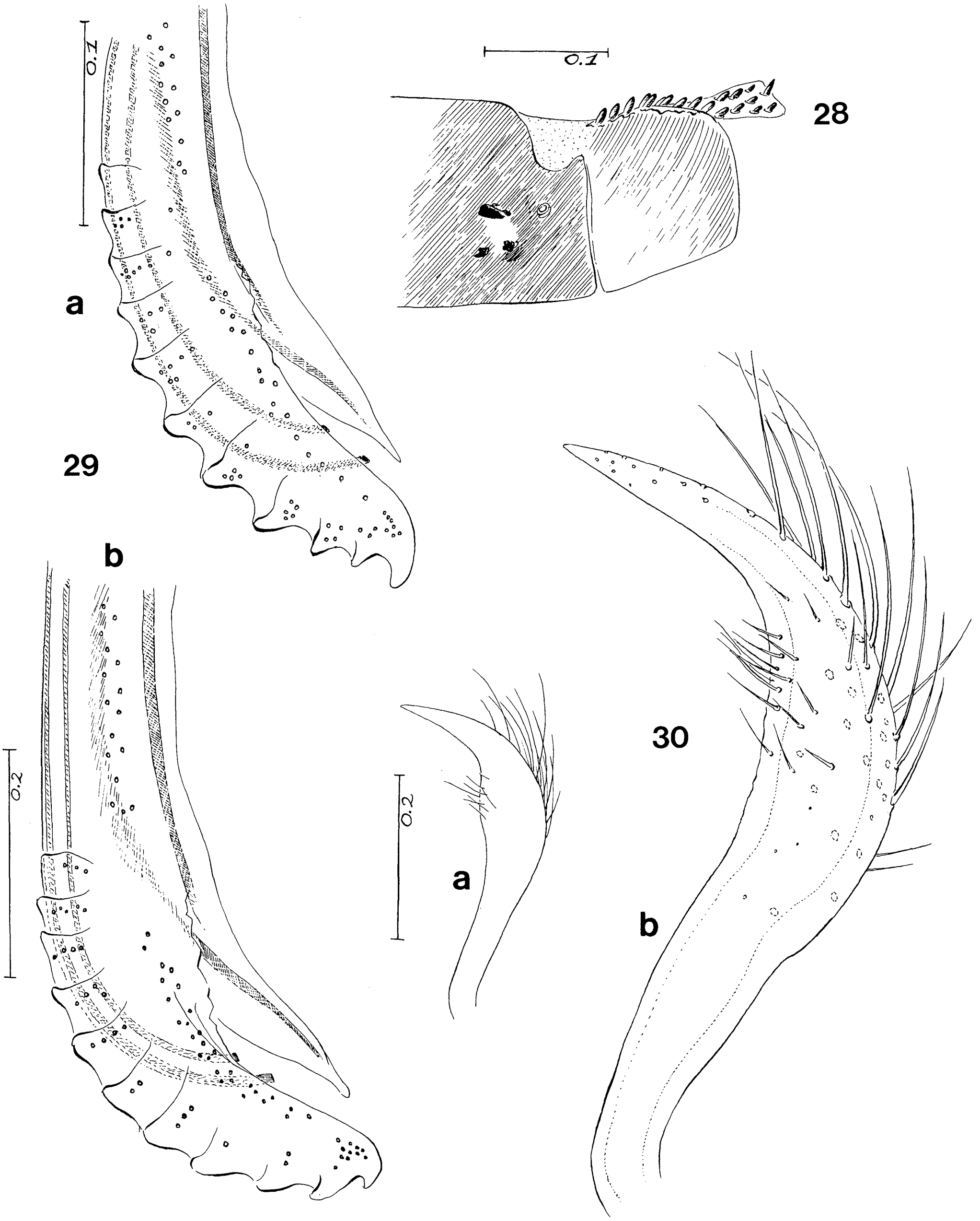


FIG. 28–30. **28.** Left lateral part of 3rd abdominal sternite and connexivum with rudiments of larval organ, stigma and grasping plate; ♂ of *S. kauaiensis.* **29.** Apex of 1 blade of the ovipositor (small circles represent sensilla): a, *S. oahuensis*; b, *S. exulans.* **30.** Left paramere of *S. exulans*: a, at lower magnification; b, at high magnification (small circles represent sensilla; larger, interrupted circles represent implantations of spines on the opposite surface).

the reverse). Genital structures are not helpful in discriminating species of this complex. Only semibrachypterous specimens of *S. intermedia* have been collected so far.

Measurements. Holotype (♂): length, 2.81 mm; width, 1.40 mm. Mean length of 8♂, 2.94 mm (min 2.8, max 3.3); width, 1.41 mm (1.35, 1.45). Length of 14 ♀: 3.37 mm (3.0, 3.7); width, 1.68 mm (1.61, 1.8).

Holotype ♂, HAWAIIAN IS: OAHU I, Mt Kaala, 18.VII.1968 (Bishop 11,415). Paratypes as follows. HAWAIIAN IS. OAHU I: Mt Kaala, 8.XII.1935, 2♂, R.L. Usinger; 3.I.1925, 1♀, Swezey; III.1954, 1♂, Ford; 14.IV.1966, 2♂,2♀, P.D. Ashlock & C. Yoshimoto; 31.I.1968, 1♀, in moss on trees, D.M. Tsuda; 18.VII.1968, 2♂,1♀, in moss on trees, W.C. Gagné. HAWAII I: Olaa, Glenwood, 3.IX.1917, 1♀, 766 m, W.M. Giffard; Olaa, 34 km from Hilo to Volcano, 8.VII.1918, 1♂,2♀, 766 m, W.M. Giffard; 29.VIII.1919, 1♀, 766 m, Giffard. MAUI I: Hana Forest Reserve, 17.III.1974, 1♀, 1375 m, on mossy tree, W.C. Gagné; Hanaula, 10.VII.1960, 1♀, 1333 m, J.A. Tenorio; Kipahulu Val Camp, 2,13–17.VIII.1967, 1♀, 1250 m, N. Wilson; Waikamoi, 16.VI.1965, 1♀, J.W. Beardsley.

Holotype in the Bishop Museum; paratypes there and in the collection of the University of Hawaii; the Hawaii State Department of Agriculture, Department of Entomology; California Academy of Science; the Polhemus collection; and the author's collection.

General remarks. Since the degree of differences between *S. intermedia* on the one hand and *S. oahuensis* and *S. procellaris* on the other hand are so small, one wonders whether *S. intermedia* is not just a taxon of intraspecific level of 1 of these 2 species. Initially I hesitated to describe it as a valid species and was rather inclined to attribute to it a subspecific rank of *S. oahuensis,* with which it shares the lack of pubescence in the center of the clavus. However, its occurrence on 3 islands, where it apparently possesses a niche different from the other species, favors its warranting the status of species. Most of the material of *S. intermedia* was collected in 5 different years from Mt Kaala, Oahu. There are no collections of *S. procellaris* from that area, and the few records of *S. oahuensis* from Mt Kaala originate from dates which are different from the *S. intermedia* records. I suppose, therefore, that *S. intermedia* and *S. oahuensis* occur on Mt Kaala at separate sites. On Hawaii, *S. intermedia* and *S. oahuensis* are recorded from the same elevation at Olaa, but not the same date. Unfortunately, exact small-scale topographic descriptions, which might reveal discrepancies in the ecological demands of the 3 species, are lacking. Three of the 13 different locality labels mention an association with moss on trees, the remaining 10 labels give no indication of habitats whatsoever. The widely distributed *S. oahuensis* has been mentioned 4 times from moss on trees, but many more records refer to a wide variety of substrates. It may thus be that *S. intermedia* is better adapted than any other species to live in the overstory, but we have not yet enough proof for this idea.

Another possibility to explain the position of *S. intermedia* as more or less intermediary between *S. oahuensis* and *S. procellaris* is to consider it a hybrid of the latter 2 species. This is very unlikely for the following reasons. *S. oahuensis* and *S. procellaris*

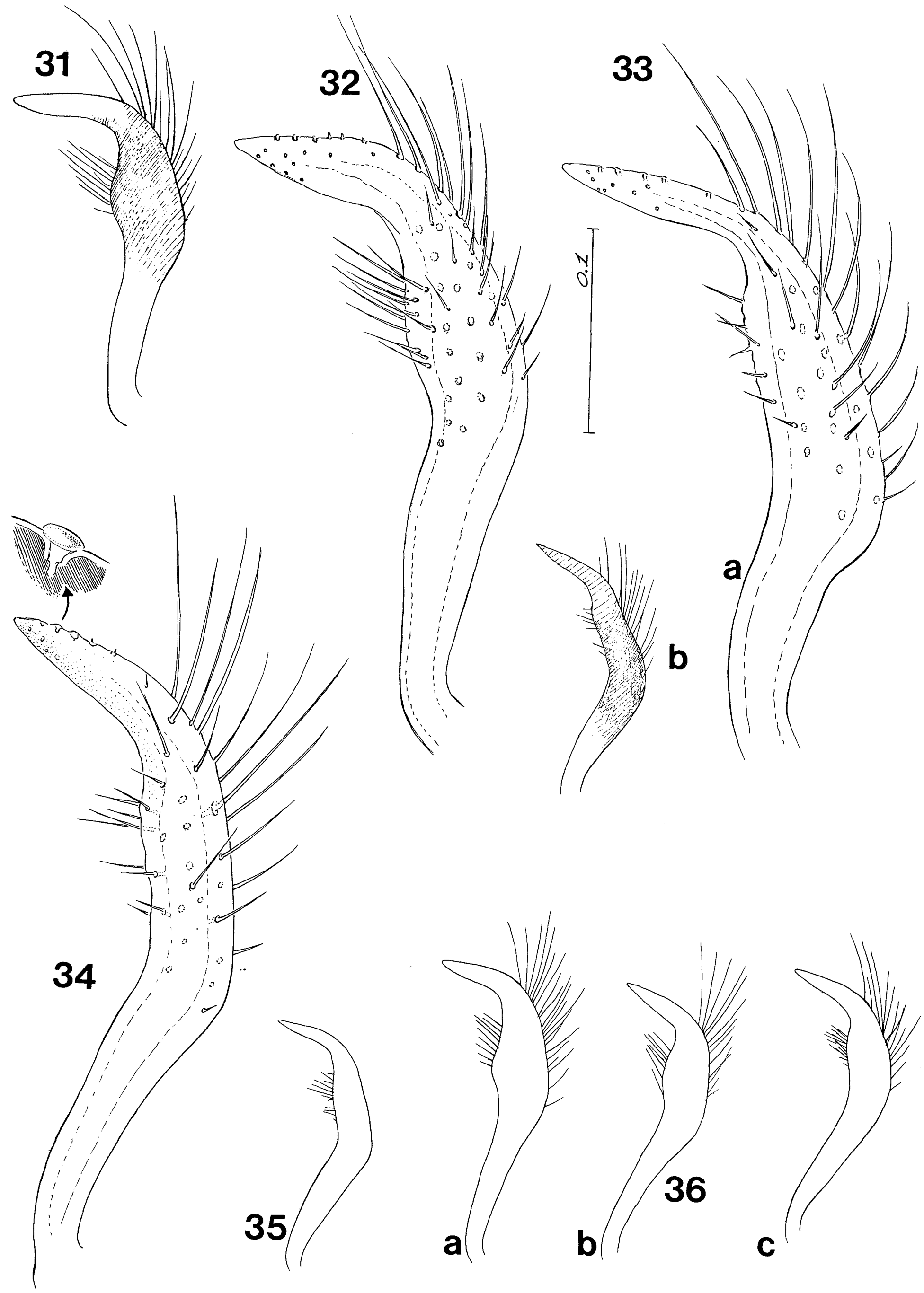


FIG. 31–36. Left parameres: **31,** *S. oahuensis*; **32,** *S. procellaris*; **33,** *S. longicornis* (a, b, different specimens); **34,** *S. kauaiensis* (arrow shows 1 sensillum in optical section); **35,** *S. nubigena* (lectotype); **36,** *S. procellaris* (a–c, specimens from different localities).

are clearly and easily defined species which were collected syntopically at some localities on Hawaii, Lanai and Oahu. The differences between both species are greater than between some of the sibling pairs described from the continents, e.g., *Saldula saltatoria* L. and *S. fucicola* J.Sb. in Europe, which remained reproductively isolated under experimental conditions (personal observations). There are many more sympatric siblings within Saldidae behaving in the field as separate populations over wide geographic areas. Eventual introgressive hybridization between the much more well-demarcated *S. oahuensis* and *S. procellaris,* with a resulting mosaic pattern of parental character states, seems to me very improbable. Examples of interspecific hybridization in animals are mostly associated with newly created or disturbed habitats (Ross 1974). This certainly does not apply to the stable environments which prevail in the localities in the Hawaiian Is favored by saldids. The fact that *S. intermedia* is found now on 3 islands, so far only in the flightless state, indicates its stable integrity as an independent taxon which probably was more widely distributed in the past.

Saldula usingeri Cobben, **new species** FIG. 10a–c

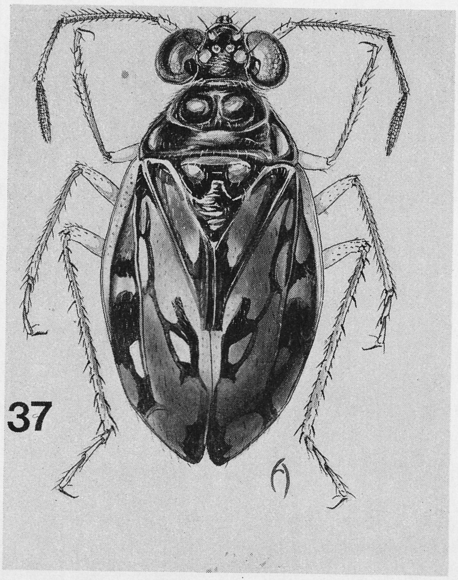
This species is very close to *S. procellaris* (clavus uniformly covered with thin pubescence, including its center), and only the few differences will be summarized here. They are the predominance of dark pigmentation of the fore wing situated in the exocorium (FIG. 10a–c) (in the mesocorium in *S. procellaris,* FIG. 7a–f); pruinose area in the medioproximal edge of the clavus 3–4× larger than in *S. procellaris*; median outline of membrane straight, left and right membrane only touching each other (in *S. procellaris* mostly somewhat convex so that there is a small overlap).

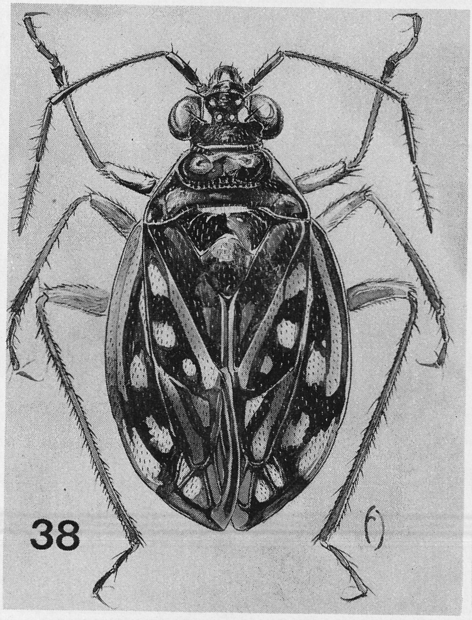
Measurements. Holotype (♂): length, 3.05 mm; width, 1.41 mm. Mean length of 4 ♂, 3.00 mm (min 2.80, max 3.10); width, 1.38 mm (1.30, 1.41). Length of 3 ♀, 3.30 mm (3.20, 3.50); width, 1.65 mm (1.60, 1.75).

Holotype ♂, HAWAIIAN IS: MAUI I, Upper Hana, Forest Reserve, greensword, mid camp, 4.VIII.1973, 1700 m, leaf litter, F.G. Howarth (BISHOP 11,416). Paratypes as follows. HAWAIIAN IS. MAUI I: same data as holotype 3♂,3♀. MOLOKAI I: Molokai Mts, 21.IX.1893, 1♀, R.C.L. Perkins; Mapulehua, Punaula Ridge, 15.VIII.1963, R.L. Usinger; Puu Kolekole, 18.VII.1963, 1333 m, 1♂, D.E. Hardy.

Holotype in the Bishop Museum; paratypes in BISHOP and in the collection of the University of Hawaii; the Hawaii State Department of Agriculture, Department of Entomology; California Academy of Science; the Polhemus collection; and the author's collection.

General remarks. The arguments given above to justify assigning species status to *S. intermedia* apply more or less also to the present taxonomic unit. The main reason for considering the 2 populations from Maui and Molokai as belonging to 1 taxonomic unit and being reproductively independent of *S. procellaris* is that the pigment eunomies of the fore wing do not match each other. FIG. 10a–c of *S. usingeri* inserted within the series of *S. procellaris* (FIG. 7b–f) would result in a discontinuous eunomy.





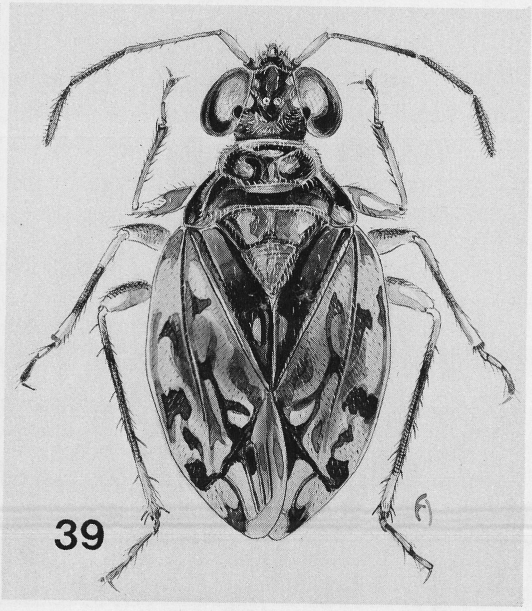


Fig. 37–39. **37.** *Saldula kauaiensis* (Oahu, Manoa, Palolo Ridge, 3.XI.1935, R.L. Usinger). [Although I have not seen this specimen, it almost certainly belongs to *S. kauaiensis,* since it is the only species from Hawaii with such a large pale area in the central part of the clavus (compare with Fig. 6c). This specimen was first identified by Zimmerman (1948, his Fig. 99, right) as *S. procellaris,* and in 1957 (p. 192) as *S. oahuensis.*] **38.** *Saldula exulans* (Oahu, Haleauau, 8.II.1936, R.L. Usinger). **39.** *Saldula oahuensis* (Oahu, 19.IX.1920, H. Swezey). Fig. 37–39 drawn by Frieda Abernathy; reprinted from *Insects of Hawaii,* Vol. 3, Fig. 99, p. 222, 1948, with permission of the editor; these superb pictures deserve to have been reproduced in the present paper as Fig. 1, but they were received after the final labeling of my figures.

The ecological demands of *S. usingeri,* so far collected only in the flightless form, are not known. The sparse records suggest that it occurs isolated from its close relatives *S. procellaris, S. oahuensis, S. intermedia, S. longicornis* and *S. nubigena.* The 6 specimens collected from only 1 locality on Maui were accompanied by only *S. exulans.* In one of the localities of *S. usingeri* on Molokai, namely Puu Kolekole, *S. procellaris* was also collected, at a time and elevation difference of 10 years and 400 m, respectively.

Saldula longicornis Cobben, **new species** FIG. 8a–c, 16, 20b, 27a–c, 33a–b

This species has been generally referred to as *S. oahuensis* Blackburn. Zimmerman (1948) added *Acanthia humifera* Kirkaldy (1908: 199) as a synonym of *S. oahuensis.* In 1951 and 1957 he concluded, after having also studied museum material outside the Honolulu collections, that 2 different species were being treated as *oahuensis.* In fact, Kirkaldy (1908) described *A. humifera* as a new species, comparing it with the description given of *A. oahuensis* by Blackburn (1888). This confusion indicates the inadequacy of the original descriptions.

Description

The description is short since it is not necessary to repeat characters of the foregoing 4 species, with which *S. longicornis* forms a complex. It is closest to *S. oahuensis* from which it differs in a more uniform wing design (FIG. 8a–c), slightly more sparse pubescence of the fore wing, and the more expanded ashy-pruinose proximal area of the clavus. The small area between the pruinose area and the apical light spot on the clavus bears no hairs (as in *S. oahuensis* and *S. intermedia*). The front legs are uniformly pale, but 1 ♂ is fuscous at the base of the femur. The pronotum shape (FIG. 16) is sometimes more sinuate laterally, resembling *S. oahuensis* (FIG. 18a), but the pubescence is less. The parandria have a wider base and are shorter (FIG. 27a–c) than in *S. oahuensis, S. procellaris, S. intermedia* and *S. usingeri* (FIG. 27d–g). The most reliable and unique character of *S. longicornis,* separating it from its related species, is of a morphometric nature, viz. its long antennae. The ratio, length of antennae/median length of pronotum (exclusive of pronotal collar) is for 4 ♂, 5.25–6.10, and for 4 ♀, 5.40–5.59. These ratios in *S. oahuensis* are for 10 ♂ and 10 ♀, respectively, 3.96–4.58 and 3.64–4.51; these latter ranges apply also for *S. procellaris, S. intermedia* and *S. usingeri.* All available specimens of *S. longicornis* are flightless, the length of the hind wing corresponding with the picture in FIG. 20b.

Measurements. Mean length of 4 ♂, 3.18 mm (min 3.10, max 3.30); width, 1.55 mm (1.50, 1.58). Length of 5 ♀, 3.52 mm (3.30, 3.65); width, 1.77 mm (1.66, 1.83).

Holotype ♂, HAWAIIAN IS: OAHU I: Honolulu Mts, 1♂, R.C.L. Perkins (BISHOP 11,417). Paratypes: HAWAIIAN IS. OAHU I: Kukuiala, 11.IV.1936, 1♂, R.L. Usinger; Maunawili, 8.XI.1906, 1♀; Tantalus, 25.II.1906, 433 m, 1♀, W.M. Giffard; Mt

Tantalus ? (label in very faint pencil), IV.1907, 1♀; Mt Tantalus, 19.V.1907, 2♂,2♀; Waianae Mts, 1♀; Oahu ?, 1♂,2♀; Sandwich Is, 1913-323 (BMNH).

The species has not yet been found outside Oahu. I have a note made when looking over the Drake Collection in Washington in 1973, that a ♂ from Kauai (Alakai Swamp, 17.VII.1920, C.N. Forbes) was grouped under *S. oahuensis.* This specimen should be restudied carefully to verify whether it is indeed this species or *S. longicornis.*

General remarks. Nothing more can be said other than that this species is an endemic of Oahu. Descriptions of the exact site where the species lives are lacking. *S. oahuensis* and *S. procellaris* have also been collected from Mt Tantalus, but in other years, so that *S. longicornis* may live in situations not occupied by other species. None of the localities of other species recorded from Oahu, such as *S. intermedia, S. kauaiensis* and even the widespread *S. exulans,* are the same as for *S. longicornis.*

Saldula nubigena (Kirkaldy) FIG. 9, 20a, 35

Acanthia nubigena Kirkaldy, 1908, Proc. Hawaii. Entomol. Soc. **1:** 199.

Saldula nubigena: Zimmerman, 1948, Insects of Hawaii, Vol. 3: 223, Fig. 100; 1951, Proc. Hawaii. Entomol. Soc. **14:** 336; 1957, Insects of Hawaii, Vol. 6: 191.—Drake & Hoberlandt, 1950, Acta Entomol. Mus. Natl. Pragae **26:** 9.

Lectotype ♂. Kirkaldy (1908) described the species from Maui, Haleakala, 1666 m. Neither sex nor number of specimens is given, but $2^{7}/_{8}$–$3^{1}/_{8}$ mm is given as the length of the species, so that Kirkaldy based his description on at least 2 specimens. There are 2 extant specimens from Kirkaldy's studied material (all I could find) in the assemblage of material from all museums. One is a ♂ with the same data on the label as mentioned by Kirkaldy; it was collected by Perkins, IV.1894, and bears a BMNH type label. The other specimen, from the Fauna Hawaiiensis Collection (BISHOP), is a ♀ with the only label information "Maui 251" ("Maui, Haleakala, IV.1894; All the small Carabids and Hemiptera by grubbing," from Perkins number code in Bishop Museum).

I selected the ♂ as the lectotype of *S. nubigena* and placed an appropriate label to that effect under the specimen. The lectotype is deposited in the British Museum.

Description

Despite the paucity of material, it is clear that we deal here with a valid species. It is close to the *S. oahuensis* complex (middle area of clavus without hairs), but is unique in its short 2nd antennal segment, which is subequal with the last segment. The ratio of segments 2/4 is 1.04–1.05, and in all other species of the *oahuensis-procellaris* group it ranges 1.28–1.60. The fore wing (FIG. 9) is distinctly semibrachypterous and the hind wing (FIG. 20a) is more reduced than in any other species. The wing design of the 2 specimens is quite the same and rather pale (FIG. 9). It seems that the clavus tends to earlier depigmentation than in *S. oahuensis* and *S. intermedia* (compare FIG. 9 with FIG. 3b and 11a, respectively), but this can be verified only when longer series become available. Although the 2 specimens present are not teneral, their acetabulae

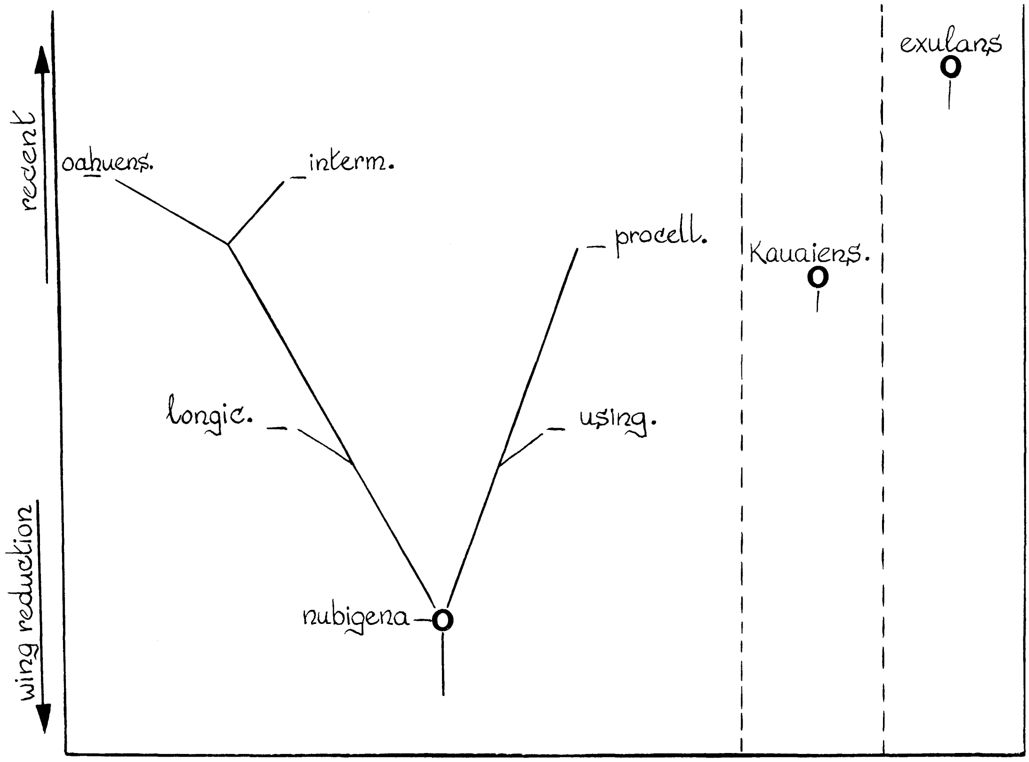


FIG. 40. Diagram of the relative time since the arrival and speciation of the *Saldula* species in the Hawaiian Archipelago. The species indicated with O represent the original colonizers (see text).

and coxae are predominantly light brownish, whereas in all other related species they are predominantly black. Parandria and paramere (FIG. 35) are more like *S. longicornis.*

Measurements. Length of ♂ (lectotype), 2.83 mm; width, 1.50 mm. Length of ♀, 3.00 mm; width, 1.68 mm.

Specimens examined. HAWAIIAN IS: MAUI I, Haleakala, IV.1894, 1666 m, 1♂ (lectotype), R.C.L. Perkins; 1♀, Maui 251 (see note above).

S. procellaris and *S. exulans* have also been recorded from Haleakala, but at elevations of 666 m.

Saldula kauaiensis Cobben, **new species** FIG. 6a–d, 22a, b, 34, 37

Description

Of the 4 new species described in this paper, *S. kauaiensis* is the most distinctive. It has the size of the *oahuensis-procellaris* complex, but it is unique by its overall shiny appearance, including the fore wings, and by the 2 sharply contrasting pale areas on the clavus. The most proximal pale area is separated from the anterior margin of the clavus by a distance of more than its width (see FIG. 6a, b and contrast with *S. exulans* which also often has an anterior colorless spot, FIG. 1b, c). In the less-pigmented individuals, constituting part of a gradual eunomic series of wing variation (FIG. 6a–d), the anterior and distal claval spots fuse. The resulting pale window of the clavus nevertheless contrasts strongly with the surrounding black pigment (FIG. 6c, d; in the other species dealt with, the boundaries between dark and light areas of the most light specimens are vague and irregular, see FIG. 1b, 3b, 9, 11a). The clavus is wide and somewhat depressed in the middle. The shiny, more or less coreaceous corium is yellowish brown and bears 3 or 4 ivory-white markings. These are surrounded by black pigment of varying degree and often by a pruinose layer; the endocorium has always a black strip along the clavus. The membrane is strongly reduced, its veins being almost absent. Although *S. kauaiensis* has in this latter respect the most reduced hemelytron structure of all the Hawaiian species, the reduction of the hind wing conforms to FIG. 20c (less reduced than in *S. nubigena,* FIG. 20a). The pubescence of *S. kauaiensis* is very sparse and short, decumbent. Parandria and paramere (FIG. 34) resemble most those of *S. longicornis.*

The accurate illustration by the artist Abernathy, first presented in Zimmerman (1948, Fig. 99, right) as *S. procellaris* and reproduced here as FIG. 37, almost certainly refers to this new species. It is of a specimen from Oahu, Manoa, Palolo Ridge, 3.XI.1935, collector R.L. Usinger, but I did not find it among the abundant material before me. The hemelytral design (clavus + corium) fits, however, exactly within the series presented here in FIG. 6a–d.

Measurements. Mean length of 4 ♂, 3.01 mm (min 2.90, max 3.25); width, 1.48 (1.37, 1.63). Length of 7 ♀, 3.39 (3.20, 3.55); width, 1.73 (1.62, 1.99).

Holotype ♂, HAWAIIAN IS: KAUAI I: Alakai Swamp, south, 1.I.1974, 1500 m, on mossy tree trunk, W.C. Gagné (BISHOP 11,414). Paratypes as follows. HAWAIIAN IS. OAHU I: Schofield-Waikane Trail, 28.IV.1938, 833 m, on moss, 2♀, E.C. Zimmerman; Koolau Mts, Kaipapau, 14.II.1939, 1♀, Y. Kondo; Koolau Mts, Waikane Trail, 20.X.1974, 650 m, on mossy branches of *Tetraplasandra meiandra,* 1♀, W.C. Gagné; Koolau Mts, Poamoho Trail, 15.II.1976, 520 m, on muddy trail, 1♂, W.C. Gagné; Wailupe, 23.I.1915, 1♀; Konahuanui, 17.VI.1917, 1♀, J.C. Bridwell; Mt Olympus, 26.VII.1936, 666–800 m, no water, 1♀, F.X. Williams. KAUAI I: Alakai Swamp, NW, 9.VII.1937, 1♀, E.C. Zimmerman; Kokee, II.1919, 1♀, J.A. Kusche; southern Mohihi Ridge, 8.VII.1937, 1♂, E.C. Zimmerman; Mt Kahili, 2.IX.1970, 800 m, on *Cheirodendron helleri,* 1♀, W.C. Gagné.

Holotype in the Bishop Museum. Paratypes in BISHOP, and in the British Museum collection; the Hawaii State Department of Agriculture, Department of Entomology; California Academy of Science; the Polhemus collection; and the author's collection.

General remarks. Three locality labels mention captures from moss, 2 of them from a level above the ground; 1 locality stresses that no open water was present and another concerned a muddy trail. However, ⅔ of all labels have no specified topographic characteristics, although most of them point to elevations above 500 m. It is clear that more accurate descriptions of the actual spots where the species occurs are needed to tell something about the ecological demands of *S. kauaiensis.* The species was collected together with *S. procellaris* on Mt Olympus, Oahu, possibly from the same spot, since both species were glued on the same card. There are no simultaneous records with other species.

DISCUSSION ON ORIGIN AND SPECIATION

The Hawaiian fauna of shore bugs consists of only 8 species of the global genus *Saldula.* These probably originated from 3 separate colonizations by transoceanic flight. *Saldula* is the largest genus of the family, and it belongs to the largest and most evolved subfamily, Saldinae (Cobben 1959, 1971). Its sole presence in the Hawaiian Archipelago is therefore not surprising. Representatives of *Saldula* are found on both continental and oceanic islands. So far there is only 1 overseas settler known that has diverged so much by long isolation that it deserves a special generic status, viz *Helenasaldula aberrans* from St. Helena (Cobben 1976). Another aberrant saldine genus, *Salduncula,* is theoretically a candidate for survival in the Hawaiian Is. All *Salduncula* species are small and long winged, and all live in intertidal situations. Four species have been described from the Seychelles, Malagasy, Samoa, Guam and the Tokara Is (Brown 1954, Drake 1961, Miyamoto 1963, Polhemus 1976).

Of the less-derived and more ancient subfamily Chiloxanthinae (some 20 recent species known), only species of the predominantly halophilous genus *Pentacora* might eventually have reached the Hawaiian Is. Modern *Pentacora* species are active flyers, and the most widespread, *P. sphacelata,* succeeded in colonizing the Galapagos Is (Polhemus 1968; for the ecology of *P. sphacelata* and other littoral saldids, see also Bahr & Schulte 1976). Another species, *P. malayensis,* occurs on Taiwan (Cobben 1980).

Families of shore bugs other than Saldidae have not been met with in the Hawaiian Is (Leptopodidae, Leotichiidae, Omaniidae). The latter family contains 4 flightless intertidal species [Red Sea, Samoa, New Caledonia, Tokara and Nauru I (Cobben 1970; Polhemus 1976)]. Species are very minute and probably can be passively dispersed over distances by rafting or storm transport. Intertidal zones and salt marshes should be inspected with scrutiny for such new additions to the Hawaiian fauna.

ORIGIN OF THE *SALDULA* SPECIES

Unfortunately not much can be hypothesized on the origin of the 8 species of the Hawaiian Is. So far, they all seem to be endemic and all show more or less well-progressed reduction of flight capacity. This is in contrast with the *Saldula* species from Micronesia, which are long-winged (Drake 1961). None of the Hawaiian species can be definitely related to continental or oceanic species described thus far. Zimmerman (1948a) suggested that the Hawaiian Saldidae represent derivatives of a common Polynesian ancestral stock. I too assume they have a Pacific rather than an American origin, as counts for the majority of the Hawaiian insect fauna (Zimmerman 1948a; Bowden & Johnson 1976). It must be said that the Indo-Pacific fauna of saldids is the least known, so that future extension of our knowledge of that region possibly will permit a more adequate discussion of the Hawaiian fauna. The Hawaiian *Saldula* species fall into 3 groups: *S. exulans, S. kauaiensis* and all the remaining closely allied species. Of these, only *S. exulans* has the hemelytral ridge, obliquely running along the subcostal lateral overfold (FIG. 2b, c). The ridge is taxonomically haphazardly distributed in Saldidae. In some otherwise uniform taxa it occurs in some species, in others it does not (e.g., present in the *S. rivularia* group, absent in the *S. scotica* group; present in *Teloleuca,* absent in *Salda*). The ridge is in general an attribute of typical representatives of the genus *Saldula* in Europe and North America (inclusive of *Micracanthia* and *Ioscytus*). Its occurrence within *Saldula* is irregular, but absence seems more the rule in species from the Indo-Pacific areas. The ridge does not show a positive relation with species which are able to fly; its presence may contribute to stronger interlocking between hemelytron and thorax-abdomen when the animal is not in flight.

WING POLYMORPHISM IN SALDIDAE

I use here the terminology of wing polymorphism given earlier (Cobben 1960). The following 5 categories are based only on the reduction of the fore wing: *macropterous,* hemelytron completely developed (FIG. 1e); *submacropterous,* membrane very slightly reduced (more or less intermediary between FIG. 1a and 1e); *semibrachypterous* (*moderately*), membrane reduced about halfway (FIG. 1b); *semibrachypterous* (*strongly*), membrane reduced to narrow strip (FIG. 6); and *brachypterous,* hemelytron with no sign of membrane (as in the intertidal *Aepophilus*).

It is clear that wing modification is of a gradual nature and that sometimes an arbitrary choice must be made for intermediary types. Lindskog (1974, 1975) commented on my use of the terms submacropterous and semibrachypterous, because he considered these terms not in accordance with a functional classification of pterygopolymorphism. Lindskog proposed the following terms instead (my terminology in parentheses): *strongly macropterous* (macropterous), fore and hind wing with full flight function; *moderately macropterous* (submacropterous), membrane slightly reduced, hind wings reaching the distal border of the membrane, capable of flight (flight muscles not atrophied); *moderately brachypterous* (submacropterous), membrane slightly reduced, hind wings not reaching the end of the membrane cells (flight muscles atrophied); and *strongly brachypterous* (semibrachypterous), membrane distinctly reduced, hind wings not surpassing hind border of corium (not able to fly).

I am a proponent of including ecophysiological aspects in classification where possible and practical. I think, however, that Lindskog's terminology contributes more to confusion. Although my terminology is concerned only with the morphological phenomena of fore wing reduction, in my key (Cobben 1960) I described in addition the extent of hind wing development by species. However, as shown in the present paper, hind wing and fore wing reduction do not always keep step with each other. Lindskog's subdivision is based on the automatic implication that macropterism means "capable of flight" and brachypterism means "not capable of flight." However, full-winged Heteroptera may reveal histolysis of the indirect flight muscles during the adult stage, as in Pyrrhocoridae and Corixidae (e.g.: Edwards 1969; Young 1965a, b; Scudder & Meredith 1972). The functional terminology of Lindskog's interpretation of macroptery and brachyptery then breaks down as a means of characterizing species on the basis of wing polymorphism. Flight-muscle polymorphism is hard to incorporate consistently within the terminology of pterygopolymorphism. Furthermore, to term Heteroptera possessing almost completely developed pairs of wings but atrophied wing muscles as "brachypterous" conflicts with the etymology of the word. It is, in addition, very confusing as regards the terminology commonly used in many other heteropterous families. This accounts in particular for Lygaeidae, in which different degrees of visible wing reduction have been definitely correlated with relative recent and historical permanencies of habitats (see e.g., Sweet 1964, Slater 1975). I will not dwell further upon this subject, which has been discussed in the literature on Heteroptera many times from different angles [see Slater (1977) in *Biotropica* **9**(4): 217–29].

Focusing the discussion toward wing reduction within Saldidae on a worldwide basis, we may generalize that species can be arranged according to overall macroptery (as regards fore wing and hind wing development, irrespective of ability to fly), submacroptery [fore wings only somewhat reduced, hind wings slightly (potential ability to fly) or more distinctly reduced (probably never able to fly)], different degrees of semibrachyptery (fore wings with considerable reduction of membrane, hind wings strongly reduced up to nearly absent, FIG. 20a–d), and brachyptery (clearly half-winged without membrane, hind wings absent). Microptery and aptery do not occur in Saldidae, for the evident reason that the lateral side of the fore wing of the female plays an essential role during copulation. Saldidae have a unique side-to-side mating posture (Cobben 1957, Leston 1957), which accounts for the remarkable shape of fore wing reduction in the brachypterous *Aepophilus bonnairei* Sign. (exocorium much less reduced than the remainder parts of corium).

The whole evolutionary process of reduction of flight capacity in Saldidae starts with flight-muscle polymorphism, subsequently accompanied by minute wing reductions and a switch mechanism for muscle development and histolysis as a direct response to environmental factors. It seems that with further reduction of flight capacities, more and more genetic control was developed to produce occasional macropterous specimens within predominantly flightless species. Indirect argument that macroptery of a normally strongly semibrachypterous saldid species has a genetic background is shown by the European halophilous *Halosalda lateralis* Fall. A series of the rare macropterous form of this species shows another eunomy of wing design when compared with a series of semibrachypterous individuals. If the total scale of

TABLE 1. The distribution of Hawaiian species of *Saldula* by island.

	ISLAND				
SALDULA SPECIES	Kauai	Oahu	Molokai	Maui	Hawaii
exulans	X	X	X	X	X
oahuensis	X	X	X	X	X
procellaris		X	X	X	X
intermedia		X		X	X
usingeri			X	X	
longicornis		X			
nubigena				X	
kauaiensis	X	X			

eunomy of a species is considered as an expression of its genome, a continuous deviation of this pattern combined with macroptery might be explained as being genetically controlled. Studies on the proportion of long-winged to short-winged forms in order to calculate dispersal patterns and centers of distribution, as has been done extensively with Carabidae (e.g., Lindroth 1963, Darlington 1971, Haeck 1971), have not yet been undertaken with Saldidae. Still, saldids form an ideal tool for this zoogeographic purpose, premised on an adequate sampling method. Macropterous *Halosalda lateralis* specimens are rare in museum collections, and sampling with pit-fall traps in saline habitats on Terschelling, one of the Dutch North Sea islands, revealed 110 specimens in 2 seasons, all semibrachypterous (I studied the samples collected in this way by Drs de Smidt in 1969/1970). However, in 1971 on the same small island, I collected within a short time and with "hand-picking" more than 10 macropterous specimens along an artificial sandy road bordering the natural habitat of the species. The same pit-fall samples contained more than 70 individuals of the "rare" macropterous *Salda littoralis*.

DISTRIBUTIONAL PATTERNS IN THE HAWAIIAN IS

The distribution of the Hawaiian species of *Saldula* is shown in TABLE 1. Lanai (very close to Molokai and Maui), the smallest of the major islands, harbors only *S. oahuensis* and *S. procellaris* and is omitted here from the discussion. *S. exulans* and *S. oahuensis* are the most widespread species, the first being the most abundant. The next species in decreasing sequence of frequency are *S. procellaris* and *S. intermedia*. The remaining 4 species are restricted to 1 or 2 islands, as far as we know now. This picture may change somewhat with more extensive searching in the future (only 2 specimens of *S. nubigena* were available).

The distribution sequence given in TABLE 1 seems to run more or less parallel with the present flight possibilities of the species expressed by differences in wing reduction.

Although it is a handicap that I have not personally made detailed observations on the ecology and flight behavior of the Hawaiian species, I can speculate to some extent on the meaning of the differential wing reduction. By analogy from what we know from other insects exhibiting wing polymorphism, it is apparently true also for saldids that wing reduction is a function of environmental factors and evolutionary time. So far, the locality data suggest that the Hawaiian saldids did not make any crucial shift to new adaptive zones. All species seem to prefer permanent moist conditions and to inhabit damp places which are much alike ecologically. Species of the *oahuensis-procellaris* complex living in normal habitats at soil level have often been collected also from the overstory. Although such partially arboreal habits seem quite deviative for saldids, I agree with Lindskog (1975) that this is not exceptional, considering the very damp conditions in rain forests. I found *S. saltatoria* L. and *S. c-album* Fieb. in Europe occasionally several metres above soil on tree trunks in very wet and shadowed situations, a habit also shared by *Salda pellucens* F. (Lindskog 1975). Saldidae are nonselective predators, their food supply being determined by the preferred niche of the species in question. The 7 small-sized species of Hawaii are morphologically very much alike (rostrum of similar length) and the locality records suggest very uniform habitats for all of them.[5] There seems, furthermore, not to be a leveling of saldid species by occurrence at different altitudes.[6]

If lack of ecological diversification between the species is true indeed, and if all species (except possibly *S. exulans*) live in equally stable environments, then the different degree of wing reduction (FIG. 20) could be a good indicator for the relative age of the species from the moment of entrance into the Hawaiian biota. This should imply the following sequence of relative ages of the Hawaiian species (from oldest towards most recent immigration and speciation: *S. nubigena, S. longicornis* + *S. usingeri, S. kauaiensis* + *S. procellaris, S. oahuensis* + *S. intermedia, S. exulans.* This sequence runs parallel with the actual abundance of the species (except for *S. intermedia*). The most widely distributed *S. exulans,* although a predominantly flightless species, is apparently able to produce a higher percentage of macropterous individuals than any other species. *S. exulans* seems to be more associated with the presence of open water than other species; its striking wing polymorphism (3 morphs, FIG. 1a, b, e) could point to its relative recentness and/or to its occupancy of less stable habitats. The microphysical conditions of the localities of the other 7 species possibly do not differ much, and are indicative of more terrestrial though permanently damp environments. The large collection of the second species in order of abundance, *S. oahuensis,* contained only 3 macropters. Semibrachyptery in this species (and its close relative *S. intermedia*) is accompanied by varying degrees of hind wing reduction (FIG.

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[5] I refer to Usinger (1942: 159), who concluded in describing the general physical conditions of the Hawaiian Islands: "Despite the great variety over the islands as a whole, there is a remarkable uniformity of conditions in any particular repeated ecological niche, so that identical physical conditions usually can be found in spots on each of the main islands."

[6] Elevation records given are mostly above 700 m. This does not automatically mean that Hawaiian saldids are typically mountain species; it is probably the consequence of dramatic changes of original biotas below 700 m by human activities (Usinger 1942).

20d). *S. procellaris,* collected only once in the macropterous state, has stronger hind wing reduction (FIG. 20c). *S. usingeri, S. longicornis* and *S. nubigena,* only known as semibrachypters, have the hind wings merely as vestiges (FIG. 20b, a). *S. kauaiensis* forms an exception in this gradual series of fore and hind wing reduction; its fore wings are more reduced (FIG. 6) than in any other Hawaiian species, but not the hind wings (FIG. 20c).

In summary, the most widespread *S. exulans* reveals pterygopolymorphism, and, to a lesser degree, so do *S. oahuensis* and *S. procellaris.* The other species are only known in the monomorphic state, although it must be admitted that much less material is available. The semibrachypterous fore wings of all Hawaiian species have retained the device underneath the apex of the clavus that serves for coupling the fully developed fore and hind wing during flight. This device is, of course, functionless in the semibrachypterous animals. The presence of this device in even the species with the strongest hind wing reduction, such as *S. nubigena, S. longicornis* and *S. usingeri,* suggests that these species might still be potentially dimorphic and create, under some circumstances, macropterous bugs.[7] However, the fact that they occur very locally and on only 1 or 2 islands probably means that macroptery plays no substantial role in these species in modern times.

The distributional picture of the Hawaiian species (see TABLE 1) does not allow us to speculate reasonably about the dispersal routes of the species. Species now apparently restricted to one island may have occurred on other islands during periods when they possessed more dispersal power than today. Fragmentary occurrence reflects therefore patterns of secondary isolation. The sequence of species given above, arranged according to their antiquity in the Hawaiian Archipelago on the basis of wing reduction, is visualized in FIG. 40 in combination with their arrangement on a tentative basis of relationship. If the dendrogram for the *oahuensis-procellaris* complex, shown in the left segment of FIG. 40, reflects the reality, it follows that the antennal formula of *S. nubigena* (2nd and 4th segment subequal in length) and the hairless area in the center of the clavus would be plesiomorphous conditions. However, the morphological divergence between the species is too meager to consider this dendrogram as a reliable cladogram.

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[7] Complete loss of the coupling device in question, as for example in the intertidal semibrachypterous *Enalosalda mexicana,* could mean that such species have lost completely the genetic switch mechanism to produce long-winged morphs.

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