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The *Calosoma* species of the Galápagos archipelago. I. Redescriptions and distribution of the species

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Summary

In this paper the species of the genus *Calosoma* WEBER, 1801 (Coleoptera, Carabidae) from the Galápagos islands are redescribed in detail. Therefore more than 800 specimens collected during recent expeditions on 14 different islands or volcanoes of the archipelago have been examined in detail and moreover measured for a large number of biometric variables. About 1.200 additional specimens were studied but not measured.
Based on single characteristics an unambiguous identification to species level is not always possible due to the very high intraspecific variability shown by some of the species. Several characters, used in previous taxonomic papers moreover seem to be influenced epigenetically or were formerly unprecisely or even erroneously described. Species identification is most easy by means of a combination of characters, especially those describing the size and shape of male genitalia. These characters were not used in previous taxonomic keys to these *Calosoma* species.
Key-words : *Calosoma*, taxonomy, distribution.

Résumé

Dans cette publication les espèces du genre *Calosoma* WEBER, 1801 (Coleoptera, Carabidae) des îles Galàpagos sont redécrites en détail. Dans ce but plus de 800 spécimens collectionnés récemment au cours d'expéditions dans 14 îles ou volcans différents de l'archipel ont été examinés en détail et mesurés pour un grand nombre de variables biométriques. De plus ou moins 1.200 spécimens fûrent étudiés sans biométrie.
Une identification des espèces n'est pas toujours possible à partir de caractères simples due à la variabilité intraspécifique très large de quelques espèces. Plusieurs caractères, utilisés dans des publications antérieures, semblent également être influencés d'une façon épigénétique ou étaient imprécisément ou même erronément décrits. L'identification des espèces est le plus facile à partir d'une combinaison de caractères, spécialement ceux qui décrivent la taille et la forme des génitalias mâles. Jadis, ces caractères ne fûrent jamais utilisés dans des clés de détermination pour ces espèces de *Calosoma*.
Mots-clefs : *Calosoma*, taxinomie, répartition.

Introduction, material and methods

The genus *Calosoma* WEBER, 1801 belongs to the relatively most studied beetles of the Galápagos archipelago. Nevertheless, until recently, there has been a lot of confusion in the taxonomic literature of these beetles from Galápagos. It is a great merrit of BASILEWSKY (1968) to have brought basic order in the formerly used nomenclature by recognizing three different species and a lot of synonymies. Moreover, a fourth species from Isla Santa Cruz was described as new by that author. Recently we started investigations on the beetles and spiders of the Galápagos islands (cfr. BAERT & MAELFAIT, 1986, BAERT *et al.*, 1989 and DESENDER *et al.*, 1988, 1989). During three expeditions (1982, 1986 and 1988; BAERT, MAELFAIT & DESENDER) we managed to sample all important islands and volcanoes of the archipelago, including the different volcanoes of Isabela and Fernandina, some of which had, until now, never been prospected for these invertebrates. We were also fortunate to have access to the collections of : (1) the Charles Darwin Research Station, (2) the Belgian entomologists N. LELEUP (1964, identified and studied by BASILEWSKY, 1968), S. JACQUEMART (1974 expedition) and BAERT & MAELFAIT (1982 expedition), deposited in the K.B.I.N. at Brussels, (3) H. and I. SCHATZ (1985 and 1987 expeditions, identified) gathered during their ecological investigations of the soil invertebrates of the Galápagos islands.
Detailed studies on our abundant *Calosoma* material showed that a number of hitherto used characters in species recognition were unprecisely or even wrongly described, adding to the already existing problems of ambiguous identification. We therefore thought it would be of general interest to redescribe the known species based on our material at hand.
In this paper the first part of our work is presented, namely the detailed redescriptions of the taxa on species rank. This paper also provides a compilation of all known distributional data for the species mentioned. To prevent redundancy and for the matter of clarity we will only mention the different islands and vegetation belts where species have been found and we refer to a former paper for all detailed data (DESENDER *et al.*, 1989). The second part of this study will deal with canonical discriminant function analyses in order to identify these species on a multivariate basis. An identification key will be added to that part of publication (DESENDER & DE DIJN, in prep.). At the moment we are analyzing in more details our infraspecific data, which pose, as usual with island fauna's, a number of methodo-

logical problems in subspecific designations. Moreover, we have not yet obtained type material from one subspecies, which needs to be checked. The results of these analyses will be presented in a future paper (DESENDER, in prep.). We will only use the genusname *Calosoma* WEBER, 1801 in this paper. We have indeed observed that important characters in subgeneric (or according to some authors generic rank) identification in many cases even show infraspecific variability not accounted for. Moreover the extreme splitting of the "family" Carabidae in many different families and the higher levelling of subgenera to genera as proposed by JEANNEL (1940) is not any longer followed by many Carabid taxonomists. Therefore, at the time being, we propose only to use the genusname *Calosoma* WEBER, 1801. As already mentioned there are also a number of problems with subspecific nomenclature of the *Calosoma* species of Galápagos, which will be dealt with in another paper.

All measurements were made with a stereomicroscope WILD M5 with a calibrated ocular. Standard total length was defined from the frontal margin of the clypeus until the apical margin of the elytra; in addition to biometric size variables, a number of meristic variables (chaetotaxy on different body parts), as well as other discontinuously varying characteristics were also noted. The male genitalia as well as female external reproductive structures (gonapophyse) were prepared in each individual and also measured. Finally dispersal power characteristics were also investigated : these include a standardized measure of flight wing development (% max allometry, cfr. DESENDER *et al.*, 1986), which is based on wing length × wing width and corrects for absolute body size differences, furthermore a measure of the functional state of indirect flight musculature and finally characteristics describing the size and puntuation of the metepisternum.

We will now describe the different species : in each case we will (1°) compile all known synonymies and references, (2°) treat the material examined, (3°) diagnose the species as far as possible, (4°) redescribe them (general size and shape, head, prothorax, abdomen and elytra, flight wings, indirect flight musculature and metapisternum, male genitalia, female external reproductive structures, color of integument) and finally (5°) summarize our data on distribution, habitat choice and zoögeographic affinities. Biometric values in these redescriptions always show mean value (minimum - maximum), expressed in mm, unless mentioned otherwise.

Results

Calosoma granatense GEHIN, 1885
(Plate I)

TYPE

Colombia (1885?, 1 ind., holotype) : exact locality unknown; Museum Hist. Nat., Paris.

SYNONYMS AND REFERENCES

Calosoma granatense GEHIN, 1885, p. 59.
Calosoma galapagoum HOWARD, 1889, p. 191 (non HOPE).
Calosoma howardi LINELL, 1898, p. 251.
Calosoma galapageium ROESCHKE, 1900, p. 59 (non HOPE).
Calosoma howardi : MUTCHLER (1925), p. 223.
Calosoma (Callistriga) galapageium : BREUNING (1927), p. 200 (non HOPE).
Calosoma howardi : BLAIR (1933), p. 472.
Calosoma howardi : MUTCHLER (1938), p. 3.
Castrida (Microcalosoma) galapageium : JEANNEL (1940), pp. 93, 98, fig. 2 (non HOPE).
Calosoma howardi : VAN DYKE (1953), pp. 7-9, pl. 1, fig. 1.
Calosoma darwinia VAN DYKE, 1953, pp. 10-11, pl. 1, figs. 3, 5.
Calosoma (Castrida) galapageium : GIDASPOW (1936), pp. 286, 289, figs. 2, 14-19, 25, 62-74 (non HOPE).
Calosoma darwinia : LINSLEY & USINGER (1966), p. 141.
Calosoma howardi : LINSLEY & USINGER (1966), p. 141.
Castrida granatense : BASILEWSKY (1968), pp. 189-200.
Castrida granatensis : LINSLEY (1977), pp. 19-20.
Castrida granatense : FRANZ (1985), pp. 75-76.
Castrida granatense : MORET (1986), pp. 92-93.

MATERIAL EXAMINED

Detailed data and biometrics were gathered from 376 males and 367 females collected on different altitudes on the islands Espanola, Floreana, Isabela, Marchena, Pinta, Pinzon, San Cristóbal, Santa Cruz, Santa Fé, Santiago, Seymour; in addition about 1.160 other specimens were identified without detailed biometrics and dissections.

DIAGNOSIS

Extremely variable species, only identified with certainty by means of a combination of characters, especially male genitalia which are slender and rather narrow at the orificium and possess a moderately long penistip (figs. 2-3); externally (fig. 1) distinguished from *C. leleuporum* by the relatively narrower head and apical part of pronotum, from *C. linelli* by the larger size and relatively longer abdomen and elytra; externally only distinguishable from *C. galapageium* by means of a combination of several characters (discriminant function analyses, DESENDER & DE DIJN, in prep.).

DESCRIPTION

(a) *General size and shape :*
Standard total length :
males : 19.20 (13.67-22.67) (n = 376)
females : 19.85 (15.84-22.84) (n = 367)
Maximal width (elytra) :
males : 8.61 (5.66-10.16)
females : 9.03 (7.00-11.00)
Body shape : cfr. fig. 1; abdomen with elytra in the mean 1.6 × wider than pronotum.

(b) *Head :*
Moderately robust, in the mean 0.72 × longer than wide; eyes prominent; frons with at each side a single supraorbital puncture inside eye; distinct fine punctuation on the head capsule with some larger punctures between the eyes; distinct dorsal longitudinal grooves between the eyes; mandibles strigose; antennae pubescent from 5th segment onwards and reaching about 4.5 segments behind basal margin of pronotum.
Labial palp (fig. 6) with penultimate segment longer than last segment and bearing a variable number of setae from 0-5 (mode = 4) with a variable position :

number of setae	0	1	2	3	4	5
number of individuals (left palp)	1	1	20	144	572	5
number of individuals (right palp)	1	2	27	137	565	11

Reduction of setation in about 22 % of the beetles; few cases of asymmetry; very few cases of hypersetation.

Mentum (fig. 5) with median process varying from sharp (fig. 5) to obtuse; chaetotaxy variable from 0-3 setae (mode = 2) :

number of setae :	0	1	2	3
number of individuals :	184	69	488	2

Obviously the presence of 2 setae is the normal condition (mode) although about 34 % of the beetles shows a reduction in setation, whereas about 10 % shows left/right asymmetry (1 or 3 setae on mentum); only 2 cases of hypersetation moreover in asymmetry.

(c) *Prothorax :*
Pronotum in the mean 1.5 × wider than long; maximal pronotal width at about 38 % of apical margin; apical and basal width of pronotum about equal; basal margin convexe, with somewhat backwards protruding hind angles; lateral margins distinct with or without middle or basal setae :

number of middle setae	0	1	2	3
number of individuals	114	116	510	3
number of basal setae	0	1	2	3
number of individuals	110	81	546	6

Mode (middle setae) = 2; mode (basal setae) = 2; about 15 % of the beetles without setae; 11 % (middle setae) - 16 % (basal setae) shows left/right asymmetry in the presence of these setae.

Pronotal disk smooth and more or less shining; fine punctuation weak to very strong on more apical and basal marginal parts of pronotum.
Posternal process at the top convexe to concave (fig. 9) with or without a brush of setae; lateral margins of central disk weak to sharp.
Profemur relatively slender (about 0.30 × longer than wide); anterior tarsi in male (fig. 4) dilated with a relatively narrow dorsal depression on the second segment; segment 1-3 ventrally bearing a dense brush of setae, exceptionnaly also a small brush on the 4the segment (only in 3 males or less than 1 %).

(d) *Abdomen and elytra :*
Elytra (fig. 1) in the mean 2.85 × longer than wide, with greatest width at about 55 % of the basal margin; elytra with more or less distinct humeral angles, more or less parallel sides; striae regular, punctate; interstices convex; fourth, eighth and twelfth interstices broken into chains by small foveae.
Mesofemur (fig. 7) with external ventral row of setae varying in number from 10-21; this characteristic is more or less positively correlated with standard total length; mesotibia in male (fig. 7) more or less arcuate with a brush of yellow-red hairs at the internal apex and a longer brush at the outer apical half.
Metafemur with external ventral row of setae varying in number from 5-15, again more or less dependent on individual body size (standard total length); metatrochanter with or without seta and rounded at tip :

number of setae on both metatrochanters	0	1	2
number of individuals	698	22	23

3 % of beetles with asymmetry in metatrochanter setation; about 3 % only possesses setae on both metatochanters.

Last sternite with a number of apical setiferous punctures varying from 1 - 11 (males : mode 4; females : mode = 6) :

number of punctures	1	2	3	4	5	6	7	8	9	10	11
number of males		24	22	259	41	19	2	6	3		
number of females	1	2	6	115	61	123	26	18	8	4	3

(e) *Flight wings, indirect flight musculature and metepisternum :*
Flight wings variable in size and shape according to the population : lowland populations mostly possess completely developed wings and are able to fly, whereas highland populations show flight wing polymorphism with wing reduction to different degrees; pl. V, fig. 1 shows the frequency distribution of wing development (% max allometry) which ranges from 35 - 143 % : beetles in the possession of functional flight muscles are shown in white collumns; the other beetles showed autolyzed or completely absent flight wing musculature; flight muscles were

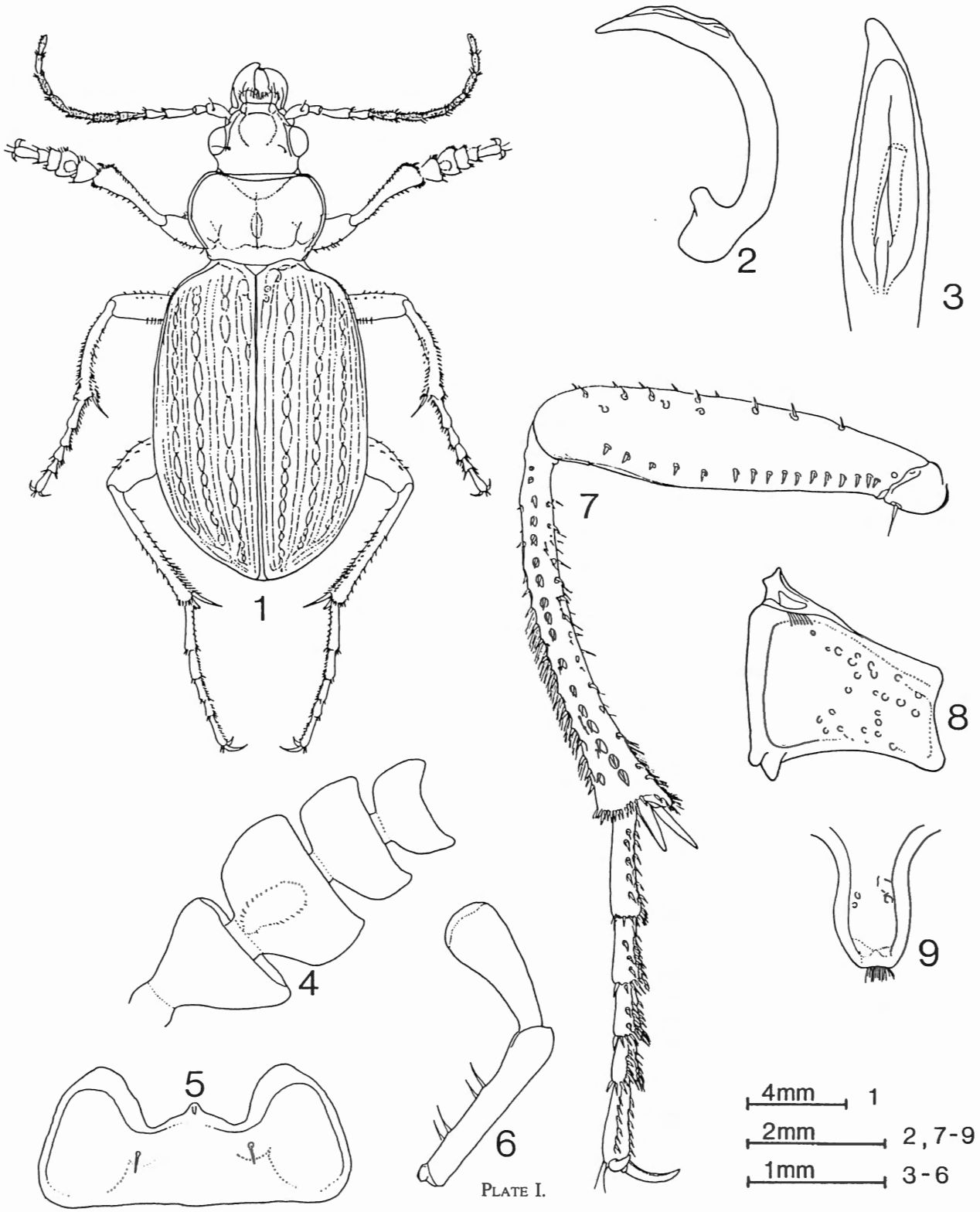

PLATE I.

Calosoma granatense *GEHIN, 1885 : male specimen, Isla Santa Cruz, CDRS, arid vegetation belt, 27.II.1986, collected at light;*

Fig. 1. – *General dorsal view.*
Fig. 2. – *Penis, lateral view.*
Fig. 3. – *Penis, dorsal view at orificium and tip.*
Fig. 4. – *Dorsal view of male protarsal segments 1-4.*
Fig. 5. – *Mentum.*
Fig. 6. – *Last and penultimate segment of labial palp.*
Fig. 7. – *External view of right middle leg.*
Fig. 8. – *Lateral view of metepisternum.*
Fig. 9. – *Prosternal process.*

never functional in beetles with wings below about 87 % of development.
Metepisternum (fig. 8) variable in shape, mostly distinctly longer than wide and with punctures varying in number from 0 - 47 (mean about 19 for males as well as females); mean number of punctures positively related to metepisternal size.

(f) *Male genitalia :*
Penis (figs. 2-3) slender and rather narrow at orificium with a moderately long and more or less arcuated penistip; membraneous part of orificium more or less symmetric.

Penis length (lateral view from tip to basis) :	4.06 (3.52-4.56)
Orificium maximal width (membraneous part) :	0.42 (0.34-0.56)
Width chitinous parts (at orificium) :	0.20 (0.12-0.26)
Penistip length :	0.42 (0.30-0.50)
Minimal penis width at basis (dorsal view)	0.39 (0.34-0.44)

(g) *Female external reproductive structures :*
Gonapophyses of usual type for *Calosoma* with numerous setae at the basis.

Leaf-like terminal process length :	0.96 (0.82-1.12)
Leaf-like terminal process width :	0.50 (0.44-0.57)

(h) *Color of the integument :*
Extremely variable : ground color from shining to dull deep black to dark piceous; surface color from blue to green to coppery iridescent, extremely variable in intensity and distribution; ventral side black to blue-green metallic black to dark piceous or brown and dull without metallic hue; extremities unicolorous black to piceous.

DISTRIBUTION, HABITAT CHOICE AND ZOÖGEOGRAPHIC AFFINITIES

Galápagos : Baltra, Darwin, Eden, Espanola, Fernandina, Floreana, Genovesa, Isabela, (Volcán Alcedo, Volcán Cerro Azul, Volcán Darwin, Volcán Sierra Negra, Volcán Wolf), Marchena, Pinta, Pinzon, Pitt, San Cristóbal, Santa Cruz, Santa Fé, Santiago, Seymour.
Occurs in many habitat types, but especially abundant in the dry arid zone and transition zone at lower altitudes; on Isabela and Fernandina also occurring at higher altitudes in pampa-habitats.
South American mainland : Colombia, Peru (Callao).
Occurring in the entire Galápagos archipelago and probably originating from the South American mainland, although there are no recent records there and there is some doubt on the older records.

Calosoma galapageium Hope, 1838
(Plate II)

TYPE

Galápagos : Isla Santiago(?) (one male, holotype, 1835) : "in the central part of one of the Islands of the Galápagos Archipelago", British Museum Nat. Hist, of London.

SYNONYMS AND REFERENCES

Calosoma galapageium Hope, 1838 : p. 130.
Calosoma galapageium : Van Dyke (1953), pp. 11-12, pl. 1, fig. 6.
Calosoma galapageium : Linsley & Usinger (1966). p. 140.
Castrida galapageium : Basilewsky (1968), pp. 203-204.
Castrida galapageium : Linsley (1977), p. 19.
Castrida galapageium : Franz (1985), p. 76.
Castrida galapageium : Moret (1986), p. 94.

MATERIAL EXAMINED

Detailed data and biometrics were gathered from 19 males and 13 females collected at higher altitudes near and at the summit of Isla Santiago.

DIAGNOSIS

This species can be distinguished, also from the closely related *C. granatense,* by means of the male genitalia, especially by the penistip which is shorter as compared to all other *Calosoma* species of Galápagos. Externally only distinguishable by means of discriminant function analysis based on a combination of several characters.

DESCRIPTION

(a) *General size and shape :*
Standard total length :
males : 16.79 (15.17-18.17) (n = 19)
females : 17.59 (15.84-18.67) (n = 13)
Maximal width (elytra) :
males : 6.90 (6.16-7.50)
females : 7.48 (6.83-8.16)
Body shape : cfr. fig. 1; abdomen with elytra in the mean 1.45 × wider than pronotum.

(b) *Head :*
Moderately robust, in the mean 0.76 × longer than wide; eyes prominent; frons with at each side a single supraorbital puncture inside eye; distinct fine punctuation on the head capsule with some larger punctures between the eyes; short and obsolete dorsal longitudinal grooves between the eyes; mandibles strigose; antennae pubescent from 5th segment onwards and reaching about 3 segments behind basal margin of pronotum.
Labial palp (fig. 6) with penultimate segment longer than last segment and bearing a variable number of setae from 2-5 (mode = 4) with a variable position :

number of setae :	2	3	4	5
number of individuals (left palp)	2	7	22	1
number of individuals (right palp)		8	24	

Reduction of setation in about 28 % of the beetles, mostly in asymmetry.

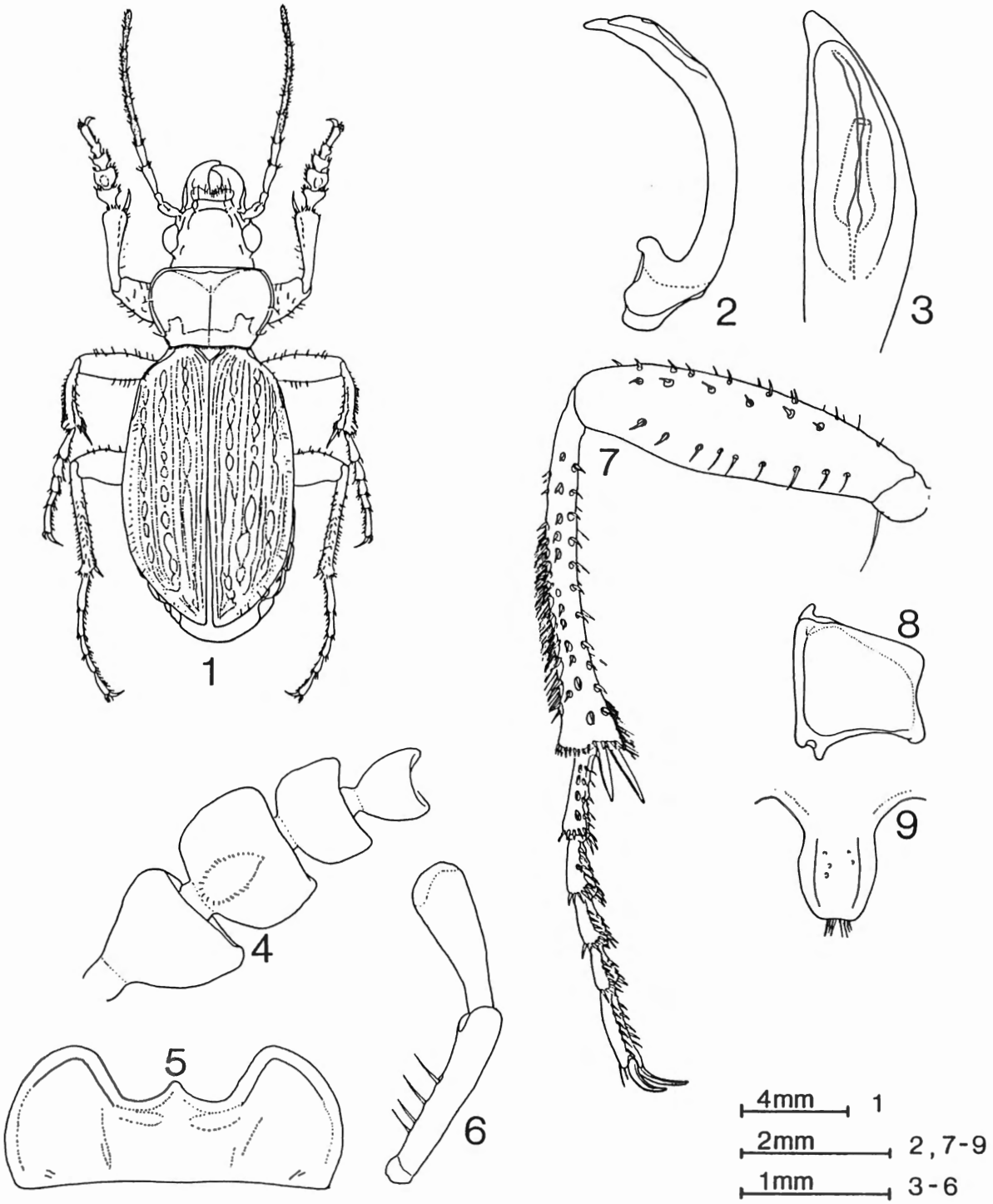

PLATE II.

Calosoma galapageium *HOPE, 1838 : male specimen, Isla Santiago, 820 m, near summit of the island, pampa vegetation, 7.III.1986; see legend plate I for further explanation.*

Mentum (fig. 5) with median process more or less sharp (fig. 5); chaetotaxy variable from 0-2 setae (mode = 0) :

number of setae	0	1	2
number of individuals :	14	8	10

Reduction in about 70 % of the beetles; about 25 % left/right asymmetry.

(c) *Prothorax :*

Pronotum in the mean 1.52 × wider than long; maximal pronotal width at about 37 % of apical margin; apical width of pronotum about 1.1 × wider than basal width; apical margin straight to concave; basal margin more or less convexe, with only very slightly backwards protruding hind angles; lateral margins distinct, always with middle and basal setae :

number of middle setae	2	3	4
number of individuals	31	1	
number of basal setae	2	3	4
number of individuals	29	2	1

Mode (middle setae) = 2; mode (basal setae) = 2; only about 6 % of the beetles shows hypersetation, mostly in asymmetry.

Pronotal disk smooth and more or less shining; fine punctuation weak on the basal marginal parts of the pronotum. Prosternal process at the top straight to slightly concave (fig. 9) with a brush of setae; 1 specimen with a seta on the central disk; lateral margins of central disk weak to sharp.
Profemur somewhat robust (about 0.33 × longer than wide); anterior tarsi in male (fig. 4) dilated (segments 1-3 only) and with a relatively narrow dorsal depression on the second segment; 4th segment about as long as wide; segment 1-3 ventrally bearing a dense brush of setae.

(d) *Abdomen and elytra :*
Elytra (fig. 1) in the mean 3.0 × longer than wide, with greatest width at about 53 % of the basal margin; elytra with somewhat less distinct humeral angles, sides more or less evenly arcuated; striae regular, more or less punctate, more or less obsolete near the margins of the elytra; interstices convexe; fourth, eighth and twelfth interstices broken into chains by small foveae, in many specimens somewhat irregular near the margins of the elytra.
Mesofemur (fig. 7) with external ventral row of setae varying in number from 9-15; mesotibia in male (fig. 7) arcuate with a brush of yellow-red hairs at the internal apex and a longer brush at the outer apical half.
Metafemur with external ventral row of setae varying in number from 6-12; metatrochanter mostly without seta and rounded at tip :

number of setae on both metatrochantes	0	1	2
number of individuals	28	3	1

9 % of beetles with asymmetry in metatrochanter setation; about 3 % only possesses setae on both metatrochanters.

Last sternite with a number of apical setiferous punctures varying from 4 - 9 (males : mode = 4; females : mode = 6) :

number of punctures	4	5	6	7	8	9
number of males	16	2	1			
number of females	1	3	5	1	2	1

(e) *Flight wings, indirect flight musculature and metepisternum :*
Flight wings reduced to different degrees but probably never any longer functional; pl. V, fig. 2 shows the frequency distribution which ranges from 11 - 25 % of maximal wing development; one beetle in the possession of functional flight muscles showed relatively larger wings (53 %); all other beetles with wing musculature completely absent.
Metepisternum (fig. 8) about quadrate and with relatively few punctures varying from 0-21 (mean about 2 for males, and about 6 for females); mean number of punctures positively related to metepisternal size.

(f) *Male genitalia :*
Penis (figs. 2-3) more or less robust and rather wide at orificium, with a very short penistip; membraneous part of orificium asymmetric.

Penis length (lateral view from tip to basis) :	4.14 (4.04-4.40)
Orificium maximal width (membraneous part) :	0.49 (0.44-0.52)
Width chitinous parts (at orificium) :	0.22 (0.16-0.26)
Penistip length :	0.24 (0.20-0.28)
Minimal penis width at basis (dorsal view) :	0.38 (0.36-0.40)

(g) *Female external reproductive structures :*
Gonapophyses of usual type for *Calosoma* with numerous setae at the basis; shape somewhat more slender as in the other *Calosoma* species.

Leaf-like terminal process length :	1.00 (0.90-1.04)
Leaf-like terminal process width :	0.45 (0.42-0.48)

(h) *Color of the integument :*
Ground color brownish black to piceous; surface colour : convexe surfaces with only slight green-blue to blue reflection; depressions somewhat more pronounced iridescent; ventral side brown to piceous; extremities unicolorous brown to piceous.

DISTRIBUTION, HABITAT CHOICE AND ZOÖGEOGRAPHIC AFFINITIES

Santiago, restricted to open grassy vegetation in the higher parts of the island; especially abundant at the summit.
Only known from the Galápagos.

Calosoma leleuporum (Basilewsky, 1968)
(Plate III)

TYPE

Galápagos : Isla Santa Cruz (holotype male, paratype male, 12-17.II.1965), "cratères du sommet"; K.B.I.N., Brussels.

SYNONYMS AND REFERENCES

Castrida leleuporum Basilewsky, 1968 : pp. 200-203, figs. 2, 3.
Castrida leleuporum : Linsley (1977), p. 20.
Castrida leleuporum : Franz (1985), p. 76.
Castrida leleuporum : Moret (1986), pp. 93-94.

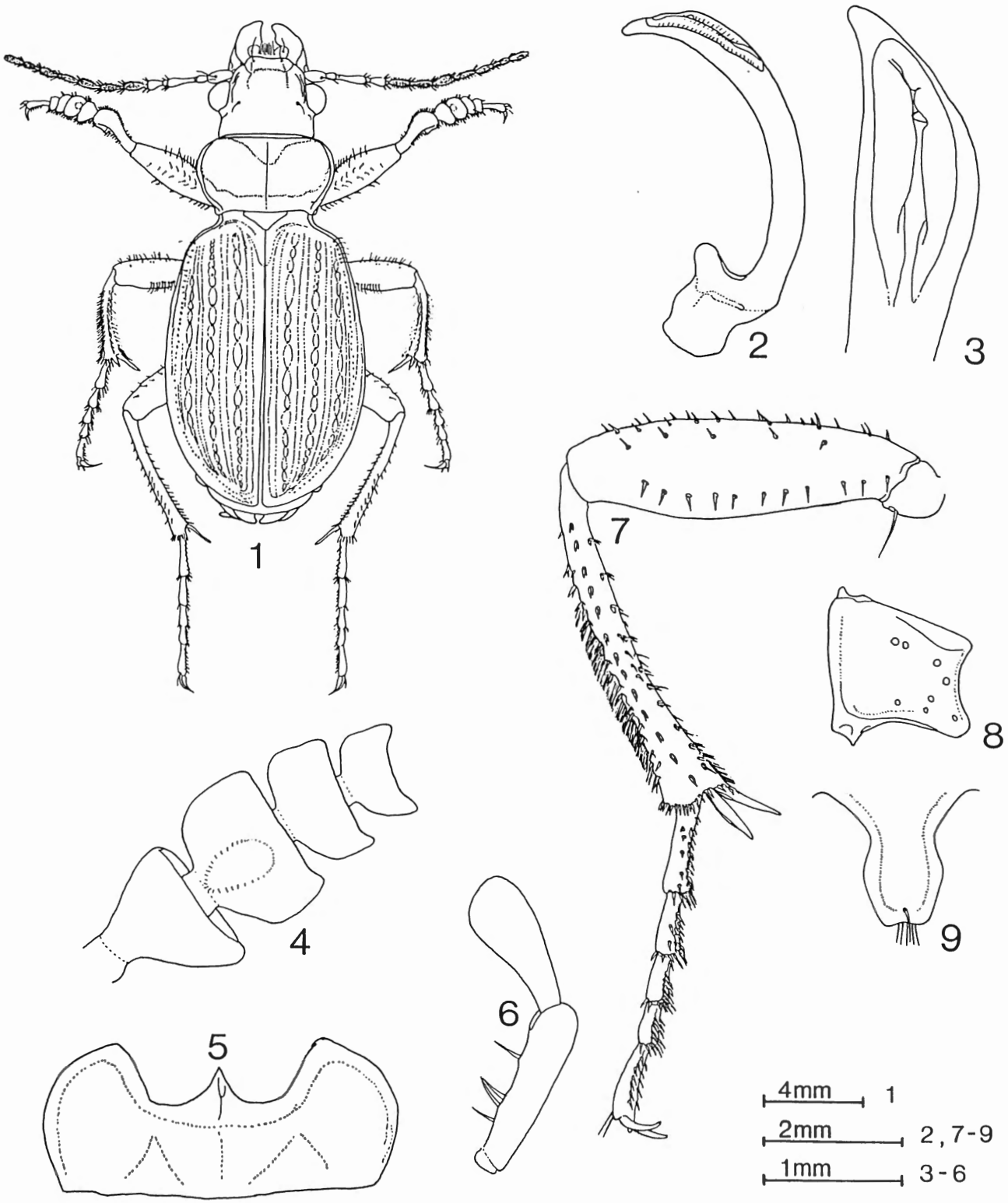

PLATE III.

Calosoma leleuporum *(BASILEWSKY, 1868) : male specimen, Isla Santa Cruz, 670 m, near summit of the island in fern-sedge vegetation belt, 13.III.1986; see legend plate I for further explanation.*

MATERIAL EXAMINED

Detailed data and biometrics were gathered from 38 males and 27 females collected near or at the summit of Isla Santa Cruz; in addition 54 specimens were identified without detailed biometrics and dissections.

DIAGNOSIS

Differing from the other *Calosoma* species of Galápagos by the relatively wider head and apical part of pronotum and by the male genitalia which are large and wide near the tip; males always possess a dense brush of setae on 4 protarsal segments as compared to 3 segments in the other species (exceptionally also a small fourth in *C. granatense*).

DESCRIPTION

(a) *General size and shape :*
Standard total length :
males : 18.27 (16.84-19.70) (n = 38)
females : 19.61 (18.34-21.17) (n = 27)
Maximal width (elytra) :
males : 7.78 (7.00-8.50)
females : 8.51 (8.00-9.33)
Body shape : cfr. fig. 1; abdomen with elytra in the mean 1.45 × wider than pronotum.

(b) *Head :*
Robust, in the mean 0.62 × longer than wide; eyes prominent; frons with at each side a single supra-orbital puncture inside eye; distinct fine punctuation on the head capsule with many larger punctures between the eyes; distinct but short dorsal longitudinal grooves between the eyes; mandibles strigose; antennae pubescent from 5th segment onwards and reaching about 4 segments behind basal margin of pronotum.
Labial palp (fig. 6) with penultimate segment longer than last segment and bearing a variable number of setae from 2-6 (mode = 4) with a variable position :

number of setae	2	3	4	5	6
number of individuals (left palp)	2	4	49	9	1
number of individuals (right palp)	1	4	50	7	3

Reduction of setation in about 9 % of the beetles; few cases of asymmetry; 15 % of beetles with hypersetation.

Mentum (fig. 5) with median process sharp (fig. 5); chaetotaxy variable from 0-3 setae (mode = 0) :

number of setae	0	1	2	3
number of individuals	38	7	19	1

Reduction in about 69 % of the beetles; about 12 % shows left/right asymmetry.

(c) *Prothorax :*
Pronotum in the mean 1.65 × wider than long; maximal pronotal width at about 35 % of apical margin; apical width of pronotum about 1.22 × wider than basal width; apical margin straigth; basal margin more or less convexe, with slightly backwards protruding hind angles; lateral margins distinct, always with middle and basal setae :

number of middle setae	1	2	3	4	5
number of individuals	1	56	7		1
number of basal setae	1	2	3	4	5
number of individuals	2	55	8		

Mode (middle setae) = 2; mode (basal setae) = 2; about 12 % of the beetles shows hypersetation, always in asymmetry.

Pronotal disk smooth; weak punctuation only on apical and basal marginal parts of the pronotum.
Prosternal process at the top mostly slightly concave (fig. 9) with a brush of setae; in several specimens also a seta on the central disk; lateral margins of central disk weak to sharp.
Profemur moderately robust (about 0.34 × longer than wide); anterior tarsal segments in male (fig. 4) all dilated and with a relatively narrow dorsal depression on the second segment; segments 1-4 ventrally bearing a dense brush of setae.

(d) *Abdomen and elytra :*
Elytra (fig. 1) in the mean 2.83 × longer than wide, with greatest width at about 52 % of the basal margin; elytra with somewhat less distinct humeral angles, sides more or less evenly arcuated; striae regular, punctate; interstices convexe; fourth, eighth and twelfth interstices broken into chains by small foveae.
Mesofemur (fig. 7) with external ventral row of setae varying in number from 9-16; mesotibia in male (fig. 7) slightly arcuate with a reduced and indistinct brush of yellow-red hairs at the internal apex and a long brush at the outer apical half.
Metafemur with external ventral row of setae varying in number from 5-11; metatrochanter mostly without seta and rounded at tip :

number of setae on both metatrochanters	0	1	2
number of individuals	61	2	2

3 % of beetles with asymmetry in metatrochanter setation; about 3 % only possesses setae on both metatrochanters.

Last sternite with a number of apical setiferous punctures varying from 2 - 10 (males : mode = 4; females : mode = 6) :

number of punctures	2	3	4	5	6	7	8	9	10
number of males	1	1	17	4	6	3	5	1	
number of females			3	3	7	3	5	3	3

About 50 % of beetles with hypersetation; 28 % with left/right asymmetry.

(e) *Flight wings, indirect flight musculature and metepisternum :*

Flight wings reduced to a relatively high degree and probably never any longer functional; pl. V, fig. 3 shows the frequency distribution which ranges from 9 - 35 % of maximal wing development; all beetles with wing musculature completely absent.

Metepisternum (fig. 8) somewhat longer than wide and with a number of punctures varying from 0-37 (mean about 11 for males as well as females); mean number of punctures positively related to metepisternal size.

(f) *Male genitalia :*

Penis (figs. 2-3) robust and wide at orificium, with a moderately short penistip; membraneous part of orificium asymmetric.

Penis length (lateral view from tip to basis) :	4.54 (4.08-4.92)
Orificium maximal width (membraneous part) :	0.55 (0.50-0.60)
Width chitinous parts (at orificium) :	0.23 (0.18-0.28)
Penistip length :	0.34 (0.28-0.38)
Minimal penis width at basis (dorsal view) :	0.41 (0.38-0.44)

(g) *Femal external reproductive structures :*

Gonapophyses of usual type for *Calosoma* with numerous setae at the basis; shape somewhat more slender as in *Calosoma granatense*.

Leaf-like terminal process length :	1.05 (0.94-1.14)
Leaf-like terminal process width :	0.50 (0.46-0.56)

(h) *Color of the integument :*

Ground color shining deep black to brownish black; surface colour : convexe surfaces with slight yellow-green reflection; depressions deep blue, blue-green to golden-green iridescent; ventral side black-brown to piceous; extremities unicolorous dark piceous to piceous.

DISTRIBUTION, HABITAT CHOICE AND ZOÖGEOGRAPHIC AFFINITIES

Santa Cruz, only in the highlands; especially numerous in *Sphagnum* bogs and humid grasslands.

Only known from the Galápagos.

Calosoma linelli MUTCHLER, 1925
(Plate IV)

TYPE

Galápagos : Isla San Cristóbal (1891, one male, holotype); U.S. National Museum, Washington.

SYNONYMS AND REFERENCES

Calosoma galapageium LINELL, 1898 : p. 250 (non HOPE).
Calosoma linelli MUTCHLER, 1925 : pp. 222-223.
Calosoma (Microcalosoma) linelli : BREUNING (1927), p. 123.
Calosoma (Microcalosoma) linelli : JEANNEL (1940), p. 99.
Calosoma linelli : VAN DYKE (1953), pp. 12-13, pl. 1, fig. 7.
Calosoma (Microcalosoma) linelli : GIDASPOW (1963), pp. 284-285, figs. 8, 12, 33, 36, 57, 58, 84.
Calosoma linelli : LINSLEY & USINGER 1966), p. 141.
Castrida linelli : BASILEWSKY (1968), pp. 204-206.
Castrida linelli : LINSLEY (1977), p. 20.
Castrida linelli : FRANZ (1985), p. 76.
Castrida linelli : MORET (1986), pp. 94-95.

MATERIAL EXAMINED

Detailed data and biometrics were gathered from 8 males and 1 female collected in the highlands close to lake El Junco on San Cristóbal.

DIAGNOSIS

Smallest species of the genus in Galápagos with a relatively wider pronotum and relatively shorter and more or less ovoid elytra; male genitalia small and narrow with relatively long and pecular tip.

DESCRIPTION

(a) *General size and shape :*

Standard total length :
males : 12.38 (11.17-13.00) (n = 8)
females : 12.67 (n = 1)
Maximal width (elytra) :
males : 5.60 (5.16-6.00)
females : 5.84
Body shape : cfr. fig. 1; abdomen with elytra in the mean only 1.36 × wider than pronotum.

(b) *Head :*

More or less robust, in the mean 0.66 × longer than wide; eyes less prominent; frons with at each side a single supraorbital puncture inside eye; fine punctuation on the head capsule; indistinct dorsal longitudinal grooves between the eyes; mandibles indistinctly strigose; antennae pubescent from 5th segment onwards and reaching about 2 segments behind basal margin of pronotum.

Labial palp (fig. 6) with penultimate segment longer than last segment and bearing a reduced number of 2-3 setae :

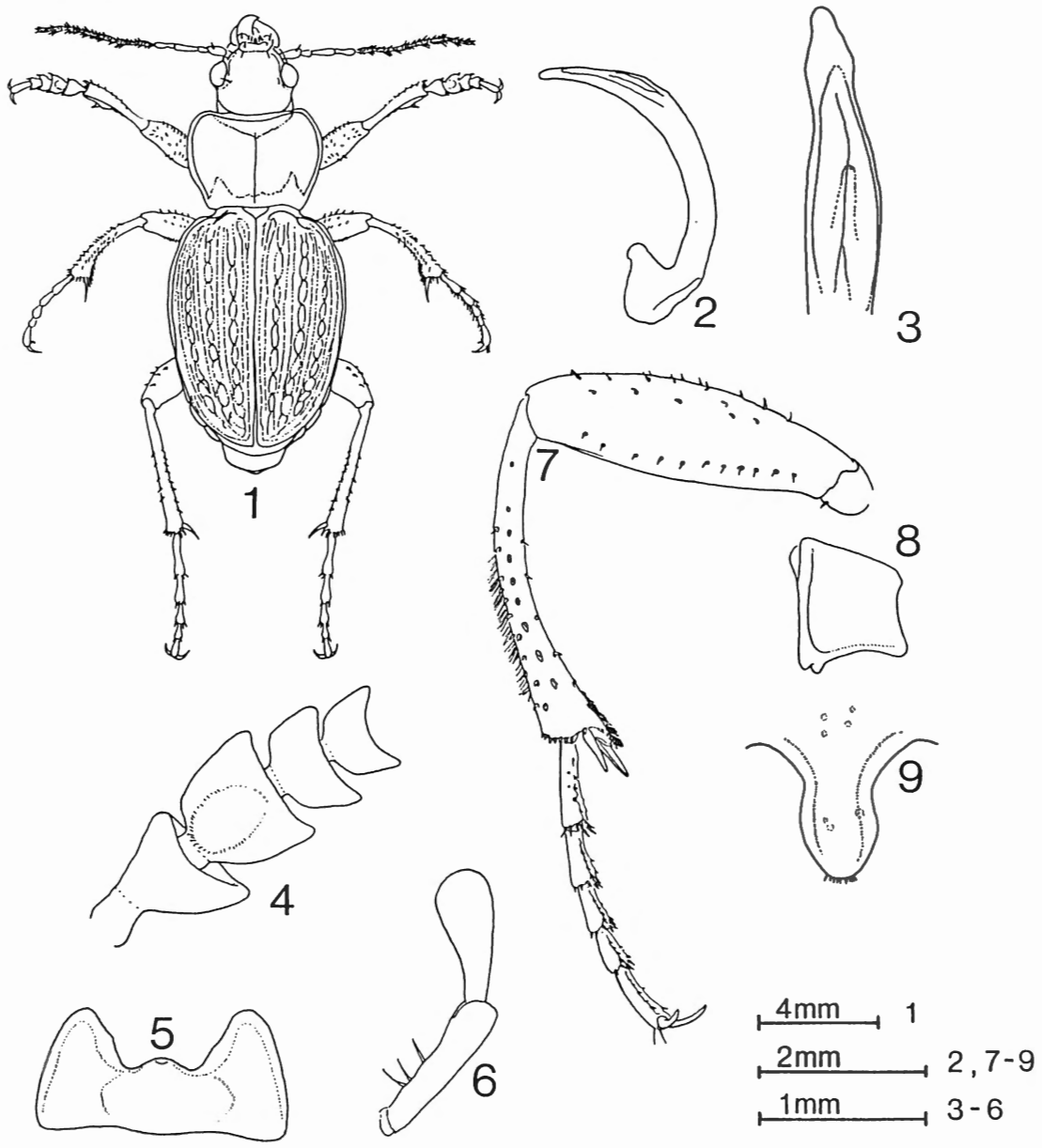

PLATE IV.

Calosoma linelli *MUTCHLER, 1925 : male specimen, Isla San Cristóbal, 570 m, near El Junco, pampa vegetation with some shrubs, 27.III.1986; see legend plate I for further explanation.*

number of setae	2	3
number of individuals (left palp)	3	6
number of individuals (right palp)	7	2

Asymmetry in most beetles.

Mentum (fig. 5) with median process reduced and obtuse (fig. 5) and without setae.

(c) *Prothorax :*
Pronotum in the mean 1.46 × wider than long; maximal pronotal width at about 38 % of apical margin; apical width somewhat smaller than basal width; apical margin slightly concave; basal margin more or less straight, with only slightly backwards protruding hind angles; lateral margins distinct, without middle or basal setae (except 1 basal seta on one side only in the female studied).
Pronotal disk smooth; weak punctuation only on basal marginal parts of the pronotum.
Prosternal process at the top convexe or straight and narrow (fig. 9) with a brush of relatively short setae; no setae on the central disk and only weakly delimited lateral margins.
Profemur moderately robust (about 0.36 × longer than wide); anterior tarsal segments in male (fig. 4) all dilated and with a relatively wide dorsal depression on the second

segment; segments 1-3 ventrally bearing a dense brush of setae.

(d) *Abdomen and elytra :*
Elytra (fig. 1) in the mean 2.63 × longer than wide, with greatest width at about 41 % of the basal margin only; elytra without distinct humeral angles, sides evenly arcuated; striae regular but shallow, more or less punctate; interstices only slightly convexe; fourth, eighth and twelfth interstices broken into chains by small foveae.
Mesofemur (fig. 7) with external ventral row of setae varying in number from 10-15; mesotibia in male (fig. 7) strongly arcuate with a brush of yellow-red hairs at the internal apex and a longer brush at the outer apical half.
Metafemur with external ventral row of setae varying in number from 5-11; metatrochanter always without seta and rounded at tip.
Last sternite with a number of apical setiferous punctures varying from 2 - 6 (males : mode = 4; female 6) :

number of punctures	2	3	4	5	6
number of males	1		7		
number of females					1

(e) *Flight wings, indirect flight musculature and metepisternum :*
Flight wings extremely reduced to a narrow rudiment; pl. V, fig. 4 shows the frequency distribution which ranges from 0.8 - 2.3 of maximal wing development; all beetles with wing musculature completely absent.
Metepisternum (fig. 8) distinctly wider than long and always without distinct punctures.

(f) *Male genitalia :*
Penis (figs. 2-3) short and narrow at orificium, with a relatively long penistip with a pecular shape; membraneous part of orificium more or less symmetric.

Penis length (lateral view from tip to basis) :	3.15 (3.00-3.32)
Orificium maximal width (membraneous part) :	0.30 (0.26-0.32)
Width chitinous parts (at orificium) :	0.12 (0.10-0.14)
Penistip length :	0.39 (0.36-0.42)
Minimal penis width at basis (dorsal view) :	0.30 (0.28-0.32)

(g) *Female external reproductive structures :*
Gonapophyses of usual type for *Calosoma* with numerous setae at the basis; shape very robust as compared to all other *Calosoma* species from Galápagos.

Leaf-like terminal process length :	0.66
Leaf-like terminal process width :	0.38

(h) *Color of the integument :*
Ground color shining to dull brown to reddish brown; surface color : convexe surfaces with more or less coppery red-yellow reflection; depressions coppery to yellow-green iridescent; ventral side reddish brown, darker near segment margins; extremities unicolorous light rufous.

DISTRIBUTION, HABITAT CHOICE AND ZOÖGEOGRAPHIC AFFINITIES

San Cristóbal, only in the highlands, mainly in open pampa-habitats.
Only known from the Galápagos.

Discussion

The redescriptions given above do agree with a lot of details mentioned by Basilewsky (1968). A comparison with Gidaspow (1963) is much more difficult, because in that paper *C. granatense* and *C. galapageium* were treated as one species. Nevertheless a number of hitherto not used or previously unprecisely described characteristics for the identification of the *Calosoma* species of Galápagos are elaborated here. The study of morphological variability extends further than in previous papers because of the very abundant material at hand which was moreover collected on more of the different islands of the entire Galápagos archipelago.
To our opinion, the most important contribution in our work concerns the detailed description and study of variability in size and shape of the male genitalia in these species. These characters do enable an easy species identification (especially when combining several independant measures in discriminant function analyses, cfr. Desender, in prep.) and were previously never used. One exception is the species *C. linelli*, wherefrom Gidaspow (1963) described the pecular shape of the penistip. We also made an attempt to use female reproductive structures in the diagnosis of the species. Spermathecae were prepared in each of the species but were very simple in structure and similar in all specimens studied. Gonapophyses showed some minor differences, be it with a rather high variability, overlapping between most species. Only the species *C. linelli* (but with only one female at hand) differed clearly from other species in the shape of the terminal leaf-like process of the gonapophyse. Gidaspow (1963) already described its shape as "slim and pointed"; from our measurements we can deduce however that this leaf-like process is much stouter as compared to all other *Calosoma* species from Galápagos.
The previous descriptions for *C. galapageium* in literature were very short, without any details on chaetotaxy or genitalia, with only a few data on body shape characteristics and only very few illustrations : these descriptions were indeed only based on 2 male specimens. The male in that species possesses a brush of setae on the ventral surface of 3 protarsal segments; Basilewsky (1968) erroneously mentioned these brushes on 4 segments which is not the case on all beetles checked by us, neither on the holotype specimen (collected by Charles Darwin), which we had the opportunity to check. In addition, we observed that a small number of *C. granatense*, a species with normally 3 such segments, also possessed a small additional brush on the 4th segment. On the other hand, we could confirm Basilewsky (1968) in the observation of 4 segments with

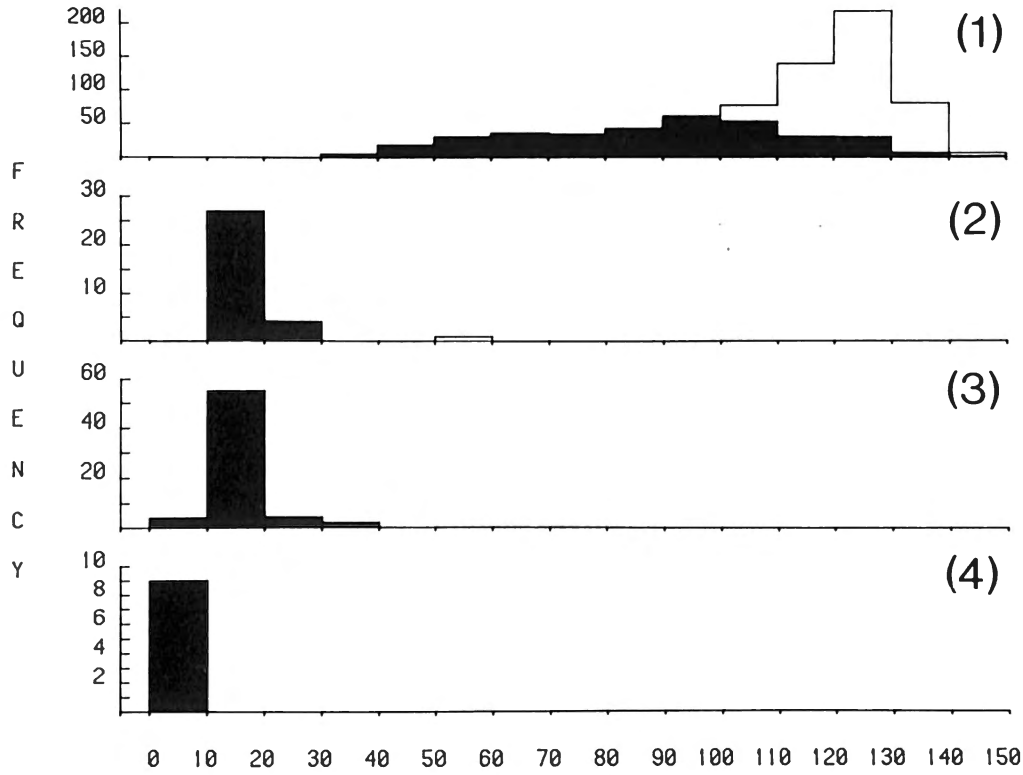

PLATE V.

Frequency distribution of wing development (% max allometry) in (1) Calosoma granatense, *(2)* C. galapageium, *(3)* C. leleuporum *and (4)* C. linelli*; white collumns : individuals with functional indirect flight muscles; black collumns : beetles with autolyzed or completely absent indirect flight muscles.*

a ventral brush in all specimens of *C. leleuporum*. For *C. linelli* the older descriptions were based on 3 specimens only. In that species, as well as in *C. galapageium* and *C. leleuporum* we had much larger samples in our collections and were thus able to define much more precisely the infraspecific variation in morphological features.

Dispersal power characteristics were not previously measured or studied in much details. From our results it follows that *C. granatense* has to be defined as a wing polymorphic beetle. As far as we know, this is the first case of wing polymorphism reported for a beetle species in Galápagos. Variation of wing development indeed continuously covers a very wide range in size and shape, sometimes even in single populations (DESENDER, in prep.). Although there are differences in mean wing development between the 4 *Calosoma* species mentioned, one can only identify with certainty *C. linelli* on the basis of this characteristic; specimens with completely developed hind wings on the other hand all belong to *C. granatense*. As shown above, *C. linelli* is not really apterous, as mentioned by several other authors, but brachypterous.

Our numerous data on chaetotaxy of pronotum, mentum, labial palp, profemur, metafemur, metatrochanter and last sternite show that most of these characters do not aid in species recognition, although we can observe a general trend of reduction in setation in *C. linelli* as opposed to the other species. There is, as already recognized by GIDASPOW (1963) and BASILEWSKY (1968) a pronounced individual variation in setation within most species. Moreover, by separatedly counting left and right setation – as was not done in previous taxonomic work on these beetles –, we observed a lot of cases of asymmetry which show that these characteristics can be influenced to a large extent by epigenetic factors. In itself this is a fascinating observation, which we will analyse on population level in the future and which could have resulted from isolation, small populations and inbreeding actions. It does however make these characters difficult to use in taxonomic work. Frequency distributions of these meristic characters were not mentioned in earlier publications. Our results reveal in many cases a much more extended variability as previously observed. This is of course most probably due to our abundant and diversified study material.

We do agree with BASILEWSKY (1968) that it is not justified to classify *C. linelli* in another subgenus as the other species. All species are clearly related, but show modifications of their body shape to a varying degree. Many of these changes can be related to a decreasing dispersal power, general size and a corresponding relative shortening of the hind body of these beetles. As already mentioned, at the time being, we propose only to use the genusname *Calosoma* WEBER, 1801 for these beetles.

Data on morphometrics will be much more elaborated in a second paper (DESENDER & DE DIJN, in prep.) on species identification by means of discriminant functions analyses. In other future papers we intend to go into more details on infraspecific morphological variation, dispersal power, habitat preference and population biology, adaptive radiation, speciation hypotheses and other aspects of the evolutionary ecology of these fascinating animals from Galápagos.

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