

# The Macaronesian *LAPAROCERUS*

NEW

**Campeones de la biodiversidad.** Un género de gorgojos bate récord de radiación evolutiva en islas oceánicas de la Macaronesia

¿PORQUÉ HAY TANTOS *LAPAROCERUS*? El enjambre de 261 especies y subespecies presentes en Madeira, Salvajes y Canarias suponen el resultado de un proceso combinado de evolución adaptativa y geográfica en archipiélagos volcánicos antiguos, que cuentan con muchas islas compartimentadas ecológicamente y sujetas a una dinámica de construcción y desmantelamiento. Una minuciosa prospección a lo largo de veinte años y los análisis filogenéticos basados en el ADN revelan la monofilia del grupo, sus relaciones internas y las rutas más plausibles de colonización, que comenzó en el Mioceno tardío.

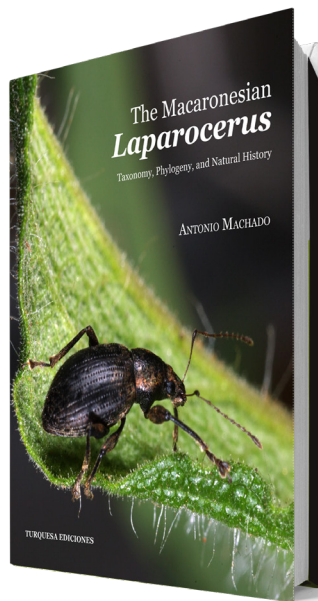
A lo largo de unos 9 millones de años las sucesivas radiaciones evolutivas generaron varios subgrupos monofiléticos, 25 en total, que ahora se reconocen como subgéneros de *Laparocerus*. Las rutas de colonización, cambios de hábitats, poblaciones aisladas por el volcanismo, dispersión por megadeslizamientos y otros factores importantes en la especiación, se discuten en detalle.

Los *Laparocerus* son coleópteros incapaces de volar y la mayoría de los taxones son exclusivos de una sola isla —diecisiete en total— habiendo ocupado prácticamente todos los hábitats, desde los matorrales costeros hasta el bosque esclerófilo, la laurisilva (bosque de nieblas), los pinares, el matorral de cumbre y el medio subterráneo (incluidos los tubos volcánicos). Reflejan así una extraordinaria plasticidad morfológica y ecológica. Solo dos especies habitan el noroeste de África, el continente más próximo, pero se trata de una retrocolonización desde Canarias. La isla más rica es Tenerife (2034 km<sup>2</sup>) con 68 especies y subespecies. En general existe una proporción de un *Laparocerus* endémico por cada 31 km<sup>2</sup>, récord no alcanzado por ningún otro grupo animal o vegetal en la Macaronesia.

Si las islas oceánicas han sido consideradas tradicionalmente como laboratorios de la evolución y “máquinas de producir especies”, los *Laparocerus* se perfilan como un grupo modelo ideal para profundizar en los fenómenos de dispersión y especiación de todo tipo. Un grupo así ofrece una imagen de grano fino de la evolución en

marcha. Para facilitar estos estudios, el presente libro de A. Machado aporta una revisión taxonómica completa del género *Laparocerus*, con descripción de las 264 especies y subespecies —duplicando el número de las previamente conocidas—, con claves de identificación, 374 macrofotografías de los imagos, 50 láminas con dibujos de las genitalias y otras piezas internas y 47 mapas de distribución. También incluye un detallado estudio morfológico (13 láminas) de una especie, incluidos los estadios preimaginales; así como capítulos dedicados a la biología reproductiva, ecología (plantas alimenticias, hábitats, etc.) y comportamiento. En resumen, su historia natural.

El autor espera que en el futuro próximo los *Laparocerus* acaben por compartir el podio de los estudios de evolución insular con los pinzones de Darwin o las *Drosophila*.



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## HISTORY

1.2 | HISTORY



Fig. 18. Daniel Louis Uyttenboogaart (b. Amsterdam, 1872–1947).

1935, Liebmann 1939, Janson 1940, Fernández 1951, Gardner & Classy 1962, Cossens 1864, Palm 1867, Israelson et al. 1982, Erber & Hinterseher 1988, Erber 1990, and Franz 1996), or in ecological studies that survey specific habitats (e.g. Peraza et al. 1986, Campos et al. 1990). Nonetheless, four authors here not listed deserve special mention, as they have focussed on Curculionidae or directly on *Laparocerus*, describing new taxa, clarifying some synonymies, or enlarging chorological knowledge of the group.

Daniel Louis Uyttenboogaart (Fig. 18) was a wealthy Dutch gentleman trained as lawyer and civil servant, who started visiting the main Canary Islands in relation to maritime commerce, and soon became interested in their beetle fauna. He collected mainly on Tenerife and Gran Canaria together with his wife Helen. He also studied the collections kept in the Madrid Natural History Museum (materials from Escalera and Ignacio Bolívar), the Museum Pietro Rossi at Milano, and the Museum Georg Frey at Basel. In addition, he examined the rich material obtained by M. Charles Alluaud in his expeditions to the Canaries (1889–1890) and to Madeira (1938), stored at the Muséum National d'Histoire Naturelle (Paris), or the Canarian co-

leoptera collected by Richard Frey and Ragnar Storå in 1931, which are kept in the Zoological Museum of the University of Helsinki. As a result, he authored seven *Laparocerus* species and provided the first comprehensive key to the genus (Uyttenboogaart 1929, 1935, 1936, 1937, 1940, Uyttenboogaart & Zumpt 1940). He also proposed the new subgenus *Wollastonicerus*, 1837—replacing *Wollastonia* Uyttenboogaart 1836 (non Heer, 1852)—with the misfortune of not having designated a type species and therefore being an unavailable name.

In his later years, Harald Lindberg (Fig. 19), curator of Botany at the University Museum of Helsinki, took an interest in the study of Coleoptera. He had at hand the copious material collected by his son the professor of Entomology, Håkan Lindberg (Fig. 466-L). Håkan was more interested in Hemiptera, making two visits to Madeira (1957 and 1959) and five to the Canary Islands (between 1947 and 1951). Harald published 5 new *Laparocerus* species in 1950 and 7 more in 1953, all from the latter archipelago. The overall results of the Finnish Canarian expeditions were jointly presented by father and son in 1958, providing a compilation of the 71 *Laparocerus* species and subspecies recorded for the Canaries—including some synonyms—accompanied by small distribution maps.

The first curculionid specialist, properly speaking, who studied the Macaronesian weevil fauna was André



Fig. 19. Harald Lindberg (b. Helsinki, 1871–1963).

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## ETHOLOGY

3.2 | ETHOLOGY

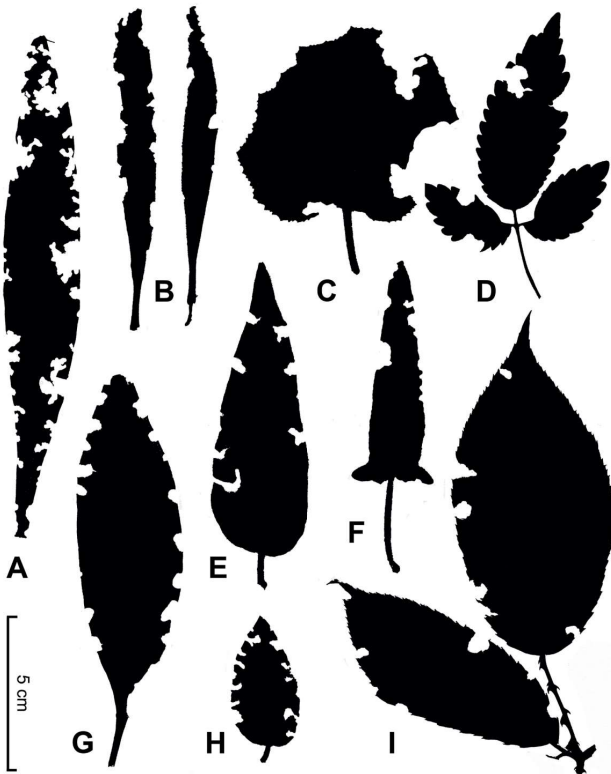
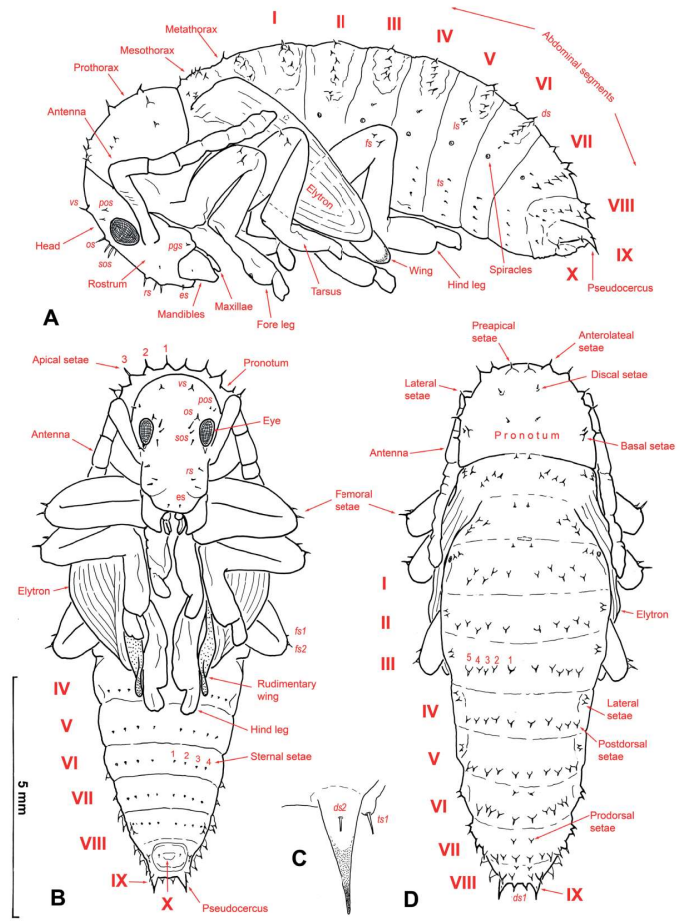


Fig. 62. *Laparocerus* feeding marks on leaves of bushes and small plants.— A: *Laparocerus distortus* on *Euphorbia mellifera* Ait.— B: *Laparocerus bentjeji delicatulus* on *Echium onosmifolium* Webb.— C: *Laparocerus crassus* on *Pericallis appendiculata* L. f.— D: *Laparocerus aeneotinctus femoralis* on *Cedronella canariensis* L.— E: *Laparocerus elongatus mucronatus* on *Gesnouinia arborea* L'Her.— F: *Laparocerus grayanus* on *Salvia canariensis* L.— G: *Laparocerus tingvaro* on *Phyllis nobla* L.— H: *Laparocerus propinquus* on *Cistus symphytifolius* L.— I: *Laparocerus sculptus* on *Rubus bollei* Focke.

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## ANATOMY

2.4 | THE PUPA



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## BIOLOGY

3.1 | BIOLOGY

The copulation lasts several minutes. The male remains in an inclined position on the back of the female's abdomen, holding on with his front and medium legs (Fig. 44-A). This does not prevent the female from moving around, without apparent difficulty. The rear ends of the copulating pair stay rather distant from each other. However, the female projects her ovipositor outwards to embrace the penis (almost half of it), while it is the long everted endophallus that penetrates into the vagina to reach in principle the bursa copulatrix, or its vicinity (Fig. 44-B).

The male may remain on top of the female for a while after having invaginated the aedeagus. Occasionally another male climbs on top of them as an additional partner.

### Oviposition

No oviposition has been observed directly. It occurs during the night. However, in the laboratory, the presence of rows of eggs hidden in folds or crevices of rigid objects such as bark, dry leaves, cracked sticks (Fig. 45 B-D) or the folds of Emden's fans—which were readily used when provided (see Methodology)—suggest that the female uses her very long ovipositor as a flexible tube to look for a convenient shelter for the eggs (Fig. 45-A). These hiding places must be narrow, since the eggs are deposited in rows from the bottom outwards, forming a layer or two, so that only the last rows are exposed, protecting the interior ones. The size

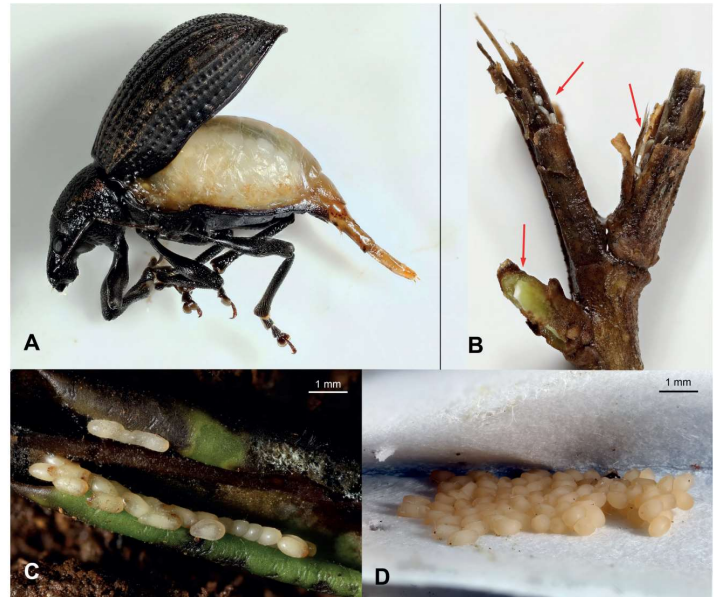


Fig. 45. A: *Laparocerus bellus* (♀) with stretched ovipositor, and elytra uplifted to show abdomen bearing 101 eggs.— B: Eggs (red arrows) of *L. ruteri* hidden in the crevices of a stick.— C: Dead leaf partially unrolled to show hidden clutch (70 eggs) of *L. ruteri*.— D: Fold of a Van Emden fan opened to show a clutch of 92 eggs of *L. bellus* five days after being laid.

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Natural enemies

**Predators.** Phytophagous insects are the basic trophic support for predators specialised in capturing insects, and less so, but important, for many other animals that complement their vegetable diet with animal proteins. In Macaronesia, considering the outstanding abundance and biomass of *Laparocerus*, they are likely one of the key food sources, together with lepidopterans (larvae) and orthopterans. Nocturnal activity, sheltering behaviour, death-feigning and procryptic colouring are indirect indicators of the palatability of the group. However, in the literature there are only a few records of predation on *Laparocerus*, but covering a wide spectrum.

Cott (1934) studied the stomach content of 195 individuals of the introduced Mediterranean tree frog (*Hyla*

*meridionalis* Boettger, 1874) mostly from Gran Canaria, and found 7 specimens (4 mm) of *Laparocerus compactus*; Machado (1985) reports *Laparocerus* remnants in droppings of the El Hierro giant lizard (*Gallotia simonyi* Steindachner, 1889) and the El Hierro common lizard (*Gallotia caesaris* (Lehrs 1914)); Pais and García (2000) found them in pellets of the red-billed chough (*Pyrrhocorax pyrrhocorax barbarus* Vaurie, 1954) on La Palma. On the high mountains of the same island Medina and García (2007) counted 75 *Laparocerus* remnants in droppings of feral cats (*Felis silvestris catus* L. 1759): 7 exx of *L. astralis*, 1 ex of *L. combrecitensis*, 7 exx of *L. laevis*, 1 ex of *L. auarita*, 1 ex of *L. tanausa*, and 69 unidentified *Laparocerus*, covering 10.2% of the total prey surveyed, with a frequency of 6.73%. Stüben (2017) deduced that chitin remnants of *Laparocerus cryptus* found under stones on

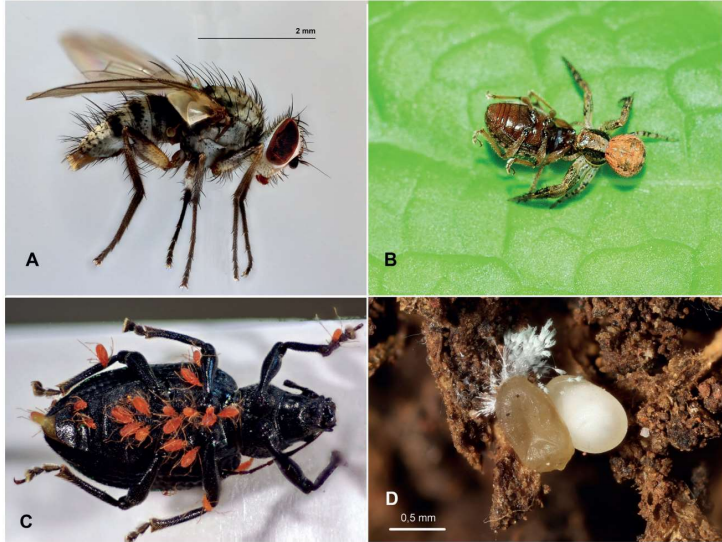


Fig. 72. Natural enemies of *Laparocerus*. A: Endoparasitic *Rondania insularis* (Bigot, 1891) ♀ (Diptera, Tachinidae). B: *Ozyptila* spider (Araneae, Thomisidae) with its prey, *Laparocerus vestitus* (photo M.A. Peña). C: *Laparocerus fernandezii* with ectoparasitic mites *Leptus tenerificus* Hatlinger, 2009 (Acarina: Erythraeidae). D: Eggs of *Laparocerus bellus* infected by *Verticillium* sp. (Fungi: Ascomycota).

DISTRIBUTION & KEYS

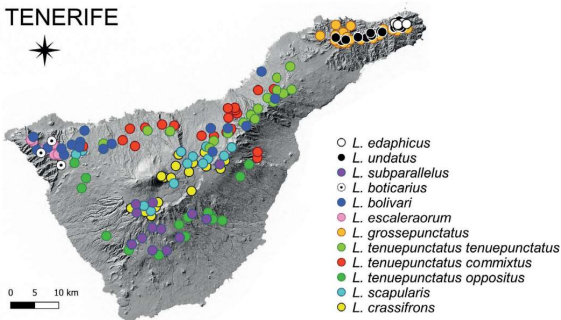


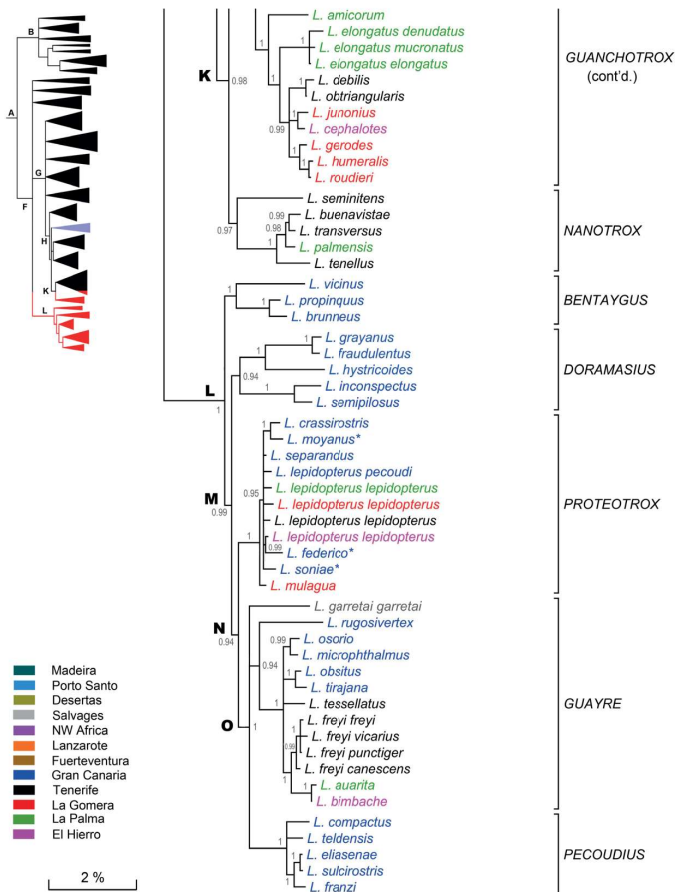
Fig. 334. Distribution of subgenus *Bencomius* on Tenerife.

The species mean genetic divergence within *Bencomius* is 8.4% and, without doubt, its segregation on Tenerife deserves a thorough phylogeographic study.

Key to species

- 1 Antennae with desmomerers 3-7 moniliform and club broad oval; integument lacking scales, only with some erect setae. Inhabiting Tenerife. . . . . *L. edaphicus* [p. 407]
- Antennae with all desmomerers longer than wide and club fusiform; integument with scales (often deliquescent) and soft setae on elytra. . . . . 2
- 2 Elytral interstriae with some separate but distinct punctures (in cases almost effaced on disc, best visible on 5<sup>th</sup> interstria). . . . . 3
- Elytral interstriae lacking distinct punctures (not to be confused with the micropunctules of the reticulate microsculpture, one per cell). . . . . 8
- 3 Size usually > 10.5 mm; scape straight; elytral with distinct humeral callus and surface slightly undulate; protibiae ♂ notably excavate inside. Inhabiting Tenerife. . . . . *L. undatus* [p. 408]
- Size < 10.5 mm; scape clearly arcuate, sinuate or bent; elytra with humeral callus not or weakly developed, and surface not undulate; protibiae at most feebly emarginate. . . . . 4

- 4 Elytra ♂ broader and more acuminate, with punctures on interstriae very conspicuous, large and foveolate, nearly as large as punctures of striae (at least on lateral interstriae); dorsum more or less flattened. . . . . 5
- Elytra ♂ narrower and elongate (L/W= 1.6.5–1.85) with punctures on interstriae shallower and much smaller than punctures of striae; dorsum of elytra convex, not flattened. . . . . 6
- 5 Eyes larger, their length 1.1× the interocular distance; elytral disc little convex; interstitial punctures on entire elytra; setae shorter. Inhabiting Tenerife (Anaga). . . . . *L. grossepunctatus* [p. 410]
- Eyes smaller, their length 0.8× the interocular distance; elytra more convex; interstitial punctures often effaced on disc, particularly on females; setae longer. Size 5.7–9.6 mm Inhabiting Tenerife (outside Anaga and Teno). . . . . *L. tenuipunctatus commixtus* [p. 414]
- 6 Pronotum with sides shortly constricted at base and straight lateral angles; rostrum slightly divergent, with slightly inflate genae; elytra with vermiculate microsculpture. Inhabiting La Palma. . . . . *L. combrecitensis* [p. 417]
- Pronotum with sides barely constricted at base and obtuse lateral angles; rostrum parallel; pregenae not inflated; elytra with irregular polygonal microsculpture. . . . . 7
- 7 Rostrum shorter (L/W= 0.75); elytral setae rather erect, longer than a tarsal claw, distant and regularly aligned



DESCRIPTIONS

*Laparocerus (Laparocerus) chaensis* Uyttenboogaart, 1940

Fig. 85.

ssp. *chaensis* Uyttenboogaart, 1940

*Laparocerus chaensis* Uyttenboogaart, 1940 p. 57 [type: NMNH]; Machado 2006a p. 2010 [syn. *vandeli*] –*Laparocerus morio*, in Wollaston 1854 p. 360 [Ilhéu Chão]; Uyttenboogaart 1947 p. 15 [syn. *chaensis*]. –*Laparocerus (Laparocerus) chaensis chaensis*, in Machado 2008b p. 314, 326 [bona species]; Machado 2013 p. 289; Machado et al. 2017 p. 15; Stüben 2017 p. 71. –*Laparocerus*, in Machado in Borges et al. 2008 p. 317; Machado 2017 p. 283; Stüben 2022 p. 592. = *Laparocerus (Laparocerus) morio vandeli* Roudier, 1958 p. 199 [type Ilhéu Chão, MNHN]; Roudier 1961 p. 63; Roudier 1963 p. 132; Erber & Hinterseher 1988, p. 172; Machado 2006a p. 2010 [lectotype; ⇒ *chaensis* Uyttenboogaart].

TYPE LOCALITY. Ilhas Desertas: Ilhéu de Chão [32°35'12"N 16°32'43"W, 70 m].

**Etymology.** The species is named after the type locality, the islet of Chão, in the Madeiran archipelago, with the suffix *-ensis* (of or from a place) to indicate belonging.

**Description.** Similar to *L. morio*, much smaller in size (length ♂ 5.9–9.2 mm, ♀ 5.7–8.3 mm); males not much larger than females; body shape more oval-elongate or elliptical; pronotum not bulky ahead, smaller (L/W= 0.8 instead of 0.9), more uniformly rounded on sides; elytra never parallel (oval-acuminate, not truncate at apex), widest before middle (about 1.6× width of pronotum), their lateral declivity smoother and microsculpture somewhat stronger, but granules almost absent; setae a trifle longer (about length of a tarsal claw). Legs (♂): metatrochanter protruding backwards as a conspicuous tooth; metatarsomeres 1-2 with internal bristles longer (>length of tarsomere); male metatibiae (Fig. 82 C-D) more pilose and less crenulate internally; outer apical margin moderately expanded outwardly, articular area wider than long, rhomboid shaped; internal emargination angled, forming a blunt heel. Aedeagus: penis body bisinuate in its concave part, with less deflexed, shorter, triangular, and blunt apical plate (dorsal view); endophallus with two basal rows of 30-31 denticles (Fig. 471-B).

**Distribution and ecology.** *Laparocerus chaensis chaensis* inhabits the islets of Chão (0.4 km<sup>2</sup>) and Bugio (3.3 km<sup>2</sup>), in the Desertas, not having been found yet in Deserta Grande, the largest islet located between the other two, and also inhabited by *L. cryptus* (Fig. 80). This is a



Fig. 85. *Laparocerus chaensis chaensis* ♂.

striking case of two related *Laparocerus* species coexisting in the same place, and it is worth investigating if *L. cryptus* was introduced onto Chão, or why *L. chaensis chaensis* is apparently absent on Deserta Grande.

In Chão, it is extraordinarily abundant in the vegetated plateau (40-80 m altitude), particularly in spring and summer (Fig. 5). It can be found aggregated in large numbers under stones. During the night it crawls to feed on shrubs like *Suaeda vera* or *Jasminum odoratissimum*, but not on *Artemisia* or existing crucifers.

**Comments.** The islet samples studied from Ilhéu de Chão and Bugio, in the Desertas, and the Ilhéu do Desembarcadouro in the extreme east of Madeira, cluster together as *L. chaensis* s. l., and show a rather high COI genetic distance from *L. morio* (9.7–11.8%) or from *L. cryptus* (11.6–12.8%), but surprisingly, less from *L. distortus* (4.3–5.0%)

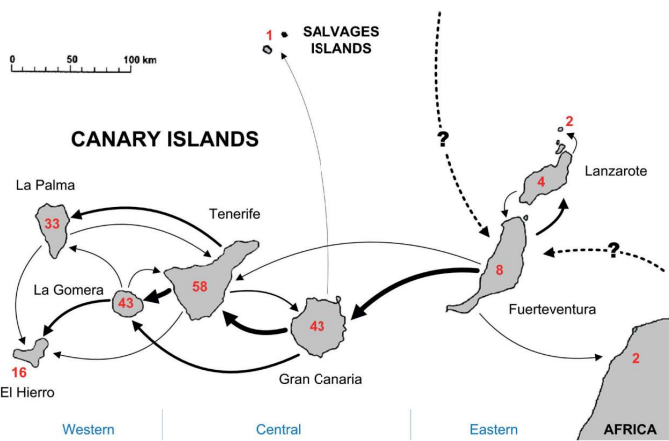


Fig. 449. Hypothetical colonisation pathways of *Laparocerus* weevils in the Canary Islands and Salvages, with numbers of species known from each island.

low the sequence 7.6 Ma > 6.3 Ma > 5.9 Ma > 4.8 Ma. Only *Lichenophagus* seems to have not reached Madeira, whereas *Atlantis*, one of the younger subclades (4.2 Ma), evolved exclusively on the latter island. *Wollastonia* takes a basal position in the Madeiran clade in the mitochondrial phylogram published in Machado et al. (2017) or when adding the COI marker, suggesting that it became extinct on Porto Santo while the clade radiated on Madeira itself much later (3.3 Ma). However, this basal position is taken by *Laparocerus* when adding the nuclear 28S rDNA marker, and it ends up as an unresolved polytomy in the full 6-gene phylogram. There is no information on what Porto Santo and the Desertas looked like in the Tortonian 7.6 Ma ago, and at present they are largely eroded and harbour a depauperate biota. Moreover, missing extinct species may have a significant impact on the deep topology of phylograms.

**THE CANARY ISLANDS.** The Canarian clade tree topology shows a more complex set of sequential polytomies divided into two branches after the initial Node F (7.4 Ma): a first branch with Nodes G-K at 6.7 Ma, 5.5 Ma, 4.7 Ma, 4.4 Ma, and 3.8 Ma (average split delay 0.7 Ma), and a second much younger branch with Nodes L-O at 4.0 Ma, 3.6 Ma,

3.3 Ma and 3.0 Ma (average split delay 0.3 Ma). Both series and their subsequent branching follow roughly an East to West direction in coherence with the pattern of decreasing age of the islands, and with increasing distance from continental Africa. However, the pattern is more complex than a simple forward stepping-stone progression as reported for some Canarian groups like *Brachyderes* (Emerson et al. 2000a), *Pimelia* (Juan et al. 1995), *Hegeter* (Juan et al. 1996), *Nesotes* (Rees et al. 2001a), *Aerostira* and *Purpuraria* (López et al. 2007), *Drosophila* (Khadem et al. 1998), or many plant genera (Marrero 2004). In *Laparocerus*, having disregarded multiple lineages arriving from the continent, other possibilities of intra-archipelago colonisation (cf. Warren & Funk 1955, Sanmartín et al. 2008) can be recognised as single or combined, and were duly commented on Part V Taxonomy.

Basal groups like *Purpuranius* and *Aridotrox* inhabit the eastern Canaries, which are the oldest islands and were joined as a single mass in the past. The remaining 14 subgenera are distributed across the central and western islands, although several are restricted to just Gran Canaria (*Faycanius*, *Doramasius*, *Bentaygus*, and *Pecoudius*). A striking exception to this division is posed by *Laparocerus*

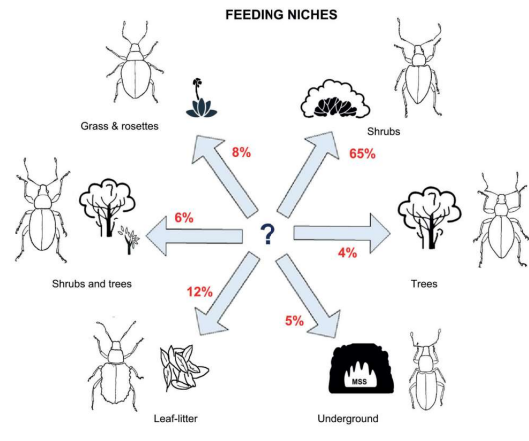


Fig. 453. Radiation of *Laparocerus* in feeding niches.

the extant habitats. The attached diagrams (Fig. 453 and Fig. 454) provide a panorama of the extent of adaptive radiation undergone by *Laparocerus*, both habitat and life-style shifts, one often associated with the other.

It has been confirmed that **laurisilva** has a Plio-Pleistocene origin, with a few older species from the Upper Miocene (Kondraskov et al. 2015). It is not a relict sample of the Tertiary flora as has been largely thought (Ciferri 1962, Axelrod 1975). Several lineages of *Laparocerus* inhabit the laurisilva (*Atlantis*, *Pseudatlantis*, *Benomius*, *Guanchothrox*, *Machadotrox*, *Fernandezius*, *Proteotrox*, etc.). They can be found high in the canopy of trees (*Laurus*, *Persea*, *Ocotea*, *Prunus*, *Myrica*, etc.), on bushes of all sizes, on the shorter plants that grow in the shade or on the more exposed cliffs and light gaps (*Aconium*, *Cedronella*, *Geranium*, *Hypericum*, *Phyllis*, *Ranunculus*, *Rubus*, *Senecio*, etc.), in the leaf-litter, and underground. In other words, *Laparocerus* were already there when laurisilva arrived and developed in Macaronesia, and their parallel conquest of this habitat is now almost complete.

(3) True tree climbers have developed in *Atlantis*, *Machadotrox*, and *Proteotrox* as in the case of *L. ellipticus* and *L. inflatus* (uncertain sedis). Most forest species are shrub feeders that may also eat the leaves of the trees and their suckers, but do not climb high.

The same applies to the **sclerophyllous forest**, which emerged in the Mediterranean under hot dry summers and cool wet winters approximately 3.4 Ma ago (Jiménez et al. 2010). The number of *Laparocerus* species feeding on plants and shrubs associated with sclerophyllous forest (e.g. *Convolvulus floridus*, *Carlina salicifolia*, *Bupleurum salicifolium*, *Gymnosporia cassinoidea*, etc.) is almost as high as in laurisilva. Good examples are *Belicarius* species on La Gomera (e.g. *L. crotchi*, *L. subnebulosus*, *L. geroles*, *L. humeralis*, *L. magnificus*) or *L. (Amyntas) bellus* on Tenerife and its sister species *L. arrochai* on La Palma feeding on *Jasminum odoratissimum*. However, a great part of these species feed also on plants of laurisilva or open shrublands. In contrast, the list of components of the sclerophyllous community that are not accepted as food by *Laparocerus* is more notable (*Boscaea*, *Dracaena*, *Juniperus*, *Marcelletia*, *Olea*, *Phoenix*, *Pistacia*, *Ruta*, etc.), while very few of the twenty laurisilva tree species are left aside (apparently only *Arbutus*, *Visnea*, and *Salix*).

The presence of *Laparocerus* adapted to the **lowland shrublands** is almost as rich as in the forest habitats, with more diversity accumulated in the less arid formations on the windward slopes. Only five lineages seem not to have colonised this habitat: *Wollastonia*, *Atlantis*, *Bentaygus*, *Benomius*, and *Guayrae*.

El autor

ANTONIO MACHADO CARRILLO (Madrid, 1953) ha sido profesor de Ecología en la Universidad de La Laguna (Tenerife, islas Canarias), director-conservador del Parque Nacional del Teide, Director del Observatorio Ambiental Granadilla, asesor de política ambiental de la Presidencia de los gobiernos español y canario, Consejero Regional de la Unión Internacional para la Conservación de la Naturaleza (UICN), y presidente del Centro Europeo de Conservación de la Naturaleza (ECNC). También ha trabajado como consultor independiente en conservación para varias organizaciones internacionales y programas de cooperación. Editor jefe del Journal for Nature Conservation (2001-2021), y miembro numerario de la Academia Canaria de la Lengua (ACL) y de la World Academy of Arts and Science (WAAS).

En la actualidad está retirado y continua feliz con sus estudios privados de Entomología. Entre otras publicaciones, destacan los siguientes libros: *Los ditíscidos de las islas Canarias* (1987), *Monografía de los carábidos de las islas Canarias* (1992), *Elenco de los coleópteros de las islas Canarias* (junto con P. Oromí, 2000), *T. Vernon Wollaston (1822-1878): un entomólogo en la Macaronesia* (2006), *La psicósfera ¿Necesitamos una nueva Ecología?* (2006), y *Ca-torze días: reflexiones sobre el sentido de la vida, la mente y más cosas* (2019).



Muestra de *Laparocerus* de la isla de La Palma

