NEW

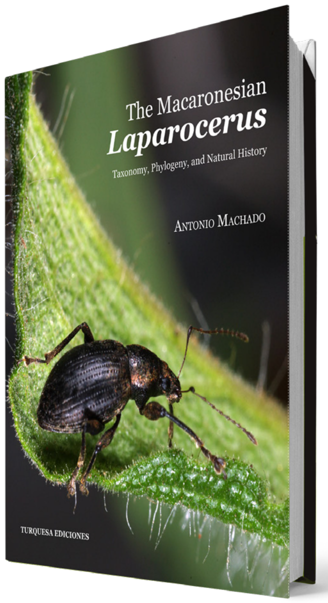
The Macaronesian

LAPAROCERUS

Champions of biodiversity. A weevil genus beats records of explosive evolutive radiation on oceanic islands in Macaronesia

Why are there so many *Laparocerus*? The swarm of 261 species and subspecies in Madeira, Salvages and the Canary Islands is the result of a blend of adaptive and non-adaptive evolution in old volcanic archipelagos. These have plenty of environmentally dissected islands subject to a dynamics of construction and deconstruction. A twenty year-long prospection and a DNA phylogenetic analysis reveal their monophyly, internal relationships, and plausible pathways of colonisation, which started in the late Miocene.

Within a timeframe of about 9 million years, sequential radiation events have generated several monophyletic groups, 25 in total, that have been recognised as subgenera of *Laparocerus*. Colonisation routes, habitat shifts, disruption of populations by volcanism, dispersal by massive landslides, and other important factors for speciation are discussed in depth.



Hardcover, 226 × 290 mm, 681 pp.
ISBN : 978-84-16785-99-5

Laparocerus weevils are all flightless and most taxa are exclusive to one single island—seventeen in total—having occupied almost all habitats, from the coastal shrublands to the sclerophyllous woodlands, evergreen cloud-forest, pine woodlands, high-mountain shrublands and the underground environment (volcanic lava-tubes). They thus show an extraordinary morphological and ecological plasticity. Only two species inhabit NW Africa, the nearest continental land, but as a result of a back-colonisation. The richest island is Tenerife (2034 km^2) with 68 species and subspecies. Overall, there is an outstanding ratio of one endemic *Laparocerus* per 31 km^2, a record not beaten by any other plant or animal genus in Macaronesia.

If oceanic islands have been traditionally considered as laboratories of evolution and species-producing machines, *Laparocerus* will become an ideal model species for broadening research into dispersal and speciation processes of all kinds. Such a group provides a fine-grain picture of nature and evolution at work.

To assist in this endeavour, this book authored by A. Machado provides a full revision of the genus *Laparocerus*, with descriptions of all 264 species and subspecies —doubling the number previously known—keys for their identification, 374 macro-photographs of the imagos, 50 plates with line-drawings of their genitalia and other internal pieces, and 47 distribution maps. It also incorporates a detailed anatomical study (13 plates) of one species including preimaginal stages, and chapters dealing with their breeding biology, ecology (food-plants, habitats, etc.), and behaviour. Their natural history, in other words.

The author hopes that in the near future *Laparocerus* will merit sharing the podium with Darwin's finches or *Drosophila* in studies of island evolution.

HISTORY

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

1935, Liebmann 1939, Janson 1940, Fernández 1951, Gardner & Classey 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.

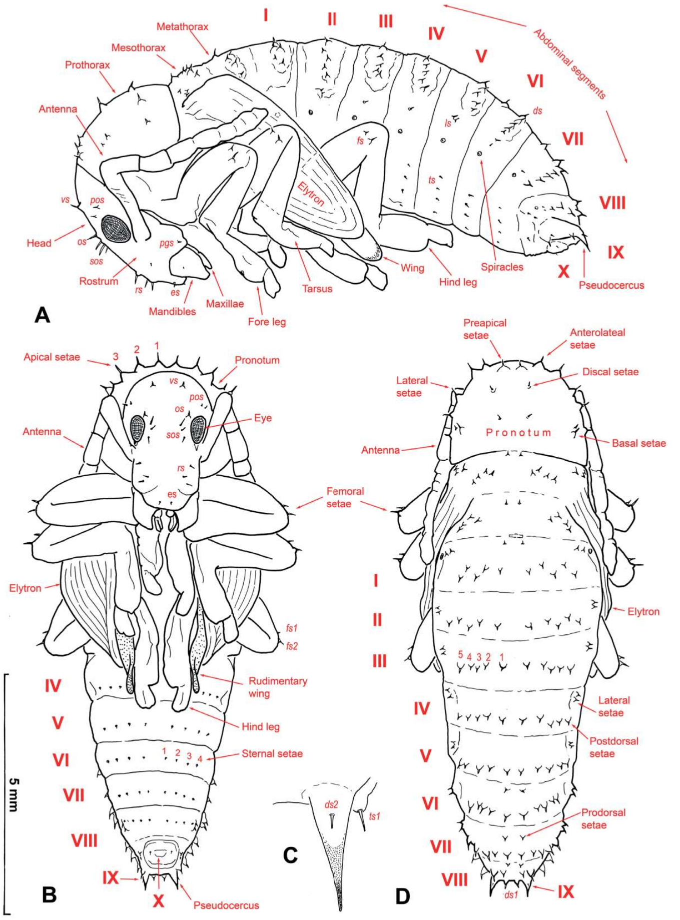
Daniel Louis Uyttenboogaart (Fig. 18) was a wealthy Dutch gentleman trained as lawyer and civil servant, who started visiting the main Canary Islands in relation to maritime commerce, and soon became interested in their beetle fauna. He collected mainly on Tenerife and Gran Canaria together with his 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 coleoptera 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).

ANATOMY



ETHOLOGY

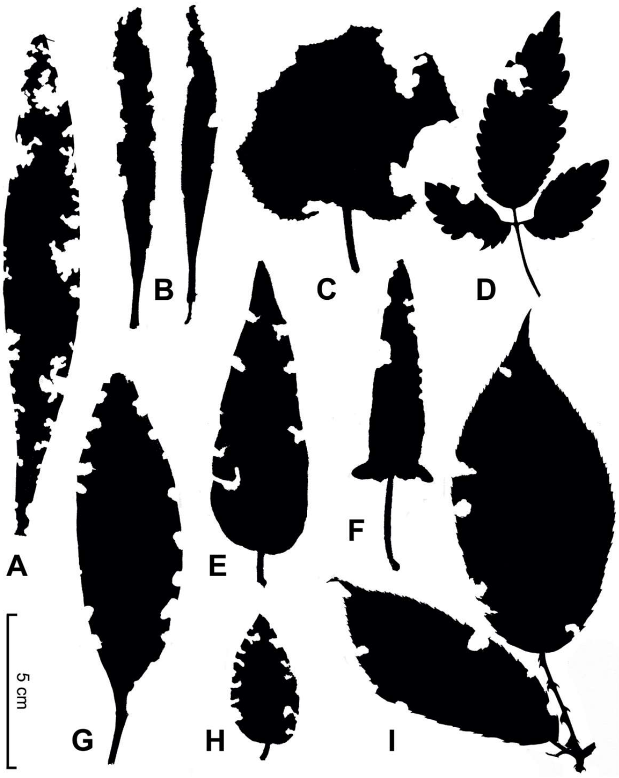


Fig. 62. *Laparocerus* feeding marks on leaves of bushes and small plants.– **A**: *Laparocerus distortus* on *Euphorbia mellifera* Ait.– **B**: *Laparocerus bentejui delicatulus* on *Echium onosmifolium* Webb.– **C**: *Laparocerus crassus* on *Pericallis appendiculata* L. f.– **D**: *Laparocerus aeneotinctus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

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

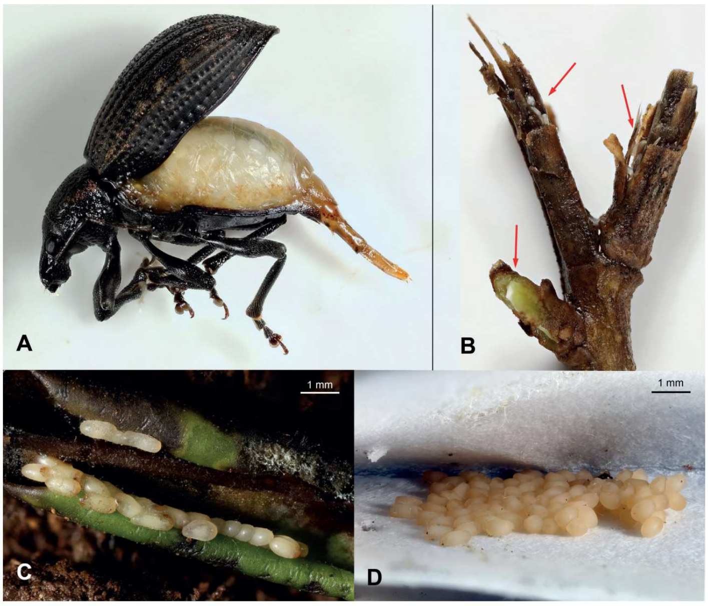


Fig. 45. **A**: *Laparocerus bellus* (♀) with stretched ovipositor, and elytra uplifted to show abdomen bearing 101 eggs.– **B**: Eggs (red arrows) of *L. ruteri* hidden in the crevices of a stick.– **C**: Dead leaf partially unrolled to show hidden clutch (70 eggs) of *L. ruteri*.– **D**: Fold of a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

ETHOLOGY

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. tanausu,* 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

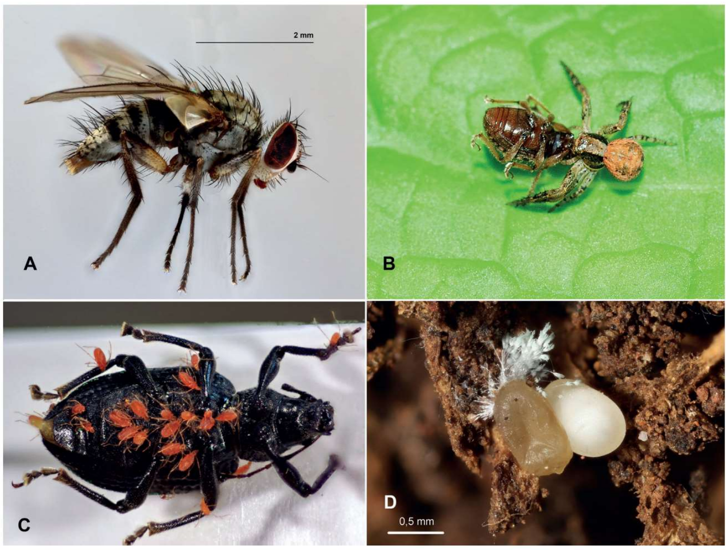
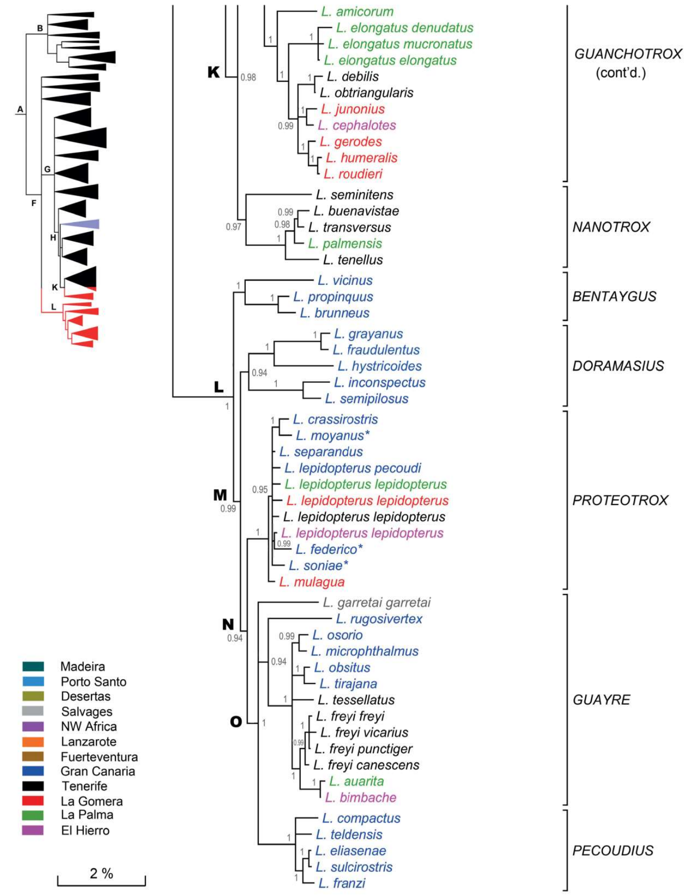


Fig. 72. Natural enemies of *Laparocerus*. **A**: Endoparasitic *Rondania insularis* (Bigot, 1891) ♀ (Diptera, Tachinidae),– **B**: *Ozyptila* spider (Araneae, Thomisidae) with its prey, *Laparocerus vestitus* (photo M.A. Peña). **C**: *Laparocerus fernandezi* with ectoparasitic mites *Leptus tenerificus*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

PHYLOGENY



DISTRIBUTION & KEYS

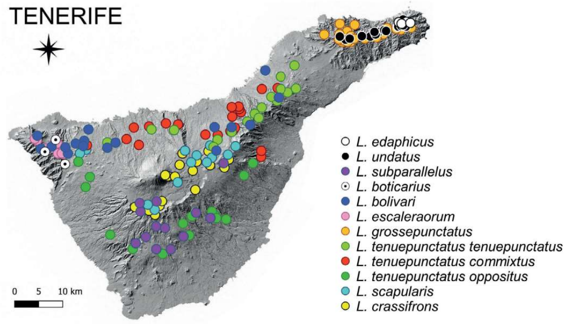


Fig. 334. Distribution of subgenus *Bencomius* on Tenerife.

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 desmomeres 3-7 moniliform and club broad oval; integument lacking scales, only with some erect setae. Inhabiting Tenerife . . . . ***L. edaphicus*** [p. 407]

– Antennae with all desmomeres longer than wide and club fusiform; integument with scales (often dehiscent) and soft setae on elytra. 2

2 Elytral interstriae with some separate but distinct punctures (in cases almost effaced on disc, best visible on 5th 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; interstrial 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; interstrial punctures often effaced on disc, particularly on females; setae longer. Size 5.7–9.6 mm Inhabiting Tenerife (outside Anaga and Teno). . . . . ***L. tenuepunctatus 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

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DESCRIPTIONS

Laparocerus (Laparocerus) chaoensis
Uyttenboogaart, 1940

Fig. 85.

ssp. ***chaoensis*** Uyttenboogaart, 1940

Laparocerus chaoensis 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. *chaoensis*].
—*Laparocerus (Laparocerus) chaoensis chaoensis*, 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; ⇒ *chaoensis* 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 **-***ēnsis* (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 outwards, 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 chaoensis chaoensis* inhabits the islets of Chão (0.4 km²) and Bugio (3.3 km²), 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 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. chaoensis chaoensis* 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.

Fig. 85. *Laparocerus chaoensis chaoensis* ♂.

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. chaoensis* 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%)

BIOGEOGRAPHY

7.2 | Colonisation

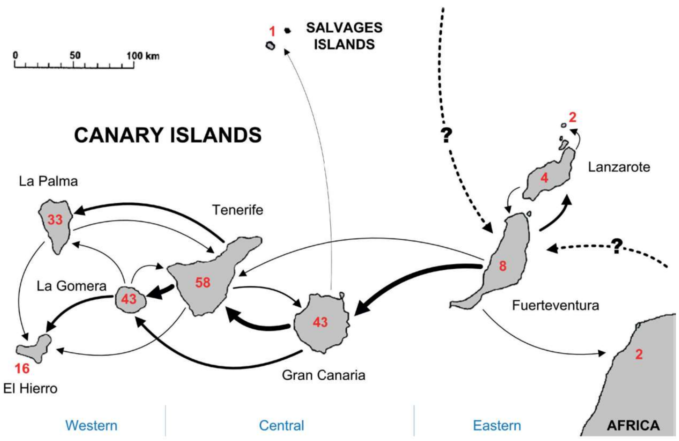

Fig. 449. Hypothetical colonisation pathways of *Laparocerus* weevils in the Canary Islands and Salvages, with numbers of species known from each island.

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. *Wollastonius* 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 28SrDNA 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), *Acrostira* 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*

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EVOLUTION

7.3 | Diversification

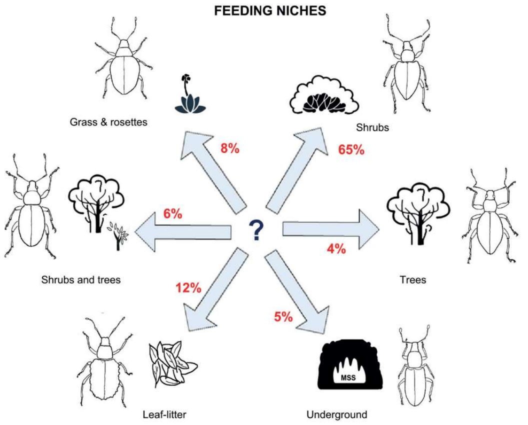

Fig. 453. Radiation of *Laparocerus* in feeding niches.

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 lifestyle 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, Bencomius, Guanchotrox, Machadotrox, Fernandezius, Proteotrox,* etc.). They can be found high in the canopy of trees[3] (*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 (*Aeonium, 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.

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 cassinoides,* etc.) is almost as high as in laurisilva. Good examples are *Belicarius* species on La Gomera (e.g. *L. crotchi, L. subnebulosus, L. gerodes, 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 (*Bosea, Dracaena, Juniperus, Marcetella, 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: *Wollastonius, Atlantis, Bentaygus, Bencomius,* and *Guayre*.

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

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ABOUT THE AUTHOR - **Antonio Machado**, PhD (Madrid, 1953) has been a lecturer in Ecology at the University of La Laguna (Tenerife, Canary Islands), superintendent of Teide National Park, Director of the Granadilla Environmental Observatory, adviser on environmental policies for the Presidency of the Spanish and Canarian Governments, Regional Councillor of the International Union for Conservation of Nature (IUCN), and President of the European Centre for Nature Conservation (ECNC). He has also worked as independent conservation consultant for several international organisations and in foreign co-operation programmes. Editor-in-chief of the Journal for Nature Conservation (2001-2021), full member of the Canarian Academy of Language and of the World Academy of Arts and Science.

He is now retired and happily continues with his private research on Entomology. Among other publications are the following books: *Los ditíscidos de las islas Canarias* (1987), *Monografía de los carábidos de las islas Canarias* (1992), *Catalogue of the Coleoptera of the Canary Islands* (co-authored with P. Oromí, 2000), *T. Vernon Wollaston (1822-1878). Un entomólogo en la Macaronesia* (2006), *The Psychosphere ¿Do we need a new Ecology* (2006), and *Fourteen days. Reflections on life, mind, and other things* (2019).

Laparocerus sample from the island of La Palma

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