



# Molecular phylogeny in endemic weevils: revision of the genera of Macaronesian Cryptorhynchinae (Coleoptera: Curculionidae)

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A molecular phylogeny and lineage age estimates are presented for the Macaronesian representatives of the weevil subfamily Cryptorhynchinae, using two mitochondrial genes (cytochrome *c* oxidase subunit 1 and 16S). The Bayesian reconstruction is supplemented by observations on morphology, ecology, and reproductive biology. The present study often corroborates the groups previously outlined in higher-level informal taxonomies. These and further groups are now assigned new taxonomic status. The following genera and subgenera are described (formerly *Acalles*): ***Aeoniacalles* gen. nov.**, ***Canariacalles* gen. nov.**, ***Ficusacalles* gen. nov.**, ***Madeiracalles* gen. nov.**, ***Silvacalles* gen. nov.** (with ***Tolpiacalles* subgen. nov.**, ***Tagasastacalles* subgen. nov.**), ***Sonchiacalles* gen. nov.**, ***Echiumacalles* gen. nov.** (monotypic), ***Lauriacalles* gen. nov.** (monotypic), and ***Pseudodichromacalles* gen. nov.** (monotypic; formerly *Dichromacalles*). For the western Palaearctic genus *Acalles* Schoenherr, 1825 the first subgenus ***Origoacalles* subgen. nov.** is described and for the genus *Onyxacalles* Stüben, 1999 the first subgenus ***Araneacalles* subgen. nov.**; *Paratorneuma* Roudier 1956 resyn. Except for one species of *Acalles* (*Origoacalles*), all of these new higher taxa are endemic to the Macaronesian Islands. All new taxa are presented, together with their host plants and further data, in a synoptic tabular overview. Based on the results of our phylogenetic analysis, we advocate the hypothesis that the evolution of the species in the new genera (of which most group into a ‘Macaronesian clade’) began in the comparatively arid succulent bush zone and that the shady and humid laurel forest of the thermo-Canarian and thermo-Madeiran zone was entered much later. Our reconstruction implies that the Canarian and Madeiran archipelagos were colonized by Cryptorhynchinae at least seven times from the continent but saw only one considerable adaptive radiation. It also becomes apparent that it is the ancestor species of the genus *Canariacalles* – and not *Pseudodichromacalles* – that features a close connection to the south-western European and north-western African species of *Dichromacalles* s.s. Finally, a key is presented for all genera and subgenera of the Macaronesian Cryptorhynchinae.

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**ADDITIONAL KEYWORDS:** 16S – Azores – Bayesian – biodiversity – Canary Islands – COI – colonization – ecology – endemism – host plants – lineage age estimates – Madeira – Selvagens – taxonomy.

## INTRODUCTION

This study is connected to the recently published, first molecular phylogeny of the species-rich weevil subfamily Cryptorhynchinae (Astrin & Stüben, 2008).

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More specifically, our focus here lies on the ‘Atlantic clade’ that was introduced in that article. The Atlantic clade encompasses the overwhelming majority of genera from the Macaronesian Islands (but also a few of those from the continental Palaearctic zones bordering the Atlantic Ocean).

The term ‘Macaronesia’ originates from the discipline of geobotany, and refers to the Atlantic, volcanic archipelagos of the Azores (nine islands), Madeira

(three islands), Selvagens (three islands), Canaries (seven islands), and Cape Verde (not considered in this study) along with a small part of western Morocco. Lanzarote and Fuerteventura, the eastern-most Canary Islands are separated from the African continent by only 115 km. The distance between Madeira and the mainland amounts to 600 km, whereas the eastern-most island of the Azores, Santa Maria, lies in the middle of the ocean, 1500 km away from the coast of mainland Portugal.

On these Macaronesian Islands occurs a highly endemic cryptorhynchine fauna. Out of the currently known 353 western Palaearctic species within the subfamily Cryptorhynchinae, 95 species (i.e. 27%) live here; and only two of these species can also be found on the mainland: *Dichromacalles dromedarius* (Boheman, 1844) and *Acalles globulipennis* Wollaston (1854). Linking this figure to the area occupied by the Macaronesian Islands, there would be one species per 109 km<sup>2</sup> of extension of land, making Macaronesian cryptorhynchine biodiversity 500 times 'denser' than for all of Europe. Cryptorhynchinae constitute almost 6% (currently 65 species) of the 1114 endemic Coleoptera (Oromí *et al.*, 2001) and about 25% of the 237 endemic Curculionioidea (Machado & Oromí, 2000) on the Canaries. In this sense, the Macaronesian Islands and particularly the Canarian and Madeiran archipelagos can be seen as a 'laboratory of evolution' for Cryptorhynchinae – similar to the entimine weevils of the genus *Laparocerus* (Machado *et al.*, 2008).

Our survey of the Macaronesian cryptorhynchine fauna started more than a decade ago with the exploration of the Canaries. Within two years, the number of species descriptions for these islands was doubled (to 61 species in total; cf. Bahr, 2000; Stüben, 2000a–h). The structure of the internal sac of the aedeagus (the endophallus; cf. Figs 2B–22B) played a crucial role in separating the Canarian species of *Acalles s.l.* from the continental European and North African species and in structuring them into informal taxonomic groups (Stüben, 2000a). Since the work of T.V. Wollaston in the mid-19<sup>th</sup> century, most Macaronesian Cryptorhynchinae (those species measuring 3–10 mm and living monophagously or oligophagously on a number of woody perennials) have been included in the genus *Acalles*. We will here use the term '*Acalles s.l.*' for those – nonmonophyletic – Macaronesian species that are not part of the taxa *Onyxacalles*, *Calacalles*, *Echinodera* (all usually smaller-sized), or the subterranean Torneumatini. Morphological analysis of the endophallus also led to a first phylogenetic hypothesis for the group (Stüben, 2000b).

Recently, we extended the survey to the archipelagos of Madeira (Stüben, 2002b) and the Azores (Stüben, 2003b, 2004b). Beyond accessing the type material (of the T.V. Wollaston Collection at the

British Museum of Natural History, London, UK), the focus lay primarily on incorporating knowledge on the ecology and life cycle of Cryptorhynchinae into any taxonomic effort undertaken. In numerous recent expeditions to the western Canary Islands, Madeira, and Porto Santo, further insights into the biology of the studied group have been gained, especially into the relationships to the respective host plants (Stüben & Germann, 2005; Germann & Stüben, 2006; Stüben, 2007b, 2008a; Stüben & Astrin, 2009 in press), which are here presented for the first time in a synoptic overview. Based on the previous research, we reflect on the molecular results obtained for this study, which – together with the morphological and ecological evidence – constitute one of the central criteria in erecting new supraspecific taxa of Macaronesian Cryptorhynchinae.

## MATERIAL AND METHODS

### TAXON SAMPLING AND LABORATORY ROUTINE

DNA sequences from 94 western Palaearctic weevils were used in this study. Eighty-nine species of Cryptorhynchinae in 24 genera (including new genera) and three outgroup taxa are represented. All autochthonous Macaronesian genera and 58 of the currently 95 Macaronesian species entered the analysis (cf. Stüben, 2009a). The outgroup consisted of the continental *Adexius scrobipennis* Gyllenhal, 1834 (Curculionidae: Molytinae), as well as *Barretonus minor* Folwaczny, 1972 (Curculionidae: Cossoninae) from the Madeiran archipelago and *Laparocerus oromii* Machado, 2008 (Curculionidae: Entiminae) from the Canary Islands. Conspecific individuals were sampled for those Macaronesian species showing a markedly disjunct distribution: *Acalles globulipennis* and *Dichromacalles dromedarius* (see below). Table 1 gives information on the analysed material.

As our focus lay on cryptorhynchine genera rather than on the deep branches of the tree, we analysed two genes of the fast-evolving mitochondrion. We sequenced part of the cytochrome *c* oxidase subunit 1 (CO1) and of the ribosomal large subunit (16S) genes and thereby obtained 52 sequences for 16S and 47 sequences for CO1 (almost all of these from Macaronesian specimens, mostly from the western Canaries and Madeira). The remaining 84 sequences (mainly continental 'reference taxa'; cf. Table 1) were taken from Astrin & Stüben (2008). Sequence length was 658 bp for CO1 and 529–544 bp for 16S (unaligned). The DNA sequences generated in this study have been submitted to GenBank (<http://www.ncbi.nlm.nih.gov/GenBank/index.html>; see Table 1 for accession numbers) and can be found in the Update Catalogue of Westpalearctic Cryptorhynchinae

**Table 1.** Collecting data, vouchers, and GenBank accession numbers

Taxon	Collecting data	Vouchers	Acc.#16S	CO1
<i>Acalles camelus</i> (Fabricius, 1792)	FRANCE: Isère, 45°06'45"N, 05°36'21"E, 1352 m, mixed forest, 2005, Stüben	JJ0017, I-0026-cam	EU286282	EU286447
<i>Acalles echinatus</i> (Germar, 1824)	CROATIA: Dalmatia, 44°31'45"N, 15°08'34"E, 927 m, <i>Fagus</i> , 2007, Stüben	JJ0193, HR-0334-ech	EU286346	EU286510
<i>Acalles fallax</i> Boheman, 1844	CROATIA: Dalmatia, 44°24'32"N, 15°34'13"E, 617 m, <i>Quercus</i> , 2007, Stüben	JJ0191, HR-0332-fal	EU286344	EU286508
<i>Acalles globulipennis</i> Wollaston, 1854	P.: Madeira, 32°45'08"N, 17°01'40"W, 1004 m, <i>Euphorbia mellifera</i> , 2008, Astrin & Stüben	JJ0430, P-528-glo	FJ716495	FJ716546
<i>Acalles globulipennis</i> Wollaston, 1854	E.: Tenerife, Anaga, 28°31'55.09"N, 16°17'24"W, 840 m, laurisilva, 2008, Astrin & Stüben	JJ0603, E-676-glo	FJ716513	FJ716562
<i>Acalles lemur lemur</i> (Germar 1824)	FRANCE: Isère, 45°26'01"N, 05°12'06"E, 448 m, <i>Quercus</i> , <i>Fagus</i> , 2005, Stüben	JJ0014, I-0010-leL	EU286281	EU286446
<i>Acalles parvulus</i> Boheman, 1837	FRANCE: Isère, 45°26'01"N, 05°12'06"E, 448 m, <i>Quercus</i> , <i>Fagus</i> , 2005, Stüben	JJ0018, I-0008-par	EU286283	EU286448
<i>Acalles pilula</i> Wollaston, 1864	E.: El Hierro, 27°44'29"N, 18°03'24"W, 895 m, <i>Laurus</i> , 2006, Stüben	JJ0080, C-0099-pil	EU286296	EU286461
<i>Acalles sierrae</i> H. Brisout, 1865	E.: Almería, 37°05'45"N, 02°57'37"W, 2285 m, <i>Erinacea anthyllis</i> , 2005, Stüben	JJ0148, E-0100-sie	EU286328	EU286492
<i>Acallobrates denticollis</i> (Germar, 1824)	CROATIA: Dalmatia, 44°31'45"N, 15°08'34"E, 927 m, <i>Fagus</i> , 2007, Stüben	JJ0192, HR-0333-den	EU286345	EU286509
<i>Acallorneuma doderoi</i> A. & F. Solari, 1908	ITALY: Sicily, 37°51'38"N, 13°23'24"E, 1200 m, <i>Quercus</i> , <i>Fraxinus</i> , 2002, Stüben	JJ0065, S-0082-dod	EU286292	EU286457
<i>Aeoniacalles aeonii</i> (Wollaston, 1864)	E.: Tenerife, Anaga, 28°33'04"N, 16°15'12"W, 831 m, <i>Aeonium cuneatum</i> , 2008, Astrin & Stüben	JJ0616, E-689-aeo	FJ716518	FJ716567
<i>Aeoniacalles</i> <i>aeonisimlis</i> (Stüben, 2000)	E.: La Gomera, 28°09'29"N, 17°09'37"W, 627 m, <i>Aeonium</i> , 2008, Astrin & Stüben	JJ0652, E-725-aes	FJ716529	FJ716577
<i>Aeoniacalles argillosus</i> (Boheman, 1837)	E.: La Palma: 28°50'36"N, 17°54'07"W, 254 m, <i>Kleinia neriifolia</i> , 2006, Stüben	JJ0152, C-0103-arg	FJ716487	FJ716539
<i>Aeoniacalles</i> <i>grancanariensis</i> (Stüben, 2000)	E.: Gran Canaria, Las Lagunetas, Barrauco La Mina, 1300 m, 1999, Stüben	JJ0691, E-752-gra	FJ716534	–
<i>Calacalles atomarius</i> Bahr, 2000	E.: Tenerife, Anaga, 28°33'38"N, 16°09'20"W, 500 m, <i>Sonchus</i> spp., <i>Aeonium cuneatum</i> , 2003, Stüben	JJ0515, E-576-ato	FJ716512	FJ716561
<i>Calacalles azoricus</i> Stüben, 2004	P.: Azores, Faial, 38°35'10"N, 28°42'04"W, 886 m, <i>Tolpis azorica</i> , 2003, Stüben	JJ0102, P-0125-azo	EU286303	EU286468
<i>Calacalles droueti</i> (Crotch, 1867)	P.: Azores, Pico, 38°27'21"N, 28°21'04"W, 811 m, <i>Euphorbia stygiana</i> , 2003, Stüben	JJ0100, P-0123-dro	EU286302	EU286467
<i>Calacalles moraguesi</i> (Desbrochers, 1898)	E.: Mallorca, 39°54'56"N, 03°03'03"E, 19 m, <i>Smilax aspera</i> , <i>Quercus ilex</i> , 2004, Stüben	JJ0379, E-484-mor	FJ716492	–
<i>Calacalles pusillus</i> Bahr, 2000	E.: Tenerife, Teno, 28°21'39"N, 16°46'19"W, 534 m, plant detritus, 2008, Astrin & Stüben	JJ0629, E-702-pus	FJ716521	FJ716570
<i>Calacalles wollastoni</i> (Chevrolat, 1852)	P.: Madeira, 32°51'31"N, 17°12'11"W, 391 m, <i>Ficus carica</i> , 2008, Astrin & Stüben	JJ0455, P-520-wol	FJ716507	FJ716557

Table 1. Continued

Taxon	Collecting data	Vouchers	Acc.#16S	CO1
<i>Canariacalles alluaudi</i> (Uyttenboogaart, 1940)	E.: Tenerife, Teno, 28°21'35"N, 16°52'05"W, 230 m, <i>Foeniculum vulgare</i> , 2008, Astrin & Stüben	JJ0636, E-709-all	FJ716523	FJ716572
<i>Coloracalles humerosus</i> (Fairmaire, 1862)	FRANCE: Gard, 43°57'03"N, 04°28'59"E, 68 m, <i>Quercus ilex</i> , 2006, Stüben	JJ0079, F-0098-hum	EU286295	EU286460
<i>Cryptorhynchus lapathi</i> (Linné, 1758)	GERMANY: 'Bienen bei Rees, Altrheinarm', 2004, Scharf	JJ0214, D-0354-lap	EU286360	EU286523
<i>Dendroacalles euphorbiacus</i> (Stüben, 2000)	E.: La Palma, 28°50'36"N, 17°54'07"W, 254 m, <i>Euphorbia regis-jubae</i> , 2006, Stüben	JJ0113, C-0138-eup	EU286310	EU286475
<i>Dendroacalles ornatus</i> (Wollaston, 1854)	P.: Madeira, 32°48'47"N, 17°08'59"W, 950 m, <i>Ocotea foetens</i> , 2008, Astrin & Stüben	JJ0432, P-530-orn	FJ716497	FJ716548
<i>Dendroacalles poneli</i> (Stüben, 2000)	E.: El Hierro, 27°43'53"N, 18°07'04"W, 725 m, <i>Euphorbia regis-jubae</i> , 2006, Stüben	JJ0114, C-0141-pon	EU286311	EU286476
<i>Dendroacalles ruteri</i> (Roudier, 1954)	E.: La Palma, 28°49'11"N, 17°54'48"W, 919 m, laurisilva, 2006, Stüben	JJ0107, C-0132-rut	EU286306	EU286471
<i>Dendroacalles sigma</i> (Wollaston, 1864)	E.: La Palma, 28°49'38"N, 17°53'46"W, 708 m, <i>Juglans regia</i> , 2006, Stüben	JJ0493, E-554-sig	FJ716510	FJ716560
<i>Dichromacalles albopictus</i> (Jacquet, 1887)	FRANCE: Provence, 43°50'59"N, 07°28'28"E, 1269 m, <i>Quercus ilex</i> , <i>Helleborus</i> , 2007, Stüben	JJ0418, F-447-alb	FJ716493	FJ716544
<i>Dichromacalles creticus</i> (Reitter, 1916)	GREECE: Crete, 35°20'44"N, 23°54'38"E, 1050 m, <i>Cichorium</i> , 2006, Bahr & Bayer	JJ0084, GR-0130-cre	EU286298	EU286463
<i>Dichromacalles dioctetianus</i> (Germar, 1817)	E.: Cádiz, 36°04'35"N, 05°25'46"W, 34 m, <i>Olea</i> , <i>Mastix</i> , 2007, Astrin & Stüben	JJ0178, E-0204-dio	EU286336	EU286500
<i>Dichromacalles dromedarius</i> (Boheman, 1844)	E.: La Palma, 28°49'50"N, 17°52'03"W, 386 m, <i>Sonchus hierrensis</i> , 2006, Stüben	JJ0104, C-0127-dro	EU286304	EU286469
<i>Dichromacalles dromedarius</i> (Boheman, 1844)	E.: Cádiz, 36°03'47"N, 05°42'04"W, 14 m, <i>Mastix</i> , <i>Ulex</i> , 2007, Astrin & Stüben	JJ0201, E-0208-dro	EU286353	EU286517
<i>Dichromacalles rolletii</i> (Germar, 1824)	ITALY: Sicily, 38°01'59"N, 14°35'56"E, 700 m, <i>Euphorbia dendroides</i> , 2005, Stüben	JJ0106, I-0129-rol	EU286305	EU286470
<i>Dichromacalles tuberculatus</i> (Rosenhauer, 1856)	E.: Cádiz, 36°04'35"N, 05°25'46"W, 34 m, <i>Olea</i> , <i>Mastix</i> , 2007, Astrin & Stüben	JJ0199, E-0203-tub	EU286351	EU286515
<i>Echinodera andalusiensis</i> Stüben, 2003	E.: Cádiz, 36°04'10"N, 05°31'48"W, 257 m, <i>Quercus suber</i> , 2007, Astrin & Stüben	JJ0200, E-0205-and	EU286352	EU286516
<i>Echinodera angulipennis</i> Wollaston, 1864	E.: Tenerife, Teno, 28°18'27"N, 16°50'29"W, 668 m, <i>Ficus carica</i> , Citrus, 2008, Astrin & Stüben	JJ0630, E-703-ang	FJ716522	FJ716571
<i>Echinodera brisouti</i> (Reitter, 1885)	GREECE: Corfu, 39°46'38"N, 19°53'21"E, 479 m, <i>Q. pubescens</i> , <i>L. nobilis</i> , <i>Asphodelus</i> , 2007, Stüben	JJ0233, KO-0370-bri	FJ716489	FJ716541



Table 1. Continued

Taxon	Collecting data	Vouchers	Acc.#16S	CO1
<i>Echinodera crenata</i> Wollaston, 1863	E.: Tenerife, 28°17'01"N, 16°34'18"W, 2172 m, <i>Spartocytisus supranubius</i> , 2008, Astrin & Stüben	JJ0639, E-712-cre	FJ716524	FJ716573
<i>Echinodera guacimara</i> Stüben & Germann, 2005	E.: Tenerife, Anaga, 28°33'42"N, 16°09'25"W, 502 m, plant detritus, 2008, Astrin & Stüben	JJ0615, E-688-gua	FJ716517	FJ716566
<i>Echinodera hystrix</i> Wollaston, 1864	E.: El Hierro, 27°44'10"N, 18°04'26"W, 796 m, laurisilva, 2006, Stüben	JJ0115, C-0142-hys	EU286312	EU286477
<i>Echinodera merkli</i> (Meyer, 1896)	GREECE: Epirus, 39°46'59"N, 21°09'09"E, 1419 m, <i>Fagus</i> , 2007, Stüben	JJ0338, EP-0385-mer	FJ716491	FJ716543
<i>Echinodera orbiculata</i> Wollaston, 1864	E.: Tenerife, Anaga, 28°33'21"N, 16°10'46"W, 808 m, <i>Laurus</i> , <i>Ixanthus</i> <i>viscosus</i> , 2008, Astrin & Stüben	JJ0610, E-683-orb	FJ716515	FJ716564
<i>Echinodera personata</i> Colonnelli, 1985	E.: Tenerife, 28°21'39"N, 16°52'12"W, 130 m, leaf-litter at roadside, 2008, Astrin & Stüben	JJ0620, E-693-per	FJ716519	FJ716568
<i>Echinodera</i> <i>pseudohystrix</i> Stüben, 2000	E.: La Gomera, 28°07'27"N, 17°13'26"W, 901 m, laurisilva, 2008, Astrin & Stüben	JJ0645, E-718-psh	FJ716527	FJ716575
<i>Echinodera siciliensis</i> Stüben, 2003	ITALY: Sicily, 38°09'00"N, 12°46'19"E, 35 m, <i>Quercus</i> , <i>Fraxinus</i> , 2006, Stüben	JJ0126, I-0153-sic	EU286315	EU286480
<i>Echinodera tenoensis</i> Stüben, 2000	E.: Tenerife, 28°21'39"N, 16°46'18"W, 520 m, <i>Foeniculum vulgare</i> , detritus, 2004, Stüben	JJ0507, E-755-ten	FJ716511	–
<i>Echiumacalles</i> <i>anagaensis</i> (Stüben, 2000)	E.: Tenerife, Anaga, 28°33'42"N, 16°09'25"W, 502 m, <i>Echium strictum</i> , 2008, Astrin & Stüben	JJ0613, E-686-ana	FJ716516	FJ716565
<i>Elliptacalles longus</i> (Desbrochers, 1892)	E.: Cádiz, 36°41'50"N, 05°26'20"W, 646 m, <i>Q. ilex</i> , <i>Ceratonia</i> , <i>Olea</i> , <i>Mastix</i> , 2007, Astrin & Stüben	JJ0176, E-0198-lon	EU286335	EU286499
<i>Ficusacalles senilis</i> <i>senilis</i> (Wollaston, 1864)	E.: El Hierro, 27°45'04"N, 17°59'02"W, 1311 m, <i>Pericallis murrayi</i> , 2006, Stüben	JJ0304, E-0259-sen	FJ716490	FJ716542
<i>Kykliocalles</i> <i>euphorbiophilus</i> Stüben, 2003	MOROCCO, High Atlas, 30°52'25"N, 08°21'26"W, 2000 m, <i>Euphorbia</i> <i>nicaeensis</i> , 2002, Stüben	JJ0197, M-0160-eup	EU286349	EU286513
<i>Kykliocalles roboris</i> (Curtis, 1834)	FRANCE: Isère, 45°18'40"N, 05°45'17"E, 1649 m, <i>Abies</i> , <i>Fagus</i> , <i>Fraxinus</i> , 2005, Stüben	JJ0168, I-0037-rob	EU286330	EU286494
<i>Lauriacalles acutus</i> (Wollaston, 1864)	E.: La Palma, 28°45'18"N, 17°46'37"W, 857 m, laurisilva, 2006, Stüben	JJ0112, C-0137-act	FJ716486	FJ716538
<i>Madeiracalles</i> <i>achadagrandsensis</i> (Stüben, 2002)	P.: Madeira, 32°47'05"N, 17°11'06"W, 1189 m, laurissilva, 2008, Astrin & Stüben	JJ0434, P-532-ach	FJ716499	FJ716550
<i>Madeiracalles cinereus</i> (Wollaston, 1860)	P.: Madeira, 32°46'49"N, 16°54'54"W, 809 m, <i>Euphorbia mellifera</i> , 2008, Stüben	JJ0452, P-516-cin	FJ716505	FJ716555
<i>Madeiracalles dispar</i> (Wollaston, 1854)	P.: Madeira, 32°47'05"N, 17°11'06"W, 1189 m, laurissilva, 2008, Astrin & Stüben	JJ0433, P-531-dis	FJ716498	FJ716549
<i>Madeiracalles</i> <i>machadoi</i> (Stüben, 2006)	P.: Madeira, 32°44'20"N, 17°06'09"W, 1295 m, <i>Cytisus scoparius</i> , 2008, Astrin & Stüben	JJ0453, P-517-mac	FJ716506	FJ716556
<i>Madeiracalles</i> <i>portosantoensis</i> (Stüben, 2002)	P.: Porto Santo, 33°04'51"N, 16°19'59"W, 397 m, <i>Quercus ilex</i> , <i>Quercus suber</i> , 2008, Astrin & Stüben	JJ0436, P-534-por	FJ716500	FJ716551

Table 1. Continued

Taxon	Collecting data	Vouchers	Acc.#16S	CO1
<i>Madeiracalles pulverosus</i> (Gemminger, 1871)	P.: Madeira, 32°49'59"N, 16°54'00"W, 35 m, <i>Olea</i> , 2008, Stüben	JJ0424, P-512-pul	FJ716494	FJ716545
<i>Madeiracalles saxicola</i> (Wollaston, 1854)	P.: Madeira, 32°42'51"N, 16°46'12"W, 239 m, <i>Euphorbia piscatoria</i> , 2008, Stüben	JJ0450, P-514-sax	FJ716504	–
<i>Madeiracalles terminalis</i> (Wollaston, 1854)	P.: Madeira, 32°49'59"N, 16°54'00"W, 35 m, <i>Olea</i> , 2008, Stüben	JJ0447, P-510-ter	FJ716502	FJ716553
<i>Onyxacalles balearicus</i> Stüben, 2005	E.: Mallorca, 39°48'47"N, 02°53'23"E, 571 m, <i>Quercus ilex</i> , 2004, Stüben	JJ0207, E-0168-bal	EU286357	EU286521
<i>Onyxacalles bermejaensis</i> Stüben, 2001	E.: Málaga, 36°39'51"N, 05°05'01"W, 1047 m, <i>Quercus ilex</i> , 2005, Stüben	JJ0198, E-0167-ber	EU286350	EU286514
<i>Onyxacalles luigionii</i> (A. & F. Solari, 1907)	CROATIA: Dalmatia, 44°32'41"N, 15°09'58"E, 1049 m, <i>Fagus</i> , 2007, Stüben	JJ0195, HR-0339-lui	EU286348	EU286512
<i>Onyxacalles maginaensis</i> Stüben, 2004	E.: Jaén, 37°43'21"N, 03°29'11"W, 1600 m, <i>Quercus ilex</i> , 2005, Stüben	JJ0147, E-0169-mag	EU286327	EU286491
<i>Onyxacalles neglectus</i> Kulbe, 1999	E.: La Gomera, 28°07'27"N, 17°13'26"W, 901 m, laurisilva, 2008, Astrin & Stüben	JJ0640, E-713-neg	FJ716525	–
<i>Onyxacalles portusveneris</i> (Mayet, 1903)	FRANCE: Gard, 43°57'03"N, 04°28'59"E, 68 m, <i>Quercus ilex</i> , 2006, Stüben	JJ0144, F-0166-por	EU286326	EU286490
<i>Onyxacalles ringeli</i> Kulbe, 1999	E.: La Palma, 28°37'37"N, 17°49'45"W, 1432 m, laurisilva, 2006, Stüben	JJ0087, C-0171-rin	EU286300	EU286465
<i>Onyxacalles valencianus</i> Germann, 2005	E.: Alicante, 38°39'34"N, 00°32'29"W, 1296 m, <i>Quercus ilex</i> , 2007, Astrin & Stüben	JJ0172, E-0180-val	EU286331	EU286495
<i>Onyxacalles verrucosus</i> (Wollaston, 1863)	E.: El Hierro, 27°44'29"N, 18°03'24"W, 895 m, <i>Laurus</i> , 2006, Stüben	JJ0137, C-0170-ver	EU286324	EU286488
<i>Paratorneuma orbatum</i> (Wollaston, 1865)	E.: La Gomera, 28°09'58"N, 17°12'11"W, 255 m, <i>Persea americana</i> , 2008, Astrin & Stüben	JJ0660, E-733-orb	FJ716532	FJ716580
<i>Paratyphloporus karamani</i> (Formánek, 1912)	CROATIA: Dalmatia, 43°27'59"N, 16°41'40"E, 280 m, <i>Olea</i> , <i>Quercus</i> , <i>Carpinus</i> , 2007, Stüben	JJ0188, HR-0312-kar	EU286342	EU286506
<i>Pseudodichromacalles fernandezi</i> (Roudier, 1954)	E.: La Gomera, 28°08'18"N, 17°12'52"W, 791 m, <i>Sonchus</i> , 2008, Astrin & Stüben	JJ0664, E-737-fer	FJ716533	FJ716581
<i>Silvacalles cedroensis</i> (Kulbe, 2000)	E.: La Gomera, 28°07'27"N, 17°13'26"W, 901 m, laurisilva, 2008, Astrin & Stüben	JJ0643, E-716-ced	FJ716526	FJ716574
<i>Silvacalles hakani tagasaste</i> (Stüben, 2000)	E.: La Palma, 28°43'18"N, 17°47'07"W, 1047 m, <i>Chaemaecytisus proliferus</i> , 2006, Stüben	JJ0154, C-0106-tag	FJ716488	FJ716540
<i>Silvacalles instabilis</i> (Wollaston, 1864)	E.: Tenerife, Teno, 28°20'00"N, 16°47'10"W, 500 m, <i>Laurus</i> , 2005, Stüben	JJ0111, C-0136-ins	EU286309	EU286474
<i>Silvacalles lepidus</i> (Kulbe, 2000)	E.: La Palma, 28°38'22"N, 17°47'54"W, 624 m, <i>Laurus</i> , 2006, Stüben	JJ0110, C-0135-lep	EU286308	EU286473
<i>Silvacalles lunulatus</i> (Wollaston, 1854)	P.: Madeira, 32°44'34"N, 16°53'40"W, 514 m, <i>Laurus</i> , 2008, Stüben	JJ0449, P-513-lun	FJ716503	FJ716554

Table 1. Continued

Taxon	Collecting data	Vouchers	Acc.#16S	CO1
<i>Silvacalles mundus</i> (Wollaston, 1964)	E.: La Palma, 28°45'18"N, 17°46'37"W, 857 m, <i>Juglans regia</i> , 2006, Stüben	JJ0108, C-0133-mun	EU286307	EU286472
<i>Silvacalles nubilosus</i> (Wollaston, 1864)	E.: Tenerife, Anaga, 28°33'21"N, 16°10'46"W, 808 m, <i>Laurus</i> , <i>Ixanthus</i> <i>viscosus</i> , 2008, Astrin & Stüben	JJ0609, E-682-nub	FJ716514	FJ716563
<i>Silvacalles pedestris</i> (Stüben, 2000)	E.: La Gomera, 28°09'15"N 17°17'36"W, 819 m, <i>Ocotea foetens</i> , 2008, Astrin & Stüben	JJ0650, E-723-ped	FJ716528	FJ716576
<i>Silvacalles tolpivorus</i> (Germann & Stüben, 2006)	E.: La Gomera, 28°09'29"N, 17°09'37"W, 627 m, <i>Tolpis proustii</i> , 2008, Astrin & Stüben	JJ0654, E-727-tol	FJ716530	FJ716578
<i>Sonchiacalles muelleri</i> (Stüben, 2000)	E.: La Palma: 28°32'15"N, 17°49'42"W, 1212 m, <i>Tolpis calderae</i> , 2006, Stüben	JJ0092, C-0112-mue	FJ716485	FJ716537
<i>Sonchiacalles</i> <i>silosensis</i> (Stüben, 2000)	E.: La Gomera, 28°09'29"N, 17°09'37"W, 627 m, <i>Sonchus gomerensis</i> , 2008, Astrin & Stüben	JJ0656, E-729-sil	FJ716531	FJ716579
<i>Sonchiacalles sonchi</i> (Stüben, 2000)	E.: Tenerife, Teno, 28°21'39"N, 16°46'19"W, 534 m, plant detritus, 2008, Astrin & Stüben	JJ0626, E-699-son	FJ716520	FJ716569
<i>Torneuma caecum</i> Wollaston, 1860	P.: Madeira, 32°42'35"N, 16°58'17"W, 384 m, <i>Ficus carica</i> , 2008, Astrin & Stüben	JJ0458, P-523-cae	FJ716509	FJ716559
<i>Torneuma deplanatum</i> <i>deplanatum</i> (Hampe, 1864)	ITALY: Sicily, 38°04'03"N, 13°11'37"E, 539 m, <i>Asphodelus albus</i> , 2006, Stüben	JJ0203, I-0305-dep	EU286354	EU286518
<i>Torneuma desilvai</i> Osella & Zuppa, 1998	P.: Madeira, 32°47'51"N, 17°02'33"W, 85 m, <i>Laurus</i> , 2008, Astrin & Stüben	JJ0431, P-529-des	FJ716496	FJ716547
<i>Torneuma maderense</i> Stüben, 2002	P.: Madeira, 32°51'25"N, 17°12'18"W, 296 m, <i>Ficus carica</i> , 2008, Astrin & Stüben	JJ0457, P-522-mad	FJ716508	FJ716558
<i>Torneuma</i> <i>picocasteloense</i> Stüben, 2002	P.: Madeira: 33°04'27"N, 16°19'25"W, 146 m, <i>Cynara cardunculus</i> , 2008, Astrin & Stüben	JJ0437, P-535-pic	FJ716501	FJ716552
Outgroup: <i>Adexius</i> <i>scrobipennis</i> Gyllenhal, 1834	FRANCE: Isère, 45°16'15"N, 05°40'44"E, 813 m, <i>Fagus</i> , <i>Fraxinus</i> , <i>Quercus</i> , 2005, Stüben	JJ0043, I-0020-AdS	EU286289	EU286454
Outgroup: <i>Barretonus</i> <i>minor</i> Folwaczny, 1972	P.: Porto Santo, 33°04'27"N, 16°19'25"W, 146 m, <i>Cynara cardunculus</i> , 2008, Astrin & Stüben	JJ0438, P-536-BAR	FJ716535	FJ716582
Outgroup: <i>Laparocerus oromii</i> Machado, 2008	E.: La Gomera, 28°08'18"N, 17°12'52"W, 791 m, <i>Persea indica</i> , 2008, Astrin & Stüben	JJ0665, E-738-LAP	FJ716536	FJ716583

Collecting data usually consist of country (E., Spain; P., Portugal), region/island, coordinates, host plant, year of collection, and the collector's name; all material determined by P. E. Stüben; vouchers (DNA, morphology) are kept at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK); GenBank accession numbers starting with 'FJ' correspond to material sequenced in this study (those starting with 'EU' are taken from Astrin & Stüben (2008); the five cases for which no CO1 sequence is available are marked by a dash (they were coded as missing in the analysis); taxa appear under their new names.

(Stüben, 2009a). The matrix of concatenated, aligned nucleotide sequences is available from the authors or in Supporting Information Appendix S1. In this alignment, the five taxa for which no CO1 sequences were available (cf. Table 1) are coded as missing information (all 'N') for this gene. Total genomic DNA vouchers and voucher specimens are deposited at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany. The dry material consulted in this study is that of the Stüben Collection (CURCULIO-Institute, Mönchengladbach, Germany). Exhaustive information on collected material and localities on the Macaronesian Islands can be found in Stüben (2009b).

DNA extraction, using the Nucleo Spin Tissue extraction kit (Macherey-Nagel, Dueren, Germany), was carried out on samples preserved in ethanol or on dried material. We extracted DNA from either two to three legs, head, and prothorax, or sometimes also the whole weevil, depending on size and conservation of the sample. Primers (also specified in the GenBank records) and PCR conditions were those used in Astrin & Stüben (2008). Double-stranded sequencing was carried out by a sequencing facility (Macrogen, Seoul, South Korea). In order to control the base calling, we checked the electropherograms by eye.

#### PHYLOGENETIC AND DIVERGENCE-DATING ANALYSES

DNA sequence alignment was performed manually (CO1) or using the MUSCLE v. 3.6 program (Edgar, 2004), run with default parameters. MODELTEST v. 3.7 (Posada & Crandall, 1998; Posada & Buckley, 2004), implementing the Bayesian information criterion (BIC), identified the general time reversible + invariable sites + gamma distribution (GTR + I +  $\Gamma$ ) model of nucleotide substitution (Lanave *et al.*, 1984) as the best-fit model for CO1 as well as for 16S (disregarding excluded positions, see below). We concatenated the sequence data from the analysed genes using BioEdit v. 7.0.4.1 (Hall, 1999), thereby obtaining an alignment length of 1224 characters. Out of these, we excluded 90 ambiguously aligned 16S positions from phylogenetic analysis in order to guarantee positional homology over the whole alignment (Wägele, 2005; for an alternative procedure see Simmons & Ochoterena, 2000). As this exclusion of positions represents a biological hypothesis (open to discussion), we specified them in the same file as the combined alignment (see Appendix S1).

The program PAUP\* v. 4.0b10 (Swofford, 2002) was used to compute the phylogenetic information content, base frequencies, and to assess homogeneity of partitions (100 replicates).

We present parallel Bayesian Markov chain Monte Carlo (MCMC) analyses for a data set consisting of the

two mitochondrial genes. These were treated together for their provenance because they form part of the same linkage unit. We used the MrBayes v. 3.1.2 software (Ronquist & Huelsenbeck, 2003) to infer Bayesian reconstructions. We implemented the model of sequence evolution as diagnosed by the BIC, while letting MrBayes equate the values of the parameters through the use of 'flat' prior distributions. Parameters were unlinked amongst partitions and also between the third vs. first plus second codon positions in CO1. The analysis was run for 20 million generations (using the default chain number and temperatures). Every 1000th tree was sampled (40 000 trees retained for the two parallel runs taken together). Burn-in was determined graphically and checked using the TRACER v. 1.4.1 software (Rambaut & Drummond, 2007). Accordingly, we retained 39 920 trees. These were used for building a 50% majority rule consensus dendrogram (with posterior probabilities). Corroborating the burn-in values of the main analysis and excluding the possibility of an attraction to local optima (Huelsenbeck & Bollback, 2001; Huelsenbeck *et al.*, 2002), two additional replicates were run for ten million generations each and with different starting seeds. These are not shown as they produced identical or near-identical results.

In order to accommodate varying nucleotide substitution rates across lineages, we performed uncorrelated, relaxed-clock estimates of divergence times with BEAST v. 1.4.8 (Drummond & Rambaut, 2007), which employs Bayesian MCMC. Using a Yule process speciation prior, we based the analyses on the topology of the MrBayes consensus tree and chose the uncorrelated lognormal (UCLN) model of rate variation in combination with the model of evolution as identified through application of the Bayesian information criterion (GTR + I +  $\Gamma$  for both partitions). The UCLN model delivers smaller 95% highest posterior densities than the uncorrelated exponential model that is also offered in BEAST (Drummond *et al.*, 2006). We ran (and later joined) two separate Bayesian analyses for 30 million generations, sampling every 1000th tree. Through TRACER we assessed the convergence of the runs and burn-in iterations (3000 trees each). Discarding the burn-in resulted in effective sample size values for the posterior probability (as for all monitored parameters) of well over 100. We calibrated the analysis by two biogeographical points (A, B; based on island ages) and – close to the root – by indirect fossil evidence (C).

A: we assume that *Onyxacalles ringeli* Kulbe (1999) originated on the island of La Palma, to which it is endemic whereas its sibling species (*Onyxacalles neglectus* Kulbe, 1999) is endemic to La Gomera and El Hierro. Therefore, we put a constraint on the age of *O. ringeli*, not allowing it to be older than 2 Myr,



which is the highest probable age of La Palma (cf. Carracedo, 2008).

B: in order to stabilize the BEAST runs, we dated the diversification of *Madeiracalles* on Madeira to 5.1–4.8 Mya. Around this time, soil formation on Madeira (the island emerged around 5.2 Mya; cf. Carvalho & Brandão, 1991; Schmincke, 1998) should have been complete and it is likely that representatives of *Madeiracalles* already living on Porto Santo (like today, *Madeiracalles portosantoensis*; Stüben, 2002b) soon reached the neighbouring island.

C: none of the analysed species is known to exist in fossil form. However, Gratshev & Zherikhin (2003) stated that almost all modern weevil subfamilies probably existed in the Palaeogene period. The fossil record for Cryptorhynchinae and Molytinae (Britton, 1960) as well as for Cossoninae (Kuschel, 1992) reaches back to the Eocene. Therefore, we loosely constrained the ingroup (Cryptorhynchinae) to be at least 34 Myr old.

The BEAST runs were checked through the program r8s (Analysis of Rates of Evolution) v. 1.71 (Sanderson, 2003). Applying the same calibration points as in BEAST, we obtained similar results that always lay well within the confidence intervals of the divergence estimates delivered by BEAST (sometimes above, sometimes below BEAST mean values; not shown).

## RESULTS AND DISCUSSION

### HOMOGENEITY OF PARTITIONS, INFORMATION CONTENT AND BASE COMPOSITION

The incongruence length difference test (Farris *et al.*, 1994) showed no significant conflict between the two partitions included in the analysis. The proportion of variable characters in the analysed CO1 fragment is 54.6%; 49.5% are parsimony informative. Out of these informative characters, two-thirds are contributed by third codon positions. In 16S with excluded ambiguous positions, variable characters make up 43.3% and informative ones 34.7%. Considering the variable characters, base composition proved to be homogeneous in both markers. An A + T bias (typical in insect mtDNA, e.g. Crozier & Crozier, 1993) existed for both mitochondrial genes. This bias was higher in 16S (72.3%) than in CO1 (63.3%), although CO1 third codon positions (77.0%) exceeded the A + T bias of 16S.

### TREE TOPOLOGY AND TAXONOMIC CHANGES BASED ON MOLECULAR RECONSTRUCTION, MORPHOLOGY AND ECOLOGY

The Bayesian reconstruction (Fig. 1A), based upon the analysis of the CO1 and 16S genes, mostly confirms the informal taxonomic groups presented in a

morphological classification of Canary Cryptorhynchinae by Stüben (2000a, Table 1). The reconstruction also corroborates the results of Astrin & Stüben (2008) by showing multiple colonization events and by recovering as natural groups with absolute or near-total support the genera *Calacalles*, *Dichromacalles*, *Echinodera*, *Onyxacalles*, and *Acalles* (the *Acalles* 'core group'), as well as the tribe Torneumatini and the Atlantic clade. Concerning the morphological tree presented by Stüben (2000b), it is noteworthy that the taxa now joined in the genus *Sonchiacalles* were already recovered as sister to the rest of the Canary clade. However, the phylogenetic 'unconnectedness' of the two forest-dwelling species groups (*Dendroacalles* and *Silvacalles*) could not be recognized by morphology alone (which is mirrored in the informal taxonomic groups).

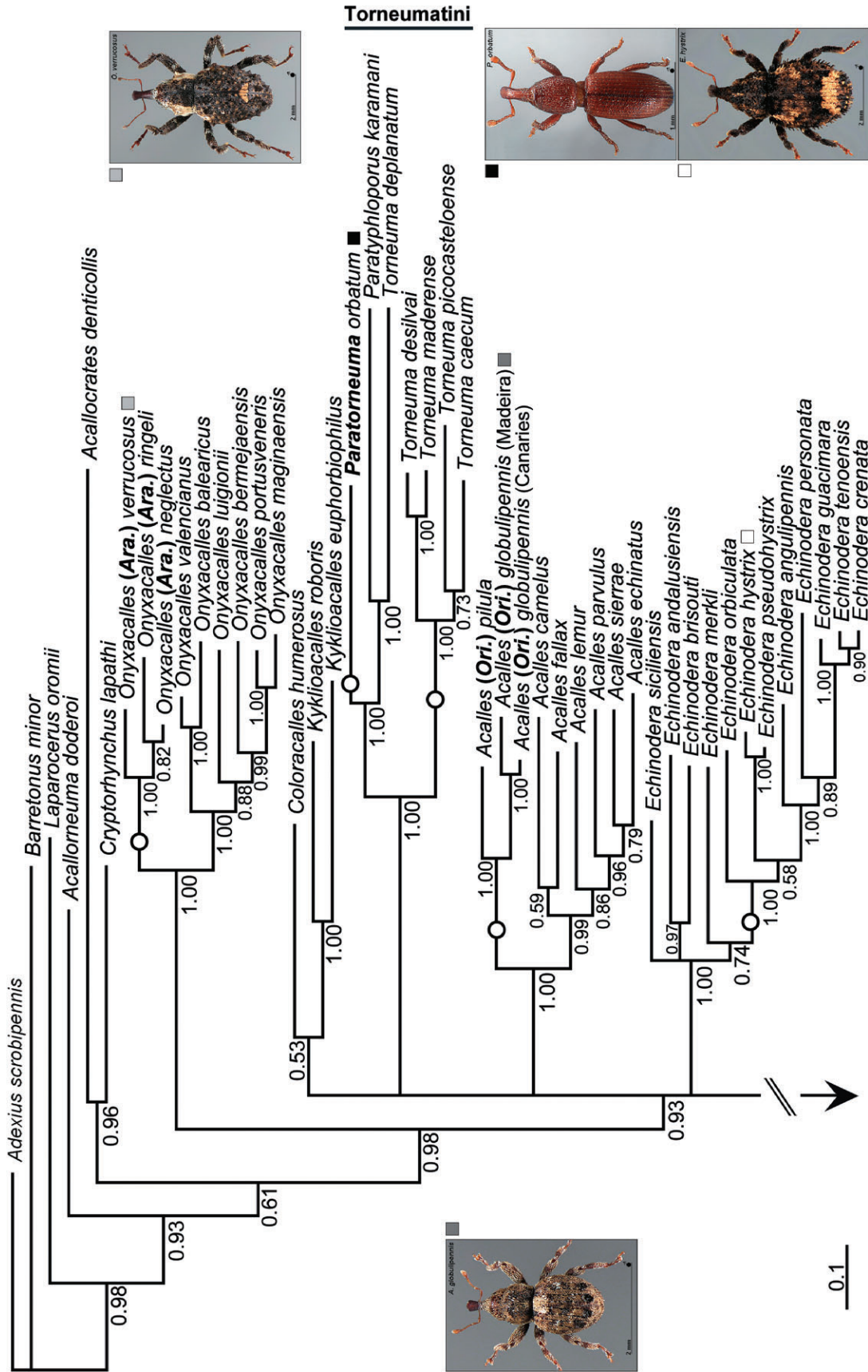
As a result of the nature of the employed genetic markers, the resolution of the tree is usually high at species and genus level (cf. e.g. the Macaronesian representatives of *Onyxacalles*, *Echinodera*, and *Acalles* forming subgroups within the respective genus with full support), whereas the relationships amongst the older, mostly continental genera and tribes often remain unclear (e.g. how does *Echinodera* relate to *Acalles* and *Kyklioacalles*?). This situation is better within the Atlantic clade (this group corresponds to the second page of the dendrogram, Fig. 1A). However, some of the support values for the highly resolved Canary clade advise caution. Within the Canary clade, there are two conspicuous suprageneric groups that can be 'banked on': *Aeoniacalles* + *Dendroacalles* and *Echiumacalles* + *Ficusacalles*.

Figures 2A–22E complement the molecular results with data on morphology, reproductive biology, and ecology. Taxonomic changes and comments are given in the last column of this tabular synopsis. Detailed reasons for the proposition of the supraspecific taxa are given in the respective discussions of each new taxon.

### LINEAGE AGE ESTIMATION

The chronogram in Figure 1B shows the estimated lineage divergence times. The calibration is based on island ages. This constitutes a strong a priori assumption and introduces a certain degree of circularity (cf. Arnedo *et al.*, 2008; Machado *et al.*, 2008). The speculative component in our calibration was to assume that the diversification of *Madeiracalles* took place shortly after the formation of Madeira (in fact, morphology does not exclude the option that it could have happened later).

How can this uncertainty be circumvented? With all sequences obtained at the same point in time and no direct fossil evidence, there remains only the



**Figure 1.** A, Bayesian 50% majority rule consensus for the two analysed mitochondrial genes. Numbers indicate nodal posterior probabilities. The scale shows the expected nucleotide substitutions per site. Abbreviations in parentheses denote subgenus (see text). Genus names in bold indicate new nomenclature. Circles mark colonization events (in black: invasive species). For many Macaronesian species, the respective host plants are depicted. The second page of the tree shows the taxa corresponding to the 'Atlantic clade'. B, chronogram based on relaxed phylogenetic analysis of the two mitochondrial genes, using the uncorrelated lognormal model of substitution rate variation. Numbers next to the nodes indicate mean divergence times (in Myr), with 95% confidence intervals of divergence times depicted as bars at the corresponding nodes. N.B. Although the underlying topology is that delivered by MrBayes, BEAST does not allow polytomies, which it resolves arbitrarily.



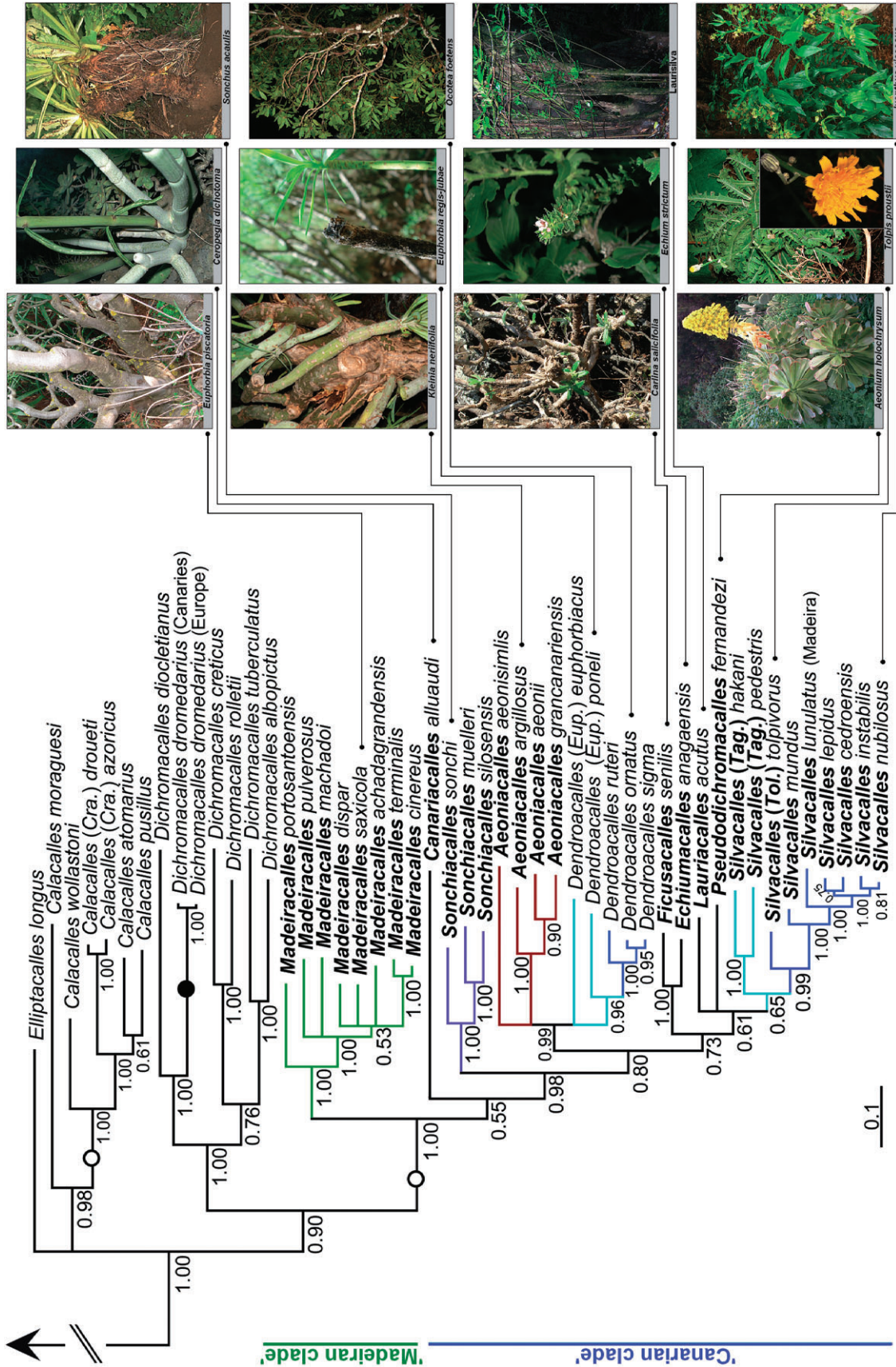


Figure 1A. Continued

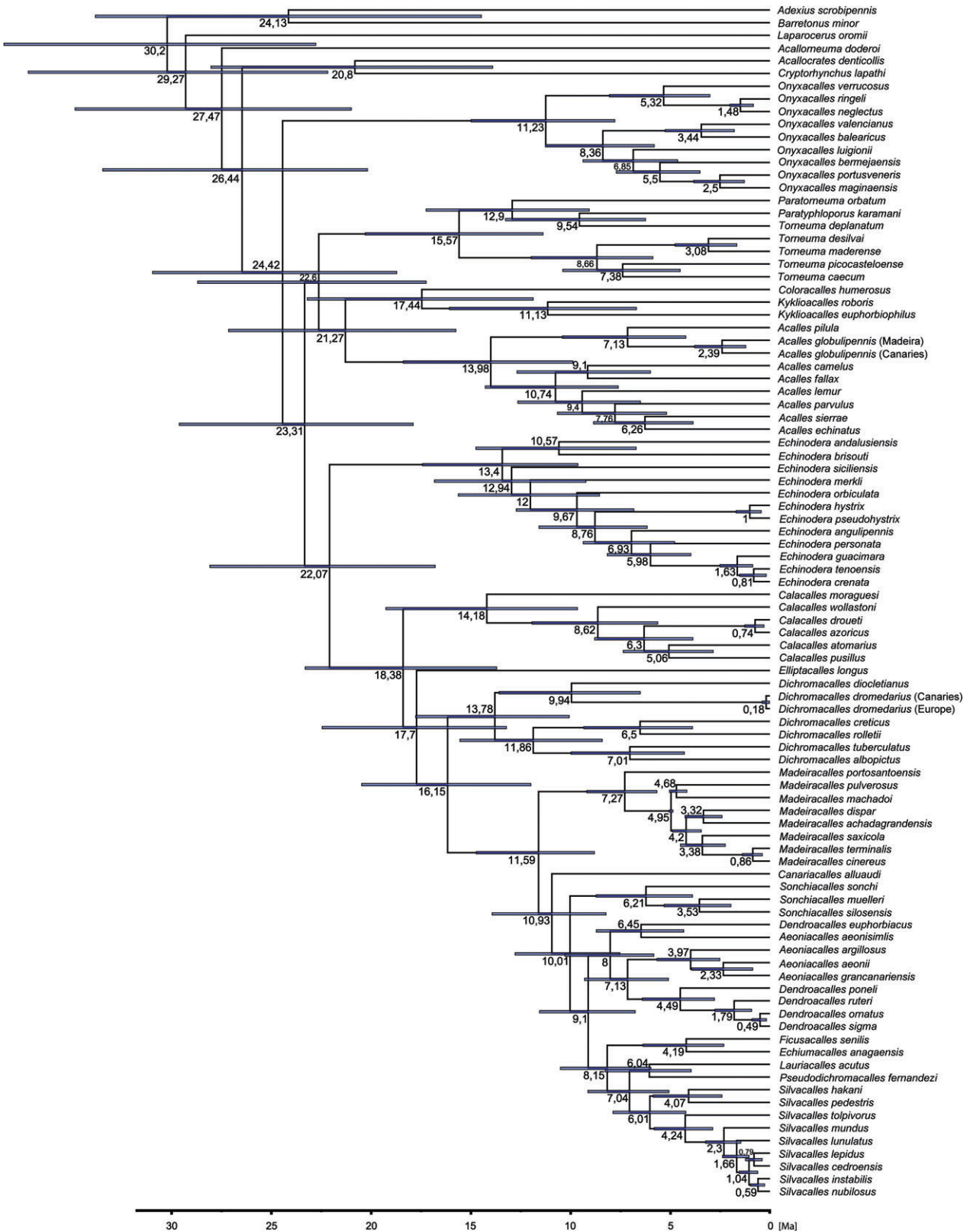
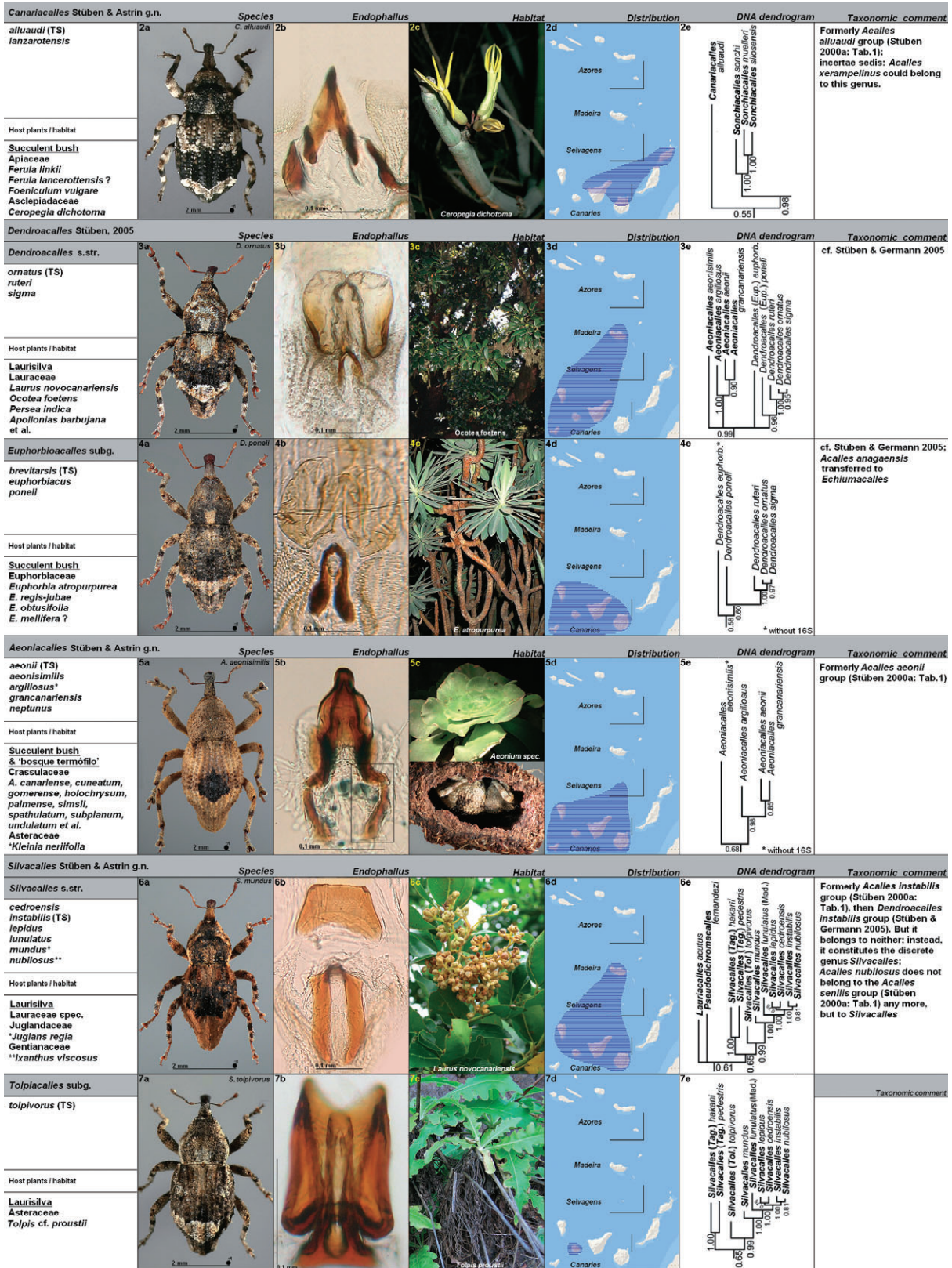


Figure 1(B). Continued





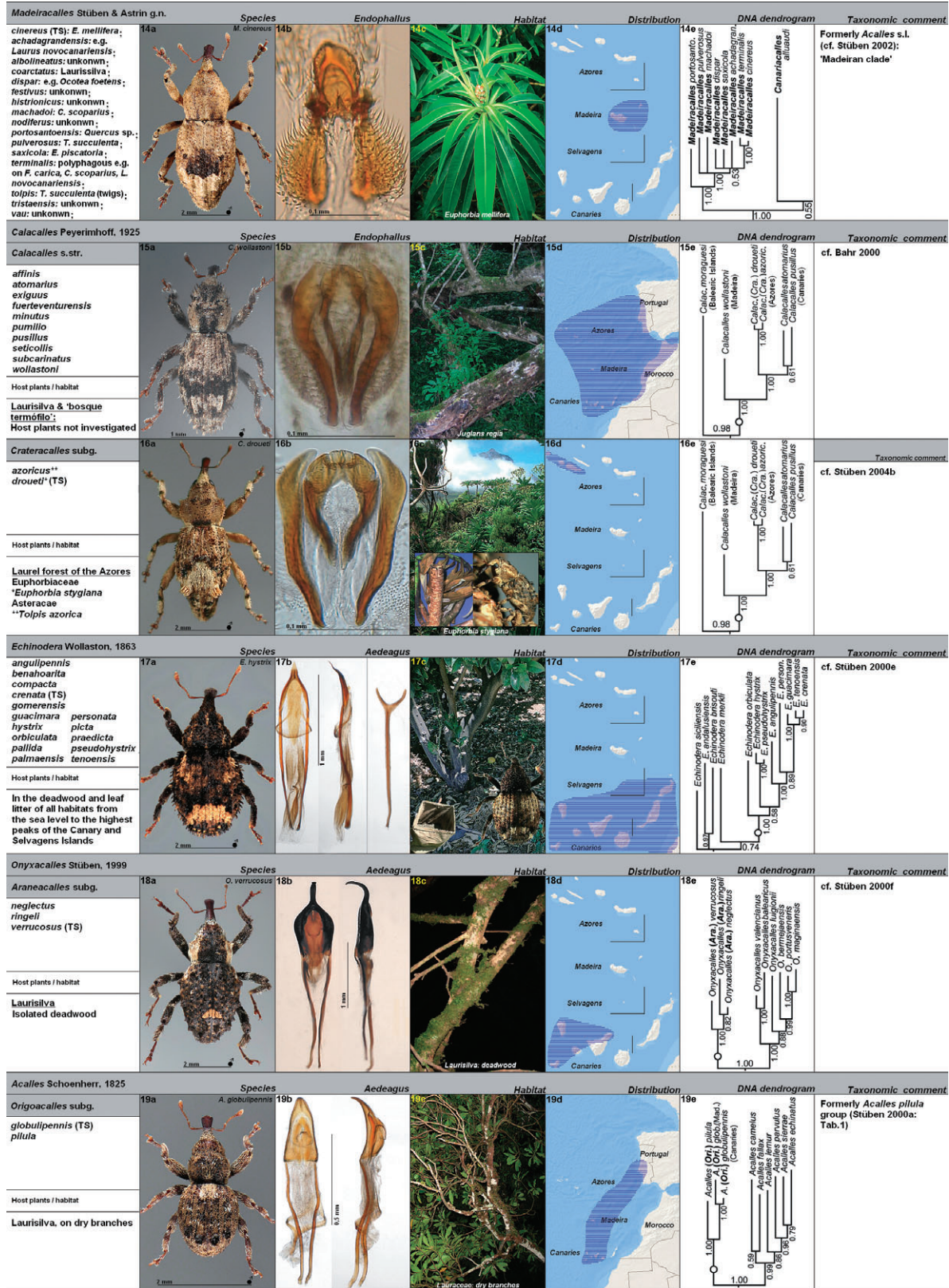
Figures 2–22. Morphological, biological, and ecological comparison of the genera and subgenera of Macaronesian Cryptorhynchinae along with the respective sections of the tree; (TS) = type species. Figures 4E and 5E show a section of the tree that results when 16S sequences for *Aeoniacalles aeonisimilis*\* and *Dendroacalles euphorbiacalles*\* are excluded.



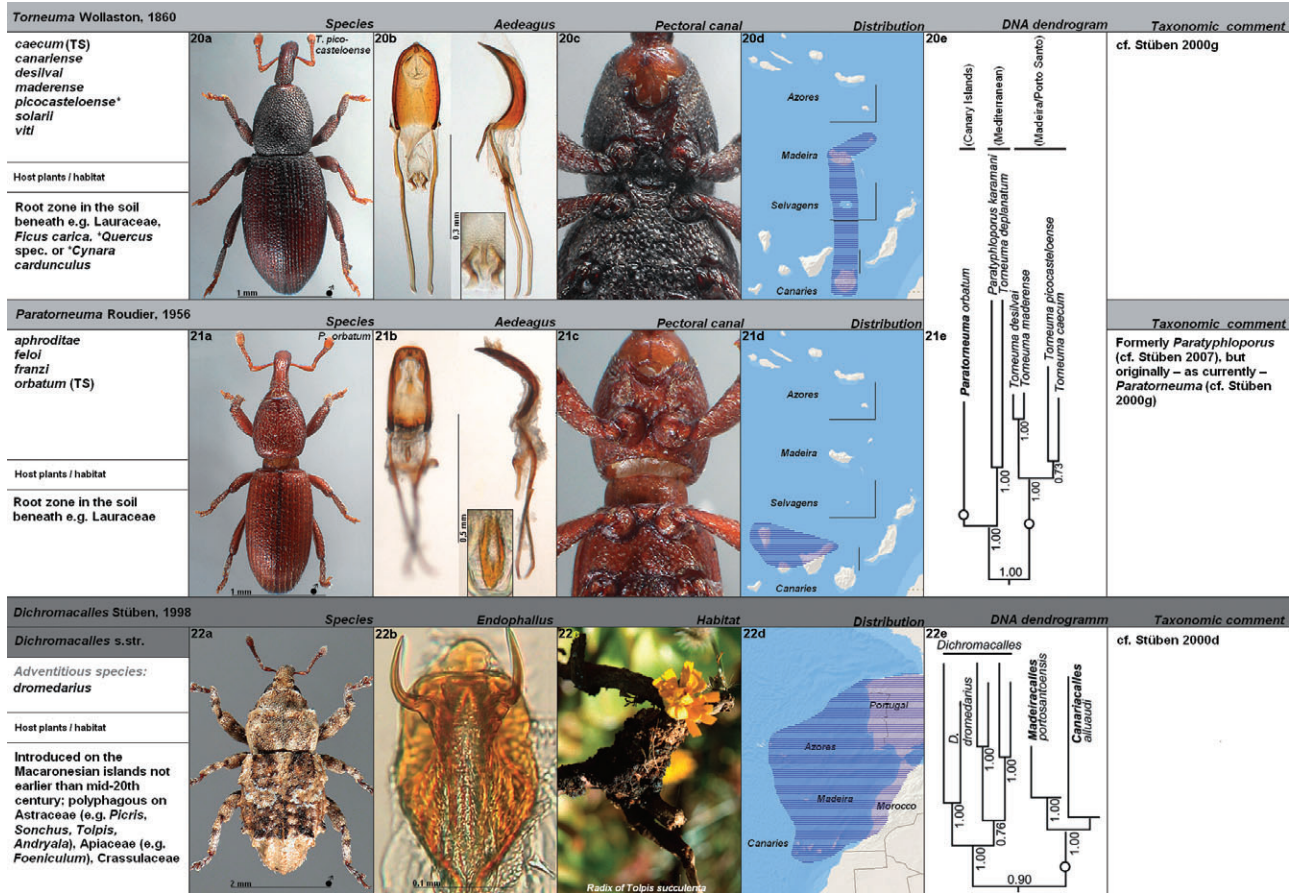
<p><b>Tagasastacalles</b> subg.</p> <p><i>hakani hakani</i> (TS) <i>hakani tagasaste pedestris</i></p> <p>Host plants / habitat</p> <p><b>Fabaceae</b> (originally "laurisilva") <i>Chamaecytisus profliferus</i></p>	<p>8a </p> <p>8b </p> <p>8c </p> <p>8d </p>	<p>8e </p>	<p>Taxonomic comment</p> <p>Formerly <i>Acalles tagasaste</i> group (Stüben 2000a; Tab.1)</p>
<p><b>Pseudodichromacalles</b> Stüben &amp; Astrin g.n.</p> <p><i>fernandezii</i> (TS)</p> <p>Host plants / habitat</p> <p><b>Succulent bush</b> <b>Apiaceae</b> <i>Foeniculum vulgare</i> <b>Asteraceae</b> <i>Sonchus acaulis</i>, <i>congestus</i>, <i>hierrensis</i>, <i>Pericallis murrayi</i> <b>Crassulaceae</b> <i>Aeonium holochrysum</i>, <i>tabuliforme</i> <i>Aeonium spec.</i> <b>Fabaceae</b> <i>Spartocytisus supranubius</i></p>	<p>9a </p> <p>9b </p> <p>9c </p> <p>9d </p>	<p>9e </p>	<p>Taxonomic comment</p> <p>Formerly a species of <i>Dichromacalles</i> (Stüben 2000d); now <i>Pseudodichromacalles</i></p>
<p><b>Lauriacalles</b> Stüben &amp; Astrin g.n.</p> <p><i>acutus</i> (TS)</p> <p>Host plants / habitat</p> <p><b>Laurisilva</b> <b>Lauraceae spec.</b></p>	<p>10a </p> <p>10b </p> <p>10c </p> <p>10d </p>	<p>10e </p>	<p>Taxonomic comment</p> <p><i>Acalles acutus</i>: formerly <i>incertae sedis</i> (Stüben &amp; Germann 2005)</p>
<p><b>Sonchiacalles</b> Stüben &amp; Astrin g.n.</p> <p><i>muelleri silosensis sonchi</i> (TS)</p> <p>Host plants / habitat</p> <p><b>Uppermost succulent bush &amp; 'bosque termófilo'</b> <b>Asteraceae</b> <i>Sonchus acaulis</i>, <i>congestus</i>, <i>hierrensis</i>, <i>palmensis</i>, <i>radicatus</i>; <i>Tolpis calderae</i>, <i>lacinata</i>, <i>proustii</i>, <i>lagopoda</i></p>	<p>11a </p> <p>11b </p> <p>11c </p> <p>11d </p>	<p>11e </p>	<p>Taxonomic comment</p> <p>Formerly <i>Acalles sonchi</i> group (Stüben 2000a; Tab.1)</p>
<p><b>Echiumacalles</b> Stüben &amp; Astrin g.n.</p> <p><i>anagaensis</i> (TS)</p> <p>Host plants / habitat</p> <p><b>Uppermost succulent bush &amp; 'bosque termófilo'</b> <b>Boraginaceae</b> <i>Echium strictum</i></p>	<p>12a </p> <p>12b </p> <p>12c </p> <p>12d </p>	<p>12e </p>	<p>Taxonomic comment</p> <p>Formerly a species of <i>Dendroacalles</i> subg. <i>Euphorbiacalles</i> (Stüben &amp; Germann 2005).</p>
<p><b>Ficusacalles</b> Stüben &amp; Astrin g.n.</p> <p><i>senilis ficvorator senilis oceanicus senilis senilis</i> (TS)</p> <p>Host plants / habitat</p> <p><b>Succulent bush &amp; 'bosque termófilo': Ficus carica</b> <b>Apiaceae</b> <i>Foeniculum vulgare</i> <b>Fabaceae</b> (e.g.) <i>Chamaecytisus profliferus</i> <b>Asteraceae</b> (e.g.) <i>Sonchus hierrensis</i> <i>Tolpis proustii</i> <i>Carlina salicifolia</i> <b>Euphorbiaceae</b> <i>Euphorbia anachoreta</i></p>	<p>13a </p> <p>13b </p> <p>13c </p> <p>13d </p>	<p>13e </p>	<p>Taxonomic comment</p> <p>Formerly <i>Acalles senilis</i> group (Stüben 2000a; Tab.1)</p>

Figures 2–22. Continued





Figures 2–22. Continued



Figures 2–22. Continued

alternative of adopting a nucleotide substitution rate from the literature. This is, however, as problematic as the biogeography-calibrated approach, as we lack a criterion on which rate to apply. In a tentative BEAST run, we relied exclusively on nucleotide substitution rates, implementing (in an uncorrelated, relaxed-clock analysis) a normal prior distribution for the per-lineage substitution rate, with a mean of 1.15% ± 0.15% (a pairwise substitution rate of 2.3% was established for insect mitochondrial DNA by DeSalle *et al.*, 1987; Brower, 1994 published 2.0% in *Drosophila*). This led to divergence estimates that were very similar to the results obtained through the biogeography-calibrated analysis, exceeding the mean estimates (of the main analysis) by usually not more than 1 Myr. Regardless of the uncertainty inherent to both approaches individually, their converging results confer a higher reliability to the estimated lineage ages.

According to the divergence estimates (which should be used cautiously because of the rather large confidence intervals), the ‘Macaronesian clade’ colonized the archipelagos between 16 and 11 Mya

(taking the 95% highest posterior densities, HPD: between 20.5 and 8.8 Mya) – this is younger than often hypothesized and can, but does not necessarily, imply that the eastern Canaries functioned as stepping stone islands.

The genus *Echinodera* started to diversify on the Canary Islands around 9.7 Mya (HPD: 12.7–6.8 Mya) (judging from the analysed species), *Acalles* (*Origoacalles*) around 7.1 Mya (HPD: 10.4–4.2 Mya) and *Onyxacalles* (*Araneacalles*) around 5.3 Mya (HPD: 8–3 Mya). By 8.7 Mya (HPD: 12–5.9 Mya), the diversification of *Torneuma* probably started on Porto Santo (where *Torneuma picocasteloense* occurs today). In addition, the genus *Calacalles* reached Macaronesia before Madeira had emerged.

#### THE CANARIAN CLADE AND THE ‘WAY OF COLONIZATION’

On the Macaronesian Islands occur 93 endemic Cryptorhynchinae as well as two introduced species: *Dichromacalles dromedarius* Boheman, 1844 (Fig. 22A, D) and *Echinoacalles franzi* Stüben, 2008a.



The distribution of a further species, *Acalles* (*Origoacalles*) *globulipennis* Wollaston, 1854, also reaches to the northern Portuguese mainland (Fig. 10A, D). Amongst the endemic taxa, the former species of *Acalles* *s.l.* in particular (see Introduction) lack closely related species on the North African and the European mainland. In the past, the degree of endemism in the *Acalles* *s.l.* species and their unique insular isolation have given rise to numerous speculations concerning the colonization and evolution of Cryptorhynchinae on the Macaronesian Islands (cf. Stüben, 2000c).

At first, much attention was given to the putatively ancient evergreen laurel forest on the volcanic Macaronesian Islands, the more so as in the Tertiary, large areas of Mediterranean Europe and North Africa were equally covered by laurel forest and because its age has been reported to be as great as 40 Myr (see Pott, 2005). Bramwell & Bramwell (1974: 79) suggested an age of about 20 Myr for the Macaronesian forest whereas other authors have proposed only 5 Myr (Kunkel, 1993). It has always been a highly speculative question: are the long-legged, bizarrely bristled, and (unlike on the adjacent mainland) tree-climbing Canarian *Acalles* *s.l.* merely relics of a time long gone? Or can we conclude from the supposedly great age of the Macaronesian laurel forest that its fauna is 'inevitably' very old too (e.g. Zerche, 1996)?

Now we can reject these hypotheses – at least for the species of *Acalles* *s.l.* The species of the genus *Canariacalles* seem very 'basal', not only in morphological terms (Stüben, 2000b: fig. 1) but also the mitochondrial phylogenetic tree of the Macaronesian Cryptorhynchinae presented here demonstrates the comparative evolutionary proximity of the direct ancestor of the species *Canariacalles alluaudi* (Uyttenboogaart, 1940) to the species of *Dichromacalles* *s.s.* (Fig. 1A; cf. description of *Canariacalles* gen. nov. below), which are widespread in the western Mediterranean and the Atlantic region. Like the species of *Dichromacalles*, *C. alluaudi* develops on host plants growing in the arid succulent belt. In our reconstruction, *C. alluaudi* appears as sister to the entire 'Canarian monophylum' with also a high likelihood (cf. nodal support) of being sister not only to the Canarian, but to the Madeiran clade as well.

This new finding corroborates the already established hypothesis (Stüben, 2000c; Stüben & Germann, 2005) that 'the colonisation and, respectively, the evolution [of the Macaronesian species of *Acalles* *s.l.*] started in the conspicuously more arid habitats of the coastal succulent belt and continued much later as adaptation to the shady and moist laurel forest of the thermo-Canarian belt' (translated from Stüben & Germann, 2005: 48). This implies that the bizarrely

shaped and specialized 'tree-climber species' (the species of *Silvacalles* *s.s.* as well as the species of *Dendroacalles*) are not only morphologically (Stüben, 2000b: fig. 1; Stüben & Germann, 2005: fig. PhyDEND), but also according to the mitochondrial dendrogram (Fig. 1A), highly derived taxa of the Macaronesian clade.

For the flightless Cryptorhynchinae, the most likely method of dispersal is over the open sea, because a physical connection to the mainland has never existed for the Macaronesian Islands. The colonization happened either by adults clinging to the bark of trees or, more likely, by any stage of development remaining inside twigs of dwarf-shrubs while floating on the sea. Even hatched imagines can remain in the sealed cell of the pupa for several weeks (Stüben, 2004a, 2005a). Such 'vessels' or swimming islands of vegetation can be for instance the woody stalks and root necks of perennial herbs (e.g. Apiaceae: *Ferula* or *Foeniculum*) or the more robust branches of several shrubs and succulents (e.g. Crassulaceae: '*Holochrysa*'), which allow the individuals within to survive a 'cruise' of several weeks over the open sea (cf. Stüben, 2000c). This route was apparently taken by the succulicole, xerothermophilic Cryptorhynchinae of the probably 'proto-*Dichromacalles*' type that originally gained a foothold on the barren lava flows of the volcanic islands. In all likelihood, it was during the long period of volcanic activity and of the continuing growth of the Macaronesian archipelagos that the evolution of the first endemic Cryptorhynchinae took place (long before soil formation led to the appearance of the Macaronesian laurel forest and before this forest reached its climax). Over hundreds of thousands of years there must have been a more or less dense cover of xerothermophilic, succulent, and spinose dwarf vegetation on the meagre lava soil. This vegetation is today typical for the arid zones of Lanzarote and Fuerteventura or on the mountainous islands at altitudes below 300 m (northern slopes) or below 800 m above sea level (southern slopes). It also occurs in dry river valleys or canyons (so-called 'barrancos'). On the northern slopes, in the belt of the trade wind clouds, dense forests developed millions of years ago (during warm periods). The recent volcanic activity on all Canarian Islands (except on La Gomera; still ongoing on La Palma) and Madeira repeatedly cut aisles into the dense cover of vegetation and thereby provided new areas for a permanent succession which has been an ideal evolutive 'arena' for the species arriving from the North African and European mainland. The colonizing individuals must already have been adapted to what they found here: succulent, woody, and often poisonous perennials (*Sonchus*, *Tolpis*, *Aeonium*, *Foeniculum*, etc.). Possibly these weevil species also had an impact on the evolution of the host plant groups as

a result of feeding on specific individuals and specific parts of the plants (Sprick & Stüben, 2000; Stüben, 2000c).

Not counting the introduced species, the Macaronesian Islands have been colonized by Cryptorhynchinae seven times independently (see circle symbol on the branches, Fig. 1A). After each of these colonization events, the species arriving at the islands underwent some form of cladogenesis. However, a considerable adaptive radiation has taken place only once, after the colonization by the *Dichromacalles*-like ancestor species of a 'Macaronesian clade'. The Macaronesian clade is formed by two distinct subgroups: the 'Madeiran clade' (= *Madeiracalles*) and the 'Canarian clade'.

#### THE MADEIRAN CLADE

There has been some speculation about the age of Madeira. Today it seems to be clear (Carracedo, 2008): that the main island of the Madeiran archipelago is much younger than the small neighbouring island Porto Santo that emerged 14 Mya. More than 5 Mya (in the Miocene–Pliocene transition) the first coral reefs formed, which is a reliable indication that after 9 Myr of subaerial volcanic activity the nascent main island Madeira was about to emerge from the sea. Tenerife and Gran Canaria are almost three times as old as Madeira (see Sziemer, 2000). Perhaps the relatively short geological history of Madeira (as an emerged island) is one of the reasons why many taxa of *Acalles s.l.* are not only very similar morphologically, but might also even stand at the beginning of a potential splitting of species (although of course we cannot anticipate further steps of evolution). Amongst the Canarian taxa of *Acalles s.l.* the morphological features are immensely more copious. Accordingly, the taxonomic work on Madeiran Cryptorhynchinae based on phenotypic characters has been much more laborious (Stüben, 2002b).

Given that the endemic taxa of *Madeiracalles* gen. nov. of the archipelago of Madeira present only such scarce morphological characters applicable to phylogenetic investigation, molecular analysis is the more promising method. Thus, for the Madeiran species of this group, the mitochondrial data show a result comparable to that recently obtained for the genus *Laparocerus* (Curculionidae: Entiminae) by Machado *et al.* (2008) – a monophyletic group representing the adelphotaxon of the Canarian clade.

The fact that *Madeiracalles portosantoensis* (Stüben, 2002b) had been discovered on Porto Santo under *Quercus ilex* and *Quercus suber* was puzzling at first (Stüben, 2002b: 124). Was this species possibly introduced along with its host plants during recent centuries? This question also seems to be solved now.

The species must have been living on Madeira already and switched host plants during the radical floral change following human exploitation of the island: *Madeiracalles portosantoensis* shows a morphological connection to the species of *Acalles s.l.* that are endemic to the Macaronesian Islands (Stüben, 2002b). As revealed by the molecular analysis, this species – living on 14-Myr-old Porto Santo – constitutes the adelphotaxon to all other species of the Madeiran clade, which probably did not evolve earlier than 5 Mya. The high morphological similarity as well as the almost unmodified basic pattern of the endophallus of the Madeiran species could also indicate a shorter period of radiation.

*Madeiracalles pulverosus* of main island Madeira is – like *M. portosantoensis* – one of the few extremely xerothermophilic, succulicole cryptorhynchine species that develop during summer within the woody root neck of full-grown shrubs of *Tolpis succulenta* Lowe living on the barren rock of the coastal belt. *Madeiracalles pulverosus* (and *Madeiracalles machadoi*) represent the sister taxa of all the remaining species of the genus *Madeiracalles*. Was it again – similar to the radiation on the Canaries – a succulicole pioneer species that colonized the dry habitats of the coastal belt of the archipelago of Madeira first, while the adaptation to the shady and moist laurel forest took place much later?

According to this scenario, two species – coming from the Canaries and already specialized on laurel forest – colonized the archipelago of Madeira very 'late' (cf. Fig. 1B): the ancestor of *Silvacalles lunulatus* (closely related species occur on La Palma and La Gomera) (Fig. 6D) and the highly derived *Dendroacalles ornatus* (Wollaston, 1854) (Fig. 3A, D), which is apparently a synonym of *Dendroacalles fortunatus* (Wollaston, 1864) described for La Gomera (cf. Stüben & Germann, 2005: 43).

Besides *Madeiracalles*, *Silvacalles lunulatus*, and *Dendroacalles ornatus*, the following taxa managed to colonize the archipelago of Madeira: *Calacalles s.s.* with only one species (cf. Fig. 15A), *Calacalles wollastoni* (Chevrolat, 1852); one 'genuine' species of *Acalles*: *Acalles (Origoacalles) globulipennis* (also occurring in the coastal belt of Portugal; Fig. 19A, D); the introduced *Dichromacalles dromedarius* (Fig. 22A, D). In addition, the Torneumatini reached the archipelago of Madeira (Figs 20, 21). The four species of *Torneuma* that are endemic to the archipelago (including the type species *Torneuma caecum* Wollaston, 1860) form a separate 'Madeiran clade' in our reconstruction (but additional '*Torneuma*' species from the European mainland and Gran Canaria still need to be collected). As sister group to the Madeiran *Torneuma* stands (with absolute support) a group comprised of *Paratorneuma orbatum* (Wollaston,

1865) from La Gomera plus the two Mediterranean species *Paratyphloporus karamani* (Formánek, 1912) and *Typhloporus deplanatus* Hampe, 1864. However, the long edges of the dendrogram do not necessarily mean that the species group of *T. deplanatus* Hampe, 1864, which is widespread in the Mediterranean, really belongs to the genus *Torneuma* (see also discussion below: Torneumatini).

## TAXONOMY

### REVISION OF THE GENERA OF THE MACARONESIAN CRYPTORHYNCHINAE

#### *Preliminary remark*

In the following, we present nine genera and two subgenera of the Macaronesian species of 'Acalles s.l.' for the first time. We share the view that taxonomic splitting should be avoided wherever possible. However, the pan-Palaeartic distribution of the group under study and the close phylogenetic ties of the Macaronesian representatives to continental taxa necessitate a taxonomic concept that is in balance with the already described genera and subgenera of Palaeartic Cryptorhynchinae (therefore, erecting several new genera cannot be avoided). Within this wider framework, the most substantial argument for the new taxa is the structure of the internal sac of the aedeagus (endophallus). In each of the continental, species-rich genera (e.g. *Dichromacalles* or *Kykliocalles*), the endophalli share a unique basic structure, and it is expedient to apply this concept to the classification of Macaronesian *Acalles* s.l. as well. In doing so it can be noted that in the 'younger' species of Madeira (not older than 5 Myr) the structure of the endophallus has changed only marginally (Figs 28–32), whereas the structures of the 'older' species of the Canary Islands show a high diversity (cf. Figs 2B–22B). According to this scenario we subsume all species from the Madeira archipelago under the new genus *Madeiracalles*, and divide the species of *Acalles* s.l. from the Canary Islands into several new genera, following the logically compelling concept that we refer to earlier in this paragraph. For the already-mentioned morphological and for compelling ecological reasons, it is not possible, e.g. to merge the Canarian genera *Ficusacalles* + *Echiuacalles*, *Lauriacalles* + *Pseudodichromacalles* or even *Dendroacalles* + *Aeoniacalles* (as one might suggest before carefully considering all the evidence). We discuss this in detail below.

#### TRIBE CRYPTORHYNCHINI SCHOENHERR, 1835

#### *DENDROACALLES* STÜBEN, 2005 (FIGS 3A–E, 4A–E)

*Type species: Acalles ornatus* Wollaston, 1854

Wollaston, 1854, 1857, 1865; Roudier, 1954; Behne, 2000; Stüben, 2000a, b, c, 2002b, 2004a, 2006, 2007b,

2008a; Stüben, Behne & Bahr, 2003; Stüben & Germann, 2005; Germann & Stüben, 2006; Astrin & Stüben, 2008; Stüben, Fabian & Astrin, 2009 in press.

#### *Compilation of the subgenera and species of the genus Dendroacalles*

(N.B. in the following (re)descriptions, bold type indicates taxa from Macaronesian locations for which DNA sequences are presented.)

#### *Dendroacalles* s.s.

***Dendroacalles ornatus* (Wollaston, 1854) – Madeira (including type locality)**

= *Acalles fortunatus* Wollaston (1864) syn. Stüben & Germann, 2005: 43 – La Gomera

***Dendroacalles sigma* (Wollaston, 1864) – La Palma**

***Dendroacalles ruteri* (Roudier, 1954) – Tenerife (including type locality), La Gomera, El Hierro, La Palma**

#### ***Euphorbioacalles* Stüben (2005) subgen.**

*Type species: Acalles brevitarsis* Wollaston, 1864

*Dendroacalles (Euphorbioacalles) brevitarsis* (Wollaston, 1864) – Gran Canaria

***Dendroacalles (Euphorbioacalles) poneli* (Stüben, 2000) – Tenerife (including type locality), La Gomera, El Hierro**

***Dendroacalles (Euphorbioacalles) euphorbiacus* (Stüben, 2000) – La Palma**

#### *Discussion*

The species of this genus have been (re)described by Stüben (2000a). Based on the analysis of morphological characters, 11 of the 29 endemic taxa of Canarian *Acalles* s.l. have been presented in a preliminary cladogram (Stüben, 2000b). Furthermore, first hypotheses on biogeography and evolution were proposed for the Canarian Cryptorhynchinae (Stüben, 2000c), especially for the species of the recently described genus *Dendroacalles* (Stüben & Germann, 2005).

In the first description of this genus, the five species of the 'Acalles instabilis-group' (now *Silvacalles*) were preliminarily included in *Dendroacalles* (Fig. 6). The reasons for the inclusion were that these species also possess a double sclerotic structure of the internal sac of the aedeagus (endophallus) (Fig. 6B), that they show an elongated, canoe-like habitus (cf. Fig. 6A), and that they belong to the ecological group of the so-called 'tree-climbers' of the Canarian and Madeiran laurel forest (Stüben *et al.*, 2009 in press; cf. Fig. 6C). According to our phylogenetic analysis, these tree-climbers represent an artificial grouping (Fig. 1A). The species of the *Dendroacalles instabilis*-group belong to the new genus *Silvacalles*. As numerous species from the



laurel forest herb layer are also included in this taxon, we also describe a subgenus, *Silvacalles* s.s., that accommodates the *instabilis*-group (fully supported in our reconstruction).

The host-plant relationships of the more xerothermophilic taxa *Dendroacalles poneli* (La Gomera, El Hierro, Tenerife: Teno Mts; Fig. 4A) and *D. euphorbiacus* (La Palma) have recently been studied much more extensively than for most species of *Dendroacalles* s.s. from the actual laurel forest (Stüben, 2004a, 2007b; Stüben & Germann, 2005; Germann & Stüben, 2006). These two species, endemic to the western Canary Islands, belong to the subgenus *Dendroacalles* (*Euphorbioacalles*) Stüben, 2005 (in Stüben & Germann, 2005). However in our analysis, this subgenus proved to be paraphyletic with respect to the *Dendroacalles* s.s. species (cf. Fig. 4E). The 'detached' position of *D. euphorbiacus* (Figs 1A, 3E) is because of the signal of the 16S gene (incomplete lineage sorting?). When analysing the genus only for CO1, *Dendroacalles* becomes monophyletic (cf. Fig. 4E).

Our phylogenetic reconstruction implies that *Dendroacalles anagaensis* (Tenerife, La Gomera) has to be separated from the genus *Dendroacalles* (to avoid polyphyly). Unlike the already-mentioned species that develop in dendriform taxa of the spurge family (Euphorbiaceae), *D. anagaensis* is the only Macaronesian cryptorhynchine species developing in *Echium strictum* L., which belongs to the borage family (Boraginaceae) (Germann, 2004). Thus, we propose the new monotypic genus *Echiumacalles* (Fig. 12A–E) to accommodate this species. As the above-mentioned double sclerotic structure of the endophallus is also characteristic for *Echiumacalles anagaensis*, this character must have evolved independently three times during the evolution of the Cryptorhynchinae on the Macaronesian archipelagos; namely in *Dendroacalles* (Figs 3B, 4B), *Silvacalles* s.s. (Fig. 6B), and *Echiumacalles* (Fig. 12B).

The aforementioned hypothesis of *Acalles* s.l. evolution pointing from the succulent belt into the laurel forest is supported by the position of the highly derived *Dendroacalles* species in the mitochondrial tree. The supposedly great age of the Macaronesian laurel forest, a forest also characteristic of warm Tertiary Europe, should not be taken to imply that this plant association also shelters life-forms of great age.

*Differential diagnosis:* See below ('Key to the genera and subgenera of Macaronesian Cryptorhynchinae').

*Distribution:* Canary Islands (except Lanzarote and Fuerteventura), Madeira.

**AEONICALLES** STÜBEN & ASTRIN GEN. NOV.

(FIG. 5A–E)

*Type species:* *Acalles aeonii* Wollaston, 1864

Wollaston, 1864, 1865; Roudier, 1954; Israelson *et al.*, 1982; Behne, 2000; Riede & Stüben, 2000; Stüben, 2000a, b, c, 2002b, 2005a, 2007b, 2008a; Bayer & Stüben, 2000; Sprick & Stüben, 2000; Stüben *et al.*, 2003; Stüben & Germann, 2005; Germann & Stüben, 2006.

*Compilation of the species of the genus Aeoniacalles*

***Aeoniacalles aeonii* (Wollaston, 1864) comb. nov. (formerly: *Acalles*) – Tenerife**

= *Acalles bodegensis* Stüben, 2000 syn. Stüben & Germann, 2005

***Aeoniacalles aeonisimilis* (Stüben, 2000) comb. nov. (formerly: *Acalles*) – La Gomera (including type locality), La Palma**

***Aeoniacalles grancanariensis* (Stüben, 2000) comb. nov. (formerly: *Acalles*) – Gran Canaria**

***Aeoniacalles argillosus* (Boheman, 1837) comb. nov. (formerly: *Acalles*) – Tenerife (including type locality), La Gomera, El Hierro, La Palma**

***Aeoniacalles neptunus* (Wollaston, 1854) comb. nov. (formerly: *Acalles*) – Selvagens**

The taxa of this new genus are identical to the species of the *Acalles aeonii*-group revised in Stüben (2000a: 35–46).

*Description*

*Size:* 3.9–9.0 mm.

*Head:* Punctures of the dark brown rostrum of the ♂ dense, deep and robust, rostrum about three-quarters as long as pronotum; rostrum of the ♀ slightly longer, conspicuously more slender and more rounded, lighter in colour, the punctures finer, more sparse and less deep – mid-line often without punctures.

*Pronotum:* 0.95–1.10× as wide as long; widest directly behind the middle, slightly rounded towards base (as in *Aeoniacalles aeonisimilis*) or narrowed almost linearly, strongly rounded towards the strong constriction at the front margin. Without mid-groove or depression. Disk of pronotum slightly convex with two dark brown marks of bristles sticking out vertically near the middle; at the front-margin with the same type of bristles. Sometimes also with diffuse dark, longitudinal marks next to the base.

*Elytra:* Elongated, 1.34–1.48× as long as wide; widest at the end of the basal third or directly in front of the middle, outline towards base and elytral slope predominantly parallel or – as in *Aeoniacalles aeonisi-*



*milis* – rounded oblong oval. Next to the apex with a lateral depression. The even intervals superelevated – often tubercle-like, the uneven intervals on the same level like punctured stripes; the latter on the disc of elytra predominantly smaller than the intervals and with finer punctures as on the flanks of elytra; here the more robust and deep punctured stripes overlap into the intervals. In the middle and behind with a broad black fascia fading into the brown colour of the basic cover anteriorly and contrasting with a zone of white scales posteriorly. Fascia on its anterior part often with a very dark tuft of bristles on the suture. There are further diffuse dark marks on the second to fourth interval at the base of elytra and sometimes next to the apex on the always lighter brown elytral slope (*Aeoniacalles grancanariensis* with a pitch-dark mark on the elytral slope). At large the colouring of the elytra is only little contrasting. The base of elytra forming almost a line.

**Legs:** Front femur long, protruding (extremely conspicuous in *Aeoniacalles argillosus*) front margin of the eye; hind femur reaching the middle of the last abdominal sternite. Basic cover of legs consisting of dense, light brown scales. Femur sparsely annulated with black, fine, and slender bristles. Tibia covered on the outer edge with short elevated bristles and on the inner surface with hair-like bristles.

**Venter:** With a deep pectoral canal. The middle of the front margin of second abdominal sternite often protruding arc-like to the first sternite. Second sternite as long as or longer than sternites 3 and 4 combined. First and second sternite predominantly covered with slender, acuminate bristles.

**Aedeagus:** The endophallus consists of a simple equal-sided, inverse v-shaped structure; the ends of this structure are attached to a 'sickle' (Fig. 5B).

**Differential diagnosis:** The species of this genus are distinguished from all other endemic taxa of the Macaronesian archipelagos by the equal-sided, inverse v-shaped structure of the internal sac of the aedeagus; the ends of this circle-like structure are attached to a 'sickle' (Fig. 5B). See also the key of the Macaronesian genera.

**Biology and ecology:** Most taxa in this genus live on several species of the orpine family (Crassulaceae), especially on endemic species of the genus *Aeonium* (cf. Fig. 5C). An exception is *Aeoniacalles argillosus*, which is monophagous on the poisonous *Kleinia neriifolia* Haw. (locally known as verode or berode, Asteraceae) (Germann & Stüben, 2008). The reports on *Euphorbia anachoreta* and/or *Cistanche phelypaea* as

host plants of *Aeoniacalles neptunus* from the Selvagens are doubtful (see Stüben, 2002b: 118). The biology of the Canarian species has been studied extensively over recent years, for instance the parallel cladogenesis (cospeciation) with the host plant (Stüben, 2000c: 303), analysis of the phytochemicals (Sprick & Stüben, 2000), description of the larvae/pupae along with their development (Bayer & Stüben, 2000; Stüben, 2005a), or the function and relevance of the stridulatory organ and its mechanism (Riede & Stüben, 2000). It has been possible to rear numerous generations of *Aeoniacalles aeonii* and *Aeoniacalles argillosus* (Stüben, 2005a; Germann & Stüben, 2006). Phylogenetically, there is a very clear connection between *Aeoniacalles* and its sister genus *Dendroacalles* (recovered together as monophylum with near-total support; cf. Fig. 1A).

As with *D. euphorbiacus* (see above), the position of *A. aeonisimilis* varies according to the analysed gene. The paraphyly of the genus *Aeoniacalles* in Figure 1 turns into monophyly when the 16S gene is excluded (cf. Fig. 5E).

**Etymology:** The name *Aeoniacalles* refers to several endemic species of the orpine family (Crassulaceae, genus *Aeonium*) that are the host plants of most of the weevils in this genus (only *A. argillosus* lives monophagously on the poisonous Asteraceae *Kleinia neriifolia* Haw.). Some species of *Aeoniacalles* have not been described yet.

**Distribution:** Endemic to the Canary Islands (except Lanzarote and Fuerteventura), Selvagens (does not occur on Madeira).

**SILVACALLES STÜBEN & ASTRIN GEN. NOV.**  
(FIGS 6A–E, 7A–E, 8A–E)

**Type species:** *Acalles instabilis* Wollaston, 1864

Wollaston, 1864, 1865; Roudier, 1954; Behne, 2000; Kulbe in: Stüben, 2000a; Riede & Stüben, 2000; Stüben, 2000a, b, c, 2002b, 2007b, 2008a; Stüben *et al.*, 2003; Stüben & Germann, 2005; Germann & Stüben, 2006; Astrin & Stüben, 2008; Stüben *et al.*, 2009 in press.

*Compilation of the subgenera and species of the genus Silvacalles*

***Silvacalles s.s.***

***Silvacalles instabilis* (Wollaston, 1864) comb. nov. (formerly: *Acalles*, *Dendroacalles*) – Tenerife (including type locality), Gran Canaria**  
***Silvacalles mundus* (Wollaston, 1864) comb. nov. (formerly: *Acalles*, *Dendroacalles*) – La Palma**  
***Silvacalles lepidus* (Kulbe, 2000) comb. nov. (formerly: *Acalles*, *Dendroacalles*) – La Palma**

*Silvacalles cedroensis* (Kulbe, 2000) **comb. nov.** (formerly: *Acalles*, *Dendroacalles*) – La Gomera

*Silvacalles lunulatus* (Wollaston, 1854) **comb. nov.** (formerly: *Acalles*, *Dendroacalles*) – Madeira

*Silvacalles nubilosus* (Wollaston, 1864) **comb. nov.** (formerly: *Acalles*) – Tenerife (including type locality), La Palma

*Tagasastacalles* **subgen. nov.**

Type species: *Acalles hakani* Roudier, 1954

*Silvacalles* (*Tagasastacalles*) *hakani hakani* (Roudier, 1954) **comb. nov.** (formerly: *Acalles*) – Tenerife

*Silvacalles* (*Tagasastacalles*) *hakani tagasaste* (Stüben, 2000) **comb. nov.** (formerly: *Acalles*) – La Palma (including type locality), El Hierro?

*Silvacalles* (*Tagasastacalles*) *pedestris* (Stüben, 2000) **comb. nov.** (formerly: *Acalles*) – La Palma (including type locality), Tenerife, El Hierro, La Palma

*Tolpiacalles* **subgen. nov.**

Type species: *Acalles* (*Tolpiacalles*) *tolpivorus* Germann & Stüben, 2006

*Silvacalles tolpivorus* (Germann & Stüben, 2006) **comb. nov.** (formerly: *Acalles*) – La Gomera

The taxa of this new genus belong mainly to the groups of *Acalles instabilis* and *Acalles tagasaste*, which have already been revised (Stüben, 2000a: 35–46). All species of this genus inhabit the thermo-Canarian belt above 400 m, namely the thermophilous shrub forest ('bosque termófilo') on the Canary Islands and the Canarian and Madeiran laurel forest.

*Description*

*Size:* 2.0–7.5 mm.

*Head:* The puce, shiny rostrum of the ♂ two-thirds and of the ♀ three-quarters as long as pronotum (shorter only in *Silvacalles tolpivorus*). The rostrum of the ♀ more slender and fine, rostrum of the ♂ slightly more robust and with more strongly punctures. The antenna unicoloured puce.

*Pronotum:* About as wide as long and the outline almost always strongly 'bellied' rounded; mid-groove either – as in most of the species – completely absent or – as in only a few species – at most with a very slight depression. Disc of pronotum with only a small, isolated pair of tufts of bristles (often only consisting of a few dark bristles sticking out vertically); on the front margin with a collar of long bristles sticking out vertically and arranged more densely in the middle. Outline of pronotum regularly rounded at all sides; disc of pronotum often convex. However, the pronotum coasts down towards the front margin flatly, often 'delta-like', with a strong lateral depression/

constriction next to the front margin. The contrasting colouring of the elytra (especially in *Silvacalles nubilosus*) is also continued on the pronotum even if large-scaled, light marks and fascia are absent.

*Elytra:* Elongated, canoe-like; 1.34× (1.23× in *S. pedestris*) to 1.60× as long as wide; widest *c.* in the middle; outline laterally slightly and towards the elytral slope rounded more strongly oval. Without shoulders next to the base; however, the sixth interval sometimes slightly protruding tooth-like; apex of elytra strongly elongated, which causes – similarly to the genus *Dendroacalles* – a 'canoe-like' habitus. Next to the apex with a slight lateral depression. On the second and fourth interval with little bristled humps and knobs, which are definitely not as steeply erected and high as in *Dendroacalles s.s.*; the colouring of the elytra extremely variable interspecifically as well as intraspecifically. Elytral slope with an almost triangular, dark mark that is extended to a broad, fuliginous fascia in *Silvacalles hakani tagasaste*.

*Legs:* Long, the front femur projecting above the front margin of pronotum; legs obscurely annulated; the femur mostly with two, the tibia with one obscure dark ring. Femur with raised, light, slender bristles; the outer edge of tibia with bristles sticking out vertically.

*Venter:* First abdominal sternite very long, longer than the second, the latter as long as or longer than both following sternites combined, fifth sternite again longer.

*Aedeagus:* Endophallus with an often tiny, fork-like structure (degenerated or lacking in *Silvacalles nubilosus*, Fig. 36B) that is terminated towards apex by a sclerotized (transparent and trapezoidal) plate that is mostly clearly wider than long in the species of the subgenus *Silvacalles s.s.* (Fig. 6B). Only *S. tolpivorus* has a clearly different, distinctive, 'goblet-like' structure of the internal sac (Fig. 7B). The three species of the subgenus *Tagasastacalles* – only with the fork-like structure of the endophallus (Fig. 8B) – also belong to this genus.

*Differential diagnosis:* The species of the new genus *Silvacalles* can be easily discriminated from the species of the new genus *Aeoniacalles* (described above): the latter have a sickle-like structure at the basal ends of the forked structure of the endophallus (Fig. 5B) which is absent in the genus *Silvacalles*.

Both species within the subgenus *Silvacalles* and the species within the genus *Dendroacalles* inhabit the dense laurel forest of the Canaries and Madeira. Therefore, confusion during determination seems

possible. However, the specimens of *Dendroacalles* are larger (3.5–7 mm) than those of *Silvacalles* s.s. (2–3 mm – *S. mundus* and *S. nubilosus* 5 mm at most). Moreover, the species of *Dendroacalles* have two plates above the forked structure of the endophallus (Figs 3B, 4B), whereas in *Silvacalles* s.s. these structures form a single, connected, trapezoidal, or square-like plate (Fig. 6B). *Silvacalles nubilosus* has a single, almost square-like, very thick, and hardly transparent plate as well, and the terminating, basal, fork-like structure is lacking or has been reduced (Fig. 36B). See also the ‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’.

**TAGASASTACALLES STÜBEN &  
ASTRIN SUBGEN. NOV. (FIG. 8A–E)**

The three (sub-)species of this subgenus live on *Chamaecytisus proliferus* Link. (escobón, tagasaste), a plant belonging to the pea family (Fabaceae) (cf. Stüben, 2007b) and have only a simple, fork-like structure in the endophallus without a second terminal, trapezoidal table (Fig. 8B). Based on the molecular tree, it is possible to include this well-supported group in the genus *Silvacalles*, to which it is joined as sister taxon (but without high posterior probability values). According to the morphological affinity to the *Silvacalles* s.s. and *S. (Tolpiacalles)* species (and in order to avoid taxonomic splitting), we include this group – as subgenus – in the genus *Silvacalles*.

*Differential diagnosis:* See below (‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’).

**TOLPIACALLES STÜBEN & ASTRIN SUBGEN. NOV.  
(FIG. 7A–E)**

The only species of this monotypic subgenus is *S. tolpiworus*, which has been described only recently (Germann & Stüben, 2006). It is monophagous on *Tolpis* cf. *proustii*, a member of the daisy family (Asteraceae). It is probably a plant endemic to La Gomera (Germann & Stüben, 2006). We place this taxon in the genus *Silvacalles* as well. On the one hand the species has a slightly different ‘goblet-like’ structure of the internal sac, a character that discriminates it from all other Macaronesian Cryptorhynchinae. On the other hand, the habitus and preference of habitat leave no doubt that it belongs in this genus (it is recovered as sister to *Silvacalles* s.s. with near-total support). Thus again the attention of the taxonomist is focussed on the biology and ecology of the higher taxa presented (cf. following section).

*Differential diagnosis:* See below (‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’).

*Biology and ecology:* All species of *Silvacalles* live in the shady and moist laurel forest of the thermo-Canarian and thermo-Madeiran belt. *Silvacalles* species are not found associated with more or less succulent plants as are, for instance, the specialized taxa of Crassulaceae growing in crevices of rock faces or *Kleinia neriifolia* (Asteraceae) of the coastal succulent belt (belonging to the plant association of the Kleinio–Euphorbietea). Instead, Lauraceae (for *Silvacalles* s.s.) and dendri-form Fabaceae (for the subgenus *Tagasastacalles*) are the host plants of these Cryptorhynchinae that prefer very moist habitats stretching across the belts of the laurel forest and the pine forest. There is another species that belongs to the group of taxa inhabiting the moist trade wind zone (including the forest areas and the upper succulent belt): the contrastingly coloured *S. nubilosus* (Fig. 36A), which is monophagous on *Ixanthus viscosus* Griseb. (Fig. 36C), a plant of the gentian family (Stüben & Germann, 2005: 70), and – conspicuous through a differing endophallus – *S. (Tolpiacalles) tolpiworus* (Fig. 7A), which lives on *Tolpis* cf. *proustii* Pit. on La Gomera (Fig. 7C).

This also applies to the species of the subgenus *Tagasastacalles*. The very variable small tree *Chamaecytisus proliferus* (‘tagasate’, Fabaceae), which belongs to the natural vegetation of the laurel forest and the pine forest (‘bosque mixto’) has been a cultivated plant of the western Canary Islands for centuries (Fig. 8C). The green shoots of the regularly pollarded trees are used as fodder. Today its use provides the only kind of protection for the species of *Tagasastacalles*, which have become very rare in their natural habitat – the remains of the endangered laurel forest (cf. Stüben, 2008a). The current populations of these cryptorhynchine species in the ‘treeless’ plantations of Tagasaste, e.g. on El Hierro should not result in the false notion that *Tagasastacalles* is a subgenus alien to the Canarian laurel (and pine) forest. This type of forest is almost extinct on El Hierro.

It is difficult to distinguish the habitat preference of the large species of *Dendroacalles* s.s. and the very small species of *Silvacalles* s.s., which both inhabit the laurel forest. However, many species of *Silvacalles* (e.g. *S. lepidus* from La Palma, *S. cedroensis* from La Gomera and *S. lunulatus* from Madeira) inhabit the margin of the laurel forest or its substitute vegetative associations. Specimens can be collected through beating dead, thin twigs and branches of especially *Laurus* spp. (Fig. 6C) or of *Myrica* (see also Kulbe, 2000). In contrast to this, the species of *Dendroacalles* s.s. inhabit exclusively the (undisturbed) primary forest (Stüben, 2007b; Fig. 3C).



*Etymology:* The name *Silvacalles* refers to the shady and moist laurel forest inhabited by this cryptorhynchine genus.

*Distribution:* Endemic to the western Canary Islands and (with only one species) on Madeira.

**LAURICALLES STÜBEN & ASTRIN GEN. NOV.**

(FIG. 10A–E)

*Type species by monotypy:* *Acalles acutus* Wollaston, 1864

Wollaston, 1864, 1865; Roudier, 1954; Israelson *et al.*, 1982; Kulbe in: Stüben, 2000a; Behne, 2000; Stüben, 2000a, b, 2007b; Stüben *et al.*, 2003; Stüben & Germann, 2005; Astrin & Stüben, 2008; Stüben *et al.*, 2009 in press.

*The species of the genus Lauriacalles*  
***Lauriacalles acutus* (Wollaston, 1864) comb. nov. (formerly: *Acalles*) – Tenerife (including type locality), La Palma**

A detailed redescription of *Lauriacalles acutus* (Wollaston, 1864) (formerly *Acalles*), the types species of the new monotypic genus, is given by Stüben (2000a: 73–75).

*Description*

*Size:* 2.9–4.9 mm.

*Head:* Rostrum of the ♂ four-fifths as long as pronotum, brown, punctures deep and close; rostrum of the ♀ as long as pronotum, punctures finer and glossy; antennae reddish-brown; insertions of the antennae in (♂) or behind (♀) the middle of the rostrum.

*Pronotum:* Slender, as long as wide or slightly longer (c. 1.04×); from the base towards the middle on the side broadening nearly rectilinearly and towards the fore-margin rounded ovally; in front of the fore-margin with a lateral depression. The pronotum is more slender than the elytra, which are 1.5× wider (Fig. 10A). On the disk of pronotum and in front of the scutellum with a small hollow followed by a furrow.

*Elytra:* 1.40–1.50× as long as wide; strongly rounded (bulbously); widest directly in front of the middle; next to the apex more slender and constricted, with a deep lateral depression. On the suture with a small bristled hump, on the second and fourth interval with two and on the third with one bristled hump; the hump of the elytral slope (on the second interval) is very high, with long, robust, and upright elevated aggregations of bristles; on this elytral slope always with a wide, triangular (less often with a v-like), white, and distinctive fascia.

*Legs:* Very long, the front femur projecting above the front margin of pronotum; femur and tibia more or less clearly annulated with one or two dark rings. Femur with raised, short, and slender bristles; the outer edge of tibia with short and clubbed bristles sticking out vertically; femur and tibia brown, tarsus reddish brown.

*Venter:* First abdominal sternite very long, longer than the second, the latter as long as or longer than both following sternites combined, fifth sternite again longer.

*Aedeagus:* Endophallus only with a single ‘fork’-shaped structure (Fig. 10B).

*Differential diagnosis:* The new genus is distinguished from the species of the genera *Dendroacalles* and *Silvacalles* s.s. by its lack of the disc-shaped structures above the fork of the endophallus (Fig. 10B vs. Figs 3B, 4B). Equally, *L. acutus* cannot be confused with the species of the genus *Aeoniacalles* described above: The latter always has a falciform structure at the basal ends of the fork-like structure of the endophallus (Fig. 5B) that is not present in *L. acutus*.

Finally *Lauriacalles* is compared with the species of the subgenus *Tagasastacalles* of the genus *Silvacalles* that also possesses a simple fork-like structure of the internal sac of the aedeagus only slightly different in shape (Fig. 8B). The elytral slope of *Lauriacalles* is covered with humps and very long and upright aggregations of bristles (sticking out almost vertically) of which the anterior ones are coloured dark brown to black and the posterior ones are light brown to white. However, the elytral slope of the species of *Tagasastacalles* is characterized by smaller humps covered with shorter bristles that are of less contrasting colouring. Furthermore, the apex of the elytra of *L. acutus* is conspicuously elongated in a ‘beak-like’ way (Fig. 10A), whereas the elytra of *S. hakani hakani*, *S. hakani tagasaste*, and *S. pedestris* have only a slight lateral depression towards the apex, which is only slightly elongated (cf. Fig. 8A). The species of *Tagasastacalles* are monophagous on *Chamaecytisus proliferus* Link. (Fig. 8C) and *L. acutus* has exclusively been collected by beating of dead twigs of several species of the laurel family (Lauraceae). Thus, confusing these groups is impossible even in the field. See also the ‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’.

*Discussion*

The affiliation of this species to any informal taxonomic group has been problematic until now. First it was placed in the group of *Acalles sigma* (Stüben, 2000a: 73), which was then separated as the genus



*Dendroacalles* s.s. However, the option of describing a new genus for the species according to morphological characters only seemed too speculative. Consequently, the species was declared *incertae sedis* with the comment that ‘according to its habitus, this species is very similar to the species of *Dendroacalles*. However, it does not have the double structure of the internal sac of the aedeagus which is typical for the genus [cf. Figs 3B, 4B vs. Fig. 10B in current paper]. Hence at present one can only speculate about the phylogenetic position of this Macaronesian species of *Acalles* as there are no results from molecular genetic investigations to recur to’. (translated from Stüben & Germann, 2005: 42).

The Bayesian analysis underlines the particular position of this new monotypic genus from the Canarian laurel forest (Fig. 1A): it appears in a trichotomy, together with the species *Pseudodichromacalles fernandezi* and the *Silvacalles* cluster. Merging these genera into one genus, maybe also including *Echiu-macalles* and *Ficusacalles*, is not an option. Neither can we consider a fusion with just the (equally monotypic) genus *Pseudodichromacalles*. The impossibility of joining *Pseudodichromacalles* and *Lauriacalles* (not even recovered as exclusive sister groups) lies in the morphological and ecological differences regarding habitat preference as well as the markedly different host plants. Whereas *L. acutus* is a species of the laurel forest (and its substitute vegetative associations or contacting plant communities on Tenerife and La Palma; Fig. 10C), *Pseudodichromacalles fernandezi* inhabits the Canarian succulent belt and prefers more arid and open areas (cf. section on biology and ecology of *Pseudodichromacalles*).

*Etymology*: The name *Lauriacalles* refers to the shady and moist laurel forest of the thermo-Canarian belt that is the habitat of this monotypic genus.

*Distribution*: Endemic to the Canary Islands Tenerife (including type locality) and La Palma (rare on this island).

**PSEUDODICHROMACALLES STÜBEN & ASTRIN**  
GEN. NOV. (FIG. 9A–E)

*Type species by monotypy*: *Acalles fernandezi* Roudier, 1954

Roudier, 1954; Lindberg, 1958; Stüben & Behne, 1998; Behne, 2000; Stüben, 2000d, 2008a; Bahr, 2001; Stüben, Behne & Bahr, 2001; Stüben & Germann, 2005.

*The species of the genus Pseudodichromacalles Pseudodichromacalles fernandezi* (Roudier, 1954) **comb. nov.** (formerly: *Acalles*, *Dichromacalles*) – Tenerife (incl. type locality), La Gomera, El Hierro

A detailed redescription of *Pseudodichromacalles fernandezi* (formerly *Dichromacalles*), the types species of the new monotypic genus *Pseudodichromacalles*, is given in Stüben (2000d: 100–102).

*Description*

*Size*: 3.3–6.6 mm.

*Head*: Rostrum (♂) very short, robust, dim, reaching half the length of pronotum, covered with bright scales and dotted closely towards the apex; shiny rostrum of the ♀ more slender, longer, light brown, dots arranged more distantly and finer; eyes small, flat, and in dorsal view only visible as narrow lines.

*Pronotum*: 1.08–1.14× as wide as long, flattened; widest at the end of the basal quarter or third, towards the fore-margin up to the lateral constriction nearly parallel-sided; the high-contrast integument with light brown and black spots.

*Elytra*: Compact, flattened; 1.48–1.55× as long as wide; widest in the middle, towards the base nearly parallel-sided, flanks with a slight lateral depression near the apex, apex not so far pushed forward as in the species of *Dendroacalles* or *Silvacalles*. The colouring (mainly of the specimens from El Hierro) is very contrasting (like the Mediterranean species of *Dichromacalles*): the basic cover is dark brown; with a crescent-like fascia in front of the base and a V-shaped, light brown (white), clearly contrasting fascia on the elytral slope (Fig. 9A). The second, fourth, and sixth intervals are protruding. At the sides of the elytra the groove-like punctures of the stripes are deep, overlapping the intervals (‘honeycombed structure’).

*Legs*: Very short, the front femur reaching the fore-margin of pronotum, the hind femur reaching the end of the third abdominal sternite. They are covered with bright scales and annular arranged black scales. The bright and small bristles of the femur are placed spaciouly.

*Venter*: The second abdominal sternite is clearly longer than sternite 3 and 4 combined; with a dark spot in front of the third sternite. Metasternum between the mesocoxae very slender and at most one-third as wide as mesocoxae in diameter.

*Aedeagus*: With a unique, o-shaped structure of the endophallus: (Fig. 9B).

*Differential diagnosis*: The complex structure of the internal sac of the aedeagus of *P. fernandezi*, which is unique amongst the Macaronesian Cryptorhynchinae,

also separates the monotypic genus *Pseudodichromacalles* from all other genera of the western Palaearctic (Fig. 9B).

*Discussion:* Unlike with *L. acutus*, the position of the type species of the new monotypic genus *Pseudodichromacalles*, *P. fernandesi*, always seemed straightforward on morphological terms. For its description, A. Roudier (1954) placed it close to the western European and North African species *Dichromacalles dioletianus* (Germar, 1817). The similarity to the habitus of the continental species of *Dichromacalles* s.s. Stüben (1998) seems obvious (Stüben, 2000c, d). However, in the morphological phylogeny, *Canariacalles alluaudi* (cf. Stüben, 2000b: fig. 1) is considered the most convincing link between the Macaronesian and continental (esp. *Dichromacalles*) Cryptorhynchinae. No other endemic species of *Acalles* s.l. seemed to establish (because of its habitus) such an evident ‘morphological connection’ to the African mainland.

Our mitochondrial reconstruction strongly supports this biogeographical trend for the Canarian *Acalles* s.l. species. It is actually the ancestor species of the genus *Canariacalles* (and not the species *P. fernandesi*) that features the close connection to the south-western European and north-western African species of *Dichromacalles* s.s.

More attention should have been paid to the conspicuously complex structure of the internal sac of the aedeagus of *P. fernandesi* (unique amongst all Cryptorhynchinae of the western Palaearctic), which differs significantly from *Dichromacalles* s.s. (cf. Fig. 9B vs. Fig. 22B). It should have been clear that especially the structure of the endophallus is of outstanding importance regarding the intrageneric grouping of western Palaearctic Cryptorhynchinae (see Stüben, 1998, 1999a, 2003a).

In addition to the DNA analysis, it is primarily this morphological character that substantiates the exceptional position of *P. fernandesi* amongst the Macaronesian Cryptorhynchinae.

*Biology and ecology:* In contrast to the numerous monophagous species amongst the Macaronesian Cryptorhynchinae, *P. fernandesi* is predominantly oligophagous to polyphagous. The biology of this species has recently been studied extensively on El Hierro (Stüben, 2008a: 327 – under the former name *Dichromacalles*). The population on El Hierro is monophagous on the endemic *Pericallis murrayi* Nord. of the daisy family (Asteraceae), whereas the populations on Tenerife prefer either *Foeniculum vulgare* Mill. of the carrot family (Apiaceae) (Teno Mts) or several species of the genera *Sonchus* (Asteraceae) and *Aeonium* (Crassulaceae) of the upper succulent belt (Anaga

Mts). *Pseudodichromacalles fernandesi* largely avoids the shady and moist laurel forest. It does not only occur below this forest, but can also be collected above 2000 m by shifting detritus under the endemic gorse species *Spartocytisus supranubius* (L.fil) in the circle of Las Cañadas, at the base of Mt Teide.

*Etymology:* The name *Pseudodichromacalles* alludes to the interesting history of research on this species since its first description by A. Roudier (1954). This name should remind and warn us that the habitus and colouring of almost all western Palaearctic Cryptorhynchinae are subject to an underestimated variability (Sprick & Stüben, 2000) because of the endophytic development of the larvae in different plant species and different parts of the plant (influence of phytochemicals), as well as in dead wood with extremely different degrees of contained moisture. This is not only often an obstacle for straightforward determination but in this case it also led to the erroneous supposition that *P. fernandesi* might be a species complex (Stüben, 2000d: 102). The specimens of *P. fernandesi*, collected by us (on El Hierro) for the first time in the stalks of the endemic *Pericallis murrayi* Nord. (Asteraceae, Fig. 9C), are very large and of a bright and contrasting colouring (see Fig. 9A). Regarding the complex structure of the internal sac of the aedeagus, there exist no differences between the specimens from El Hierro and those from *Foeniculum vulgare* on Tenerife, which are conspicuously smaller and rather unicoloured. Molecular analyses mirror this finding (J. J. Astrin & P. E. Stüben, unpubl. data).

*Distribution:* Endemic to the Canary Islands of Tenerife (including type locality), La Gomera, and El Hierro.

**SONCHIACALLES STÜBEN & ASTRIN GEN. NOV.**

(FIGS 11A–E, 33)

*Type species:* *Acalles sonchi* Stüben, 2000

Bayer & Stüben, 2000; Behne, 2000; Riede & Stüben, 2000; Sprick & Stüben, 2000; Stüben, 2000a, b, c, 2002b, 2007b, 2008a; Stüben *et al.*, 2003; Stüben & Germann, 2005; Germann & Stüben, 2006.

*Compilation of the species of the genus*

***Sonchiacalles***

***Sonchiacalles sonchi* (Stüben, 2000) comb. nov. (formerly: *Acalles*) – Tenerife (including type locality), La Gomera, La Palma**

***Sonchiacalles silosensis* (Stüben, 2000) comb. nov. (formerly: *Acalles*) – Tenerife (including type locality), La Gomera**

***Sonchiacalles muelleri* (Stüben, 2000) comb. nov.  
(formerly: *Acalles*) – La Palma (including type  
locality), El Hierro**

The taxa of this new genus belong to the *Acalles sonchi*-group which has been revised several years ago (Stüben, 2000a: 46–53).

*Description*

*Size:* 3.8–8.6 mm.

*Head:* Rostrum short, reaching two-thirds of length of pronotum; rostrum of ♂ wider, more robust and with dense and deep punctures going from the base to the apex.

*Pronotum:* 1.00–1.10× as wide as long; widest in the middle, outline almost linearly narrowed towards base and towards the constriction at the front margin regularly – in robust specimens strongly bellied – rounded. Punctures of pronotum very fine; pronotum sparsely covered with very small, dark bristles; without a clearly visible mid-groove or depression. The colouring corresponds with the darker basic cover of the elytra. Disc of pronotum flattened, the outline forming – in lateral view – together with the crown line of the elytra a straight line.

*Elytra:* Very elongated, often flattened; 1.40–1.76× as long as wide; widest in the middle, outline between middle and base mostly parallel (in *Sonchiacalles muelleri* slightly rounded), flanks with a slight lateral depression near the apex; the apex rounded obtuse angled. Punctured stripes on the disc of elytra fine up to the second interval, becoming more robust and pit-like and deeper towards the flanks where the punctures clearly overlap the intervals. The colouring is very contrasting: the basic cover is dark brown. On the first third there is a falciform fascia and on the slope of elytra a V-shaped, light brown, clearly contrasting fascia (Fig. 11A) with aggregations of bristles on the even, slightly elevated intervals. Here the acuminate bristles are at most 2× as long as wide. The flanks only sparsely covered with tiny bristles.

*Legs:* Short, the front femur reaching the front margin of the eyes, the hind femur reaching the last abdominal sternite. Tibia conspicuously annulated dark brown and black.

*Venter:* First abdominal sternite longer than the second, the second longer than sternite 3 and 4 combined. Metasternum between the midcoxae very slender and at most half as wide as midcoxae in diameter.

*Aedeagus:* With a simple, inverse v-shaped structure of the internal sac (Fig. 11B).

*Differential diagnosis:* The species of this new genus are easily distinguished from the species of the genus *Aeoniacalles*, to which they are not particularly related. The metasternum is more slender between the midcoxae, the elytra are conspicuously longer and more flattened, the legs are shorter and the endophallus without a basal ‘sickle’. See also the ‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’.

*Biology and ecology:* The species of this new genus live concealed on several endemic taxa of the genera *Sonchus* and *Tolpis* (cf. Fig. 11C) on the western Canary Islands. They can be found at altitudes between 200 and 700 m at the upper limit of the succulent belt in the transition zone to the former thermophilous shrub-forest (‘bosque termófilo’), which is largely deforested today. The stridulatory organ and its mechanism (Riede & Stüben, 2000) and the complex breeding behaviour of *Sonchiacalles muelleri* (Stüben, 2000a, 2008a) have been studied extensively. The similar habitus, breeding behaviour, and larval development within *Tolpis* latex resulted in the hypothesis of *Sonchiacalles* being closely related to *Madeiracalles pulverosus* (Gemminger, 1871) of Madeira (Stüben, 2002b). However, according to the molecular dendrogram this does not seem to be the case. Instead, *M. pulverosus* belongs to the discrete Madeiran clade (Fig. 1A).

Most of the more than 30 species of *Sonchus s.l.* of the Canaries are woody perennials and thus there might well be further undiscovered species of *Sonchiacalles*. Did the evolution of *Sonchiacalles* (like the radiation of *Aeoniacalles*) follow its endemic host plants (cf. Kim *et al.*, 2008) in a parallel cladogenesis (see Stüben, 2000c)? Concerning the cryptic speciation in *Liparthrum* bark beetles (Curculionidae: Scolytinae) Jordal, Kirkendall & Harkestad (2004) showed that these species, which are associated with different Macaronesian Euphorbiaceae, are clearly monophyletic.

*Etymology:* The name *Sonchiacalles* refers to the host plant relationship of *S. sonchi* and *S. silosensis*.

*Distribution:* Endemic to the western Canary Islands (apparently not on Madeira).

***ECHIUMACALLES* STÜBEN & ASTRIN GEN. NOV.  
(FIG. 12A–E)**

*Type species by monotypy:* *Acalles anagaensis* Stüben, 2000



Behne, 2000; Stüben, 2000a; Sprick & Stüben, 2000; Stüben *et al.*, 2003; Germann, 2004; Stüben & Germann, 2005; Germann & Stüben, 2006.

*The species of the genus Echiuacalles*  
***Echiuacalles anagaensis* (Stüben, 2000) comb. nov. (formerly: *Acalles*, *Dendroacalles*) – Tenerife: Anaga Mts (including type locality), La Gomera**

An extensive description of the only species of this genus, *Echiuacalles anagaensis* (Stüben, 2000) (formerly: *Acalles*, *Dendroacalles*), is presented in Stüben (2000a: 80–82).

#### Description

*Size:* 4.8–5.9 mm.

*Head:* Rostrum of the ♂ short, dark brown, with deep and close punctures, half as long as – or slightly longer than – the pronotum; the rubiginous rostrum of the ♀ three-quarters as long as pronotum, more slender and more distantly dotted; the second antennomere one-quarter shorter than the first, the third antennomere slightly longer than wide and the following antennomeres globular.

*Pronotum:* 1.06–1.16× as long as wide, widest at the end of the basal second fifth, at the sides towards the base narrowing rectilinear, towards the foremargin more rounded with a lateral depression; without a hollow on the disk of pronotum; at the front margin and on the disk of pronotum with same accumulations of dark, two to three times as long as wide, upright bristles; at the sides of the pronotum with a small white fascia.

*Elytra:* Elongated, ‘canoe-like’; 1.51–1.55× as long as wide, widest at the end of the basal quarter, in the middle weakly rounded laterally, towards the apex nearly narrowing rectilinear. A peculiar characteristic is the deep black (nearly isosceles) triangular fascia on the elytral slope (Fig. 12A).

*Legs:* Short; the front femur reaching the foremargin of pronotum; the hind femur reaching the penultimate sternite; femur annulated with one, tibia with two dark rings.

*Venter:* The second abdominal sternite maximum as long as both following sternites combined; with most fine, bright bristles long and slender. Metasternum between the mesocoxae very slender and at most half as wide as mesocoxae in diameter.

*Aedeagus:* Endophallus only with a double ‘mushroom-shaped’ structure (Fig. 12B).

*Differential diagnosis:* The genus can be easily distinguished from the other taxa of the Canarian archipelago by the flattened, conspicuously elongated habitus, the monophagous host plant relation (*Echium strictum*) and especially by the deep black, equal-sided triangular mark on the elytral slope. Although all species of *Dendroacalles* and also some species of *Silvacalles* also present a double structure of the internal sac of aedeagus, there is no further species with a ‘mushroom-shaped’ structure of the endophallus (Fig. 12B). See also the ‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’.

*Discussion:* Placing the single species of this new genus into any of the existing higher taxa of the Macaronesian Islands always seemed problematic. Only preliminarily was it joined with the succulicole species of the genus *Dendroacalles*: the *Acalles euphorbiacus*-group (Stüben, 2000a: 82), which now represents the subgenus *Euphorbioacalles* Stüben (2005). Once again the only reason for this taxonomic decision lay in the double structure of the internal sac (Fig. 12B). Meanwhile, it has been proven (Germann, 2004; Stüben & Germann, 2005) that *Echiuacalles anagaensis* is the only cryptorhynchine species of the entire western Palaearctic region living monophagously on a species of Boraginaceae (*Echium strictum* L.) (Fig. 12C). It has an elongated, flattened habitus (Fig. 12A) and is therefore distinct from the more ‘compact’ species of *Euphorbioacalles* (Fig. 4A) that develop on representatives of the spruce family (Euphorbiaceae). The mitochondrial reconstruction clearly rejects the hypothesis of *Echiuacalles anagaensis* belonging to the genus *Dendroacalles*. However, the tree also shows a conspicuously high (and fully supported) proximity of *Echiuacalles anagaensis* to *Ficusacalles senilis* (Fig. 1A). Nevertheless, morphological and ecological reasons forbid the joining of these two genera. The species of *Ficusacalles* live in other habitats and on different host plants on the Canary and Selvagens Islands (see below) and have a more robust and ‘compact’ habitus while also featuring a distinct endophallic shape (cf. Fig. 13A–E). This led to our decision to establish the new monotypic genus *Echiuacalles*.

*Etymology and biology:* The name *Echiuacalles* refers to the host plant of *Echiuacalles anagaensis* (type locality: Anaga Mts, Tenerife), *Echium strictum*. Recently, *Echiuacalles anagaensis* was also found on *Echium strictum* on the island of La Gomera (Germann & Stüben, 2006). Germann (2004) extensively describes the discovery of the host plant and its distribution on Tenerife. The verification of a member of the borage family (Boraginaceae) as host plant of a

cryptorhynchine species was quite a surprise after a long period of studying – without success – numerous Canarian and Madeiran plants of this family, especially as these plants use phytochemicals like pyrrolizidine alkaloids (usually strongly toxic to insects) as a defence strategy against herbivores. The genus *Echium* is represented on the Canary Islands by 23 species out of which 22 are endemic. This suggests that it might be worthwhile to look for further new species of *Echiumacalles* on all Macaronesian Islands, especially investigating plants of the borage family.

*Distribution:* Only known from the Anaga Mountains on Tenerife and from La Gomera.

***FICUSACALLES* STÜBEN & ASTRIN GEN. NOV.**  
(FIG. 13A–E)

*Type species: Acalles senilis* Wollaston, 1864

Wollaston, 1864, 1865; de Marseul, 1875; Roudier, 1954; Franz, 1996; Arechavaleta, Zurita & Oromí, 2000: 93; Behne, 2000; Sprick & Stüben, 2000; Stüben, 2000a, 2007b, 2008a; Stüben *et al.*, 2003; Stüben & Germann, 2005.

*Compilation of the species of the genus*

***Ficusacalles***

***Ficusacalles senilis senilis* (Wollaston, 1864) comb. nov. (formerly: *Acalles*) – El Hierro (including type locality), Tenerife, northern La Palma**

*Ficusacalles senilis fivorator* (Stüben, 2007) comb. nov. (formerly: *Acalles*) – southern La Palma (including type locality)

*Ficusacalles senilis oceanicus* (Stüben, 2002) comb. nov. (formerly: *Acalles*) – Selvagens (including type locality)

*Description*

*Size:* 3.30–5.50 mm (without rostrum).

The species of the new genus are very variable regarding habitus and colouring.

*Pronotum:* As long as wide or slightly wider; widest behind the middle, outline towards base only slightly rounded, narrowed in a straight line or rounded long oval to ‘bellied’; with a slight depression next to the front margin. Contrastingly coloured as for the elytra in recently emerged specimens. Often with slender mid-groove or wide and shallow depression. Disc of pronotum sometimes with an aggregation of bristles on both sides of the mid-groove.

*Elytra:* 1.35–1.45× as long as wide; widest anterior to the middle, *c.* at the end of the second fifth (from the base); from the middle towards the apex of elytra

almost lineally narrowed or rounded long oval, apex of elytra protruding ‘beak-like’, flanks with depression in the range of second and third sternite; elytra without shoulders; disc of elytra anterior to the middle with light (beige) scales covering the first and second interval; the first three intervals near the middle with a triangular mark of dense black scales. Slope of elytra with light (beige) scales forming either a broad fascia or covering the entire slope. With a falciform, white fascia on each elytron going from the basal edges to the second interval directly in front of the middle. Elytra with pit-shaped punctures becoming deeper towards the flanks. Intervals clearly wider than punctured stripes; scutellar stripe with a black, elongated aggregation of bristles in the middle of elytra; second interval with a predominantly light, elongated aggregation of bristles next to the base and a shortly oval aggregation of bristles directly behind the middle; third interval with a small, oval, bristled hump anterior to the middle; fourth interval again with an elongated, even aggregation of bristles. Humps are present primarily in the nominotypic taxon *Acalles senilis senilis* (type locality: El Hierro). These structures are conspicuously more flat in the other subspecies and the aggregation of the bristles are often abraded in older specimens.

*Legs:* Front femur reaching the front margin of eyes, hind femur ending far from the apex of elytra. Legs sparsely covered with short, predominantly light bristles that are close-fitting at the femur and erect at the tibia.

*Head:* Eyes slightly oval, rounded towards the front and tapering towards the underside of rostrum. Rostrum of ♂ dark brown, short, at most 3.80× as long as wide, with dense and fine punctures next to the apex (mid-line without punctures) and with a dense cover of light scales between base and insertion of antenna; rostrum of ♀ longer, brighter, narrower between the insertions of antenna, with scales only next to the base and finer and more spacious punctures at the apex.

*Venter:* Second abdominal sternite as long as sternites 3 and 4 combined; second sternite covered with light, rounded scales partly overlapping like tiles and in addition with a few short and slender bristles.

*Aedeagus:* With a conspicuous, big, long, and parallel balk-shaped structure of the internal sac (Fig. 13B).

*Differential diagnosis:* This new genus is characterized by the conspicuously big, parallel, balk-shaped structure of the internal sac of the aedeagus (cf. Fig. 13B) and therefore the genus can be easily dis-

tinguished from all other species of Macaronesian Cryptorhynchinae. See also the 'Key to the genera and subgenera of Macaronesian Cryptorhynchinae'.

**Biology and ecology:** Specimens of *F. senilis senilis* and *F. senilis ficvorator* have been collected by beating dead twigs of *Ficus carica* L. on the western islands of the Canarian archipelago (cf. Fig. 13C). The biology and ecology of *F. senilis ficvorator* of La Palma as well as rearing studies using twigs of the genus *Ficus*, a typical cultivated plant of the Canary Islands, have been described in detail (Stüben, 2007b: 218–220). On Tenerife and El Hierro *F. senilis senilis* lives predominantly on *Foeniculum vulgare* Mill., which is a common shrub on fallow land. In these habitats one can beat numerous specimens from the lower dead stalks of robust plants at night. The development takes place in these dead stalks. The species of this new genus seem to be extraordinarily oligophagous to polyphagous. On El Hierro *F. senilis senilis* is 'omnipresent', living – amongst other woody perennials – on *Carlina salicifolia*, *Sonchus hierrensis*, *Tolpis proustii*, and *Chamaecytisus proliferus*. Therefore, it is not a big surprise that even the endemic *Euphorbia anachoreta* Svent. of the spurge family (Euphorbiaceae) has been reported as host plant for *F. senilis oceanicus* of the Selvagens (cf. Stüben, 2000a: 132).

The variability of *F. senilis* correlates with the high number of host plants. There are contrastingly black and white coloured specimens as well as unicoloured white or grey individuals. Stüben (2008a: 324) attributed this variability primarily to the differences in nutrition, especially to the influence of several phytochemicals during larval development (not only to the 'ageing' of the integument). Thus phenotypically, the species of this genus cannot be easily discriminated. The only reliable morphological character is the endophallus.

**Etymology:** The name *Ficusacalles* refers to the host-plant relation of the Canarian species of this genus, which can be beaten from savaged plants of the Mediterranean fig tree (*Ficus carica*) at night.

**Distribution:** Only known from the western Canary Islands Tenerife, La Palma, and El Hierro as well as from the Selvagens.

**CANARIACALLES STÜBEN & ASTRIN GEN. NOV.**  
(FIGS 2A–E, 23A, 24B)

**Type species:** *Acalles neptunus alluaudi* Uyttenboogaart, 1940

Wollaston, 1864; Uyttenboogaart, 1940; Roudier, 1954; Lindberg, 1958; Bayer & Stüben, 2000; Riede &

Stüben, 2000; Sprick & Stüben, 2000; Stüben, 2000a, b, c; Behne, 2000; Stüben *et al.*, 2003; Stüben & Germann, 2005.

*Compilation of the species of the genus*

**Canariacalles**

**Canariacalles alluaudi** (Uyttenboogaart, 1940)

**comb. nov. (formerly: Acalles)** – Gran Canaria (incl. type locality), **Tenerife**

= *Acalles haraldi* Roudier, 1954 syn. Stüben, 2000: 32  
*Canariacalles lanzarotensis* (Stüben, 2000) comb. nov. (formerly: *Acalles*) – Lanzarote (incl. type locality)

? *Canariacalles xerampelinus* (Wollaston, 1864) (formerly: *Acalles*) – Tenerife: Agua García (incl. type locality) – *incertae sedis*

**Description**

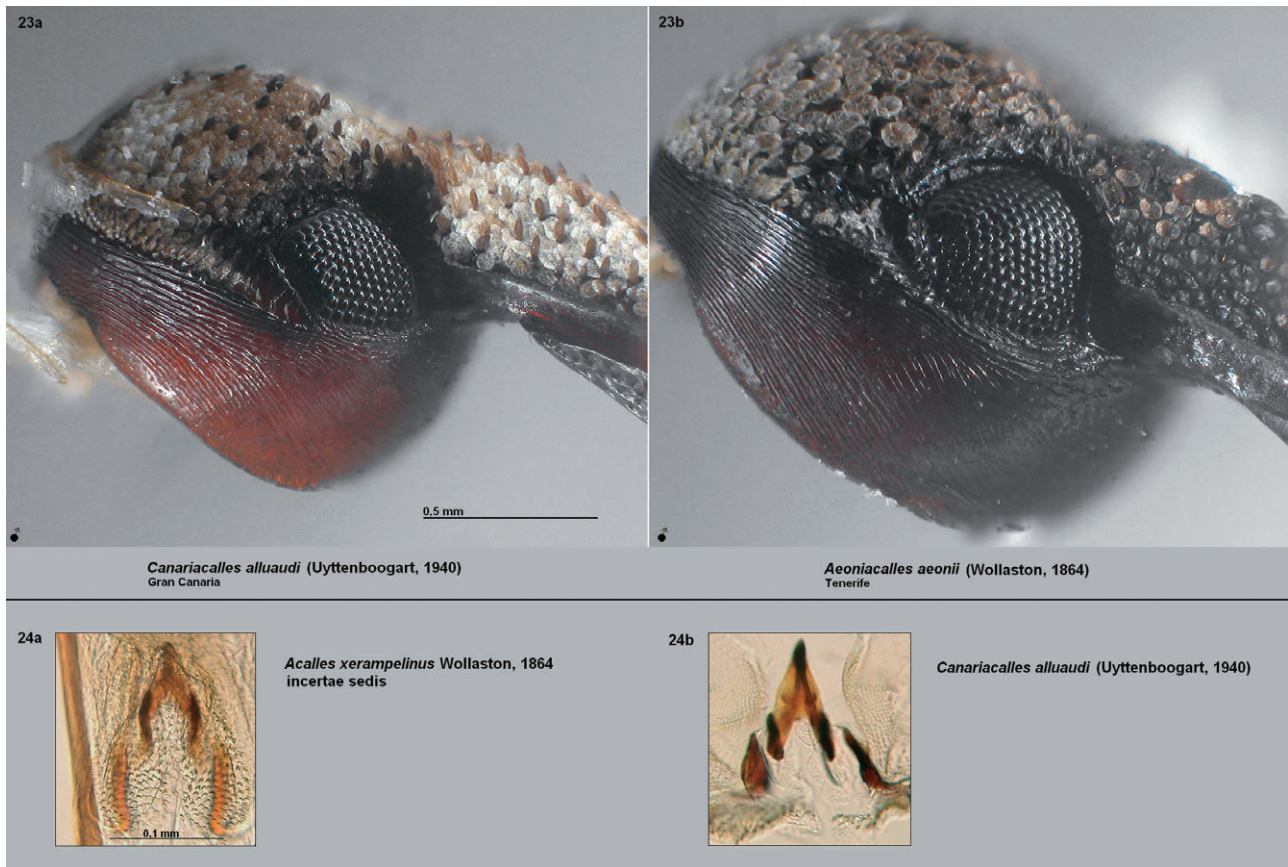
**Size:** 3.4–7.0 mm

**Head:** Rostrum in both sexes shorter than pronotum; basal half of rostrum either sparsely covered with scales (♀) or rostrum with a dense cover of scales that sometimes exceeds the insertion of the antenna (♂). The rostrum of the ♂ is conspicuously more robust, darker brown, and has more dense punctures in the apical part. Eyes rhombic.

**Pronotum:** 1.02–1.12× as wide as long; widest directly behind the middle; behind the front margin of pronotum either with an abrupt constriction, which causes an angular outline or without such constriction, which causes a regularly rounded outline. The disc of pronotum is complanate. The basic cover consists of light brown to brown scales mixed with a few pale dark brown marks. Under the dense cover of scales the fine punctures is almost invisible.

**Elytra:** Wide, angular, and robust; 1.28–1.31× as long as wide; widest behind the steeply sloped shoulders at the end of the first fifth, outline towards apex almost parallel (or slightly narrowed) to the posterior end of the broad dark fascia. Apex oval rounded without constriction. Crown line of elytra in lateral view at the disc of elytra almost a straight line on the same level as the crest of pronotum and sloping steeply behind the broad posterior fascia. The punctured stripes consisting of pit-like punctures that are even on the flanks of elytra always narrower than the punctures of the complanate intervals. On the posterior part of the dark brown fascia that spans over the whole width of the elytra there is a conspicuous longitudinal knob on the second and fourth interval, also the scutellar stripe is slightly superelevated here. Eighth interval immediately behind the base with knob-like swelling covered with light scales. The





**Figures 23–24.** 23, *Canariacalles* with rhombic eyes (in lateral view) in comparison with *Aeoniacalles*. 24, endophallus of *Acalles xerampelinus* in comparison with *Canariacalles alluadi*.

dense basic cover consists of tiny brown scales that shade into a dark brown cover of scales on the longitudinal knobs as well as on the posterior fascia. On the intervals the tiny, light brown, scaly bristles are arranged in one or two lines and separated from each other by 4–10× bristle length. The base of elytra protruding half-moon-like towards the suture.

**Legs:** Short, the front femur reaching the eye, the hind femur ending far from the apex of elytra only slightly protruding from the posterior dark fascia. The light brown scaly bristles on the femur are inconspicuous and very short; tibia annulated with belts of black scales.

**Venter:** Second abdominal sternite longer than sternites 3 and 4 combined; first and second sternite covered with small, shortly oval to circular bristles. The interspace between midcoxae of metasternum very narrow and at most half as wide as midcoxae.

**Aedeagus:** The inverse v-shaped structure of the internal sac discontinued in the midsection (Fig. 2B).

**Differential diagnosis and discussion:** The species of the new genus *Canariacalles* are distinguished from all other Macaronesian Cryptorhynchinae by the rhombic shape of the eyes (Fig. 23), the extremely robust habitus (Fig. 2A), and the inverse v-shaped structure of the internal sac of the aedeagus, which is discontinued in the midsection (Fig. 2B).

There is only one further species presenting an almost identical structure of the internal sac: *Acalles xerampelinus* Wollaston (1864) (Fig. 24A, B). This is the only cryptorhynchine species that until today was impossible to recover from the laurel forest of Tenerife (type locality: Agua García). According to Wollaston (1864), this species has been collected only a few times in the mountains of Anaga and Teno. It is obviously not a xerothermophilic species of the coastal succulent belt, but it probably belongs to the herbaceous vegetation of the laurel forest of the Canaries (potentially being monophagous on a species of the carrot family, an Apiaceae). Given the fact that *Acalles xerampelinus* has a conspicuously different habitus from the species of the new genus *Canariacalles* and that there is no alternative option of

classification, we here declare it *incertae sedis*. See also the ‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’.

The common ancestor of the *Dichromacalles* and *Canariacalles* species very likely represents the ‘missing link’ between the Macaronesian (or at least Canarian) species and the mainland. The morphological similarity to species of *Dichromacalles*, as for, e.g. *Dichromacalles dromedarius*, has already been pointed out (see Stüben, 2000b: fig. 1) and is corroborated by our mitochondrial phylogeny (Fig. 1A, cf. see also discussion of *P. fernandezi*).

**Biology and ecology:** In the Teno Mountains of Tenerife, *Canariacalles alluaudi* predominantly develops – often associated with *Dichromacalles dromedarius* – in dead stalks of *Foeniculum vulgare* Mill. (Stüben, 2000a: 32). However, adults of *Canariacalles alluaudi* have also been observed feeding on the poisonous succulent *Ceropegia dichotoma* Haw. (Fig. 2C). *Canariacalles alluaudi* larvae have been successfully reared on stems of *Ceropegia* until the second instar (Stüben & Germann, 2005: 68). However, the species of the new genus live mainly on species of the carrot family (Apiaceae). On Gran Canaria (Tenteniguada, 700 m) during summer (July), we observed numerous larvae, pupae, and imagines still in their cocoons at about 10–20 cm below soil surface, in the dead stems of the Apiaceae *Ferula linkii* Webb (Stüben, 2000a: 32). The larvae and pupae have been described by Bayer & Stüben, (2000). The stridulatory organ of this species motivated the study on the sonic defence of Cryptorhynchinae. Such a defence strategy is adopted by those taxa of the weevil subfamily that develop in woody plants forming a resonating body (Riede & Stüben, 2000). The development of *Canariacalles* in the stalks or root necks of several species of the carrot family (Apiaceae) shows many similarities to *Dichromacalles* development that mainly takes place in species of the daisy family (Asteraceae) (Stüben & Behne, 1998; Bahr, 2001).

*Canariacalles alluaudi* has not been reported from the eastern islands Fuerteventura and Lanzarote but on the latter the genus is represented by *Canariacalles lanzarotensis*, which we consider to be the sister species of *Canariacalles alluaudi* because of their morphological similarity (not sequenced).

**Etymology:** The name *Canariacalles* refers to the supposition that the common ancestor of the species of this genus, early ‘Canarian islanders’, and of the species of *Dichromacalles s.s.* of northern Africa and western Europe very likely represents the ‘missing link’ to the North African mainland. The succulicolous way of life of these two groups allows the assumption

that the colonization of the Canary Islands took its beginning in the arid succulent belt of the eastern islands.

**Distribution:** As yet only known from the eastern islands Lanzarote and Gran Canaria as well as the central western island Tenerife.

*DICHROMACALLES* STÜBEN, 1998 (FIG. 22A–E)

**Type species:** *Rhynchaenus dioeletianus* Germar, 1817 – Croatia (including type locality), south-west Europe, north-west Africa

Boheman, 1844; Brisout *et al.*, 1864; Solari & Solari, 1907; Hoffmann, 1958; Stüben & Behne, 1998; Bayer & Stüben, 2000; Riede & Stüben, 2000; Sprick & Stüben, 2000; Stüben, 2000b, c, d, 2002b, 2004b, 2005b, 2007b, 2008a; Bahr, 2001; Stüben *et al.*, 2001; Stüben & Germann, 2005; Astrin & Stüben, 2008.

*Compilation of the species of the genus*

***Dichromacalles* of the Macaronesian Islands**

***Dichromacalles dromedarius* (Boheman, 1844)**

(formerly: *Acalles*) – Canary Islands, Madeira, Azores, Portugal (including type locality), **south-west Europe**, north-west Africa

= *Acalles fasciculatus* Boheman (1844) syn. Bahr (2001: 126).

= *Acalles plagiatofasciatus* Costa, 1847 syn. Bahr (2001: 126).

= *Acalles impressicollis* Lucas, 1849 syn. Bahr (2001: 126).

**Discussion:** The widespread *Dichromacalles dioeletianus* presumably lives on all Canary Islands in an altitude between 50 and 2000 m (until now not reported from Fuerteventura). Individuals of this species have often been found in great abundance on plants of the daisy family (Asteraceae: *Sonchus* sp., *Tolpis* sp., *Andryala pinnatifida* Ait., *Picris echioides* L., etc.), on umbelliferous plants (Apiaceae, e.g. *Foeniculum* sp.) and sporadically also on plants of the orpine family (Crassulaceae) (P. E. Stüben, pers. observ.). Hence *Dichromacalles dioeletianus* is markedly polyphagous and on its host plants it is socialized with several other species of Cryptorhynchinae.

In the year 1971, the first Canarian *D. dromedarius* specimens were reported for Tenerife. According to the current omnipresence of this species on the Canary Islands, Madeira, and the Azores, we exclude the possibility that this species – not found during the extensive collecting of T. V. Wollaston in the mid-19<sup>th</sup> century – could have simply been overlooked before (cf. also minimal genetic distance – in Fig. 1A – separating a Euro-

pean and a Canarian specimen). Hence it is undoubtedly an adventitious species that was introduced for instance with plants of the daisy family [Tempère & Péricart (1989) mention the cotton thistle (*Onopordon illyricum* L.) as host plant in south-western Europe; we also found *D. dromedarius* on several ligneous perennials in the coastal belts of Morocco, southern Spain, and Portugal]. Spreading very rapidly, *D. diocletianus* is the only recent settler from the mainland on the Macaronesian Islands. On Madeira, it lives (amongst others) on *Tolpis succulenta* (Fig. 22C) and thus it has become a serious competitor of the endemic *Madeiracalles pulverosus* and *Madeiracalles tolpis* (Stüben, 2002b: 147).

*Distribution:* Presumably present on all Canary Islands (hitherto no report only for Fuerteventura); also on Madeira and the Azores (although not reported from all of the islands within these archipelagos). See also the 'Key to the genera and subgenera of Macaronesian Cryptorhynchinae'.

**MADEIRACALLES STÜBEN & ASTRIN GEN. NOV.**  
(FIGS 14A–E, 25–32, 34)

*Type species:* *Acalles dispar* Wollaston, 1854  
Wollaston, 1854, 1857, 1865; Lundblad, 1958; Stüben, 2002b; Stüben *et al.*, 2003; Stüben & Astrin, 2009 in press.

*Compilation of the species of the genus*

***Madeiracalles***

***Madeiracalles achadagrandensis* (Stüben, 2002) comb. nov. (formerly: *Acalles*) – Madeira**

*Madeiracalles albolineatus* (Wollaston, 1854) comb. nov. (formerly: *Acalles*) – Madeira

***Madeiracalles cinereus* (Wollaston, 1860) comb. nov. (formerly: *Acalles*) – Madeira**

*Madeiracalles coarctatus* (Wollaston, 1857) comb. nov. (formerly: *Acalles*) – Madeira

***Madeiracalles dispar* (Wollaston, 1854) comb. nov. (formerly: *Acalles*) – Madeira**

*Madeiracalles festivus* (Wollaston, 1857) comb. nov. (formerly: *Acalles*) – Madeira

*Madeiracalles histrionicus* (Wollaston, 1857) comb. nov. (formerly: *Acalles*) – Porto Santo

***Madeiracalles machadoi* (Stüben, 2006) comb. nov. (formerly: *Acalles*) – Madeira**

*Madeiracalles nodiferus* (Wollaston, 1854) comb. nov. (formerly: *Acalles*) – Madeira

***Madeiracalles portosantoensis* (Stüben, 2002) comb. nov. (formerly: *Acalles*) – Porto Santo**

***Madeiracalles pulverosus* (Gemminger, 1871) (nec. *Acalles pulverulentus* Wollaston, 1854) comb. nov. (formerly: *Acalles*) – Madeira**

= *Acalles oblitus* Wollaston (1854) syn. (Stüben & Astrin, 2009, in press)

***Madeiracalles saxicola* (Wollaston, 1854) comb. nov. (formerly: *Acalles*) – Deserta Grande (including type locality), Madeira**

***Madeiracalles terminalis* (Wollaston, 1854) comb. nov. (formerly: *Acalles*) – Madeira**  
= *Acalles terminalis* var.  $\beta$  Wollaston (1854) syn. (Stüben, 2002)

*Madeiracalles tolpis* (Stüben, 2002) comb. nov. (formerly: *Acalles*) – Madeira

*Madeiracalles tristaensis* (Stüben, 2002) comb. nov. (formerly: *Acalles*) – Madeira

*Madeiracalles vau* (Wollaston, 1854) comb. nov. (formerly: *Acalles*) – Madeira

*Description*

*Size:* 2.5 (*M. tolpis*)–7.2 mm (*M. nodiferus*)

*Head:* Eyes circular; the reddish-brown rostrum of the ♂ with dense and oval punctures, the basal third covered with brown scales; length: approximately two-thirds of length of pronotum. The rostrum of the ♀ more slender, conspicuously longer (four-fifths of length of pronotum), with finer and less dense punctures and basal third only sparsely covered with scales.

*Pronotum:* 1.04–1.14× (–1.22× *M. tristaensis*) as long as wide; widest in the middle; outline rounded evenly oval or 'bellied' (as in robust specimens of *M. pulverosus*). Disc of pronotum with aggregations of dark brown bristles sticking out vertically on both sides of the often only fine mid groove or shallow mid-depression.

*Elytra:* Elongated, 'canoe-like': 1.27–1.51× (1.53–1.68× *M. tristaensis*) as long as wide; widest directly in front of the middle (or at the end of the basal third); elytra, often rounded elliptically, the anterior sixth part steeply sloped towards the base of elytra; towards the apex beginning with a lateral depression (somewhat concave on the flanks), the apex itself elongated 'beak-like'. The integument is very variable. Between a more or less unicoloured dark brown and a light brown or beige basic colouring there are all imaginable changes and crossovers, although always with a light, v-shaped fascia on the elytral slope and often with a diffuse pale-white scutellar mark at the base. Moreover, most of the species have a light falciform fascia extending from the sixth interval at the base to the scutellar stripe in the middle of the elytra. Elytra with numerous protuberances covered with bristles, the biggest, often elongated and high-piled aggregations of bristles are situated on the second interval of the elytral slope.



*Legs:* Long; front femur reaching posterior margin of eye; tibia with short, often ‘erinaceous’ distant bristles; femur with sloping, raised bristles; tibia annulated with belts of dark brown to black scales.

*Venter:* Second abdominal sternite as long as sternites 3 and 4 combined.

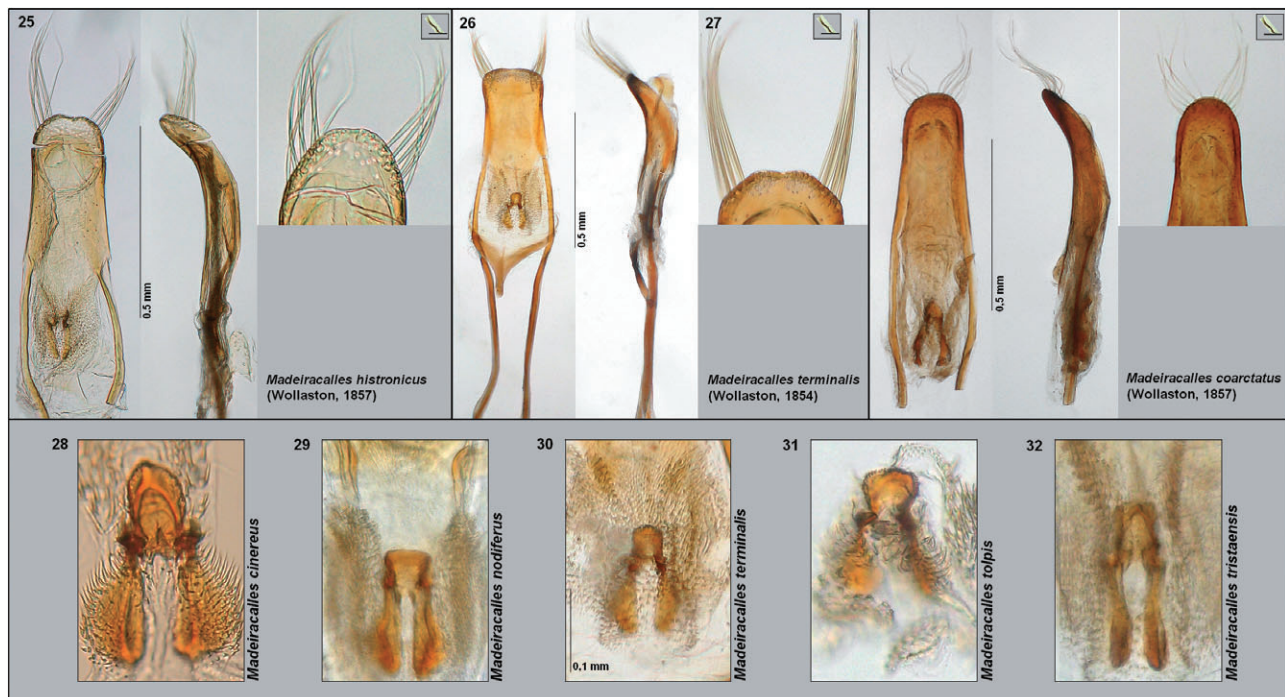
*Aedeagus:* Median lobe always with very long capillary bristles (Figs 25–27); endophallus very small and ‘complex’, besides the inverse v-shaped basic structure there is (except for three minor variances) a clearly cognizable basic pattern (Figs 28–32).

*Differential diagnosis and discussion:* According to the structure of the internal sac there are only subtle differences amongst most *Madeiracalles* species (Figs 28–32); the interspecific variability is much higher in the Canarian clade. As a result of this, splitting up the morphologically very ‘homogeneous’ genus *Madeiracalles* into subgenera does not make sense, especially when striving for comparability/equivalence of supraspecific taxa in all Macaronesian Cryptorhynchinae. See also the ‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’.

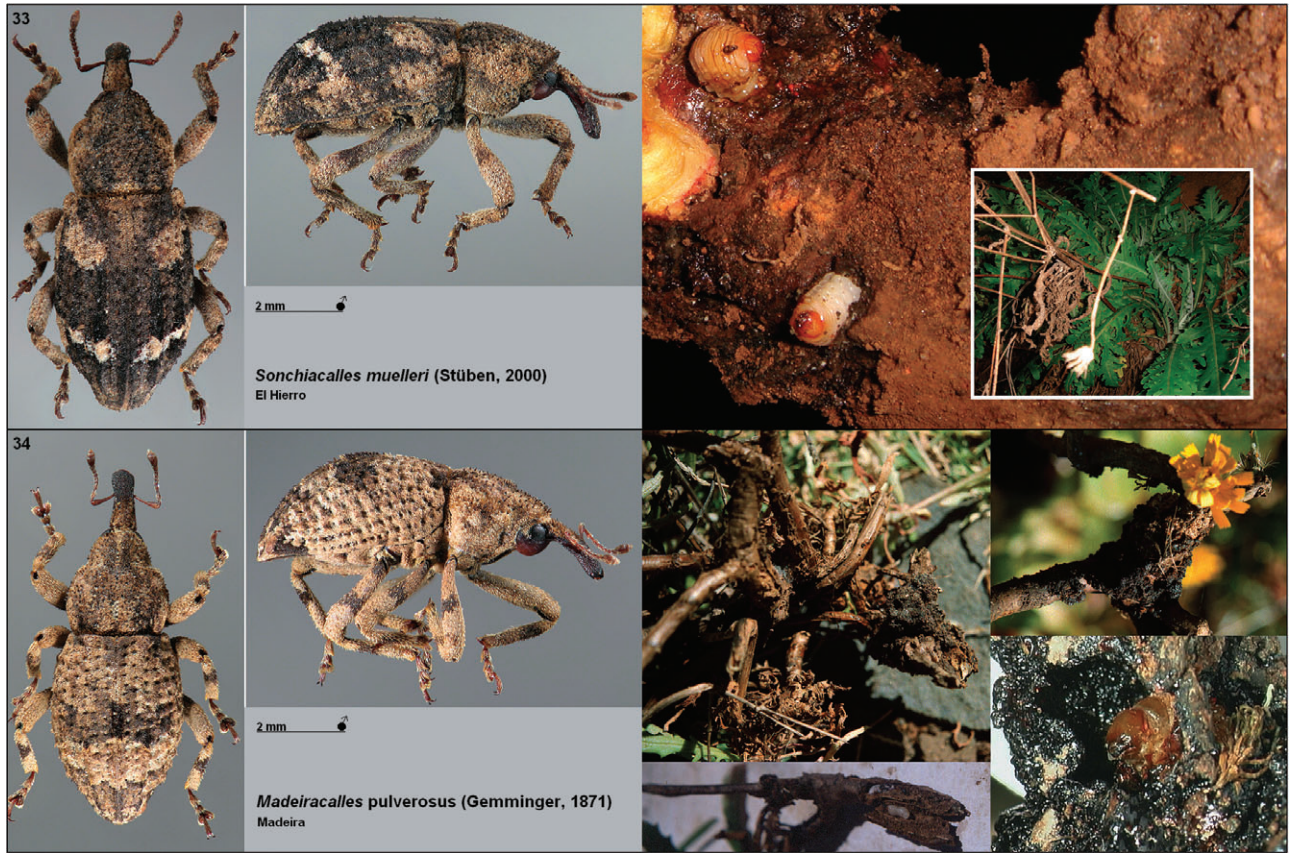
The species of *Madeiracalles* represent a monophyletic group forming the so-called ‘Madeiran clade’ (cf. Fig. 1A). This group is distinguished from the Canar-

ian genera by (1) the conspicuously long and slender, capillary bristles on the median lobe of the aedeagus (Figs 25–27); and (2) the ‘complex’ inverse v-shaped structure of the endophallus, which shows a clearly comprehensible basic pattern and is doubtlessly homologous amongst the species of *Madeiracalles* (Figs 28–32).

*Biology and ecology:* On the Canary Islands, instances of radiative cospeciation of some Cryptorhynchinae with their host plants (of the genera *Aeonium*, *Sonchus*, and *Tolpis*) have been ascertained (Sprick & Stüben, 2000; Stüben, 2000c). However, on Madeira there is no evidence for such an evolution. No Madeiran cryptorhynchine species is known to develop on *Aeonium* and *Sonchus*. *Madeiracalles pulverosus* lives on *Tolpis succulenta* (the name seems to suggest it, but *Madeiracalles tolpis* does not belong in this root-drilling group, even though it develops in thin twigs of *Tolpis succulenta*). *Madeiracalles pulverosus* shows the same larval development and breeding behaviour as *Sonchiacalles muelleri* of the Canary Islands. The larvae and pupae of *M. pulverosus* behave in the same way in the chambers (made of latex and agglutinated small stones) at the root neck of *Tolpis succulenta* (Stüben, 2002b) as those of *Sonchiacalles muelleri*, e.g. on *Tolpis calderae* (La Palma) or *Tolpis proustii* (El Hierro) (Stüben, 2000a, 2008a) (Figs 33, 34). Nev-



**Figures 25–32.** 25–27, *Madeiracalles* is distinguished from the Canarian genera by the conspicuously long and slender, capillary bristles on the median lobe of the aedeagus. 28–32, the ‘complex’ inverse v-shaped structure of the endophallus shows a clearly comprehensible basic pattern and is doubtlessly homologous amongst the species of *Madeiracalles*.



**Figures 33–34.** *Sonchiacalles muelleri* has the same larval development, the adults show identical breeding behaviour and the larvae and pupae behave in the same way in the chambers (made of latex and agglutinated small stones) at the root neck of, e.g. *Tolpis proustii* on El Hierro as *Madeiracalles pulverosus* in the roots of *Tolpis succulenta* on Madeira.

ertheless, the dendrogram shows that the two species are not directly related (cf. Fig. 1A), which takes us to the conclusion that this seemingly complex behavioural pattern has obviously evolved in parallel.

We suggest that in the colonization of Porto Santo (and later of Madeira), the same evolutive pattern took effect as on the Canary Islands. In addition, in this archipelago, the pioneer species were those xerothermophilic ones preferring the coastal succulent belt, e.g. the ancestor of the extremely xerothermophilic *Madeiracalles portosantoensis* (from the Pico do Castelo on Porto Santo) or the succulicole, coastal *M. pulverosus* that develops in the root neck of *Tolpis succulenta* on the sun-exposed rocks of Madeira during summer. The colonization of the shady and moist laurel forests of Madeira obviously started much later (even if according to the phylogenetic analysis the extremely xerothermophilic *Madeiracalles saxicola*, which develops in *Euphorbia piscatoria* and has been described from the arid island Deserta Grande, does not fully fit in; cf. Fig. 1A). Today most of the Cryptorhynchinae of Madeira are highly adapted to the laurel forest, e.g. *Madeiracalles*

*cinereus* (Fig. 14A) that lives in the trade wind zone of the moist laurel forest and develops in thin twigs of a dendriform species of Euphorbiaceae, *Euphorbia mellifera* (Stüben, 2002b; Stüben & Astrin, 2009 in press) (Fig. 14C).

*Etymology:* The name *Madeiracalles* refers to the Madeiran clade as recovered in our analysis for the monophyletic group of former *Acalles* s.l. species from the archipelago of Madeira.

*Distribution:* Endemic to the archipelago of Madeira.

CALACALLES PEYERIMHOFF, 1925  
(FIGS 15A–E, 16A–E)

*Type species:* *Acalles (Calacalles) theryi* de Peyerimhoff, 1925 – Morocco (including type locality), Portugal

Wollaston, 1864; de Peyerimhoff, 1925; Uyttenboogaart, 1939; Roudier, 1954; Bahr, 2000; Behne, 2000;



Stüben *et al.*, 2001; Stüben, 2002b, 2003b, 2004b, c, 2005b; Germann & Stüben, 2006; Astrin & Stüben, 2008.

*Compilation of the subgenera and species of the genus Calacalles of the Macaronesian Islands*

**Calacalles s.s.**

*Calacalles affinis* Bahr, 2000 – Tenerife

**Calacalles atomarius** Bahr, 2000 – Tenerife

*Calacalles exiguus* Bahr, 2000 – Tenerife (including type locality), La Palma

*Calacalles fuerteventurensis* Bahr, 2000 – Fuerteventura (including type locality), Lanzarote

*Calacalles minutus* Bahr, 2000 – La Gomera (including type locality), Tenerife

*Calacalles pumilio* Bahr, 2000 – Tenerife (including type locality), La Gomera

**Calacalles pusillus** Bahr, 2000 – Tenerife (including type locality), La Gomera, Gran Canaria

*Calacalles seticollis* Wollaston, 1864 – El Hierro (including type locality), La Palma, Tenerife, La Gomera

= *Acalles wollastoni palmensis* Roudier, 1954 syn. Bahr, 2000: 121

= *Acalles zumpti* Uyttenboogaart, 1939 syn. Bahr, 2000: 122

*Calacalles subcarinatus* (Israelson, 1984) – Azores: Flores (including type locality), Faial, São. Jorge, Terceira, Pico, São. Miguel, Santa Maria

**Calacalles wollastoni** (Chevrolat, 1852) – Madeira (including type locality), Porto Santo

= *Acalles cylindricollis* Wollaston, 1964 syn. Wollaston, 1865: 280

**Crateracalles** Stüben, 2004 subgen.

*Type species: Acalles droueti* Crotch, 1867

**Calacalles (Crateracalles) droueti** (Crotch, 1867) – Azores: Flores (including type locality), Faial, Pico

**Calacalles (Crateracalles) azoricus** (Stüben, 2004) – Azores: Faial (including type locality)

*Discussion:* The genus *Calacalles* was revised several years ago for the species of the Canary Islands (Bahr, 2000). Stüben (2004b) added the subgenus *Crateracalles* from the Azores. The transfer from *Acalles* to *Calacalles* was mainly motivated (1) by the extraordinary size (the specimens of this subgenus are three times longer than the specimens of *Calacalles s.s.*); (2) by the characteristics of the elytra (with strong bristle-tufts) and pronotum (with a saucer-shaped rim of thorns); and (3) by their different host plant interactions. Although these criteria all left some uncertainty regarding the transfer, only the similar ‘shell-shaped’ structures of the internal sac of the aedeagus

retain some morphological significance for the inclusion in *Calacalles* (cf. Figs 15B, 16B).

The molecular analysis of the set of available species confirms (maximal support value) the genus *Calacalles* as a natural group. Even the noticeably large species *C. droueti* and *C. azoricus* of the islands Faial, Pico, and Flores are now corroborated as part of the genus. The reconstruction shows that the subgenus *Calacalles s.s.* is paraphyletic with regard to the subgenus *Crateracalles* (cf. Fig. 1A).

However, there remain numerous questions and issues. It is doubtful whether – after investigating further Canarian samples – the hypothesis of Bahr (2000), who proposed a ‘multi-insular’ distribution for several *Calacalles* species, will hold. The claim of synonymy for *Calacalles wollastoni palmensis* (Roudier, 1954) is questionable, as is the usefulness of some exoskeletal characters that provide only scarce criteria for a convincing species discrimination (e.g. antennae with six or seven antennomeres, respectively; or elytra projecting above the pronotum).

According to our molecular analysis, the Macaronesian *Calacalles s.s.*, which are amongst the smallest Cryptorhynchinae (cf. Fig. 15A; body lengths of 1.5–2.5 mm), are derived from an ancestor species of those *Calacalles* living in North Africa and on the Iberian Peninsula as well as on the adjoining islands. *Calacalles moraguesi* (Desbrochers, 1898) of Mallorca and Menorca (analysed in this study) is closely related to *Calacalles theryi* (de Peyerimhoff, 1925) of the Atlantic coastal belt of Portugal and Morocco.

Preliminary studies towards a revision of the genus *Calacalles* are currently being undertaken (J. J. Astrin & P. E. Stüben, unpubl. data).

*Differential diagnosis:* Distinguishing *Calacalles* from the other genera of Macaronesian Cryptorhynchinae is not difficult and can be carried out quickly with the ‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’ (see below).

*Distribution:* Macaronesian Islands (except Selvagens), Iberian Peninsula (including Balearic Islands), North Africa.

ACALLES SCHOENHERR, 1825

**ORIGOACALLES** STÜBEN & ASTRIN SUBGEN. NOV.

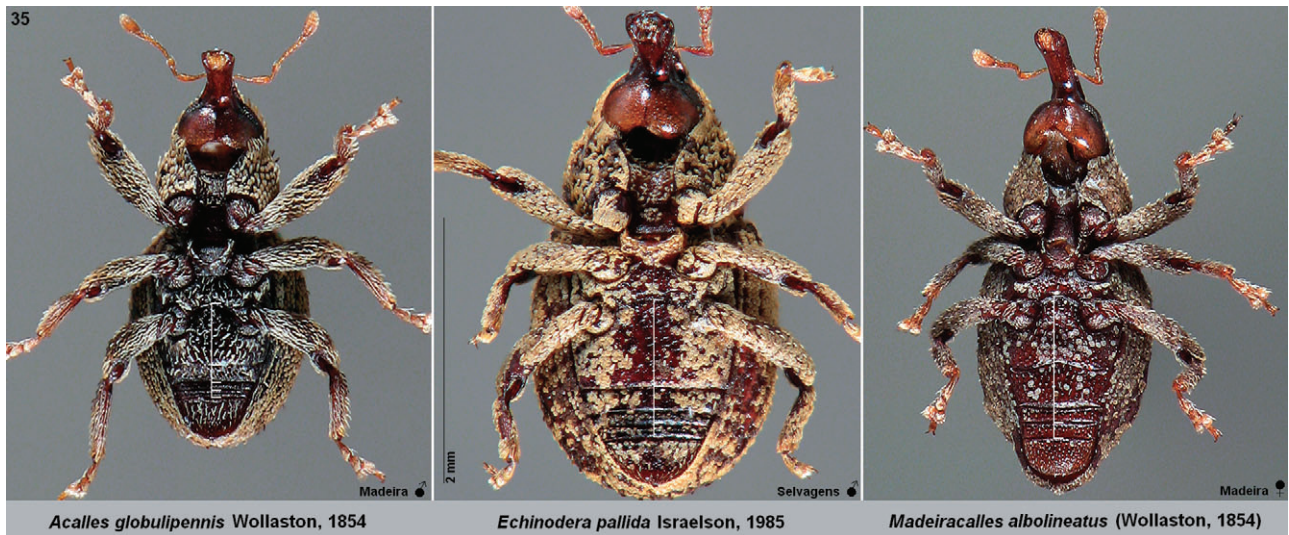
(FIGS 19A–E, 35)

*Type species of the genus Acalles: Acalles camelus* (Fabricius, 1792) – Germany (including type locality), Europe

*Type species of the subgenus Origoacalles: Acalles globulipennis* Wollaston (1854)

Wollaston, 1854, 1857, 1864, 1865; de Marseul, 1875; Lundblad, 1958; Behne, 2000; Stüben, 2000a, c,





**Figure 35.** *Acalles globulipennis* and *Echinodera pallida*: first abdominal sternite clearly longer than the three following (very narrow) segments combined (here vs. *Madeiracalles albolineatus*: first abdominal sternite maximally as long as the three following sternites combined (second sternite as long as or longer than sternite 3 and 4 combined).

2002b, 2008a; Stüben *et al.*, 2003; Stüben & Germann, 2005; Germann & Stüben, 2006; Astrin & Stüben, 2008.

*Compilation of the species of the subgenus*

***Origoacalles* subgen. nov.**

***Acalles (Origoacalles) globulipennis* Wollaston (1854) comb. nov. (formerly: *Acalles* s.s.) – Madeira (including type locality), Tenerife, Gran Canaria, Mainland Portugal = *Acalles pilula* var.  $\beta$  *seminulum* Wollaston (1864) syn. Stüben 2000: 85 – Tenerife**

***Acalles (Origoacalles) pilula* Wollaston (1864) comb. nov. (formerly: *Acalles* s.s.) – La Palma (including type locality), Tenerife (Teno), La Gomera, El Hierro**

*Description*

**Head:** The big, flat, and almost circular eyes covering the entire flanks of the head are noticeable. The rostrum of the ♂ is reddish brown, slender, finely punctured, two-thirds as long as the pronotum, and densely covered with light scales almost reaching the antennal insertion, the rostrum of the ♀ is clearly longer reaching three-quarters of the pronotum length.

**Pronotum:** 0.95–1.05× as long as wide; widest behind the middle, outline in dorsal view regularly rounded to the fore and hind margin, only robust specimens show an indicated lateral constriction close to the fore margin. The dense and fine punctures separated by narrow ridges only. The almost circular scales are the

same colour as the scales of the elytra. The prolongation of the light and narrow lateral fascia, which starts on the fore half of the elytra is continued and widened on the flanks of the pronotum. The disc of the pronotum is convex without mid groove or depression. The light scutellar spot of the elytra is continued on the middle of the base of pronotum. The elytra are considerably wider than the pronotum (up to two elytral intervals).

**Elytra:** Shortly oval, 1.10–1.20× as long as wide (Fig. 19A); widest shortly in front of the middle to immediately behind the base and therefore of quite variable outline (almost spherical, shortly oval, or inversely egg-shaped). The narrow stripes are situated almost on the same level as the much wider intervals and consist of extremely fine punctures. There are robust black tufts of bristles on the first and third interval of the elytral slope. Further black tufts of bristles are situated behind a spot of light (beige) scales on the anterior third of the elytra on the first (also indicated on the third) interval. The brown integument consists of circular, predominantly isolated scales.

**Legs:** Particularly tibia and tarsus (light) reddish brown. The front femur reaches the fore margin of the pronotum, the hind femur reaches the tip of the elytra. The slender, light scales are raised on the femur and stick out vertically on the outer edge of the tibia.

*Venter*: Metasternum between midcoxae as wide as midcoxae in diameter; sternites predominantly with long, slender bristles (depending on the degree of abrasion hair-like as well). The first sternite is – as in *Echinodera* – longer than the three following combined (Fig. 35).

*Aedeagus*: Triangular, ending acute-angled; resembling the aedeagus of the Central European *Acalles* like *A. misellus* Boheman (1844), *A. fallax* Boheman (1844), and *A. papei* A. & F. Solari, 1905, etc. (Stüben *et al.*, 2003) – and is separated from this species by lacking the structure of the internal sac (Fig. 19B).

*Differential diagnosis and discussion*: According to the habitus, *Acalles* s.s. of the European mainland and *Origoacalles* are very similar (and their status as sister taxa is fully supported in the tree). The most conspicuous character of both taxa is the almost ‘globular’ to shortly oval outline of the elytra. The elytra are only 1.2× as long as high and decline almost perpendicularly in lateral view (cf. Fig. 19A). In addition, according to the acuminately tapering apex of the aedeagus, both species of *Origoacalles* are comparable with the *Acalles* s.s. species of the western Palaearctic that also have such ‘triangular’ aedeagi (cf. Fig. 19B). Amongst others this group includes *Acalles sintraniensis* Stüben, 1999, *Acalles papei* A. & F. Solari, 1905, *Acalles kippenbergi* Dieckmann, 1982, *Acalles tibialis* (Weise, 1891), *Acalles ptinoides* (Marsham, 1802), *Acalles petryszaki* Dieckmann, 1982, *Acalles echinatus* (Germar, 1824), *Acalles fallax* Boheman (1844), *Acalles misellus* Boheman (1844), and *Acalles almeriaensis* Stüben, 2001. The mentioned combination of characters is absent in all other species of Macaronesian Cryptorhynchinae.

However, the species of *Origoacalles* also share two significant characters with the species of *Echinodera*: (1) the first abdominal sternite is clearly longer than the three following, very short sternites taken together (in *Acalles* s.s. maximally as long as the three following sternites combined); (2) as in *Echinodera*, the structure of the internal sac of aedeagus is lacking (this structure is always present in *Acalles* s.s. and in all other Macaronesian species) (cf. Figs 17B, 19B). See also the ‘Key to the genera and subgenera of Macaronesian Cryptorhynchinae’.

Probably only studies on population genetics would reveal whether these Atlantic species could have colonized Madeira first (coming from the Iberian Peninsula) and spread afterwards (as opposed to the more ‘usual’ direction of colonization; Stüben, 2000c) – to the Canary Islands, with a further species, *Acalles pilula*, evolving on the western islands (cf. Fig. 19D). The species of *Origoacalles* are specialized on decay-

ing twigs of dead wood (cf. Fig. 19C) and form an absolutely discrete group with no phylogenetic contact to any other Macaronesian Cryptorhynchinae.

*Etymology*: *Origoacalles* (origo, Latin: origin, provenance): the mitochondrial tree shows the species of *Origoacalles* as the sister group to *Acalles* s.s. and the genus shares some morphological characters with the genus *Echinodera*. The habitus of the *Origoacalles* species is consistent with that of the European species of *Acalles* s.s.

*Distribution*: Western Canary Islands, Madeira, Portugal.

*ECHINODERA* WOLLASTON, 1863 (FIGS 17A–E, 35)

*Type species of the genus Echinodera*: *Echinodera crenata* Wollaston, 1863

Wollaston, 1863, 1864, 1865; de Marseul, 1875; Uyttenboogaart, 1937, 1940; Roudier, 1954; Lindberg, 1958; Stüben, 1998, 2000e, 2002b, 2003b, 2007b, 2008a; Behne, 2000; Riede & Stüben, 2000; Stüben *et al.*, 2001; Stüben & Germann, 2005; Germann & Stüben, 2006; Astrin & Stüben, 2008.

*Compilation of species of the subgenus Echinodera s.s. of the Macaronesian Islands*:

***Echinodera crenata* Wollaston, 1863 – Tenerife**

***Echinodera angulipennis* Wollaston, 1864 – Tenerife**

***Echinodera orbiculata* Wollaston, 1864 – Tenerife**

***Echinodera personata* Colonnelli, 1985 – Tenerife**

***Echinodera tenoensis* Stüben, 2000 – Tenerife**

***Echinodera guacimara* Stüben & Germann, 2005 – Tenerife**

*Echinodera benahoarita* Stüben, 2000 – La Palma

*Echinodera palmaensis* Stüben, 2000 – La Palma

***Echinodera hystrix* Wollaston, 1864 – El Hierro (including type locality), La Palma**

***Echinodera pseudohystrix* Stüben, 2000 – La Gomera**

*Echinodera praedicta* Germann & Stüben, 2006 – La Gomera

*Echinodera gomerensis* Stüben, 2000 – La Gomera

*Echinodera compacta* Wollaston, 1864 – Gran Canaria

*Echinodera picta* Wollaston, 1864 – Fuerteventura (including type locality), Lanzarote

*Echinodera pallida* Israelson, 1985 – Selvagens

*Discussion*: The genus *Echinodera*, which is represented by many species on the Canary Islands, has not colonized the archipelago of Madeira or the

Azores. Only *Echinodera pallida* successfully spread to the very small Selvagens, located between the Canaries and Madeira. Independently from the former *Acalles* s.l. species, *Echinodera* colonized – like, e.g. the genus *Onyxacalles* – the Canary Islands from the mainland and underwent an adaptive radiation. *Echinodera* inhabits areas from the dry, coastal, succulent vegetation up to the high mountains like the caldera of the Pico del Teide of Tenerife (*Echinodera crenata*) or the Roque de Los Muchachos of La Palma (*Echinodera benahoarita*) (Stüben, 2000c: fig. 6; Germann & Stüben 2006: 165: fig. KONV).

All western Canary Islands show a segregation of these host plant-independent *Echinodera* species according to climatic altitudinal belts (Stüben, 2000e; Germann & Stüben, 2006: 165: fig. KONV). It can only be clarified by breeding and cross-breeding experiments or by further molecular studies whether the long-bristled, uniformly brownish *Echinodera* species of the laurel forest and the short-bristled, black-and-white coloured species of the coastal succulent belt repeatedly originated as discrete species on each island or if these forms merely result from intraspecific phenotypic variability (because of, e.g. larval development) along an altitudinal or moisture gradient, i.e. as modifications. An extensive combined molecular and morphological study of the genera *Echinodera* and *Ruteria* is under way (J. J. Astrin & P. E. Stüben, unpubl. data).

*Differential diagnosis:* See below ('Key to the genera and subgenera of Macaronesian Cryptorhynchinae').

*Distribution:* All Canary Islands, Selvagens (absent on Madeira and the Azores).

*ONYXACALLES* STÜBEN, 1999 (FIG. 18A–E)

*ARANEACALLES* STÜBEN & ASTRIN SUBGEN. NOV.

*Type species of the genus Onyxacalles:* *Acalles luigi-nii* Solari, 1907 – Italy: Lazio (type locality), SW-Europe

*Type species of the subgenus Araneacalles:* *Acalles verrucosus* Wollaston, 1863

Wollaston, 1863, 1864, 1865; de Marseul, 1875; Uyttenboogaart, 1940; Uyttenboogaart & Zumpt, 1940; Roudier, 1954; Lindberg, 1958; Oromí, 1984; García, Ortega & Pérez Sánchez, 1993; Behne, 2000; Riede & Stüben, 2000; Stüben, 1999b, 2000c, f, 2002a, 2003c, 2007b, 2008a; Stüben & Wolf, 2001; Stüben *et al.*, 2001; Germann & Stüben, 2004, 2006; Stüben & Germann, 2005; Astrin & Stüben, 2008.

*Compilation of the species of the subgenus*

*Araneacalles* subgen. nov.

*Onyxacalles (Araneacalles) verrucosus* (Wollaston, 1863) comb. nov. (formerly: *Onyxacalles* s.s.) – Tenerife (including type locality), El Hierro

*Onyxacalles (Araneacalles) neglectus* (Kulbe, 1999) comb. nov. (formerly: *Onyxacalles* s.s.) – La Gomera (including type locality), El Hierro

*Onyxacalles (Araneacalles) ringeli* (Kulbe, 1999) comb. nov. (formerly: *Onyxacalles* s.s.) – La Palma

*Description*

*Size:* 3.1–5.5 mm

*Head:* The slender, reddish brown and fine dotted rostrum of the ♂ as long as the pronotum, the rostrum of ♀ longer than the pronotum.

*Pronotum:* 1.1–1.2× as wide as long, widest at the end of the basal quarter, at the side regularly rounded, only robust specimens show a slight lateral constriction in front of the fore margin; disk of pronotum – covered with black scales – without a hollow; however, with a small dent behind the scutellum and on each side with an accumulation of some upright bristles. Pronotum laterally with a large, white (sometimes with reddish brown) fascia, which silhouetted in high contrast against the dark, nearly black integument of the whole habitus (Fig. 18A).

*Elytra:* Short- and long-oval, 1.2–1.4× as long as wide, widest at the end of the basal quarter, at the side regularly rounded, apex acute-oval, egg-shaped rounded; on the first interval with six, on the third and fifth intervals with three tapered and black humps of bristles, the bristles on the fifth interval sometimes a little bit brighter; on the elytral slope with a short, distinctive white fascia on the sutural strip and the first interval (Fig. 18A). The whole integument consists of oval, dark brown and black scales; only behind the middle on the seventh interval (covered from the hind femur) and on the sixth interval in front of the elytral base with a small white spot.

*Legs:* Very long, arachnoid. The front femur reaches the insertions of the antennae (the middle of rostrum); femura annulated with white spots; the outer edge of tibia with bristles sticking out vertically (upright erinaceous).



*Venter*: Second abdominal sternite a little bit longer than sternite 3 and 4 combined; Metasternum between the mesocoxae as wide as mesocoxae in diameter.

*Aedeagus*: With a long and narrow hook-shaped apex, characteristic for the species of the genus *Onyxacalles* (Fig. 18B).

*Discussion and differential diagnosis*: This group of species occurring on the western Canary Islands has already been discussed in a revision of the genus *Onyxacalles* (Stüben, 1999b). In this work Kulbe (1999) separated *Onyxacalles neglectus* and *Onyxacalles ringeli* from *Onyxacalles verrucosus* Wollaston, 1863.

According to our analysis, the three Canarian species of *Onyxacalles* represent the sister group of *Onyxacalles* s.s. of the European mainland. Regarding their habitus (cf. Fig. 18A) and the distinctive hook-shaped apex of the aedeagus (cf. Fig. 18B), the Canarian species definitely belong to the genus *Onyxacalles*, as corroborated by the total support values of the *Onyxacalles* clade. Besides the characters already mentioned, the uncommonly long and slender ('spidery') legs and the very long rostrum (especially in comparison to the eastern European species of *Onyxacalles*) justify establishing a separate subgenus. *Araneacalles* is distinguished from all other Macaronesian Cryptorhynchinae by the characters described here. See also the 'Key to the genera and subgenera of Macaronesian Cryptorhynchinae'.

It took a long time to find the evolutionary link between the 'Atlantic fraction' of *Onyxacalles* and the south-westernmost species of this genus from the Alps and the Pyrenees. This gap was recently closed by new descriptions from the Iberian Peninsula and north-west Africa (Stüben & Wolf, 2001; Stüben, 2002a, 2003c). Furthermore, the scattered populations of *Onyxacalles* depend on standing deadwood within intact patches of natural forest. Thus, *Onyxacalles* populations have become rare or are highly endangered.

*Biology and ecology*: The species of the Canarian subgenus *Araneacalles* have nocturnal habits and live in dense natural forest – just like *Onyxacalles* s.s. in Europe, North Africa, and Asia Minor. The three Canarian species depend on natural laurel forest and especially on deadwood, something that does not apply for most of the other Macaronesian Cryptorhynchinae that live in trees and shrubs (cf. Fig. 18C). The species group is endemic to the western islands Tenerife, La Gomera, El Hierro, and La Palma. The rearing of this group turned out to be very difficult.

*Etymology*: The name *Araneacalles* refers to the uncommonly long, spidery legs of the three species of *Onyxacalles* which occur on the Canaries.

*Distribution*: Endemic to the four western Canary Islands.

#### TRIBE TORNEUMATINI BEDEL, 1884

##### *TORNEUMA* WOLLASTON, 1860 (FIG. 20A–E)

*Type species of the genus Torneuma*: *Torneuma caecum* Wollaston, 1860

Wollaston, 1860, 1865; Roudier, 1956, 1965; González, 1971; Osella & Osella, 1984; Osella & Zuppa, 1998; Behne, 2000; Stüben, 2000g, 2002b, 2007a, 2008b.

*Compilation of species of the genus Torneuma the Macaronesian Islands*

***Torneuma caecum* Wollaston, 1860 – Madeira**  
= *Torneuma brincki* Roudier, 1965 syn. (González, 1971: 7)

***Torneuma desilvai* Osella & Zuppa, 1998 – Madeira**

***Torneuma maderense* Stüben, 2002 – Madeira**  
***Torneuma picocasteloense* Stüben, 2002 – Porto Santo**

*Torneuma canariense* Osella & Osella, 1984 – Gran Canaria

*Torneuma solarii* Osella & Osella, 1984 – Gran Canaria

*Torneuma viti* Osella & Osella, 1984 – Gran Canaria (cf. discussion below)

##### **PARATORNEUMA** ROUDIER, 1956 RESYN. (FIG. 21A–E)

(lastly: *Paratyphloporus* Solari, 1937, (Stüben, 2007) – Mediterranean)

*Type species of the genus Paratorneuma*: *Torneuma orbatum* Wollaston, 1865 (Roudier, 1956);

Wollaston, 1865; F. Solari, 1937; Roudier, 1956; González, 1971; Franz, 1981; Osella & Osella, 1984; Osella, 1986; Behne, 2000; Stüben, 2000g, 2007a, 2008b; Germann & Stüben, 2006.

*Compilation of species of the genus Paratorneuma*  
***Paratorneuma orbatum* (Wollaston, 1865) – La Gomera**

*Paratorneuma aphroditae* Germann & Stüben, 2006 – La Gomera

*Paratorneuma feloi* (Stüben, 2007) – Tenerife

*Paratorneuma franzi* González, 1971 – Tenerife

*Paratorneuma lindrothi* Franz, 1981 – La Palma

## KEY TO THE GENERA AND SUBGENERA OF MACARONESIAN CRYPTORHYNCHINAE

(quod vide Stüben, 2000h, 2008b: 'Key to the genera and some species of the subfamily Cryptorhynchinae from the West Palaearctic region (without Macaronesia)'; in parentheses: the number of species on each island)

1. Eyes absent; subterranean species.....Tribe: Torneumatini.....2
    - With eyes; species inhabiting leaf-litter, decaying wood or phytophagous on green plants..Tribe: Cryptorhynchini.....3
  2. With a constantly deep pectoral canal, from the foremargin of the prosternum to the mesocoxae, terminating between mesocoxae in a similarly deep-lying mesosternal receptaculum (Fig. 20C). Distribution: Madeira (3), Porto Santo (1), Gran Canaria (3).....Genus: *Torneuma* Wollaston, 1860
    - In front of procoxae with a deep or a shallow pectoral canal that ascends directly in front of or between the procoxae. From this point, it descends steeply to the mesosternal receptaculum. (The area directly in front of or between the procoxae is always raised in the species of this genus.) The procoxae have contact to one another (Fig. 21C). Distribution: La Gomera (2), Tenerife (2), La Palma (1).....Genus: *Paratorneuma* Roudier, 1956
  3. First abdominal sternite clearly longer than the three following (very narrow) segments combined (Fig. 35). Internal sac of aedeagus without a sclerotized structure (Figs 17B, 19B).....4
    - First abdominal sternite maximum (at most) as long as the three following sternites combined (second sternite as long as or longer than sternite 3 and 4 combined) (Fig. 35). Internal sac of aedeagus with a sclerotized structure (e.g. Figs 2B, 3B, 15B, 28–32).....5
  4. Eyes smaller and oval, at the sides of the head, in dorsal view only visible as narrow lines; in lateral view the eyes do not exceed the upper margin of the antennal groove. Elytral intervals with separate bristles, arranged in single rows and very distant from one another. The aedeagus always with an S-shaped, long, tapering, not sclerotized ('translucent') apex (Fig. 17B). Distribution: Tenerife (6), La Palma (3), La Gomera (3), Gran Canaria (1), Fuerteventura/Lanzarote (1), Selvagens (1).....Genus: *Echinodera* Wollaston, 1863
    - Eyes larger and round; their position further up: expanded to the frons and well visible in dorsal view. Elytra with large tufts of bristles on the first and third intervals (well visible on the elytral slope). Aedeagus without an S-shaped, long, tapering apex (Fig. 19B). Distribution: Tenerife / Gran Canaria / Madeira (1), Tenerife (Teno) / La Gomera / El Hierro (1).  
.....Genus: *Acalles* Schoenherr, 1825  
.....Subgenus: ***Origoacalles*** Stüben & Astrin **subgen. nov.**
  5. Pronotum with a rim of few long, strong, and clearly raised spicular bristles or thorns (Figs 15A, 16A). Genus: *Calacalles* de Peyerimhoff, 1925.....6
    - Pronotum (and elytra) always densely covered with finer, close-fitting, or erected bristles, with bristle-crests or bristle-bumps.....7
  6. On average smaller species: < 3.0 mm (without rostrum); intervals of elytra with single-row arranged bristles (Fig. 15A). Distribution: Canaries (8), Madeira (1), Azores (1).....Subgenus: *Calacalles* s.s.
    - On average taller species: > 3.5 mm (without rostrum); elytra with strong bristle-tufts (and pronotum with a saucer-shaped rim of thorns) (Fig. 16A). Distribution: Azores (2).....Subgenus: *Crateracalles* Stüben, 2004
  7. 'Spherical' habitus and long legs; the mostly black-scaled pronotum with clearly contrasting lateral light yellow to white sides (Fig. 18A); aedeagus with a long and narrow hook-shaped apex (Fig. 18B). Distribution: Western Canary Islands (3).....Genus: *Onyxacalles* Stüben, 1999  
.....Subgenus: ***Araneacalles*** Stüben & Astrin **subgen. nov.**
    - Slender (mostly oblong, 'prow-shaped') habitus; lateral parts of pronotum without an extended light marking of scales; aedeagus without a hook-shaped apex, simply rounded. Formerly *Acalles* s.l. and *Dichromacalles* (cf. Stüben, 2000a, d).....8
  8. Rostrum shorter: <4–4.5× as long as wide; habitus more stout, elytra flatter and broader, towards the apex more broadly rounded. Genera of the Macaronesian succulent bush and the thermophilous forest.....9
    - Rostrum longer: >5–7× as long as wide; habitus more slender, apex of elytra extremely produced, 'prow-shaped'. (Most species from the Macaronesian laurel forest and amongst others from Crassulaceae.).....13
- 'Broad-nosed' species*
9. Aedeagus with a small Π-shaped structure inside the internal sac (endophallus) (Fig. 22B). Only with a single species on nearly all Macaronesian Islands: the introduced *Dichromacalles dromedaries* (Fig. 22A) immigrated from south-western Europe or/and north-western Africa.....Genus: *Dichromacalles* Stüben, 1998
    - Aedeagus without a Π-shaped structure inside the internal sac.....10
  10. With rhombic eyes (in lateral view, Fig. 23A) and with wide, on the top flattened, short oval and towards the apex equably rounded elytra (not elongated beak-shaped). Distribution: Gran Canaria/Tenerife (1), Lanzarote (1) [incertae sedis: *Acalles xerampelinus* Wollaston (1864); perhaps this species belongs to *Canariacalles* (cf. Fig. 24A)].....Genus: ***Canariacalles*** Stüben & Astrin **gen. nov.**

- Eyes rounded towards the frons (Fig. 23B).....11
- 11. Endophallus: unique amongst all western Palaearctic species, with a large Ω-shaped structure (Fig. 9B). Distribution: western Canary Islands (1).....Genus (monotypic): ***Pseudodichromacalles*** Stüben & Astrin **gen. nov.** (*Pseudodichromacalles fernandezi* (Roudier, 1954))
- Endophallus: with a small, fork-shaped structure. Mono- or oligophagous species from *Sonchus* and *Tolpis*....12
- 12. Only known from the western Canary Islands (Fig. 11D) (3).....Genus: ***Sonchiacalles*** Stüben & Astrin **gen. nov.**
- A single species from Madeira on *Tolpis succulenta*, cf. Fig. 34) (1) [*Madeiracalles pulversosus* (Gemming, 1871)].....Genus (pars): ***Madeiracalles*** Stüben & Astrin **gen. nov.**

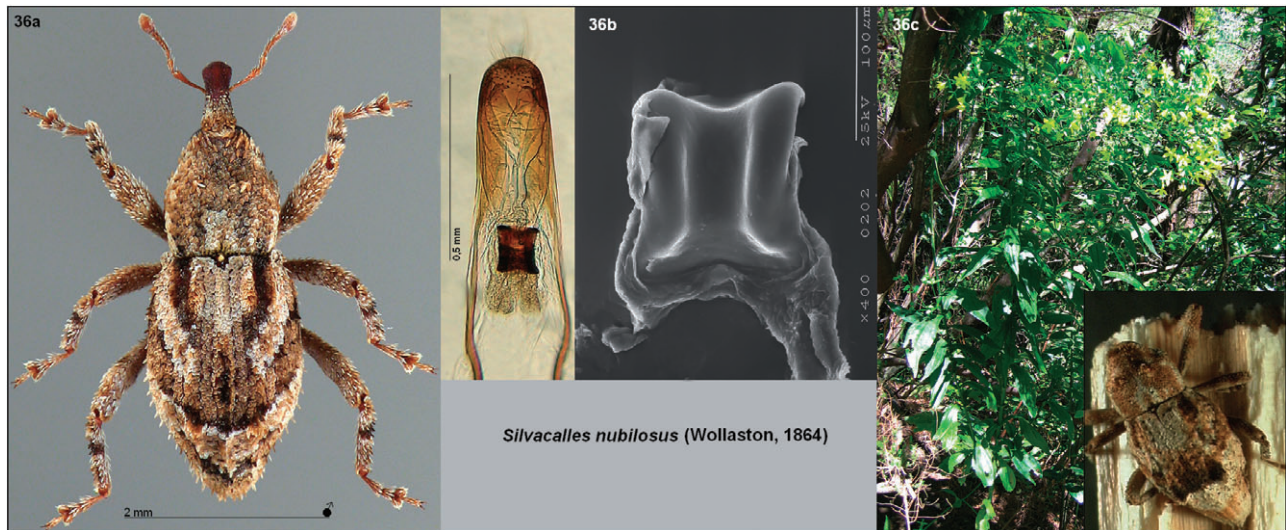
*‘Long-nosed’ species*

The following genera/subgenera – species with a very variable habitus – are distinguished quickly and safely by the study of the sclerotized structure of the endophallus.

- 13. Aedeagus with a double structure of the endophallus, consisting of a ‘fork’ (dividers) and one or two disk-shaped structures above (Figs 3B, 4B, 6B, 12B).....14
- Endophallus only with a single ‘fork’-shaped (Figs 5B, 8B, 10B, 14B), ‘beam’-shaped (Fig. 13B), or ‘cup’-shaped structure (Fig. 7B) .....17
- 14. Species smaller: < 3 mm (*S. mundus* < 4 mm); endophallus with a single, wider and longer, trapezoidal sclerotized (transparent) disk above the ‘fork’-shaped structure (Fig. 6B). Distribution: Gran Canaria/Tenerife (1)/La Palma (2)/La Gomera (1)/Madeira (1).....Genus (pars): ***Silvacalles*** s.s. Stüben & Astrin **gen. nov.**
- Species larger: > 3.5 mm (up to 7 mm); endophallus with two sclerotized (transparent) and usually drop-shaped disks above the ‘fork’-shaped structure (Figs 3B, 4B, 12B)..... 15
- 15. Habitus flat, elongate, with a black, isosceles triangular spot on the elytral slope (Fig. 12A). The single species develops on *Echium strictum* on La Gomera and Tenerife (1).....Genus (monotypic): ***Echiumacalles*** Stüben & Astrin **gen. nov.** [*Echiumacalles anagaensis* (Stüben, 2000)]
- Habitus more arched (lateral view); without such a spot on the elytral slope. Genus *Dendroacalles* Stüben, 2005 ..... 16
- 16. The strong humps on the second interval of the elytral slope with long, robust, and upright aggregations of elevated bristles. Rostrum longer (rostrum of females nearly as long as the pronotum). Species living in the shadowy-humid laurel forest (cf. Fig. 3C): Distribution: Canaries/Madeira (3).....Subgenus: *Dendroacalles* s.s. Stüben, 2005 (in Stüben & Germann, 2005)
- The flat humps on the second interval of the elytral slope with short erected bristles. Rostrum shorter (rostrum of females attaining three-quarters of the length of the pronotum).The host plants of these species are the dendriform Euphorbiaceae of the succulent bush (cf. Fig. 4C). Distribution: Canaries (3)..... Subgenus: *Euphorbioacalles* Stüben, 2005 (in Stüben & Germann, 2005)
- 17. Species from the Madeira archipelago (Fig. 14D) (15).....Genus (pars): ***Madeiracalles*** Stüben & Astrin **gen. nov.**
- Species from the Canaries and Selvagens..... 18
- 18. On the second interval of the elytral slope with strong humps and with long, robust, and upright elevated aggregations of bristles; on this elytral slope with a wide, triangular, white spot, too. A tree-climbing species of the laurel forest (Fig. 10C). Distribution: Tenerife/La Palma (1).....Genus (monotypic): ***Lauriacalles*** Stüben & Astrin **gen. nov.** (*Lauriacalles acutus* (Wollaston, 1864))
- On the second interval of the elytral slope with flat humps and with very short bristles (species that never develop on Lauraceae)..... 19
- 19. Endophallus with a ‘fork’-shaped structure and terminally with a sickle-shaped structure: (Fig. 5B). Species from *Aeonium* spp., another species from *Kleinia neriifolia*. Distribution: Canaries (4), Selvagens (1).....Genus: ***Aeoniacalles*** Stüben & Astrin **gen. nov.**
- Without a sickle-shaped structure of the endophallus.....20
- 20. With a peculiar, 2.5× as long as wide, parallel balk-shaped structure of the endophallus (Fig. 13B). Distribution: western Canaries (2), Selvagens (1).....Genus: ***Ficusacalles*** Stüben & Astrin **gen. nov.**
- Without such a structure of the endophallus.....21
- 21. Endophallus with a balk-shaped, square and strong sclerotized structure (Fig. 36A, B). A single species feeding on *Ixanthus viscosus* (in the ‘laurisilva’). Distribution: Tenerife/La Palma (1).....Genus (pars): ***Silvacalles*** s.s. Stüben & Astrin **gen. nov.** (*Silvacalles nubilosus* Wollaston, 1864)



- ‘Fork’-shaped (Fig. 8B) or ‘cup’-shaped (Fig. 7B) structure of the endophallus Genus (pars): *Silvacalles* Stüben & Astrin **gen. nov.**.....22
- 22. ‘Fork’-shaped structure of the endophallus (Fig. 8B). All from the dendriform Fabaceae *Chamaecytisus proliferus* Link. (‘tagasaste’). Distribution: western Canary Islands (3).....  
.....Subgenus: *Tagasastacalles* Stüben & Astrin **subgen. nov.**
- A single species (La Gomera) feeding on *Tolpis* cf. *proustii* with a ‘cup’-shaped structure of the endophallus (Fig. 7B).....  
...Subgenus (monotypic) *Tolpiacalles* Stüben & Astrin **subgen. nov.** (*Silvacalles* (Tol.) *tolpivorus* (Germann & Stüben, 2006)



**Figure 36.** A, *Silvacalles nubilosus* (in dorsal view). B, aedeagus in ventral view (left), endophallus (right). C, *Ixanthus viscosus* Griseb., the host plant of *S. nubilosus*.

**Discussion (Torneumatini):** The supraspecific classification of Torneumatini has always been a problem for taxonomists working exclusively morphologically (Stüben, 2007a). The taxa of this tribe all have a very similar habitus. Furthermore, biological and ecological arguments are hard to apply because the animals live subterraneously. In the past the only decisive character was the pectoral canal, which is either present and fully developed (*Torneuma*; Fig. 20C), only present as a shallow depression in front of the praecoxae (*Paratyphloporus*; Fig. 21C) or totally absent (*Pseudotorneuma*). In a recent study, Torneumatini was classified using this character as well as the structure of the internal sac of the aedeagus (Stüben, 2007a).

The simple classification suggested in this study bore in mind the practice of science and was an attempt to settle the taxonomic confusion that had resulted from almost 150 years of research on Torneumatini. It was always clear that the supposition of a continuous evolutionary transformation process (fully developed pectoral canal reaching midcoxae →

pectoral canal only as shallow depression in front of the praecoxae → pectoral canal absent) would only deliver a heuristic/pragmatic, typological classification (Stüben, 2007a: 95). We cannot even be certain about the polarity of this transformation series (although it is more likely that the fully developed pectoral canal constitutes the ancestral character state for Torneumatini; see above).

The genus *Paratorneuma* Roudier (1956) (pectoral canal developed as a shallow depression in front of the praecoxae; Fig. 21C) was at first interpreted as a younger synonym of *Paratyphloporus* Solari, 1937 (Stüben, 2007a). According to this definition, the species belonging to this genus included not only Mediterranean taxa (e.g. the type species of *Paratyphloporus*: *Torneuma karamani* Formánek, 1912), but also some Canarian species like *Paratyphloporus franzi* (González, 1971) (originally *Paratorneuma*) and the new species *Paratyphloporus feloi* Stüben, 2007. However, the option was kept open: ‘If future molecular results should indicate the plausibility of parallel evolution between Canarian

and South European Torneumatini, thus rendering the groups paraphyletic, a separation and thereby a re-synonymization of the genus *Paratorneuma* Roudier (1956) with the type species *Torneuma orbatum* Woll. (La Gomera) will be required' (translated from Stüben, 2007a: 39).

According to our molecular dendrogram (from which many southern European species of *Torneuma* are absent), the pectoral canal of Torneumatini has been reduced twice (Fig. 1A): on the Canary Islands and in the Mediterranean independently. Now we have to consider four genera of Torneumatini and await further molecular results (sufficient material fit for sequencing has yet to be collected) in order to determine whether the species-rich Mediterranean group around the type species *Torneuma deplanatum deplanatum* (Hampe, 1864) requires one more taxon: namely *Typhloporus* Hampe, 1864.

*Differential diagnosis:* See also the 'Key to the genera and subgenera of Macaronesian Cryptorhynchinae'.

*Distribution:* Canary Islands, Madeira, Porto Santo, Mediterranean.

*ECHINOACALLES* STÜBEN, 2008

*Type species of the monotypic genus Echinoacalles: Echinoacalles franzi* Stüben, 2008  
Stüben, 2008: 321–323.

*Annotation:* This monotypic genus, which is only known from El Hierro (type locality: Las Montañetas), the smallest and westernmost island of the Canaries, is only mentioned for the sake of completeness [it is neither considered in the tabular synopsis (Figs 2A–22D) nor in the key]. From today's perspective, it can be deduced from its habitus and from the describing author's unsuccessful search for further specimens at the type locality (the description was based on one individual) that the species does not belong to the Canarian fauna. Presumably it was recently introduced with potting soil (from South or Central America?) or was mislabelled or transported with the collecting equipment.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Nexus file containing the molecular phylogenetic data matrix and MrBayes block used in this study.

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