

Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic Cryptorhynchinae (Coleoptera : Curculionidae)

Jonas J. Astrin^A and Peter E. Stüben^B

^AZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany. Email: j.astrin.zfmk@uni-bonn.de

^BCurculio Institute, Hauweg 62, D-41066 Mönchengladbach, Germany. Email: p.stueben@t-online.de

Abstract. A phylogeny is presented for the western Palaearctic representatives of the weevil subfamily Cryptorhynchinae using a combination of phenotypic and genotypic characters. This phylogeny is the first for the extremely species-rich Cryptorhynchinae to use molecular data (mitochondrial CO1 and 16S as well as nuclear ribosomal 28S). The results of this study show the need for molecular tools within this morphologically cryptic group of weevils and provide a scaffold based on which genus assignment can be tested. The present study mostly corroborates the current subdivision into genera (but many of the subgeneric groups are questioned). Three new genera are described: *Montanacalles* gen. nov. (type species: *Kyklioacalles nevadaensis* Stüben, 2001), *Coloracalles* gen. nov. (type species: *Acalles humerosus* Fairmaire, 1862) and *Elliptacalles* gen. nov. (type species: *Acalles longus* Desbrochers, 1892). Relevant external characters and the male genitalia of all discussed taxa are illustrated. Three species are transferred to different genera: *Kyklioacalles aubei* (Boheman, 1837) (formerly: *Acalles*), *Ruteria major* (Solari A. & F., 1907) and *Ruteria minosi* (Bahr & Bayer, 2005) (both formerly *Echinodera*).

Introduction

With probably more than 6000 described species, the weevil subfamily Cryptorhynchinae Schönherr, 1825 is among the most diverse animal subfamilies. Its species show a variety of forms; in temperate regions, on which we focus here, they are mostly small, inconspicuously coloured and almost always flightless. Their larvae develop in stressed, dying parts of lignified plants (roots or branches). If disturbed, members of the Cryptorhynchinae enter a characteristic state of thanatosis in which the rostrum is retracted into a canal on the pro- and mesosternum and the legs are folded in parallel manner. The subfamily includes more than 500 genera, of which more than half are monotypic (Alonso-Zarazaga and Lyal 1999). The subfamily Cryptorhynchinae has an almost worldwide distribution. However, phylogenetic studies on it are very rare, especially above genus level (but see Stüben and Germann 2005 for the Canary Islands; Paulay 1985 covers the cryptorhynchine fauna of Rapa island, consisting of a single genus). Apart from a negative collecting bias for this group (e.g. many species are leaf litter inhabitants), the rarity of phylogenetic studies is probably due to the high rate of endemism and frequent morphological crypsis of its members (cf. Figs 5–10). Although this seems to indicate the suitability of molecular markers in cryptorhynchine systematics, no molecular phylogeny exists so far for the subfamily. In fact, molecular data on the group are generally very scarce (GenBank registers sequences for only 15 species, Oct. 2007; www.ncbi.nlm.nih.gov/Genbank/).

Using a combination of molecular and morphological characters, we focus on western Palaearctic (mostly European)

Cryptorhynchinae species in our analysis – an especially morphologically cryptic group. Through the creation of several new genera during the last decade, the classification for this group has been fundamentally rearranged (cf. Savitsky 1997; Stüben 1998, 1999a, 1999b, 2003, 2004; Stüben and Behne 1998; Bahr 2000; Stüben and Germann 2005). Thus, our primary goal was to test the consistency of current genus-level taxa. This task could be addressed satisfyingly within the study's setup, leading also to the creation of three new genera: the genus *Coloracalles* with the type species *C. humerosus* (Fairmaire, 1862), *Elliptacalles* with the type species *E. longus* (Desbrochers, 1892) and *Montanacalles* with the type species *M. nevadaensis* (Stüben, 2001). Additionally, it leads to the transfer of three species to other genera: *Acalles aubei* Boheman, 1837 (now *Kyklioacalles*), *Echinodera major* (Solari A. & F., 1907) and *Echinodera minosi* Bahr & Bayer, 2005 (both now *Ruteria*). Furthermore, we investigate the suitability of current subgeneric divisions in the group, of which some proved monophyletic, but several others paraphyletic. We also comment on 'deeper' cryptorhynchine relationships and their classification into tribes. Our data can serve as a template for the assignment to genera of morphologically problematic new species. This is an important aspect for the taxonomy of the group, since many cryptorhynchine species are still being described in the western Palaearctic region. In fact, the last decade saw an increase in species number of more than 100% (there are currently 350 recognised cryptorhynchine species in the western Palaearctic; Stüben 2008).

Materials and methods

Taxon sampling and vouchering

For morphological reconstruction, 22 species (cf. Fig. 4) from 13 cryptorhynchine genera were studied. We always included the type species for the respective genus. Addition of congeners served the purpose of increasing compatibility with the molecular dataset and to investigate cases of dubious taxonomy. We examined 10–20 samples per species from the Curculio Institute collection (cf. authors' addresses), always covering most of the respective species' known geographic distribution. Our outgroup comparison centred on *Adexius scrobipennis* Gyllenhal, 1834 – a member of the weevil subfamily Molytinae and thus a close relative of the Cryptorhynchinae (Wink *et al.* 1997). But for its lack of the rostral canal (typical for Cryptorhynchinae species), the habitus of *A. scrobipennis* and the absence of a structured internal sack of the aedeagus (intromittent organ) make it easy to mistake it for an *Echinodera* Wollaston, 1863 species (one of the ingroups).

For molecular analysis, we obtained DNA sequences from 83 weevils: 74 cryptorhynchine species (in 17 genera) and the outgroup taxon (*A. scrobipennis*). Multiple individuals per species were sampled in cases relevant within this study or in cases where a considerable distance separates the collecting localities. With the exception of three Cryptorhynchinae species from the Neotropics, all beetles were collected in the Palaearctic. Appendix 1 lists the analysed material along with the collecting data. Voucher specimens (or tissue) and total genomic DNA vouchers are deposited at the ZFMK (cf. authors' addresses) and can be accessed under the voucher numbers specified in Appendix 1.

Of the current 19 western Palaearctic cryptorhynchine genera, 15 are treated here (cf. Catalogue of Western Palaearctic Cryptorhynchinae, Stüben 2008a, and counting the new genera described in this study).

Morphological characters and genetic markers

In total, we sampled 36 adult morphological characters. The characters studied were obtained from rostrum and pectoral canal (four characters), head (four), pronotum (eight), elytra (10), legs (two), ventral view (two), male genitalia (five) and the spiculum ventrale (one). A description of the morphological characters can be found in Appendix 2. The corresponding data matrix appears in Appendix 3.

Most of the molecular characters used in this study are mitochondrial (and thus fast-evolving) because our focus lay on cryptorhynchine genera rather than on deep branches. We sequenced part of the cytochrome *c* oxidase subunit 1 (CO1) and part of the ribosomal large subunit (16S) genes. To complement these with a nuclear marker, we also sequenced a fragment of the ribosomal 28S gene from the D6–D7 region. Sequence lengths (unaligned) were as follows: 659 bp for CO1, 528–541 bp for 16S and 305–553 bp for 28S. The DNA sequences generated in this study have been submitted to GenBank (Accession Numbers EU286281–EU286526). The matrix of concatenated, aligned nucleotide sequences is available from the authors or can be downloaded as an Accessory Publication from the *Invertebrate Systematics* website. Taxa not analysed molecularly but present in the morphological dataset were not included in the concatenated alignment to avoid artefacts in reconstruction (otherwise arising through the prevalence of missing characters for the respective taxon).

DNA extraction, amplification and sequencing

DNA isolation, using the Nucleo Spin Tissue extraction kit (Macherey–Nagel, Düren, Germany), was carried out on samples preserved in ethanol or on dried material. We extracted DNA from either 2–3 legs, head and prothorax or, in some cases, the whole weevil, depending on the size and conservation of the sample. PCR reaction mixes (50 µL) contained 125 nmol MgCl₂, 5 µL 10× PCR buffer, 25 pmol of forward and reverse primer each, 5 pmol deoxyribonucleotide triphosphates (dNTPs), 1.75 units of *Taq* polymerase and 5 µL total undiluted DNA template. The laboratory chemicals were purchased from Sigma–Aldrich (Steinheim, Germany). We used the Qiagen (Hilden, Germany) Multiplex PCR kit in cases where the regular protocol failed. PCR primers – newly designed for the group under study – are given in Table 1. Thermal cycling was performed on blocks of the type GeneAmp PCR System 2700 (Applied Biosystems, Foster City, CA, USA). PCR programs followed the 'Touch Down' routine (Palumbi 1996) or, in the case of CO1, a combination of 'Touch Down' and 'Step Up' routines. For 16S: first cycle set (15 repeats): 35 s denaturation at 94°C, 35 s annealing at 55°C (–1°C per cycle) and 60 s extension at 72°C. Second cycle set (25 repeats): 35 s denaturation at 94°C, 35 s annealing at 40°C and 50 s extension at 72°C. For 28S: same as for 16S, but with annealing temperatures at 65°C and 50°C. For

Table 1. Sequences of CO1, 16S and 28S primers

Primer positions are based on Folmer *et al.* (1994) for CO1 and on Crandall and Fitzpatrick (1996) for 16S

Gene	Direction	Primer	Sequence (5'→3')
CO1	fw	LCO1490-JJ	CHACWAAYCATAAAGATATYGG
	rev	HCO2198-JJ	AWACTTCVGGRTGVCCAAARAATCA
16S	fw	16S-1472-JJ	AGATAGAAACCRACCTGG
	alternative fw	16S1472-JJ-al	GGTCCTTTCGTAATAA
	rev	16S-ar-JJ	CRCTGTTTATTAATAAACAT
	alternative rev	16Sar-JJ-al	CCTGTWTATTAATAAACATGGC
28S	fw	28SJJ-a	ATGGATGGCGCTGAAGCGTCGT
	alternative fw	28SJJ-a-al	CCTGAAATGGATGGCGCTGAAGCG
	rev	28SJJ-b	CCGACGAACTCTCTTGCGGAGG

CO1: annealing temperatures at 70°C and 55°C, with a decrease of 2°C per cycle in the first cycle set. Double stranded sequencing was carried out either by a sequencing facility (Macrogen, Seoul, South Korea; using ABI 3730XL sequencers) or on a CEQ 8000 sequencer (Beckman Coulter, Fullerton, CA, USA).

Phylogenetic analyses

DNA sequence alignment was performed manually (CO1) or using the MUSCLE ver. 3.6 programme (Edgar 2004a, 2004b), run with default parameters for 400 000 iterations. Subsequently, we improved the output alignments by making use of MUSCLE's 'refine' option. ModelTest ver. 3.7 (Posada and Crandall 1998; Posada and Buckley 2004), implementing the Bayesian information criterion (BIC; Schwarz 1978), identified the transversion (TVM)+proportion of invariable sites (I)+gamma distribution (Γ) model of nucleotide substitution (a submodel of general time reversible (GTR; Lanave *et al.* 1984)) as the best-fit model for CO1, the Hasegawa–Kishino–Yano (HKY)+I+ Γ model (Hasegawa *et al.* 1985) for 16S and the Kimura two-parameter (K2P)+ Γ model (Kimura 1980) for 28S (sample size=number of alignment taxa multiplied by characters; disregarding excluded positions, see below). We concatenated the sequence data from the three analysed genes and added the morphological data. Thereby, we obtained an alignment (in the following referred to as 'combined alignment') with a total length of 1926 characters. Of these, we excluded 391 ambiguously aligned positions from phylogenetic analysis to guarantee positional homology over the whole alignment (Wägele 2005; for an alternative procedure see Simmons and Ochoterena 2000). For reproducibility, excluded positions are specified in the same file as the combined alignment (cf. Accessory Publication from *Invertebrate Systematics* website). The excluded parts of the matrix correspond to insertion/deletion (indel) events of the ribosomal genes, in their majority localised in the highly variable, partially tandem-repeated 28S-D7a expansion segment. Indels can be very useful in taxonomy (Astrin *et al.* 2006); however, in phylogenetics, they potentially disturb the analysis if directly included (Morrison and Ellis 1997; Wägele 2005; but see Giribet and Wheeler 1999). As a 'precautionary principle' (Astrin *et al.* 2007) that does not disturb the analysis, we favour excluding part of the information in the dataset rather than risking biased reconstructions – especially when considering that the phylogenetic signal for the more terminal sections of the tree should in theory already be strong thanks to the inclusion of mitochondrial genes (with their elevated mutation and fixation rates).

We present Bayesian Metropolis-coupled Markov chain Monte Carlo analyses for two datasets: the mitochondrial genes (treated together for their provenance from a single linkage unit) and the combined alignment. The low information content and consequently poor resolution of the 28S reconstruction (owing in part to its overall relatively high conservation, see below) did not justify its separate representation, so that it is only considered in combination with morphology and mitochondrial sequences. We used the MrBayes ver. 3.1.2 software (Huelsenbeck and Ronquist 2001;

Ronquist and Huelsenbeck 2003) to infer Bayesian reconstructions. For each gene partition, we implemented the model of sequence evolution as diagnosed by the BIC (i.e. degrees of freedom in nucleotide substitution, rate distribution across sites and assuming or rejecting a fraction of invariable sites), but not the exact parameters, which were equated by MrBayes through the use of 'flat' prior distributions (on objective Bayesian analysis, see Berger 2006). Parameters were unlinked among partitions and also between the 3rd versus 1st plus 2nd codon positions in CO1 (cf. Accessory Publication from the *Invertebrate Systematics* website: MrBayes block within Nexus file). For comparison, additional shorter runs were conducted with exact BIC parameters (these are also specified in the Nexus file, they deliver a highly similar topology and are not considered further). We ran two independent replicates for 10 million generations per analysis (each with one cold chain and three chains of different temperature). Every 1000th tree was sampled (20 000 trees retained). Negative log-likelihood score stabilisation was determined in a separate visualisation. Accordingly, we retained 19 886 trees for combined and 19 908 trees for mitochondrial analysis. These were used for building 50%-majority rule consensus phylograms (with posterior probabilities). Corroborating the burn-in values of the main analyses and excluding the possibility of an attraction to local optima (Huelsenbeck and Bollback 2001, Huelsenbeck *et al.* 2002), four additional replicates for each dataset (not considered further) were run with a million generations each and with different starting seeds.

In addition to the Bayesian phylograms, we constructed a maximum parsimony (MP) tree for the combined alignment using PAUP* ver. 4.0b10 (Swofford 2002; this program was also used to compute the phylogenetic information content and to assess homogeneity of partitions using 100 replicates per run). Because of the expected saturation at CO1 3rd codon positions (cf. e.g. Gleeson *et al.* 1998; Astrin *et al.* 2007; Ros and Breeuwer 2007, but see Björklund 1999), these sites were excluded from MP analysis to reduce the noise in the reconstruction (which indeed seemed to increase in a tentative cladogram including 3rd codon positions). We furthermore excluded the same characters as in the Bayesian analysis. The remaining gaps were treated as fifth character states. The MP heuristic search was conducted with tree-bisection-reconnection (TBR) branch swapping for 5000 replicates (random stepwise addition of taxa) and used equal weights. The resulting 143 equally parsimonious trees (length: 2906 steps, consistency index (CI): 0.32, retention index (RI): 0.61) were used to construct a strict consensus. Nodal support is given in the form of bootstrap values (Felsenstein 1985), heuristically determined through 1000 pseudoreplicate matrices.

In the reconstruction based on morphological characters alone, a maximum parsimony heuristic search (using equal weights) was conducted in PAUP*. Thereby, we obtained 27 equally parsimonious cladograms (length: 76 steps, CI: 0.47, RI: 0.71) that were used to compute a strict consensus. To show character state distributions on the tree, the Winclada ver. 1.00.08 programme (Nixon 2002) was used (in combination with Hennig86 ver. 1.5, Farris 1988, which delivered the same strict consensus topology as PAUP*).

Results and Discussion

Homogeneity of partitions and information content

The incongruence length difference test (ILD; Farris *et al.* 1994) showed no conflict between morphological and molecular genetic data included in the analysis. Mitochondrial and nuclear sequence data proved to be equally free of conflict (for the potential shortcomings of the ILD test see e.g. Yoder *et al.* 2001; Darlu and Lecointre 2002).

The proportion of variable characters in our CO1 partition (including 3rd positions) is 54.3%; 49.6% are parsimony informative. Excluding the positions of dubious alignment, variable characters in 16S constitute 45.5% of the alignment and informative ones constitute 39.5%. Again, not considering excluded positions, 28S variable characters make up 32.8% and informative characters only 9.25%.

Morphology versus molecules

Our morphological matrix contains fewer taxa than the molecular matrix (23 instead of 83) and focuses on type species as well as those congeners that warrant comparability with the molecular data. We also analysed cases of dubious genus assignment. Thus, the morphological reconstruction focuses on genus-level questions and is not distended by uninformative polytomies below genus level. These would otherwise be bound to occur owing to the high morphological stasis of the group and the extreme difficulty in obtaining more than the sampled 36 morphological characters (splitting up characters would have multiplied the existing evidence; cf. Wägele 2005).

Morphology (Fig. 4) and DNA sequence analysis (as assessed through the inference based on mitochondrial partitions alone, Fig. 3) converged in outlining the same genus-level taxonomic problems in the dataset (see below, cf. Fig. 1). Beyond this aspect, i.e. above genus-level, almost no similarities were found between the reconstructions inferred from the respective types of evidence. This is not surprising when we consider the morphological homoplasy and crypsis of the group. These place constraints on the study of cryptorhynchine systematics in so far as it is based on morphology alone. For example, the majority of morphological features (e.g. absence of the endophallus) presented by the genera *Echinodera* Wollaston, 1863 and *Ruteria* Roudier, 1954 have often been considered as plesiomorphic, a hypothesis also supported by the morphological cladogram in this study (Fig. 4). However, molecular data suggests these are in fact derived (secondary reduction).

Current genera of western Palaearctic Cryptorhynchinae

The phylogenetic reconstructions (Figs 1–4) consistently recovered many of the sampled cryptorhynchine genera as monophyletic groups. This holds true for the genera *Acallocrates* Reitter, 1913, *Calacalles* Peyerimhoff, 1926, *Dendroacalles* Stüben, 2005, *Dichromacalles* Stüben, 1998, *Onyxacalles* Stüben, 1999 and *Torneuma* Wollaston, 1860 (the latter sampled with more than one species only in morphology). *Kyklioacalles* Stüben, 1999 and *Ruteria* show paraphyly. *Acalles* Schönherr, 1825 as well as *Echinodera* proved to be polyphyletic.

With the few taxonomic changes suggested below (three new genera and three transfers; all based on tree topology and on

morphological re-investigation of the respective species), *Acalles*, *Kyklioacalles* and, depending on the reconstruction, also *Ruteria* (paraphyletic for MP, Fig. 2) and *Echinodera* (paraphyletic for Bayesian analysis, Figs 1, 3) are monophyletic for the taxa studied. For these taxa, our findings thus suggest that the current classification of western Palaearctic Cryptorhynchinae is mostly coherent. The phylograms further represent the genera as always fully supported, distinct ‘units’ (in the eye of the observer) that are separated from each other by a considerable evolutionary distance (if considering *Echinodera/Ruteria* together).

The genera Echinodera and Ruteria

Echinodera major and *Echinodera minosi* were recovered with full support as nested within *Ruteria* (in MP, both species and *Ruteria* are basal to *Echinodera*).

Echinodera major has in the past been brought in connection with *Echinodera* s. str. (Caldara, 1973), in particular with *E. variegata* (Boheman, 1837) (*E. major* = *Acalles variegatus* ab. *grossus* Frieser, 1955 syn. (Stüben, 1998)). So far, only the lectotype from the Museo Civico di Storia Naturale, Milano was known. Ample new material from Dalmatia (Curculio Institute collection) now morphologically corroborates the necessity to transfer *E. major* to the genus *Ruteria*: the completely rounded, large eyes protruding the upper margin of the antennal groove (the small eyes of *Echinodera* do not protrude) and the form of the aedeagus, which is comparable with those of *Ruteria hypocrita* Boheman, 1837 and *Ruteria graeca* Caldara, 1973. Consequently, we transfer *Echinodera major* to *Ruteria*, resulting in the new combination *Ruteria major* (Solari A. & F., 1907).

In the original description of *E. minosi*, Bahr and Bayer (2005) failed to notice the large eyes protruding from the upper margin of the antennal groove and the elongated tip of the aedeagus. These morphological characters, along with the molecular evidence, suggest an inclusion in *Ruteria*. Therefore, we transfer *Echinodera minosi* to the genus *Ruteria*, resulting in the new combination *Ruteria minosi* (Bahr & Bayer, 2005).

Addendum: *Ruteria major* and *Ruteria minosi* on average both measure more than 4.0 mm in length and thereby match the other 14, comparably ‘large’ *Ruteria* species. The roughly 70 described *Echinodera* species are smaller, measuring only 2–3 mm.

In the Bayesian reconstructions, *Ruteria* consistently appears nested within *Echinodera* (with high support in mitochondrial analyses and medium support in combined analyses). However, the cladogram (Fig. 2) recovers no such grouping. Further molecular investigations are necessary (and are currently being arranged) to clarify the relationships between and within these taxa, testing the feasibility of a synonymisation and a potential subgenus *Echinodera* (*Ruteria*) (cf. Roudier 1954).

The genus Acalles

Since the work of Solari and Solari (1907) and for many following decades, morphologically problematic cryptorhynchine species were often assigned to the genus *Acalles*, as long as they showed some overall outward resemblance. This practice resulted in a polyphyletic genus within which morphological homoplasy abounded (Stüben and Behne 1998). Obviously, some effects

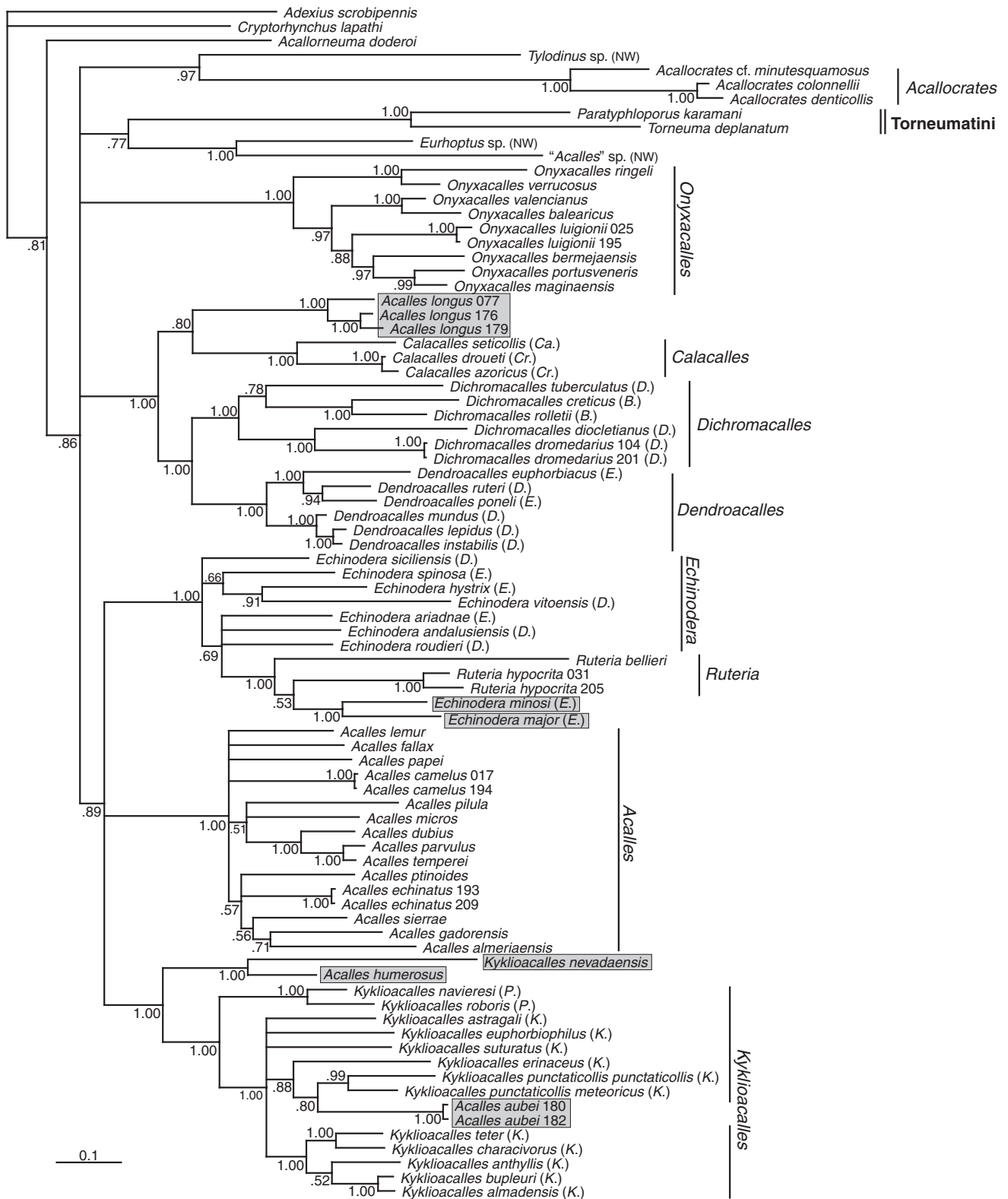


Fig. 1. Combined Bayesian 50% majority rule consensus for morphology, mitochondrial partitions and 28S. Posterior probability values are indicated at the respective nodes. Taxonomic changes appear in this tree under their old names, but are highlighted. Initials in parentheses behind taxon names indicate the corresponding subgenus (see text). As in the other trees, numerals behind taxon names stand for DNA voucher numbers (cf. Appendix 1; only given in cases of multiple individuals per species). NW = New World.

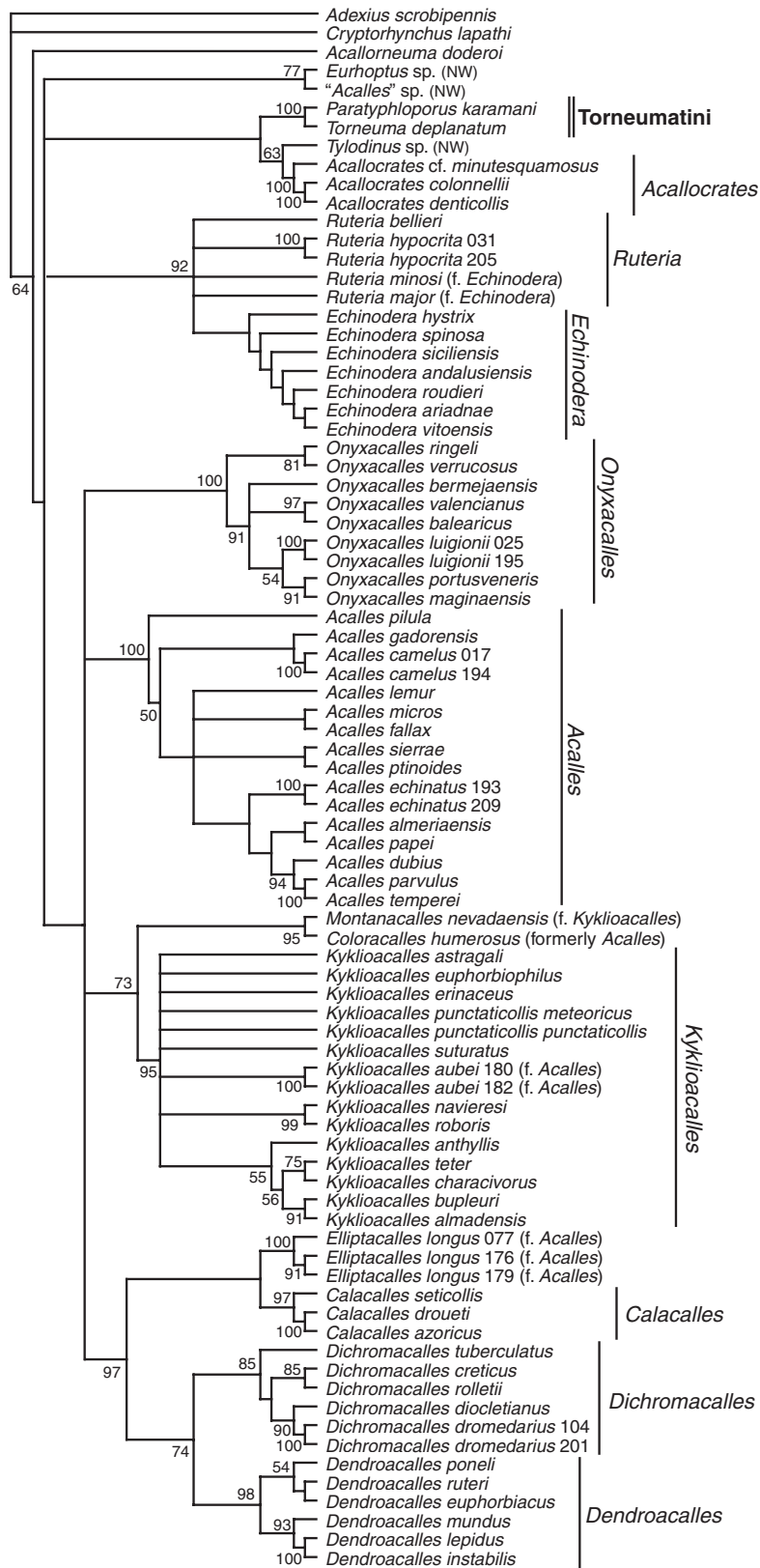


Fig. 2. Combined maximum parsimony strict consensus for morphology, mitochondrial partitions and 28S. Bootstrap values are indicated at the respective nodes. Taxonomic changes appear under their new name, followed by their former genus name in parentheses (f. = formerly).

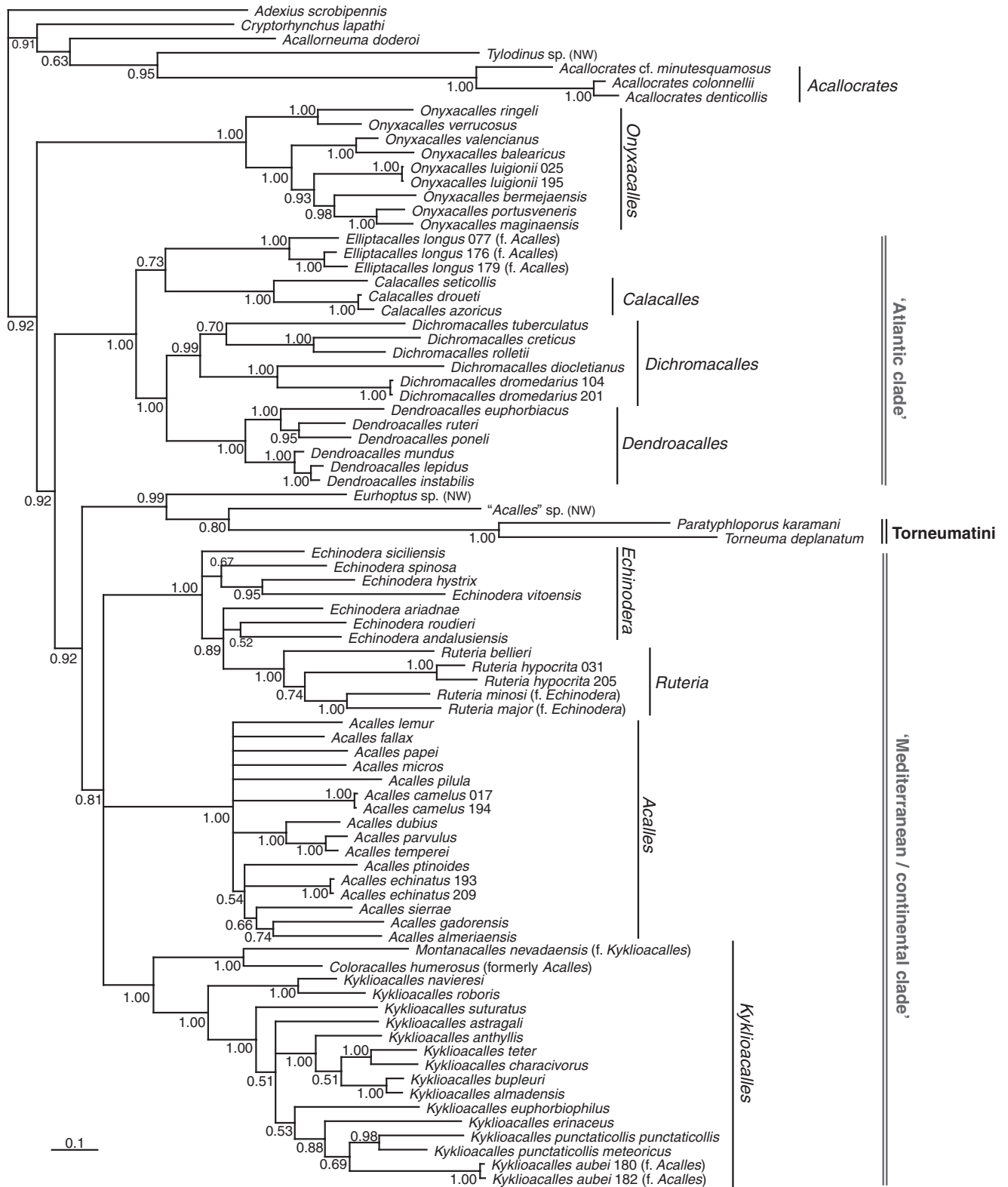


Fig. 3. Bayesian consensus for the mitochondrial CO1 and 16S genes with posterior probabilities. Unofficial higher level taxonomy is denoted by quotes and double bars.

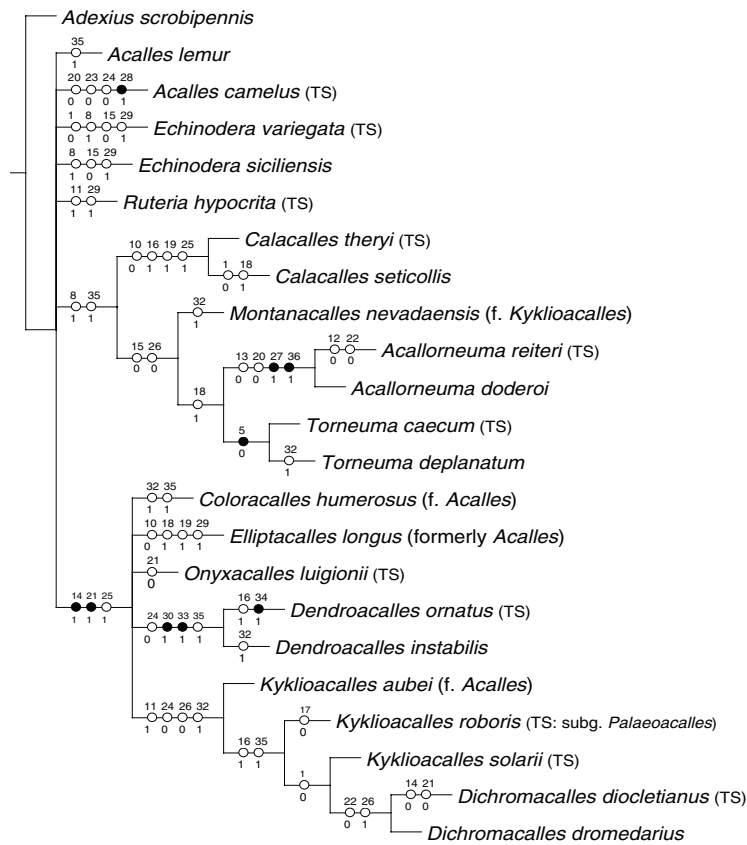


Fig. 4. Rooted maximum parsimony strict consensus for morphological data alone with character state distributions (cf. Appendix 3). TS = type species.

of this practice can still be detected (we remove three *Acalles* species from the genus, see below). Nevertheless, in our reconstructions, the type species *Acalles camelus* Fabricius, 1792 falls into a clearly confined clade of congeners. This proves that the genus *Acalles* can be reduced to a monophyletic ‘core group’.

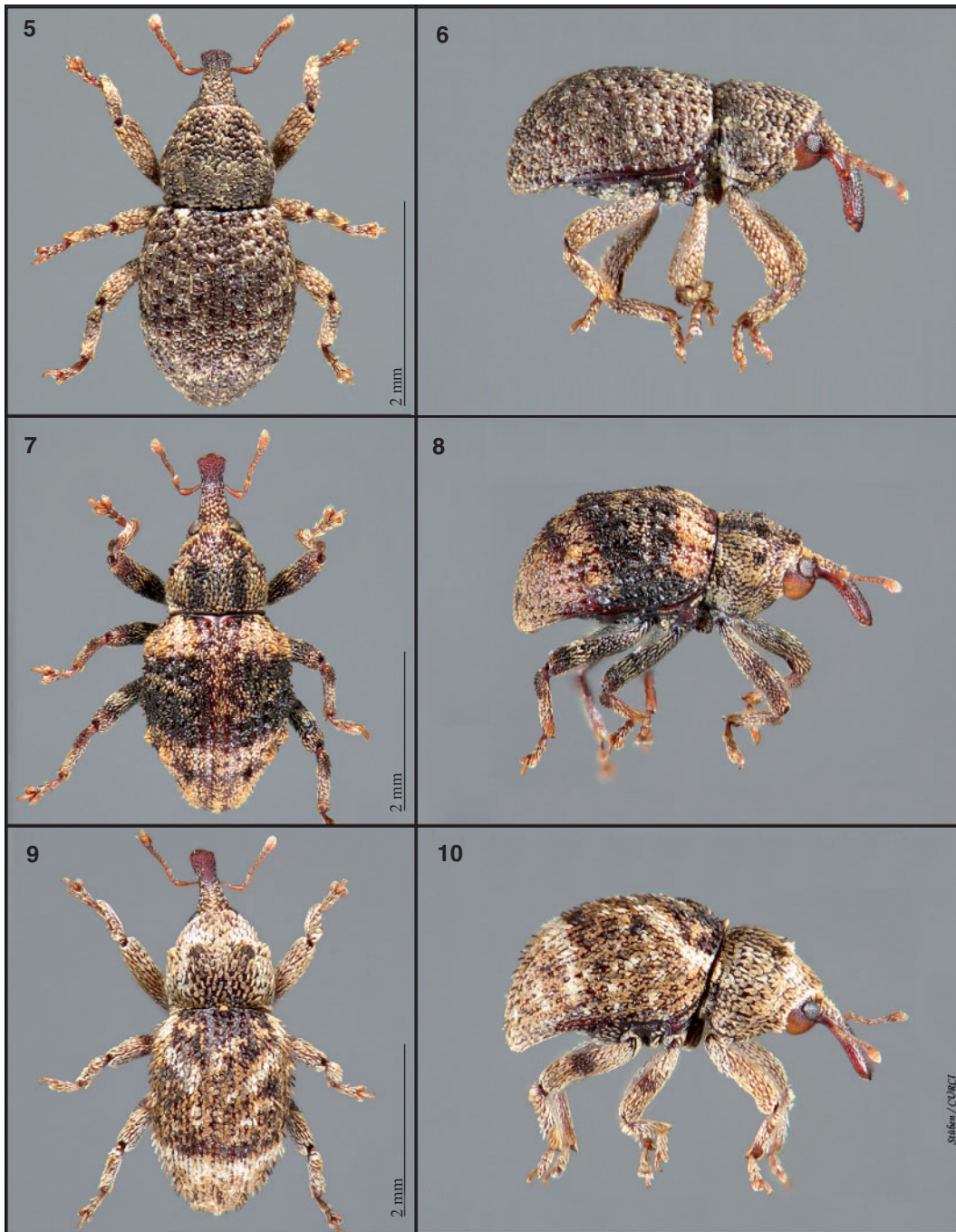
Although not all *Acalles* specimens in the present analysis come from the European continent (*A. pilula* Wollaston, 1864 is from the Canary Islands), a Mexican animal identified according to the literature (Papp 1979) as *Acalles* sp. clearly is not part of the *Acalles* ‘core group’ (see below; cf. Anderson 2008 on New World *Acalles*). This cautions us to test molecularly the hypotheses upon which assignment of new species to genera is to be based – at least in dubious cases within the studied group.

In our phylogenetic reconstructions, *Acalles aubei* falls into the genus *Kyklioacalles* with very high or total support. Morphologically, *A. aubei* has already been compared with *Kyklioacalles provincialis* (Hoffmann, 1960), a species to which *A. aubei* shows a considerable similarity regarding the habitus and the structure of the internal sack of the aedeagus (Stüben and Wolf 1998). In fact, even though the basal cycle-shaped structure of the endophallus typical for *Kyklioacalles* is only very weakly developed in *A. aubei* genitalia, this species is morphologically – and genetically – much closer to the *Kyklioacalles* species. We therefore transfer *Acalles aubei* to

this genus, resulting in the new combination *Kyklioacalles aubei* (Boheman, 1837).

Three new genera: *Coloracalles*, *Elliptacalles*, *Montanacalles*
Acalles longus Desbrochers, 1892 (cf. Figs 9, 10) forms a clade with *Calacalles*, *Dendroacalles* and *Dichromacalles* in our trees (different in the morphological cladogram, but here also separated from *Acalles*). It is shown as adelphotaxon to *Calacalles* (medium support in Bayesian, no support in MP analyses). We transfer *Acalles longus* to the new genus *Elliptacalles*, which is described in the following section, resulting in the new combination *Elliptacalles longus* (Desbrochers, 1892). Genetic distances between the Italian (cf. Fig. 1, #077) and two Spanish specimens in the phylograms as well as morphological observations (see below) suggest the possibility of *Elliptacalles longus* in fact consisting of more than one species.

Acalles humerosus Fairmaire, 1862 (Figs 7, 8) and *Kyklioacalles nevadaensis* Stüben, 2001 (Figs 5, 6) cluster together and appear as sister to *Kyklioacalles* with high support in the mitochondrial and combined reconstructions. If arguing based only on the molecular framework, one could think of simply transferring *Acalles humerosus* to *Kyklioacalles*, thereby avoiding the creation of yet more monotypic genera in Cryptorhynchinae (see above). However, morphological investigation forbids such a procedure (see next chapter and Figs 13–19). In the same way, it rules out the option to join



Figs 5–10. Habitus of the new genera described in this study (dorsal and lateral views). 5, 6, *Montanacalles nevadaensis* ♂, Sierra Nevada, Spain, holotype. 7, 8, *Coloracalles humerosus* ♂, Pyrénées-Orientales, France. 9, 10, *Elliptacalles longus* ♂, Sicily, Italy.

Acalles humerosus and *Kykliaacalles nevadaensis* in a separate, new genus (this morphological impossibility is also mirrored in the morphological cladogram, Fig. 4). Thus, we propose the transfer of *Acalles humerosus* to the new genus *Coloracalles*, and of *Kykliaacalles nevadaensis* into the new genus *Montanacalles* (both genera are described in the next chapter). This results in the new combinations *Coloracalles humerosus*

(Fairmaire, 1862) and *Montanacalles nevadaensis* (Stüben, 2001).

Subgenera of western Palaearctic Cryptorhynchinae

In Fig. 1, the initial letters of the corresponding subfamily are given. The subgeneric division was corroborated for *Kykliaacalles* s. str. Stüben, 1999 and *Kykliaacalles* subg.

Palaeocalles Stüben, 2003. Equally, the subgenera *Calacalles* s. str. Peyerimhoff, 1925 and *Calacalles* subg. *Crateracalles* Stüben, 2004 showed no conflict for the (three) species sampled.

However, questions were also brought up that need to be clarified in separate generic revisions. *Dichromacalles* s. str. Stüben, 1998 proved to be paraphyletic with regard to *Dichromacalles* subg. *Balcanacalles* Stüben & Behne, 1998. Reciprocal paraphyly became apparent in *Echinodera* s. str. Wollaston, 1863 and *Echinodera* subg. *Dieckmannia* Stüben, 1998. *Dendroacalles* s. str. Stüben, 2005 is also affected by paraphyly with regard to *Dendroacalles* subg. *Euphorbioacalles* Stüben, 2005 in the reconstruction (the genus *Dendroacalles* will be dealt with in a combined molecular and morphological revision on all Macaronesian Cryptorhynchinae).

Relationships among genera

The resolution of the deeper sections of the phylogenetic trees was mixed. Whereas *Acallorneuma* and *Cryptorhynchus* Illiger, 1807 always appear as sister to the remainder of the analysed Cryptorhynchinae, the mitochondrial Bayesian reconstruction also groups *Acallobrates* and *Tylodinus* Champion, 1905 together with these. Mitochondrial data alone produce a highly resolved tree: *Onyxacalles* basal to the 'Atlantic clade' (see below), which is itself sister to the remaining taxa (cf. Fig. 3). Combined Bayesian analysis (Fig. 1) places *Onyxacalles* and the Atlantic clade in a polytomy also including a 'Mediterranean/continental clade' (comprising *Acalles*, *Kyklioacalles* and *Echinodera/Ruteria*, a group recovered also in mitochondrial reconstruction, but not in MP). The combined cladogram (cf. Fig. 2) is even less resolved and, with the exception of the Atlantic clade, recovers alternative higher-level groupings. These heterogeneous findings suggest the cautious use of the information delivered by the deeper 'mitochondrial' nodes (even if well supported, cf. Wägele and Mayer 2007). Nevertheless, regarding the division into cryptorhynchine tribes according to Alonso-Zarazaga and Lyal (1999), we observe that a revision seems to be necessary: Torneumatini Bedel, 1884 (monophyletic for the two genera sampled) always appears credibly nested within Cryptorhynchini Schönherr, 1825.

Contradicting a common belief, our reconstructions prove that the western Palaearctic Cryptorhynchinae does not seem to constitute a natural grouping, as the Mexican samples were not recovered as outgroups: *Eurhoptus* LeConte, 1876 and the '*Acalles*' sp. showed an affinity with Torneumatini and *Tylodinus* is associated with *Acallobrates*, although the phenomenon of long-branch attraction (cf. Bergsten 2005) between the genetically highly divergent samples cannot be excluded. This fact should be considered in future phylogenetic efforts.

As an informal higher-level taxonomic approach, we denominate 'Atlantic clade' a monophylum constituted by the genera *Calacalles*, *Dichromacalles*, *Dendroacalles* and *Elliptacalles*. Such a group is consistently and credibly recovered in all reconstructions that are based on molecular data. Furthermore, *Dendroacalles* is connected with *Dichromacalles* and *Calacalles* with *Elliptacalles*. The

inclusion of *Elliptacalles* in the Atlantic clade is not supported by any known morphological evidence (and is not supported by 28S alone).

Taxonomy: description of three new genera

Family **CURCULIONIDAE** Latreille

Subfamily **CRYPTORHYNCHINAE** Schönherr

Genus ***Coloracalles***, gen. nov.

(Figs 7, 8, 17–19)

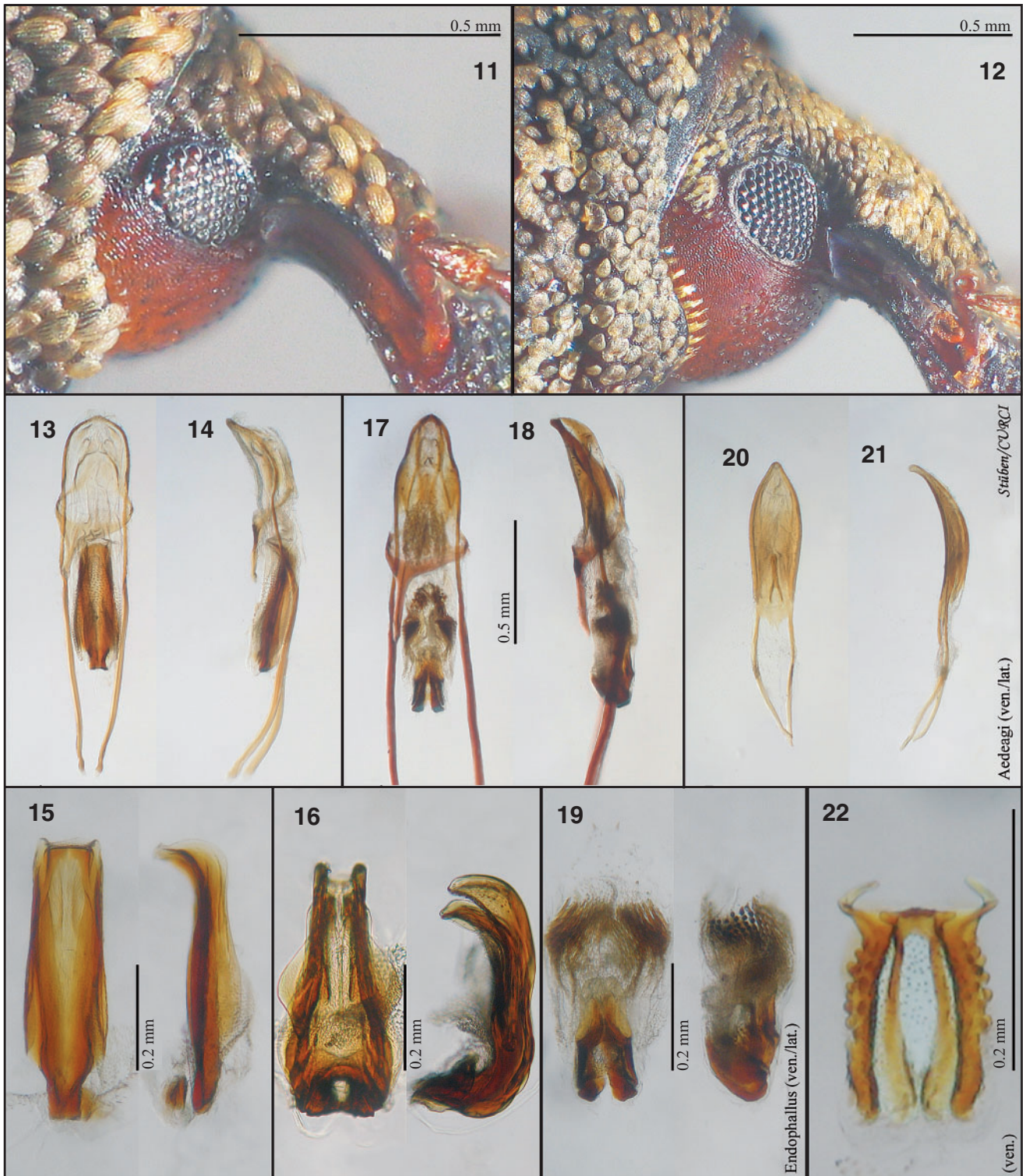
Type species by monotypy: *Acalles humerosus* Fairmaire, 1862: 557.

Acalles Fairmaire, 1862: 557. – Brisout, 1864: 456–457; Meyer, 1896: 30–31; Solari A. & F., 1907: 527; Porta, 1932: 189; Hustache, 1936: 106; Hoffmann, 1958: 1385; Bahr & Stüben, 2002: 44–45; Stüben, Behne & Bahr, 2003: 45.

Material examined

Holotype. ♂, France: 'Pyrénées-Orientales, Le Vernet, leg. M. v. Bruck', coll. Muséum National d'Histoire naturelle Paris (MHNP).

Other material examined. **France: Aquitaine:** 2 ex., Cambes, Dep. Gironde (33), (44°44'03"N, 0°27'48"W); **France: Languedoc-Roussillon:** 5 ex., 3 km W Pic Neulos, Chaîne des Albères, Dep. Pyrénées-Orientales (66), 800 m, (42°28'00"N, 2°53'53"E); 14 ex., 4 km W Pic Neulos, Chaîne des Albères, Dep. Pyrénées-Orientales (66), 750 m, (42°28'28"N, 2°53'27"E); 7 ex., 6 km W Pic Neulos, Chaîne des Albères, Dep. Pyrénées-Orientales (66), 450 m, (42°28'03"N, 2°52'31"E), coll. Bahr; 18 ex., 6 km W Pic Neulos, Chaîne des Albères, Dep. Pyrénées-Orientales (66), 450 m, (42°28'03"N, 2°52'31"E); 4 ex., Axat, Dep. Aude (11), 400 m, (42°48'25"N, 2°13'50"E); 1 ex., Cazalrenoux, Ft de Pique Mourre, Dep. Aude (11), (43°12'05"N, 1°56'52"E); 1 ex., Col de la Baraque NE Lamelouze, Dep. Gard (30), 650 m, (44°12'38"N, 3°58'05"E); 33 ex., Forêt de Sorède, Dep. Pyrénées-Orientales (66), 250 m, (42°31'57"N, 2°57'06"E), coll. Bahr; 82 ex., Forêt de Sorède, Dep. Pyrénées-Orientales (66), 250 m, (42°31'57"N, 2°57'06"E); 32 ex., Forêt de Sorède (Sorete), Vallee Heureuse, Dep. Pyrénées-Orientales (66), 250 m, 42°30'33"N, 2°57'47"E; 1 ex., Le Vernet-Saint-Esprit, Dep. Pyrénées-Orientales (66), (42°42'42"N 2°52'30"E); 1 ex., Mosset 10 km NW Prades, Dep. Pyrénées-Orientales (66), 800 m, (42°40'05"N, 2°20'53"E); 8 ex., Roquefort-de-Sault, Pyrénées-Orientales, Dep. Aude (11), 800 m, (42°45'02"N, 2°11'52"E); 5 ex., Vernet-les-Bains, Dep. Pyrénées-Orientales (66), 600 m, (42°33'04"N, 2°22'42"E); **France: Provence-Alpes-Côte d'Azur:** 1 ex., Forêt de Vensaque SE Carpentras, Dep. Vaucluse (84), 300 m, (43°57'57"N, 5°10'28"E); 2 ex., Georges de la Nesque 5 km E Villes-sur-Auzon, Dep. Vaucluse (84), 500 m, (44°03'30"N, 5°17'33"E); 1 ex., Georges de la Nesque 5 km E Villes-sur-Auzon, Dep. Vaucluse (84), 400 m, (44°03'30"N, 5°17'33"E); **France: Rhône-Alpes:** 2 ex., Ruoms, Dep. Ardèche (07), (44°27'00"N, 4°20'47"E); **Italy: Campania:** 3 ex., Massa Lubrense NW Nerano, Prov. di Napoli (NA), 100 m, (40°36'27"N, 14°20'28"E); 1 ex., Monti Picentini 6 km E Montecorvino Rovella, Prov. Salerno (SA), 500 m, (40°42'23"N, 15°04'32"E); 2 ex., Mte. Faito SW Gragnano, Prov. di Napoli (NA), 300 m, (40°40'25"N, 14°29'04"E), coll. Wolf; **Spain: Catalonia:** 3 ex., 3 km W Vallirana, Prov. Barcelona, 360 m, (41°23'13"N, 1°53'33"E), coll. Bahr; 6 ex., 3 km W Vallirana, Prov. Barcelona, 360 m, (41°23'13"N, 1°53'33"E); 6 ex., 7 km S Vidreres, Prov. Girona, (41°42'51"N, 2°50'31"E), coll. DEI; 2 ex., El Brull N La Garriga, NW Montseny, Prov. Barcelona, 850 m, (41°49'02"N, 2°18'55"E), coll. Bahr; 3 ex., El Brull N La Garriga, NW Montseny, Prov. Barcelona, 850 m, (41°49'02"N, 2°18'55"E); 3 ex., Olzinelles SE Sant Celoni, Prov. Barcelona, 200 m, (41°40'01"N, 2°30'55"E); 2 ex., Parc nat. de Sant Llorenç del Munt SE Manresa, Canal del Sal, Prov. Barcelona, 800 m, (41°40'49"N, 1°58'49"E); 1 ex., Sant Llorenç



Figs 11–22. 11, 12, Eyes/rostra in lateral view. 11, *Montanacalles nevadaensis* ♂, Sierra Nevada, Spain; 12, *Kykliocalles anthyllis* ♂, Sierra Nevada, Spain. 13–22, Male genitalia (after dissection) of the new genera and of two reference species. Upper row: entire aedeagi, lower row: endophalli. 13, 14, *Montanacalles nevadaensis*; 15, *Montanacalles nevadaensis*; 16, *Kykliocalles editorum*; 17, 18, *Coloracalles humerosus*; 19, *Coloracalles humerosus*; 20, 21, *Ellipticalles longus*; 22, *Dichromacalles albopictus*.

dos Munts NE Rupit, Prov. Barcelona, 800 m, (42°03'06"N, 2°28'35"E); 16 ex., Sant Boi de Llobregat, Prov. Barcelona, 130 m, 41°20'39"N, 2°00'45"E; 2 ex., Santa Pellaia N, Sierra de las Gavarres, Prov. Girona, 250 m, (41°55'03"N, 2°54'52"E); 3 ex., Santa Pellaia N, Sierra de las Gavarres, Prov. Girona, 250 m, (41°55'03"N, 2°54'52"E), coll. Bahr; 4 ex., Sierra de Monserrat NW Barcelona, 1100 m, (41°38'24"N, 1°51'13"E); 2 ex., Sierra de Montseny, Prov. Barcelona, (41°46'07"N, 2°23'56"E); **Tunisia:** 2 ex., Ghardimaou-Foret de Feidja, di. Statir, 880 m; 1 ex., Jendouba env. Mts. De Tébourouk, (36°30'28"N, 8°41'01"E), coll. Bahr. All material in collection Stüben if not otherwise mentioned.

Diagnosis

Acalles humerosus Fairmaire, 1862, the type species of the new genus *Coloracalles*, is distinguished from all other members of the Cryptorhynchinae by characters of the integument (cf. Bahr and Stüben 2002), most importantly the spots of pale brown scales next to the base and on the slope of the elytra (Figs 7, 8). The form of the median lobe and the structure of the internal sack of the aedeagus are unique among the Cryptorhynchinae of the western Palaearctic region (cf. generic key of Stüben, in press).

Description

Size. 2.9–3.5 mm (without rostrum)

Elytra. Box-shaped, 1.14–1.32 × as long as wide; outline in the central part parallel; narrowing in straight way in front of the base and equally in front of the apex. Integument contrastingly coloured: primary colour dark brown with extensive spots of pale-brown to reddish-brown scales next to base and on elytral slope. Instead of scutellum presence of a pale-brown, shiny, triangular and bald spot at base of scutellar stripe. On intervals 2, 4 and 6 with short, dense tufts of bristles next to base and on elytral slope. Stripes on disc of elytra more narrow than intervals, on flanks wider and with much coarser punctures. Intervals domed. Reinforcing effect through presence of bristle tufts on intervals.

Pronotum. 1.25–1.30 × as wide as long; much narrower than elytra; spherically rounded laterally and thereby clearly separated from base of elytra. Integument consists of short-oval scales, round scales only on disc of pronotum. Scales not overlapping each other, so that the dark undercoat and its fine punctures are clearly visible. Scales on the flanks coloured full of contrast, predominantly pale brown or reddish-brown, dark brown scales dominating only at the front margin as well as along the middle line. Disc of pronotum with short, black tufts of bristles and without depression or groove.

Legs. Long; front femora reaching further than the front margin of the eyes; hind femora reaching the middle of the last sternite. Legs covered with flat, elongated, dark or light-brown bristles.

Ventral view. First and second sternite coarsely punctured, with a short bristle in each puncture cavity. In the middle of the first sternite a big, deep cavity (♂). The fifth sternite punctured and bristled finely.

Head. Rostrum of male curved and scaled from the base to the insertions of the antennae. Rostrum of female straighter and only scaled at the base. In both sexes, rostrum narrows towards the middle and (apart from the slightly domed middle line) punctured sparsely and fine. Big, laterally inserted eyes clearly protrude the upper margin of the antennal groove.

Male genitalia. Median lobe of aedeagus becoming slender like a bottleneck next to the apex (Figs 17, 18); internal sack with a complex, 'three-dimensional' structure (Fig. 19).

Remarks

The next relative of *Coloracalles humerosus* in our analysis, the single species of the new genus *Montanacalles*, *M. nevadaensis*, is characterised – in contrast to *C. humerosus* – by small, oval eyes not protruding the upper margin of the antennal groove (Figs 6, 8, 11). In addition, its elytra lack bristle tufts (Figs 5, 8) and its integument consists of dense scales that cover the shiny undercoat almost completely.

Distribution

South-western Europe, Tunisia. The species occurs in dense woods of holm oak (*Quercus ilex*).

Etymology

The name *Coloracalles* refers to the clearly defined, contrasting colours of the elytral integument of the type species *Acalles humerosus*.

Genus *Elliptacalles*, gen. nov.

(Figs 9, 10, 20, 21)

Type species by monotypy: *Acalles longus* Desbrochers, 1892: 99.

Acalles Desbrochers, 1892: 99. – Meyer, 1896: 36; Solari A. & F., 1907: 528; Porta, 1932: 190; Hustache, 1936: 109; Stüben, Behne & Bahr, 2003: 51–52 (designation of lectotype).

Material examined

Lectotype. 1♂, Algeria: 'Edough' – 'longus type Db.' – 'Es Musaeo Desbrochers 1914' – 'LECTOTYPUS: *Acalles longus* Desb., des. Stüben & Bahr 1999'. coll. Muséum National d'Histoire naturelle Paris (MHNP): coll. Desbrochers.

Paralectotype. 1♀, data as for lectotype – 'PARALECTOTYPUS: *Acalles longus* Desb., des. Stüben & Bahr 1999'. coll. Muséum National d'Histoire naturelle Paris (MHNP): coll. Desbrochers.

Other material examined. **Italy: Calabria:** 5 ex., 1.5 km NE Bagnara Calabria, Prov. Reggio di Calabria (35), 200 m, (38°17'15"N, 15°49'06"E); 1 ex., Gambarie, Aspromonte N.P., Prov. di Reggio Calabria, (38°10'18"N, 15°50'22"E); 3 ex., Sant' Eufemia d'Aspromonte, Prov. di Reggio di Calabria, (38°15'59"N, 15°50'58"E); **Italy: Sicilia:** 4 ex., 4 km SW Castelbuono, P.R. Madonie, Piano Sempria, Prov. di Palermo (4), 1420 m, (37°54'01"N, 14°04'09"E); 1 ex., 6 km SW Godrano, Bosco Ficuzza, Mte. Rocca Busambra, Prov. di Palermo (14), 1200 m, (37°51'38"N, 13°23'24"E); 1 ex., R.N. Carcaci, Mte. Carcaci 6, 5 km E Prizzi, Prov. di Palermo (16), 1100 m, (37°43'10"N, 13°30'20"E), coll. Behne; 6 ex., 6 km SW Carini, Montagna Longa, 647 m, (38°07'10"N 13°08'31"E); **Morocco:** 1 ex., High Atlas, 56 km SW Asni, Tizi-n-Test, 2000 m, (30°52'25"N, 8°21'26"W), coll. Germann; **Spain: Andalucía:** 2 ex., Málaga: Sierra Bermeja, Los Reales N Estepona, 1400 m, (36°29'11"N, 5°12'24"W); 7 ex., San Roque, Sierra de Luna, Prov. Cádiz, 600 m, (36°13'09"N, 5°24'08"W); 1 ex., Sierra Bermeja, 5 km S Jubrique, Prov. Málaga, 800 m, (36°33'11"N, 5°11'36"W); 2 ex., Sierra de Luna SW Algeciras, Prov. Cádiz, 500 m, (36°07'00"N, 5°32'56"W); 1 ex., 26 km E Jaén, Sierra Mágina, 1663 m, (37°44'06"N, 3°30'09"W); 1 ex., Prov. Cádiz, 2.5 km N Ubrique, Sierra de Ubrique, 646 m, (36°41'50"N, 5°26'20"W); 1 ex., Prov. Málaga, 16 km N Estepona, Sierra Bermeja, near Jubrique, 557 m, (36°33'49"N, 5°12'27"W). All material in collection Stüben if not otherwise mentioned.

Diagnosis

The three-coloured integument is rich in contrast (Figs 9, 10). It is the most noticeable character of the new genus' type species *Acalles longus* Desbrochers, 1892. Unlike the *Dichromacalles* species from the Mediterranean (also contrastingly coloured; Stüben and Behne 1998), *Elliptacalles longus* has a much longer rostrum, elongated, inversely egg-shaped elytra, the pronotum is longer than broad and finally, it has a simple fork-like structure of the internal sack (more complex and 'three-dimensional' in *Dichromacalles*; cf. Fig. 22). This pattern of characters is unique among the Cryptorhynchinae species of the western Palaearctic.

Description

Size. 2.4–4.3 mm (without rostrum)

Elytra. Elliptic, inversely egg-shaped, 1.43–1.53× as long as wide, widest spot next to the base of elytra, acute-ovaly rounded towards apex. Integument contrastingly coloured: predominantly dark brown, with two white fasciae, one on disc of elytra and one on elytral slope. These fasciae are interrupted by spots of yellow-brown scales. Scutellum acutely rising. Intervals 2, 4 and 6 with clearly denser and longer bristles forming a line. Scales scattered and not covering the dark brown, shiny undercoat. Stripes on disc of elytra with elongated punctures, as wide as intervals, on flanks clearly wider and with coarser punctures.

Pronotum. Slightly longer than wide; narrower than elytra; rounded long-oval, becoming narrower towards base and thereby clearly separated from elytra. Integument consisting of round scales and long-oval bristles rising from undercoat, the latter forming small tufts of bristles on disc of pronotum. The dark brown, shiny, finely punctured undercoat clearly visible next to base. Puncture cavities separated by slender, shiny ridges. Crescent-shaped, white fascia of scales on disc of elytra continues on flanks, which are contrastingly coloured. Disc of pronotum 'spherically' rounded, without depression or groove.

Legs. Front femora reaching the centre of the eyes, hind femora reaching the last sternite. Legs sparsely covered with flat, long and pale bristles.

Ventral view. First and second sternite punctured coarsely, with a long light bristle in each puncture cavity. Sternites 3–5 punctured finely. First sternite slightly longer than the three following sternites together.

Head. Rostrum slender and long, at least 4× (♂) or 5× (♀) as long as wide, punctured sparsely and finely, reddish-brown and shiny; clearly narrowed at the insertions of the antennae.

Male genitalia. Median lobe of aedeagus conspicuously long, acutely rounded; with simple fork-like structure of the internal sack (Figs 20, 21).

Remarks

Morphological studies suggest that *Elliptacalles longus* (type locality: Algeria, Mt Edough, Bône) might turn out to be a complex of species. One of the authors (P.E.S.) collected large specimens in Sicily that are different from specimens from Calabria (Aspromonte), southern Spain and Morocco (High Atlas) regarding the elytral scaling, the outline of the aedeagus and the fork-like structure of the internal sack. Future targeted

molecular studies might result in the descriptions of new *Elliptacalles* species.

Distribution

Southern Spain, southern Italy, North Africa.

Etymology

The name *Elliptacalles* refers to the unique elliptical outline of the elytra in the type species *Acalles longus*.

Genus *Montanacalles*, gen. nov.

(Figs 5, 6, 11, 13–15)

Type species by monotypy: *Kyklioacalles nevadaensis* Stüben, 2001: 156–158.

Kyklioacalles Stüben, 2001: 156–158; Stüben, Behne & Bahr, 2001: 69; Stüben, 2002: 221; Stüben, 2003: 141–142; Stüben, 2006: 219.

Material examined

Holotype. 1♂, 'Spain: Almería, Sierra Nevada, Süd-Seite, 3 km N Bayárcal, 1500 m, Quercus ilex-Wald, N37°02'49"/W02°59'52"', 17.4.2001, leg. Stüben (33)', coll. CURCULIO-Institut (Mönchengladbach).

Paratypes. 2♀, data as for holotype, 1♀ coll. Stüben, 1♀ coll. CURCULIO-Institut (Mönchengladbach).

Other material examined. **Spain: Andalucía:** 5 ex., 11 km NW Láujar, Sierra Nevada, near Bayárcal, 1469 m, (37°02'42"N, 2°59'55"W); 2 ex., 14 km NW Láujar, Sierra Nevada, 2283 m, (37°05'14"N, 2°59'47"W); 1 ex., 11 km NW Láujar de Andarax, Sierra Nevada, near Bayárcal, 1291 m, (37°02'27"N, 3°00'12"W). All material in collection Stüben.

Diagnosis

Kyklioacalles nevadaensis Stüben, 2001, the type species of the new monotypic genus *Montanacalles*, is distinguished from the genus *Kyklioacalles* (to which it had been assigned preliminarily) by the pattern of bristles on the elytral intervals (see Stüben 1999a): the very long bristles form a line and lie flat on the densely scaled undercoat (Figs 5, 6). There is no species of the genus *Kyklioacalles* with both densely covering scales and long bristles lying flat on the undercoat. Further differences are the small, oval eyes, which do not protrude the upper margin of the antennal groove (Figs 11, 12) and the absence of the basal, cycle-shaped structure of the endophallus, a character typical for the genus *Kyklioacalles*.

Description

Size. 3.0–3.5 mm (without rostrum)

Elytra. Cylindrical; 1.16–1.25× as long as wide; widest spot in anterior half of elytra; narrowing only slightly towards base and regularly rounded towards apex. Integument consists of tiny round, dark-brown scales that completely cover the undercoat except for the slender stripes of punctures. Beige bristles, about twice as long as wide, are inserted at the base of each puncture cavity. More noticeable (and distinguishing the species clearly from the genus *Kyklioacalles*) are the bristles forming a line on the elytral intervals: long, slender, beige, 3–4× as long as wide, lying flat on the undercoat and with the same distance between two bristles as their individual length. Elytra lack tufts, accumulations of bristles or knobs. Monotonously dark-brown undercoat interrupted by only a few blurred spots of pale scales, but regularly carrying two beige patches on each elytron at the

base of the third and the sixth interval. The light patch on the third interval is particularly clearly defined.

Pronotum. 1.12–1.15 × as wide as long, broadest point at the end of the basal third. Scales dark brown and slightly bigger than scales of elytra. Only the flanks ‘sprinkled’ by a few lighter scales. Disc of pronotum flattened in same way as disc of elytra. Without depression or groove.

Legs. Short; front femora reaching front margin of the eyes, hind femora not reaching apex of elytra. Legs sparsely covered with pale, oval bristles. The latter predominantly twice as long as wide and sticking out only slightly from undercoat.

Ventral view. Scales of first and second sternite beige and nearly round, but not covering the reddish-brown undercoat completely. Sternites 3–5 with clearly smaller and slightly darker scales; second sternite sloping down to the third; first sternite with slight depression in the middle.

Head. Small, oval eyes not protruding upper margins of antennal grooves. Rostrum in male dark brown, punctured strongly and dense; the basal half covered with big scales; hook-shaped in lateral view. Rostrum in female narrower and ~20% longer than rostrum of male; in lateral view regularly arch-shaped; scale cover of basal half less dense. Second antennomere elongated, but only 0.75 × as long as first antennomere; antennomeres 3–7 approximately globular, resembling a string of beads.

Male genitalia. Internal sack of aedeagus conspicuously big and complex, consisting of an elongated structure with parallel outline (Fig. 15). ‘Collar-shaped’ structure in the upper part (typical for the genus *Kykliaocalles*, Fig. 16). However, no cycle-shaped structure at the basal part of endophallus. Median lobe broadly rounded (Figs 13, 14).

Distribution

Southern Spain, only known from the Sierra Nevada. The specimens were collected from the shifted litter of briar patches (e.g. of *Erinacea anthyllis*) underneath holm oaks (*Quercus ilex*).

Etymology

The name *Montanacalles* refers to the type locality of the type species *Kykliaocalles nevadaensis* in the eastern foothills of the Sierra Nevada.

Acknowledgements

This work was supported by the Deutsche Forschungsgemeinschaft (grant WA 530/36-1). We are indebted to R. Anderson, F. Bahr, Ch. Bayer, T. Clayhills, J. Longino, S. Scharf and R. Stejskal for contributing specimens. We also thank C. Etzbauer for the ordering of laboratory consumables and two anonymous referees, B. Misof, J. Skuhrovec, W. Wägele, R. Anderson, T. Swinehart, Ch. Bayer, K. Meusemann, L. Behne and the ZFMK laboratory crew for discussions or information.

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Manuscript received 14 November 2007, accepted 29 July 2008

Appendix 1. Collecting and voucher data for the sequenced weevils

Collecting data usually consist of country, region, coordinates, year of collection and the collector's name. Vouchers (DNA, morphology/tissue) are kept at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK). GenBank accession numbers are given in the text. LT = lectotype, PT = paratype

Taxon	Collecting data	Vouchers
' <i>Acalles</i> ' sp.	Mexico, Chiapas, 16°44'41"N 92°41'19"W, 2600 m, 2007, Longino	JJ221, X-0361-AcS
<i>Acalles almeriaensis</i> Stüben, 2001	Spain, Almería, 37°02'27"N 03°00'12"W, 1291 m, 2007, Astrin & Stüben	JJ174, E-0186-alm
<i>Acalles camelus</i> (Fabricius, 1792)	France, Isère, 45°06'45"N 05°36'21"E, 1352 m, 2005, Stüben	JJ017, I-0026-cam
<i>Acalles camelus</i> (Fabricius, 1792)	Croatia, Dalmatia, 44°32'41"N 15°09'58"E, 1049 m, 2007, Stüben	JJ194, HR-336-cam
<i>Acalles dubius</i> Solari A. & F., 1907	Germany, Rheinland-Pfalz, 50°27'52"N 07°13'29"E, 291 m, 2005, Stüben	JJ033, M-0066-dub
<i>Acalles echinatus</i> (Germar, 1824)	Croatia, Dalmatia, 44°31'45"N 15°08'34"E, 927 m, 2007, Stüben	JJ193, HR-334-ech
<i>Acalles echinatus</i> (Germar, 1824)	Finland, Iniö Salmis, 5–10 m, 2006, Clayhills	JJ209, FIN-0232-ech
<i>Acalles fallax</i> Bohman, 1844	Croatia, Dalmatia, 44°24'32"N 15°34'13"E, 617 m, 2007, Stüben	JJ191, HR-332-fal
<i>Acalles gadorensis</i> Stüben, 2001	Spain, Murcia, 37°52'07"N 01°33'46"W, 1361 m, 2005, Stüben	JJ078, E-0097-gad
<i>Acalles lemur lemur</i> (Germar, 1824)	France, Isère, 45°26'01"N 05°12'06"E, 448 m, 2005, Stüben	JJ014, I-0010-leL
<i>Acalles micros</i> Dieckmann, 1982	France, Isère, 45°06'45"N 05°36'21"E, 1352 m, 2005, Stüben	JJ164, I-0030-mic
<i>Acalles papei</i> Solari A. & F., 1905	Croatia, Dalmatia, 43°54'20"N 16°10'01"E, 738 m, 2007, Stüben	JJ190, HR-327-pap
<i>Acalles parvulus</i> Boheman, 1837	France, Isère, 45°26'01"N 05°12'06"E, 448 m, 2005, Stüben	JJ018, I-0008-par
<i>Acalles pilula</i> Wollaston, 1864	Spain, Canary Isl.: El Hierro, 27°44'29"N 18°03'24"W, 895 m, 2006, Stüben	JJ080, C-0099-pil
<i>Acalles ptinoides</i> (Marshall, 1802)	Germany, Niederrhein, 51°11'56"N 06°15'38"E, 2007, Stüben	JJ210, D-0256-pti
<i>Acalles sierrae</i> H. Brisout, 1865	Spain, Almería, 37°05'45"N 02°57'37"W, 2285 m, 2005, Stüben	JJ148, E-0100-sie
<i>Acalles temperei</i> Péricart, 1987	France, Isère, 45°16'15"N 05°40'13"E, 719 m, 2005, Stüben	JJ019, I-0023-tem
<i>Acallocrates cf. minutusquamosus</i>	France, Var, 43°19'42"N 05°45'17"E, 703 m, 2006, Stüben	JJ185, F-0262-min
<i>Acallocrates colonnellii</i> Bahr, 2003	Slovenia, Sv. Ana env., 20 km NE of Maribor, 2006, Stejskal	JJ083, SLO-0119-col
<i>Acallocrates denticollis</i> (Germar, 1824)	Croatia, Dalmatia, 44°31'45"N 15°08'34"E, 927 m, 2007, Stüben	JJ192, HR-333-den
<i>Acallorneuma doderoi</i> Solari A. & F., 1908	Italy, Sicily, 37°51'38"N 13°23'24"E, 1200 m, 2002, Stüben	JJ065, S-0082-dod
<i>Calacalles azoricus</i> Stüben, 2004	Portugal, Azores: Faial, 38°35'10"N 28°42'04"W, 886 m, 2003, Stüben	JJ102, P-0125-azo
<i>Calacalles droueti</i> (Crotch, 1867)	Portugal, Azores: Pico, 38°27'21"N 28°21'04"W, 811 m, 2003, Stüben	JJ100, P-0123-dro
<i>Calacalles seticollis</i> (Wollaston, 1864)	Spain, Canary Isl.: La Palma, 28°43'18"N 17°47'07"W, 1047 m, 2006, Stüben	JJ098, C-0121-set
<i>Coloracalles humerosus</i> (Fairmaire, 1862)	France, Gard, 43°57'03"N 04°28'59"E, 68 m, 2006, Stüben	JJ079, F-0098-hum
<i>Cryptorhynchus lapathi</i> (Linné, 1758)	Germany, 'Bienen bei Rees, Altrheinarm', 2004, Scharf	JJ214, D-0354-lap
<i>Dendroacalles euphorbiacus</i> (Stüben, 2000)	Spain, Canary Isl.: La Palma, 28°50'36"N 17°54'07"W, 254 m, 2006, Stüben	JJ113, C-0138-eup
<i>Dendroacalles instabilis</i> (Wollaston, 1864)	Spain, Canary Isl.: Tenerife, 28°20'00"N 16°47'10"W, 500 m, 2005, Stüben	JJ111, C-0136-ins
<i>Dendroacalles lepidus</i> (Kulbe, 2000)	Spain, Canary Isl.: La Palma, 28°38'22"N 17°47'54"W, 624 m, 2006, Stüben	JJ110, C-0135-lep
<i>Dendroacalles mundus</i> (Wollaston, 1964)	Spain, Canary Isl.: La Palma, 28°45'18"N 17°46'37"W, 857 m, 2006, Stüben	JJ108, C-0133-mun
<i>Dendroacalles poneli</i> (Stüben, 2000)	Spain, Canary Isl.: El Hierro, 27°43'53"N 18°07'04"W, 725 m, 2006, Stüben	JJ114, C-0141-pon
<i>Dendroacalles ruteri</i> (Roudier, 1954)	Spain, Canary Isl.: La Palma, 28°49'11"N 17°54'48"W, 919 m, 2006, Stüben	JJ107, C-0132-rut
<i>Dichromacalles creticus</i> (Reitter, 1916)	Greece, Crete, 35°20'44"N 23°54'38"E, 1050 m, 2006, Bahr & Bayer	JJ084, GR-0130-cre
<i>Dichromacalles diocletianus</i> (Germar, 1817)	Spain, Cádiz, 36°04'35"N 05°25'46"W, 34 m, 2007, Astrin & Stüben	JJ178, E-0204-dio
<i>Dichromacalles dromedarius</i> (Boheman, 1844)	Spain, Canary Isl.: La Palma, 28°49'50"N 17°52'03"W, 386 m, 2006, Stüben	JJ104, C-0127-dro
<i>Dichromacalles dromedarius</i> (Boheman, 1844)	Spain, Cádiz, 36°03'47"N 05°42'04"W, 14 m, 2007, Astrin & Stüben	JJ201, E-0208-dro
<i>Dichromacalles rolletii</i> (Germar, 1824)	Italy, Sicily: 38°01'59"N 14°35'56"E, 700 m, 2005, Stüben	JJ106, I-0129-rol
<i>Dichromacalles tuberculatus</i> (Rosenhauer, 1856)	Spain, Cádiz, 36°04'35"N 05°25'46"W, 34 m, 2007, Astrin & Stüben	JJ199, E-0203-tub
<i>Echinodera andalusiensis</i> Stüben 2003	Spain, Cádiz, 36°04'10"N 05°31'48" W, 257 m, 2007, Astrin & Stüben	JJ200, E-0205-and
<i>Echinodera aridnae</i> Bahr & Bayer 2005	Greece, Crete, 35°14'51"N 24°10'30"E, 900 m, 2006, Bahr & Bayer	JJ124, GR-0151-ari
<i>Echinodera hystrix</i> Wollaston 1864 (LT)	Spain, Canary Isl.: El Hierro, 27°44'10"N 18°04'26"W, 796 m, 2006, Stüben	JJ115, C-0142-hys
<i>Echinodera roudieri</i> Stüben 1998	Spain, Alicante, 38°41'38"N 00°09'42"W, 1106 m, 2005, Stüben	JJ128, E-0155-rou
<i>Echinodera siciliensis</i> Stüben 2003	Italy, Sicily, 38°09'00"N 12°46'19"E, 35 m, 2006, Stüben	JJ126, I-0153-sic
<i>Echinodera spinosa</i> Stüben 2006	Spain, Málaga, 36°39'51"N 05°05'01"W, 1047 m, 2005, Stüben	JJ122, E-0149-spi
<i>Echinodera vitoensis</i> Stüben 2006	Italy, Sicily, 38°09'00"N 12°46'19"E, 35 m, 2006, Stüben	JJ127, I-0154-vit
<i>Elliptacalles longus</i> (Desbrochers, 1892)	Italy, Sicily, 38°07'10"N 13°08'31"E, 647 m, 2006, Stüben	JJ077, I-0096-lon
<i>Elliptacalles longus</i> (Desbrochers, 1892)	Spain, Cádiz, 36°41'50"N 05°26'20"W, 646 m, 2007, Astrin & Stüben	JJ176, E-0198-lon
<i>Elliptacalles longus</i> (Desbrochers, 1892)	Spain, Málaga, 36°33'49"N 05°12'27"W, 557 m, 2007, Astrin & Stüben	JJ179, E-0213-lon
<i>Eurhoptus</i> sp.	Mexico, Chiapas, 16°44'41"N 92°41'19"W, 2600 m, 2007, Longino	JJ219, X-0359-EuS
<i>Kyklioacalles almadensis</i> Stüben, 2004	Spain, Jaén, 37°45'53"N 03°23'19"W, 1328 m, 2005, Stüben	JJ133, E-0161-alm
<i>Kyklioacalles anthyllis</i> Stüben, 2004 (PT)	Spain, Jaén, 37°50'23"N 02°59'26"W, 1577 m, 2003, Stüben	JJ062, E-0079-ant
<i>Kyklioacalles astragali</i> Stüben, 2003 (PT)	Spain, Granada, 37°22'09"N 02°50'55"W, 2200 m, 2001, Stüben	JJ060, E-0077-ast

Appendix 1. (continued)

Taxon	Collecting data	Vouchers
<i>Kyklioacalles aubei</i> (Boheman, 1837)	Slovenia, Sv. Ana env., 20 km NE of Maribor, 2006, Stejskal	JJ180, SLO-0224-aub
<i>Kyklioacalles aubei</i> (Boheman, 1837)	France, Isère, 45°24'18"N 04°56'26"E, 325 m, 2006, Stüben	JJ182, F-0226-aub
<i>Kyklioacalles bupleuri</i> Stüben, 2004	Tunisia, Tell Atlas, 35°50'23"N 9°22'36"E, 1050 m, 2003, Stüben	JJ131, T-0158-bup
<i>Kyklioacalles characivorus</i> Stüben, 2005	Italy, Sardinia, 39°49'36"N 09°22'27"E, 960 m, 2005, Stüben	JJ132, I-0159-cha
<i>Kyklioacalles erinaceus</i> Stüben, 2003	Spain, Alicante, 38°39'34"N 00°32'29"W, 1296 m, 2007, Astrin & Stüben	JJ173, E-0181-eri
<i>Kyklioacalles euphorbiophilus</i> Stüben, 2003	Morocco, High Atlas, 30°52'25"N 08°21'26"W, 2000 m, 2002, Stüben	JJ197, M-0160-eup
<i>Kyklioacalles navieresi</i> (Boheman, 1837)	France, Isère, 45°26'01"N 05°12'06"E, 448 m, 2005, Stüben	JJ022, I-0007-nav
<i>Kyklioacalles punctaticollis meteoricus</i> (Meyer, 1909)	Spain, Alicante, 38°41'57"N 00°10'32"W, 1074 m, 2005, Stüben	JJ143, E-0165-met
<i>Kyklioacalles punctaticollis punctaticollis</i> (Lucas, 1849)	Spain, Jaén, 37°44'06"N 03°30'09"W, 1663 m, 2005, Stüben	JJ134, E-0162-pun
<i>Kyklioacalles roboris</i> (Curtis, 1834)	France, Isère, 45°18'40"N 05°45'17"E, 1649 m, 2005, Stüben	JJ168, I-0037-rob
<i>Kyklioacalles suturatus</i> (Dieckmann, 1983)	Czechia, Moravia mer., Podyji National Park, Sealsfielduv K., 2006, Stejskal	JJ129, CZ-0156-sut
<i>Kyklioacalles teter</i> (Boheman, 1844)	Italy, Sicily, 37°57'08"N 13°32'50"E, 570 m, 2006, Stüben	JJ130, I-0157-tet
<i>Montanacalles nevadaensis</i> (Stüben, 2001)	Spain, Almeria, 37°02'27"N 03°00'12"W, 1291 m, 2007, Astrin & Stüben	JJ175, E-0189-nev
<i>Onyxacalles balearicus</i> Stüben, 2005 (PT)	Spain, Balearic Isl.: Mallorca, 39°48'47"N 02°53'23"E, 571 m, 2004, Stüben	JJ207, E-0168-bal
<i>Onyxacalles bermejaensis</i> Stüben, 2001	Spain, Málaga, 36°39'51"N 05°05'01"W, 1047 m, 2005, Stüben	JJ198, E-0167-ber
<i>Onyxacalles luigionii</i> (Solari A. & F., 1907)	France, Isère, 45°06'45"N 05°36'21"E, 1352 m, 2005, Stüben	JJ025, I-0027-lui
<i>Onyxacalles luigionii</i> (Solari A. & F., 1907)	Croatia, Dalmatia, 44°32'41"N 15°09'58"E, 1049 m, 2007, Stüben	JJ195, HR-339-lui
<i>Onyxacalles maginaensis</i> Stüben, 2004	Spain, Jaén, 37°43'21"N 03°29'11"W, 1600 m, 2005, Stüben	JJ147, E-0169-mag
<i>Onyxacalles portusveneris</i> (Mayet, 1903)	France, Gard, 43°57'03"N 04°28'59"E, 68 m, 2006, Stüben	JJ144, F-0166-por
<i>Onyxacalles ringeli</i> Kulbe, 1999	Spain, Canary Isl.: La Palma 28°37'37"N 17°49'45"W, 1432 m, 2006, Stüben	JJ087, C-0171-rin
<i>Onyxacalles valencianus</i> Germann, 2005	Spain, Alicante, 38°39'34"N 00°32'29"W, 1296 m, 2007, Astrin & Stüben	JJ172, E-0180-val
<i>Onyxacalles verrucosus</i> (Wollaston, 1863)	Spain, Canary Isl.: El Hierro, 27°44'29"N 18°03'24"W, 895 m, 2006, Stüben	JJ137, C-0170-ver
<i>Paratyphloporus karamani</i> (Formánek, 1912)	Croatia, Dalmatia, 43°27'59"N 16°41'40"E, 280 m, 2007, Stüben	JJ188, HR-312-kar
<i>Ruteria bellieri bellieri</i> (Reiche, 1860)	Italy, Sicily, 37°55'33"N 13°35'48"E, 581 m, 2006, Stüben	JJ187, I-0298-bel
<i>Ruteria hypocrita</i> (Boheman, 1837)	Germany, Rheinland-Pfalz, 50°08'46"N 07°12'39"E, 279 m, 2005, Stüben	JJ031, M-0047-hyp
<i>Ruteria hypocrita</i> (Boheman, 1837)	Croatia, Dalmatia, 44°31'45"N 15°08'34"E, 927 m, 2007, Stüben	JJ205, HR-335-hyp
<i>Ruteria major</i> (Solari A. & F., 1907)	Croatia, Dalmatia, 43°21'26"N 16°59'18"E, 415 m, 2007, Stüben	JJ204, HR-319-maj
<i>Ruteria minosi</i> (Bahr & Bayer, 2005)	Greece, Crete, 35°14'51"N 24°10'30"E, 900 m, 2006, Bahr & Bayer	JJ085, GR-0150-min
<i>Torneuma deplanatum deplanatum</i> (Hampe, 1864)	Italy, Sicily, 38°04'03"N 13°11'37"E, 539 m, 2006, Stüben	JJ203, I-0305-dep
<i>Tylodinus</i> sp.	Mexico, Chiapas, 16°44'41"N 92°41'19"W, 2600 m, 2007, Longino	JJ220, X-0360-TyS
Molytinae: <i>Adexius scrobipennis</i> Gyllenhal, 1834	France, Isère, 45°16'15"N 05°40'44"E, 813 m, 2005, Stüben	JJ043, I-0020-AdS

Appendix 2. Morphological characters used in the phylogenetic analyses

Additive binary coding (multi-column coding) was used to code ordered multistate transformation series

Rostrum/pectoral canal

- (1,2) Rostrum (♂) short, at most 3× as long as (between insertions of antennae) wide (0,0); rostrum (♂) longer, 3×–4× as long as wide (1,0); rostrum (♂) very long, slender, rounded like a stem, at least 4× as long as wide (1,1).
 (3) Antennal groove visible in dorsal view (0); antennal groove lateral (1).
 (4) Without pectoral canal (0); with pectoral canal (1).

Head

- (5,6) Without eyes (0,0); eyes small, long oval (1,0); eyes larger, more rounded (1,1).
 (7,8) Eyes standing close to each other, almost completely visible in dorsal view (0,0); eyes lateral (1,0); eyes latero-ventral, not protruding the upper margin of the antennal groove, not visible in dorsal view (1,1).

Pronotum

- (9) Pronotum wider than long or at most as long as wide (0); pronotum clearly longer than wide (1).
 (10,11) Disc of pronotum symmetrically 'spherically' domed (0,0); disc of pronotum flattened (1,0); disc of pronotum deepened, with median groove(s) or depression (1,1).
 (12) Punctures of pronotum coarse, 'pit-like' (0); punctures of pronotum fine (1).
 (13–14) Pronotum bald (bare of scales), with only a few scattered bristles (0,0); pronotum with flat scales and only a few scattered bristles (1,0); pronotum with flat scales and with tufts of bristles (1,1).
 (15,16) Lateral parts of pronotum curved regularly (often oblong-oval) between middle and fore margin (0,0); pronotum with a slight constriction in front of the fore margin (1,0); lateral parts of pronotum with deep constriction in front of the fore margin and front of pronotum-disc flattened 'delta-like' (1,1).

Elytra

- (17–18) Elytra almost 'spherical' (at most 1.10× as long as wide) (0,0); elytra 'short-oval' (1.20×–1.40× as long as wide) (1,0); elytra 'elongated' conspicuously (at least 1.40× as long as wide) (1,1).
 (19) Disc of elytrae flat, flanks sloping slightly (0); disc of elytrae domed, flanks steeply sloping, compressed (1).
 (20,21) Elytra almost bald (bare of scales), with only a few scattered bristles (0,0); elytra with scales lying flat and only a few scattered bristles (1,0); elytra with scales lying flat and with tufts of bristles (1,1).
 (22) Elytral stripes wider than intervals, elytral punctures coarse, 'pit-like' (0); elytral stripes slender, elytral punctures fine (often elongated) (1).
 (23,24) Elytral intervals tuberculated coarsely and regularly (0,0); elytral intervals with scattered knobs placed irregularly (1,0); elytral intervals flattened or curved regularly (1,1).
 (25) Colour scheme of elytra – except for the light fascia on the elytral slope – predominantly uniform and with poor contrast (0); colour scheme of elytra composed of two or three colours, clearly defined and rich in contrast (1).
 (26) Without a light fascia on the elytral slope (0); the light fascia on the elytral slope is clearly defined (1).

Legs

- (27) Front femur without tooth (0); front femur with tooth (1).
 (28) Front tibia (♂) straight (0); front tibia (♂) – next to the apical thorn – curved inwards (1).

Ventral view

- (29) First sternite at most as long as the following three sternites together (second sternite at least as long as third and fourth sternite together) (0); first sternite clearly longer than the three following, extremely short sternites together (1).
 (30) Edge of elytra next to the second and third sternite either rounded long-ovally or almost straight (0); edge of elytra next to the second and third sternite clearly concave (in dorsal view elytra protruding 'beak-like') (1).

Male genitalia

- (31,32) Internal sack of aedeagus without sclerotized structure (0,0); internal sack of aedeagus with parallel or fork-like 'simple' (two-dimensional) structure (1,0); internal sack of aedeagus with a highly 'complex' (three-dimensional) structure (1,1).
 (33,34) Internal sack of aedeagus with a single sclerotized structure (0,0); internal sack of aedeagus with a double sclerotized structure consisting of a fork and only one plate (1,0); internal sack of aedeagus with a double sclerotized structure consisting of a fork and two plates (1,1).
 (35) Median lobe of aedeagus conspicuously long, the apex pointed or hook-shaped (0); median lobe of aedeagus short and regularly rounded (1).

Spiculum ventrale

- (36) Apodeme of spiculum ventrale very long (0); apodeme of spiculum ventrale very short (1).

Appendix 3. Data matrix for the 36 morphological characters used in the analysis
 ? = missing character

	Characters			
	000000001 1234567890	111111112 1234567890	222222223 1234567890	33333 123456
<i>Adexius scrobipennis</i>	000010000	000000000	000000000	00??00
<i>Montanacalles nevadaensis</i>	1011101101	0110001001	0111000000	110010
<i>Coloracalles humerosus</i>	1011111001	0111101001	1111110000	110010
<i>Torneuma caecum</i>	101100??11	0110001101	0111000000	100010
<i>Torneuma deplanatum</i>	101100??11	0110001101	0111000000	110010
<i>Kyklioacalles roboris</i>	1011111001	1111110001	1110100000	110010
<i>Kyklioacalles solarii</i>	0011111001	1111111001	1110100000	110010
<i>Kyklioacalles aubei</i>	1011111001	1111101001	1110100000	110000
<i>Calacalles theryi</i>	1011101110	0110111011	0111110000	100010
<i>Calacalles seticollis</i>	0011101110	0110111111	0111110000	100010
<i>Elliptacalles longus</i>	1111111000	0111101111	1111110010	100000
<i>Dichromacalles diocletianus</i>	0011111001	1110111001	0010110000	110010
<i>Dichromacalles dromedarius</i>	0011111001	1111111001	1010110000	110010
<i>Dendroacalles ornatus</i>	1111111001	0111111001	1110110001	101110
<i>Dendroacalles instabilis</i>	1111111001	0111101001	1110110001	111010
<i>Acalles lemur</i>	1011111001	0110101001	0111010000	100010
<i>Acalles camelus</i>	1011111001	0110101000	0100010100	100000
<i>Onyxacalles luigionii</i>	1111111001	0111101001	0111110000	100000
<i>Acallorneuma reiteri</i>	1011101111	0000001100	0011001000	100011
<i>Acallorneuma doderoi</i>	1011101111	0100001100	0111001000	100011
<i>Echinodera variegata</i>	0011101101	0110000001	0111010010	00??00
<i>Echinodera siciliensis</i>	1011101101	0110000001	0111010010	00??00
<i>Ruteria hypocrita</i>	1011111001	1110100001	0111010010	00??00