

Molecular and morphological systematics of soil-inhabiting Cryptorhynchinae of the genus *Acallorneuma* and the tribe Torneumatini (Coleoptera: Curculionidae), with description of two new species

With 23 figures, 3 keys and 2 tables

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Summary

Starting from an ecological classification of the morphotypes of apterous western Palaearctic Cryptorhynchinae, molecular systematic and morphological results for the monophyletic weevil genus *Acallorneuma* MAINARDI, 1906 and the tribe Torneumatini BEDEL, 1884 are presented. Based on the mitochondrial CO1 barcoding region, we discuss the limits of comparative morphology in the uniform *Acallorneuma* species. A catalogue and a pictorial key of all 8 species of *Acallorneuma* are provided. In a second step we compare morphology-based systematics of the genus *Acallorneuma* with our molecular reconstruction. Finally, we focus on the related blind, equally wingless and uniform, currently 71 species of the tribe Torneumatini living deep in the soil. This overview of the present state of research shows that molecular intrageneric resolution is highly dependent on the number of sampled species, especially in those cases with particularly long edges in the dendrogram. But although Torneumatini sampling was not complete due to the elusiveness of these subterranean species, some taxonomic changes could still be implemented: *Torneuma* s. str. with the type species *Torneuma caecum* WOLLASTON, 1860 occurs only on the Madeira archipelago. The species of the subgenus *Paratyphloporus* SOLARI, 1937 stat. nov. - only from the western Canary Islands(!) - must be transferred into the genus subgenus *Paratorneuma* ROUDIER, 1956 stat. nov. For all other species of the Mediterranean area and the eastern Canary Islands, the systematic classification needs to be remade (incertae sedis, see also appendix 2). *Torneuma deplanatum deplanatum* (HAMPE, 1864) is the type species of the subgenus *Typhloporus* that includes some, but not all Mediterranean species with a constantly deep and wide pectoral canal, which - as it now seems likely - was developed several times. Two new species are described: *Torneuma* (s. str.) *isamberto* STÜBEN spec. nov. from Madeira and *Torneuma* (s.l.) *cadizensis* STÜBEN spec. nov. from the south of Spain. In both cases keys are given to differentiate from the closely related species.

Key words

Acallorneuma, Torneumatini, *Torneuma*, Bayesian analysis, Integrative Taxonomy, morphology, CO1, new species, taxonomic changes, Western Palaearctic, Spain, Portugal, Canary Islands, Madeira

Zusammenfassung

Ausgehend von ökologischen (idealtypischen) Einordnungen der flugunfähigen, westpaläarktischen Cryptorhynchinae werden molekulare und morphologische Ergebnisse zur monophyletischen Rüsselkäfer-Gattung *Acallorneuma* MAINARDI, 1906 und zu den subterrestrisch lebenden Arten des Tribus Torneumatini BEDEL, 1884 vorgestellt. Ein Katalog und ein Bilderschlüssel zu den 8 validen Arten der *Acallorneuma* leitet eine Diskussion über die begrenzten Möglichkeiten einer rein morphologischen Analyse der uniformen Arten des Genus *Acallorneuma* ein. In einem weiteren Schritt wird die morphologische Systematik mit der molekularen Rekonstruktion der Verwandtschaftsverhältnisse anhand einer Region des mitochondrialen CO1 Gens verglichen. Im zweiten Teil der Arbeit wenden wir uns den gegenwärtig 71 bekannten, blinden, flügellosen und weitgehend kryptischen, tief im Erdreich lebenden Arten der Torneumatini zu. Die molekulare Analyse zeigt zwischen den Arten erhebliche p-Distanzen, macht aber auch deutlich, dass die Rekonstruktion der Verwandtschaftsverhältnisse ganz entscheidend von der Anzahl der Arten und Proben abhängig ist. Dennoch wurden einige taxonomische Änderungen vorgenommen: *Torneuma* s. str. mit der Typusart *Torneuma caecum* WOLLASTON, 1860 gibt es nur auf dem Madeira Archipel! Die Arten des Subgenus *Paratyphloporus* SOLARI, 1937 stat. nov. – und zwar nur die von den Kanarischen Inseln – gehören in das Subgenus *Paratorneuma* ROUDIER, 1956 stat. nov. Für alle anderen Arten aus dem mediterranen Gebiet und den östlichen kanarischen Inseln ist eine endgültige Klassifikation zur Zeit noch nicht möglich (*incertae sedis*), auch wenn erste Gruppen - eingeteilt vor allem nach der Innensackstruktur des Aedoeagus - hier bereits vorgestellt werden (siehe Anhang 2). *Torneuma deplanatum deplanatum* (HAMPE, 1864) ist die Typusart des Subgenus *Typhloporus* und schließt einige, aber eben nicht alle mediterranen Arten mit einem konstant tiefen Rüsselkanal ein, der – das zeigen unsere vergleichenden Studien – offensichtlich mehrere Male in der Evolution ausgebildet wurde. Zwei neue Arten werden abschließend beschrieben: *Torneuma* (s. str.) *isambertoi* STÜBEN spec. nov. von Madeira and *Torneuma* (s.l.) *cadizensis* STÜBEN spec. nov. aus dem Süden Spaniens. Für beide Arten werden Schlüssel mit den nächst verwandten Arten präsentiert.

1. Introduction

1.1 Ecological-morphological considerations

Cryptorhynchinae occur in almost all terrestrial habitats. Within the deciduous and the evergreen western Palearctic forests these habitats reach from canopies over trunks, shrub layer and herbaceous layer down to the leaf litter zone (Fig. 1). Cryptorhynchinae also live in the humus-rich topsoil or among calcareous or volcanic rocks of the subsoil. Their larvae feed on dying twigs, root crowns or roots of lignified (also poisonous) stressed plants that have previously been damaged e.g. by wind or rockfall.

It is noticeable that the morphological variability within genera is highest in the canopy and upper zones of the understory. Morphological similarity among congeneric species conspicuously increases closer to the soil level. Thus, leaf litter-dwelling species of the genus *Echinodera* show only limited exoskeletal differences, and an unambiguous identification by external morphology is highly difficult in *Acallorneuma* species living in the topsoil. Without consideration of the male genital, morphological identification becomes virtually impossible in the subterranean, blind and extremely uniform-looking species of Torneumatini.

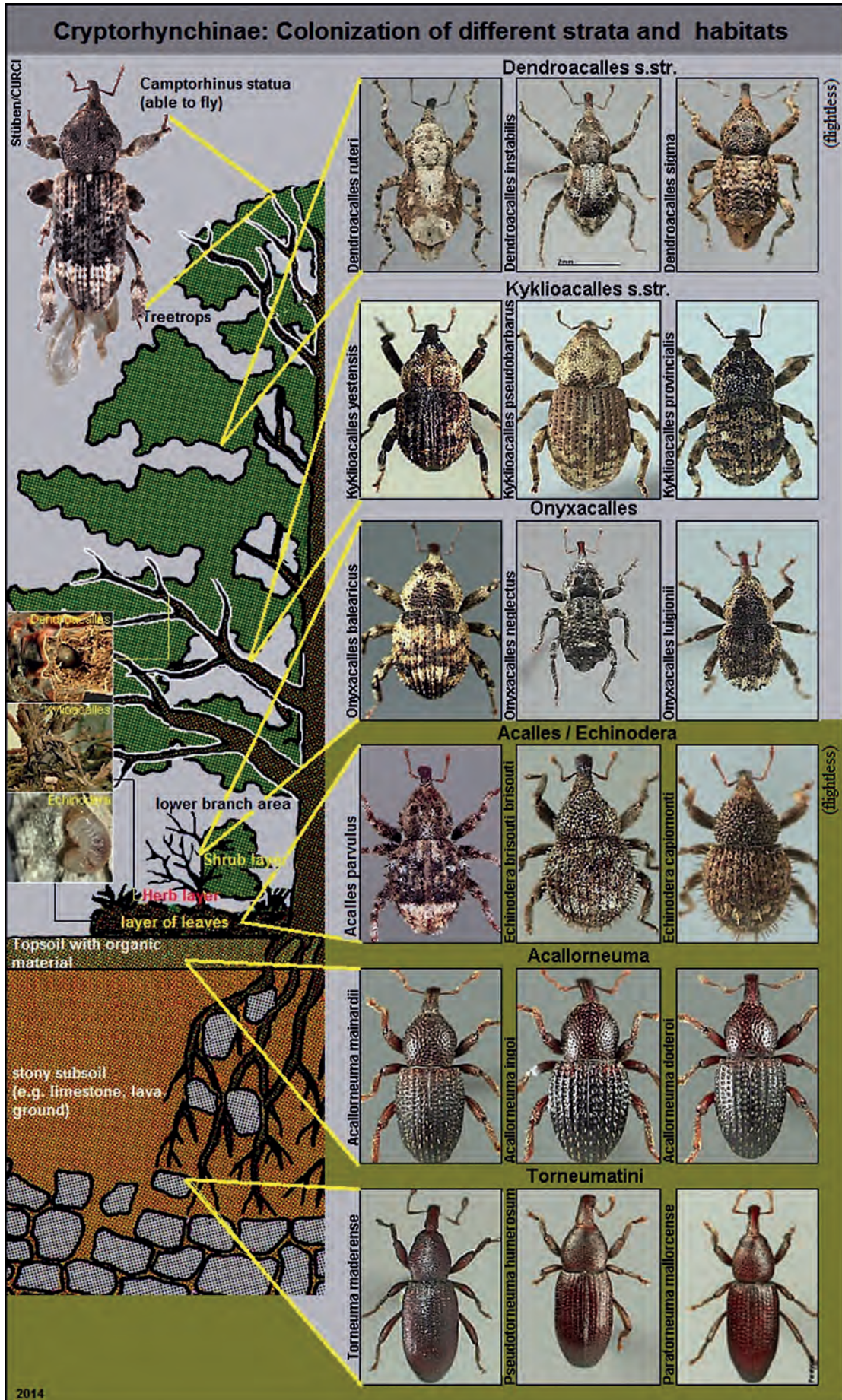
In the following, some typical body plans of flightless Cryptorhynchinae are exemplarily presented (see also Fig. 1):

Species of *Dendroacalles* / *Silvacalles* s. str. live among the higher branches up to the canopy layer of the Macaronesian laurel forest. Long-legged, rich in forms and colours and partly with bizarre scales and prominently protruding setae or bristle tufts (molecular studies in: STÜBEN & ASTRIN 2010a).

Species of *Kyklioacalles* s. str. live in the upper herbaceous layer (e.g. on Fabaceae or Euphorbiaceae) often of woodless habitats in West and Southwest Europe and Northwest Africa. However, there are also representatives of the genus *Kyklioacalles* in Central and Southeast Europe inhabiting the lower understory layer of deciduous forests. These species of the subgenus *Palaeoacalles* possess somewhat longer legs than their South European relatives with a cylindrical appearance, often smooth elytra and contrasting, spotted coloration (molecular studies in: STÜBEN & ASTRIN 2010b).

Species of *Onyxacalles* have nocturnal habits and their activity is centered around the tree trunks and stumps of the deciduous and the evergreen broad-leaved forests of Europe, North Africa and the Canary Islands. Predominantly black species, often marked with only a few bright elytral bands. Species identification based on elytral contour and bristles and on pronotum form is considerably more difficult than in the above-mentioned genera (molecular studies in: STÜBEN & ASTRIN 2012).

Fig. 1 (opposite): Ideotypic attribution (by stratum inhabited) of the genera and morphotypes of apterous western Palearctic Cryptorhynchinae. The flyer *Camptorhinus statua* is listed here in comparison to the wingless species of highly divergent genera of Cryptorhynchinae s. str., but it is not closely related to these.



Species of *Acalles* can be collected by sieving from the top layer of leaf litter in Central European forests or the detritus of low shrubs in Central and Southern Europe. *Acalles* specimens are brown and low in visual contrast, without conspicuous elytral marks or bands; in most cases also without bristle tufts or elytral protuberances. Without knowledge on aedeagi, species identification can often be very challenging, in some cases even impossible (molecular studies in: SCHÜTTE & STÜBEN 2015).

Species of *Echinodera* occur mainly in the Mediterranean area and on the Macaronesian islands, often as endemics, and can be collected in considerable numbers from the bottommost, often moist layer of forest leaf litter. Other than the above species, these Cryptorhynchinae can usually not be collected by beating of shrubs or branches. Legs are very short, eyes narrow and partly reduced; overall body shape is oval. Species are hard to tell apart and punctuation of the pronotum, number of elytral bristles and shape of the aedeagus all need to be carefully scrutinized (molecular studies in: ASTRIN & STÜBEN 2010).

Species of *Acallornewma* inhabit the uppermost thin soil layer among calcareous rocks in the southwestern Mediterranean zone, with numerous endemics. The inclusion of *Acallornewma* within Cryptorhynchinae has yet to be validated (doubts arise e.g. from STÜBEN et al. 2015, similarly for *Acallocrates* and Torneumatini). *Acallornewma* species are characterized by uncontrasting brown, flattened species, nearly 'bald', without protruding bristles. Eyes very small, strongly reduced. Species very difficult or impossible to tell apart without inspection of the aedeagus (morphological studies in: STÜBEN 2006a).

Torneumatini encompass Mediterranean and Macaronesian, almost exclusively endemic species that always follow a subterranean way of life and are associated with roots in often calcareous or volcanic rocks. All characters mentioned above are strongly reduced in this group: eyeless, extremely flattened, short-legged, nearly 'bald', light brown species; virtually indistinguishable based on outward exoskeletal characters. For morphological species identification, inspection of the aedeagus and its internal sac is indispensable (morphological studies in: STÜBEN 2007).

The increasingly complex habitat structures illustrated in figure 1 are interestingly mirrored – to some degree – by the phylogenetic reconstruction for western Palearctic genera of Cryptorhynchinae based on the mitochondrial COI + 16S and nuclear 28S genes (see STÜBEN et al. 2013: fig. 1). Indeed and generalizing, it can be said, that – for example – the Macaronesian tree climbers, the species of *Dendro-* and *Silvacalles* (STÜBEN et al. 2009), appear as highly derived, younger taxa, whereas the *Acallornewma* and Torneumatini living near or within the soil are certainly older. It could be shown for the first species of

Acallornewma that they are around 30 million years old, whereas the species of *Dendroacalles* formed 7 millions of years ago, and some species of *Silvacalles* only separated just 600,000 years ago. The *Kyklioacalles* of the lower strata can be classified between these evolutionary tendencies: they probably have developed around 17 million years ago (STÜBEN & ASTRIN 2010b: fig. 1B).

It is questionable and not always helpful if such distinct genera and ecological classifications are partly 'leveled out' by molecular analyses based on mostly conservative (nuclear) genes. This low 'resolution' at genus level leaves something to be desired in the light of worldwide thousands of described Cryptorhynchinae species. And these sometimes lead to far-fetched proposals suggesting e.g. that a "splitting" in several Western Palearctic genera could not be helpful and „Torneumatini (represented solely by [one specimen of] *Torneuma* in [the] analysis) appear to be part of the *Acalles* group“ (RIEDEL et al. 2016: 9) – without having to preoccupy oneself with the substantial morphological and mitochondrial differences among the only 6 species-rich genera of the ca. 400 Cryptorhynchinae species in the Western Palearctic; overlooking the fact that the habitat and host requirements of these species are completely different!

However, the different morphotypes (body plans) described above show a marked correlation with the ecological stratification in a tree/shrub community: in western Palearctic Cryptorhynchinae, intrageneric morphological variability is highest in the canopy-dwelling taxa, decreases in the species living closer to the soil ('epigaion') and reaches almost complete uniformity in exoskeletal characters in the soil-dwelling taxa ('edaphon'). In other words: the higher and brighter the inhabited layer, the larger the morphological differences among congeneric species, enabling easier and faster phenotypic identifications.

This also has substantial consequences for phylogenetic approaches in western Palearctic Cryptorhynchinae. In this group, classification at genus level is still straightforward based on clear and practically useful morphological, ecological and molecular differences (a fact not recognized by RIEDEL et al. 2016, who muse about western Palearctic cryptorhynchine genera while ignoring 98.7 % of the group's diversity). However at species level, the situation changes gradually: Recognizing evolutionary novelties on a morphological basis, without associated molecular analyses (like DNA sequencing), is still very well possible in species of *Dendroacalles* (STÜBEN & GERMANN 2005), *Dichromacalles* (STÜBEN & BEHNE 1998) or *Kyklioacalles* (STÜBEN 1999, 2003), but becomes much more challenging for species of *Acalles* s. str. (SCHÜTTE & STÜBEN 2015). Ultimately, for the strongly uniform epigeous or edaphic species, phylogenetic reconstructions based exclusively on morphological characters would be impractical. It is already difficult to discern, without additional infor-

mation, morphological differences among the scarce, reduced exoskeletal characters of species belonging to the genus *Echinodera*, or even more so in the subterraneously living species of *Acallornewma* and *Torneumatini*. Within a cladistics analysis, interpretation of character polarity and character weighting based on morphology alone becomes impossible in such a scenario. The minimal changes and displacements in lengths, distances, length-width ratios of elytral setae or the minimal differences in puncture size and distance on the elytral intervals or on the pronotum are possibly sufficient for a simple dichotomous differential diagnosis of a species description. They do not, however, offer appropriate guidance for establishing a character matrix and reconstructing the underlying evolution.

These realizations from practical work in the mentioned species match the conclusions from purely morphological studies by the first author (STÜBEN 2006a, 2007): species delimitation and plain dichotomous differential diagnosis require studies on morphology, ecology and reproductive biology; these however do not suffice to adequately meet the challenges of reconstructing a phylogeny in subterranean *Acallornewma* and *Torneumatini* species. In such morphologically cryptic cases, molecular analysis offers the most promising choice (STÜBEN 2006a, 2007), as many more characters are available than from comparative morphology (cf. TAUTZ 2006).

The present work aims mostly at answering three distinct questions:

1. What do we have to take into account when describing mostly uniform (not cryptic) species of *Acallornewma*, and where do we reach the limits of comparative morphology?
2. What can we learn from the molecular reconstruction of *Acallornewma* phylogeny and where are the differences from purely morphological reconstruction (for example by OSELLA & ZUPPA 2002)?
3. What can be said about genus-level systematics and taxonomy of the soil-dwelling higher taxa of *Torneumatini*?

1.2 Material and methods

A molecular phylogeny of the western Palearctic weevil genera *Acallornewma* MAINARDI, 1906 and *Torneuma* WOLLASTON, 1860 is presented here in a Bayesian analysis (Fig. 3). In total the dataset contains 7 *Acallornewma* species, 11 *Torneuma* species, 2 *Paratornewma* species and 1 *Paratyphloporus* species. Furthermore, we included 4 *Kyklioacalles* (Cryptorhynchinae) sequences as outgroup taxa. Collecting and vouchering information as well as GenBank accession numbers are given in Appendix 1. We sequenced the (5') barcoding section of the CO1 gene.

Altogether 22 sequences were generated specifically for this study, the remaining 20 sequences were taken from previous studies of the ZFMK and Curculio Institute. Sequence length was 658 bp for CO1. Total genomic DNA vouchers and voucher specimens are deposited at the Zoological Research Museum Alexander Koenig (ZFMK). The laboratory routine followed SCHÜTTE et al. 2013, except samples marked with a star* in Appendix 1, which were processed as described in ASTRIN & STÜBEN (2008). In both cases the same primers were used (ASTRIN & STÜBEN 2008), based on the typical barcoding primers (FOLMER et al. 1994):

LCO1490-JJ 5'-CHACWAAYCATAAAGATATYGG-3'
and HCO2198-JJ 5'-AWACTTCVGGRTGVCCAAARA
ATCA-3'.

DNA sequence alignment has been performed with Biomatters Geneious 6.1.8 (<http://www.geneious.com>, KEARSE et al. 2012), with the integrated MUSCLE plugin by using default parameters (DRUMMOND et al. 2012). Sequences were 658 nucleotides in length. For two sequences we could not retrieve the full length. *Acallornewma doderoi* (I-0120-dod): 572nt; *Torneuma cadizensis* spec. nov. 100-PST Spain-Cadiz: 657 nucleotides. Missing characters have been coded as 'N'. jModeltest 0.1.1 (POSADA 2008), implementing the Bayesian information criterion (BIC, SCHWARZ 1978), identified the HKY+I+G model of nucleotide substitution (HASEGAWA et al. 1985) as the best-fit model for the CO1 alignment provided. The sequence data of the mitochondrial CO1 gene was used in parallel Bayesian Markov chain Monte Carlo (MCMC) analyses, as implemented in MrBayes ver. 3.2.0 (RONQUIST & HUELSENBECK 2003). We applied the model of sequence evolution diagnosed by the BIC (nst=2 rates=invgamma). Parameters were unlinked between the 3rd versus 1st plus 2nd codon positions. Analyses were run for 40 million generations using the default chain number and temperatures, sampling 40,000 trees (average standard deviation of split frequencies: 0.000816). Every 1,000th tree was sampled. Negative log-likelihood score stabilisation was determined graphically. Accordingly, we retained 39,000 trees. These were used for building a 50 %-majority rule consensus dendrogram with posterior probability values. Geneious was used to display the tree and also to calculate uncorrected (*p*-)distances provided in Fig. 7 and within the text.

2. The genus and the species of *Acallorneuma*, and the limit to a comparative morphology

2.1 Key to the genera

The genus *Acallorneuma* (and the tribe Torneumatini) can be distinguished from all other Western Palaearctic genera of the subfamily Cryptorhynchinae (Coleoptera: Curculionoidea) by the following characteristics:

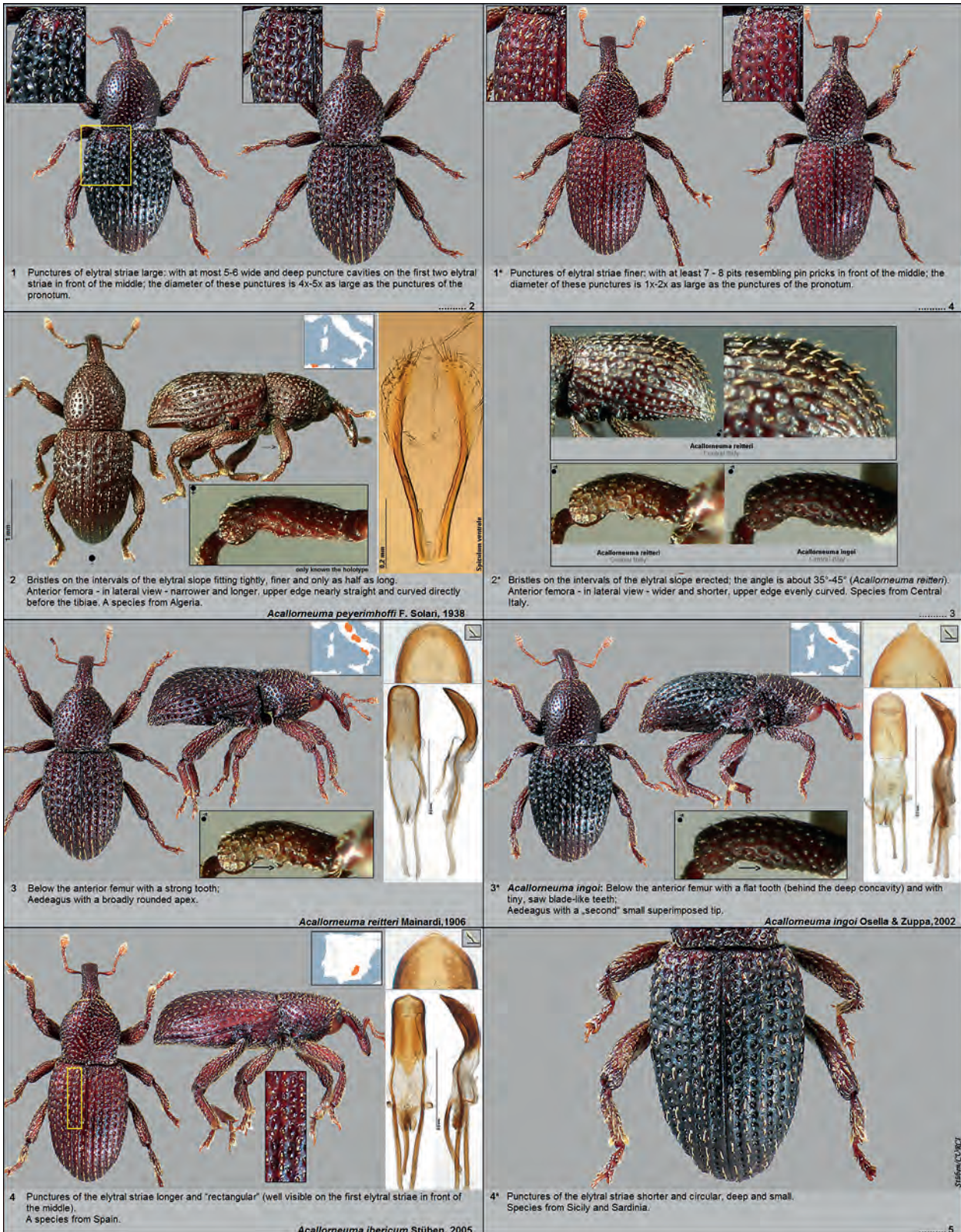


Fig. 2: Pictorial key to the species of the genus *Acallorneuma*.

- 1. Eyes lacking; subterranean species. Torneumatini
- 1*. With eyes; species inhabiting leaf-litter, decaying wood or living on plants. 2
- 2. Anterior femora edentate. all other Western Palearctic Cryptorhynchinae:
e.g. *Acalles*, *Acallocrates*, *Calacalles*, *Dendroacalles*,
Dichromacalles, *Echinodera*, *Kyklioacalles*, *Onyxacalles*
- 2*. Anterior femora with a tooth, sometimes very small. 3
- 3. Elytra covered densely with scales, bristles and bristle tufts. Mostly species with wings living on trees and in tree crowns. (*Gasterocercus*, *Camptorhinus*, *Cryptorhynchus*)

(*Camptorhinus status* is a not closely related flyer of all other Cryptorhynchinae s. str. In addition, we also include the flightless species *Poggionymus crassus* COLONNELLI, 1983 with a large tooth on the bottom side of the anterior femora; probably introduced to Sardinia).
- 3*. Elytra bare of scales, only with free-standing bristles on the intervals, in a single row and very distant from one another. Species wingless, living between decaying leaves of the upper soil layer. Length: 2.5–3.5 mm. Distribution: western Mediterranean area (Fig. 2). *Acallorhynchus* MAINARDI, 1906

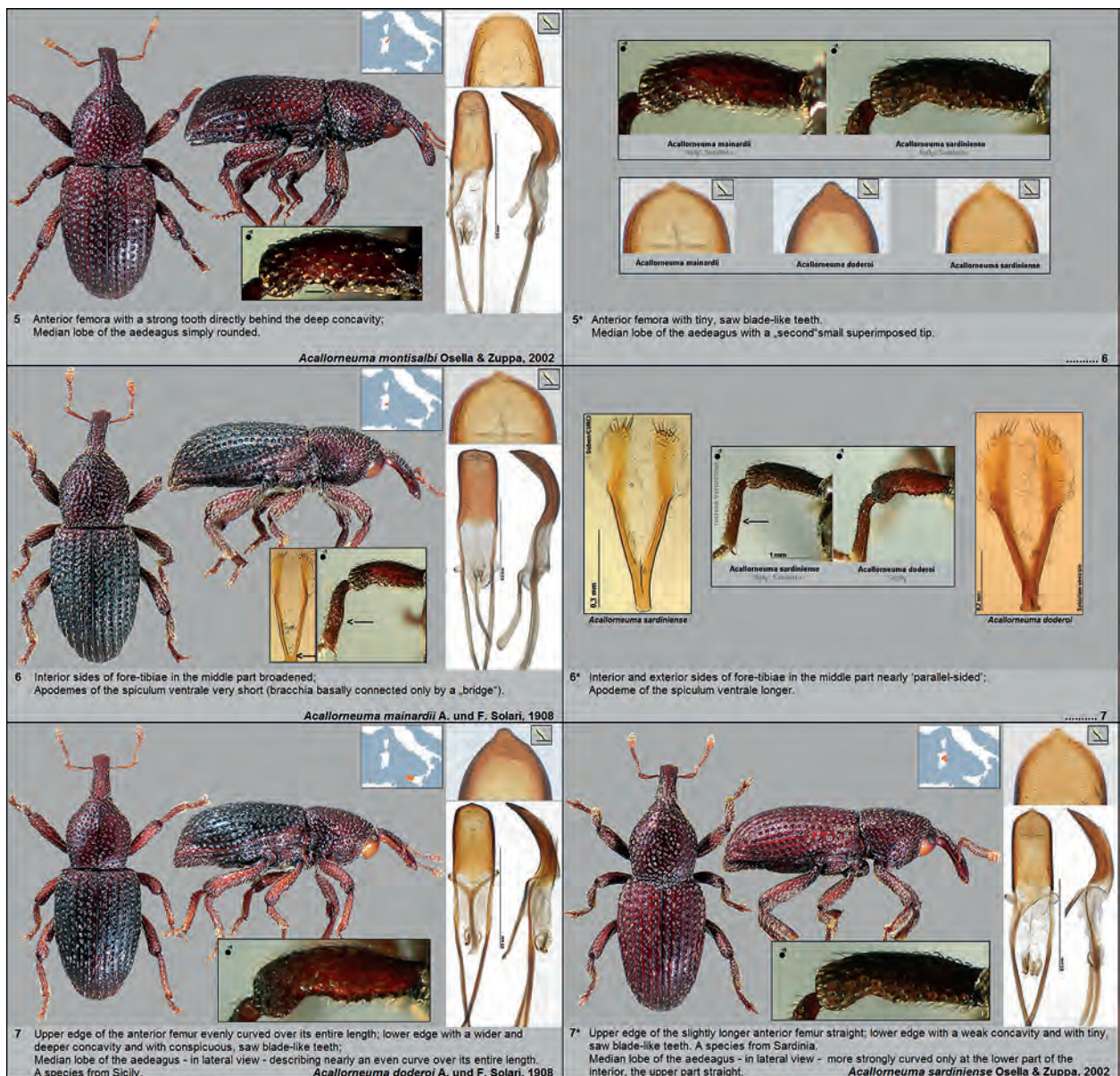


Fig. 2: (continued): Pictorial key to the species of the genus *Acallorhynchus*.

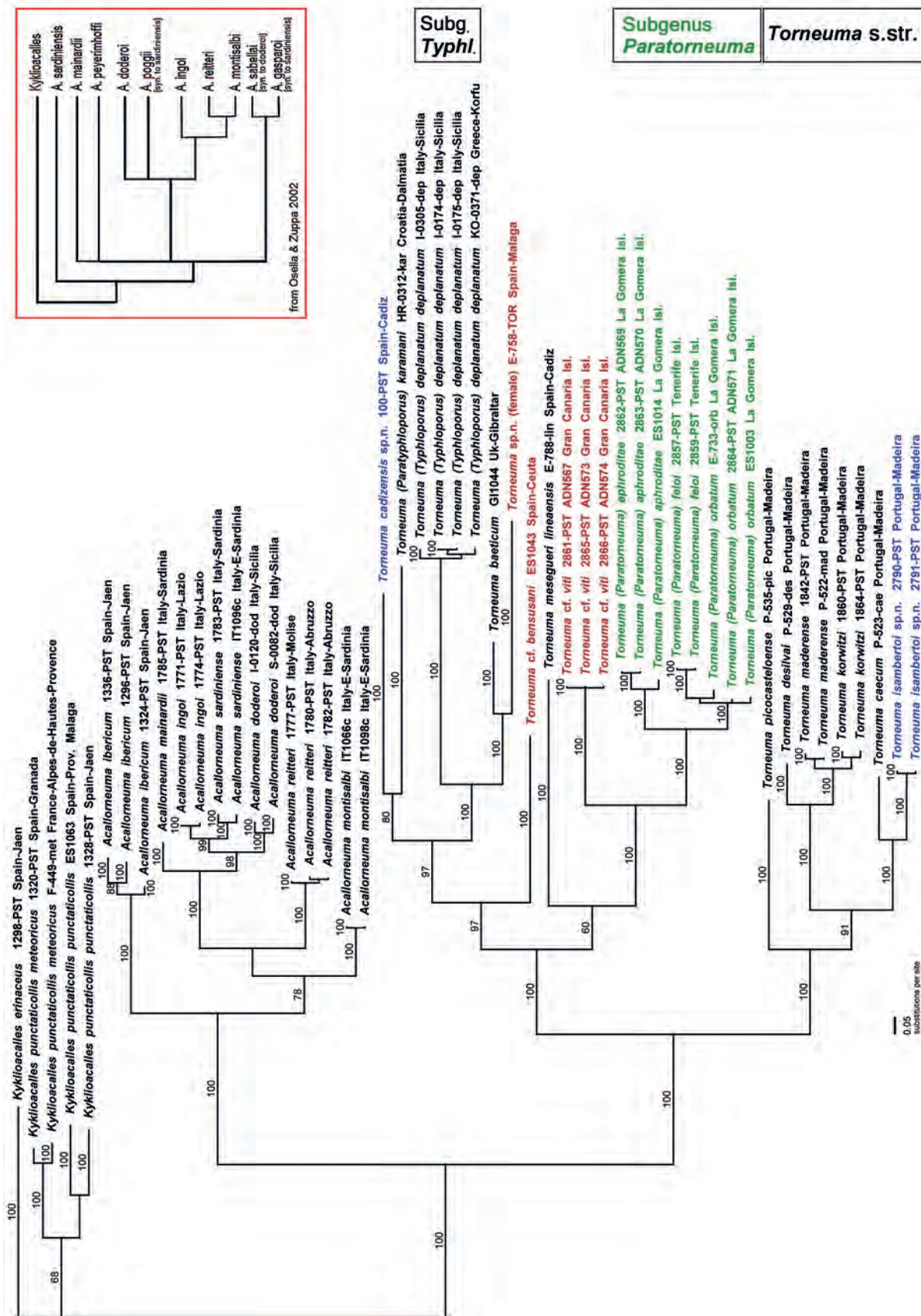


Fig. 3: Bayesian consensus tree (50 % majority rule) for CO1.

2.2 Catalogue of the species of *Acallornewma*

Species included in the molecular analysis are printed in bold.

l.t. = locus typicus

Genus *Acallornewma* MAINARDI, 1906: 151 type species
Acallornewma reitteri MAINARDI, 1906

doderoi A. & F. SOLARI, 1909: 275 E: IT (Sicily)

sabellai OSELLA & ZUPPA, 2002: 448 (synonymised by STÜBEN, 2006)

ibericum STÜBEN, 2005: 87 E: SP

ingoi OSELLA & ZUPPA, 2002: 445 E: IT (mainland)

mainardii A. & F. SOLARI, 1909: 275 E: IT (Sardegna)

montisalbi OSELLA & ZUPPA, 2002: 452 E: IT (Sardegna)

peyerimhoffi, F. SOLARI 1938: 29 N: AG

reitteri MAINARDI, 1906: 151 E: IT

sardiniense OSELLA & ZUPPA, 2002: 454 E: IT (Sardegna)

gasparoi OSELLA & ZUPPA, 2002: 455 (synonymised by STÜBEN, 2006)

poggii OSELLA & ZUPPA, 2002: 453 (synonymised by STÜBEN, 2006)

The morphological characters mentioned below enable differential diagnosis and offer a rough orientation among the 8 valid species of *Acallornewma*. Focus characters are 1) the median lobe of the aedeagus, 2) elytral punctuation or form and arrangement of bristles on the elytral intervals and 3) species-specific ventral indentation of front femora (see pictorial key). However these characters do not suffice for a phylogenetic reconstruction as shown below.

2.3 Key to the species of the genus *Acallornewma*

Even with such a pictorial key (Fig. 2), it is difficult to identify unambiguously the often uniform species of *Acallornewma*. Furthermore, there remains the question whether accurate species assignments can also be performed on females. OSELLA & ZUPPA seem to believe this is feasible, as they depict the spiculum ventrale and the spermatheca in comparative tables of their revision of *Acallornewma* (OSELLA & ZUPPA 2002), and even base their species descriptions mainly on the female genital, sometimes considering only a single female (e.g. in *Acallornewma sabellai* syn. or – based on three females – in *Acallornewma poggii* syn.). The first author has demonstrated that, with the exception of very few characters of the spiculum ventrale (apodeme length, form of brachia), the female genital is unfit to characterize species of *Acallornewma* adequately (STÜBEN 2006a). When larger series of specimens are available for investigation, the high variability of the spiculum ventrale (ibid. Tab. 454.14) and also (to a lesser extent) of the spermatheca become apparent. OSELLA & ZUPPA (2002) failed to prove the stability of these in fact unspecific characters, especially with regard to

the species *Acallornewma reitteri*, where many specimens were available to them and where they acknowledged the high variability (OSELLA & ZUPPA 2002: fig. 6a–c).

The high variability of the spiculum ventrale is typical not only for species of the genus *Acallornewma*, but for all Cryptorhynchinae of the Western Palaearctic. Unambiguous (re-) description of species belonging to the genus *Acallornewma* – or in fact to any other genus of Cryptorhynchinae – should therefore never be based solely on female specimens, especially not exclusively on the spiculum ventrale (in more detail: STÜBEN 2006a).

Concluding, we hold that the few (mostly male) morphological characters used here in compiling the *Acallornewma* key can serve as a first orientation aid within the genus, but do not – as with the uniform Torneumatini (see below) – constitute a sufficiently solid basis as to induce hypotheses on species relationship.

3. Morphological and molecular systematics of the species of *Acallornewma* Mainardi

Our molecular analysis is based on 15 individuals belonging to 7 of 8 valid *Acallornewma* species (sequence of *Acallornewma peyerimhoffi* is not yet available). The resulting phylogeny shows marked differences from the first reconstruction for the genus obtained by OSELLA and ZUPPA (2002) in their ‘analisi filogenetica del genere *Acallornewma* MAINARDI, 1906’. We have reproduced their ‘morphological’ (i.e. morphology-derived) tree in Fig. 3 (top right). Using the same weevil genus as a model system, we can thus contrast two different character systems typically used in phylogenetics against each other. TAUTZ (2006) holds that morphological and molecular trees have to be considered independently from one another. However, striking inconsistencies should prompt us to search for erroneous assumptions or glitches in either method. It has to be noted that *Acallornewma ibericum* STÜBEN from southern Spain could not yet be included in the analyses of OSELLA & ZUPPA (2002), as it was described at a later point (STÜBEN et al. 2005). Regarding the other taxa, phylogenetic placement varies considerably between the morphological tree and the molecular dendrogram presented here.

The taxa *Acallornewma gasparoi* OSELLA & ZUPPA 2002 and *A. poggii* OSELLA & ZUPPA 2002, both synonymized (STÜBEN 2006a) with *A. sardiniense* OSELLA & ZUPPA 2002, appear at different positions in the morphological tree. The species *A. sabellai* OSELLA & ZUPPA 2002 has been synonymized by STÜBEN (2006a) based on both morphological and mitochondrial 16S data (see also ASTRIN et al. 2012) with the species *A. doderoi* A. & F. SOLARI 1908,

equally described from Sicily. It appears closely related with *A. gasparoi*, the above-mentioned synonym of *A. sardiniense*. This species from Sardinia, according to our molecular analyses the sister taxon of the central Italian species *A. ingoi* OSELLA & ZUPPA 2002 appears, in the morphological reconstruction, as sister to all other *Acallornewma* species. Apart from the species pair *A. reitteri* (central Italy) and *A. montisalbi* (Sardinia), there exist almost no similarities between the trees. How can these differences be explained?

1. First of all we have to consider the imbalance between number of species vs. number of characters within the morphological reconstruction, an aspect often underestimated in morphology-based phylogenetics. It is difficult to imagine that, like in the present case, 15 characters should suffice to establish a meaningful cladogram (HENNIG 1966) for 10 ingroup species (cf. OSELLA & ZUPPA 2002: 464). In cases of morphological uniformity such as the present, DNA sequence analysis seems to be the better option as it offers many more (quantifiable) characters at species level.

Within an integrative taxonomic framework, it has been frequently shown that DNA-based phylogenies prompted the search for new morphological characters, led to modified character weighting or helped in unmasking plesiomorphic morphological characters. Molecular data have long since become an important corrective for morphologically-oriented taxonomists.

2. A purely morphological phylogenetic reconstruction does not gain additional precision or meaningfulness by subdividing already analyzed characters into several subcharacters. Such a practice merely leads to multiplication of the existing evidence. Over-splitting of characters has to be critically kept in mind when considering the characters connected to the spiculum ventrale (female genitalia) or the median lobe of the aedeagus (male genitalia) (see OSELLA & ZUPPA 2002: Table II). Splitting complex characters into various components would be justified, however, if a gradual evolutionary increase in character complexity had been proven. Otherwise, complex characters are weighted too strongly just because they 'strike the eye', or because they fit the picture that already exists in the experienced taxonomist's / systematist's mind, a common danger in purely morphological phylogenies. It is not our intention to criticize such an intuitive phylogenetic approach by experienced taxonomists – on the contrary, the resulting concepts often show striking concordance with 'proper', quantitative molecular phylogenies without room for interpretation. If this was not the case, we would have to redefine the largest part of insect systematics.

Thus, our critique is mostly directed at a-posteriori pseudo-legitimations of such intuitive phylogenetic concepts, which – in morphologically highly similar taxa

– expose themselves to the suspicion of manipulative selection of characters.

3. Conspicuously, numerous morphological detail homologies are missing from the analysis, as almost half of the species in the character matrix feature question marks, coding for an undefined character state (see OSELLA & ZUPPA 2002: Tab. III). This applies especially to the species *A. sabellai* and *A. poggi*, both described based on females, without information on the male genital. Phylogenetic analysis is thus supported by only eleven characters, and the question arises whether or not it makes sense to compile phylogenetic matrices when dealing with species affected by such a degree of morphological stasis, especially when based on a single sex. In such a scenario, there always exists the risk (among other effects) that synonymous species are not even recovered as sister taxa, as in our example *Acallornewma sardiniense* OSELLA & ZUPPA, 2002 = *Acallornewma gasparoi* OSELLA & ZUPPA, 2002 syn. = *Acallornewma poggii* OSELLA & ZUPPA, 2002 syn. or *Acallornewma doderoi* A. & F. SOLARI, 1908 = *Acallornewma sabellai* OSELLA & ZUPPA, 2002 syn.) (cf. OSELLA & ZUPPA 2002: fig. 10).

By this we do not deny the usefulness of purely phenotype-based phylogenetic analysis (see SUDHAUS 2006). However, in similar organisms, which show only a few characteristics as result of the adaptation to a life in the soil and karst (like the species of Torneumatini and *Acallornewma*, see Introduction), it can lead to considerable misconceptions as shown below.

In *Acallornewma*, OSELLA & ZUPPA (2002) perceived morphological similarity with the species close to *Kykliocalles punctaticollis* (LUCAS, 1849) – the species that today are grouped into the subgenus *Glaberacalles* STÜBEN & ASTRIN 2010, with equally almost 'bald', flattened and elongate elytra. This comparison brings both genera into close evolutionary relationship ('affinità' is mentioned). However, molecular phylogenetic reconstructions of western Palaearctic Cryptorhynchinae have shown that the genus *Kykliocalles* is in fact – contrary to the proposal of Osella and Zuppa – highly derived and not closely related to the 'basal' *Acallornewma* (STÜBEN & ASTRIN 2010b, STÜBEN & SCHÜTTE 2013). Closest to *Kykliocalles* are the genera *Coloracalles* and *Montanacalles*. Together with *Kykliocalles*, they form the sister group to the genera *Acalles*, *Onyxacalles* and *Echinodera* (ASTRIN et al. 2012). The equally flat and elongate build, almost without setae, of the *Kykliocalles* subgenus *Glaberacalles* results from a similar, partly soil-related mode of life on and between roots and root crowns, e.g. on various Fabaceae species (see details in STÜBEN 2006b). The flattened build could well be the result of convergent or parallel evolution (starting from the originally tree-dwelling *Kykliocalles* s. str. species and species of the subgenus *Palaeocalles* with strongly curved elytra). For the species of *Acallornewma*, species that hide away

among the upper rock crevices during the hot summer months, a flattened body shape is a functional necessity. The same applies to the species of *Glaberacalles*. But these adaptational (better: eco-functional) similarities in body plan cannot prompt the conclusion that both taxa are necessarily closely related. In fact, *Acallorneuma* species always cluster very ‘basally’ (often in conjunction with *Acallocrates*) in the various molecular western Palaearctic Cryptorhynchinae trees (ASTRIN et al. 2012, STÜBEN et al. 2013), and it cannot even be taken for granted that their inclusion within the subfamily Cryptorhynchinae is justified.

4. Intergeneric classification of the Torneumatini BEDEL, 1884

Even more uniform than *Acallorneuma* are the species of the tribe Torneumatini. If not for the partly complex internal sac structures of the aedeagus (endophallus), one would have to speak of cryptic species in most Torneumatini. The currently 71 valid species and subspecies in the tribe have been assigned, according to length and form of the pectoral canal, into initially three, later four genera (STÜBEN 2007, see Fig. 4):

– *Pseudotorneuma* SOLARI, 1937: lacks a pectoral canal or a mesosternal receptaculum between the mid-coxae;

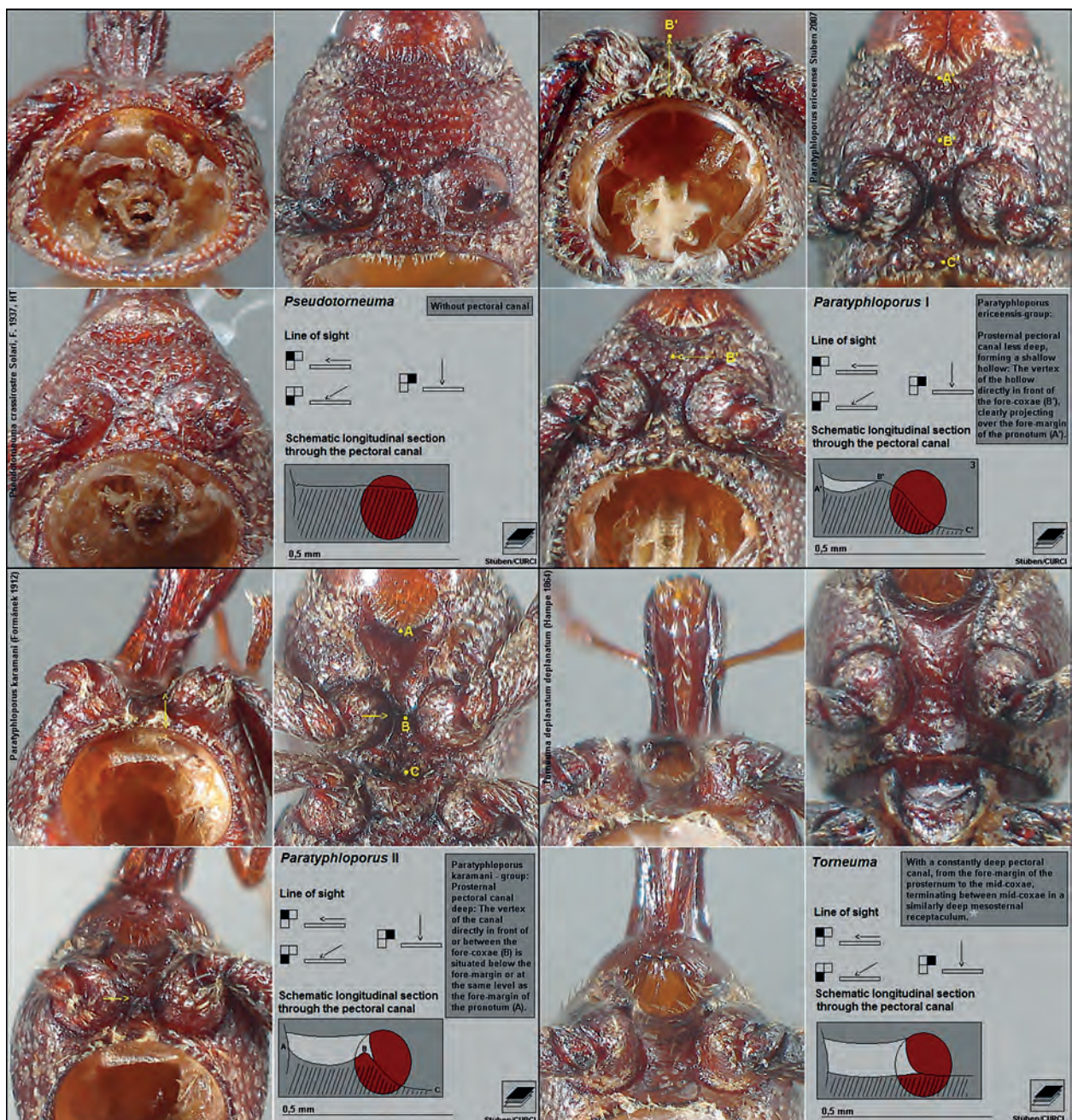


Fig. 4: Heuristic subdivision of Torneumatini by form of the pectoral canal (according to STÜBEN 2007) for fast species assignment to groups and species, based on the simplest hypothesis of a continuous transformation series.

– *Paratyphloporus* SOLARI, 1937: with pectoral canal that forms only a flat depression in front of the fore-coxae (*Paratyphloporus* I) or that ascends right before or between the fore-coxae, to drop steeply from here towards the mesosternal receptaculum (*Paratyphloporus* II);

– *Torneuma* WOLLASTON, 1860: with a constantly deep, tube-formed pectoral canal, reaching from the anterior margin of the prosternum to the mid-coxae and ending between the mid-coxae in an equally deep mesosternal receptaculum.

This preliminary subdivision (see Fig. 4), oriented at morphologically easily evaluable characters as the pectoral canal and mesosternal receptaculum, was meant as a useful provisional solution from early on (see STÜBEN 2007). Such heuristic instruments cannot convey any meaning on character polarity. Therefore the question could not be addressed whether Torneumatini originally completely lacked any pectoral canal (this seems to be the notion of ROUDIER 1956), or if instead the lack of a canal constitutes a secondary reduction. If we were dealing with a gradual mode of evolution, we would always find transitional forms (as intermediate character states) and would never be able to define (sub)genus-specific characters with certainty or conclusively.

In fact, recent molecular phylogenetic reconstructions (e.g. STÜBEN & ASTRIN 2010a) have shown that the pectoral canal has been acquired and reduced several times in Torneumatini evolution. As a first approximation, we currently reach the following conclusions:

1. The species of *Torneuma* s. str. occur only on the Madeira archipelago (see tree in Fig. 3). Besides the type species *Torneuma caecum* WOLLASTON, 1860, they contain five additional species: *T. picocasteloense* STÜBEN, 2002, *T. desilvai* G. OSELLA & ZUPPA, 1998, *T. korwitzii* STÜBEN & SCHÜTTE 2015, *T. maderense* STÜBEN, 2002 and the new species *T. isambertoi* STÜBEN spec. nov. (see description and key below).

2. The subgenus *Paratornewma* ROUDIER, 1956 stat. nov. from the western Canary Islands with the type species *Torneuma (Paratornewma) orbatum* WOLLASTON, 1865 (La Gomera) includes the species *T. (Paratornewma) aphroditae* (GERMANN & STÜBEN, 2006) (La Gomera), *T. (Paratornewma) franzi* (GONZÁLEZ, 1971) (Tenerife), *T. (Paratornewma) lindrothi* (FRANZ, 1981) (La Palma) and *T. (Paratornewma) feloi* (STÜBEN, 2007) (La Palma), an originally described species of the genus *Paratyphloporus*. All these species were – in the meantime – ‘erroneously’ transferred by the first author into the genus *Paratyphloporus* SOLARI, 1937 with the type species *Paratyphloporus karamani* (FORMÁNEK, 1912) from the Dalmatian coast, because also these species evolved the pectoral canal in form of a more or less shallow depression in front of the fore-coxae (STÜBEN 2007, 2008). However,

it was overlooked, that the rhomboid-like structures of the internal sac of the aedeagus of the *Paratornewma* species from the Canary Islands are very different from the complex structures of the *Paratyphloporus* species from the Mediterranean area (see the figures in STÜBEN 2007). Furthermore, the latter also have a deeper depression in front of the fore-coxae and/or these fore-coxae are far away from each other. In other words: although the more or less deep canal of the rostrum in front of the fore-coxae is present in both genera – reaching its highest point between the coxae and dropping steeply from here towards the mesosternal receptaculum –, it seems to be clear that both genera are not closely related as we had stated previously. It should therefore be presumed that we are here confronted with a convergent evolution of a reduction of the rostrum-canal, which leads de facto to the total loss of the rostrum-canal in the case of the few North African *Pseudotornewma* species.

What can we say conclusively about the three species from Gran Canaria, *T. viti*, *T. solarii* and *T. canariense* (all described by G. & M. OSELLA, 1984)? At this time, the molecular basis is too little and the high molecular p-distances of the mitochondrial CO1 gene do not allow to include the species into the subgenus *Paratornewma*. Furthermore, the rostrum-canal of these species from the eastern Canary Islands is clearly deeper, the fore-coxae are wider compared to the *Paratornewma* species, the elytrae are longer and the internal sac of the aedeagus, consisting of two parallel bars or lines, is different from the species of the western Canary Islands. Therefore these last three species cannot be directly allocated currently to a subgenus.

3. Most Mediterranean species, which also have a fully developed pectoral canal, should be grouped – after resynonymizing – to the subgenus *Typhloporus* HAMPE, 1864 with the type species *Typhloporus deplanatum deplanatum* HAMPE, 1864 (see Fig. 3).

However and for the time being, they are considered *incertae sedis* with regard to a subgenus until more molecular data of more Mediterranean species are available.

4. What does this mean in practice? Even though most Torneumatini cannot be told apart by exoskeletal characters, using the partly complex structure of the internal sac of the aedeagus usually allows easy assignment of specimens to individual groups (cf. STÜBEN 2007 with clear, copiously illustrated identification keys and scroll images). The speciose Mediterranean subgenus *Typhloporus* thus can be subdivided into ‘broad-nosed’ and ‘long-nosed’ species, the latter further into a *T. damryi*, a *T. robustum*, a *T. tuniseum*, a *T. convexiusculum* and a *T. siculum* group according to the internal sac structure (see Appendix 2).

We eagerly await if this preliminary classification into morphological groups (particularly with regard to the

structure of the internal sac of the aedeagus and the depth of the rostrum channel) will hold in the light of a molecular phylogenetic reconstruction by using more genes. But the fact that ‘not more’ than 21 out of 71 species of Torneumatini could be analyzed molecularly in the last eight years exemplifies how much patience we will have to muster until a conclusive systematic classification will be reached: the search for these subterranean species in the Mediterranean area and on the Macaronesian islands is among the most difficult, but also among the most urgent tasks in present-day Cryptorhynchinae research. (Neither sieving nor floating techniques seem to have predictable success – even in places where Torneumatini species have previously been found). Therefore, and keeping in mind the conspicuously long branches of the dendrogram (CO1 *p*-distances among species mostly 15 % or above), it would be premature (see Fig. 3) to formally consider a homogeneous *Typhloporus* subclade.

5. Taxonomy

Preliminary remark: A quick and unambiguous determination of Torneumatini species should always begin with a meticulous examination of the structure of the male endophallus. An identification of females is not promis-

ing considering the high number of species and also in the light of the taxonomic ‘meaninglessness’ of female genitalia in the tribe. Description of new species based on a single female should be avoided and make morphological revision or simple species description impossible in whole or in part! A molecular analysis should be obligatory in any such case.

5.1. *Torneuma* s. str. *isambertoi* STÜBEN spec. nov.

Family: Curculionidae LATREILLE, 1802

Subfamily: Cryptorhynchinae SCHOENHERR, 1825

Tribe: Torneumatini BEDEL, 1884

Genus: *Torneuma* WOLLASTON, 1860

Subgenus: *Torneuma* s. str.

Type species: *Torneuma caecum* WOLLASTON, 1860 (type locality: Madeira)

Key to the *Torneuma* s. str. species from the archipelago of Madeira

1. Elytra short-oval, broad: < 1.68 x as long as wide: (Fig. 8–9). 2
- 1*. Elytra oblong-oval, narrow: > 1.80 x as long as wide: (Fig. 5–6, 10–11). 3
2. Elytra more convex, broadest position in or behind the center; sides of pronotum from the center to the front-margin nearly narrowing rectilinearly: (Fig. 8); aedeagus: apex of the median lobe in ventral view with less distinct tip, sharply rounded (Fig. 14). Madeira. Body length: 1.95–2.05 mm. *Torneuma caecum* WOLLASTON, 1860 = *Torneuma brincki* ROUDIER, 1965 syn.
- 2*. Elytra strongly flattened, broadest position in front of the center, more oval; sides of pronotum evenly rounded: (Fig. 9); aedeagus: apex of the median lobe in ventral view with a distinct tip (Fig. 15). Porto Santo. Body length: 2.25–3.00 mm. *Torneuma picocasteloense* STÜBEN, 2002
3. Elytra longer, ogival-shaped in front of the apex (more clearly in females) (Fig. 6); median lobe of the aedeagus 9x–10x as long as wide (Fig. 13). Madeira (Paul do Mar): Body length: 2.40–3.20 mm. *Torneuma korwitzi* STÜBEN & SCHÜTTE, 2015
- 3*. Elytra shorter, ovally rounded towards the apex (without flat dents on each side immediately before the apex) (Fig. 5, 10–11); median lobe of the aedeagus at most 2.2x as long as wide (Fig. 12, 16–17). 4
4. Lower part of the interior sides of fore-tibiae (♂) ‘sickle-shaped’; aedeagus: median lobe in the middle part convex and more acuminate: (Fig. 16). Habitus: (Fig. 10); Madeira (Sao Vicente, Cruta do Cardal). Body length: 2.25–3.15 mm. *Torneuma desilvai* OSELLA & ZUPPA, 1998
- 4*. Interior sides of the fore-tibiae (♂) nearly straight; aedeagus: median lobe parallel or narrowing rectilinearly and less acuminate: (Fig. 12, 17). 5
5. Elytra more slender and more curved (Fig. 11); aedeagus longer (2.2x as long as wide) and the structure of internal sac different (Fig. 17). Body length: 2.25–2.95 mm. *Torneuma maderense* STÜBEN, 2002
- 5*. Elytra slightly broader and flatter (Fig. 5); aedeagus shorter (1.9x as long as wide) and the structure of internal sac different (Fig. 12). Body length: 2.50–2.80 mm. *Torneuma isambertoi* STÜBEN spec. nov.

Type material: Holotype (HT): 1 ♂, “Madeira, Paul do Mar, 32°45'34"N 17°13'43"W, 62 m, banana terraces under *Ficus carica* and *Euphorbia piscatoria*, sifting, 4.4.2015, leg. Stüben (20)”, coll. Curculio-Institute, D-Mönchengladbach. / **Paratype (PT):** 5 ♂, 4 ♀, same locality as for holotype, 4.4.2015, 2.7.2014, coll. Stüben, Curculio-Institute and ZFMK (Bonn).

DNA type: 1 ♂, data as for holotype, collector's no: 2790-PST, DNA no: ZFMK-DNA-0169166963, GenBank acc.: KU170192 (COI).

Description (Fig. 5, 12):

Length: 2.5–2.8 mm (without rostrum).

Venter: With a constantly deep and wide pectoral canal, from the fore-margin of the prosternum to the mid-coxae, terminating between the mid-coxae in an equally deep mesosternal receptaculum (Fig. 5); fore-margin of the prosternum low-cut, forming an arc of a circle; the ground between the prae-coxae slightly lifted, dropping down towards the mesosternal receptaculum. The



Fig. 5: *Torneuma isambertoi* sp. n., ♂, holotype.

distance between the prae-coxae is large, as is their diameter. The brink of the mesosternal receptaculum is semicircular and sharp-edged; base of the receptaculum with a step. 1st and 2nd abdominal segment of the male with a wide and flat hollow.

Head & Rostrum: Without eyes; *T. isambertoii* belongs to the 'long-nosed' species: rostrum brown, 3.50x (♂) and 3.70x (♀) as long as wide between the insertions of the antennae; with a fine median edge and on each side with a conspicuous and elongated edge; insertions of the

antennae near the apex, approximately at the end of the first quarter (♂) or first third (♀).

Pronotum: 1.18–1.20x as long as wide; widest at the end of the basal third of the pronotum; narrowing rectilinearly laterally towards the fore-margin, clearly less rounded than towards base. Disc of pronotum flattened, with fine, not deep punctures, covered with numerous round scales. The fore-margin of the pronotum with a slight indentation in the middle.



Fig. 6: *Torneuma korwitzii* STÜBEN & SCHÜTTE 2015, ♂, holotypus.

Elytra: Brown-russet, strongly flattened and elongate, 1.80x (♀) – 1.90x (♂) as long as wide; elytra in both sexes approximately parallel-sided ('cylindrical') in the middle, ovals rounded directly in front of the apex; base line

of elytra curved slightly S-shaped. The puncture stripes clearly more slender than the slightly arched intervals. These are covered with a single row of very fine, short and hardly discernible bristles.

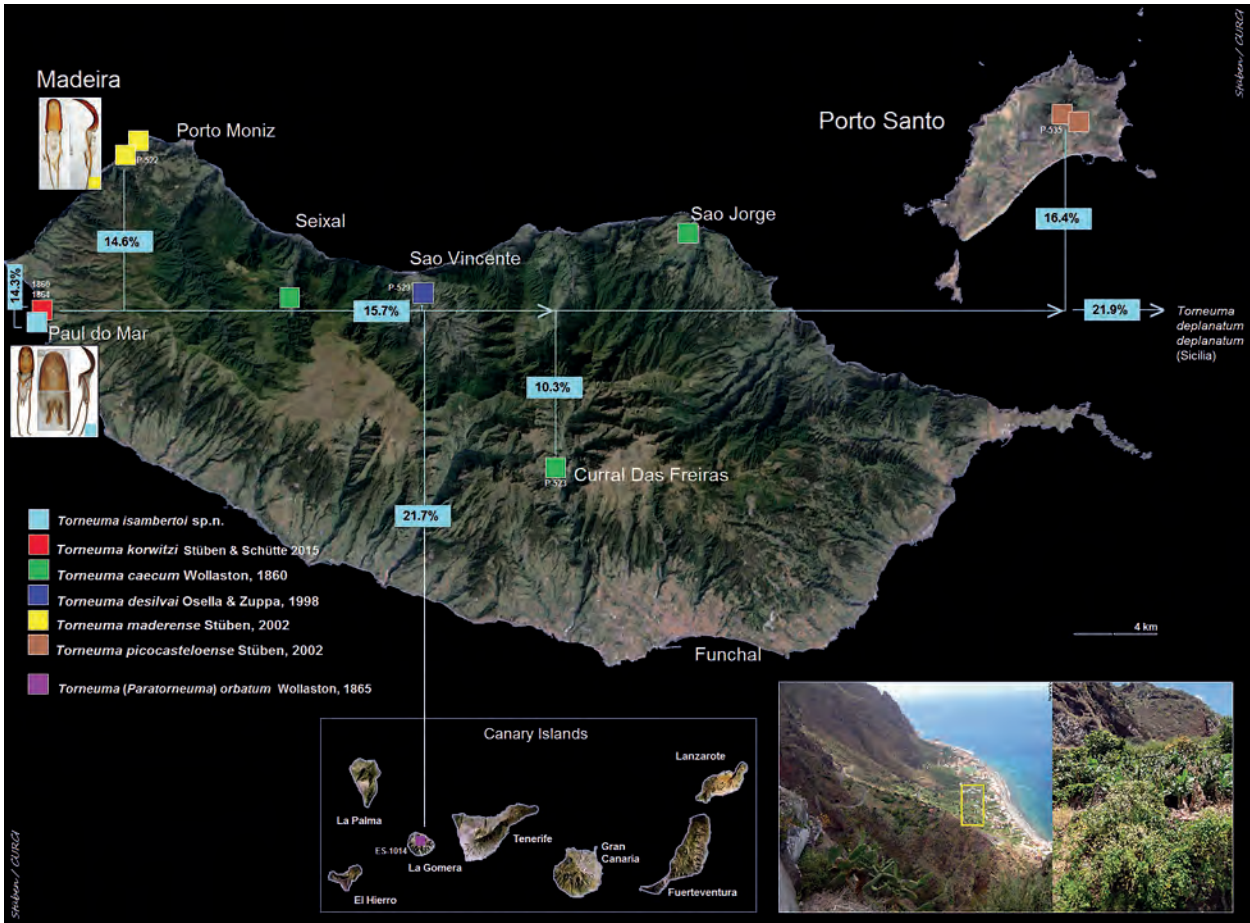


Fig. 7: Distribution of the *Torneuma* (s. str.)-species and *p*-distances of the mitochondrial COI gene between *Torneuma isambertoi* and the related species from the Madeira Archipelago (see also dendrogram Fig. 3); below right: habitat of *T. isambertoi*, Madeira: Paul do Mar.

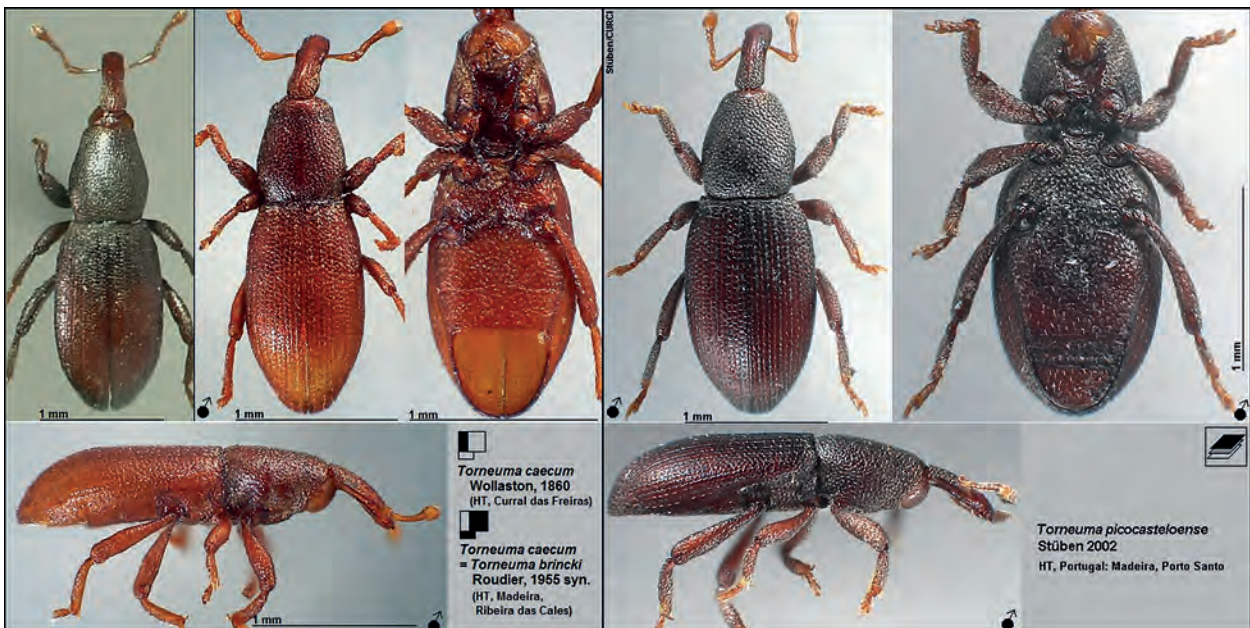


Fig. 8: *Torneuma* s. str. *caecum* (habitus).

Fig. 9: *Torneuma* s. str. *picocasteloense* (habitus).

Aedeagus: Median lobe 1.9x as long as wide, viewed laterally it forms approximately a right angle (Fig. 12).

Etymology: The new species is dedicated to Isamberto Silva (Madeira, Funchal), who has supported the first author with his excellent expert knowledge to collect the Curculionidae on the Desertas Islands. As a “Vigilante da Natureza” he is doing outstanding conservation work on the Madeira archipelago. His collection of insects and molluscs is unique.

Ecology: The new species was sieved out of dead and broken branches (detritus) by the first author in the

ground under *Ficus carica* and *Euphorbia piscatoria* always together with *Torneuma korwitzi* (Fig. 7, bottom right) in the proportion 1:3 from the banana plantations near Paul do Mar (Madeira).

Distribution: So far this species is only known from the southwest of Madeira (Portugal). An overview of the species, collecting localities and the populations of all *Torneuma* species known from the Madeira Archipelago as well as the *p*-distances of the mitochondrial COI gene between *Torneuma isamberto* and the related species are presented here in map: (Fig. 7).

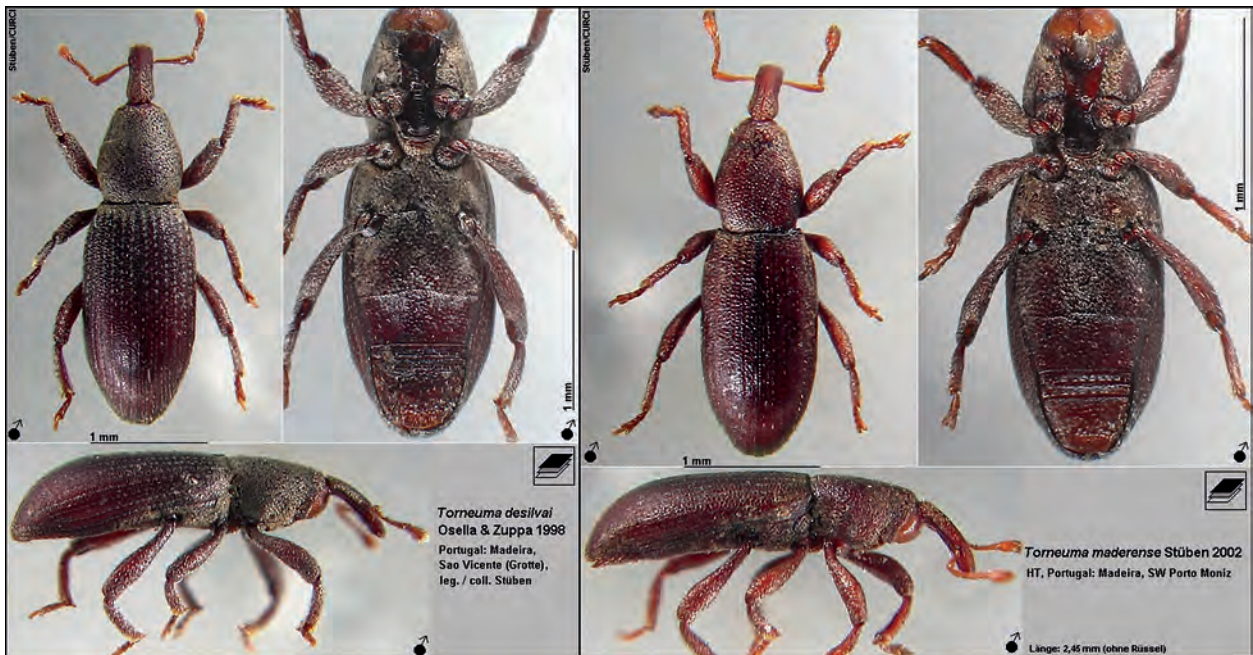


Fig. 10: *Torneuma* s. str. *desilvai* (habitus).

Fig. 11: *Torneuma* s. str. *maderense* (habitus).

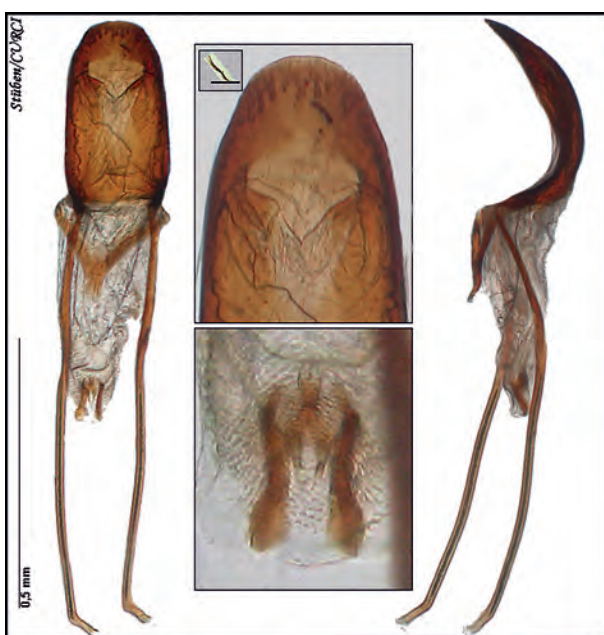


Fig. 12: *Torneuma isamberto* spec. nov., aedeagus, HT.

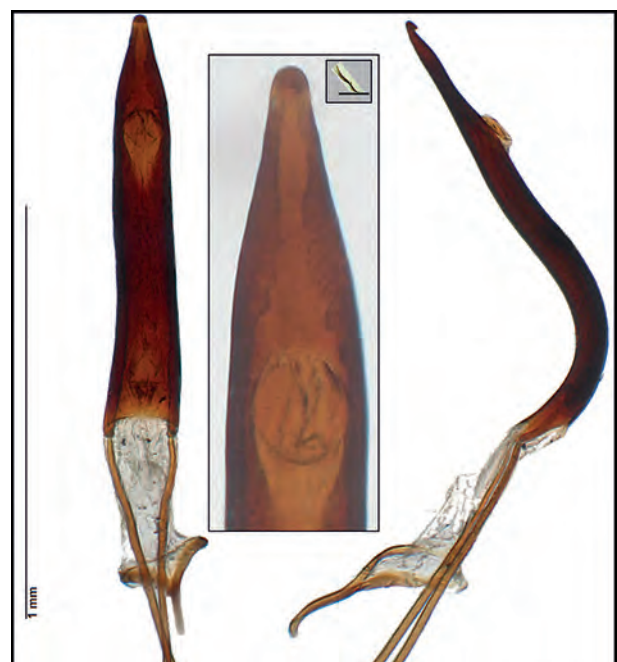


Fig. 13: *Torneuma korwitzi*, aedeagus, HT.

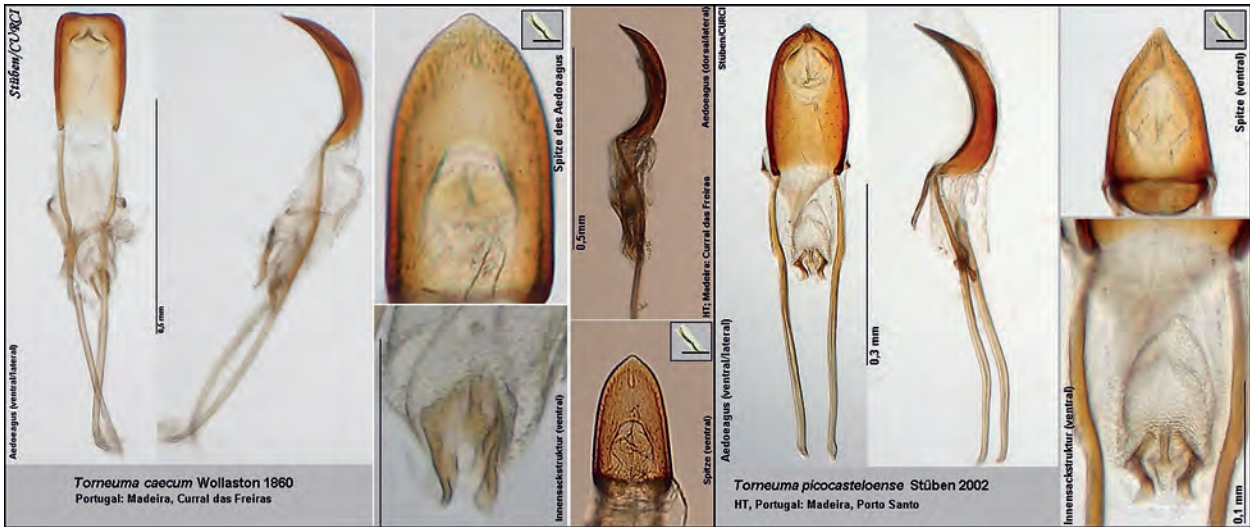


Fig. 14: *Torneuma caecum* (aedeagus).

Fig. 15: *Torneuma picocasteloense* (aedeagus), HT.

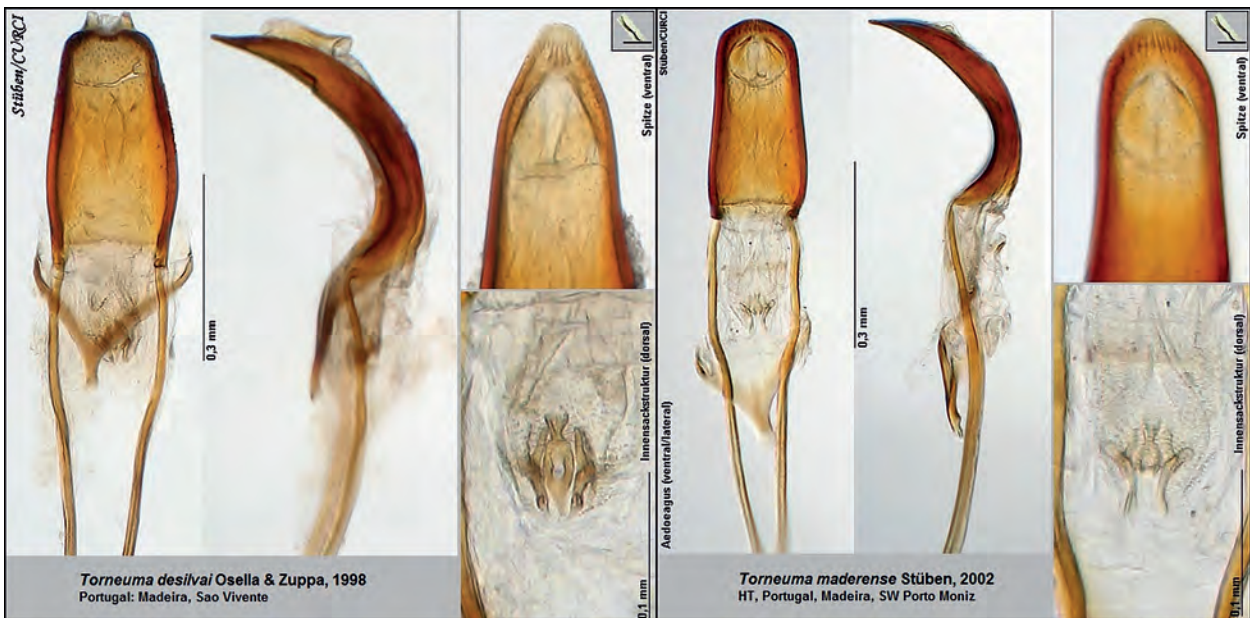


Fig. 16: *Torneuma desilvai* (aedeagus).

Fig. 17: *Torneuma* s. str. *maderense* (aedeagus), HT.

5.2. *Torneuma* s.l. *cadizensis* STÜBEN spec. nov.

Family: Curculionidae LATREILLE, 1802

Subfamily: Cryptorhynchinae SCHOENHERR, 1825

Tribe: Torneumatini BEDEL, 1884

Genus: *Torneuma* WOLLASTON, 1860

Group: *Torneuma robustum*

Type material: Holotype (HT): 1 ♂, “Spain: Cadiz, La Linea, Sierra Cabonera: Puerto Higuerón, Cordel Ruta Verde, N36°13'16" W5°20'59", 147 m, 28.9.2010, Quercus coccifera, leg. J.L. Torres”, coll. Curculio-Institute, D-Mönchengladbach.

DNAtype: data as for holotype, collector’s no: 100-PST, DNA no: ZFMK-DNA-0100417927, GenBank acc.: KC783806 (CO1).

Description of the holotype (Fig. 18, 20):

Length: 3.25 mm (without rostrum).

Venter: With a constantly deep and wide pectoral canal, from the fore-margin of the prosternum to the mid-coxae, terminating between the mid-coxae in an equally deep mesosternal receptaculum (Fig. 18); the distance between the prae-coxae is large, as is their diameter. The brink of the mesosternal receptaculum is semicircular and sharp-edged; base of the receptaculum with a step. 1st and 2nd abdominal segment of the male with a wide and flat hollow.

Head & Rostrum: Without eyes; *T. cadizensis* belongs to the 'long-nosed' species: rostrum brown, 3.8x (♂) as long as wide between the insertions of the antennae, without a mid-edge, but on each side with a short edge; insertions of the antennae near the apex, approximately at the end of the first third (♂).

Pronotum: 1.16x as long as wide; widest at the end of the basal second fifths of the pronotum; narrowing

rectilinearly laterally towards the fore-margin, clearly less rounded than towards base. Disc of pronotum flattened, with fine, deep and extensively placed punctures, covered with numerous round scales and isolated, scarce bristles. The fore-margin of the pronotum with a slight indentation in the middle.

Elytra: Brown-russet, flattened (much flatter and broader than those of *T. morandae*, see Fig. 19), 1.72x (♂) as



Fig. 18: *Torneuma cadizensis* spec. nov., HT.

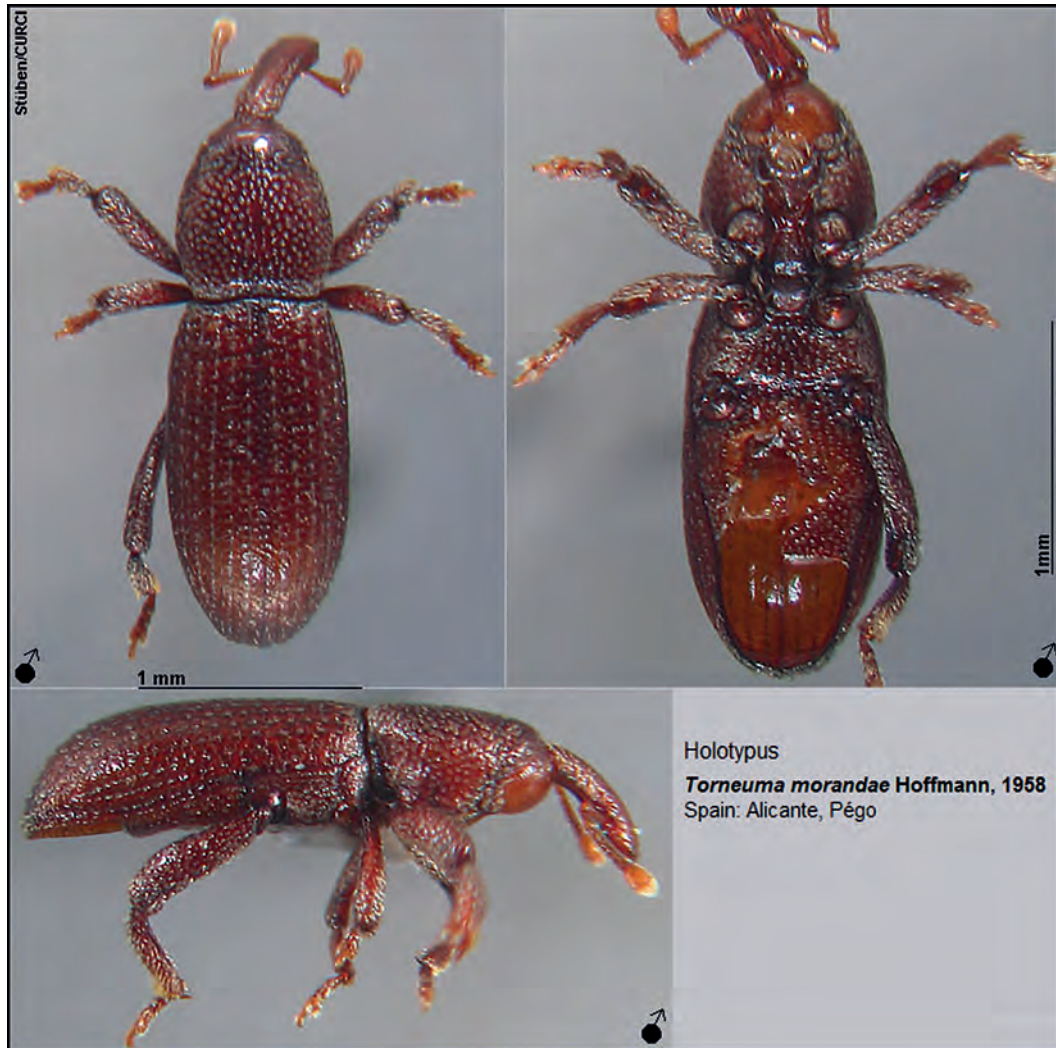


Fig. 19: *Torneuma morandae* HOFFMANN, 1958, HT.

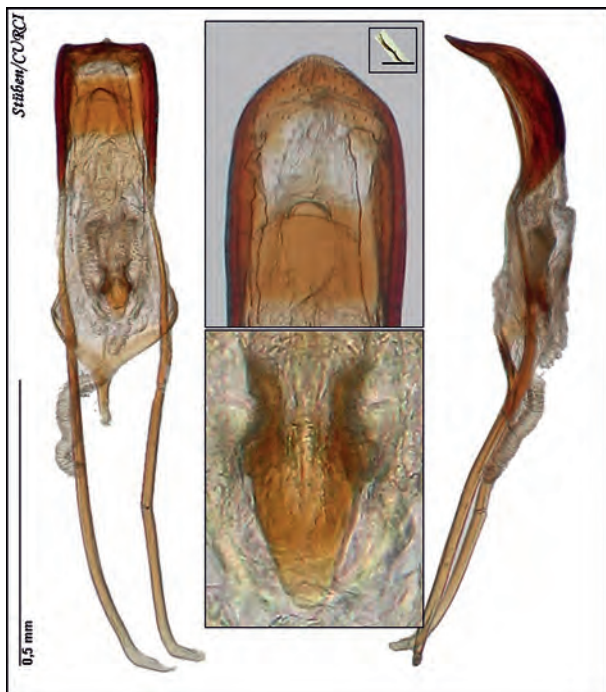


Fig. 20: *Torneuma cadizensis* spec. nov., aedeagus, HT.

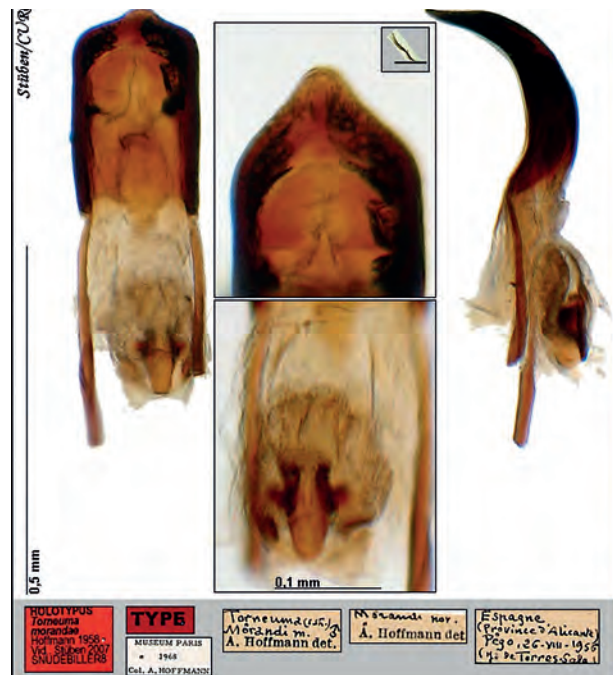


Fig. 21: *Torneuma morandae* HOFFMANN, 1958, aedeagus, HT.

Key to the species of the *Torneuma robustum* group with a simply V-shaped endophallus

Note: This group contains in the broadest sense almost a dozen additional species with a more complex and larger structure of the endophallus (see Fig. ‘Tab.Tor.6.1’ and the pictorial keys in STÜBEN 2007, and Fig. ‘Trob’ in STÜBEN 2009).

1. Elytra broad: < 1.65x as long as wide; lateral margins of the prosternal pectoral canal semicircularly rounded. 2
- 1*. Elytra more slender: > 1.72x as long as wide; lateral margins of the prosternal pectoral canal nearly straight or weakly S-shaped. 3
2. Habitus broad; premucro small, more inconspicuous, Morocco (Tanger). Body length: 2.40–2.60 mm.
Torneuma robustum (DIECK 1869)
= *Crypharis tingitana* DIECK 1869
= *Crypharis strigirostris* FAIRMAIRE 1873
- 2*. Habitus slightly more slender; premucro large; Morocco (Tanger). Body length: 2.60 mm.
Torneuma robustum var. *tingitanum* (DIECK 1869)
infrasubspecific name (ICZN: 2000: 45.5)
3. Punctures of the very narrow elytral striae: on the two first elytral striae from base until center of elytra with at least 12 very fine, deeply penetrated (often a little oblong) punctures; pronotum densely punctured. Italy: island of Lampedusa. Body length: 2.50–2.90 mm. *Torneuma exstinguendum* MAGNANO & MIFSUD 2001
- 3*. Punctures of the wider elytral striae: from the base until the middle of elytra with at most 10 strong punctures or puncture cavities; pronotum sparsely punctured. 4
4. Pronotum barely longer than broad, more or less square-shaped; elytra cylindrical. Spain (Alicante). Body length: 2.35 mm. *Torneuma morandae* HOFFMANN 1958
- 4*. Pronotum 1.16x as long as wide; from the center towards the fore-margin laterally narrowing rectilinearly; elytra much flatter and broader. Spain (Cadiz). Body length: 3.25 mm. *Torneuma cadizensis* STÜBEN spec. nov.



Fig. 22: Type locality of *Torneuma cadizensis* spec. nov. near La Línea de la Concepción (Spain: Cadiz) under *Quercus coccifera* (i.l. Torres, photo: Torres).

long as wide; elytra approximately parallel-sided in the middle, ovally rounded directly in front of the apex; base line of elytra curved slightly S-shaped. Puncture stripes on the front half almost as broad as the arched intervals, on the posterior half clearly more slender. These intervals are covered with a single row of very fine, but easily discernable bristles.

Aedeagus: Median lobe 1.45x as long as wide, with a simply V-shaped structure of internal sac (Fig. 20) characteristic for the species of the *T. robustum* group (see key below and also Fig. 21).

Etymology: The species name refers to the province of Cádiz (Spain), in which the new species was found near La Línea de la Concepción (Fig. 22).

Ecology: The single specimen of the new species was collected by the first author's colleague J.L. Torres (Spain, La Línea) under *Quercus coccifera*.

Distribution: So far this species is only known from the Sierra Cabonera near La Línea de la Concepción in the south of Spain.

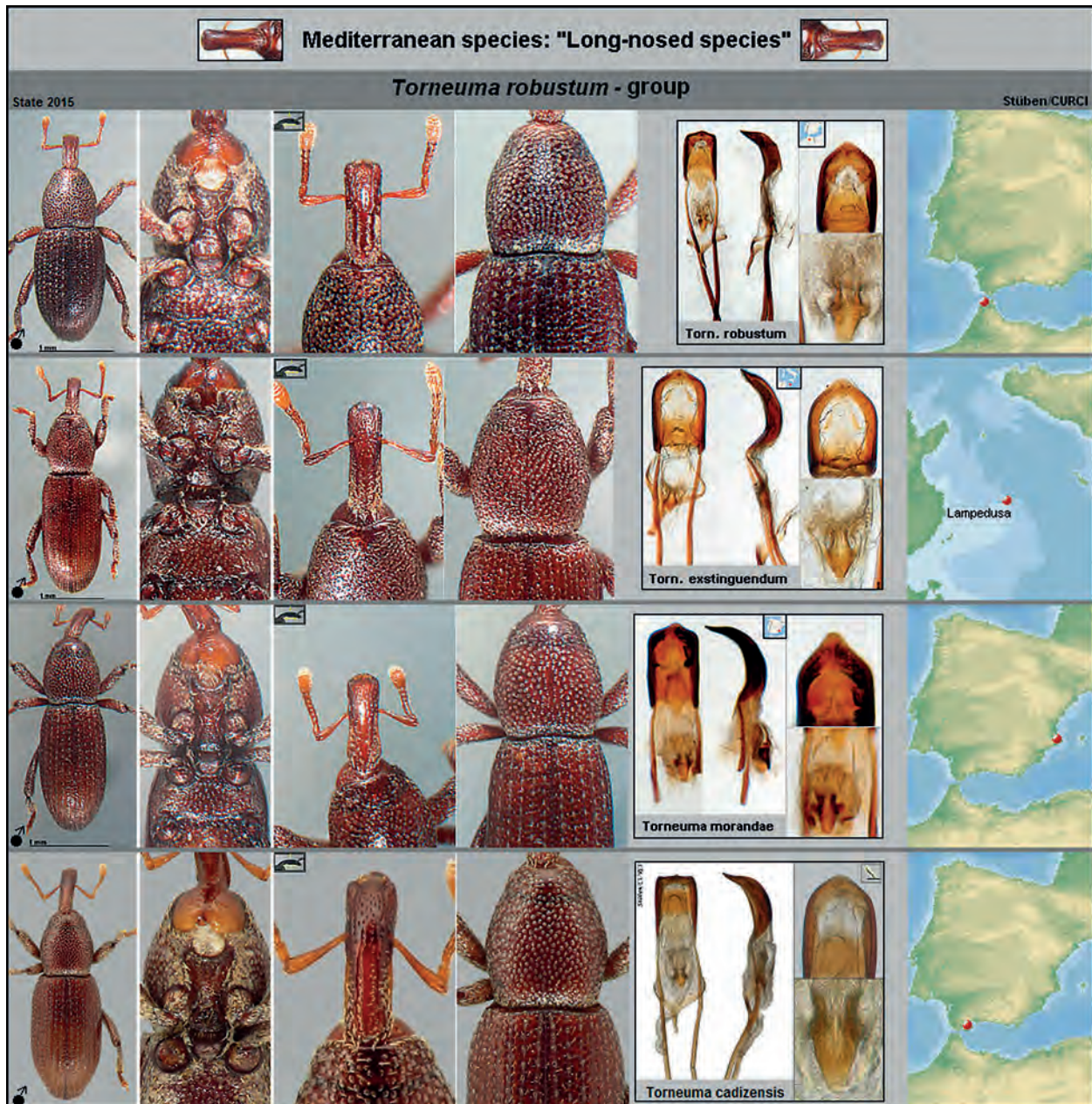


Fig. 23: Species of the *Torneuma robustum* group with a V-shaped endophallus in comparison.

Acknowledgements

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Appendix 1

Table 1: Collecting data, voucher numbers and GenBank accession numbers for the analysed material. Collecting dates are given in the format dd.mm.yyyy.

Country abbreviations: ES-Spain, IT-Italy, PT-Portugal.

30 GenBank acc. numbers (without star marking) are published in this study for the first time. 15 GenBank acc. numbers marked with a star* were taken from ASTRIN et al. 2012.

2 GenBank acc. numbers marked with two stars** were taken from STÜBEN et al. 2013.

3 GenBank acc. numbers marked with three stars*** were taken from STÜBEN & SCHÜTTE 2015.

Taxon	Collecting Data	Collectors no. ZFMK Tissue no. ZFMK DNA no. COI Genbank acc.
<i>Acallornewma doderoi</i> A. & F. SOLARI, 1909	IT, Sicilia, 5 km E Partinico, Santuario del Romitello, N38°02'37" E13°09'51", <i>Quercus ilex</i> , <i>Fraxinus</i> , 720 m, 10.10.2006, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	I-0120-dod ZFMK-TIS-cI0120 ZFMK-DNA-0100400689 GU987795*
<i>Acallornewma doderoi</i> A. & F. SOLARI, 1909	IT, Sicilia, 6 km SW Godrano, Bosco Ficuzza, Mte. Rocca Busambra, N37°51'38" E13°23'24", <i>Quercus</i> , <i>Fraxinus</i> , 1200 m, 16.10.2002, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	S-0082-dod ZFMK-TIS-cS0082 ZFMK-DNA-0100400941 EU286457*
	ES, Jaen, Sierra de Cazorla: N of Arroyo Frio, N38°00'13" W02°53'10", <i>Quercus ilex</i> , <i>Smilax</i> , 762 m, 14.05.2013, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1296-PST ZFMK-TIS-4112 ZFMK-DNA-0100426180 KJ867608
<i>Acallornewma ibericum</i> STÜBEN, 2005	ES, Jaen, Sierra Magina: SE of Torres, N37°44'46" W03°29'53", <i>Erinacea anthyllis</i> , <i>Quercus ilex</i> , <i>Astragalus</i> spec., <i>Bupleurum</i> , 1527 m, 19.05.2013, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1324-PST ZFMK-TIS-4140 ZFMK-DNA-0100426145 KJ867616
<i>Acallornewma ibericum</i> STÜBEN, 2005	ES, Jaen, S of La Guardia: Sierra de la Pandera, N37°40'20" W03°41'48", <i>Erinacea anthyllis</i> , <i>Cytisus</i> spec., 1223 m, 19.05.2013, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1336-PST ZFMK-DNA-0100426140 ZFMK-TIS-4152 KJ867619
<i>Acallornewma ingoi</i> OSELLA & ZUPPA, 2002	IT, Lazio, Alvito, S. Onófría, Val de Rio, N41°44'19" E13°43'41", <i>Carpinus</i> , 840 m, 05.05.2014, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1771-PST ZFMK-TIS-24095 ZFMK-DNA-0171624093 KP776642
<i>Acallornewma ingoi</i> OSELLA & ZUPPA, 2002	IT, Lazio, above S. Donato Val Di Comino: La grotta dei tedeschi, N41°43'67" E13°48'45", <i>Carpinus</i> , 995 m, 06.05.2014, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1774-PST ZFMK-TIS-24098 ZFMK-DNA-0171624090 KP776636
<i>Acallornewma mainardii</i> A. & F. SOLARI, 1909	IT, Sardinia, NW Ussassai: above Cant. Arqueri, N39°48'60" E09°21'59", <i>Quercus</i> , 976 m, 11.05.2014, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1785-PST ZFMK-TIS-24109 ZFMK-DNA-0171624076 KP776638
<i>Acallornewma montisalbi</i> OSELLA & ZUPPA, 2002	IT, E-Sardinia, W Siniscola: Monte Albo, N40°33'37" E09°38'01", <i>Quercus ilex</i> , 778 m, 26.09.2010, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	IT1066c ZFMK-TIS-cIT1066c ZFMK-DNA-JJ1066 KP776635
<i>Acallornewma montisalbi</i> OSELLA & ZUPPA, 2002	IT, E-Sardinia, SW Siniscola: Monte Albo, N40°32'07" E09°36'13", <i>Quercus ilex</i> , 748 m, 26.09.2010, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	IT1098c ZFMK-TIS-cIT1098c ZFMK-DNA-JJ1098 KP776633

Taxon	Collecting Data	Collectors no. ZFMK Tissue no. ZFMK DNA no. COI Genbank acc.
<i>Acallorneuma reitteri</i> MAINARDI, 1906	IT, Molise, Montenero Val Cocchiara, N41°43'22" E14°04'54", <i>Quercus</i> , <i>Rubus</i> , <i>Fraxinus</i> , 915 m, 06.05.2014, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1777-PST ZFMK-TIS-24101 ZFMK-DNA-0171624087 KP776641
<i>Acallorneuma reitteri</i> MAINARDI, 1906	IT, Abruzzo, Castèl di Ieri, Forca Caruso: Cantoni- niera, N42°04'16" E13°42'17", <i>Corylus</i> , <i>Acer</i> , 1092 m, 07.05.2014, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1780-PST ZFMK-TIS-24104 ZFMK-DNA-0171624084 KP776639
<i>Acallorneuma reitteri</i> MAINARDI, 1906	IT, Abruzzo, Castèl di Ieri, Forca Caruso: Cantoni- era, N42°04'16" E13°42'17", <i>Corylus</i> , <i>Acer</i> , 1092 m, 07.05.2014, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1782-PST ZFMK-TIS-24106 ZFMK-DNA-0171624073 KP776640
<i>Acallorneuma sardiniense</i> OSELLA & ZUPPA, 2002	IT, Sardinia, N Tortoli: P. Pedra Longa, N40°01'16" E09°41'17", <i>Pistacia</i> , 343 m, 10.05.2014, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1783-PST ZFMK-TIS-24107 ZFMK-DNA-0171624074 KU170191
<i>Acallorneuma sardiniense</i> OSELLA & ZUPPA, 2002	IT, E-Sardinia, N Dorgali: M. Tuttavista (Gipfel), N40°22'46" E09°38'22", <i>Quercus ilex</i> , 801 m, 06.10.2010, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	IT1096c ZFMK-TIS-cIT1096c ZFMK-DNA-JJ1096 JX181781**
<i>Kyklioacalles erinaceus</i> STÜBEN, 2003	ES, Jaen, Sierra de Cazorla: N of Arroyo Frio, N38°00'13" W02°53'10", <i>Quercus ilex</i> , <i>Smilax</i> , 762 m, 14.05.2013, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1298-PST ZFMK-TIS-4114 ZFMK-DNA-0100426167 KJ867609
<i>Kyklioacalles punctaticollis meteoricus</i> (P. MEYER, 1909)	ES, Granada, E of Baul, Sierra de Baza: Santa Barbara, N37°23'10" W02°50'55", <i>Bupleurum</i> , <i>Astragalus spec.</i> , 1911 m, 17.05.2013, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1320-PST ZFMK-TIS-4136 ZFMK-DNA-0100426156 KJ867614
<i>Kyklioacalles punctaticollis meteoricus</i> (P. MEYER, 1909)	France, Alpes-de-Hautes-Provence, 11 km NE Castellane, near Soleilhas, Col de St. Barnabé, N43°51'55" E06°37'52", <i>Helleborus</i> , broom, 1368 m, 30.12.2007, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	F-449-met ZFMK-TIS-cF449 ZFMK-DNA-0100400234 GU981489*
<i>Kyklioacalles punctaticollis punctaticollis</i> (LUCAS, 1849)	ES, Prov. Málaga, Algatocin: near Opayar, N36°34'39" W05°18'13", 576 m, 17.08.2010, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	ES1063 ZFMK-TIS-cES1063' ZFMK-DNA-JJ1063 KU170190
<i>Kyklioacalles punctaticollis punctaticollis</i> (LUCAS, 1849)	ES, Jaen, Sierra Magina: SE of Torres, N37°44'46" W03°29'53", <i>Erinacea anthyllis</i> , <i>Quercus ilex</i> , <i>Astragalus spec.</i> , <i>Bupleurum</i> , 1527 m, 19.05.2013, leg. Stüben, P. & Schütte, A., det. Stüben, P., Coll. ZFMK	1328-PST ZFMK-TIS-4144 ZFMK-DNA-0100426149 KJ867618
<i>Torneuma (Paratorneuma) aphroditae</i> GERMANN & STÜBEN, 2006 comb. nov. formerly: <i>Paratyphloporus</i>	ES, Canary Islands, La Gomera, S Hermigua, El Cedro: Meriga, 28°09'12"N 17°14'13"W, <i>Laurisilva</i> , <i>Persea indica</i> , stream valley, soil sample from type locality, 829 m, 28.12.2009, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	ES1014 ZFMK-TIS-cES1014 ZFMK-DNA-JJ1014 JX181783**

Taxon	Collecting Data	Collectors no. ZFMK Tissue no. ZFMK DNA no. COI Genbank acc.
<i>Torneuma (Paratorneuma) aphroditae</i> GERMANN & STÜBEN, 2006 comb. nov. formerly: <i>Paratyphloporus</i>	ES, La Gomera, Parque Nacional de Garajonay: 500 m SW Eremita de Nuestra Señora de Lourdes: Campamento viejo, MSS trap, N28°07'11.4" W17°13'33.2", 991 m, 17.11.2013, leg. Oromí, P., det. Stüben, P.	2862-PST_ADN569 n.a. n.a. KX246402
<i>Torneuma (Paratorneuma) aphroditae</i> GERMANN & STÜBEN, 2006 comb. nov. formerly: <i>Paratyphloporus</i>	ES, La Gomera, Parque Nacional de Garajonay: 500 m SW Eremita de Nuestra Señora de Lourdes: Campamento viejo, MSS trap, N28°07'11.4" W17°13'33.2", 991 m, 17.11.2013, leg. Oromí, P., det. Stüben, P.	2863-PST_ADN570 n.a. n.a. KX246403
<i>Torneuma (Paratorneuma) feloi</i> (STÜBEN, 2007) comb. nov. formerly: <i>Paratyphloporus</i>	ES, Canary Islands, Tenerife, Balo Blanco (Lavada de Tierra), N28°21'58" W16°35'14", washing soil, 660 m, 15.10.2009, leg. Oromí, P. & López, H., det. Stüben, P., Coll. ZFMK	2857-PST ZFMK-TIS-4252 ZFMK-DNA-FC17941527 KX246399
<i>Torneuma (Paratorneuma) feloi</i> (STÜBEN, 2007) comb. nov. formerly: <i>Paratyphloporus</i>	ES, Canary Islands, Tenerife, Balo Blanco (Lavada de Tierra), N28°21'58" W16°35'14", MSS trap, 660 m, 10.02.2014, le. Oromí, P. & López, H., det. Stüben, P., Coll. ZFMK	2859-PST ZFMK-TIS-4254 ZFMK-DNA-FC17941543 KX246400
<i>Torneuma (Paratorneuma) orbatum</i> (WOLLASTON, 1865)	ES, Canary Islands, La Gomera, Hermigua, Ibo Alfaro, N28°09'58" W17°12'11", <i>Persea</i> , 255 m, 09.10.2008, leg. Astrin, J. & Stüben, P., det. Stüben, P., Coll. ZFMK	E-733-orb ZFMK-TIS-cE733 ZFMK-DNA-0100404822 FJ716580'
<i>Torneuma (Paratorneuma) orbatum</i> (WOLLASTON, 1865)	ES, Canary Islands, La Gomera, S Hermigua, El Cedro: behind Aceviños, 28°08'02"N 17°13'44"W, <i>Persea indica</i> , 890 m, 04.12.2009, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	ES1003 ZFMK-TIS-cES1003 ZFMK-DNA-JJ1003 KP776634
<i>Torneuma (Paratorneuma) orbatum</i> (WOLLASTON, 1865)	ES, La Gomera, Parque Nacional de Garajonay, 500 m E Eremita de Nuestra Señora de Lourdes: Reventón Oscuro, N28°07'27" W17°12'58.5", MSS trap, 1071 m, 16.11.2013, leg. Oromí, P., det. Stüben, P.	2864-PST_ADN571 n.a. n.a. KX246404
<i>Torneuma (Paratyphloporus) karamani</i> (FORMÁNEK, 1912)	Croatia, Dalmatia, 21 km E Split, Mosor Mts., N Omis, Gata, N43°27'59" E16°41'40", Olea, Quercus, Carpinus, 280 m, 02.07.2007, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	HR-0312-kar ZFMK-TIS-cHR0312 ZFMK-DNA-0100400108 EU286506'
<i>Torneuma baeticum</i> STÜBEN, 2007	UK, Gibraltar, Engineer Road, Upper Rock, 36°07'26N 5°20'50"W, <i>Ficus carica</i> , 160 m, 03.02.2010, leg. Perez & Bensusan, det. Perez and Bensusan, Coll. ZFMK	GI1044 ZFMK-TIS-cGI1044 ZFMK-DNA-JJ1044 KP776630
<i>Torneuma cf. bensusani</i>	ES, Ceuta, Mirador Isabel II, 35°53'33"N 5°21'47"W, <i>Asphodelus</i> sp., 207 m, 08.05.2010, leg. Bensusan & Guillem, det. Bensusan and Guillem, Coll. ZFMK	ES1043 ZFMK-TIS-cES1043 ZFMK-DNA-JJ1043 KP776632
<i>Torneuma</i> (s. l.) <i>cadizensis</i> sp. n. STÜBEN, 2016	ES, Cádiz, La Linea, Sierra Carbonera, Puerto Higueron, Cordel Ruta Verde cribando Bajo Coscoja, N36°13'17" W5°20'60", <i>Quercus coceifera</i> , 155 m, 28.09.2010, leg. Torres, J. L., det. Stüben, P., Coll. ZFMK	100-PST ZFMK-DNA-0100417927 KC783806
<i>Torneuma</i> (s. str.) <i>caecum</i> WOLLASTON, 1860	PT, Madeira, 1 km S Curral das Freiras, Seara Velha, N32°42'35" W16°58'17", <i>Ficus carica</i> , 384 m, 20.03.2008, leg. Astrin, J. & Stüben, P., det. Astrin, J. and Stüben, P., Coll. ZFMK	P-523-cae ZFMK-TIS-cP523 ZFMK-DNA-0100400286 FJ716559'

Taxon	Collecting Data	Collectors no. ZFMK Tissue no. ZFMK DNA no. COI Genbank acc.
<i>Torneuma</i> (s. str.) <i>desilvai</i> OSELLA & ZUPPA, 1998	PT, Madeira, São Vicent, N32°47'51" W17°02'33", <i>Laurus azorica</i> , 85 m, 22.03.2008, leg. Astrin, J. & Stüben, P., det. Astrin, J. and Stüben, P., Coll. ZFMK	P-529-des ZFMK-TIS-cP529 ZFMK-DNA-0100400638 FJ716547*
<i>Torneuma</i> (s. str.) <i>isambertoii</i> sp. n. STÜBEN, 2016	PT, Madeira, Paul do Mar (20), N32°45'34" W17°13'43", under <i>Ficus carica</i> , E. piscatorial, 62 m, 04.04.2015, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	2790-PST ZFMK-TIS-26144 ZFMK-DNA-0169166963 KU170192
<i>Torneuma</i> (s. str.) <i>isambertoii</i> sp. n. STÜBEN, 2016	PT, Madeira, Paul do Mar (20), N32°45'34" W17°13'43", under <i>Ficus carica</i> , E. piscatorial, 62 m, 04.04.2015, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	2791-PST ZFMK-TIS-26145 ZFMK-DNA-0169166951 KU170193
<i>Torneuma</i> (s. str.) <i>korwitzii</i> STÜBEN, 2015	PT, Madeira, Paul do Mar, N32°45'34" W17°13'43", <i>Ficus</i> , 62 m, 02.07.2014, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	1860-PST ZFMK-TIS-26063 ZFMK-DNA-0171606097 KP776628***
<i>Torneuma</i> (s. str.) <i>korwitzii</i> STÜBEN, 2015	PT, Madeira, Paul do Mar, N32°45'34" W17°13'43", <i>Ficus</i> , 62 m, 02.07.2014, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	1864-PST ZFMK-TIS-26067 ZFMK-DNA-0171606101 KP776629***
<i>Torneuma</i> (s. str.) <i>maderense</i> STÜBEN, 2002	PT, Madeira, W Porto Moniz, Santa Madalena: Rib. do Tristao, N32°51'20" W17°12'21", Moraceae, 154 m, 29.06.2014, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	1842-PST ZFMK-TIS-26045 ZFMK-DNA-0171606127 KP869115***
<i>Torneuma</i> (s. str.) <i>maderense</i> STÜBEN, 2002	PT, Madeira, 3,5 km W Porto Moniz, Santa Madalena, N32°51'25" W17°12'18", <i>Ficus carica</i> , 296 m, 19.03.2008, leg. Astrin, J. & Stüben, P., det. Astrin, J. and Stüben, P., Coll. ZFMK	P-522-mad ZFMK-TIS-cP522 ZFMK-DNA-0100400291 FJ716558*
<i>Torneuma meseguerei lineensis</i> STÜBEN, 2009	ES, Cádiz, La Línea, Sierra Carbonera, between Puerto Higuerón and Zabal Alto, N36°12' W05°19', <i>Pistacia lentiscus</i> , 09.10.2008, leg. Torres, J. L., det. Torres, J. L., Coll. ZFMK	E-788-lin ZFMK-DNA-0100405063 ZFMK-TIS-cE788 GU988047*
<i>Torneuma</i> (s. str.) <i>picocasteloense</i> STÜBEN, 2002	PT, Madeira, Porto Santo, 2,5 km N Vila Baleira, Pico Castelo - Pico do Facho, N33°04'27" W16°19'25", <i>Cynara cardunculus</i> , 146 m, 26.03.2008, leg. Astrin, J. & Stüben, P., det. Astrin, J. and Stüben, P., Coll. ZFMK	P-535-pic ZFMK-DNA-0100400629 ZFMK-TIS-cP535 FJ716552*
<i>Torneuma</i> sp. ♀	ES, Málaga, E Málaga, Macharaviaya, N36°45'54" W04°12'47", <i>Olea europaea</i> , <i>Ulex</i> , 218 m, 06.01.2009, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	E-758-TOR ZFMK-TIS-cE758 ZFMK-DNA-0100405061 GU988048*
<i>Torneuma</i> cf. <i>viti</i>	ES, Gran Canaria, Barranco de Los Rios: Los Berrazales, N28°04'08" W15°39'22.5", MSS trap, 503 m, 30.12.2013, leg. López, H., det. Stüben, P., Coll. ZFMK	2861-PST_ADN567 n.a. n.a. KX246401
<i>Torneuma</i> cf. <i>viti</i>	ES, Gran Canaria, Barranco de Los Rios: Los Berrazales, N28°04'08" W15°39'23", MSS trap, 499 m, 30.12.2013, leg. López, H., det. Stüben, P., Coll. ZFMK	2865-PST_ADN573 n.a. n.a. KX246405

Taxon	Collecting Data	Collectors no. ZFMK Tissue no. ZFMK DNA no. COI Genbank acc.
<i>Torneuma cf. viti</i>	ES, Gran Canaria, Barranco de Los Rios: Los Berrazales, N28°04'08" W15°39'23", MSS trap, 499 m, 30.12.2013, leg. López, H., det. Stüben, P., Coll. ZFMK	2866-PST_ADN574 n.a. n.a. KX246406
<i>Torneuma (Typhloporus) deplanatum deplanatum</i> (HAMPE, 1864)	IT, Sicilia, 6 km SW Carini, Montagna Longa, N38°07'10" E13°08'31", <i>Asphodelus albus</i> , 647 m, 09.10.2006, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	I-0174-dep ZFMK-TIS-cI0174 ZFMK-DNA-0100400681 GU987789'
<i>Torneuma (Typhloporus) deplanatum deplanatum</i> (HAMPE, 1864)	IT, Sicilia, 10 km W Palermo, Monte Cuccio, Pass Torretta, N38°07'47" E13°14'55", <i>Asphodelus albus</i> , 577 m, 05.10.2006, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	I-0175-dep ZFMK-TIS-cI0175 ZFMK-DNA-0100400682 GU987790'
<i>Torneuma (Typhloporus) deplanatum deplanatum</i> (HAMPE, 1864)	IT, Sicilia, 8 km S Carini, W M. Gibilmesì, N38°04'03" E13°11'37", <i>Asphodelus albus</i> , 539 m, 10.10.2006, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	I-0305-dep ZFMK-TIS-cI0305 ZFMK-DNA-0100400382 EU286518'
<i>Torneuma (Typhloporus) deplanatum deplanatum</i> (HAMPE, 1864)	Greece, Korfu, 18 km N Kerkyra, Loutsès, Megali Grava, N39°46'38" E19°53'21", <i>Quercus pubescens</i> , <i>Laurus nobilis</i> , <i>Asphodelus</i> , 479 m, 23.09.2007, leg. Stüben, P., det. Stüben, P., Coll. ZFMK	KO-0371-dep ZFMK-TIS-cKO0371 ZFMK-DNA-0100400462 GU987874'

Appendix 2

Currently classification of the tribe Torneumatini BEDEL, 1884

GENUS *Subtorneuma* HOFFMANN, 1961: 36, **stat. nov.**, (upgraded from subgenus of *Torneuma* WOLLASTON, 1860, see differential diagnosis in: STÜBEN 2007), type species *Torneuma (Subtorneuma) normandi* HOFFMANN, 1961

Tornatum OSELLA, 1986: 7, type species *Torneuma syriacum* REITTER 1889

besucheti OSELLA, 1986: 13, **Turkey**

normandi HOFFMANN, 1961, **Algeria**

loebli OSELLA, 1986: 11, **Turkey**

syriacum galilaeum OSELLA, 1986: 11, **Israel**

syriacum simoni MEYER, 1895: 295, **Israel**

diversum OSELLA, 1986: 11

syriacum syriacum REITTER, 1889: 39, **Lebanon**

GENUS *Torneuma* WOLLASTON, 1860: 453, type species *Torneuma caecum* WOLLASTON, 1860

Coelotyphloporus SOLARI 1937: 16, type species *Torneuma curtulum* F. SOLARI, 1937

Crypharis FAIRMAIRE 1868: 498, type species *Crypharis planidorsis* FAIRMAIRE, 1868

Pseudotyphloporus SOLARI 1937: 17, type species *Torneuma grouvellei* DESBROCHERS, 1889

subgenus *Torneuma s. str.*

caecum WOLLASTON, 1860: 455, **Maderia**

brincki ROUDIER, 1965: 45

picocasteloense STÜBEN, 2002: 152, **Maderia**

desilvai OSELLA & ZUPPA, 1998: 4, **Maderia**

korwitzi STÜBEN & SCHÜTTE 2015: 1, **Maderia**

maderense STÜBEN, 2002: 151, **Maderia**

isambertoii STÜBEN, 2016, **Maderia**

subgenus *Paratorneuma* ROUDIER, 1956: 132, resyn., stat. nov. (downgraded to subgenus of *Torneuma* WOLLASTON, 1860), type species *Torneuma orbatum* WOLLASTON, 1865
aphroditae GERMANN & STÜBEN, 2006: 167, (*Paratorneuma*), **Canary Islands: La Gomera**
felo STÜBEN, 2007: 102 (*Paratyphloporus*), **Canary Islands: Tenerife**
franzi GONZÁLEZ, 1971: 7, (*Paratorneuma*), **Canary Islands: Tenerife**
lindrothi FRANZ 1981: 331, (*Paratorneuma*), **Canary Islands: La Palma**
orbatum WOLLASTON, 1865: 48, **Canary Islands: La Gomera**

incertae sedis (see above; belong perhaps to the same or a closely related subgenus)

canariense G. & M. OSELLA, 1986: 57, **Canary Islands: Gran Canaria**

solarii G. & M. OSELLA, 1986: 59, **Canary Islands: Gran Canaria**

viti G. & M. OSELLA, 1986: 54, **Canary Islands: Gran Canaria**

mesegueroi lineaensis STÜBEN, 2009: 99, **Spain**

mesegueroi mesegueroi GONZÁLEZ, 1971: 11, **Spain**

subgenus *Paratyphloporus* SOLARI, 1937: 16, stat. nov. (downgraded to subgenus of *Torneuma* WOLLASTON, 1860), type species *Torneuma karamani* FORMÁNEK, 1912

karamani FORMÁNEK, 1912: 232 (*Torneuma*), **Croatia**

zoufali REITTER, 1913: 66 (*Torneuma*), **Bosnia & Herzegovina**

incertae sedis (see above; belong perhaps to the same or a closely related subgenus)

besucheti GONZÁLEZ, 1966: 104 (*Pseudotorneuma*), **Spain (Majorca)**

mallorcense STÜBEN, 2005: 118 (*Paratorneuma*)

ericeensis STÜBEN, 2007: 97, (*Paratyphloporus*), **Italy (Sicily)**

subgenus *Pseudotorneuma* SOLARI, 1937: 16 stat. nov. (downgraded to subgenus of *Torneuma* WOLLASTON, 1860), type species *Torneuma subplanum* DESBROCHERS, 1889

crassirostre F. SOLARI, 1937: 18 (*Pseudotorneuma*), **Algeria**

humerosum F. SOLARI, 1937: 18 (*Pseudotorneuma*), **Algeria**

vaulogeri NORMAND, 1937: 257

subplanum DESBROCHERS, 1889: clviii, **Algeria**

zariquieyi ROUDIER, 1954: 101 E: SP (*Pseudotorneuma*), **Spain (Balearics)**

subgenus *Somodytes* GONZÁLEZ, 1970: 47, type species *Somodytes escolai* GONZÁLEZ, 1970

escolai GONZÁLEZ, 1970: 49 (*Somodytes*), **Spain**

subgenus *Typhloporus* HAMPE 1864: 191 resyn., (downgraded to subgenus of *Torneuma* WOLLASTON, 1860), type species *Typhloporus deplanatus* HAMPE, 1864

deplanatum abbazzii STÜBEN, 2007: 51, **Italy (Sardinia)**

deplanatum deplanatum HAMPE, 1864: 192 (*Typhloporus*), **Greece (Corfu), Italy, Algeria**

andreinii A. & F. SOLARI 1909: 277

championi A. & F. SOLARI, 1909: 278

hipponense NORMAND, 1937: 259

planidorsis FAIRMAIRE, 1868: 498 (*Crypharis*)

rosaliae ROTTENBERG, 1871: 240 (*Crypharis*)

setiferus BRISOUT, 1870: 296 (*Baridius*)

deplanatum oberthueri FAIRMAIRE, 1876: 38 (*Crypharis*), **Algeria**

deplanatum raymondi PERRIS, 1869: 28 (*Crypharis*), **Italy (Sardinia)**

sardoum DESBROCHERS, 1889: clix

deplanatum teuladense STÜBEN, 2007: 55, **Italy (Sardinia)**

Further groups of *Torneuma* s.l. (see also STÜBEN 2007) that cannot be allocated morphologically and/or molecularly to one of the above-mentioned genera or subgenera.

“Long-nosed species”

T. damry group

damryi PERRIS, 1875: 10 (*Crypharis*), **France, Italy**
grouvellei grouvellei DESBROCHERS, 1889: clviii, **France, Italy**
grouvellei liguricum STÜBEN, 2007b: 60, **Italy**

T. robustum group

robustum DIECK, 1869: 355 (*Crypharis*), **Morocco**
strigirostris FAIRMAIRE, 1873: 346 (*Crypharis*)
tingitana DIECK, 1869: 356 (*Crypharis*)
cadizensis STÜBEN, 2016, **Spain**
extinguendum MAGNANO & MIFSUD, 2001: 455, **Italy (Lampedusa)**
morandae HOFFMANN, 1958: 194, **Spain**

baeticum STÜBEN, 2007: 44, **Spain**
maltense MAGNANO & MIFSUD, 2001: 453, **Italy (Sardinia), Malta**
ficuzzense STÜBEN, 2007: 57, **Italy (Sicily)**
angelae MAGRINI & PALADINI 2015: 63, **Italy (Sicily)**
longipenne PIC, 1910: 89, **Portugal**
stanviti STÜBEN, 2008: 97, **Spain**
torresi STÜBEN, 2009: 97, **Spain**
trogodytis STÜBEN, 2009: 95, **Morocco**

incertae sedis

lagaudei F. SOLARI, 1955: 158, **France**
mateui ROUDIER, 1954: 100, **Spain**
bensusani STÜBEN, 2010: 1, **Spain**
penaensis GERMANN & BRAUNERT 2014: 562, **Portugal**

“Broad-nosed species”**T. tunisium group**

tuniseum F. SOLARI, 1937: 19, **Tunisia**
rugosum NORMAND, 1937: 259
attenuatum NORMAND, 1937: 260
boiteli NORMAND, 1937: 260, **Algeria, Tunisia**

T. siculum group

siculum elegantulum NORMAND, 1937: 261, **Algeria**
siculum siculum RAGUSA, 1881: 43, **Italy (Sicily)**
minutum MEYER, 1895: 293, **Italy (Sardinia)**
clandestinum MAGNANO & MIFSUD, 2001: 458, **Italy (Lampedusa)**
strictum MAGNANO & MIFSUD, 2001: 452, **Malta**
curtulum curtulum F. SOLARI, 1937: 19, **Italy (Sardinia)**
curtulum vastum STÜBEN, 2007: 75, **Italy (Sardinia)**
istanense alhaurinense STÜBEN, 2008: 100, **Spain**
istanense istanense STÜBEN, 2008: 98, **Spain**

T. convexiusculum group

convexiusculum convexiusculum FAIRMAIRE, 1873: 347 (*Crypharis*), **Algeria**
convexiusculum theryi DESBROCHERS, 1889: clviii, **France, Algeria, Tunisia**
rectirostris HOFFMANN, 1956: 70
incallidum NORMAND, 1937: 260

incertae sedis

serpentinum STÜBEN, 2007: 78, **Portugal**
longicolle TOURNIER, 1874: ccx (*Crypharis*), **Algeria (type missing)**
subterraneum FAIRMAIRE, 1873: 347 (*Crypharis*), **Algeria (type missing)**