

# The Namaini, a new weevil tribe with six new genera from South Africa (Coleoptera: Curculionidae: Entiminae)

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Based on a phylogenetic analysis of a large number of mainly undescribed edaphic Entiminae from South Africa, a new tribe of entimine weevils is described, which includes six new genera. Taxa included in **Namaini trib. nov.** are clustered into seven clades that are used to delimit the following genera: *Nama*, type genus of the tribe, plus the new genera *Cederbergia gen. nov.*, *Cervellaea gen. nov.*, *Namaquania gen. nov.*, *Pentamerica gen. nov.*, *Springbokia gen. nov.* and *Yamalaka gen. nov.* A key to the genera is given and four new species are described.

ADDITIONAL KEYWORDS: Bayesian Inference – edaphic weevils – new taxa – phylogenetic analysis – South Africa.

## INTRODUCTION

Recent research on weevils in previously poorly explored regions has resulted in an increase of the species number for that region by a factor of about five (Oberprieler *et al.*, 2007; Meregalli, 2013, 2020). When a single genus has been studied, particularly of edaphic, or of any non-vagile, apterous weevils, the species number has increased by a factor of 100 or more [e.g. Anderson (2010) for *Theognete* Champion, 1902; Riedel *et al.* (2013); Riedel & Narakusumu (2019) for *Trigonopterus* Fauvel, 1863]. Research specifically designed to sample weevils highly adapted to peculiar, scarcely investigated habitats in regions presenting a high level of biodiversity and endemism generally results in the discovery of large numbers of undescribed taxa, not only at the species- and genus-rank, but occasionally even at higher ranks (Zherikhin,

1987; Oberprieler *et al.*, 2007) and their taxonomic treatment can be challenging (see for example Tänzler *et al.*, 2012). A simple nomenclatural description of the new taxa increases knowledge on biodiversity of these regions and helps characterize the local ecosystems; however, in view of the still uncertain classification of the Curculionoidea (Oberprieler *et al.*, 2007), it may result in a somewhat subjective, opinion-based taxonomy, that lacks a rigorous ranking of the new taxa (Jordal *et al.*, 2014). Preliminary phylogenetic assessment of the new taxa, inferring their relationships and suggesting their placement within a framework of the present day classification, is therefore desirable, so that the new taxa can be described based on sound relationships (Pons *et al.*, 2006; Tänzler *et al.*, 2012).

## THE NAMA-GROUP PLAN OF THE PROJECT

### TACKLING THE TAXA OF THE NAMA-GROUP

The genus *Nama* Borovec & Meregalli, 2013 was described for four species of small edaphic

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Entiminae, collected in Richtersveld National Park, Northern Cape Province, Republic of South Africa (Borovec & Meregalli, 2013). Further collecting trips in the Republic of South Africa and southern Namibia, as well as the examination of extensive material deposited in private collections and in some European, North American and South African museums yielded specimens from over 60 more populations, whose morphology suggested possible affinities with the species already described in the genus *Nama*. All these specimens are defined here as belonging to the “*Nama*-group”.

Several questions arose when we tried to infer a proper classification of these taxa. First of all, are all these apparently related taxa truly belonging to a monophyletic unit? And, if any clade is delimited, in which tribe should these be placed? Is it possible to recognize within the clade, single units separated by discontinuities to be regarded as distinct genera and how many different species can be recognized among these specimens?

We had to address several biases and difficulties: (1) only two taxa sharing morphological similarities with the *Nama*-group were previously known: *Trachyphloeosoma brevicolle* Voss, 1974 and *Trachyphloeus brevis* Boheman, 1842 (which do not belong to the genera to which they were first assigned), all the others being undescribed; (2) no other apparently related taxa from the western part of South Africa (actually, from the entire sub-Saharan region) are known; and (3) there is no phylogenetic reconstruction for any of the South African members of the subfamily. When the four species of *Nama* were described, it was already doubtful that they could be referred to as a single genus, because of the great morphological variation among them (Borovec & Meregalli, 2013). The large number of new taxa that were subsequently sampled reinforced this opinion and underlined the great diversity and complexity of the *Nama*-group. Trying to identify monophyletic units, we have performed a phylogenetic analysis of these edaphic Entiminae, based on the sequences of the mitochondrial cytochrome c oxidase subunit I (*mt-Cox1* hereafter). The set of species that were analysed included sequences of a few other edaphic South African Entiminae found during our expeditions, not always identified at the species level and possibly undescribed, but whose morphology allowed their identification at genus rank: *Cycliscus* sp., *Phaylomerinthus* sp. n. 1 and *Ph.* sp. n. 2 (Embrithini) and *Oosomus* sp. (Oosomini). *Philetaerobius nidicola* Marshall, 1923 [Entiminae *incertae sedis* (Borovec et al., 2018)], an Entiminae strongly differentiated morphologically, was used as one of the outgroups.

#### RELATIONSHIPS OF THE NAMA-GROUP WITHIN THE SUBFAMILY ENTIMINAE

The relationships of the *Nama*-group at the tribal rank in the subfamily Entiminae were assessed using the data resulting from the molecular analysis. Adaptive morphological characters in these highly specialized edaphic weevils are often subject to too high a level of homoplasy to be truly informative when applied to higher rank taxa. Terricolous entimines, regardless of their phylogenetic affinities, are in fact generally wingless, often with more globular elytra, with, in dorsal view, a declivity covering the apex of the elytra, often broad, erect or suberect setae, eyes with a reduced number of ommatidia, short and robust antennae, legs and tarsi, with the apex of protibiae often armed with distinct stout spines and sometimes also lobed, metacoxae shifted from the longitudinal axis of body to the elytral borders and a wide and obtuse metaventral process. We retrieved *mt-Cox1* sequences, obtained with the same primers that we used, of taxa belonging to several tribes of the Entiminae from GenBank. We choose a species of the type-genus of the tribe, when available, or one of another genus of the same tribe, if this genus was included in a clade together with the type genus of the tribe in Gillett et al. (2018), or if the two genera are closely related morphologically. As the outgroup, *Bagous exilis* du Val, 1854, belonging to the subfamily Bagoinae and not related to the Entiminae, was chosen. Four species among those belonging to the *Nama*-group were added to the Entiminae-tribe analysis, to understand if they clustered in an independent clade or were associated with another tribe.

#### PHYLOGENETIC STRUCTURE OF THE NAMA-GROUP

In our study we tried to circumscribe monophyletic units to be considered as genera, according to the results of the molecular phylogeny based on *mt-Cox1*. The sequence data of this gene have been extensively used for recognizing relationships, and also for tackling hyperdiverse and mostly undescribed faunas (Tänzler et al., 2012). The molecular region chosen generally proved to be a powerful tool in phylogenetic studies, particularly to recognize low-rank affinities, even though in some individual lineages high error rates have been detected (Hendrich et al., 2010) and some criticism was raised. However, in the Entiminae, the mitochondrial genome proved to offer sound information on reciprocal affinities (Gillett et al., 2018).

As a further outgroup we used the Palaearctic *Trachyphloeus spinimanus* Germar 1824, because the genus *Nama* shares several morphological traits with the Trachyphloeini: a rostral epifrons with well-defined

and visible borders along the entire length, at base as wide as the space between anterior borders of eyes, dorsally placed antennal sockets, a rostrum that is wider than long, posteriorly continuous with the head, not separated from it by a transverse sulcus, trisetose mandibles, elytra without laterally protruding humeral calli in dorsal view, the entire dorsal and ventral part of body densely squamose, all femora unarmed, tibiae with short mucro, lacking spurs, metatibiae lacking corbels and short and robust legs and antennae, all the species are wingless.

#### P-DISTANCE ANALYSIS

The p-distance among the clades and among taxa was evaluated for both base- and amino acid sequences to evaluate the intergeneric and interspecific variation. There is no clear-cut threshold to discriminate between inter- and intraspecific variation, even though differences below 3–4% (= p-distance 0.03–0.04) in the sequence of *mt-Cox1* for allopatric populations can usually be applied to metapopulations of the same species, and differences of more than 6% are considered as good indicators of distinct species (Hebert *et al.*, 2003). These data were confirmed by other studies carried out on apterous, specialized and scarcely moving weevils [i.e. Meregalli *et al.* (2018) for *Dichotrachelus*]. However, Riedel *et al.* (2010) found that intraspecific variation could even reach 8.8% in *Trigonopterus*, and interspecific variation in that genus was also high, around 20%.

The procedures implemented to the study allowed us to identify the taxa belonging to the *Nama*-group, to assess its monophyly and to infer its phylogenetic structure, recognizing the monophyletic groups that were used to delimitate taxa at genus-rank.

## MATERIAL AND METHODS

### SAMPLE COLLECTION

Field work was conducted in October 2011 (Western Cape, Northern Cape), September 2012 (Western Cape, Northern Cape, southern Namibia), September 2013 (Western Cape, Northern Cape, southern Namibia), November 2016 (Western Cape, Northern Cape), November 2018 (Northern Cape, Western Cape) and October 2019 (Western Cape). The main collecting method used was sifting below large shrubs of the Euphorbiaceae, mainly *Euphorbia dregeana* E.Mey. ex Boiss. and *Euphorbia mauritanica* L., under Aizoaceae, mainly *Aizoon africanum* (L.) Klak, and occasionally below large shrubs of other flowering plant families. In a few instances some specimens were found by late evening and night sweeping of grasses. Sample locations were selected based on the

presence and number of large shrubs, offering good shelter to arthropods, and on the presence of good litter accumulation. About 5–10 L of soil were collected at each locality (quantity depending on the number of shrubs and characteristics of the litter below them) and placed in a thin layer in the sun for half an hour, to directly collect specimens that started moving. Soil was then stored in cotton bags, that were carefully opened twice a day to look for specimens, for at least 1 week, or until no additional specimens appeared, and then safely disposed of. Weevils climbed up towards the top of the bag, and were collected in tubes with ethyl acetate or with absolute ethanol. A three-digit field number was assigned to each morphospecies of edaphic weevil: first digit, the expedition (1 = 2011, 2 = 2012, 3 = 2013, 4 = 2016, 5 = 2018, 6 = 2019); second and third digit, the sequential number of the collecting site. When more than one morphospecies was found at a site, a letter was added to differentiate them (i.e. 335\_a and 335\_b).

Collected specimens were prepared dry on mounting cards. Dissected female genitalia were embedded in Solakryl BMX, and dried male genitalia were glued to the same mounting card as the insect, or conserved in glycerol in mini vials pinned together with the respective specimen.

### PHYLOGENETIC ANALYSIS

Specimens used for molecular analysis were usually preserved in small vials in ethanol, but in some cases they were mounted dry on cards. Such specimens used for the study were first rehydrated in 2 mL of a solution composed of 10 mM Tris-HCl pH 8.5, 30 mM NaCl, 5 mM EDTA for 24 h. Total DNA was extracted by placing the whole animal body in 400 µL of 5 M guanidine-isothiocyanate. The head + pronotum was separated from the rest of the body to maximize DNA extraction. Specimens were later preserved in a vial with 95% ethanol, or remounted and glued onto a card. Removal of proteins was accomplished by adding 400 µL of 4 M sodium perchlorate followed by chloroform extraction. Total DNA was precipitated from the upper phase by isopropyl alcohol precipitation and resuspended in TE buffer. A fragment of mitochondrial cytochrome oxidase subunit I (*mt-Cox1*) was amplified with primers based on Folmer *et al.* (1994) modified as in Astrin & Stüben (2008): fw: LCO1490-JJ (sequence 5'→3': CHACWAAYCATAAAGATATYGG); rev: HCO2198-JJ (sequence 5'→3'AWACTTTCVGG RTGVCCAAARAATCA). All PCRs were performed in a volume of 20 µL with HotStarTaq Master Mix (Qiagen). Amplification of DNA was done as follows: 15 min of initial denaturation (95 °C) followed by ten cycles of 30 s at 94 °C, 45 s at 60 to 50 °C (lowering the annealing temperature in each cycle by 1°C), 2 min at

72 °C followed by 30 cycles of 30 s at 94 °C, 45 s at 50 °C, 2 min at 72 °C and a final extension cycle of 15 min at 72 °C. The reaction products were purified by agarose gel electrophoresis and successive purification from the gel. Sequencing was performed by an external service (Genechron, Roma). Both strands were sequenced. Forward and reverse chromatograms were checked with Chromas (<http://technelysium.com.au/wp/chromas/>) using default parameters and ambiguities were corrected manually. The *mt-Cox1* sequences had no indels after alignment, and no stop codons were detected, so the presence of NUMT pseudogenes was excluded. Multiple sequence alignment of both strands was performed with MEGA-X (Tamura *et al.*, 2013), after reversing and complementing the reverse strand, with the Muscle alignment option. The sequences were trimmed at the extremes and the final sequences that were used for the analysis were 658 bp long. The correspondence with the codons was obtained by deleting the first nucleotide, thus the analyses were conducted on a segment of 657 bp. All the sequences used for the phylogenetic analysis were deposited in GenBank. Since it was not possible to examine the chromatograms of the sequences retrieved from GenBank, their quality was checked by comparing for congruity, when possible, with the sequences of different accessions of the same species, or of related species of the same genus. Only sequences differing from the others in only few sites were used.

Pairwise distance was calculated with MEGA-X, implementing the p-distance model. Bayesian inference (BI hereafter) was estimated using MrBayes v.3.2. Two runs with four chains were run for 2 000 000 generations, sampling every 500 generations. The chains were left free to sample all the models of the GTR family using reversible jump Monte Carlo Markov chain (MCMC) (Huelsenbeck *et al.*, 2004). Heterogeneity of substitution rates among different sites was modelled with a four categories discretized  $\Gamma$  distribution, with a proportion of invariables. The matrix was partitioned so that substitution rates could vary according to the nucleotide position in the codon. The first 25% of generations were discarded (burn-in) and convergence was evaluated with the average standard deviation of split frequencies. Goodness of mixing was assessed looking at the acceptance rate of swaps between adjacent chains, following Ronquist *et al.* (2012). After a first analysis, the temperature was lowered to 0.05 in order to improve swaps between chains. The resulting consensus tree was examined with Figtree (Rambaut, 2014).

There has been considerable debate about the validity of the supports obtained in phylogenetic analyses (Hillis & Bull, 1993; Wheeler & Pickett, 2008). To better evaluate the credibility of the monophyletic groups, we tested each clade on MrBayes by respectively

constraining the clade to be always present (positive constraint) or absent (negative constraint) in the sampled trees, and estimating the difference of the marginal likelihoods of the two analyses [Bayes Factor (BF)]. For some clades whose affinity was scarcely supported, the alternative topologies were also tested. The stepping-stone algorithm (Xie *et al.*, 2011), provided in the Mr Bayes program, was implemented with 50 steps and a total length of 255 000 generations, with the first step discarded as burn-in. A topology was considered as supported when the marginal likelihood of the positive constraint was better than the negative constraint by at least 5 log units, as indicated by Kass & Raftery (1995).

#### MORPHOLOGICAL SYNAPOMORPHIES

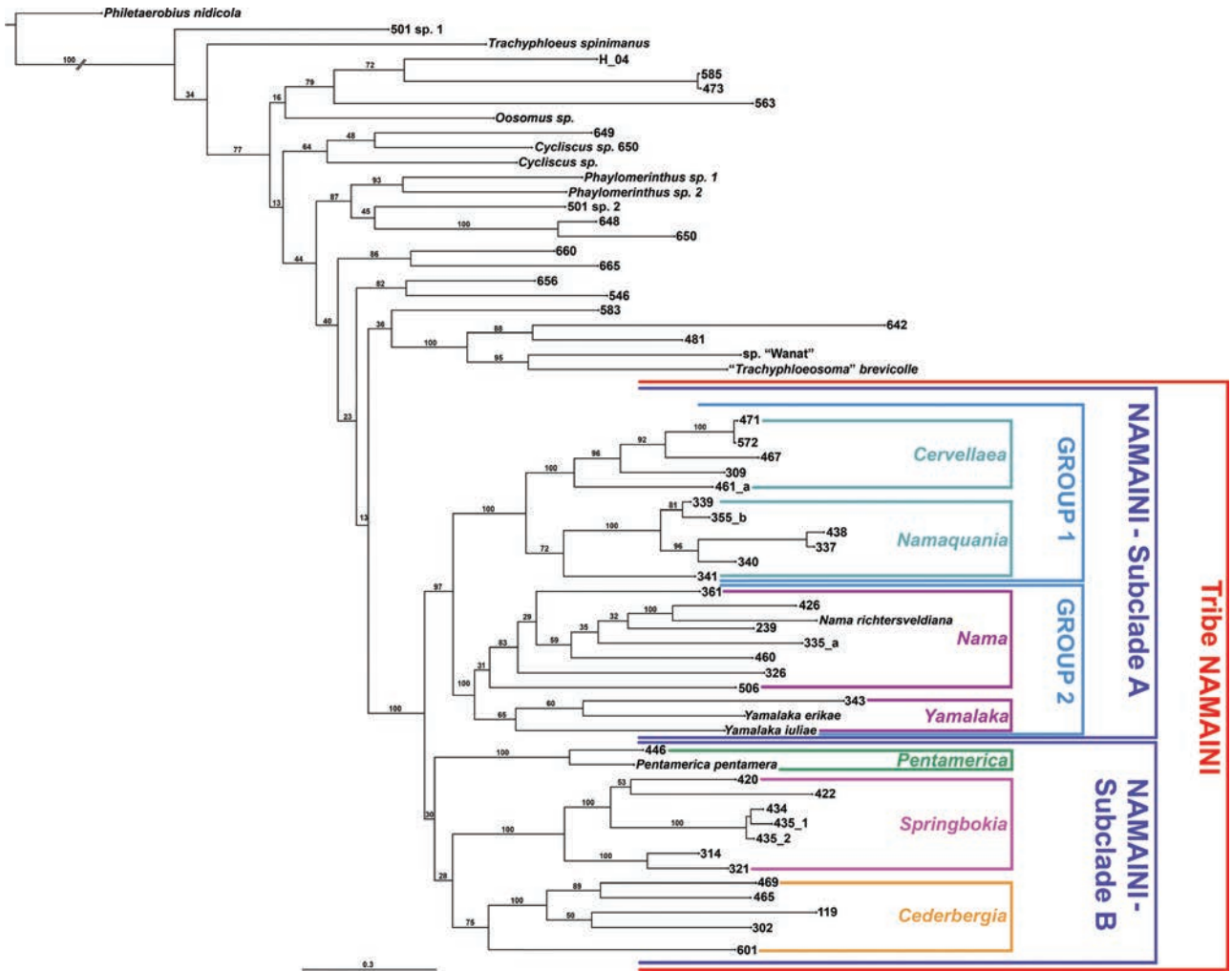
Based on the results of the phylogenetic analysis, all species that were included in the phylogenetic tree were visually examined based on external characters and genitalia to recognize synapomorphies; this to obtain a morphological characterization of the genera. Based on these synapomorphies, all taxa that could not be sequenced were referred to one of the genera.

## RESULTS

### PHYLOGENETIC ANALYSIS

Most edaphic taxa of the Entiminae that were sequenced, including those previously described in the genus *Nama*, cluster in a maximally supported clade (which is described below as the new tribe Namaini) (Fig. 1). This clade is composed of two major subclades. Subclade A is strongly supported (97% post probability in BI) and is composed of two maximally supported groups (Group 1 and Group 2). Each of these groups includes two clades that we consider here as genera (the new genera *Cervellaea* and *Namaquania* in Group 1, and *Nama* and the new genus *Yamalaka* in Group 2). *Nama* includes *Nama richtersveldiana* Borovec & Meregalli, 2013, the type species, and two of the other three species originally described as *Nama* are placed in the new genus *Yamalaka*. All these clades were strongly supported also by the BF, with values always higher than 10 and even up to 40.

Subclade B is not statistically supported (30% pp), probably due to the uncertain placement of the new genus *Pentamerica* (described below). However, each of the three clades within subclade B is strongly supported, two having maximal support and the third one with 75% pp, and all have high values of the BF. These monophyletic groups represent three more new genera (*Cederbergia*, *Pentamerica* and *Springbokia*).



**Figure 1.** The *Nama*-group phylogeny, Bayesian Inference consensus tree, all branches are shown. Branch post probability support is indicated on the branches, in percentage. Scale bar unit: expected substitutions per site.

The position of *Pentamerica*, that includes the fourth of the species originally described as *Nama*, *Nama pentamera* Borovec & Meregalli, 2013, is tested with the application of the BF, alternatively constraining it to be monophyletic with the genera of Subclade A or with those of Subclade B. The BF vaguely associated it with Subclade A rather than with Subclade B, where it is placed by the BI, but only by two units of marginal likelihood (ML = -14367 vs. -14369), a value not significant according to Kass & Raftery (1995). The affinities between the three genera in Subclade B were also tested, and in this case the BF strongly indicates closer relationships of *Pentamerica* with *Springbokia* rather than with *Cederbergia* (BF = 12, ML = -14372 vs. -14374). A group of species, including “*Trachyphloeosoma brevicolle*”, clusters as sister to the Namaini clade. The other edaphic species that were analysed cluster in various groups, in part corresponding to different

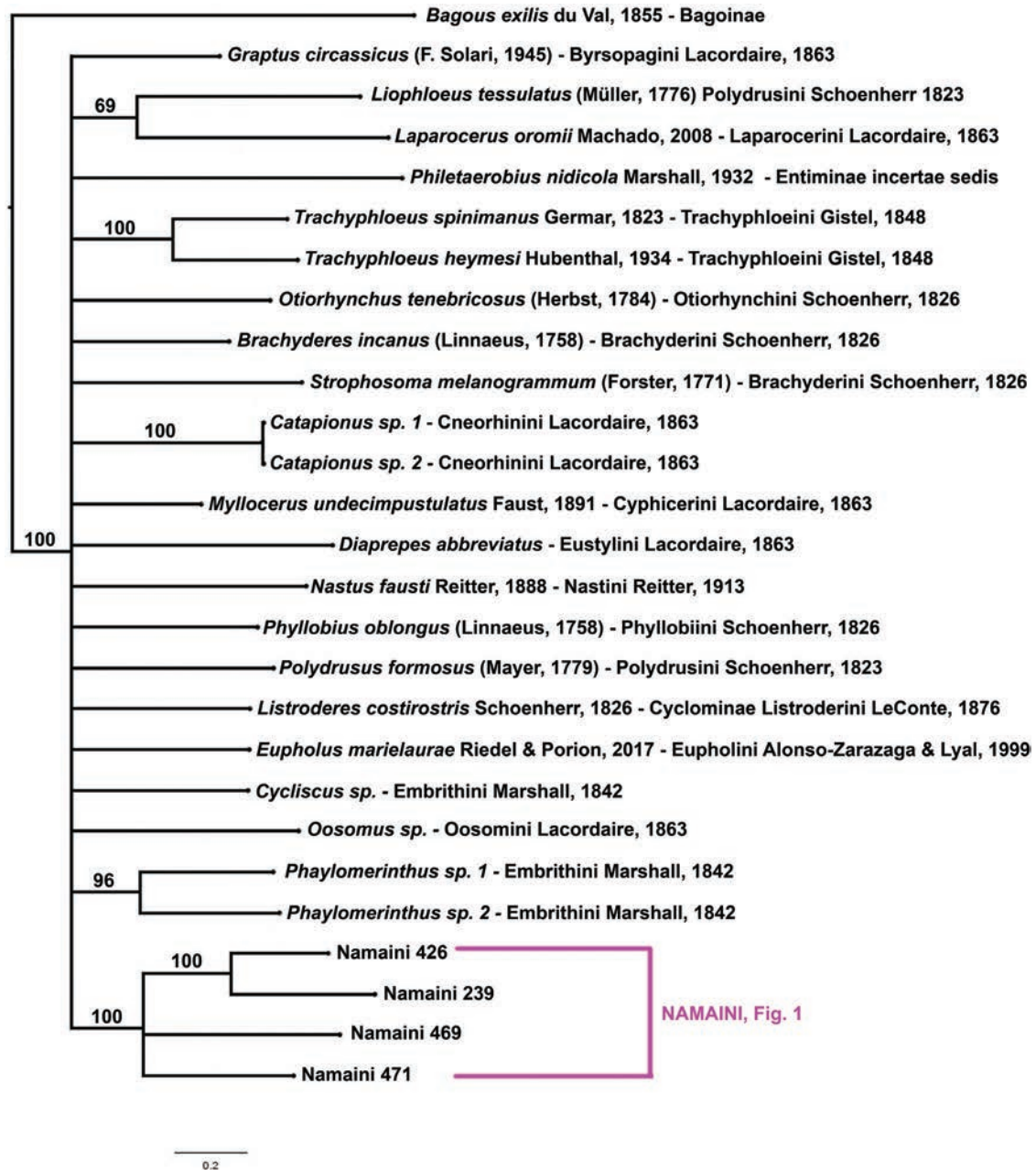
tribes. These species are not discussed in the present paper.

RELATIONSHIPS OF THE NAMAINI WITH OTHER TRIBES OF THE ENTIMINAE

The species of Namaini, as defined by the previous analysis, cluster in a maximally supported clade also in this analysis, with no indication of any relationship with other tribes of the Entiminae (Fig. 2).

P-DISTANCE

The p-distance evaluated between species of the Namaini and the two outgroups, *Philtaerobius nidicola* and *Trachyphloeus spinimanus*, varies between 0.17 and 0.22 with a mean distance of 0.195 and a median distance of 0.191. The p-distance between the two subclades of the *Namaini* is generally



**Figure 2.** The Namaini tribe in the Entiminae, Bayesian Inference consensus tree (50% majority rule). Branch post probability support is indicated on the branches, in percentage. Scale bar unit: expected substitutions per site.

a little lower, approximately between 0.15 and 0.18. The taxa included in *Cervellaea* differ from those in *Namaquania* approximately by 0.12 to 0.15, whereas the reciprocal difference among taxa of the other genera is generally higher, comprised between 0.15 and 0.18. The interspecific distances among the taxa within each genus varies depending on the taxa, from 0.04 for what appear to be isolated metapopulations of the same taxon, to more than 0.18. Intraspecific distance is only

available for a few taxa, and it is always limited, lower than 0.01. Also, intrapopulation distance is scarce in the few cases that were tested (Table S1).

#### MT-COX1 SEQUENCES

The aligned sequences of the taxa included in the Namaini were examined with MEGA-X. The sites conserved among all the taxa were 382/657 (53.6%),

and the amino acids (aa) conserved were 173/219 (79%). This confirmed that in the majority of cases the substitution regarded the third nucleotide of the codon, not resulting in a variation of the aa. The rate of variation differed among the genera. *Cervellaea*: sites conserved 511/657 (77.8%), aa 210/219 (95.9%); *Namaquania*: sites conserved 524/657 (79.8%), aa 213/219 (97.6%); *Nama*: sites conserved 427/657 (65%), aa 194/219 (88.6%); *Yamalaka*: sites conserved 492/657 (74.9%), aa 205/219 (93.6%); *Pentamerica*: sites conserved 587/657 (89.3%), aa 229/229 (100%); *Springbokia*: sites 479/657 (72.9%), aa 208/219 (95%); *Cederbergia*: sites conserved 460/657 (70%), aa 207/219 (94.5%). The species of *Cervellaea* shared some molecular synapomorphies, in particular they had a thymine in site 295 of the 657 chain (vs. an adenine in all other taxa of the Namaini), a cytosine in site 296 vs. a guanine in all other taxa, an adenine in site 484 (vs. a cytosine or a thymine) and a thymine replacing a cytosine in site 485. Regarding the aa chain, *Cervellaea* differed from all other taxa of Namaini for a methionine replacing a proline or a leucine in position 162 of the 219 aa long chain and again a methionine replacing a valine or an isoleucine in position 199. The species of *Namaquania*, that, together with *Cervellaea*, formed Group 1 of Subclade A, differed in their sequence from those of the later for an adenine in sites 24 (a thymine in *Cervellaea*) and 471 (a thymine or a cytosine in *Cervellaea*), and a cytosine in sites 484 and 485 (vs. respectively an adenine and a thymine, in *Cervellaea*, respectively). All species of *Nama* and *Yamalaka* (Subclade A, Group 2) shared an adenine in site 241, instead of a cytosine or a thymine, and a thymine instead of a guanine in site 511. In the aa chain, the species of *Nama* had an isoleucine replacing a methionine in position 19, a synapomorphy shared with the species of *Springbokia*, and a methionine replacing a leucine in position 81, in this case the synapomorphy was shared with the species of *Yamalaka*, as is also the case of a serine replacing an alanine in position 171. A few molecular synapomorphies were also found in *Pentamerica*, a thymine replacing a guanine or an adenine in site 472, another thymine replacing a cytosine or an adenine in site 484 and an adenine replacing a cytosine in site 485; the last two substitutions resulting in the replacement of a proline with an isoleucine. In site 496, the two species of *Pentamerica* shared a thymine with all the other taxa of Subclade B (usually a guanine for the species of Subclade A). This was the only molecular synapomorphy shared by all the species of Subclade B and it determined the substitution of an alanine with a serine in position 166 of the aa chain for all these species. All species in *Springbokia* have a thymine replacing an adenine in site 291 (character shared with species 460 of *Nama*). An adenine in site 379

was shared by all the taxa of the genus, and almost all the taxa of *Cederbergia*, whereas in all the other taxa of the Namaini there was a guanine in this site. This determined the substitution of a valine with an isoleucine in the aa chain in position 127. The species in *Cederbergia* shared an adenine in site 352 and a guanine (vs. a cytosine) in site 353, that determined the constant presence of a serine in position 118 of the aa chain (fasta file with the sequences supplied in Table S2).

## DISCUSSION

THE *NAMA*-GROUP RELATIONSHIPS IN THE ENTIMINAE  
The species of the *Nama*-group cluster in a clade distinct from all other Entiminae and no relationships with taxa of other tribes of Entiminae were found. The tribal classification of the subfamily Entiminae is still debated, and even its monophyly seems questionable (McKenna *et al.*, 2009; Gillett *et al.*, 2014, 2018). The tribes, as presently defined (Alonso-Zarazaga & Lyal, 1999), can be used only in a historical, traditional sense, and do not represent the evolutionary structure of the subfamily. Relationships among the tribes is contrasting in papers dealing with the Curculionoidea (McKenna *et al.*, 2009; Haran *et al.*, 2013; Gillett *et al.*, 2014). In particular, Gillett *et al.* (2018) demonstrated that most of the tribes, in their present composition, are para- or polyphyletic. Most of the South African genera were referred to tribes native to the Palaearctic region without a critical analysis of the characters. One of the most important attempts at a reclassification of the Afrotropical entimines was by Marshall (1942). Based on chaetotaxy of the mandibles, he split entimines with “otiorhynchine”-type antennal scrobes (scrobes entirely visible in dorsal view, in profile not forming narrow furrow mostly directed downwards) into two main groups: a group with the mandible bearing only three setae and a group where the mandible bears more or less numerous setae. This mandible chaetotaxy seems to reflect relationships and is still used today, for example, for the redefinition of the tribe Embrithini (Borovec & Oberprieler, 2013). Using this character, the Afrotropical entimines with “otiorhynchine”-type scrobes, lacking laterally prominent humeral calli and having trisetose mandibles, were included in the tribes Embrithini, Oosomini, “Peritelini” and “Trachyphloeini”, even though the attribution of the Afrotropical genera to the latter two tribes is questionable. A detailed discussion and a differential diagnosis of the Namaini vs. the other Afrotropical entimine tribes is given in the *Remarks* section of the treatment of the tribe.

Since the *mt-Cox1* analysis shows that no close relationships exist between the *Nama*-group and any of

the other tribes of Entiminae—as defined by their type-genus—of which *mt-Cox1* sequences were available, the *Nama*-group is here assigned to a new tribe, the Namaini.

#### PHYLOGENETIC LINEAGES IN THE TRIBE NAMAINI

Our study reveals that the tribe Namaini includes seven monophyletic units, each used to define genus-rank taxa.

The two main subclades, Subclade A and Subclade B, that compose the Namaini clade, might suggest that the tribe is composed of two distinct subtribes. However, the second subclade has no statistical support, and indeed the affinities of *Pentamerica* could not be determined. Therefore, a subdivision of the tribe into subtribes is not justified. The two genera composing the first group of Subclade A have maximal support and are clearly well delimited by molecular sequences, with some molecular and morphological synapomorphies. The taxa included in each of the two genera are morphologically uniform, with a p-distance usually around 0.09–0.10. Therefore, the attribution of the taxa whose sequences were not available to *Cervellaea* or *Namaquania* was relatively easy. The relationships of *Nama* with *Yamalaka*, the two genera composing the second groups of Subclade A, are sound. Both genera are composed of relatively well-differentiated taxa, both in their morphology and *mt-Cox1* sequences, with a p-distance of about 0.15. The remaining genera appear to be isolated and their reciprocal relationships could not be clearly disclosed.

The placement of *Pentamerica* is uncertain, since no sound evidence correlating it to either of the two subclades was obtained, neither by the Bayesian inference (associating it to Subclade B, but only with 30% pp) nor by the Bayes factor (associating it to Subclade A, but with BF = 2). The molecular sequences confirm this uncertainty, with the nucleotides of some sites shared with taxa of *Nama* (Subclade A) and those of other sites shared with taxa of *Springbokia* (Subclade B). *Springbokia* is clearly defined by morphology and *mt-Cox1* sequences; the p-distances among the taxa vary between 0.10 and 0.15. Finally, four of the taxa that cluster in *Cedebergia* appear to be reciprocally closely related, also based on their morphology, while the other species, 601, is more isolated, also geographically.

In the present paper the new tribe and the new genera corresponding to these monophyletic units are described. Due to the complexity of the Namaini and the large number of new species, only the type species of each new genus are described here. The other taxa of the various genera are listed with their locality code and their formal descriptions will be the subject of further papers.

In the taxonomic part of the paper only the main diagnosis of all the new taxa have been reported. The

detailed morphological descriptions of each taxon, the discussions on the reciprocal relationships and the differential diagnoses are added in [Supporting Information, File S1](#).

#### TAXONOMY

##### NAMAINI BOROVEC & MEREGALLI, TRIB. NOV.

*Type genus:* *Nama* Borovec & Meregalli, 2013, here designated.

*Zoobank registration:* urn:lsid:zoobank.org:act:944D0242-515B-4A1E-9C2C-62A14267062E

*Diagnostic description.* Subfamily Entiminae. Small size, 1.4–4.9 mm; body densely squamose, flightless; rostrum short and wide, posteriorly continuous with head; epifrons at base reaching inner margins of eyes, mostly with U- or V-shaped stria on dorsum; frons with a few exceptions densely squamose; antennal sockets in dorsal view hardly visible, furrow-shaped to narrowly reniform, laterally slightly to distinctly enlarged posteriad, directed towards eye or above eye; eyes small to middle sized; antennal scapes mostly robust; anterior margin of pronotum laterally without ocular lobes or vibrissae; elytral humeral calli not developed; metaventral process wide, distinctly wider than transverse diameter of metacoxa; femora unarmed; metatibiae lacking corbels; claws free, distinctly divaricate; *Ventrites* densely squamose, only exceptionally glabrous; female sternite VIII with long and slender apodeme terminating at base or inside of plate; gonocoxites with apical styli.

*Distribution:* South Africa (Western and Northern Cape), Namibia (Karas).

*Remarks:* The Namaini is a small tribe of entimines, comprising seven genera, six of which are described here. They are native to the south-western part of South Africa and adjacent Namibia. This tribe is clearly delimited by *mt-Cox1* sequences, and it can also be characterized by morphological traits. The new tribe underlines the limits of the traditional practice of referring Afrotropical genera to Palaeartic tribes, a procedure that often leads to polyphyletic taxa, particularly in the case of these wingless, highly adapted and scarcely vagile edaphic species.

Because of the free claws and absence of metatibial corbels, the Namaini could be associated with the Oosomini Lacordaire, 1863, a tribe mainly restricted to South Africa, comprising genera of small- to middle-sized weevils. However, at present it is not clearly delimited and in its present composition it seems to be polyphyletic. Therefore, only species belonging to the



type genus *Oosomus* Schoenherr, 1834, collected in the course of our expeditions, were used for the molecular analysis, and no relationship of this genus with the Namaini was indicated. According to its morphological characters, the Namaini differ from the Oosomini by the following characters: rostrum conspicuously wider than long (either wider than long, or in some genera elongate to a different degree in the Oosomini), frons densely squamose (glabrous in the Oosomini), eyes small, often placed in the lower part of head (moderately large, positioned dorsally in the Oosomini), scapes short, robust (long, slender in the Oosomini), mesepimera moderately large, subtriangular (small, narrow in the Oosomini), metacoxae separated by 1.5–2.0 × their width (as wide as width of coxa in the Oosomini), suture between ventrite 1 and 2 straight, slightly sinuate or deeply arched (straight in the Oosomini), appressed scales greyish to brownish, always lacking a metallic sheen (with a greenish or bluish sheen in some taxa in the Oosomini).

The Namaini is easily differentiated from the Embrithini, another Afrotropical entimine tribe with trisetose mandibles. The Namaini has free claws (all genera of the Embrithini have species with connate claws), absence of metatibial corbels (wide or narrow, densely setose or squamose corbels in the Embrithini) and the rostrum continuous with the head (rostrum separated by a broad depression or a transverse stria in the Embrithini).

There is a group of genera in the eastern part of South Africa that are provisionally maintained in the tribe Trachyphloeini (see Borovec & Skuhrovec, 2017), because in the absence of molecular data, it is difficult to determine if they really belong to this primarily Palaearctic tribe, showing a disjunct distribution (no species or genus of true Trachyphloeini is known from subtropical and tropical parts of Africa), or if the morphological similarity is due to homoplastic sharing of adaptive characters in edaphic species. However, the Namaini can be distinguished from these genera by the same traits indicated for the Embrithini, except the metatibial corbels, also lacking in the species of these genera.

Alonso-Zarazaga & Lyal (1999) also reported the tribe Otorhynchini for the Afrotropical region, represented by the genus *Sciobius* Schoenherr, 1823, and four other small genera known from South Africa and Madagascar. These five genera differ from the Palaearctic genera referred to the Otorhynchini and their placement is yet unclear. However, the Namaini differs from these Afrotropical Otorhynchini by the rostrum not expanded laterally to form pterygia (forming pterygia in the Otorhynchini), the squamose frons (glabrous in the Otorhynchini), the antennal scapes short and robust (slender and long in the Otorhynchini) and the tibiae lacking spur (with spur in all tibiae in the Otorhynchini).

The tribe Peritelini includes almost 30 genera and a large number of species in the Palaearctic region, mainly in its south-western part, and these differ from the almost 40 Afrotropical genera referred to the Peritelini known mainly from East Africa. Both groups of this tribe, the Palaearctic as well as the Afrotropical Peritelini, differ from the Namaini by having connate claws, and the Afrotropical genera also by a slender stria separating the rostrum from the head.

#### SUBCLADE A - GROUP 1

##### *CERVELLAEA* BOROVEC & MEREGALLI, GEN. NOV.

*Zoobank registration:* urn:lsid:zoobank.org:act:E0FDE5CC-1C9D-4B01-B419-9A85A96F45A5

*Type species:* *Cervellaea coheni* Borovec & Meregalli, here designated.

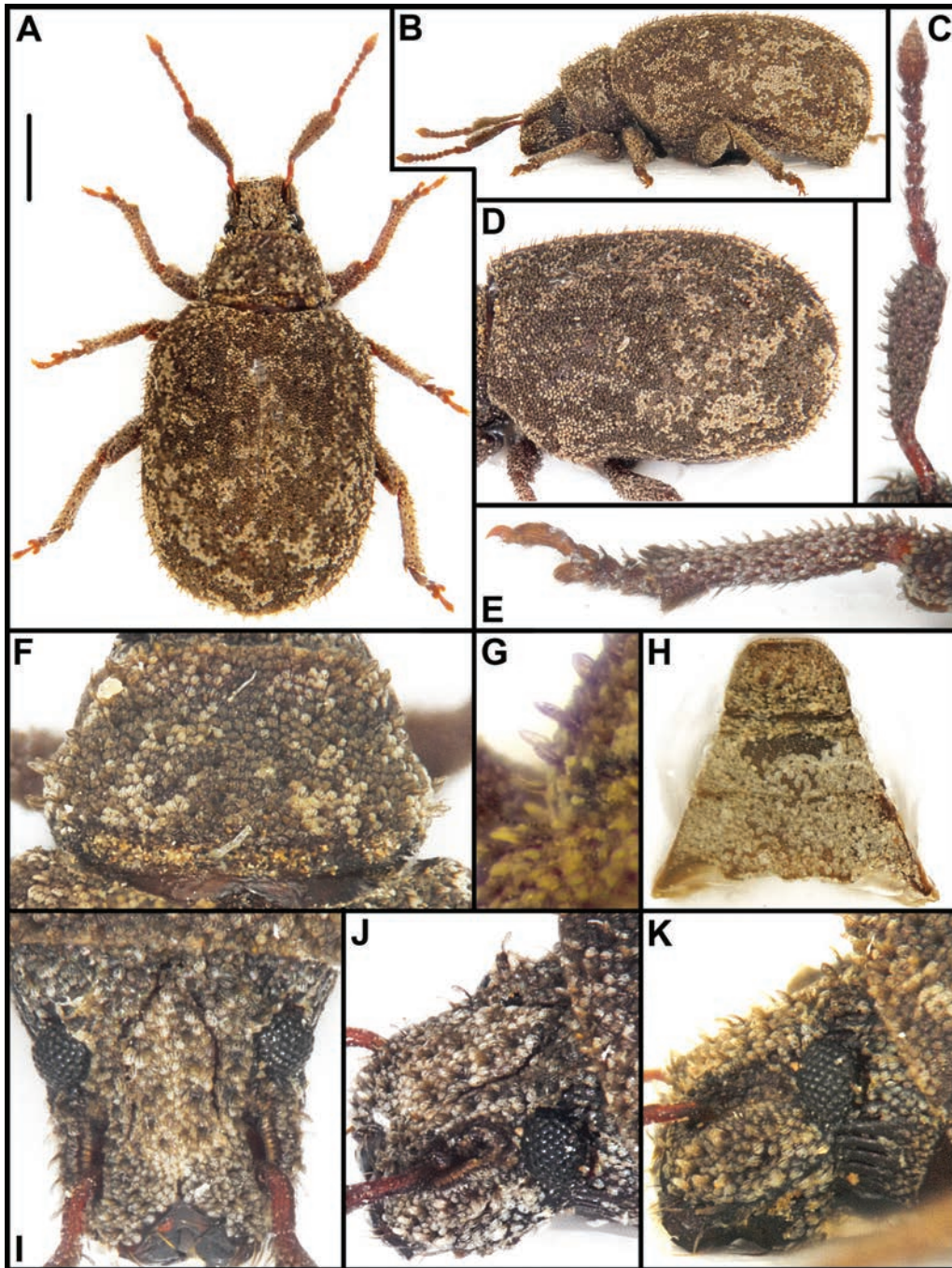
*Diagnostic description:* Middle-sized Namaini 2.9–4.4 mm long; rostrum with U-shaped stria on epifrons; ventral border of rostrum in profile short, conspicuously shorter than rostral thickness; frons densely squamose; gena and subgena densely squamose; antennal sockets in dorsal view narrowly reniform, in profile not reaching eyes, slender, directed above eyes; antennal scapes conspicuously enlarged apicad, at apex distinctly wider than club; tibiae long and slender; tarsi long and slender, onychium distinctly longer than segment 3; ventrites squamose; suture between ventrite 1 and 2 straight; tegmen with weakly sclerotized short parameres; female sternite VIII with long and slender apodeme terminating at base of plate and forming short basal margins, its plate small, rhombus-shaped to oval.

*Etymology:* We name this genus after our colleague and friend Piero Cervella (1959–2019), researcher at the Department of Life Sciences of the University of Turin, who set up the sequencing protocol and discussed the preliminary results of the study with much interest. The gender is feminine.

*Included taxa and distribution:* In addition to the type species, seven additional taxa are included in *Cervellaea*, based on the *mt-Cox1* analysis and/or their morphology. They are distributed in South Africa, in the western and south-western part of the Northern Cape (Fig. 12).

##### *CERVELLAEA COHENI* BOROVEC & MEREGALLI, SP. NOV. (FIGS 3, 10B, I, P, 11B, I, P)

*Zoobank registration:* urn:lsid:zoobank.org:act:B0DDDC9E-453F-4ED4-B2E5-1CF3DAB4B059



**Figure 3.** *Cervellaea coheni*, paratype. A, body, dorsal view. B, body, lateral view. C, antenna. D, elytra, dorso-lateral view. E, protibia. F, pronotum. G, pronotum, detail of scales at side. H, ventrites, male. I, J, K, rostrum respectively dorsal, dorso-lateral and lateral view. Bar: 1 mm.

*Diagnostic description:* Body length 2.88–3.44 mm, holotype 3.37 mm. Erect setae on elytra short, lanceolate, apically pointed, forming one regular row on each interval, about as long as a third to a quarter the width of one interstria; rostrum subparallel-sided with straight sides; epifrons with concave sides, dorsally

slightly shallowed with distinct V-shaped stria; scapes at base distinctly S-shaped; elytra long oval; onychium almost twice as long as previous segment; penis short, widest at base and evenly tapered apicad with rounded tip; endophallus with complex, many times distorted sclerite; spermatheca with ramus long, straight,

almost twice as long as wide and collum small, about isodiametric, distant from ramus.

*Etymology*: During our 2016 expedition, the extraordinary artist Leonard Cohen (1934–2016) passed away, and we wish to name this species after him. Because Piero Cervella had an excellent knowledge of music, it is appropriate to associate this specific epithet with a genus named after him.

*Ecology*: The specimens were sifted from litter of dead leaves and branches under large shrubby *Euphorbia*.

*Type material*: Holotype: ♂, species 471: RSA, Western Cape, Cederberg Mts., Between Cederberg and Ceres, 32°37.576'S, 19°23.405'E, 639 m, 24.xi.2016, R. Borovec & M. Meregalli lgg., sifting of detritus, dead leaves and branches below shrubby *Euphorbia* (TMSA). Paratypes: same data as the holotype, 22 ex (MMTI, RBSC); species 572: RSA, Western Cape, Cederberg Mts., entrance Nuwerust Rest Camp, 32°33.722'S, 19°22.607'E, 560 m, 13.xi.2018, R. Borovec & M. Meregalli lgg., sifting of litter under *Euphorbia mauritanica*, 179 ex. (BMNH, MMTI, NMPC, RBSC, SANC, TMSA).

#### **NAMAQUANIA BOROVEC & MEREGALLI, GEN. NOV.**

*Zoobank registration*: urn:lsid:zoobank.org:act:FBD76D02-3A0B-4BD0-BF03-35A0E599D73F

Type species: *Namaquania andreai* Borovec & Meregalli, here designated.

*Diagnostic description*: Middle-sized Namaini 2.4–4.1 mm long; rostrum continuous with head, with U-shaped stria on epifrons; ventral border of rostrum in profile short, conspicuously shorter than rostral thickness; frons densely squamose; gena and subgena densely squamose; antennal sockets in dorsal view narrowly reniform, in profile not reaching eyes, enlarged posteriad, directed towards eyes; antennal scapes slender, at apex as wide as clubs; metaventral process 1.5 × wider than transverse diameter of metacoxa; tibiae long and slender; tarsi long and slender, onychium distinctly longer than segment 3; ventrites squamose; suture between ventrite 1 and 2 slightly sinuose; tegmen with weakly sclerotized short parameres; female sternite VIII with long and slender apodeme terminating at base of plate and forming short basal margins, its plate small, rhombus-shaped to oval.

*Etymology*: The genus name refers to the Namaqualand, an arid region of South Africa (Northern Cape Province) and southern Namibia, originally inhabited

by Nama and Khoisan tribes, from where the majority of the species were collected. The gender is feminine.

*Included taxa and distribution*: In addition to the type species, seven additional taxa are included in *Namaquania*, based on the *mt-Cox1* analysis and/or their morphology. They are distributed in South Africa: Northern Cape, northern part of Southern Cape and in southern Namibia (Fig. 13).

#### **NAMAQUANIA ANDREAI BOROVEC & MEREGALLI, SP. NOV.**

(FIGS 4, 10D, K, R, 11D, K, R)

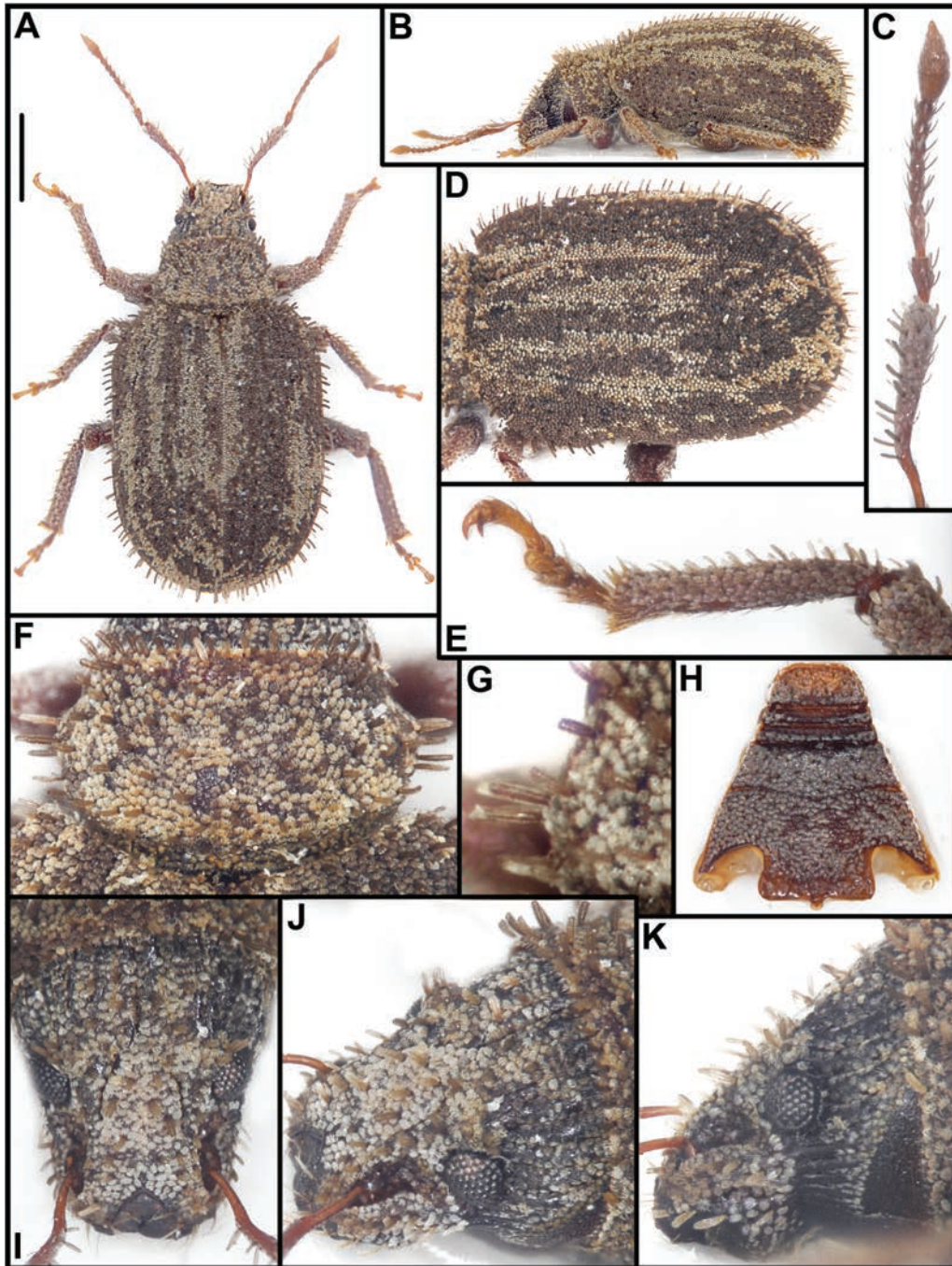
*Zoobank registration*: urn:lsid:zoobank.org:act:74773254-8DB7-4141-BD6F-E9B902826415

*Diagnostic description*: Body length 2.43–3.32 mm, holotype 3.16 mm. Elytra with erect setae short, narrowly subspatulate, apically truncated, forming a single row on each interstria, slightly shorter than half the width of one interstria; rostrum slightly tapered anteriorly with straight sides; epifrons with slightly concave sides, dorsally broadly shallowly depressed with U-shaped stria; scapes slightly simply curved at basal third; elytra long oval; penis short, widest at base, evenly tapered apically with regularly rounded tip; endophallus with one long curved and two shorter, hook-shaped sclerites; spermatheca with ramus robust, straight, about twice as long as wide and collum less than half as long as wide as ramus, subtriangular.

*Etymology*: We name this species after our friend Andrea Battisti, a former student of one of the authors (M.M.), who participated in our 2013 expedition and shared the windy days and the freezing nights with us in the field, enthusiastically helping us in the collection of these weevils.

*Ecology*: The specimens were sifted from litter of dead leaves and branches under large shrubs of *Euphorbia*.

*Type material*: Holotype: ♂, species 337. RSA, Northern Cape, 20 km S Eksteefontein, above Ratelfontein, 28°28'57.398"S, 17°20'062"E, 805 m, 16.ix.2013, R. Borovec, A. Battisti, M. Meregalli lgg., sifting of detritus, dead leaves and branches below shrubby *Euphorbia* (TMSA). Paratypes: same data as the holotype, 14 ex (MMTI, RBSC); species 336\_a. RSA, Northern Cape, 20 km S Eksteefontein, E Ratelfontein, 28°57.017"S, 17°21.008"E, 690 m, 16.ix.2013, R. Borovec, A. Battisti, M. Meregalli lgg., sifting of detritus, dead leaves and branches below shrubby *Euphorbia*, 12 ex (BMNH, MMTI, NMPC, RBSC, SANC, TMSA).



**Figure 4.** *Namaquania andreai*, paratype. A, body, dorsal view. B, body, lateral view. C, antenna. D, elytra, dorso-lateral view. E, protibia. F, pronotum. G, pronotum, detail of scales at side. H, ventrites, male. I, J, K, rostrum respectively dorsal, dorso-lateral and lateral view. Bar: 1 mm.

SUBCLADE A - GROUP 2

*NAMA* Borovec & Meregalli, 2013

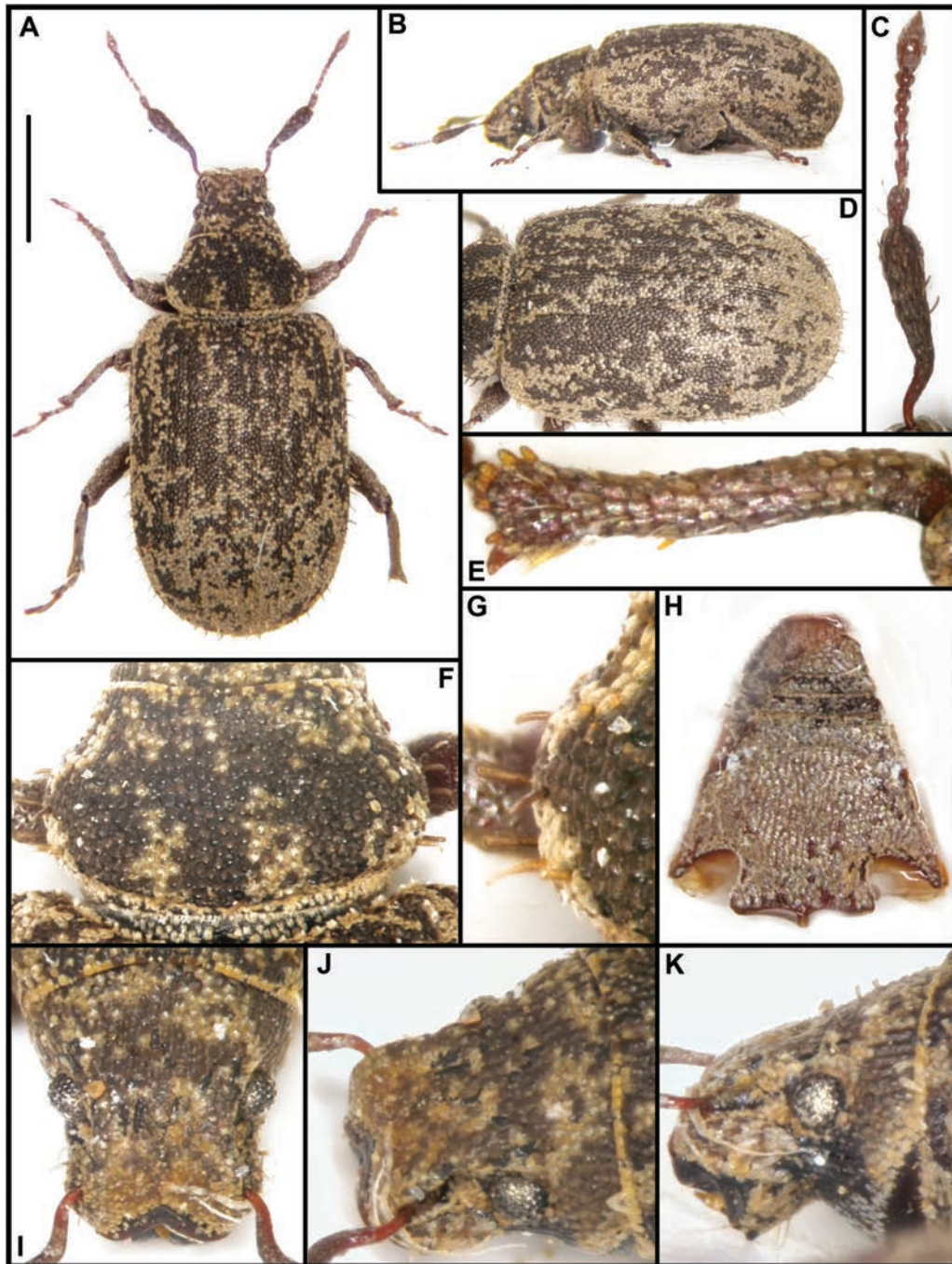
*Nama* Borovec & Meregalli, 2013: p.502 (original description); Borovec & Skuhrovec [2017: p.523 (note)].

*Type species: Nama richtersveldiana* Borovec & Meregalli, 2013: p.504 (original description) (Figs 5, 10C, J, Q, 11C, J, Q).

*Amended diagnosis:* Namaini of variable size, 1.7–4.9 mm long; epifrons wide, occupying majority of dorsal

part of rostrum, posteriorly continuous with head; ventral border of rostrum in profile short, conspicuously shorter than rostral thickness; frons squamose; gena and subgena densely squamose; antennal sockets in dorsal view invisible or hardly visible, in profile subtriangular, posteriorly enlarged, with ventral margin

directed to middle of eyes and dorsal margin parallel with dorsal border of rostrum; pronotum in some species conspicuously laterally lengthened to dorsolaterally flattened lobes; all tibiae in apical part distinctly enlarged laterally, apically rounded, armed with sparse, stout spines; tarsi long and slender; ventrites squamose;



**Figure 5.** *Nama richtersveldiana*, paratype. A, body, dorsal view. B, body, lateral view. C, antenna. D, elytra, dorso-lateral view. E, protibia. F, pronotum. G, pronotum, detail of scales at side. H, ventrites, female. I, J, K, rostrum respectively dorsal, dorso-lateral and lateral view. Bar: 1 mm.

tegmen with weakly sclerotized parameres; female sternite VIII with long and slender apodeme, terminating inside of plate, plate oval, wider than long; gonocoxites with short styli, only slightly longer than wide.

*Included taxa and distribution:* In addition to the type species, *Nama richtersveldiana*, fourteen taxa are included in *Nama*, based on the *mt-Cox1* analysis and/or their morphology. They are distributed in South Africa: Northern Cape and northern part of Southern Cape (Fig. 14).

#### YAMALAKA BOROVEC & MEREGALLI, GEN. NOV.

*Zoobank registration:* urn:lsid:zoobank.org:act:537D2C1A-33B5-4B55-A8DF-F625C0D3F5B6

Type species: *Nama erikae* Borovec & Meregalli, 2013: p.508, here designated (Figs 6, 10G, N, U, 11G, N, U).

*Diagnostic description:* Very small to small Namaini 1.7–2.4 mm long; rostrum continuous with head with U-shaped stria on epifrons; ventral border of rostrum in profile short, conspicuously shorter than rostral thickness; frons squamose; gena and subgena densely squamose; antennal sockets in dorsal view narrowly reniform, laterally subtriangular, longer than wide, not reaching eyes; procoxal cavities placed in middle of prosternum; metatibiae with apical surface densely squamose; ventrites squamose; tegmen with parameres; female sternite VIII with long and slender apodeme, terminating just inside of plate, plate oval to widely oval; gonocoxites with long apical styli.

*Etymology:* During our 2013 trip with our colleague Andrea Battisti, we camped one night in an area with several large burrows of an unknown animal, possibly an aardvark [*Orycteropus afer* (Pallas, 1766)]. We did not know what it was and the fantasy name Yamalaka was coined. Since then we always think of a Yamalaka following and protecting us during our expeditions. We name this genus after our fictional protector.

*Included taxa and distribution:* In addition to the type species, *Yamalaka erikae* (Borovec & Meregalli, 2013) **comb. nov.**, *Yamalaka iuliae* (Borovec & Meregalli, 2013) **comb. nov.** and five additional taxa are included in *Yamalaka*, based on the *mt-Cox1* analysis and/or their morphology. They are distributed in South Africa: Northern Cape (Fig. 15).

#### SUBCLADE B

#### PENTAMERICA BOROVEC & MEREGALLI, GEN. NOV.

*Zoobank registration:* urn:lsid:zoobank.org:act:A67A110A-640A-4293-A658-DA4849C7C4D8

Type species: *Nama pentamera* Borovec & Meregalli, 2013: p.506, here designated (Figs 7, 10E, L, S, 11E, L, S).

*Diagnostic description:* Very small Namaini 1.7–2.1 mm long; rostrum short and wide with epifrons conspicuously tapered apicad with straight sides; frons large, occupying almost apical half of rostrum, glabrous, matt; epistome hardly visible; gena and subgena glabrous, smooth; antennal sockets in dorsal view reniform, well visible, in lateral view short, subtriangular, not reaching eyes, with ventral margin directed to dorsal margin of eyes; scapes in apical two-thirds conspicuously thickened, widest before apex; funicles 5-segmented; procoxal cavities placed closer to anterior margin of prosternum; protibiae widest at basal third and slightly evenly tapered anteriorly, at apex not enlarged outside or inside; apical surface of metatibiae glabrous; ventrites glabrous; suture between ventrites 1 and 2 arched; tegmen with short basally connected parameres; female sternite VIII with apodeme long and terminating inside of plate; plate lengthened apically to well sclerotized process, distinctly constricted before tip; gonocoxites with tip well sclerotized, slightly curved and sharpened, lacking styli.

*Etymology:* The name is derived from Greek πέντε, five, and μέρος, part. The species belonging to this genus appear to be characterized by the antennal funicle composed of five segments, hence the name. The gender is feminine.

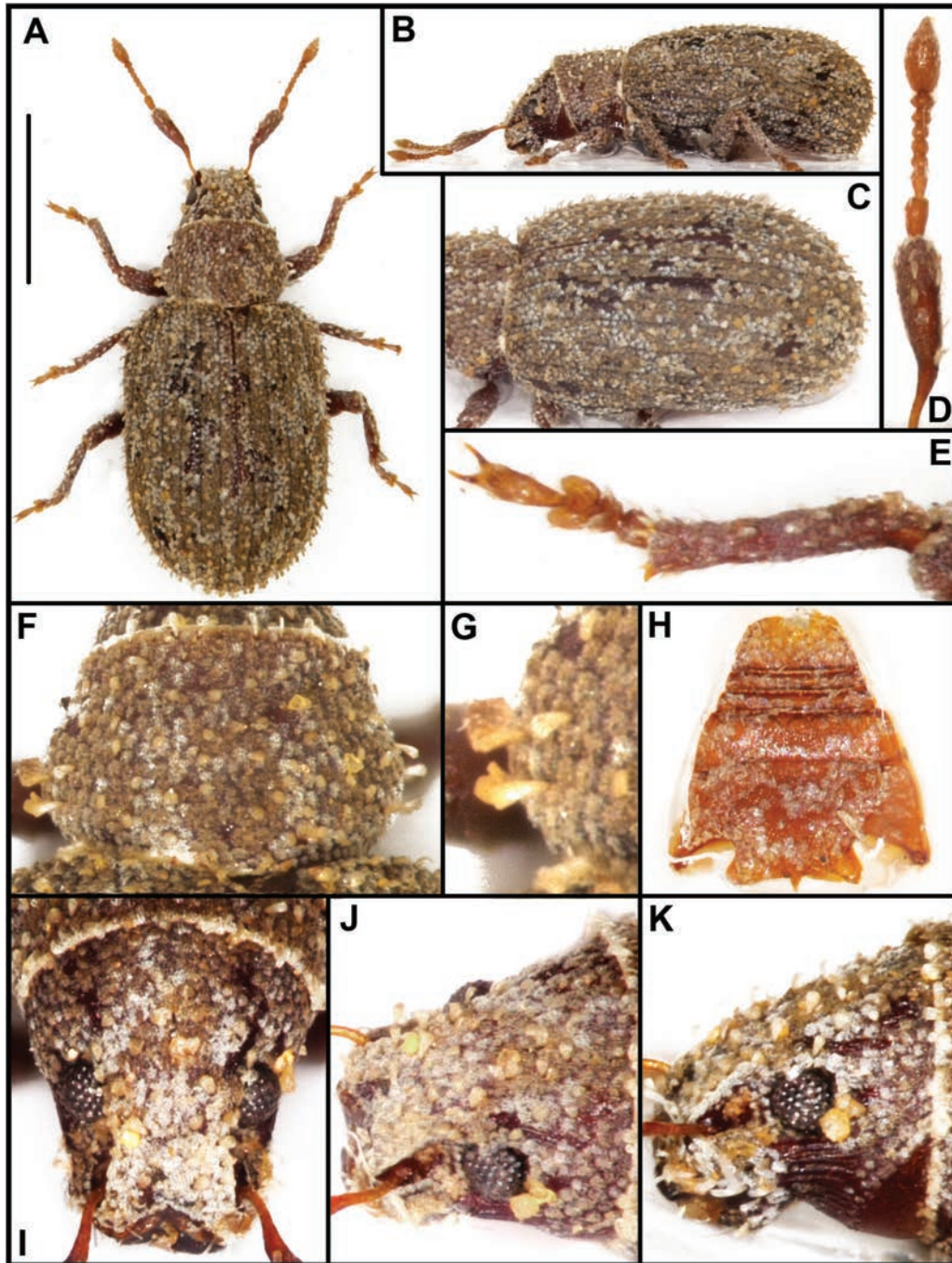
*Included taxa and distribution:* In addition to the type species, *Pentamerica pentamera* (Borovec & Meregalli, 2013) **comb. nov.**, only one more taxon is included in the genus, based on the *mt-Cox1* analysis and its morphology. The two species are known from South Africa: Northern Cape, Richtersveld National Park (Fig. 13).

#### SPRINGBOKIA BOROVEC & MEREGALLI, GEN. NOV.

*Zoobank registration:* urn:lsid:zoobank.org:act:DDE8F03E-13CB-4EB2-A61D-001AAD8FE1A8

Type species: *Springbokia sacculus* Borovec & Meregalli, here designated.

*Diagnostic description:* Very small Namaini, 1.4–2.1 mm long; rostrum short and wide with epifrons distinctly tapering anteriorly; frons squamose; gena glabrous and smooth, subgena in narrow middle part glabrous, laterally densely squamose, squamose parts subtriangular; antennal sockets in dorsal view narrowly reniform, in profile subtriangular, reaching eyes, with ventral margin touching ventral margin of eyes and

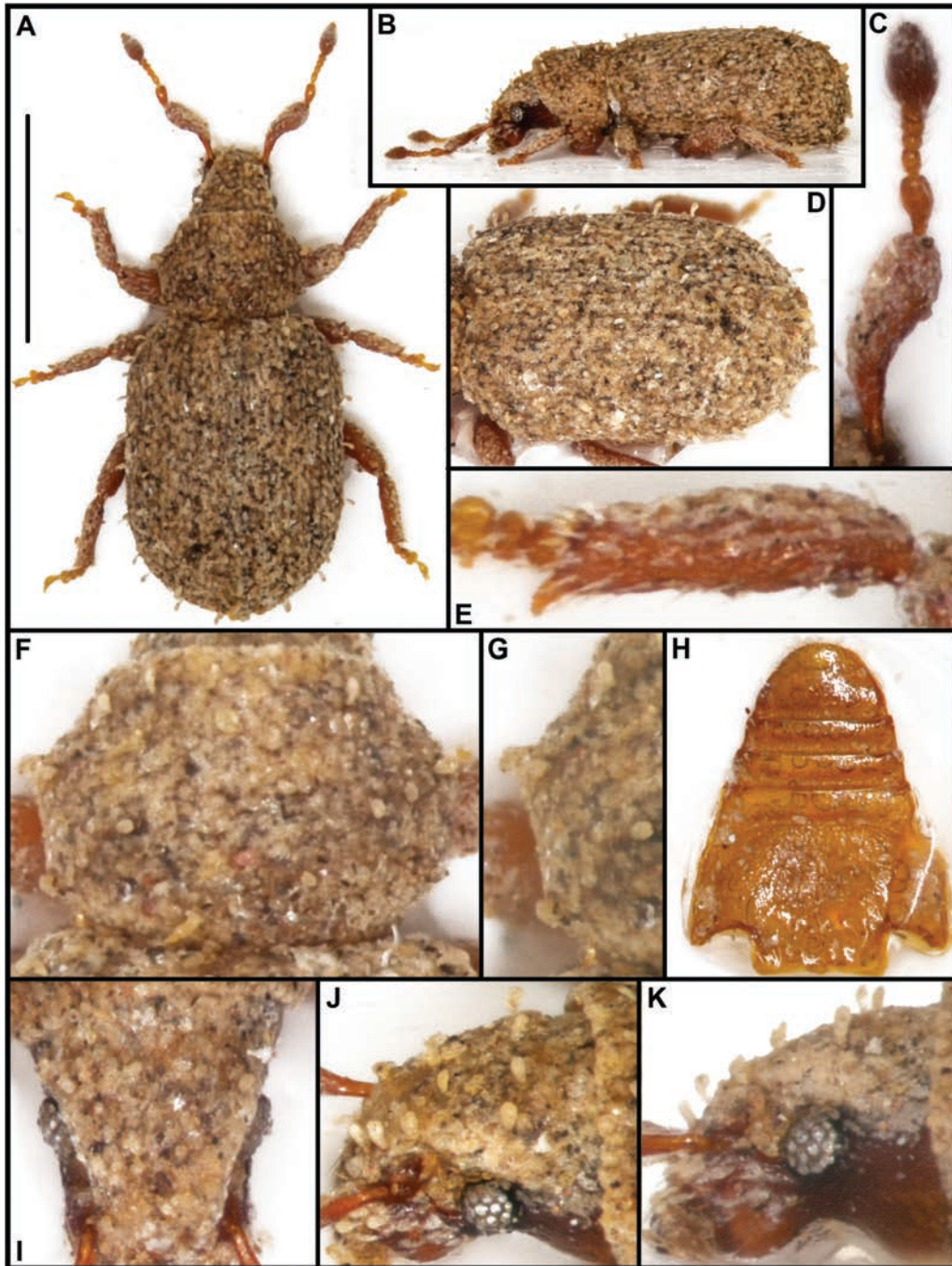


**Figure 6.** *Yamalaka erikae*, paratype. A, body, dorsal view. B, body, lateral view. C, antenna. D, elytra, dorso-lateral view. E, protibia. F, pronotum. G, pronotum, detail of scales at side. H, ventrites, male. I, J, K, rostrum respectively dorsal, dorso-lateral and lateral view. Bar: 1 mm.

dorsal margin directed above eyes; antennal funicles 6-segmented; procoxal cavities placed closer to anterior margin of pronotum; apical surface of metatibiae glabrous; ventrites squamose; suture between ventrites 1 and 2 arched; tegmen without parameres; female

sternite VIII with long and slender apodeme terminating inside of plate, plate distinctly wider than long.

*Etymology:* The name of the genus is derived from the town of Springbok, the largest town in the



**Figure 7.** *Pentamerica pentamera*, paratype. A, body, dorsal view. B, body, lateral view. C, elytra, dorso-lateral view. D, pronotum. E, protibia. F, pronotum. G, pronotum, detail of side. H, ventrites, female. I, J, K, rostrum respectively dorsal, dorso-lateral and lateral view. Bar: 1 mm.

Namaqualand area in the Northern Cape Province, in the surroundings of which the first specimens of this genus were collected in the course of the first expedition to South Africa. The gender is feminine.

*Included taxa and distribution:* In addition to the type species, nine additional taxa are included in *Springbokia*, based on the *mt-Cox1* analysis and/or their morphology. They are distributed in South Africa: Northern Cape Province (Fig. 16).

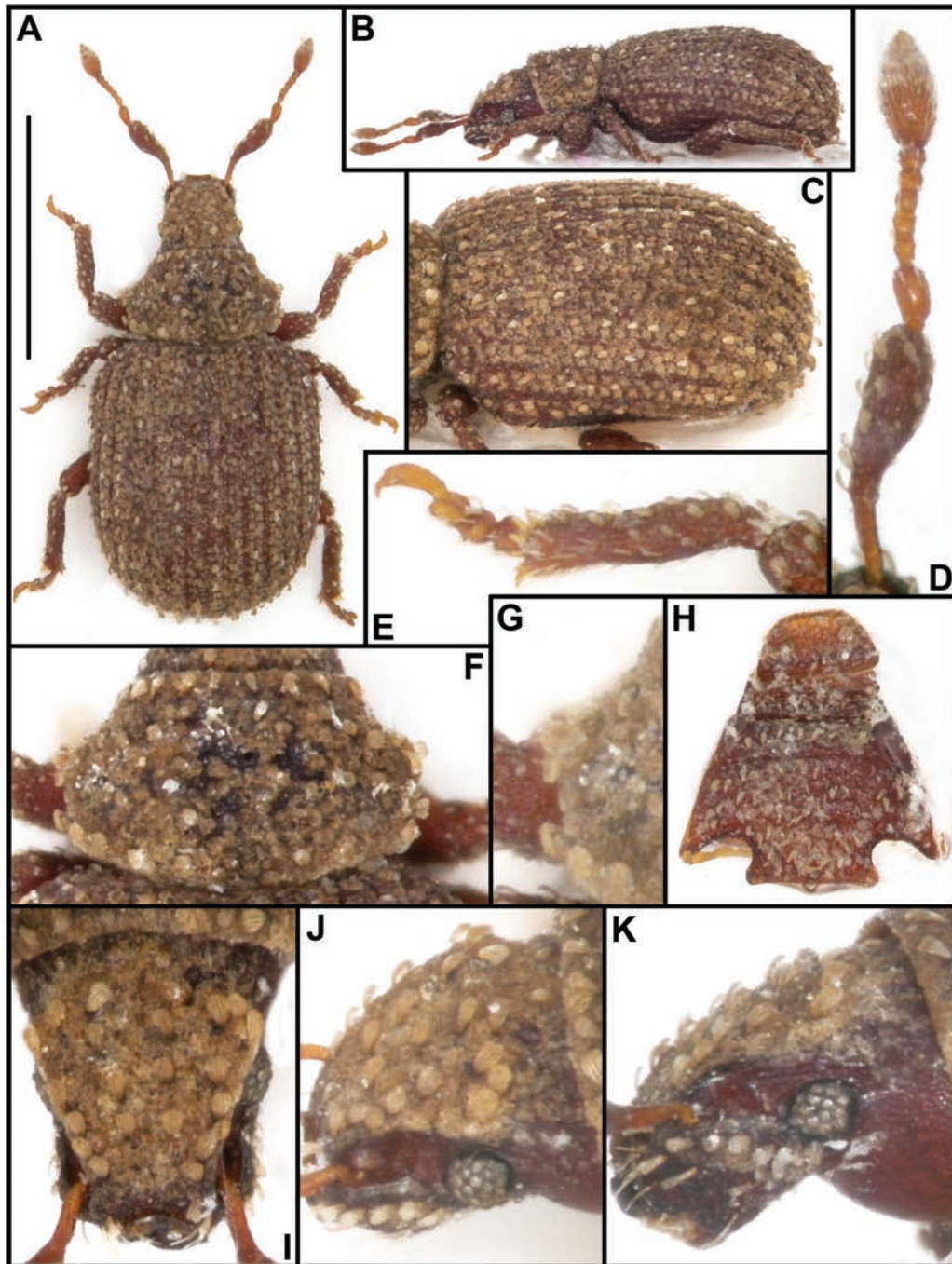


*SPRINGBOKIA SACCULUS* BOROVEC & MEREGALLI, SP.  
NOV.

(FIGS 8, 10F, M, T, 11F, M, T)

Zoobank registration: urn:lsid:zoobank.org:act:E716D353-E73B-4A54-9D65-9F8EBDF982DF

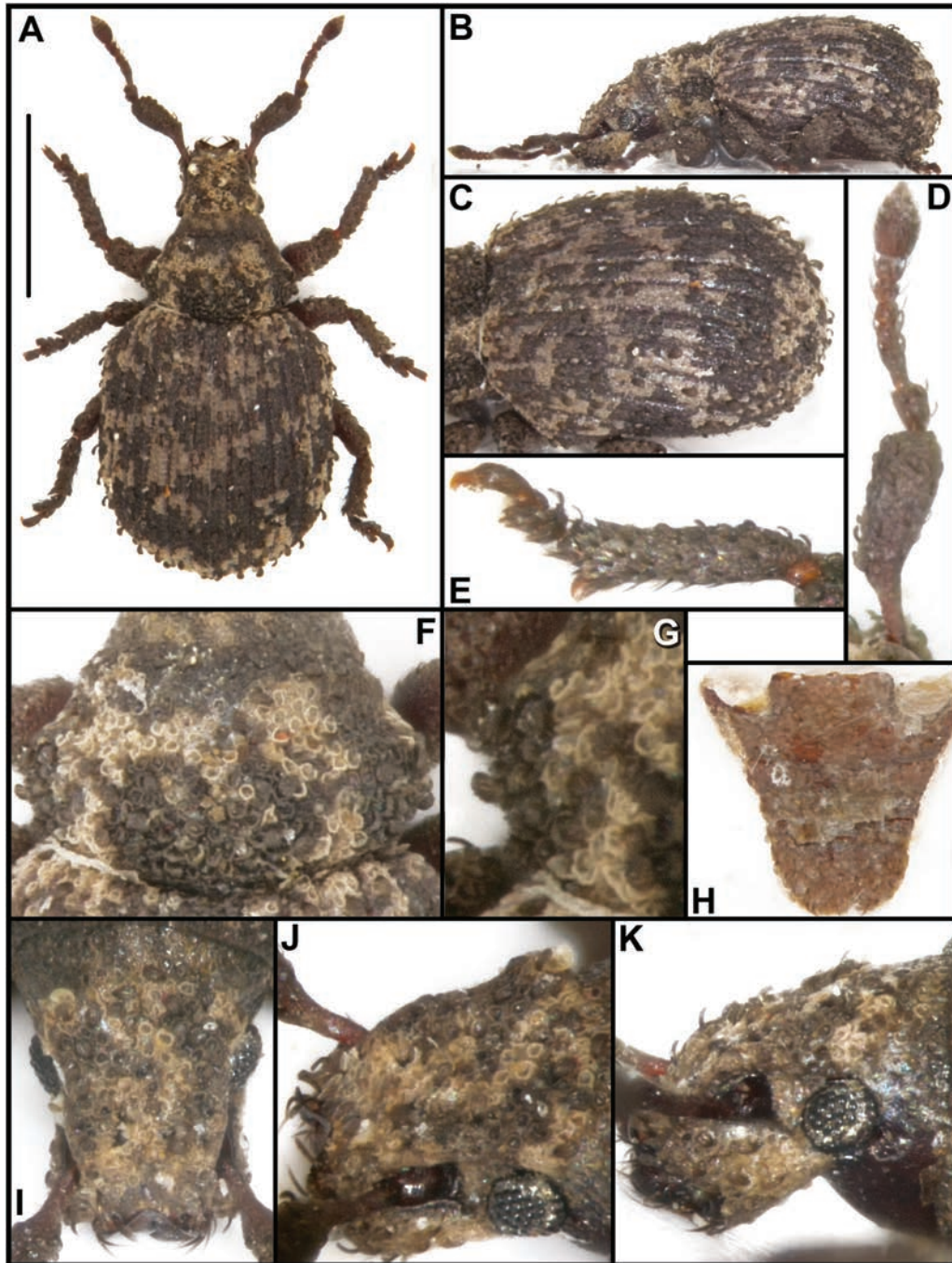
*Diagnostic description:* Body length 1.44–1.91 mm, holotype 1.63 mm. Elytra with one regular row of short semi-appressed setae on each interstria, at most as long as half the width of interstria, subspatulate, apically rounded; rostrum subparallel-sided with



**Figure 8.** *Springbokia sacculus*, paratype. A, body, dorsal view. B, body, lateral view. C, antenna. D, elytra, dorso-lateral view. E, protibia. F, pronotum. G, pronotum, detail of scales at side. H, ventrites, male. I, J, K, rostrum respectively dorsal, dorso-lateral and lateral view. Bar: 1 mm.

## KEY TO THE GENERA OF THE NAMAINI

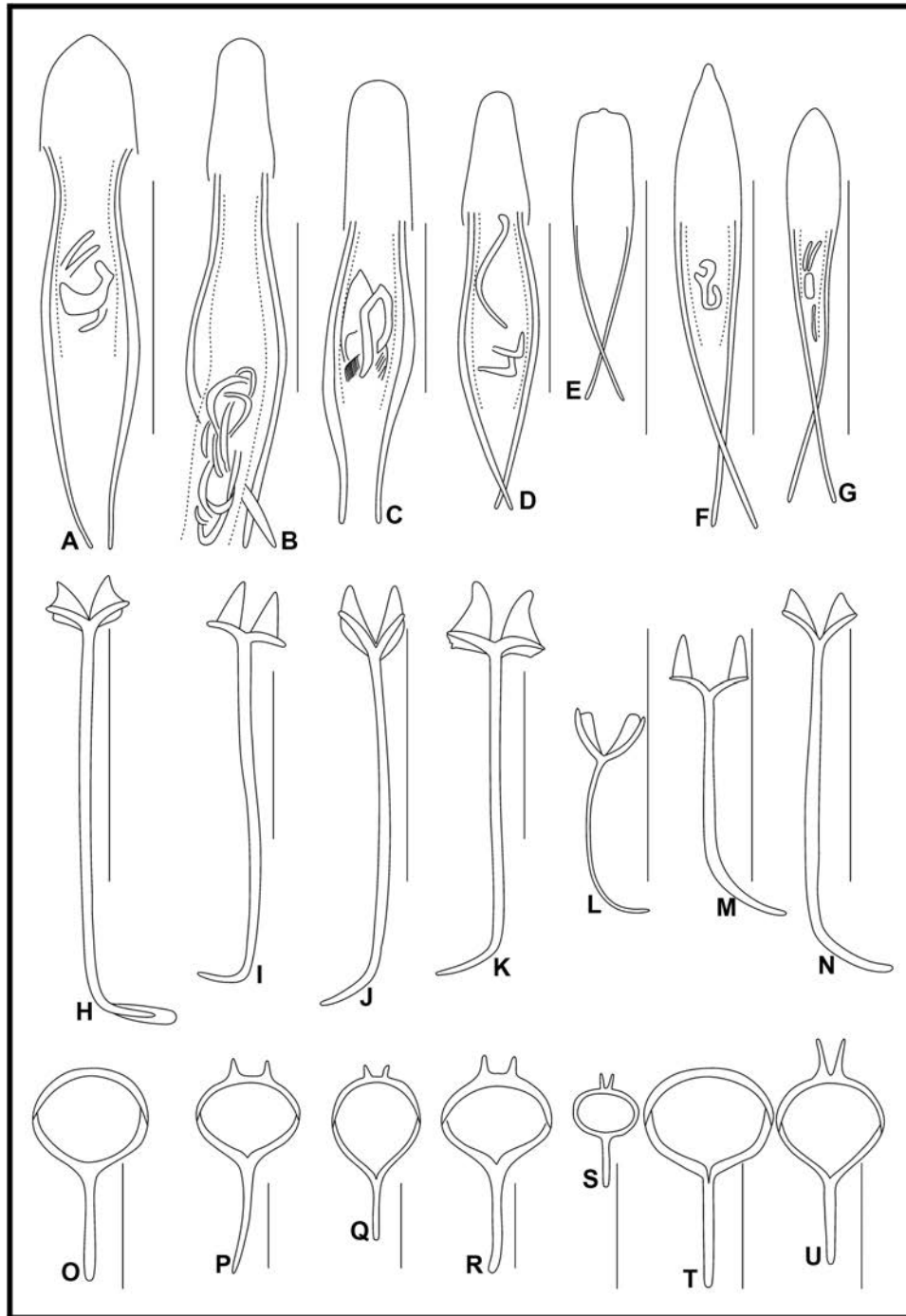
1. Antennal sockets in lateral view reaching eyes. Epifrons flat, at most with slender median longitudinal stria. Eyes with less than 35 ommatidia. Subgenera glabrous at least in middle part..... 2
  - Antennal sockets in lateral view separated from anterior margin of eyes by squamose stripe shorter than eye diameter. Epifrons usually with U- or V-shaped stria open anteriorly, posteriorly reaching vertex. Eyes with more than 35 ommatidia. Subgenera densely squamosa..... 3
2. Frons densely squamose. Epistome posteriorly carinate. Antennal funicle 6-segmented. Antennal sockets in profile reaching eyes with ventral margin touching ventral margin of eyes. Subgenera in narrow middle part glabrous, laterally densely squamose. Protibiae of uniform width along the entire length. Ventrites densely squamose. Plate of sternite VIII of females apically rounded. Gonocoxites with apical styli. Size 1.4–2.1 mm ..... *Springbokia*
  - Frons glabrous, matt. Epistome hardly visible, posteriorly not separated from frons. Antennal funicle 5-segmented. Antennal sockets in profile not directly reaching eyes, with ventral margin directed to dorsal margin of eyes. Subgenera glabrous, only narrow lateral part sparsely squamose. Protibiae widest at basal third, slightly narrowed apicad. Ventrites glabrous. Sternite VIII of females with plate apically lengthened, forming distinct apical process. Gonocoxites lacking styli. Size 1.7–2.1 mm ..... *Pentamerica*
3. Antennal sockets in dorsal view hardly visible as narrow furrow; in lateral view narrowly furrow-shaped, with ventral margin well edged, reaching ventral margin of eye and dorsal margin barely noticeable, vanishing before eyes. Procoxae touching anterior margin of prosternum. Tegmen lacking parameres. Ventral border of rostrum in profile long, equally long as rostral thickness. Gena glabrous. Size 1.8–2.6 mm ..... *Cederbergia*
  - Antennal sockets in dorsal view visible in anterior half to two-thirds of length as narrowly reniform; in lateral view with dorsal and ventral margin equally developed. Procoxae in middle or before middle of pronotum, not touching anterior margin of prosternum. Tegmen with parameres, these sometimes weakly sclerotized. Ventral border of rostrum in profile short, conspicuously shorter than rostral thickness. Gena in apical half densely squamosa..... 4
4. Abdominal ventrite 2 long, as long as or longer than ventrites 3 and 4 combined. Suture between ventrites 1 and 2 straight or slightly sinuose. Tibiae long and slender, protibiae 4.6–6.7 × longer than wide, apically fringed by short setae. Apodeme of sternite VIII of females terminating at base of plate and creating short basal margins. Appressed elytral scales small, 6–8 across width of interstria, raised setae create 1–2 dense irregular rows on each interstria..... 5
  - Abdominal ventrite 2 short, as long as ventrite 3 or 4. Suture between ventrites 1 and 2 deeply arched. Tibiae short and robust, protibiae 4.3–5.9 × longer than wide, apically armed with short and sparse spines. Apodeme of sternite VIII of females terminating inside of plate, basal margin of plate membranous. Appressed elytral scales bigger, 3–5 across width of interstria, raised setae create one regular row on each interstria..... 6
5. Antennal sockets in lateral view narrow, slightly enlarged posteriorly, with ventral border directed against dorsal border of eye and dorsal border directed above eye. Antennal scapes conspicuously enlarged apicad, at apex distinctly wider than club. Suture between ventrite 1 and 2 straight. Size 2.9–4.4 mm ..... *Cervellaea*
  - Antennal sockets in lateral view wide, distinctly enlarged posteriorly, with ventral border directed against ventral border of eyes and dorsal border directed against dorsal border of eyes. Antennal scapes slightly enlarged apicad, at apex at most as wide as club. Suture between ventrite 1 and 2 slightly sinuose. Size 2.4–4.1 mm ..... *Namaquania*
6. Epifrons narrow, at apex 0.5–0.7 × wide as rostrum. Protibiae apically subtruncated, laterally slightly enlarged, armed with sparse, short, fine or stout yellowish spines. Pronotum in all species with sides regularly rounded. Gonocoxites with long styli, distinctly longer than wide. Size 1.7–2.4 mm ..... *Yamalaka*
  - Epifrons wide, at apex 0.7–0.9 × wide as rostrum. Protibiae apically distinctly rounded, laterally distinctly enlarged, armed with conspicuous, sparse, stout yellow or black spines. Some species with conspicuous, laterally prominent lobes in basal half of pronotum. Gonocoxites with short styli, only slightly longer than wide. Size 1.7–4.9 mm ..... *Nama*



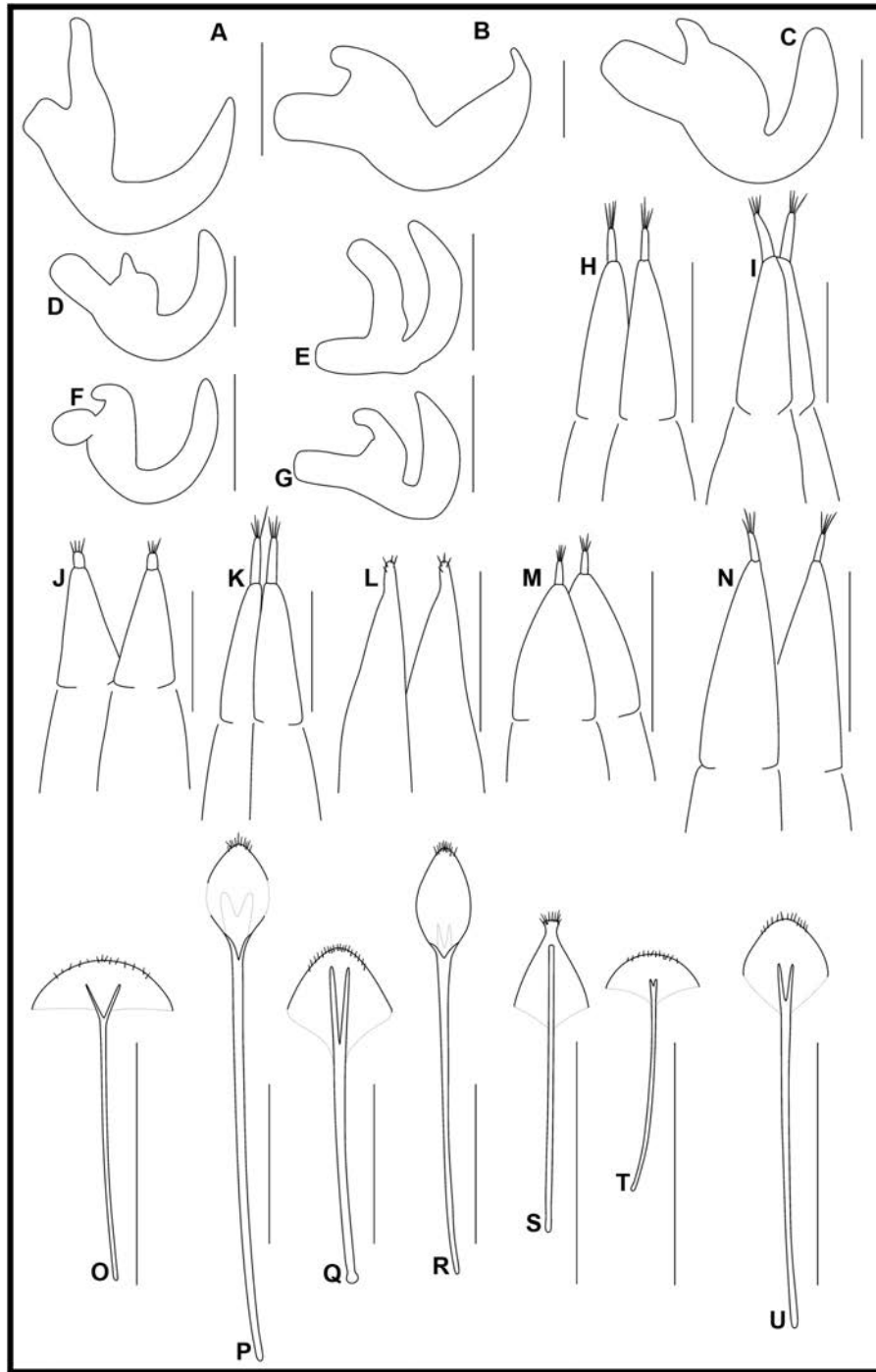
**Figure 9.** *Cederbergia indecora*, paratype. A, body, dorsal view. B, body, lateral view. C, elytra, dorso-lateral view. D, antenna. E, protibia. F, pronotum. G, pronotum, detail of scales at side. H, ventrites, male. I, J, K, rostrum respectively dorsal, dorso-lateral and lateral view. Bar: 1 mm.

straight sides; epifrons wide, regularly flat; antennal sockets in lateral view with ventral border reaching ventral border of eyes and dorsal border directed above eyes and vanishing there; scapes curved at midlength, at apical half robust, widest at middle

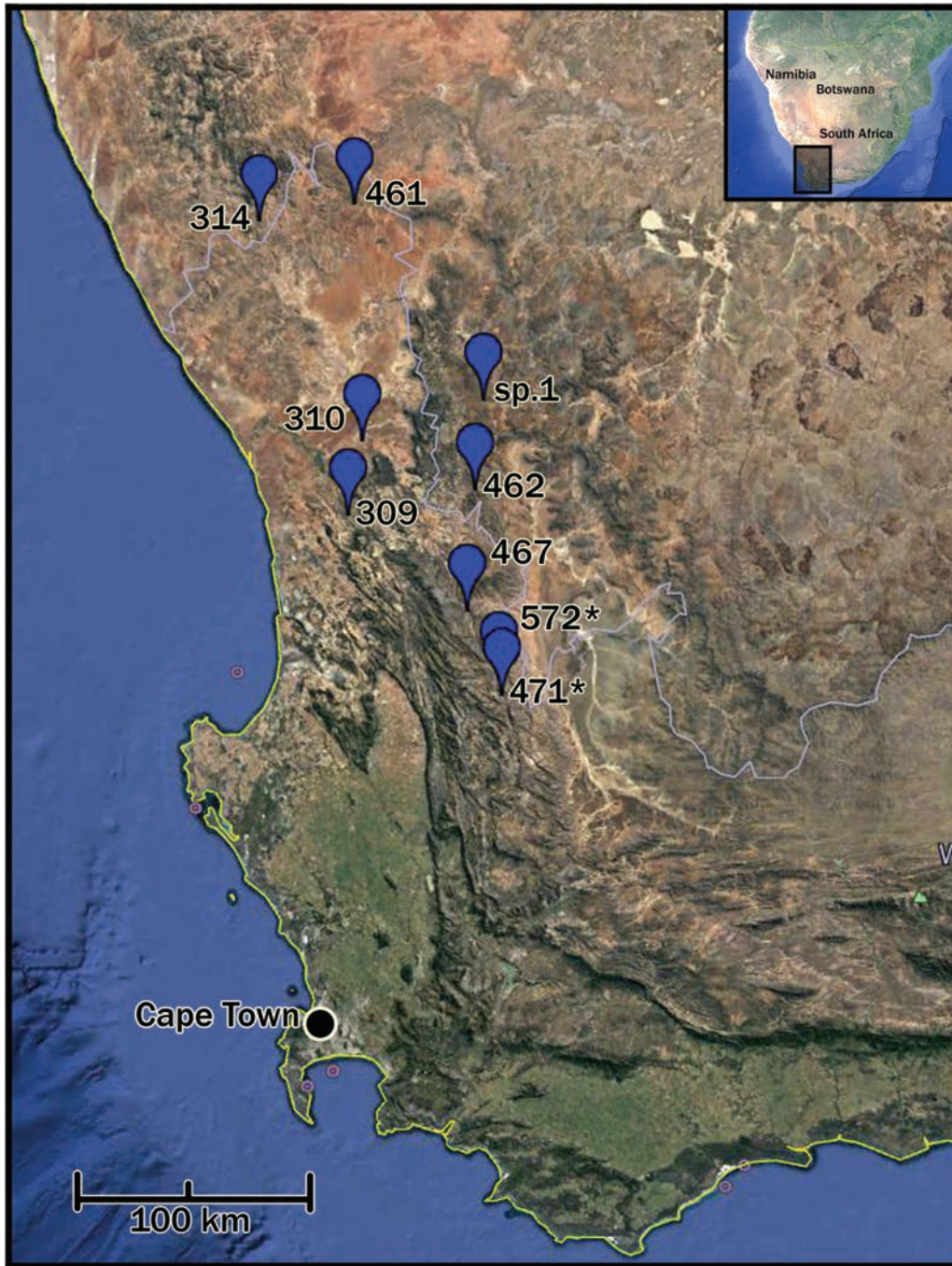
of apical half, here as wide as clubs; elytra short oval; protibiae robust, apically subtruncated with a dense fringe of yellowish long setae; penis regularly triangular, from base evenly tapered apicad to sharp tip; endophallus short with elongate sclerite;



**Figure 10.** Male terminalia. Penis with temones: (A) *Cederbergia indecora*, paratype, (B) *Cervellaea coheni*, paratype, (C) *Nama richtersveldiana*, paratype, (D) *Namaquania andreaei*, paratype, (E) *Pentamerica pentamera*, paratype, (F) *Springbokia sacculus*, paratype, (G) *Yamalaka erikae*, paratype. Scale bars: 0.50 mm. Sternite IX: (H) *Cederbergia indecora*, paratype, (I) *Cervellaea coheni*, paratype, (J) *Nama richtersveldiana*, paratype, (K) *Namaquania andreaei*, paratype, (L) *Pentamerica pentamera*, paratype, (M) *Springbokia sacculus*, paratype, (N) *Yamalaka erikae*, paratype. Scale bars: 0.50 mm. Tegmen: (O) *Cederbergia indecora*, paratype, (P) *Cervellaea coheni*, paratype, (Q) *Nama richtersveldiana*, paratype, (R) *Namaquania andreaei*, paratype, (S) *Pentamerica pentamera*, paratype, (T) *Springbokia sacculus*, paratype, (U) *Yamalaka erikae*, paratype. Scale bars: 0.25 mm.



**Figure 11.** Female terminalia. Spermatheca: (A) *Cederbergia indecora*, paratype, (B) *Cervellaea coheni*, paratype, (C) *Nama richtersveldiana*, paratype, (D) *Namaquania andreaei*, paratype, (E) *Pentamerica pentamera*, paratype, (F) *Springbokia sacculus*, paratype, (G) *Yamalaka erikae*, paratype. Scale bars: 0.10 mm. Gonocoxites: (H) *Cederbergia indecora*, paratype, (I) *Cervellaea coheni*, paratype, (J) *Nama richtersveldiana*, paratype, (K) *Namaquania andreaei*, paratype, (L) *Pentamerica pentamera*, paratype, (M) *Springbokia sacculus*, paratype, (N) *Yamalaka erikae*, paratype. Scale bars: 0.25 mm. Sternite VIII: (O) *Cederbergia indecora*, paratype, (P) *Cervellaea coheni*, paratype, (Q) *Nama richtersveldiana*, paratype, (R) *Namaquania andreaei*, paratype, (S) *Pentamerica pentamera*, paratype, (T) *Springbokia sacculus*, paratype, (U) *Yamalaka erikae*, paratype. Scale bars: 0.50 mm.



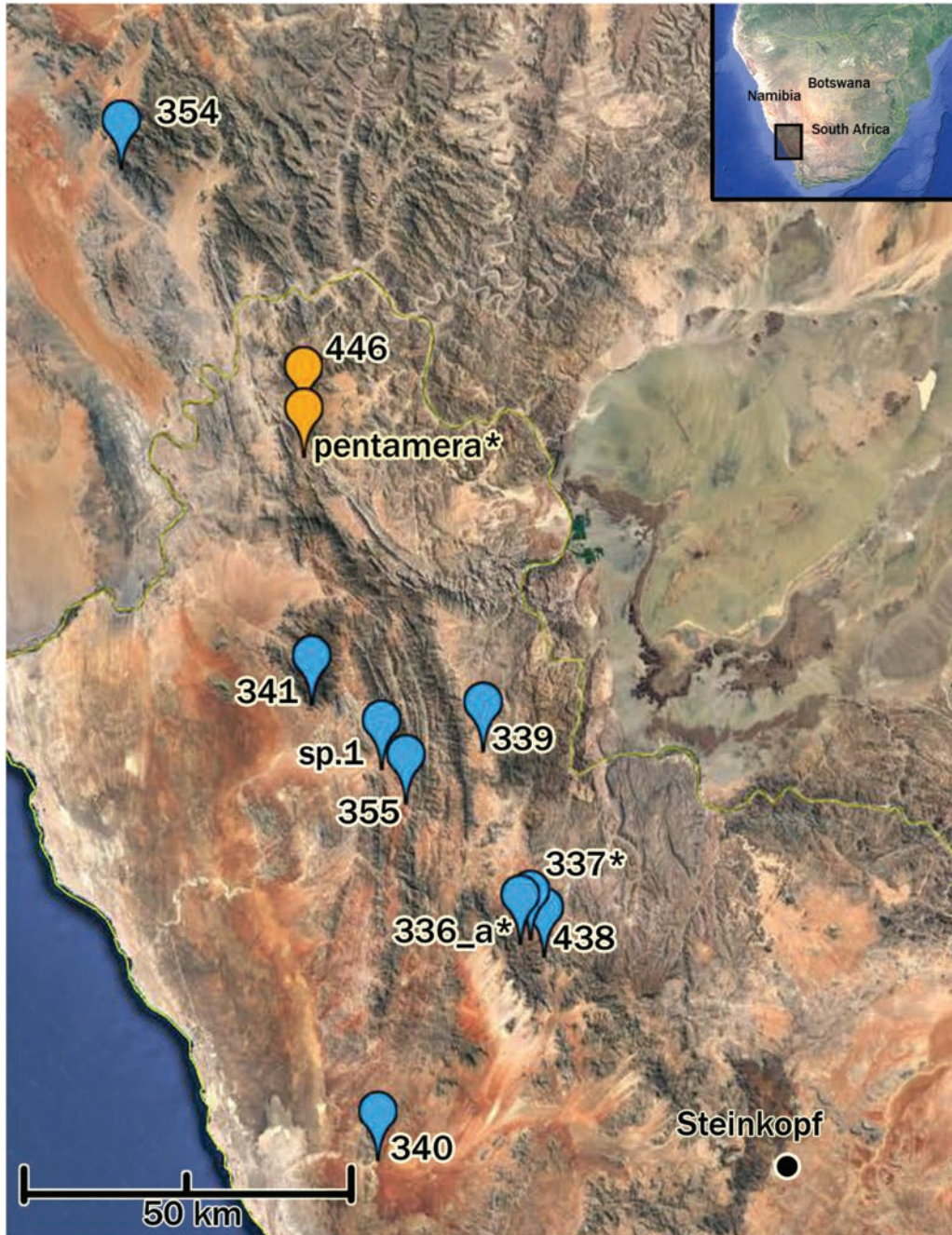
**Figure 12.** Distribution map of the genus *Cervellaea*. \* = type species. Map data: Google Earth, Maxar Technologies, used according to Google Earth Terms of Service.

spermatheca with ramus distinctly bigger than collum, almost as long as wide; collum short, elongate, slender, curved at tip.

*Etymology.* From the Latin *sacculus*, a small bag, in reference to the method of collecting these weevils. Noun in apposition. All specimens were collected

over the course of several days from inside a small bag containing soil sifted from under *Euphorbia* shrubs.

*Ecology:* The specimens were sifted from soil below large shrubs of *Euphorbia dregeana*, in karroo-type vegetation.



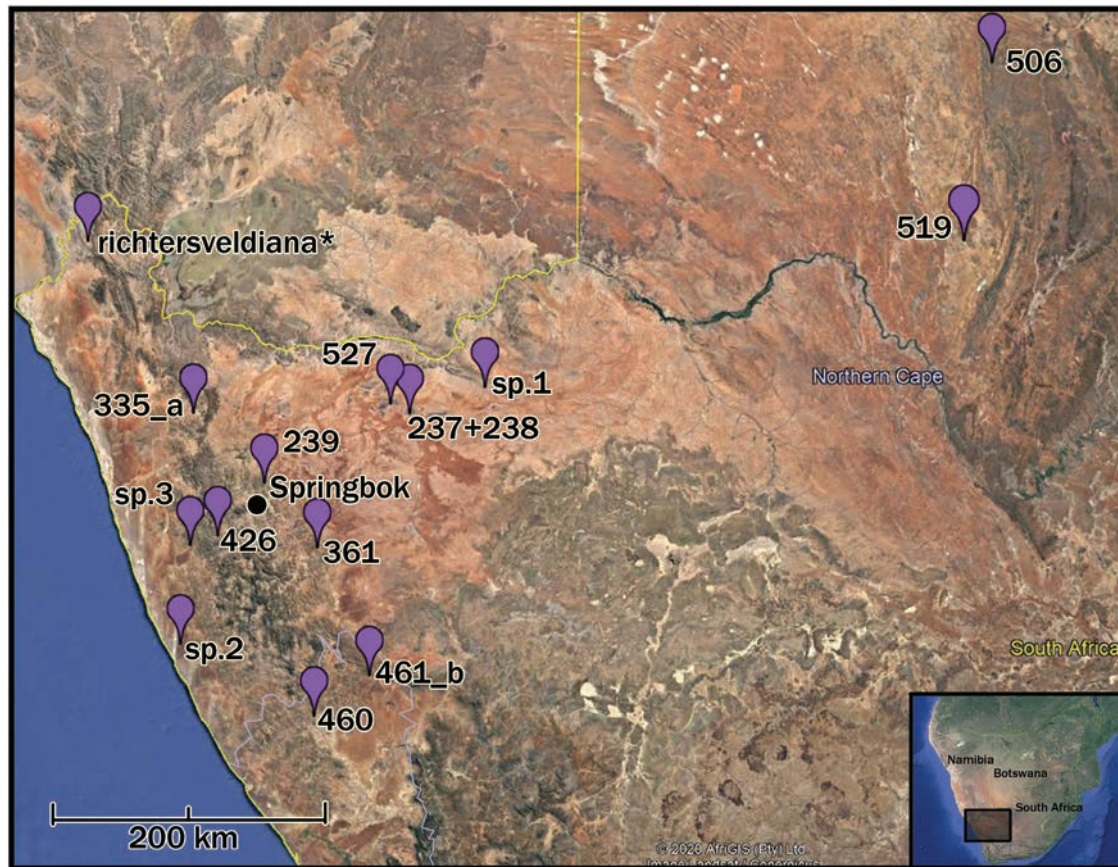
**Figure 13.** Distribution map of the genera *Namaquania* (blue markers) and *Pentamerica* (yellow markers). \* = type species. Map data: Google Earth, Maxar Technologies, used according to Google Earth Terms of Service.

*Type material:* Holotype: species 422, ♂, RSA (South Africa), Northern Cape, Namaqua NP, E Wildeperdehoek Pass, 29°56.837'S, 17°38.276'E, 496 m, 13.xi.2016, sifting of detritus, dead leaves and branches below shrubby *Euphorbia*, R. Borovec, M. Meregalli lgg. (TMSA). Paratypes: same data as the holotype, 47 ex (RBSC, MMTI, TMSA, SANC, BMNH, NMPC).

**CEDERBERGIA BOROVEC & MEREGALLI, GEN. NOV.**

*Zoobank registration:* Zoobank.org/urn:lsid:zoobank.org:act:A35B84F3-F62B-4D54-965F-88BA8863A4C4

*Type species:* *Cederbergia indecora* Borovec & Meregalli, here designated.



**Figure 14.** Distribution map of the genus *Nama*. \* = type species. Map data: Google Earth, Maxar Technologies, used according to Google Earth Terms of Service.

*Diagnostic description:* Small Namaini 1.8–2.6 mm; rostrum continuous with head with U-shaped stria on epifrons; frons squamose; gena glabrous and smooth, subgena densely squamose; antennal sockets in dorsal view hardly visible as narrow furrows, laterally with ventral margin directed to ventral margin of eyes and dorsal margin poorly noticeable, vanishing before eyes; procoxal cavities touching anterior margin of pronotum; apical surface of metatibiae squamose; abdominal ventrites densely squamose; suture between ventrites 1 and 2 conspicuously arched; tegmen lacking parameres; female sternite VIII with long and slender apodeme terminating inside of plate, plate wider than long.

*Etymology:* *Cederbergia* is derived from the Cederberg Mountains, rock formations located approximately 300 km north of Cape Town, where the majority of the taxa attributed to this genus were found. The gender is feminine.

*Included taxa and distribution:* In addition to the type species, 12 additional taxa are included in *Cederbergia*, based on the *mt-Cox1* analysis and/or

their morphology. They are distributed in South Africa: Western Cape (Fig. 17).

***CEDERBERGIA INDECORA* BOROVEC & MEREGALLI, SP. NOV.**

(FIGS 9, 10A, H, O, 11A, H, O)

*Zoobank registration:* urn:lsid:zoobank.org:act:5FBAB9E6-3508-48DF-92A3-F2D7ED1F6DDE

*Diagnostic description:* Body length 2.06–2.39 mm, holotype 2.08 mm. Semi-erect setae on elytra short, sparse, subspatulate, forming a regular row on each interstria, about as long as half the width of interstria; rostrum indistinctly tapered anteriorly with straight sides; epifrons wide, evenly tapered anteriorly with straight sides, broadly shallowly depressed on entire surface; epistome elongated anteriorly, forming two teeth, longer Pakhuis Pass, 32 in males; scapes robust, curved at basal third, at apical two-thirds evenly enlarged, at apex conspicuously wider than clubs; elytra short oval; protibiae robust with outer and inner

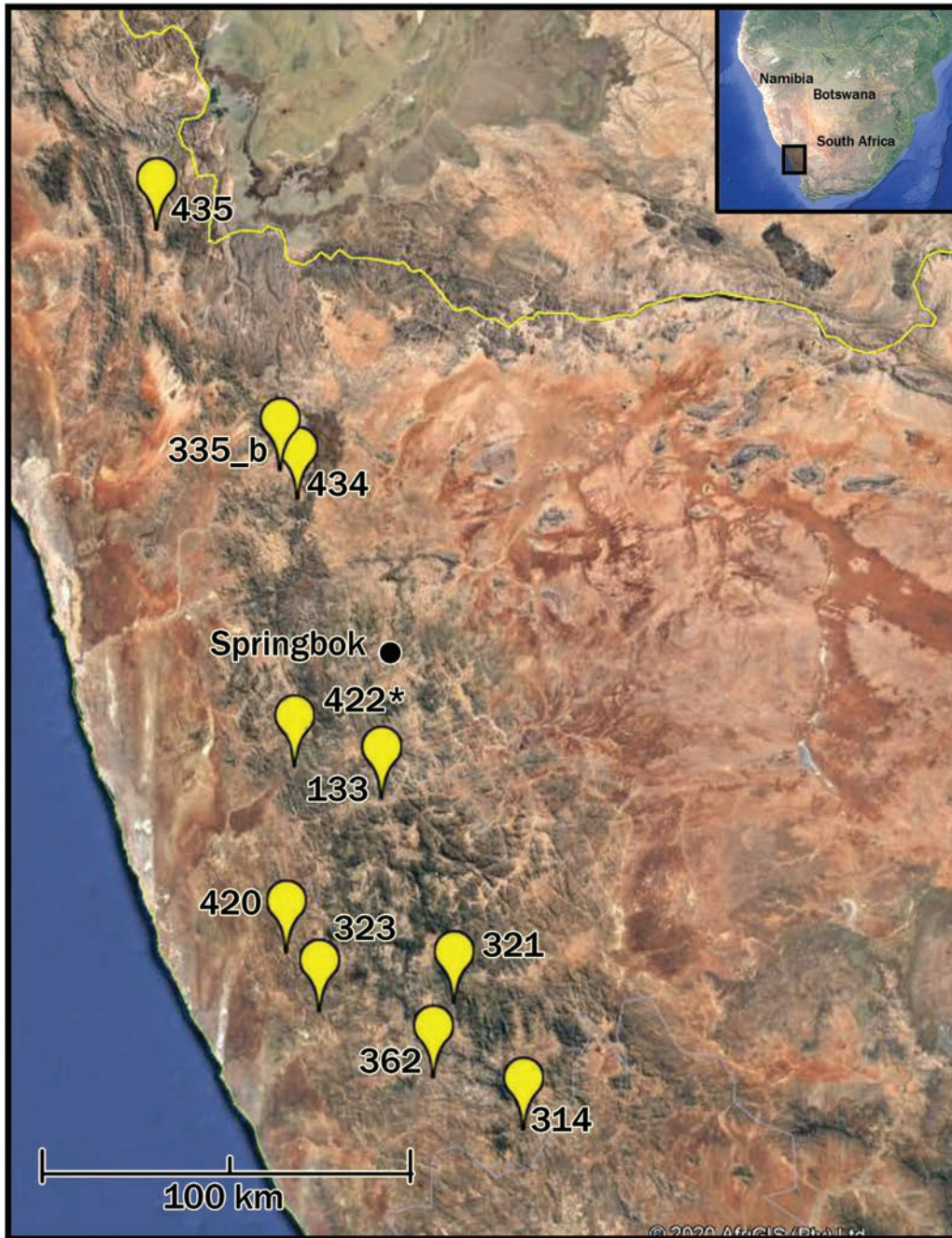




**Figure 15.** Distribution map of the genus *Yamalaka*. \* = type species. Map data: Google Earth, Maxar Technologies, used according to Google Earth Terms of Service.

side almost straight, apically rounded with a fringe of dense, black bristles; penis short, subparallel-sided, apically subtriangular with rounded tip; endophallus with two short, moderately wide sclerites; spermatheca with ramus short, slightly shorter than wide and conspicuously shorter than the slender and straight, tube-shaped nodulus.

*Etymology:* The specimens were collected by sifting dead leaves and decomposing humus at the margin of the parking area of the Pakhuis Pass, below a broad and high shrub, with branches reaching the ground and offering good shelter. The entire undershrub was filled with every type of trash, hence the name of the species, *indecora*, from the Latin *indecorus*, indecent.



**Figure 16.** Distribution map of the genus *Springbokia*. \* = type locality. Map data: Google Earth, Maxar Technologies, used according to Google Earth Terms of Service.

*Ecology:* The specimens were sifted from litter of dead leaves and branches under shrubby small trees in fynbos vegetation.

*Type material:* Holotype: species 465, ♂, RSA, Western Cape, Cederberg Mts., Pakhuis Pass, 32°08.979'S,

19°01.750'E, 1002 m, 22.xi.2016, R. Borovec lgg., sifting of detritus and dead leaves and branches below trees and shrubs (TMSA). Paratypes: same data as the holotype, 21 ex. (BMNH, MMTI, NMPC, RBSC, SANC, TMSA); same data as the holotype, 10.xi.2018, 4 ex. R. Borovec et M. Meregalli lgg. (MMTI, RBSC).



**Figure 17.** Distribution map of the genus *Cederbergia*. \* = type locality. Map data: Google Earth, Maxar Technologies, used according to Google Earth Terms of Service.

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2016: SANParks: Permit number CRC/2016/035–2012/V1; Northern Cape: ODB 2399/2016; Cape Nature: AAA041-00158-0056. 2018: SANParks: Permit number MERM/AGR/035–2012/2017–2022/V1; Northern Cape: ODB 2399/2016 renewed; Cape Nature: AAA041-00158-0056. 2019: SANParks: Permit number MERM/AGR/035–2012/2017–2022/V1; Cape Nature: CN44-28-11324. The authors declare that they have no conflict of interest.

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Contributions to the paper: M.M. and R.B.: general general structuring of the study and field sampling; M.M.: phylogenetic analysis and discussion of the results; R.B.: morphological descriptions, discussion on classification of the Entiminae; P.C., A.S., S.O., I.T.: DNA extraction, sequencing and contribution to the analysis of the results; O.N.: general management of the study.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**File S1.** Detailed descriptions of the taxa, comparative remarks and various notes.

**Table S1.** Estimates of Evolutionary Divergence between Sequences. The number of base differences per site from between sequences are shown. This analysis involved 38 nucleotide sequences. Codon positions included were 1st + 2nd + 3rd. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There were a total of 688 positions in the final dataset. Evolutionary analyses were conducted in MEGA X.

**Table S2.** *Mt-Cox1* sequences of the specimens examined.