Pythiopina, an enigmatic subtribe of darkling beetles (Coleoptera: Tenebrionidae: Pedinini): taxonomic revision, microtomography, ecological niche models and phylogenetic position

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Abstract. Morphological, anatomical, and distributional data concerning the South African endemic beetle subtribe Pythiopina (Tenebrionidae: Pedinini) are revised. Five species, representing two genera, are recognized. Included in this total is one new species (Meglyphus mariae Kamiński sp.n.). The following species are placed in synonymy: Meglyphus ciliatipes [=Meglyphus calitzensis syn.n.]; Meglyphus laenoides [=Meglyphus andreaei syn.n.; =Meglyphus namaqua syn.n.]. Microtomographic models for all valid Pythiopina species, including the holotype of the newly described species, are presented and analysed. Endoskeleton morphology (specifically characters of the tentorium and metendosternite) proved to be informative at the specific and generic levels. An identification key is provided to all known species of the subtribe. Environmental niche models are presented for the majority of species. A molecular phylogeny of Pedinini based on six genetic loci (28S: D1–D3 region; 28S: D4–D5 region, COII, ArgK, CAD2, wg) was also produced to explore the phylogenetic position of Pythiopina. This analysis is the first to include representatives of all seven subtribes of Pedinini, and supports a sister relationship between Pythiopina and the Palaearctic subtribe Dendarina. Results also suggest the existence of a second pair of sister taxa within Pedinini (in addition to Melambiina) with an amphitropical African distribution. This published work has been registered in ZooBank, http://zoobank.org/urn:lsid:zoobank.org:pub:285AD87A-46B1-4FE9-BC57-949EA1F70D49.

Introduction

Pythiopina Koch (Tenebrionidae: Tenebrioninae) is one of the smallest and least studied subtribes within Pedinini Eschscholtz (Bouchard et al., 2005, 2011). At present, it is represented by two flightless southern African genera, Pythiopus Koch (monotypic) and Meglyphus Motschulsky (hitherto seven species). To date, only three papers dealing with the taxonomy of this group have been published (Koch, 1953, 1955; Robiche, 2010).

Moreover, no previous attempts have been made to investigate the phylogenetic relationships of Pythiopina with the other subtribes of Pedinini. Due to the presence of an elongate metaventrite in all members of the subtribe – a feature often associated with macropterous darkling beetle species – it was interpreted as a presumably old and separate lineage, without direct connections to other pedinoid beetles (Koch, 1956).

Pythiopina specimens are very scarce in most entomology collections, and therefore several species are known only from a few specimens which were collected in a single location (e.g. Meglyphus ciliatipes Koch, Meglyphus calitzensis Koch and Meglyphus namaqua Koch). However, the major taxonomic uncertainty within Pythiopina concerns Meglyphus, which was
transferred to this subtribe based on the result of a taxonomic revision made by Koch (1955). While working on his paper, Koch was unable to study the holotype of *Meglyphus laenoides* Motschulsky, which is the type species of the genus, and, at that time, was the only known representative of the species (Motschulsky, 1872). Based on the material available to him, Koch distinguished six species, including five new ones that he wanted to describe. In order to do so, he was forced to base his interpretation of *M. laenoides* solely on the original diagnosis. He admitted that Motschulsky’s (1872) description can be applied to a variety of available morphotypes; however, he picked one and referred to it as ‘*M. laenoides* sensu meo’. This approach was especially precarious because, according to Koch’s interpretation, there were no diagnostic characters for female specimens and Motschulsky did not specify the sex of his holotype.

Koch’s (1955) decision had strong implications for the taxonomy of Pythiopina. Without examining Motschulsky’s *M. laenoides* holotype, it was impossible to determine whether Motschulsky (1872) and Koch (1955) were referring to the same species when describing *Meglyphus* morphology, and if all of Koch’s species were valid. To address this problem a taxonomic revision of the whole genus, based on complete type material, was performed. Additionally, to present a coherent description of the whole subtribe, the anatomy of *Pythiopus* was also analysed. Furthermore, because the relation of Pythiopina with other subtribes remained ambiguous (Koch, 1955, 1956), a preliminary phylogenetic analysis of Pedinini was performed. Based on the obtained results, a revised definition of Pythiopina is given.

**Material and methods**

**Revision of Pythiopina**

The revisionary part of this study was based on material from the Ditsong National Museum of Natural History, Pretoria, South Africa (TMNH), the Field Museum of Natural History, Chicago, USA (FMNH), the Museum and Institute of Zoology of the Polish Academy of Sciences (MIZ PAS), the Staatliches Museum für Naturkunde Stuttgart (SMNS), and the Zoological Museum of Moscow State University, Moscow, Russia (ZM MSU). The original label data for the specimens is given in quotation marks and separated by a comma. Each line of the original label data is separated by a forward slash. The morphological terminology follows that of Matthews *et al.* (2010), with additional specialized terms used for the male and female terminalia (Banaszkiewicz, 2006; Iwan & Kamiński, 2016). Terminalia were investigated using standard methodology (see Iwan & Kamiński, 2016). Morphological measurements were recorded using a filar micrometer. Images were taken using a Canon 1000D (Japan) body with accordion bellows and a Canon Macro Lens EF 100 mm (Japan), and with a Hitachi S-3400N (Japan) SEM in MIZ PAS.

**μCT analysis**

X-ray microtomographic (μCT) analyses were performed at MIZ PAS using a SkyScan 1172 system (SkyScan, 2008). During the scanning processes, the X-ray source was set to a voltage of 40 kV and a current of 250 mA. Images were obtained with no binning mode. Due to their specific body shape, the specimens were scanned using four to five oversized scans (Raś & Kamiński, 2013; Iwan *et al.*, 2015). Reconstruction was performed using NReacon software v. 1.6.4.7), and the segmentation process was conducted in CTAN v. 1.11.10. Specimen anatomy was later investigated in blender v. 2.77. During the μCT analyses, each Pythiopina species was represented by a single type specimen; holotype in the case of *Meglyphus mariae* Kamiński sp.n., and paratype material for all other taxa. All models are available in the supplementary material.

**Distributional patterns**

The distribution of species was illustrated using Quantum GIS (QGIS) v. 2.4. The raster layer used for creating the digital elevation model was downloaded from the WorldClim website (http://www.worldclim.org/). The division of the Afrotropical Realm into ecoregions was adopted after Olson *et al.* (2001). The concept of Coleoptera zones follows Endrödy-Younga (1978) and the digital version of this biogeographic division was created during a previous study (Kamiński, 2015a). The names of the Coleoptera zones where the specimens were collected are given in brackets in the distribution section for a particular species. The information in this section includes both previously published and newly analysed data.

The environmental niches of Pythiopina species were modelled using a presence-only method due to the lack of reliable absence data. Maximum entropy modelling (MaxEnt) was used, as it has been shown to have outstanding performance with small datasets when compared with other techniques (Elith *et al.*, 2006; Hernandez *et al.*, 2006). *Meglyphus mariae* sp.n. was not included in the analysis due to the scarcity of distributional data. For the MaxEnt calculations, a set of WorldClim (Hijmans *et al.*, 2005) environmental layers (continuous variables, resolution of 30 s) and a rasterized layer of Afrotropical ecoregions (categorical variable) from Olson *et al.* (2001) were used. The analysis was restricted to the southern part of Africa (the area south of 21.00°S). Models were run 50 times, with random test percentage set to 25 and ‘subsample’ as the sampling technique. The model evaluation was assessed by estimating the area under the curve (AUC) value (Fielding & Bell, 1997). Geographic overlaps between niches of particular species pairs were calculated as the proportion of shared cells of suitable conditions to the sum of ranges modelled for these species. Estimates of overlap were conducted using minimum training presence criterion as thresholds for probability of occurrence and the qgis software. Moreover, Schoener’s D (Schoener, 1968) and I (Warren *et al.*, 2008) indices were calculated in ENMTOOLS software (Warren *et al.*, 2010). Both measures give pairwise niche overlap, with values ranging from 0 (no overlap) to 1 (identical niche models). Identity test, implemented in ENMTOOLS, was used to check if the habitat suitability scores generated by models from two species exhibit statistically significant ecological differences.
Table 1. Subtribal classification of Pedinini.

| Subtribe                  | Distribution                  | References                                      |
|---------------------------|-------------------------------|-------------------------------------------------|
| Dendarina Mulsant and Rey | Western Palearctic            | Iwan & Löbl (2008)                              |
| Eurynotina Mulsant and Rey| Endemic to Southern Africa    | Kamiński (2016)                                 |
| Leichenina Mulsant        | Australasia, Afrotropic, Indomalaya, Neotropic (introduced) and Palearctic | Gridelli (1939) and Dunford & Steiner (2007)   |
| Melambina Mulsant and Rey | Afrotropic and western Palearctic | Kamiński (2011, 2015c) and Leo & Liberto (2011) |
| Pedinina* Eschscholtz     | North and central Afrotropic and Palearctic | Iwan & Löbl (2008)                              |
| Platynotina Mulsant and Rey| Afrotropic, Indomalaya, Nearctic, Neotropic and Palearctic (Canary Islands, Egypt) | Iwan (2002) and Kamiński (2015b)               |
| Pythiopina Koch           | Endemic to Southern Africa    | Present paper                                    |

*Subtribe Loensina Koch (see Bouchard et al., 2011, 2005) is interpreted here as a synonym of Pedinina (see Kamiński & Iwan, 2017).

Phylogenetic position of Pythiopina

In order to investigate the relationships of Pythiopina with the other subtribes of beetles belonging to Pedinini, a preliminary phylogenetic analysis of the whole tribe was performed. Fourteen taxa representing all seven subtribes of Pedinini were included (Kamiński & Iwan, 2017). For the currently accepted subtribal classification, see Table 1. Representatives of Opatrini were used as outgroups, as a close affiliation between Opatrini and Pedinini has been postulated by many authors (e.g. Koch, 1956; Medvedev, 1968; Doyen & Tschinkel, 1982). Voucher specimens (Table S1) are deposited in the entomological collection of MIZ PAS.

DNA extraction and sequencing

DNA was extracted from specimens using DNeasy Blood and Tissue kits (Qiagen Inc., Valencia, CA, U.S.A.) following the manufacturer’s protocols. Extractions were performed on whole head capsules, after cutting the occipital membrane and associated tissues connecting it to the rest of the body. After tissue digestion, each head was reassociated with its respective body, thus leaving relatively intact voucher specimens in which the head capsule could easily be glued back on when the specimens were removed from ethanol and mounted.

DNA was amplified and sequenced for six loci from five genes: 28S rRNA (28S, 1698 bp) D1–D3 and D4–D5 regions, cytochrome c oxidase II (COII, 654 bp), wingless (wg, 435 bp), CAD/ rudimentary (CAD2 sensu Moulton and Wiegmann 2004, 711 bp), and arginine kinase (ArgK, 669 bp). PCRs were performed in 25 μL reactions on either (Thermo Scientific, Waltham, MA, U.S.A.) or (BioRad iCycler, San Diego, CA, U.S.A.) thermocyclers using TaKaRa Ex Taq (TaKaRa, Mountain View, CA, U.S.A.) following the manufacturers’ protocols. Primer pairs and amplification conditions are described in Wild & Maddison (2008) and Kanda et al. (2015). PCR clean-up, quantification and sequencing were performed at the University of Arizona’s Genomic and Technology Core Facility (UAGC). Sequencing was done on a 3730 XL Applied Biosystems automatic sequencer.

Assembly of multiple chromatograms of each gene fragment and initial base calls were made with PHRED v. 0.020425.c (Green & Ewing, 2002) and PHRAP v. 0.990319 (Green, 1999) as orchestrated by Mesquite’s CHROMASEQ v. 1.12 package (Maddison & Maddison, 2014) with subsequent modifications by CHROMASEQ and manual inspection.

DNA analyses

Nucleotides were aligned in MESQUITE 3.11 (Maddison & Maddison, 2016). The 28S matrices (D1–D3 and D4–D5) were aligned with MAFFT v. 7.130b (Katoh & Standley, 2013) using the L-INS-i method. Protein-coding genes were manually aligned and checked based on their translated amino acid sequences. The genes either had no indels (ArgK, COII, and wg) or one- to two-amino-acid deletion (CAD2) in reference to the other taxa in the matrix. All nucleotide alignments were also combined into a single concatenated dataset for partitioning and phylogenetic analyses (Appendix S1).

Data partitions and the model of evolution for each partition were both inferred using PARTITIONFINDER v. 1.1.1 (Lanfear et al., 2012) and the concatenated dataset, initially partitioned by gene and codon position (for protein coding genes). Examined models were restricted to those available in MBAYES (Ronquist et al., 2012) and RAXML (Stamatakis, 2014). Models were compared using greedy searches and the Bayesian information criteria (BIC). The suggested optimal partitions (Table 2) were implemented for most subsequent analyses in each program, with exceptions discussed later.

Maximum parsimony (MP) analyses were conducted using PAUP*4.0a150 (Swofford, 2002) and TNT (Goloboff et al., 2008) with gaps treated as either missing data or a fifth state. A variety of heuristic [random stepwise additions 100–1000, with

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Results

Revision

The material examined during the present study allowed for the testing of species hypotheses for the majority of taxa (except M. ferreri) hitherto classified in Pythiopina. Results support the maintenance of both genera (Pythiopus and Meglyphus) currently classified within this subtribe, as both genera are easily characterized by the presence of autapomorphic features (Figs 6, 8). On the other hand, newly identified specimens allowed more detailed analyses of morphological variability within already known species. This resulted in the discovery of a new species (M. mariae sp.n.) and following taxonomic decisions: M. ciliatipes (= M. calitzensis syn.n.); M. laenoides (= M. andreaei Koch syn.n.; = M. namaqua syn.n.). General dorsal morphology of all valid Pythiopina species is presented in Fig. 1.

During the µCT analysis, three-dimensional models of all analysed species were constructed. The resolution of these visualisations enables detailed, digital investigation of the morphology of these taxa, including external and internal structures (STL models S1–5). Moreover, as this dataset contains models of type specimens representing all currently valid species, it can be treated as a reference for future taxonomic studies. However, as stated by Simonsen & Kitching (2014) this approach does not remove the need for real dissections and morphological expertise. Finally, analysis of the internal skeletal structures resulted in discovery of potentially phylogenetically informative characters (Figs 2, 3).

The morphology of tentoria observed in the 3D models revealed similarities between all Meglyphus species (Fig. 2A–D). In all cases, the anterior margins of the posterior tentorial arms are angled towards the midline (breadth ratio at the base/anterior tip of posterior tentorial arms = 2.6–6.2) (frontal view). Moreover, the anterior tentorial arms emerge laterally from the posterior tentorial arms. Finally, all species of Meglyphus are characterized by having a relatively long base on the posterior tentorial arms. On the other hand, in the case of Pythiopus the anterior margins of the posterior tentorial arms diverge slightly (breadth ratio at the base/anterior tip of posterior tentorial arms = 0.3) – forming a wide clearance in the frontal view (Fig. 2E). Unlike in Meglyphus, the anterior tentorial arms emerge dorsally from the posterior tentorial arms. Moreover, the base of the posterior tentorial arms is relatively narrow.

Analysis of metendosternite structure revealed a different image. A great similarity of this body element was reported between M. laenoides and Pythiopus cornutipes Koch (Fig. 3). In both cases, metendosternites are equipped with relatively elongated bases (total length:width ratio = 0.9–1.0), median perforations (length:width ratio = 2.0–3.0) and keels (length:width ratio = 3.3–4.6). Moreover, furcal arms seem to be subparallel in relation to the metaventrite (lateral view) (α = 10.0–18.0°; Fig. 3C, E). The remaining species of Meglyphus seem to have wider metendosternites (metendosternite, length:width ratio = 0.6–0.7; median perforation, length:width ratio = 0.6–1.2; keel, length:width ratio = 1.6–2.4) (Fig. 3A, B, D), while the value of the angle α reported for these taxa varies between 22.0° and 34.0°.

All results obtained during the revisionary part of this work are summarized in the ‘Taxonomy’ section.

Distribution

A database containing 43 localities for five Pythiopina species was compiled during this study (Fig. 4A). For most of the species several localities were obtained. Only M. mariae sp.n. is currently known from a single locality. Based on all specimens examined or reported in the literature, representatives of the investigated subtribe inhabit six ecoregions and three Coleoptera zones in southern Africa. The northernmost locality for the whole subtribe was reported for P. cornutipes (Fig. 4A). Details concerning distribution of particular species are presented in the Taxonomy section.

Environmental niche models generated for Pythiopina species showed high specificity, with average AUC values for the test dataset ranging from 0.991 to 0.996 (Fig. 4B–E). These models showed little overprediction outside of the locations included in analyses. The most crucial variables for each prediction were different. Maximum temperature for the warmest month was most important for predicting the distribution of P. cornutipes, mean temperature of wettest quarter for M. laenoides, mean temperature of driest quarter for M. bradleayi, and plant cover for M. ciliatipes. Models acquired for particular species do not predict the distributions of others (Fig. 4B–E).
Fig. 1. General dorsal morphology of species representing Pythiopina: (A, B) Meglyphus bradleyi; (C, D) Meglyphus ciliatipes; (E, F) Meglyphus laenoides (type species of Meglyphus); (G, H) Meglyphus mariae sp.n.; (I) Pythiopus cornutipectus (type species of Pythiopus). (A, C, E, G, I) males; (B, D, F, H) females. Scale bar = 2.00 mm.

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Distributional overlap ranged from 1.0% to 22.0%; however, in most cases the obtained values were relatively low (Table 3). Overlapping areas between *Meglyphus bradleyi*–*M. ciliatipes* and *M. bradleyi*–*M. laenoides* occurred near the western edge of Nama Karoo, while those between *M. ciliatipes*–*P. cornutipectus* and *M. laenoides*–*P. cornutipectus* close to the northern border of Succulent Karoo. The highest percentage of shared area was reported for the *M. ciliatipes*–*M. laenoides* pairing (Table 3). Predictions acquired for these taxa suggest that they can be found sympatrically through the Succulent Karoo ecoregion (Fig. 4). Divergences of ecological niches, measured by $D$ and $I$ indices, were revealed for most of the investigated species pairs (Table 3).

**Phylogenetic position**

All parsimony analyses recovered identical results depending on how gaps were treated. Analyses with gaps treated as missing data resulted in two most parsimonious trees ($L = 3080$, consistency index (CI) = 0.57, retention index (RI) = 0.43), and those with gaps treated as a fifth state also resulted in two most parsimonious trees ($L = 3144$, CI = 0.57, RI = 0.43). Recovered topologies differed only in the placement of *Pedinus femoralis* (L.). Bayesian analyses recovered robust topologies based on majority-rule consensus of 30,002 sampled trees each. For Bayesian analyses using the models of evolution recommended by *PARTITIONFINDER* (Fig. 5A), the final topology had
Fig. 3. X-ray microtomographic models of metendosternites of species representing Pythiopina: (A) Meglyphus bradleyi; (B) Meglyphus ciliatipes; (C) Meglyphus laenoides; (D) Meglyphus mariae sp.n.; (E) Pythiopus cornutipectus. Lateral (top) and dorsal (bottom) projections are provided. Abbreviations: w, total width height of metendosternites; l, length height of metendosternites; h, height of metendosternites; α, angle between base of sternum and furcal arms. Scale bars = 100 μm. [Colour figure can be viewed at wileyonlinelibrary.com].

an average standard deviation of split frequencies = 0.00076 and log-likelihood score of −18,835. Analyses applying the GTR + Γ model to all partitions resulted in a similar average standard deviation of split frequencies value of 0.00075, but a log-likelihood score of −17,640. RAXML log-likelihood values were −19,062 without partitions and −18,173 with partitions, both using the GTR + Γ model as recommended in the program manual. All resulting trees were rooted with Opatrum sabulosum (L.) (Opatrina).

Recovered Bayesian and ML topologies varied depending on the evolutionary models and partitioning schemes used, with the highest log-likelihood score recovered in partitioned analyses using the GTR + Γ model for all partitions. All analyses were largely congruent, differing only in the monophyly of the genus Phylan Dejean, 1821, and the placement of Pedinus femoralis (L.) and Leichenum canaliculatum variegatum (Klug, 1833). Phylan was recovered as monophyletic in all parsimony analyses and Bayesian analyses using only GTR + Γ. The genus was paraphyletic in relation to Dendarus Latreille, 1829 in all other analyses. Leichenum canaliculatum (Leichenina) was recovered as sister to most of the subtribes (Fig. 5A) in the MP, Bayesian with recommended models, and unpartitioned ML analyses. It was recovered in a sister-group relationship with P. femoralis (Pedinina) in the partitioned ML and

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Fig. 4. Distribution of Pythiopina: (A) analysed localities; (B–E) distribution models obtained for selected species and (F, G) amphitropical disjunction in distribution of Melambiina and Pythiopina+Dendarina clade. Minimum training presence criterion was used as thresholds for probability of occurrence. Average area under the curve (AUC) value for each analysis is presented. Models were generated using a set of WorldClim (Hijmans et al., 2005) environmental layers and a rasterized layer of the Afrotropical ecoregions from Olson et al. (2001). Distribution and diversity of Melambiina after Kamiński (2011, 2015c) and Leo & Liberto (2011); Dendarina after Iwan & Löbl (2008) (modified). [Colour figure can be viewed at wileyonlinelibrary.com].

Bayesian with GTR+Γ only analyses (Fig. 5B), with both found at the base of a Melambiina + (Pythiopina + Dendarina) clade. In the MP, Bayesian with recommended models, and unpartitioned ML analyses, P. femoralis was not closely associated with L. canaliculatum, but instead moved from Pedinina + (Melambiina + (Pythiopina + Dendarina)) – in Bayesian with recommended models and unpartitioned ML – to Pedinina + (Pythiopina + Dendarina) or Pedinina + Melambiina in the MP trees, resulting in a basal polytomy of Pedinina + Melambiina + (Pythiopina + Dendarina) in the MP majority-rule consensus. All analyses, regardless of analytical method, partitioning or evolutionary models, recovered Pythiopina (Meglyphus) as the sister taxa to Dendarina (Dendarus and Phylan) (Fig. 5A, B).

Discussion

Phylogenetic position

The phylogeny presented in current paper is the first to illustrate relationships between all Pedinini subtribes (Fig. 5);
subtribes within Pedinini (e.g. Dendarina, Eurynotina, Loensina, (see Antoine, 1956; Koch, 1956; Medvedev, 1968; Iwan, 2002).

Ticanus santandRey) and Platynotina (e.g. Angolositus Pedinina (e.g. not all Pythiopina species have divided eyes, similarly for some

However, this is not supported by either the reconstructed molecular phylogeny or a broader examination of the taxa. Namely, not all Pythiopina species have divided eyes, similarly for some Pedinina (e.g. Cabirutus Strand); on the other hand, several Melambiina (e.g. Melambius Multasent and Rey, Litoborus Multasent and Rey) and Platynotina (e.g. Angolositus Koch, Atrocrypticus Iwan), have eyes split in half by the extended canthus (see Antoine, 1956; Koch, 1956; Medvedev, 1968; Iwan, 2002). Moreover, dilated male protosomeres occur in several different subtribes within Pedinini (e.g. Dendarina, Eurynotina, Loensina, Melambiina) as well as the nonabbreviated epipleuron (Koch, 1956; Kamińska, 2016). Furthermore, within Pedinina the met- tum is tripartite, with a protruding medial lobe and exposed lateral lobes. Therefore, available morphological data seem to be in accordance with the molecular hypothesis presented in this paper (Fig. 5).

The taxonomic distinctiveness of Pythiopina and Dendarina is not unequivocal, as the latter entity is currently defined only by the absence of autapomorphic features reported for the first, e.g. the metasternum is not elongate (Koch, 1956; Medvedev, 1968). However, this is probably caused only by the lack of adequate morphological studies. Most of the conceptual works concerning Pedinini are dated to the first half of 20th Century (Antoine, 1942; Español, 1945; Koch, 1948), which is an era before Pythiopina was proposed. Due to this, Dendarina was customarily compared with Pedinina. Therefore, in the light of current knowledge it would be premature to propose a synonymy between Pythiopina and Dendarina before completing a more detailed study of their relationship, including the examination of additional Dendarina taxa.

### Biogeographic remarks

From the biogeographic point of view, Melambiina display an amphitropical distribution (Fig. 4F), with two separate biodi- versity hotspots located on opposite edges of Africa (Mediterranean Basin and southern Africa) and only a few enigmatic taxa in between (Koch, 1956; Kamińska, 2011). This type of distribution is also shared by many other groups of organisms (e.g. Coleman et al., 2003; Biondi & D’Alessandro, 2008; Kirk-Spriggs & McGregor, 2009). According to the presented phylogeny for Pedinini, the Pythiopina + Dendarina clade also follows this pattern (Fig. 4G). The commonly accepted sce- nario explaining the origin of this distributional pattern was proposed by Balinsky (1962), who hypothesized that southwestern Africa and the Horn of Africa were connected by a corridor of drier habitat. It is thought that this linkage expanded to its maxima during the Pleistocene glacial periods (Verdcourt, 1969; van Zinderen Bakker, 1975; Goldblatt, 1978). This scenario invokes vicariance as the main cause of the origin of the disjunctions and seems to be widely supported by both plant and animal studies (Verdcourt, 1969; van Zinderen Bakker, 1975; Goldblatt, 1978; Biondi & D’Alessandro, 2008). However, data presented by Kergoat et al., 2014a suggest that Den- darina diverged from Melambiina in the middle Cretaceous (~ 100.00 Ma); therefore according to this estimate, the origin of the amphitropical distributions within Pedinini should be linked to some other paleoclimatic events. In light of these results, it is possible to hypothesize that the Cretaceous reduc- tion of the arid zones might have played a crucial role in the evolution of the Pythiopina + Dendarina clade (Hallam, 1984; Füllmi, 2011). However, future studies are required to calibrate more accurately the phylogenetic events within Pedinini and analyse the biogeographic history of this group. Nevertheless, the discovery of amphitropical distributions on the African continent within two sister clades (Melambiina and

| Species pair | Percentage overlap | $D$ | $I$ |
|-------------|-------------------|----|----|
| Meglyphus bradleyi versus Meglyphus ciliatipes | 1.9 | 0.227<sup>a</sup> | 0.530<sup>a</sup> |
| M. bradleyi versus Meglyphus laenoides | 3.5 | 0.221<sup>a</sup> | 0.485<sup>a</sup> |
| M. bradleyi versus Pythiopina cornutipectus | 1.0 | 0.284<sup>a</sup> | 0.612<sup>a</sup> |
| M. ciliatipes versus M. laenoides | 22.0 | 0.521 | 0.781 |
| M. ciliatipes versus P. cornutipectus | 1.1 | 0.284<sup>a</sup> | 0.537<sup>a</sup> |
| M. laenoides versus P. cornutipectus | 10.0 | 0.499 | 0.766 |

<sup>a</sup>Value significant (Identity test). Percentage of overlapping was calculated using the minimum training presence criterion as thresholds for probability of occurrence. For definitions of Schoener’s $D$ and $I$ indices, see Warren et al., 2008.

some previous studies included only a few representatives of Dendarina and Melambiina (Kergoat et al., 2014a,b). All reconstructed topologies, regardless of methodology, support a sister-group relationship between Pythiopina and Dendarina. From a morphological point of view, this relation is supported by the following characters: aedeagal tegmen composed of two parts, parameres short (length ratio of parameres to the whole tegmen maximally equals 0.3), penis equipped with a pair of clavae, abdominal process wide (width at least 2× distance between mesocoxae), and mentum flat (not covering cardii and basistipites; lateral wings shielded by the middle part) (Figs 6A–C, 7). The latter character is only shared by Melambiina outside of Pythiopina and Dendarina (Kamińska, 2015c), which according to the presented phylogeny is sister to the Pythiopina-Dendarina clade (Fig. 5). Several taxa currently classified within Dendarina were often placed in Melambiina and vice versa (Kamińska, 2011). However, the latter entity is sharply separated from the Pythiopina + Dendarina clade by having unipartite (composed of a single part) aedeagal tegmen (e.g. Español, 1945, 1958; Antoine, 1956; Koch, 1956; Iwan, 2001, 2004).

On the other hand, Koch (1956) implied that besides Dendarina, Pythiopina might be close to Pedinina mainly due to the following characters: eyes divided by canthus, epipleuron not abbreviated, aedeagal tegmen composed of two parts (base and parameres), and frequently dilated protosomeres in males. However, this is not supported by either the reconstructed molecular phylogeny or a broader examination of the taxa. Namely, not all Pythiopina species have divided eyes, similarly for some Pedinina (e.g. Cabirutus Strand); on the other hand, several Melambiina (e.g. Melambius Multasent and Rey, Litoborus Multasent and Rey) and Platynotina (e.g. Angolositus Koch, Atrocryptic aratus Iwan) have eyes split in half by the extended canthus (see Antoine, 1956; Koch, 1956; Medvedev, 1968; Iwan, 2002). Moreover, dilated male protosomeres occur in several different subtribes within Pedinini (e.g. Dendarina, Eurynotina, Loensina,
Fig. 5. Preliminary phylogeny of the tribe Pedinini (16 taxa, 4167 bp) based on molecular markers [28S: D1–D3; D4–D5 regions; cytochrome c oxidase II (COII), arginine kinase (ArgK), CAD/ rudimentary (CAD2) and wingless (wg)]. (A) Bayesian majority rule consensus with inferred evolutionary models from partitionfinder v1.1.1 (20 million generations, 0.25 burn-in). (B) Maximum likelihood (ML) topology from raxml (GTR + Γ with recommended partitions). Posterior probabilities are displayed above branches, and bootstrap values (1000 rapid raxml bootstrap replicates) are shown below. MP, maximum parsimony. [Colour figure can be viewed at wileyonlinelibrary.com].
Pythiopina (Pythiopina-Dendarina) provides an interesting background for future biogeographical studies.

An examination of the compiled distributional data for Pythiopina highlighted a potentially interesting pattern within the subtribe – allopatric yet closely distributed taxa – so ecological niche modelling was performed to check for potential biases in the analysed material (Fig. 4B–E). Although some small areas were predicted for any species pair, allowing potential areas of sympathy to be identified, in general the geographic regions of high environmental suitability for each species were clearly delimited (Fig. 4B–E). Hence, the resulting ecological niche models supported initial observations from the raw data (Fig. 4A). It is believed that allopatric distributions may originate when a geographic barrier develops faster than adaptation of a particular taxon to the new ecological conditions (e.g. Wiens, 2004). In this case, populations on each side of the barrier would have the same ecological requirements (niche conservatism). If this were the scenario for Pythiopina, the generated distributional models for particular species should overlap significantly (Kozak & Wiens, 2006). However, as mentioned earlier, the revealed niche overlap between species is relatively small (Table 3). Therefore, it is probable that taxonomic differentiations in Pythiopina involved processes of adaptation to differing environments (Jaime et al., 2015). For example, in contrast to other species, M. bradleayi occurs in an area with significantly lower mean temperatures during the driest quarter (Fig. 4B). In summary, the revealed distributional patterns of Pythiopina species make them a potentially interesting group within which to study speciation mechanisms. Future studies would benefit from a detailed molecular phylogeny, which should include all known species of this subtribe.

**Taxonomy**

Studied material, morphology and distributional data concerning previously described taxa representing Pythiopina are presented in Appendix S2.

**Subtribe Pythiopina Koch**

Pythiopini Koch, 1953: 245. - Koch, 1955: 450; 1956: 38; Medvedev, 1968: 13; Iwan, 2001: 352; Robiche, 2010: 169.

Pythiopina Koch, 1953. - Iwan, 2004: 737; Bouchard et al., 2005: 502; 2011: 67.

**Diagnosis.** Within Pedinini, this subtribe is similar to Dendarina, Eurynotina, Pedinina and Platynotina in having the aedeagal tegmen composed of parameres and a basal piece (composed of a single part in Leichenina, Loensina and Melambiina; see Koch, 1956; Kamiński, 2015b). From Eurynotina and Platynotina, Pythiopina can be distinguished by having a non-stridulatory gula (e.g. Iwan, 2002; Kamiński, 2015c, 2016). Moreover, it is easily differentiated from Eurynotina based on the presence of clavae on the male genitalia (absent in Eurynotina) (Fig. 7C–F). Pythiopina can be distinguished from Pedinina by having short parameres (basal part of tegmen longer than parameres; opposite in Pedinina) (Iwan, 2004). Pythiopina can also be separated from all other subtribes of Pedinini based on the elongate metasternum (which is not correlated with the development of wings, as the body is apterous; length ratio of metasternum to metacoxa = 1.7–2.0) present in all known species.

Moreover, Pythiopina can also be distinguished from all other subtribes based on the following character combination: apical segment of maxillary palps with relatively small sensory field (not occupying the whole outer edge) (Fig. 6A), canthus subparallel in basal part (Fig. 1), dorsally eyes shielded by longitudinal keel (Fig. 6F, G), and elytral humerus dentate, strongly protruding laterad (Fig. 6L, M).

**Key to the genera of Pythiopina**

1. Body size: 2.8–4.5 mm. Third antennomere short (the ratio of its length to the length of the second antennomere = 0.9–1.0); fifth antennomere short (the ratio of its length to width = 1.0) (Fig. 6D). Eyes reduced (three rows of ommatidia visible on the dorsal side; maximally a single row is present between temples and genae) (Fig. 6F). Disc of pronotum rounded. Base of pronotum straight (Fig. 1A–H). Scutellum triangular (Fig. 6M).

   Intercoxal process of the prosternum narrow and depressed apically (not angular) (Fig. 6H). Surface of prosternum with coarse punctuation (Fig. 6H). Mesoventrite without processes. Metaventrite relatively short (ratio between the distance of meso- and metacoxae to the diameter of mesocoxa = 1.5). The underside of male third protarsomere tomentose (Fig. 8B). Male protibiae more strongly expanded towards apex, most frequently equipped with sharp postmedian tooth (however, see Fig. 8A–D). .................. Meglyphus

   – Body size: 6.0–8.5 mm. Third antennomere elongated (the ratio of its length to the length of the second antennomere = 2.0); fifth antennomere elongated (length/width ratio = 1.5) (Fig. 6E). Eyes relatively well developed (four rows of ommatidia visible on the dorsal side; two rows present between temples and genae) (Fig. 6G). Disc of pronotum cordiform. Base of pronotum sinoidial (Fig. 1I). Scutellum widely rounded (Fig. 6L). Intercoxal process of the prosternum wide and not depressed apically. Surface of prosternum with fine punctuation and two elongated setae in the middle (Fig. 6I). Mesoventrite with globular process. Metaventrite elongated (ratio between the distance of meso- and metacoxae to the diameter of mesocoxa = 3.0). The underside of male protarsi not tomentose (Fig. 8E). Male protibiae slender, with longitudinal median dilatation (Fig. 8E). .......................... Pythiopus

**Genus Meglyphus Motschulsky**

Meglyphus Motschulsky, 1872: 38.- Koch, 1955: 452; 1956: 38; Medvedev, 1968: 10; Iwan, 2001: 352; 2004: 739.

**Diagnosis.** The phylogenetic distinctness of this genus is grounded by the following autapomorphies: (i) eyes reduced
Fig. 6. Diagnostic characters of species representing Pythiopina: (A–C) mentum; (D, E) antenna; (F, G) eye; (H, I) intercoxal process of prosternum; (J, K) hind coxa; and (L, M) scutellum. (M) Meglyphus bradleyi; (F, H) Meglyphus ciliatipes; (A, D, J) Meglyphus laenoides; (B) Meglyphus mariae sp.n.; (C, E, G, I, K, L) Pythiopus cornutipunctus.
Pythiopina, an enigmatic subtribe of darkling beetles

Fig. 7. Structure of female (A, B) and male (C–F) terminalia of species representing Meglyphus: (A, C) M. bradleyi; (B, D) M. ciliatipes; (E) M. laenoides; (F) M. mariae sp.n. Dorsal (top) and ventral (bottom) views of aedeagal tegmina are presented for every species. Scale bar = 200.0 μm.

(two rows of ommatidia visible on the dorsal side; maximally a single row is present between temples and genae) (Fig. 6F); (ii) intercoxal process of the prosternum narrow and depressed apically (Fig. 6H); (iii) the underside of male third protarsomere tomentose (Fig. 8B); (iv) male protibiae strongly extended towards apex, most frequently equipped with sharp postmedian tooth (Fig. 8A–D). For other characters separating this genus from Pythiopus see the identification key to the genera of Pythiopina.

Species included (4). M. bradleyi, M. ciliatipes, M. laenoides, M. mariae sp.n.

Key to the species of Meglyphus

1. Sides of the apical part of mentum parallel (Fig. 6A). Pronotum elongated (length:width ratio = 1.1), ovoid (Fig. 1E, F). Male metatibiae medially curved, without setation.................................. Meglyphus laenoides – Sides of the apical part of mentum narrowing towards apex (Fig. 6B). Pronotum widened (length:width ratio = 0.9). Male metatibiae of other shape.............................(2)

2. Pronotal base angular (Fig. 1G, H). Elytra elongated (length:width ratio = 1.8). Elytral intervals with fine punctures (Fig. 1G, H). Male metatibiae straight. Male metafemorae with median denticle on inner side (Fig. 1G). ................................................................. Meglyphus mariae Kamiński sp.n. – Pronotal base rounded (Fig. 1A–D). Elytra widened (length:width ratio = 1.6). Elytral intervals with coarse punctures (Fig. 1A–D). Male metatibiae curved. Male metafemorae simple .............................................(3)

3. Elytra covered with dense setae (Fig 6M). Third protarsomeres in males strongly dilated. Underside of second and third protarsomeres tomentose (Fig. 8A). Male protibiae with median dilatation. Male fifth ventrite with circular depression ......................... Meglyphus bradleyi – Elytra glabrous (Fig. 1C, D). Third protarsomeres in males slightly widened (Fig. 8B). Underside of third protarsomeres tomentose, second one glabrous (Fig. 8B). Male protibiae with sharp postmedian tooth. Male fifth ventrite without circular depression ..................... Meglyphus ciliatipes

Meglyphus bradleyi Koch
(Figs 1A, B, 2A, 3A, 4A, B, 6M, 7A, C, 8A)

Meglyphus bradleyi Koch, 1955: 453.

Diagnosis. This species is similar to M. ciliatipes and M. mariae sp.n. having mentum with sides narrowing towards apex (Fig. 6B) and relatively widened protibiae (Fig. 8B, C, D). Moreover, it shares with M. mariae sp.n. unique structure of male protarsi (strongly dilated) (Fig. 8A, D). Meglyphus bradleyi can be distinguished from all above-mentioned species by different structure of elytral intervals (Fig. 6M), male profemorae (Figs 8A) and fifth ventrite (with circular depression in males).

Meglyphus ciliatipes Koch
(Figs 1C, D, 2B, 3B, 4A, C, 5, 6F, M, 7B, D, 8B, 9)

Meglyphus ciliatipes Koch, 1955: 455. = Meglyphus calitzensis Koch, 1955: 455 syn.n.

Diagnosis. This species is similar to M. laenoides, having relatively narrow third tarsomeres in male protibiae (Figs 8B,
Fig. 8. Structure of male front legs of species representing Pythiopina: (A) Meglyphus bradleyi; (B) Meglyphus ciliatipes; (C) Meglyphus laenoides; (D) Meglyphus mariae sp.n.; (E) Pythiopus cornutipectus. Dorsal (left) and ventral (right) views are presented. Moreover, in case of M. ciliatipes and P. cornutipectus close-ups of the underside of the front tibiae are provided; for M. laenoides, the structure of the female front tibia and tarsus is illustrated. Scale bars = 500.0 μm.

C). Both species differ by the structure of mentum (subparallel sides in M. laenoides, Fig. 6A) and pronotum (Fig. 1C–F). Meglyphus ciliatipes can be distinguished from all its congeners in having a glabrous underside of second protarsomeres in males (Fig. 8B).

Habitat notes. The individuals of this species were recently collected within the borders of the Anysberg Nature Reserve. The newly acquired specimens were found under the stones in a dried riverbed. For habitat photographs see Fig. 9. Specimens were collected under permit number AAA007-00183-0056 issued by the Chief Executive Officer, Western Cape Nature Conservation Board.

Meglyphus laenoides Motschulsky
(Figs 1E, F, 2C, 3C, 4A, D, 6A, D, I, 7E, 8C)
Meglyphus laenoides Motschulsky, 1872: 41.- Koch, 1955: 452.

= Meglyphus andraeci Koch, 1955: 455 syn.n.- Koch, 1956: 37.
= Meglyphus namaqua Koch, 1955: 455 syn.n.

Diagnosis. This species can be distinguished from its other congeners by a unique structure of mentum (Fig. 6A), pronotum (Fig. 1E, F) and male protibiae (Fig. 8C).

Habitat notes. One of the investigated labels suggests a relationship of this species with African ant Tetramorium quadrispinosum Emery, 1886 junior synonym of Tetramorium sericeiventre Emery, 1877.

Meglyphus mariae Kamiński sp.n.
http://zoobank.org/urn:lsid:zoobank.org:act:BD95B5FE-9E80-4F46-9737-CA274353E75B
(Figs 1G, H, 2D, 3D, 4A, 6B, 7F, 8D)
Material examined. Holotype, female (TNHM): ‘S. Afr.: SW Cape Prov/Clanwilliam river/32.09°S–18.53°E’, ‘29.8.1989; E-Y: 2674/flowering meadow/Endrödy & Klimaszewski’. The microtomographic model of the holotype is available as the supplement to this publication (STL model S4). Paratypes, two males and female: same data as holotype.

Etymology. Meglyphus mariae is named in honour of my daughter, Maria Antonina Kamińska, born 9 June 2016 (Warsaw, Poland).

Diagnosis. This species is similar to M. bradleyi in sharing the following male features: strongly widened third and
Morphology. Body. Length = 3.5–4.0 mm. Habitus as in Fig. 1G, H.

Dorsal side of head dull, with conspicuous punctures (two to three diameters apart). Frontoelypeal suture extremely fine. Canthus subparallel in basal part. Clypeal emargination relatively shallow (clypeal emargination width/depth ratio ca. 6:1). Labrum wide (width:length ratio ≈ 3:0); delicately emarginated in the middle. Sides of mentum parallel. Mentum flat, not covering cardines or basistipites, cordiform. Submentum pentagonal. Apical segment of maxillary palpus triangular (with all sides of equal length); with relatively large sensory field (occupying more than half of the proximal edge). Second segment of maxillary palpus wide (length:width ratio ≈ 1.3). Palpifer with two setae located near base; with internal sulcus for maxillary palpus visible from ventral view. Anterior tentorial pits circular. Dorsally eye shielded by longitudinal keel. Three rows of facets visible in the dorsal part of eye; eye completely divided by canthus; two rows visible on the ventral side. Antenna relatively long (length of antenna/maximal length of pronotum ≈ 1:3). Antennomere short (the ratio of its length to the length of the second antennomere = 0.9–1.0); fifth antennomere short (length:width ratio = 1:0). Antennomeres 5–10 transverse.

Pronotum equal to or slightly narrower than elytra (width ratio elytra/pronotum ≈ 1:2). Length:width ratio of pronotal disc ≈ 0.9. Pronotal disc dull; covered with conspicuous punctures (two to four diameters apart); covered with short setae. Lateral sides of pronotal disc subparallel in basal part; widest in the middle; without apophyal depressive. Lateral emargination of pronotum narrow and complete; basal emargination complete (clearly visible, relatively broad); anterior widely interrupted middle. Middle of prosternum glabrous. Pronotal hypomeron dull, with longitudinal rugosites. Intercostal process of prosternum depressed apically. Procoxae situated closely (width ratio of procoxa and intercoxal process ≈ 6:0).

Elytra dull; glabrous. Elytral striae not impressed, visible as nine rows of conspicuous punctures on each elytron (one to two diameters apart). Intervals flat, with fine punctures (six to seven diameters apart). Elytral base straight; not emarginate. Epipleuron straight in most of its length, narrowing at the level of fifth abdominal ventrite; slightly narrower than the neighbouring elytral interval; situated ventrally, only the apical part is visible in dorsal aspect near the elytral slope. Elytral humerus dentate, strongly protruding laterad. Scutellum relatively small; rounded. Metathoracic wings absent.

Mesoventrite without processes. Metaventrite relatively short (length ratio cavity of hind coxa/metaventrite between the insertions of mid and hind coxae ≈ 0.7). Process of first abdominal ventrite wide (ratio of distances between mid- and meta coxae ≈ 0.5). Fifth abdominal ventrite unbordered; in males, without median circular depression, with circular protuberances in the middle.

Mesotrochanters nearly entirely covered by mesofemora; metatrochanters entirely concerned by metafemora; both equipped with a single setae. Metatrochantin merged with metacoxae (however, with conspicuous suture). Metacoxae rounded. The underside of male second and third protarsomere tomentose; third protarsomere wide (at least 1.5× wider than the second one). Male protibia with cavity near apical part; metafemora with a median denticle. Female legs simple (protibiae evenly widened toward apex).

Aedeagal tegmen (Fig. 7F) not flattened. Parameres evenly narrowing towards apex; nearly completely divided. Clavae narrowing towards apex; sharpened apically. Penis relatively narrow. Ovipositor relatively short (length ratio body/ovipositor ≈ 11:0). Paraproct shorter than coxites. Paraproct shield valvifer and part of second lobe. Valvifer wide and short (breadth:length ratio ≈ 4:6); second and third lobe of coxites elongated. Apical lobe narrow and situated on the lateral side of the third one. Gonostyli situated laterally. Vagina and bursa copulatrix without sclerites. Spermatheca with thin ducts; connected with bursa copulatrix by a thin canal. Spiculum ventrale short (width:height ratio ≈ 5:0).

Microtomography. Base of posterior tentorial arms relatively long (base length:width of head capsule ratio ≈ 0:4); originates just behind posterior eye margin and terminates on occipital foramen. Posterior tentorial arms triangular in shape (lateral view), their upper margins are shorter than the base (Fig. 2D); in anterior parts angled towards the midline (breadth ratio at the base/anterior tip of posterior tentorial arms ≈ 5:3) (Fig. 2D). Tentorial bridge situated in the anterior part of the upper edge of the posterior tentorial arms (distance from posterior tip to posterior arms base ratio ≈ 0:8); strut-like; relatively narrow (width ratio tentorial bridge:head capsule ≈ 0:1). Opposite tentorial sides connected exclusively by tentorial bridge. Laminenteronium is not developed. Anterior tentorial arms relatively long (length:width of head capsule ratio ≈ 0:5); first emerges laterally, while in posterior halves antero-laterally. In the place where anterior tentorial arms change their directions they are widened and start forming a plate, which is directed laterally.

Metendosternite relatively wide (maximal length:width ratio ≈ 0:7) and short (length ratio metendosternite to body ≈ 0:1) (Fig. 3D). Furcal arms reaching almost one third of body height; directed dorso-laterally (angle between base of sternum and furcal arms, α ≈ 24.0°); relatively narrow (width ratio furcal arm to maximal width of metendosternite ≈ 0:1). Median perforation of transverse ridge occupies dorsal plane of stalk; widened (length of perforation to its width ≈ 0:6). Keel relatively long (height:ratio ≈ 1:6). Length of stalk keel measured at base is shorter than its maximal length (basal length of keel: maximal length of keel base ratio ≈ 2:1).

Distribution. This species has been collected in the following ecoregions of South Africa (Cape Zone): Lowland fynbos and renosterveld (Fig. 4A).
Genus Pythiopus Koch

*Pythiopus* Koch, 1953: 245.- Koch, 1955: 452; Medvedev, 1968: 10; Iwan, 2001: 352; 2004: 739; Bouchard et al., 2005: 511; 2011: 424.

*Diagnosis.* The phylogenetic distinctness of this genus is grounded by the following autapomorphies: (i) pronotum cordiform (Fig. 1I); (ii) scutellum widely rounded (Fig. 6L); (iii) surface of prosternum with fine punctuation and two elongated setae in the middle (Fig. 6I); (iv) mesoventrite with globular process. For other characters separating this genus from *Meglyphus*, see the identification key to the genera of Pythiopina.

*Species included (monotypic).* *Pythiopus cornutipectus.*

*Pythiopus cornutipectus* Koch

(Figs 1I, 2E, 3E, 4A, E, 6C, G, I, K, L, 8E)

*Pythiopus cornutipectus* Koch, 1953: 249.- Koch, 1955: 452; 1956: 38.

*Diagnosis.* See the diagnosis of the genus *Pythiopus*.

*Species excluded from Pythiopina.*

*Meglyphus ferreri* Robiché

*Meglyphus ferreri* Robiché, 2010: 169.

*Type data. Holotype.* male (collection of Robiché G.): 'Mozambique, Prov. Tete, Chipembere, 21-25.XII.2009, leg. Robiché G. et Meissonnier G., in coll. Robiché G'.

*Justification.* Despite the fact that the authors of this paper were unable to investigate the morphology of the holotype of this species, it is clear that *M. ferreri* does not fit the current interpretation of *Meglyphus* or *Pythiopus*. According to the initial description, this species is *inter alia* characterized by well-developed eyes, narrow base of pronotum, obtuse elytral humerus, male protibiae with longitudinal insertions (Robiché, 2010). None of these features were reported for Pythiopina. Moreover, the morphology of the aedeagal tegmen of *M. ferreri* is not consistent with that revealed for *Meglyphus* and *Pythiopus* (Fig. 7). However, it is highly probable that this species represents the tribe Pedinini (presence of clavae on aedeagal tegmen; see Iwan, 2001, 2004).

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12255

Appendix S1. Concatenated dataset of nucleotide alignments used for phylogenetic analyses.

STL model S1. Three-dimensional model of *Meglyphus bradleyi* (paratype). Link: Raš, Marcin, 2017, 'Pythiopina, an enigmatic subtribe of darkling beetles (Pedinini): taxonomic revision, microtomography, ecological niche models and phylogenetic position', doi:10.7910/DVN/IKYGGS, Harvard Dataverse, V1; *Meglyphus bradleyi* (paratype).stl [fileName] doi:10.7910/DVN/IKYGGS.

STL model S2. Three-dimensional model of *Meglyphus ciliatipes* (paratype). Link: Raš, Marcin, 2017, 'Pythiopina, an enigmatic subtribe of darkling beetles (Pedinini): taxonomic revision, microtomography, ecological niche models and phylogenetic position', doi:10.7910/DVN/IKYGGS, Harvard Dataverse, V1; *Meglyphus ciliatipes* (paratype).stl [fileName] doi:10.7910/DVN/IKYGGS.

STL model S3. Three-dimensional model of *Meglyphus laenoides* (paratype). Link: Raš, Marcin, 2017, 'Pythiopina, an enigmatic subtribe of darkling beetles (Pedinini): taxonomic revision, microtomography, ecological niche models and phylogenetic position', doi:10.7910/DVN/IKYGGS, Harvard Dataverse, V1; *Meglyphus laenoides* (paratype).stl [fileName] doi:10.7910/DVN/IKYGGS.

STL model S4. Three-dimensional model of *Meglyphus mariae* sp.n. (holotype). Link: Raš, Marcin, 2017, 'Pythiopina, an enigmatic subtribe of darkling beetles (Pedinini): taxonomic revision, microtomography, ecological niche models and phylogenetic position', doi:10.7910/DVN/IKYGGS, Harvard Dataverse, V1; *Meglyphus mariae* sp.n. (holotype).stl [fileName] doi:10.7910/DVN/IKYGGS.

STL model S5. Three-dimensional model of *Pythiopus cornutipectus* (paratype). Link: Raš, Marcin, 2017, 'Pythiopina, an enigmatic subtribe of darkling beetles (Pedinini): taxonomic revision, microtomography, ecological niche models and phylogenetic position', doi:10.7910/DVN/IKYGGS, Harvard Dataverse, V1; *Pythiopus cornutipectus* (paratype).stl [fileName] doi:10.7910/DVN/IKYGGS.

Appendix S2. Studied material, morphology and distributional data concerning previously described taxa representing Pythiopina.

Table S1. Taxa sequenced for analyses with collection data, voucher numbers and GenBank accession IDs for DNA sequences.

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