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Do the members of the rare African bee genus *Anthidioma* (Megachilidae, Anthidiini) deserve distinct genus status?

Max KASPAREK & Michael KUHLMANN

A b s t r a c t : The bee genus *Anthidioma* PASTEELS, 1984, is considered endemic to southern Africa and comprises only two dark species lacking the carinae and maculations typical for most anthidiines. Their taxonomic status has remained ambiguous mainly because both species have been known only from single females. We describe here the hitherto unknown male of *A. chalicodomoides* PASTEELS, 1984, and found that the specialized hairs on the sterna and the two pairs of black sternal combs allow us to attribute it to the genus *Pseudoanthidium*. In an analysis of the sequence of the mitochondrial COI gene, the species turned out to be nested within the *Pseudoanthidium* clade and is closely related to the Palearctic members of the *P. scapulare* and *P. ochrognathum* groups and some other Palearctic species with very similar sternal apparatus. The genus *Anthidioma* PASTEELS, 1984 is hereby suggested to be regarded as a junior synonym of *Pseudoanthidium* FRIESE, 1898. Due to the large number of undescribed species in both the Afrotropical and Palearctic realms, there are many missing links that do not yet allow us to suggest a sound, well-justified subgeneric classification.

Key words : *Pseudoanthidium*, wool carder bees, South Africa, Namibia, taxonomy

Introduction

The genus *Anthidioma* has been erected by PASTEELS (1984) in order to accommodate two species of wool-carder bees from southern Africa: *Anthidioma chalicodomoides* PASTEELS, 1984, from the Western Cape Province, South Africa, and *A. murinum* PASTEELS, 1984, from the area which is Namibia today. The females of both species are characterized by the absence of carinae on the preoccipital ridge, the omaulus, and the scutellum, by flat terga without raised margins, long mandibles with seven teeth, and by basitarsi with bristles. MICHENER & GRISWOLD (1994) transferred *Anthidioma murina* to *Afranthidium* s. str., while GRISWOLD & GONZALEZ (2013) described a new species, *A. obibense* GRISWOLD & GONZALEZ, 2013, from Namibia and affiliated it to *Anthidioma*.

Both *A. chalicodomoides* and *A. obibense*, as well as *A. murina* which has been transferred to *Afranthidium*, have been known only from single females. Their taxonomic classification has therefore always been ambiguous and the placement in a distinct genus not well justified. In an attempt to clarify the taxonomic relationships within the Anthidiini, LITMAN et al. (2016) found close taxonomic relationships of *Anthidioma* with the genus *Anthidium*, while they did not formally suggest not to maintain the generic status.

The second author succeeded in collecting several specimens of *A. chalicodomoides* in

western South Africa, notably including a male, that is regarded to be inevitable for clarifying the taxonomic position. The male is described here for the first time which enables a reappraisal of the systematics of *Anthidioma* based on its morphology. We substantiate our morphological results with a genetic analysis of the 'barcoding region' of the mitochondrial cytochrome c oxidase subunit 1 gene (COI).

Methods

DNA extraction, PCR amplification, and sequencing were conducted by the Canadian Centre for DNA Barcoding (CCDB), Guelph, using standardised high-throughput protocols (<http://ccdb.ca/resources>). The mitochondrial cytochrome c oxidase subunit 1 gene (COI) was sequenced, with LepF1 as forward, LepR1 as reverse, and LepF1 as sequence primer (HEBERT et al. 2004). The results were submitted to Barcode of Life Data System (BOLD; RATNASINGHAM & HEBERT 2007), a cloud-based data storage and analysis platform developed by CCDB (www.barcodinglife.com). DNA alignments were made with the Muscle Alignment, run on MEGA11 software (TAMURA et al. 2021). Neighbor Joining (NJ) Tree phylogenetic analysis was performed using MEGA version 11.0.11 (KUMAR et al. 2018), and bootstrap values were determined from 1000 replications using the Tamura-Nei (TN93) model.

Five species of *Afranthidium* (*A. alternans* (KLUG, 1832), *A. carduele* (MORAWITZ, 1876), *A. lebanense* (MAVROMOUSTAKIS, 1955), *A. pusillum* (MORAWITZ, 1895), and *A. schultzei* (FRIESE, 1897)) and five species of *Anthidium* (*A. cingulatum* LATREILLE, 1909, *A. manicatum* (LINNAEUS, 1758), *A. florentinum* (FABRICIUS, 1775), *A. punctatum* LATREILLE, 1809, and *A. undulatum* DOURS, 1873) were used as outgroups (CMK). These two genera belong like *Pseudoanthidium* to "Series B" of the Anthidiini sensu MICHENER (2007) or the "*Anthidium* group" sensu LITMAN et al. (2016).

The genetic analysis was limited to Palaearctic and Afrotropical species of *Pseudoanthidium*, utilizing DNA sequences of ≥ 500 base pairs while excluding contaminants, sequences with stop-codons, and taxa with unclear species-level identification. For taxa with larger series available, only a selected number of samples were included in the analysis. The examined material included DNA sequences downloaded from the BOLD database.

The term "species group" is employed here to denote a cluster of closely related species below the genus level. Species within a species group share common character traits, thereby setting them apart from other species within the same genus. The members of a species group may not always represent the closest relatives within the genus, and the term itself does not denote a specific taxonomic rank. Furthermore, "species complex" is considered synonymous with "species group" within this context.

Images were taken with a digital microscope (Keyence VHX-5000) using the VH-Z20R/Z20T (20x to 200x) zoom lens and the OP-42305 super diffused illumination adapter. Images were stacked for extended depth-of-field.

Permits for fieldwork and wild bee collecting in South Africa were granted to M. Kuhlmann by Cape Nature for Western Cape Province (permit numbers 202/1999, 250/2000, 368/2001, AAA004-00212-0035, AAA004-00446-0035, AAA004-01055-0035, 0056-AAA008-00076, CN44-87-21440) and by Northern Cape Department of Environment and Nature Conservation for Northern Cape Province (025/2002, 056/2003,

0055/04, 0332/05, 0648/06, 0317/07, FAUNA 074/2008, FAUNA 1299/2008, FAUNA 082/2010, FAUNA 557/2011, FAUNA 638/2012, FAUNA 155/2013, FAUNA 1213/2014, FAUNA 0529/2016, FAUNA 0345/2017, FAUNA 0461/2022).

Abbreviations

CMK.....Collection Max Kasperek, Heidelberg

RCMKResearch collection of M. Kuhlmann, Zoological Museum of Kiel University, Kiel, Germany

Results

"Anthidioma" chalicodomoides PASTEELS, 1984 (Figs 1-3)

Holotype (not examined). Female, South Africa, Cape Province, Clanwilliam, B. Don (Biedouw) Valley, 25.ix.1977, B. V. Whitehead leg., Iziko South African Museum, Cape Town, South Africa (data after PASTEELS 1984).

Material examined (all South Africa): 15 km NW Nieuwoudtville, Farm Zoetfontein E, Fynbos (31°14'05"S 19°02'50"E), 775 m, 07.x.2022, 1♀, M. Kuhlmann leg. (CMK, mk1352); *Ibid.*; 11.viii.2023, 1♂ (RCMK: zmk059); Roggeveld Mts., 2km SE Farm Allemansdam (31°49'32"S 19°59'55"E), 1290 m, 20.09.2022, 2♀♀, M. Kuhlmann leg. (SCMK: zmk060, zmk061); 15 km NW Nieuwoudtville, Farm Engelsepunt, Fynbos (31°14'31''S 18°59'08''E), 830 m, 24.ix.2003, 1♀, K. Timmermann leg. (RCMK); 12 km NW Nieuwoudtville, Farm Avontuur, Fynbos (31°16'18''S, 19°02'55''E), 770 m, 10.ix.2009, 1♀, M. Kuhlmann leg. (RCMK); Cederberg Mts., road to Algeria, Olifants River bridge (32°21'55''S 18°57'06''E), 150 m, 8.ix.2017, 3♀♀, M. Kuhlmann leg. (RCMK).

Diagnosis: In accordance with PASTEELS (1984) and GRISWOLD & GONZALEZ (2013), the female can be recognized by the following combination of characters: body integument mostly black with rich long pubescence; clypeus with strong longitudinal ridges on the disc and without a thickened distal rim; scutum, scutellum, and terga densely punctate; and T6 vertical in profile, with the distal margin medially projected. The male, described here for the first time, is characterised by its black body integument with rich pubescence (as in the female); fine integumental punctation throughout; long, waved and hooked hairs on S3; a small, black comb next to the middle of S5, and a stronger black comb at the apex of a lateral arm of S3.

Description: The female is re-described here, while the hitherto unknown male is described for the first time.

Female: 8–9 mm. Head: Clypeus with strong, coarsely punctate, protruding longitudinal ridges (Figure 2A); apical part abruptly sloping inward; lower end with smooth, triangular surface; mandible slender, shining with small, shallow, scattered punctures (Figure 3A); strong apical, subapical, and uppermost teeth, and 4–5 minute teeth in between; antenna black; dense, long white hairs on lower face and lower gena, obscuring the sculpture, especially the clypeus; vertex hairs less dense, greyish-brown. Mesosoma: Black, scattered greyish hairs, but dense white pubescence on mesepisternum; scutellum and axillae crescent-shaped in dorsal view, median scutellar emargination absent; in profile, scutellum rounded in the middle and angulate laterally; very little overhanging propodeum; propodeum shagreened; pronotal lobe low, carinate. Metasoma: Black, terga with scattered

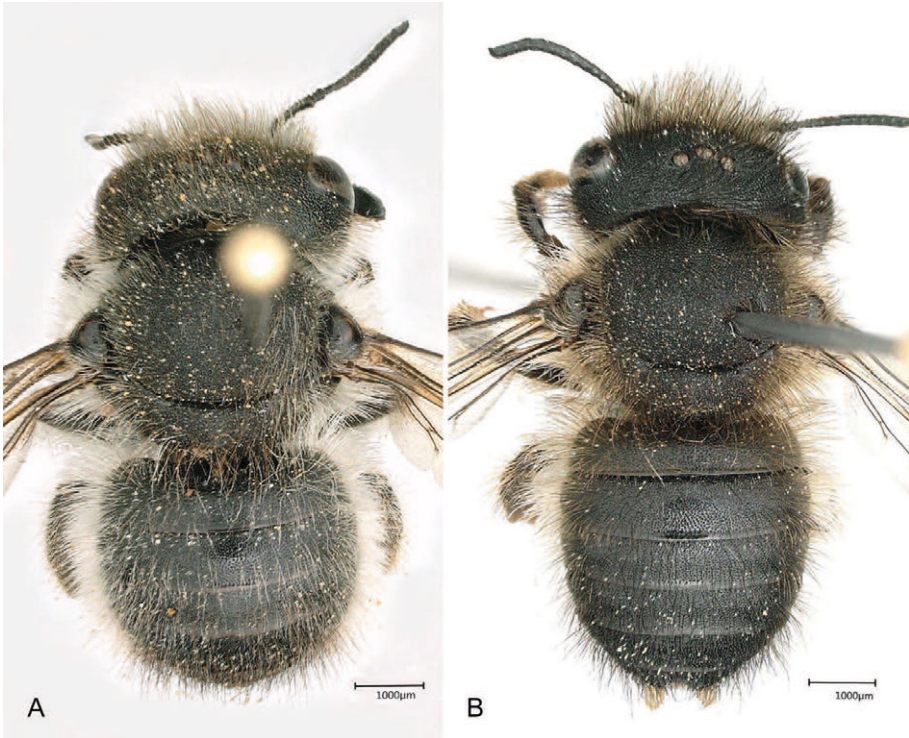


Fig. 1. Habitus of *Pseudoanthidium chalicodomoides* PASTEELS, 1984, from South Africa. **A.** Female; **B.** Male.

greyish pubescence, denser laterally (Figure 2C); hairs on T4–T6 dark brown; T1–T3 almost equally wide, T4–T6 tapering towards apex; punctuation fine, uniform, interstices up to one puncture diameter, but mostly less; no conspicuous distinction between disc and depression; smooth apical margin about one antennal width; edges protrude slightly upwards; T6 vertical in profile, distal margin horizontally projecting, small apical median emargination; scopa golden except for some grey bristles beneath horizontal projection of T6. Legs: Black, with greyish to light yellow-brown pubescence; inner faces of basitarsi with dark yellow-brown bristles.

Male. 9 mm. Black without light maculation (Figure 1); long white, greyish and yellowish pubescence. Head: Long, dense pubescence on lower face, silvery on clypeus, yellowish grey around antennal sockets, on lower gena, and on preoccipital ridge; scattered yellowish grey hairs on vertex; clypeus obscured by hairs; mandible black with three strong teeth separated by sharp incisions (Figure 3B); uppermost tooth the strongest; antenna black. Mesosoma: As in female; pronotal lobe low with shallow lamella. Metasoma: Similar to female. T6 and T7 with deep median emargination of the apical margin; S2 with apical fringe of long hairs; S3 with two rows of modified hairs: the inner row with cork-screw-like hairs, the outer row with longer, apically hooked hairs (Figure 3D); S4 with median, deep V-shaped incision; S5 with a small black comb on each side of the middle (distance between combs approximately 3.5 comb-widths) and a strong black comb at the

apex of a short lateral arm (Figure 3E); inner comb width approximately 12, outer comb with approximately 14 digits); hidden S7 deeply, and S8 shallowly bilobed. **Genitalia** (Figure 3E): Penis valves slender, not fused, tapering toward the apex; apex acute; gonocoxite slender; gonostylus leaf-shaped, slightly curved at the sides, protruding far beyond penis valve. **Legs**: Black, with long reddish-yellowish hairs; inner face of hind basitarsus densely covered with reddish bristles.

Genetic Analysis. We obtained the COI gene sequences of three females (SCMK: ZMK060, ZMK061; CMK: MK1352), all with a complete set of 658 base pairs (bp), and fully barcode-compliant as per BOLD quality standards.

In the identification tool provided by BOLD, the top 100 nearest neighbours revealed 21 species, with 71.4% belonging to *Pseudoanthidium*, 19.0% to *Afranidium*, and 4.8% each to *Pseudoheriades* (Osmiini) and the Nearctic *Trachusa mitchelli*. All hits with a genetic match of >88% belonged to the *Pseudoanthidium scapulare* group.

The analysis of phylogenetic relationships using the Neighbor Joining (NJ) methodology revealed that "*Anthidioma*" *chalicodomoides* is unambiguously nested within the *Pseudoanthidium* clade (Figure 4). Its closest relatives are the members of the *Pseudoanthidium scapulare* and *P. ochrognathum* groups, with "*Anthidioma*" *chalicodomoides* placed basally to them. Afrotropical relatives include species whose identity still needs to be confirmed. Due to the high number of undescribed species in *Pseudoanthidium*, a sound sub-generic division is not yet possible. The Palearctic taxa for which genetic data were available, could be assigned to seven different lineages.

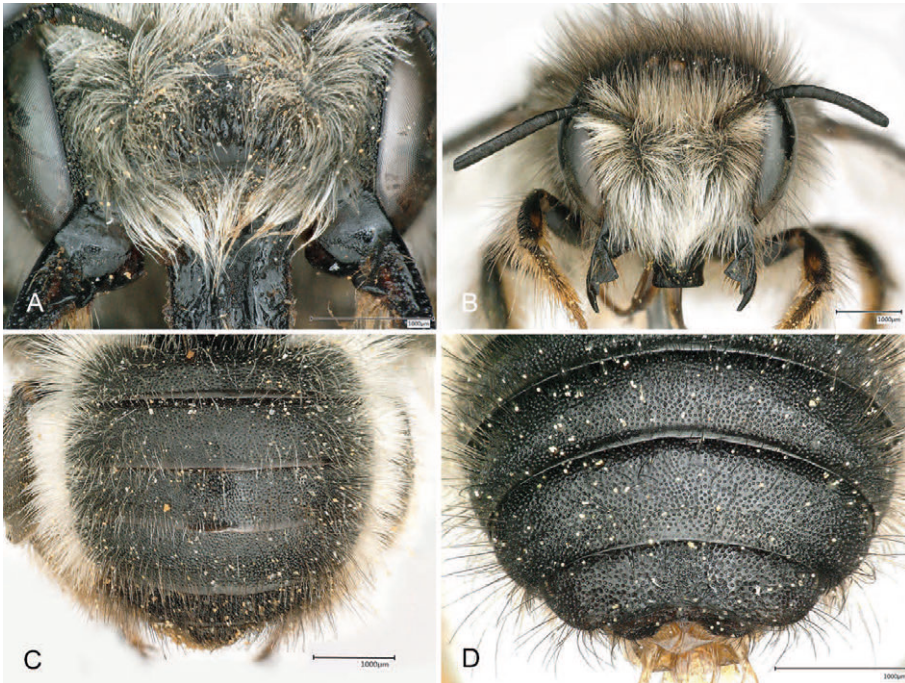


Fig. 2. *Pseudoanthidium chalicodomoides* PASTEELS, 1984. **A.** Face of the female. **B.** Face of the male; **C.** Terga of the female. **D.** Terga of the male.

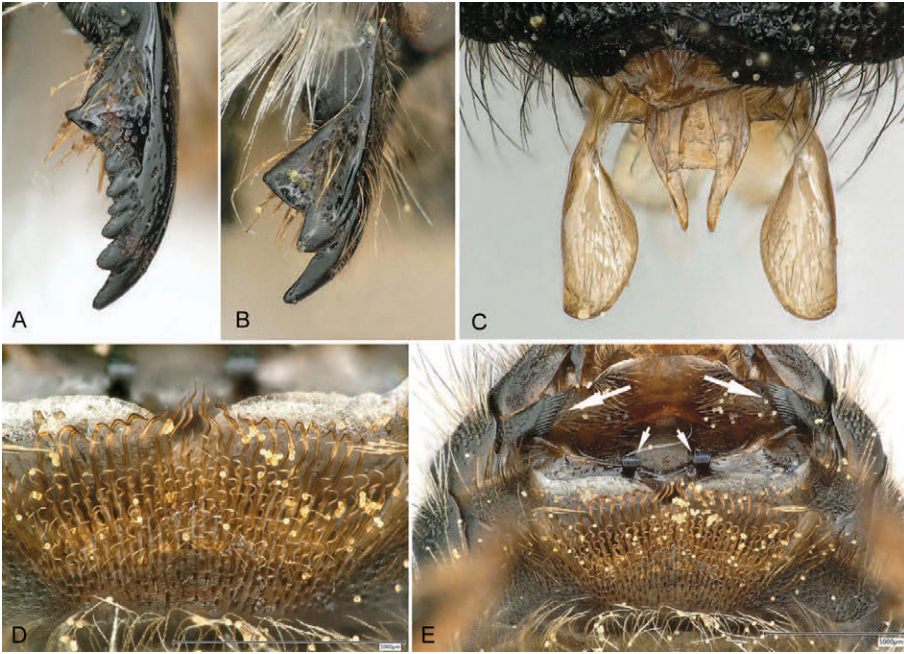


Fig. 3. *Pseudoanthidium chalicodomoides* (PASTEELS, 1984), from South Africa. **A.** Female mandible. **B.** Male mandible. **C.** Male genitalia. **D.** Corkscrew-like and apically hooked hairs on sternum 3 (S3) of the male. **E.** Sterna of the male with modified hairs on S3 and black combs on S5 (white arrows).

Distribution and habitat: The species seems to be endemic to the Fynbos region of southern Africa, occurring between the Cederberg Mts. (Clanwilliam area) in the south, the Roggeveld Mts. south of Calvinia in the east and the Bokkeveld plateau (Nieuwoudtville vicinity) in the north (Figure 5). It was found predominantly on sandy soils with typical Fynbos vegetation, characterised by evergreen, hard-leaved Mediterranean-type shrubland. It was collected visiting the flowers of Asteraceae for pollen, indicating an apparent oligolectic behaviour.

Taxonomic conclusion on generic status: Based on the morphological and genetic results, we transfer the two described species of *Anthidioma*, *A. chalicodomoides* and *A. murina*, to the genus *Pseudoanthidium* as follows:

Genus: *Pseudoanthidium* FRIESE, 1898

Syn.: *Anthidioma* PASTEELS, 1984

Pseudoanthidium chalicodomoides (PASTEELS, 1984)

Pseudoanthidium obibense (GRISWOLD & GONZALEZ, 2013)

These two species seem to be closely related with the Palaearctic *Pseudoanthidium scapulare* and the *P. ochrognathum* groups.

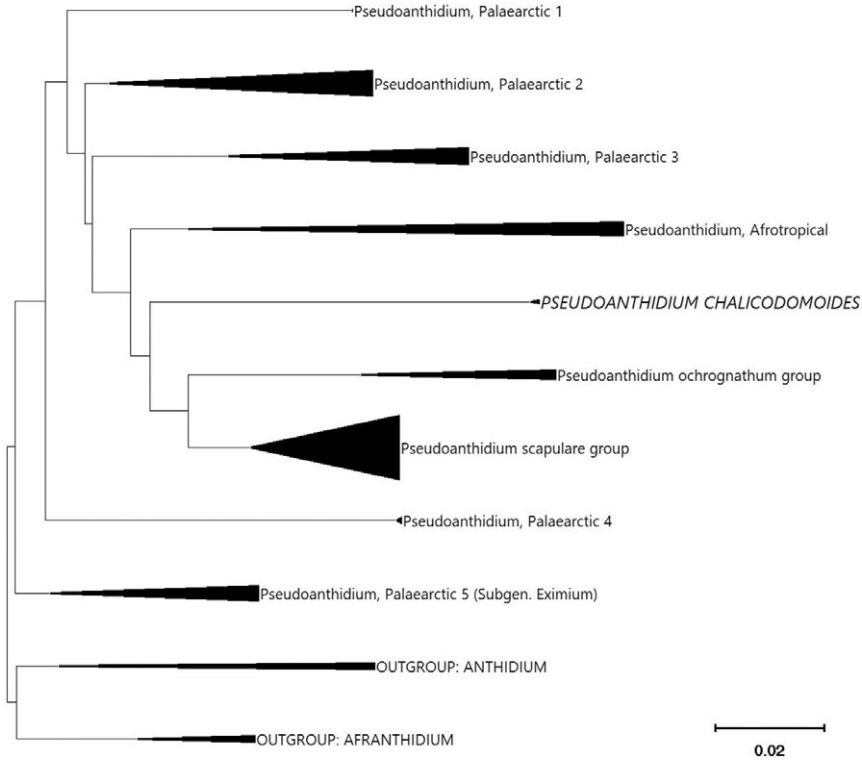


Fig. 4. Genetic relationships within the genus *Pseudoanthidium* as inferred from the DNA sequences of the barcoding region of the mitochondrial COI gene. Five selected species each of the genera *Anthidium* and *Afranthidium* were used as outgroup. For the sake of clarity, the sequences of closely related species were collapsed and classified according to their geographic origin.

Discussion

The genus *Anthidioma* was found to be a junior synonym of *Pseudoanthidium*, and the two described species are transferred to *Pseudoanthidium*. The presence of combs on the ventral metasoma of the male is a character not found in *Afranthidium*, *Anthidium*, and *Serapista*, the three other genera belonging to the "*Anthidium* group" sensu LITMAN et al. (2016). On the other hand, combs on the male sterna have been reported from at least 11 of 38 genera of Anthidiini. According to information compiled after MICHENER (2007), these include *Anthidiellum* COCKERELL (S5 with marginal comb), *Bathanthidium* MAVROMOUSTAKIS (median comb on S4 and S5), *Dianthidium* COCKERELL (comb on S5), *Hypanthioides* MOURE (S3 with median marginal comb or S4 with small but strong basal median comb or S5 with apical comb), *Pachyanthidium* FRIESE (S5 with a broad apical comb), *Plesianthidium* CAMERON (S4 with comb or S5 with apical comb), *Paranthidium*



Fig. 5. Distribution of *Pseudoanthidium chalicodomoides* PASTEEELS, 1984 (red dots) and *P. obibense* GRISWOLD & GONZALEZ, 2013 (violet dots). Records after PASTEEELS (1984), GRISWOLD & GONZALEZ (2013), ASCHER & PICKERING (2024), and this paper. The question mark stands for a record for which no further details are available.

COCKERELL & COCKERELL (S4 with median comb, S5 with lateral comb), *Pseudoanthidium* FRIESE (S5 with two pairs on combs), *Rhodanthidium* ISENSEE (S4 and/or S5 with marginal and/or median comb), *Stelis* PANZER (combs on S3 and/or S4, see figures in KASPAREK 2015), and *Trachusa* PANZER (combs on S4 and S5). In most of these genera, combs are not found in all members but are confined to certain species groups or subgenera. Therefore, it seems that combs have emerged during evolution independently both within a group and in different genera. This is also supported by the fact that the location and structure of the combs, as well as their size and type of bristles, do not follow a unique pattern but vary between the species and genera. The character of two pairs of combs, with one of them being placed at the apex of lateral combs, seems to be a unique feature for the relevant species of the genus *Pseudoanthidium*. Additionally, the specific arrangement of corkscrew-like and apically hooked hairs on S3 represents a distinctive character trait observed exclusively in certain species within the *Pseudoanthidium* genus.

Straight, unmodified penis valves and spoon-, leaf- or paddle-shaped gonostyli are a characteristic feature of members belonging to the *Pseudoanthidium* genus (see e.g. photographs in KASPAREK 2022: 173). In contrast, species within the *Anthidium* genus typically exhibit extended penis valves with curved, twisted, apically hooked, or otherwise modified

structures. The genitalia of *Afranthidium* species remain inadequately understood; however, they encompass varieties such as fused penis valves, slender, elongated, and parallel-sided gonostyli, as well as significantly enlarged penis valves, among others (MICHENER 2007). The structure of the genitalia of "*Anthidioma*" *chalicodomoides* thus corresponds to that of *Pseudoanthidium*, but not *Anthidium* or *Afranthidium*.

The close relationship of "*Anthidioma*" with the genus *Anthidium* that was suggested by LITMAN et al. (2016) could not be confirmed. Their analysis was based on female characters only and lacked genetic data. Their finding that "*Anthidioma*" *chalicodomoides* is in a polytomy with the genus *Anthidium* as found in a Maximum Likelihood (ML) analysis (Table S3 in LITMAN et al. 2016) and that the species is nested within the nominate subgenus of *Anthidium* as revealed in a phylogenetic tree based on Bayesian analyses of morphological traits concatenated with genetic data (Table S2 in LITMAN et al. 2016) may be influenced by this lack of genetic data.

In general, the subgeneric division of the genus *Pseudoanthidium* is poorly understood. Just recently, LITMAN et al. (2016) transferred three Afrotropical species groups to *Pseudoanthidium*, which have previously been regarded as subgenera of *Afranthidium*. Additionally, they moved the Palearctic genus *Neanthidium* PASTEELS, 1969 into *Pseudoanthidium*. Also in the Palearctic, the situation is complex and poorly understood, and KASPAREK & EBMER (2023) found that the classical distinction between species assigned to the nominate subgenus or to the subgenus *Royanthidium* cannot be maintained. Additionally, it appears that only a small portion of the species of *Pseudoanthidium* have been described, and there are still many "missing links" that must be found in order to get a better understanding of the phylogenetic relationships. Due to the numerous unresolved taxonomic questions, we currently refrain from a subgeneric assignment of *P. chalicodomoides*.

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Zusammenfassung

Die Bienengattung *Anthidioma* PASTEELS, 1984, gilt als endemisch im südlichen Afrika und umfasst nur zwei dunkle Arten, denen die für die meisten Anthidiini typischen Carinae und Farbmuster fehlen. Der taxonomische Status dieser beiden Arten war bisher nicht eindeutig, da sie nur von einzelnen Weibchen bekannt waren. Wir beschreiben hier das bisher unbekannte Männchen von *A. chalicodomoides* PASTEELS, 1984. Die spezialisierte Behaarung der Sterna und die zwei Paare schwarzer Sternalkämme entspricht einem Muster, das nur von der Gattung *Pseudoanthidium* bekannt ist. Bei einer Analyse der DNA Sequenz des mitochondrialen COI-Gens stellte sich heraus, dass die Art im Stammbaum innerhalb der *Pseudoanthidium*-Klade liegt und eng mit den paläarktischen Mitgliedern der *P. scapulare* und *P. ochrognathum* Artgruppen sowie einigen anderen paläarktischen Arten mit sehr ähnlichem Sternalapparat verwandt ist. Wir schlagen daher vor, die Gattung *Anthidioma* als jüngeres Synonym von *Pseudoanthidium* FRIESE, 1898 anzusehen. Aufgrund der großen Anzahl unbeschriebener Arten sowohl in der Afrotropis als auch in der Paläarktis gibt es viele "missing links", die es uns noch nicht erlauben, eine solide, gut begründete Untergattungseinteilung vorzuschlagen und *A. chalicodomoides* entsprechend zuzuordnen.

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Authors' addresses:

Dr. Max KASPAREK
Mönchhofstr. 16, D-69120 Heidelberg, Germany
E-mail: Kasperek@t-online.de

Prof. Dr. Michael KUHLMANN
Zoological Museum, Christian-Albrechts-Universität
Hegewischstraße 3, D-24105 Kiel, Germany
E-mail: mkuhlmann@zoolmuseum.uni-kiel.de

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