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ARTICLE

The wool carder bee *Pseudoanthidium alpinum* (MORAWITZ, 1873): identity of the enigmatic type species of the genus *Pseudoanthidium* (Hymenoptera: Megachilidae: Anthidiini)

Max KASPAREK¹  • Andreas Werner EBMER² 

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Abstract

Pseudoanthidium FRIESE is a species-rich genus of wool carder bees (Anthidiini) in the Old World. *Pseudoanthidium alpinum* (MORAWITZ, 1873), originally described from the Caucasus Mountains, was chosen as the type species of the genus, although it was insufficiently known. A genetic analysis of the mitochondrial cytochrome c oxidase I (COI) gene (barcoding gene) of new material now allowed the unequivocal assignment of males and females to each other and proved the conspecificity of material from Spain, Greece and Georgia. It turned out that the males with their specialized hairs and combs on the metasomal sterna correspond to the characteristics of *Pseudoanthidium* s. str., but females with their fully exposed, protruding clypeal apex to the subgenus *Royanthidium* PASTEELS, 1969. A similar combination of male and female characters was also found in three other species of *Pseudoanthidium*. As the protruding clypeal apex is thus found in both subgenera, this trait proves to be inappropriate for subgeneric classification and indicates that the definition of the subgenus *Royanthidium* needs to be revised.

Keywords | Anthidiine bees • infrageneric division • subgenera • taxonomy • subgenus *Royanthidium*

L'Abeille cotonnière *Pseudoanthidium alpinum* (MORAWITZ, 1873): identité de l'énigmatique espèce-type du genre *Pseudoanthidium* (Hymenoptera : Megachilidae : Anthidiini)

Résumé

Pseudoanthidium FRIESE est un genre regroupant de nombreuses espèces d'abeilles cardeuses (Anthidiini) de l'Ancien Monde. *Pseudoanthidium alpinum* (MORAWITZ, 1873), initialement décrite des montagnes du Caucase, a été choisie comme espèce-type représentant le genre, bien qu'elle fût insuffisamment connue. Une analyse génétique du gène mitochondrial de la cytochrome c oxydase I (COI) obtenu à partir de matériel plus récent a permis d'apparier sans ambiguïté les sexes mâle et femelle tout en prouvant la conspécificité de matériel provenant d'Espagne, de Grèce et de Géorgie. Il est apparu que les mâles avec leurs poils spécialisés et leurs peignes sur les sterna métagastriques correspondent aux caractéristiques de *Pseudoanthidium* s. str., alors que les femelles avec leur marge clypéale entièrement rebordée et saillante relèvent du sous-genre *Royanthidium* PASTEELS, 1969. Une combinaison similaire de caractères mâles et femelles a également été observée chez trois autres espèces de *Pseudoanthidium*. Comme l'apex clypéal saillant se retrouve donc dans les deux sous-genres, ce trait s'avère inapproprié pour une classification subgénérique et indique que la définition du sous-genre *Royanthidium* doit être révisée.

Mots-clefs | Anthidiini • division infragénérique • sous-genres • taxonomie • sous-genre *Royanthidium*

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INTRODUCTION

Pseudoanthidium FRIESE is a species-rich genus of wool carder bees (Anthidiini) of the Old World and 12 subgenera are recognized in the Palaearctic, Indo-Malayan and Afrotropical regions (LITMAN *et al.*, 2016, 2021; MICHENER,

2007; KASPAREK, 2021). Most species have not yet been fully characterized and the genus includes many still undescribed species, even in the Western Palaearctic (LITMAN *et al.*, 2016; KASPAREK, *unpubl.*). The inter- and intrageneric relationships

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are still poorly understood.

When Heinrich FRIESE established the subgenus *Anthidium* (*Pseudoanthidium*) to accommodate five anthidiine species with males and females with black faces and usually unarmed apical terga (FRIESE, 1898), he did not nominate a type species of this subgenus. Therefore, SANDHOUSE (1943) selected a type species and chose *Anthidium alpinum* MORAWITZ, 1873 for this purpose, a species that had been described from the Caucasus. Later, PASTEELS (1969) elevated *Pseudoanthidium* to the genus rank and noted that the designation of *alpinum* as the type species was not very appropriate as this taxon was known at that time only from a single male from the Caucasus and had unclear relationships with *Anthidium barbatum* MOCSÁRY, 1884, which was known then from Hungary and Spain and that FRIESE regarded as possible synonyms with *Anthidium alpinum*.

Doubts remained about the taxonomic identity of *Pseudoanthidium alpinum*. MICHENER & GRISWOLD (1994) noted that they had seen specimens of various species identified as *alpinum*. "One of them agrees with the original

description, having a black clypeus in the male, an unusual feature, and we believe it is true *alpinum*. All of them, however, agree in subgeneric characters with *Paranthidiellum* which we therefore place as a synonym of *Pseudoanthidium*." MICHENER & GRISWOLD (1994) further remarked that PASTEELS (1969) and WARNCKE (1980) placed *Anthidium barbatum* MOCSÁRY, 1884 and *A. serraticeps* FRIESE, 1917 in the synonymy of *A. alpinum*, but stated that "this cannot be correct for the type of *serraticeps* in Berlin is a larger, robust species of the subgenus *Royanthidium*; it is a female with a bare, projecting dentate clypeal margin." MICHENER (2007) concluded that "the application of the name *Pseudoanthidium* s. str. is probably correct, but a possible doubt is justified by the insufficient knowledge of the type species."

New material of both sexes from different parts of the distribution allowed reassessment of the taxonomic status of *P. alpinum*. By sequencing the mitochondrial cytochrome c oxidase I (COI) gene, it was possible to confirm the shared identity of the two sexes and to draw conclusions on the subgeneric division of the genus *Pseudoanthidium*.

METHODS

The morphological terminology used in the descriptions follows MICHENER (2007).

DNA extraction, PCR amplification and sequencing were conducted by the Canadian Centre for DNA Barcoding (CCDB), Guelph, using standardised high-throughput protocols (<https://ccdb.ca/resources/>). The mitochondrial cytochrome c oxidase subunit I gene (COI) was sequenced, and the results were submitted to the *Barcode of Life Data System* (BOLD), a cloud-based data storage and analysis platform developed by CCDB (<https://www.boldsystems.org/>). DNA alignments were made with the Clustal Alignment, run on MEGAX software. Genetic distance was calculated as the number of base substitutions per site from the estimation of the net average between groups of sequences. Analyses were conducted using the KIMURA 2-parameter model (KIMURA,

1980).

Sequences from the 648-base pair (bp) barcode region of the mitochondrial COI gene were recovered from three specimens of *P. alpinum*, and all of them were fully barcode compliant (two specimens with 658 bp, one with 620 bp). In BOLD, COI sequences over 500 bp are evaluated for inclusion into BINs if they meet the quality standards. The sequences will be made publicly available in BOLD.

Abbreviations

CMK	Collection Max KASPAREK, Heidelberg (Germany)
OLL	Oberösterreichisches Landesmuseum, Linz (Austria)
ZISP	Zoological Institute, St. Petersburg (Russia)
ZMB	Museum für Naturkunde, Berlin (Germany)
S1, S2, ...	Sternum 1, sternum 2, ...
T1, T2, ...	Tergum 1, tergum 2, ...

TAXONOMIC ASSESSMENT

1. *Pseudoanthidium alpinum* (MORAWITZ, 1873)

- *Anthidium alpinum* MORAWITZ, 1873. Holotype in SIZK examined (see below).
- *Anthidium barbatum* MOCSÁRY, 1884. Budapest, Hungary (see below).
- *Anthidium serraticeps* FRIESE, 1917. Holotype in ZMB examined, synonymy confirmed (see below).
- non *Pseudoanthidium alpinum gregoriense* NOBILE, 1990. LITMAN *et al.*, (2021) found that the material corresponds with *P. stigmaticorne* (DOURS, 1873).
- non *Pseudoanthidium gregoriense* NOBILE, 1990. *P. a. gregoriense* elevated to species rank by NOBILE (1995). LITMAN *et al.*, (2021) found that the material corresponds with *P. stigmaticorne* (DOURS, 1873).

Type material examined

Holotype: ♂, Russia (Dagestan): Kurush (41°17' N, 47°50' E)

("Alp. Cauc. Curush., 8175 / FAUST [= name of the collector] / *alpinum* MOR. type"). Photographs examined (ZISP) (figure 1).

Other material examined

(4 ♀♀, 3 ♂♂). Georgia: 1 ♂, Gori env. (42°00.182' N, 44°08.880' E), 747 m, 31.V.-01.VI.2019, W. GROSSER *leg.* (OLL; oll959) [COI sequence available]. – Greece: 1 ♀, Peloponnese: Lakonia, Taygetos (36°57' N 22°21' E), 1000 m, 30.V.1981, E. & J. HÜTTINGER *leg.* (CMK; ms3618). 1 ♀, Evritania, Timfristos, above Karpenisi (38.55.54° N, 21.48.06° E), 1650 m, 15.VII.1998, A. W. EBMER *leg.* (private collection A. W. EBMER, awe003). 1 ♀, Evritania: Tymfristos [Timfristos] (c. 38°56' N, 21°49' E), 1432 m, 17.VII.1976, K. GUICHARD *leg.*, coll. BMNH(E) 2001–229 (*Pseudoanthidium barbatum* MOCS. J. PASTEELS det. 1976). – Israel: 1 ♀, 10 km E Kiryat Gat (31.597° N, 34.837° E), 13.V.2019, M. HALADA *leg.* (OLL, oll958) [COI sequence available]. – Kazakhstan: 1 ♀, Bajanaul National Park (50°49.08' N, 75°20.40' E), 410 m, 10.VI.2008, W.-H. LIEBIG *leg.* – Romania: 1 ♀, Sibiu:

Ocna Sibiului (VII-bürg. Salzburg), 1900, holotype of *Anthidium serraticeps* FRIESE (ZMB). – Spain: 1 ♀, Murcia, Sierra Espuna (37°52' N, 01°33' E), 1377 m, 21.VI.2021, I. CROSS leg. (coll. T. WOOD; tjw001) [COI sequence available]; 1 ♂, Teruel: Albaracin, 08.-11.VIII.1931, J. OGILVIE leg. (ZMB) [this record

listed by FRIESE (1898, 1911) as “Barcelona”]; 1 ♂, Teruel: Ródenas: Los Pozuelos, 1390 m, 28.VI.2021, L. CASTRO leg. (coll. F. J. ORTIZ-SÁNCHEZ; jos001; see ORTIZ-SÁNCHEZ *et al.*, 2022). – Turkey: 1 ♀, Nevşehir, Ürgüp, 04.VI.1978, M. SCHWARZ leg. (OLL, oll1055).

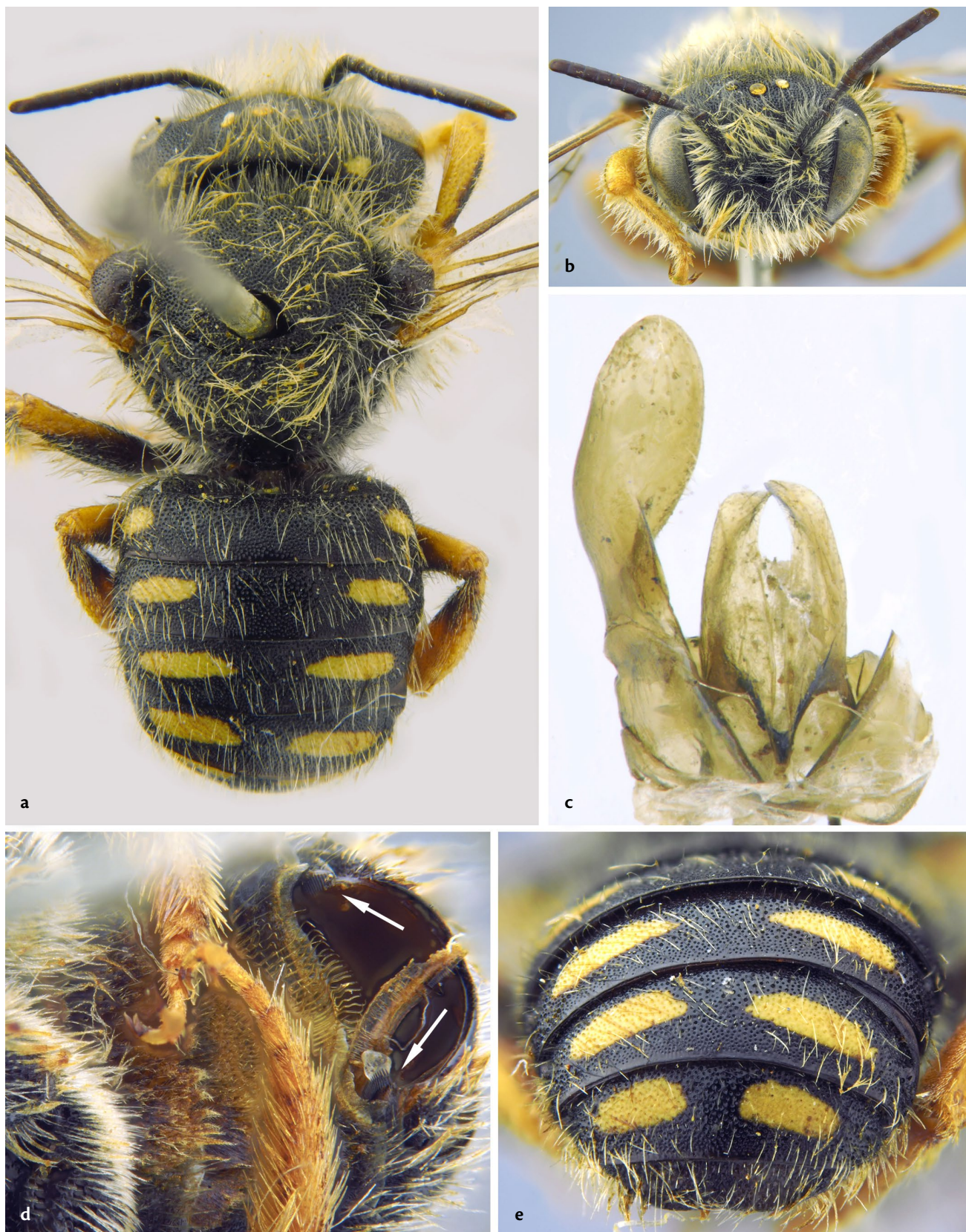


Figure 1. Holotype of *Pseudoanthidium alpinum* (MORAWITZ, 1873), a male, deposited in ZISP (St. Petersburg). **a.** Habitus. **b.** Head. **c.** Genitalia. **d.** Sterna. **e.** Apical terga. The arrows in (d) point at the black combs at the apices of the projections of S5. Photograph: Yulia ASTAFUROVA, SIZK.

Material not examined

Budapest, Hungary (J. FRIVÁLDZSKY *leg.*) (Holotype of *A. barbatum*) (MOCSÁRY, 1884).

Diagnosis

Overall, a dark *Pseudoanthidium* species. The male is characterized by a mat of dense, felt-like pubescence on S2–S3 combined with orange tibiae and tarsi, an apically unnotched gonostylus and a fine, regular punctation of the metasomal terga (figures 3a–b, 4a). The female is characterized by a fully exposed, convexly protruding clypeal apex with six to nine blunt teeth, combined with yellow mandibles with dark teeth, a finely punctated clypeus (impunctate regions absent), a black scutum, and orange tibiae and tarsi.

Genetic Analysis

COI sequences were successfully derived from three specimens of *P. alpinum*: a female from Israel, a female from Spain and a male from Georgia (see detailed data under “other material examined”). The male from Georgia has a genetic distance of 0.98% from the female from Spain and 1.08% from the female from Israel. This low distance can be taken as clear indication that all three specimens are conspecific, and that the male specimen examined here is conspecific with the females examined.

In the phylogenetic tree, the closest clades are those of *Pseudoanthidium ochrognathum* and *P. melanurum*. The inter-group genetic distance between *P. alpinum* and *P. ochrognathum* is 11.8%, and the inter-group distance between *P. alpinum* and *P. melanurum* 13.0%.

Re-description

See previous descriptions in MORAWITZ (1873) (female),

WARNCKE (1980) (male; female included in key, but not properly described) and KASPAREK (2022) (including photographs of male and female).

Female

7–8 mm. **Head:** Black with a pale yellow triangular spot behind the eye (figure 2a); lower paraocular area black as the rest of the face (Greece, Israel) or brownish-yellow (Turkey, Romania, Spain); clypeal apex fully exposed, coarsely denticulate with six to nine blunt teeth (median teeth larger than lateral ones) (figure 7); apex convexly protruding; punctation of clypeus dense and regular, slightly denser apically than at base; small impunctate (or less punctate) shining area in the lower supra-clypeal area; mandible yellow at base, with a smooth transition over reddish-brown to the five black teeth; vertex length approximately 3 ocellar diameters; head with fine punctation. **Mesosoma:** Scutum slightly convexly curved upward; black; punctation fine throughout, shining; scutellum and axillae together crescent-shaped; scutellum with a large pale-yellow spot on each side (figure 2a). **Legs:** Femora black anteriorly, orange to red-brown posteriorly; tibiae and tarsi red-brown. **Metasoma:** T1–T6 with pale yellow maculation laterally; size of yellow maculae variable (the spots on T1 and T2 of the specimen from Spain are very small) (figures 1a, 2b); T6 triangular in dorsal view; laterally not bulging; black. Color of scopa varies between dark brown to black (Romania, Spain, Turkey) and yellow-brown or light red-brown (Israel, Greece).

Male

7–8 mm. **Head:** Head black except for a minute yellow spot behind the eye (figure 2b); face with dense long yellowish-grey pubescence; clypeus with silvery white pubescence covering underlying surface; mandible yellow with some red-brown in the transient zone to the dark brown teeth; small

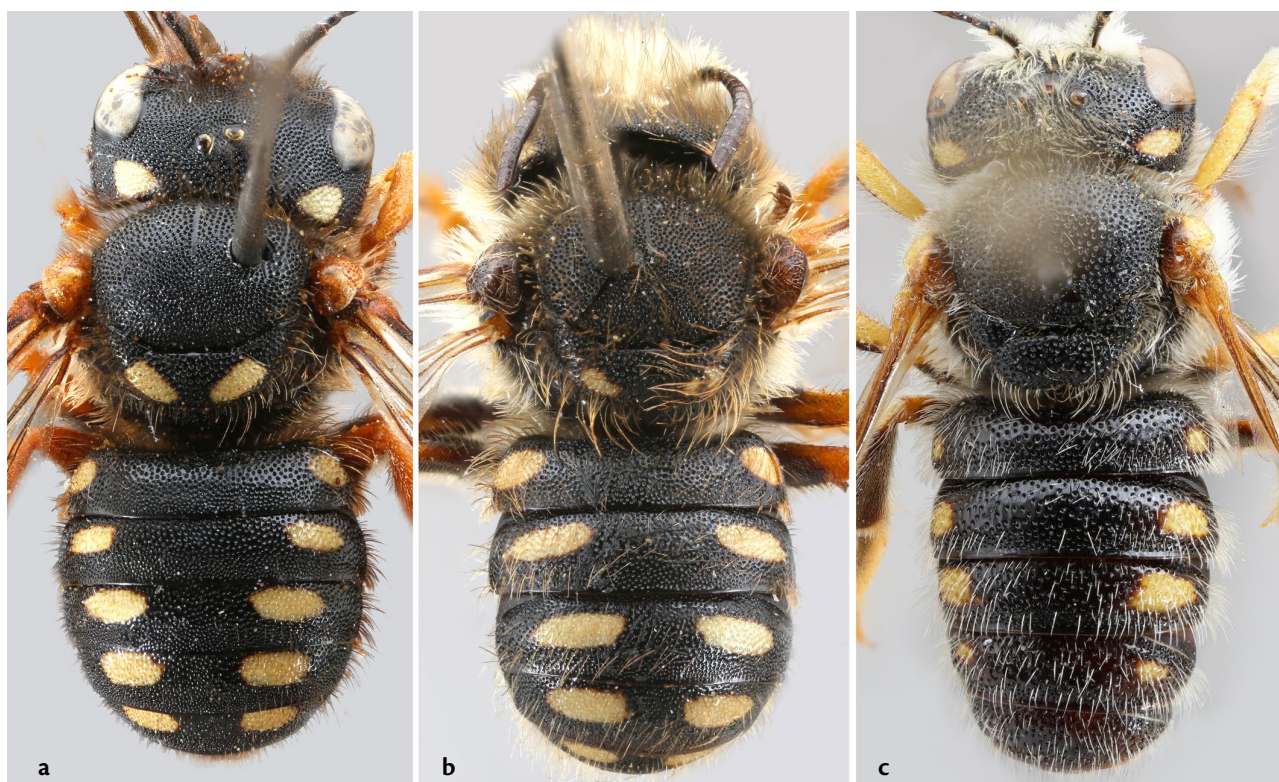


Figure 2. *Pseudoanthidium alpinum* from Greece (a. Female. b. Male) and *P. puncticolle* from Turkmenistan (c. male).



Figure 3. Males of *Pseudoanthidium alpinum* (a–b), *P. aff. alpinum* from Turkey (c–d) and *P. puncticolle* (e–f). Note the fine punctation of the scutum, scutellum and terga in *P. alpinum*, and the coarse punctation with larger punctures and larger interstices in *P. puncticolle*. Additionally, the scutellum is flat with a straight apical margin in *P. alpinum* (a & c), whereas it is swollen with a shallow median emargination in *P. puncticolle* (e, red arrow).

impunctate (or less punctate) shining area at the interface between the clypeal base and the supraclypeal area; antenna flat, dark brown to black. **Mesosoma:** Scutum, scutellum and axillae black (a specimen from Greece with a yellow spot on the scutellum), with fine and dense punctation (figures 3a–b); posterior margin of scutellum rounded; legs orange-red; femora and sometimes tibiae partly black. A felt-like pubescence on the hind metatarsi as described by WARNCKE (1980) was not noted. **Metasoma:** T1–T5 with pale yellow to sulphur yellow lateral maculations (figure 2b); T6 black; T7 brown with shallow apical emargination (figure 3b); S1 with dense fringe of felt-like branched hairs at apical margin; S2 entirely covered with a mat of dense, felt-like pubescence consisting of branched hairs (strong hairs with short,

unbranched side branches); S3 with similar felt-like pubescence, but less dense and emarginate in the middle; S4 divided in the middle; only small patches of felt-like hairs laterally, and long, straight hairs in the middle (figure 4a); S5 widely emarginate and with a lateral projection with a black comb apicolaterally (figure 5a). Gonostylus elongate, apex rounded (not notched or emarginate as in many other species of the genus) (figures 1c, 6a–b).

Remarks on synonymy

Anthidium barbatum MOCSÁRY, 1884. Described by MOCSÁRY (1884) based on a single male from Budapest,



Figure 4. Metasoma of male *Pseudoanthidium alpinum* (a) and *P. puncticolle* (b) in ventral view. Note the dense felt-like coverage. The red arrow points to the light lateral comb on S5 of *P. puncticolle* (the comb is black in *P. alpinum* but not visible in the photograph).

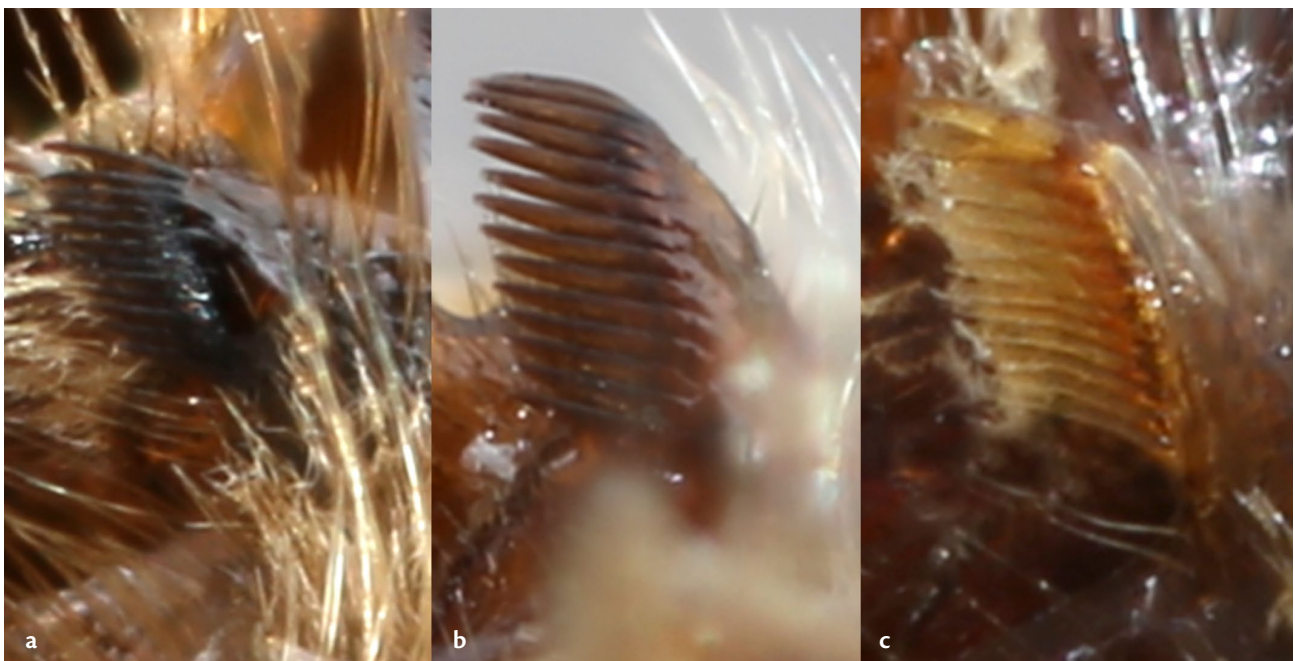


Figure 5. Apicolateral comb on the lateral arm of S5 in the male of *Pseudoanthidium alpinum* (a. Spain), *P. aff. alpinum* (b. Turkey) and *P. puncticolle* (c. Turkmenistan).

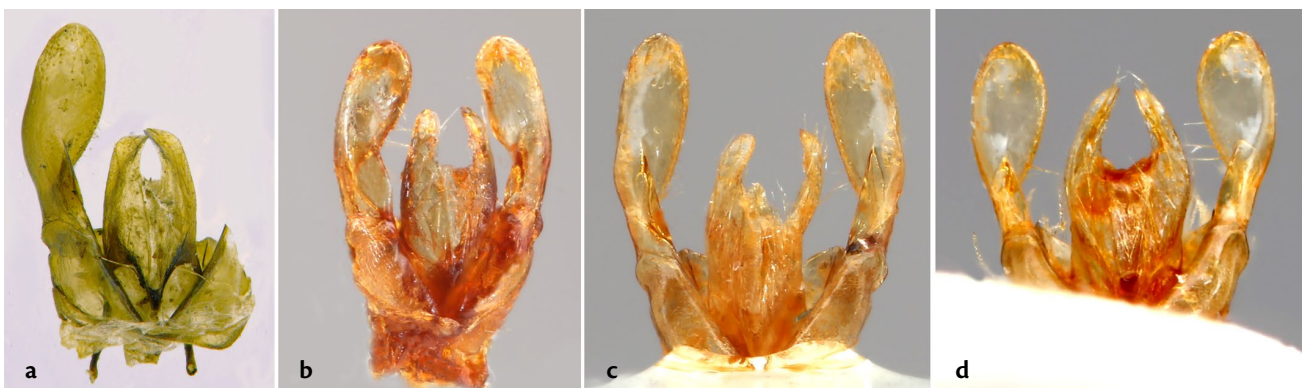


Figure 6. Male genitalia of *Pseudoanthidium alpinum* (a. holotype from Caucasus; b. Greece), c. *P. aff. alpinum* from Turkey and d. *P. puncticolle* from Turkmenistan.



Figure 7. Face of a female of *Pseudoanthidium alpinum* from Greece (A. W. EBMER leg.). Note the fully exposed apical margin of the clypeus.

Hungary (J. FRIVÁLDZSKY leg.). FRIESE (1898) examined the specimen and suspected that it is a synonymy with *Anthidium alpinum*. The only difference to other *alpinum* he noted was the absence of light maculation on T1 and T2. Actually, MOCSÁRY (1884) mentioned the yellow maculation, round on T1 and oval on T2. WARNCKE (1980) followed FRIESE (1898) in his assessment and treated *barbatum* as a junior synonym of *alpinum*. For a revised definition of the genus *Pseudoanthidium*, PASTEELS (1969) did not have access to the type material of *alpinum* deposited in ZISP (St. Petersburg), but instead examined the type of *barbatum* in ZMB (Berlin). This, he said, “is in accordance with the spirit, if not the letter, of FRIESE” [Note: PASTEELS (1969) at one point spoke about *Proanthidium* instead of *Pseudoanthidium*, which seems to be an error]. Nevertheless, MICHENER & GRISWOLD (1994) questioned the synonymy (see above under introduction). Additionally, ZSOLT (2011) listed *Anthidium barbatum* MOCSÁRY, 1884 as an extinct species in Hungary and HARIS (2016) included *Pseudoanthidium barbatum* (MOCSÁRY, 1884) in his list on the Carpathian Basin as a valid species, apparently without having seen new material.

***Anthidium serraticeps* FRIESE, 1917.** Described by FRIESE (1917) based on a single female collected in Salzburg (today: Ocna Sibiului) in Transylvania (Romania) in July 1900. The type in ZMB was examined by H. BISCHOFF (in: MAVROMOUSTAKIS 1954), G. VAN DER ZANDEN and by J. PASTEELS and regarded as *A. barbatum*. Also WARNCKE (1980) put it in synonymy with *alpinum*, but MICHENER & GRISWOLD (1994) thought that this taxon cannot be synonymous with *alpinum* because of the fully exposed and coarsely denticulate clypeal apex which is typical for the female members of the subgenus *Royanthidium* (see also introduction). HARIS (2016) regarded this taxon as a valid species. A recent examination by M. K. confirmed that *A. serraticeps* is a junior synonym of *alpinum* (figure 8).

Remarks. For the date of publication of the species description by MORAWITZ, see EBMER (2021). The name “*alpinum*” may be misleading. MORAWITZ (1873) refers to the north-eastern Caucasus as the alpine region.

Distribution

Pseudoanthidium alpinum has a wide distribution and has

been recorded in Kazakhstan, Russia (Dagestan), Georgia, Israel, Turkey, Greece, Romania, Hungary and Spain (details under “materials”) (figure 9). Additionally, FRIESE (1911) mentioned Jaffa [Haifa, Israel] (19.IV.1899) and Tenerife [Canary Islands]. Confirmation is needed, particularly for the record from the Canary Islands.

The type locality is situated at 2492 m above sea level in the transition zone between the semiarid and the montane region of Dagestan (HOLUBEC & KRIVKA, 2006: 41), but the species was also found in the foothills of the Caucasus in Georgia at 747 m. In Greece, it was found at Mount Timfristos at altitudes of 1,494 m and at 1,650 m, and in the Peloponnese at 1,000 m, in Spain at 1,377 m and 1,390 m and in Central Turkey at 1,070 m. It was collected at altitudes below 500 m in Hungary (120 m), Romania (386 m), Israel (218 m) and Kazakhstan (410 m). The altitudinal distribution thus extends from nearly sea level up to the high mountainous region at almost 2,500 m.

Relationships

The male of *P. alpinum* is very similar to the male of *P. puncticolle* (MORAWITZ, 1888) found in Central Asia (WARNCKE, 1980). Both species exhibit a similar color pattern, except for the clypeus and lower paraocular area. In *P. puncticolle*, these areas are pale yellow, while in *P. alpinum*, they are black, with, at most, some yellow present in the paraocular area. They also share a dense felt-like pubescence on S2–S3 (figure 4) and the shape of the genitalia (figure 6). However, the male of *P. puncticolle* distinctively differs from *P. alpinum* due to its noticeable coarser integument punctation on the head, mesosoma and terga. In particular, the punctures on the abdominal terga are larger, deeper, more widely spaced, and exhibit greater irregularity in *P. puncticolle* compared to *P. alpinum* (figure 3). The female of *P. puncticolle* has a striking coloration, characterized by abundant yellow and reddish-yellow maculations on the head, mesosoma, and metasoma (figure 10). This coloration sets it apart significantly from the female of *P. alpinum*. Moreover, it differs by featuring an impunctate area on the basal part of the clypeus and a less protruding, almost straight clypeal apex (figure 11b). Similar to the male, the female also displays coarser punctation on the scutum and terga (figure 10c).

A combination characterized by a protruding clypeal apex in the female and modified sternal hairs in the male was also observed in *P. obscuratum* (MORAWITZ, 1875) (figure 12) and *P. rhombiferum* (FRIESE, 1917) (figure 11). However, unlike *P. alpinum* and *P. puncticolle*, the males of these two species lack the felt-like pubescence on S2–S3. Additionally, T6 and T7 of these two species have a complex structure (figure 11e), which is simple in *P. alpinum* and *P. puncticolle*. The females of *P. obscuratum* and *P. rhombiferum* can be distinguished from *P. alpinum* by their straight to shallowly emarginate clypeal apex, whereas the clypeal apex is convexly protruding in *P. alpinum*.

2. *Pseudoanthidium aff. alpinum*

Material

1 ♂, Turkey: Obruk/Konya, 7.VI.1968, M. SCHWARZ leg. (OLL, WARNCKE collection) (Figures 3c, 3d, 5b, 6c). Listed as a new occurrence location of *alpinum* by WARNCKE (1980).



Figure 8. Holotype of *Anthidium serraticeps* MOCSÁRY, 1884, regarded as a synonym of *Pseudoanthidium alpinum* (MORAWITZ, 1873) (ZMB).

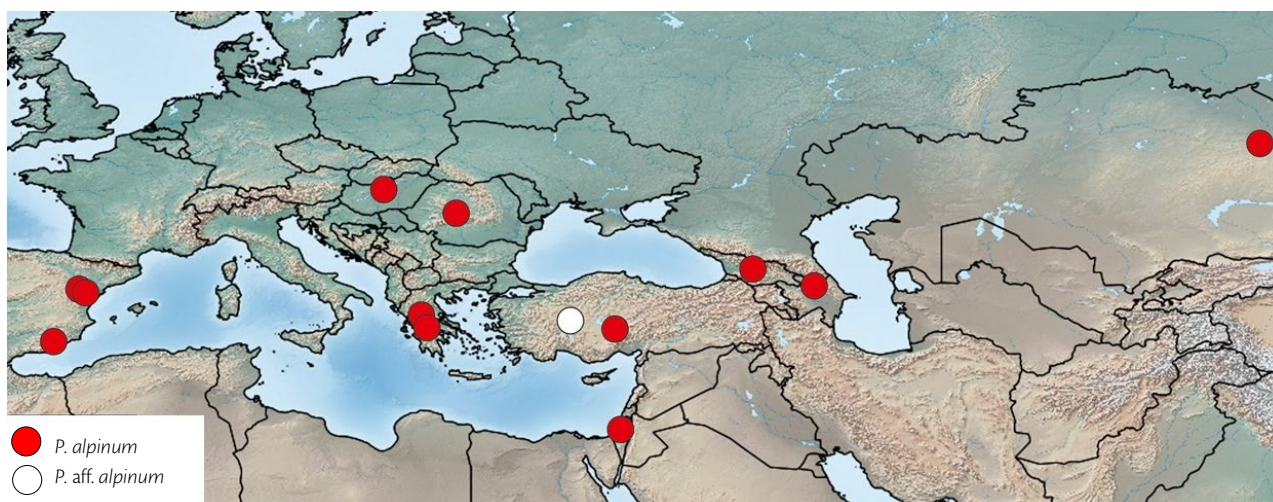


Figure 9. Distribution of *Pseudoanthidium alpinum* and a record of a specimen whose identity could not be definitively clarified (*P. aff. alpinum*).



Figure 10. Female of *Pseudoanthidium puncticolle* (MORAWITZ, 1888) from Turkmenistan (material from CMK). **a.** Habitus lateral. **b.** Head in oblique view. **c.** Preoccipital region and scutum. Note the protruding clypeus (**b**) and the coarse punctation on head and scutum (**c**).

Diagnosis

Clypeus and lower paraocular area pale yellow. The pale-yellow macula behind the eye larger than in “true” *P. alpinum* (i.e. those examined here and listed under material). Pubescence of face much less dense than in “true” *P. alpinum*. Scutum with short yellow anterior band and scutellum with yellow spot. Yellow maculations on terga larger than in “true” *P. alpinum*. Punctuation on scutum, scutellum and terga conspicuously coarser than in “true” *P. alpinum* (figures 3c–3d). Pubescence of sterna similar to *P. alpinum* with a mat of dense felt-like branched hairs on the apical margin of S1, on S2 and S3 and some remnants on S4 laterally. Apical margin of S3 convexly protruding, with long, undulating hairs. Apical margin of S4 straight, laterally protruding; S5 with small light comb on each side of the middle basically, and lateral arm with dark apical comb (figure 5b); apex of gonostylus not emarginate, as in “true” *P. alpinum* (the species of the closely related *P. scapulare* complex except for *P. canariense*, which is endemic to the

Canary Islands, and *P. tropicum* from southern Iran, have notched gonostyli).

This specimen is thus distinct from *P. alpinum* particularly by the yellow maculation on the face, a coarser punctuation on the scutum, scutellum and terga and light combs on S5 (not black as in *P. alpinum*), but agrees with *P. alpinum* in particular in the presence and extension of the felted hairs on S1–S3 and the shape of the genitalia. The specimen is clearly distinct from *P. rhombiferum* (FRIESE, 1917) by the regularly rounded T6 (two lateral bulges in *P. rhombiferum*) (figure 11). While characters such as punctuation and coloration of the integument are relatively constant in *P. alpinum* across the distribution area extending from the Iberian Peninsula to Central Asia, this male from Central Anatolia shows traits that are beyond the normal range of variation in *P. alpinum*. However, if these distinguishing characters are not confirmed by more material, it is suggested not to establish a taxonomic rank for it.



Figure 11. *Pseudoanthidium rhombiferum* (FRIESE, 1917). **a.** Habitus dorsal of a male (holotype from Syria). **b.** Female face showing the protruding clypeus (Palestine). **c.** Female apical terga (Palestine). **d.** Apical sterna of male with modified hairs of S3 and black combs on S5 (Palestine). **e.** Apical terga of male (Palestine).

3. Subgeneric classification

According to MICHENER (2007), the main character to distinguish the nominate subgenus of *Pseudoanthidium* from the subgenus *Royanthidium* is the clypeal apex of the female, which is fully exposed in *Royanthidium*, but largely hidden by hair in *Pseudoanthidium* s.str. According to this classification, the female of *Pseudoanthidium alpinum* would

be assigned to *Royanthidium*, the male to *Pseudoanthidium* s. str. With the help of genetic barcoding, we confirmed that the males and females examined belong to the same taxon.

Key to the solution of this dilemma is the exposed versus hidden apical clypeal margin. Our data show that an exposed clypeal margin is present in some of the species of *Pseudoanthidium* s.str. and in all species of *Royanthidium*.



Figure 12. Male of *Pseudoanthidium obscuratum* (MORAWITZ, 1875) from Kyrgyzstan (CMK). **a.** Habitus. **b.** Head. **c.** Ventral side of metasoma. The red arrows indicate the combs of S5 and the waved hairs on S3.

This trait is therefore not suitable for subgeneric classification. On the other hand, it is still not clear whether the males of all *Pseudoanthidium* s. str. species actually have specialized hooked and waved hairs and combs on the metasomal sterna. Out of the approximately 28 recognized species in the nominate subgenus, eight are known only from one of the two sexes, and this is mostly the female (KASPAREK, unpubl.). Additionally, the descriptions of some of the less-known species are not complete insofar as they do not describe the structures of the ventral metasoma. Clearly distinguishable species clusters within the nominate subgenus include the *Pseudoanthidium scapulare* complex (females with a clypeal apex hidden by hair, males with specialized hairs and combs on the ventral side of the metasoma) (sensu LITMAN *et al.*, 2021), the species closely

related to *Pseudoanthidium ochrognathum* (both sexes with omaular carina, males with specialized hairs and combs on the ventral side of the metasoma) (sensu KASPAREK *et al.*, 2023), while the interrelationships of most members of the genus are not known. *Pseudoanthidium alpinum* thus forms together with *P. puncticolle*, *P. rhombiferum* (FRIESE, 1917) and *P. obscuratum* (MORAWITZ, 1875) (figures 11–12) a group a pair of species with the males having specialized hairs and combs on the metasomal sterna, and females with an exposed, protruding clypeal apex. As many *Pseudoanthidium* species are known from only one sex, it can be expected that there are more species with the same combination of male and female traits. The validity of the subgenus *Royanthidium* needs to be reviewed.

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