ARTHROPOD SYSTEMATICS
& PHYLOGENY

78 (3): 361–377
2020

SENCKENBERG

Review of the genus *Dinetus* Panzer, 1806 (Hymenoptera: Crabronidae: Dinetinae) with descriptions of new subgenera and new species

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Accepted on October 01, 2020.
Published online at www.senckenberg.de/arthropod-systematics on November 11, 2020.

Editor in charge: Klaus-Dieter Klass

Abstract. One new species of *Dinetus* is described and illustrated: *D. hameri* Notton sp.n. from the United Arab Emirates; *D. politus* stat. rev. is raised in rank to a full species (formerly a subspecies of *D. cereolus*). Two new subgenera are described: *Dentidinetus* Olszewski, Notton & Kitching subg.n. and *Venustidinetus* Olszewski, Notton & Kitching subg.n. and all known species are assigned to subgenera. An illustrated key for identification of world *Dinetus* species is given and a phylogenetic analysis of *Dinetus* based on morphological characters is presented.

Key words. Hymenoptera, Crabronidae, Dinetinae, *Dinetus*, new species, United Arab Emirates, phylogeny.

1. Introduction

The genus *Dinetus* includes species with a small body size (4–8 mm), and is distinguished by the combination of two discoidal cells, two submarginal cells, and a short, apically truncate radial cell; inner eye margins converging dorsally; ventral mandibular margin with a stout tooth medially; prothorax collar almost as high as mesothorax; foretarsus of female with a distinct rake of more or less flattened setae, male with rake usually inconspicuous; mid tibia with two spurs; male antennae long, flagellum with medial segments thickened and flattened with large tyloids ventrally, tapering apically, usually spiraled in dry specimens. We consider there are 16 currently valid species of *Dinetus* worldwide; in addition to the 14 catalogued by Pulawski (2020) we consider the subspecies *D. cereolus politus* Turner, 1917 as a full species here because it is quite different from the nominotypical subspecies in numerous characters; see key below), and we describe one more new species. We also describe two new subgenera based on the results of our phylogenetic analysis. *Dinetus* species are mostly Palaearctic, occurring in northern Africa, the Arabian Peninsula and central Asia, but with one extending into Northern India (Pulawski 2018). Representatives of *Dinetus* live in open sunlit areas, with scant vegetation. Females dig holes in loose ground (usually sandy) using well-developed tarsal rakes on the front legs. A narrow, crooked burrow (several to twenty centimetres long) usually leads to a number of brood cells, which the female provisions with small Hemiptera (Bohart & Menke 1974).

De Beaumont (1960) recognised that *Dinetus* included widely disparate taxa and recognised three informal species groups for the six species known to him, i.e., *pictus* group (*D. pictus* (Linnaeus, 1758), *D. simplicipes* Saunders, 1910), *dentipes* group (*D. dentipes* Saunders, 1910 only) and *cereolus* group (*D. cereolus* Morice, 1897, *D. pulawskii* de Beaumont, 1960 and *D. venustus* de Beaumont, 1957), based on characters of size, punctuation, disposition of ocelli, clypeal shape, pilosity and wing venation. Since then various authors have assigned 14 of the species as follows: *pictus* group (2 species); *dentipes* group (6 species) and *cereolus* group (6 species) (Mokrousov & Khedher, 2020). We were interested to investigate further the nature of these groups. We therefore first checked the characters provided for de Beaumont's species groups and found that we agreed with his conclusions. We then found that each of the nine species described by other authors since de Beaumont's paper, and the one new species described here, fitted easily into his species groups as follows: *pictus* group (*D. pictus*, *D. simplicipes*); *dentipes* group (*D. dentipes*, *D. arenarius* Kazenas, 1993, *D. psammophilus* Kazenas, 1977, *D. rakhimovi* Mokrusov & Khedher, 2020, *D. turanicus* Kazenas, 1993 and *D. wojciechi* Kazenas, 1998); and *cereolus* group (*D. cereolus*, *D. hameri* **sp.n.**, *D. nabataeus* de Beaumont, 1960, *D. politus* Turner, 1917, *D. porcellaneus* Guichard, 1980, *D. pulawskii*, *D. tunisiensis* Khedher & Mokrusov, 2020 and *D. venustus*). Thus it appeared that the groups were robust and predictive. As the genus now contains 16 species, we considered that a formal phylogenetic analysis would be useful to discover whether any structure was present that might justify the erection of subgenera, and to provide a robust classification. The explicit purpose of the analysis was to test the hypothesis whether the three species groups recognised by de Beaumont (1960), as expanded by us, are each monophyletic.

2. Material and methods

Institutional acronyms are as follows: Natural History Museum, London, United Kingdom (NHMUK); Nicolaus Copernicus University, Toruń, Poland (NCU); Oxford University Museum of Natural History, Oxford, United Kingdom (OUMNH). Images of NHMUK specimens were prepared using a Canon EOS 550D digital camera connected to a Leica M125 stereomicroscope, with images processed using Helicon Focus image stacking software. Specimens from NHMUK specimens used in the study were assigned unique NHMUK specimen numbers, and associated data and images were recorded on the NHMUK database, and will be made publicly available through the NHMUK Data Portal (Natural History Museum 2014). Images of NCU specimens were prepared using an M205C Leica stereomicroscope with an integrated high-resolution Leica DFC495 digital camera and associated Leica Application Suite 4.4.0 software (Leica Microsystems, Switzerland). Morphological terminology largely follows Bohart & Menke (1976) with some terms updated following the Hymenoptera Anatomy Ontology (Yoder et al. 2010). Antennomeres are referred to as scape, pedicel, and then by numbers A3 – 13; metasomal tergites: T1 – 7; metasomal sternites: S1 – 7. Distribution data cited in the key are derived from specimen labels, supplemented by literature records from Baker (2004), de Beaumont (1960), Du et al. (2019), Guichard (1980, 1991), Kazenas (1973, 1977, 1993, 1998, 1999), Mokrousov & Khedher (2020), Pulawski (2018) and Schmid-Egger (2011). The identification key includes all species except for females of *D. simplicipes* and males of *D. cereolus*, *D. hameri*, *D. politus* and *D. rakhimovi*, which are unknown; females of *D. simplicipes* and *D. wojciechi* were unavailable to us but were included on the basis of characters derived from de Beaumont (1960) and Kazenas (1998, 1999); females of *D. tunisiensis* were unavailable to us, but were included in the key on the basis of characters given in Mokrousov & Khdeher (2020).

3. Taxonomy

3.1. Diagnosis of subgenera

3.1.1. *Dinetus* Panzer, 1806

Dinetus Panzer, 1806: 191. Type species: *Crabro pictus* Fabricius, 1793, designated by Latreille, 1810: 438.

Dinetus Jurine, 1807: 207, junior homonym of *Dinetus* Panzer, 1806. Type species: *Crabro pictus* Fabricius, 1793 by monotypy.

3.1.2. Subgenus *Dinetus* Panzer, 1806

Diagnosis. Upper face, post-ocellar area and mesoscutum densely and conspicuously punctate in both sexes; ocular ocellar length greater than hind ocellar diameter; apex of subdiscoidal cell subrectangular; mesoscutum with setae dense but minute, barely visible; cu-a joining after the fork of M and Cu by at least 5 × length of cu-a. Males with dense fringe of setae on S6 and tuft of setae on S7; A12 and 13 much narrower and longer than A11; fore tarsus with rake spines flattened and clearly different from larger setae on fore tarsus.

Included species. *D. pictus* and *D. simplicipes*.

3.1.3. Subgenus *Dentidinetus* Olszewski, Notton & Kitching subg.n.

Diagnosis. Upper face, post-ocellar area and mesoscutum more or less punctate, but less densely than for subgenus *Dinetus*, usually obscured by pubescence; ocular ocellar length usually equal to or less than hind ocellar diameter; apex of subdiscoidal cell subrectangular; cu-a joining after the fork of M and Cu by 2 – 4 × length of cu-a; mesoscutum with setae dense, mostly as long as, or longer than, diameter of hind ocellus, flattened and with strong silvery reflection, obscuring cuticle. Females with ocular ocellar length equal to or less than hind ocellar diameter. Males without setal tufts on apical sterna; A12 and 13 similar in proportions and shape to A11; fore tarsus, rake spines not flattened.

Included species. *D. arenarius*, *D. dentipes*, *D. psammophilus*, *D. rakhimovi, D. turanicus* and *D. wojciechi*.

Nomenclature. Type species here designated: *D. dentipes*.

Etymology. Named after the type species *D. dentipes*, the subgenus name is a combination of the prefix *denti-* with the genus name *Dinetus* and takes masculine gender.

3.1.4. Subgenus *Venustidinetus* Olszewski, Notton & Kitching subg.n.

Diagnosis. Upper face, post-ocellar area and mesoscutum impunctate or at most insignificantly punctate in females, more or less punctate in males of some species, but less densely so than for subgenus *Dinetus*; ocular ocellar length usually equal to or less than hind ocellar diameter except for males of *D. pulawskii* (1.0 – 1.2 ×) and *D. tunisiensis* sp.n. (1.6 ×); apex of subdiscoidal cell oblique; if setae present on mesoscutum then sparse, scattered, flattened and with strong silvery reflection, usually much shorter than diameter of hind ocellus; cu-a joining joining at or very close to fork of M and Cu. Males without setal tufts on apical sterna; A12 and 13 similar in proportions and shape to A11; fore tarsus, rake spines not flattened.

Included species. *D. cereolus*, *D. politus*, *D. hameri* sp.n., *D. nabataeus*, *D. porcellaneus*, *D. pulawskii, D. tunisiensis* and *D. venustus*.

Nomenclature. Type species here designated: *D. venustus*.

Etymology. Named after the type species *D. venustus*, the subgenus name is a combination of the prefix *venusti-* with the genus name *Dinetus* and takes masculine gender.

3.2. Descriptions of new species

Dinetus (*Venustidinetus*) *hameri* Notton sp.n.

(Figs. 25, 51 – 54)

Etymology. Named after the collector Ian L. Hamer; for brief details of his collecting in the Arabian Peninsula, see Baker (2004).

Diagnosis. This species is distinguished by the following combination of characters: frons and vertex sparsely punctured; ocular ocellar length slightly shorter than smallest hind ocellar diameter; apex of subdiscoidal cell oblique; mesoscutum with only a few scattered setae; propodeum laterally with dense silvery appressed pubescence; fore femur of female slender, longest ventral setae longer than width of femur.

Description. Female. ***Head***: Clypeus centrally convex, smooth and bare, laterally with appressed silvery pubescence, ventral margin with narrow transparent truncate projection, which has square corners. Frons and vertex sparsely punctured, ocellar area with fine punctures. Frons and vertex with only sparse pubescence, almost bare. Ocular ocellar length slightly shorter than the smallest diameter of the hind ocellus. Distance between hind ocelli almost twice ocular ocellar length (5.5 : 3). A3 about 7 × as long as wide (20 : 3) and as long as scape (excluding radicle). ***Mesosoma***: Pronotum with dense silvery pubescence on posterior margin and pronotal lobe. Mesoscutum shining, almost smooth, with fine reticulate sculpture, with only a few scattered punctures and associated setae, almost bare. Propodeum medio-dorsally with fine granular sculpture crossed by fine transverse striae, and with distinct medial groove; laterally with dense silvery appressed pubescence, the dorsal and posterior faces bare medially, the lateral face bare anteriorly. ***Metasoma***: Metasoma almost smooth, with fine reticulate sculpture, with silvery appressed pubescence laterally on posterior margins of T1 – 3. Pygidial plate slightly convex, shining, without punctures. ***Legs***: Coxae 1 and 2 with longitudinal keel anterior to apical foramen. Coxae 2 and 3 dorsally with silvery appressed pubescence. Fore femur slender (43 : 11), posteriorly covered with silvery appressed pubescence, longest ventral setae longer than width of femur. Rake spines of fore basitarsus longer apically, the longest seta not as long as the length of the fore basitarsus. ***Colour***: Head yellow, interocellar area and vertex immediately behind dark brown. Mandible yellow, apical third brown. Scape and pedicel yellow, darkened dorsally. Flagellum brown becoming a little darker apically. Pronotum yellow, except anterior and posterior margins, including pronotal lobe, marked with cream. Tegula yellow. Mesopleuron largely brown, marked with cream next to pronotal lobe and with yellow along posterior margin. Mesoscutum mostly dark brown, lateral margins yellow. Mesoscutellum and axilla cream. Propodeum yellow. T1 – 3 and 6 yellow, posterior margins of T1 – 3 marked with cream, the cream mark more or less narrowing medially. T4 – 5 dark brown. Legs yellow, coxae, trochanters and femora with dark marks dorsally; fore femur posteriorly and hind tibia dorsally cream. ***Fore wing***: Vein between subdiscoidal and discoidal cells oblique. Marginal cell short, 1.9 × as long as wide, apically truncate. Second submarginal cell subtriangular, obtuse, the outer edge almost vertical. ***Hind wing***: Vein cu-a joining the fork of M and Cu. — **Male.** Unknown.

Type material. Holotype, ♀. UNITED ARAB EMIRATES: Remah, 10.iv.1988, leg. I. L. Hamer, NHMUK010812655, deposited in NHMUK.

3.3. Supplementary data

Dinetus (*Dentidinetus*) *rakhimovi* Mokrousov & Khedher, 2020

(Figs. 4, 17, 40 – 46)

Study material. IRAN: 1♀, Kerman, Doulatabad [30°29′34.9″N 57°46′09.7″E], 469 m above sea level, 12.v.2017, leg. K. Szpila, deposited in NCU.

***Dinetus* (*Venustidinetus*) *tunisiensis* Khedher & Mokrousov, 2020**

(Figs. 13, 26, 30, 47–50)

Study material. MOROCCO: 1♂, southern Morocco, Taroudant Road, 30 km west of Ouarzazate, 19.iv.1987, leg. M. Edwards, NHMUK010812654, deposited in NHMUK.

3.4. Key to species of the genus *Dinetus* Panzer ♂ and ♀

1 Frons and vertex densely punctured, dull (Fig. 3). Males with dense fringe of setae on S6 and tuft of setae at apex of S7 (Fig. 5) (subgenus *Dinetus*) **2**

1' Frons and gena usually sparsely punctured (Fig. 4) if more densely punctured, then punctures separated by at least their diameter and interspaces are shining. Males without dense fringe of setae on S6 and without tuft of setae at apex of S7 (Fig. 6) **3**

2 ♀♀ propodeal dorsum regularly finely striate, striae posteriorly transverse, anteriorly oblique to longitudinal (Fig. 9). ♂♂: propodeal dorsum regularly striate (Fig. 8); A10 and A11 very long, A10 almost 8 × as long as wide (Fig. 10), foretarsal rake distinct. (Distribution: Europe, Kazakhstan) .... ***D. pictus* (Fabricius)**

2' ♀♀ unknown. ♂♂: propodeal dorsum, largely coriaceous (Fig. 7); A10 and A11 short, A10 2.5 × as long as wide (Fig. 11), foretarsal rake indistinct. (Distribution: Algeria) .... ***D. simplicipes* Saunders**

3 Apex of subdiscoidal cell almost vertical (Fig. 12). Mesoscutum with dense silvery appressed setae obscuring cuticle, the setae mostly as long as, or longer than, diameter of hind ocellus (subgenus *Dentidinetus*) **4**

3' Apex of subdiscoidal cell oblique (Fig. 13). Mesoscutum with at most a few sparse setae, the setae usually much shorter than diameter of hind ocellus (subgenus *Venustidinetus*) **9**

4 Frons with appressed silver setae and short erect setae, the latter less than 0.5 × as long as width of anterior ocellus (Fig. 14) **5**

4' Frons with appressed silver setae and long erect setae, the latter at least 1.5 × as long as width of anterior ocellus (Fig. 15) **6**

5 ♀♀ and ♂♂: propodeal dorsum yellow, with thin black margin, its bare part broad. ♀♀: ventral margin of clypeus with two rounded teeth close to each other; longest rake spines on fore basitarsus as long as fore basitarsus (Fig. 16). ♂♂: fore trochanter ventrally with blunt projection (Fig. 20). (Distribution: Kazakhstan) .... ***D. psammophilus* Kazenas**

5' ♀♀ only: propodeal dorsum black, its bare part narrow. ventral margin of clypeus with two sharp teeth separated from one another (Fig. 46); longest rake spines on fore basitarsus clearly shorter than fore basitarsus (Fig. 17). ♂♂: unknown. (Distribution: Iran, Uzbekistan) ... ***D. rakhimovi* Mokrousov & Khedher**

6 Propodeal dorsum black with parallel yellow borders. ♂♂: fore femur without a tooth ventrally (Figs. 18, 19) **7**

6' Propodeal dorsum black. ♂♂: fore femur with ventral tooth (Figs. 23, 24) **8**

7 ♀♀ and ♂♂: mid and hind legs mostly yellow, flagellum mostly dark. ♀♀: ventral margin of mandible with conspicuously developed tooth. ♂♂: fore trochanter without tooth (Fig. 18). (Distribution: Kazakhstan, Turkmenistan) ..... ***D. turanicus* Kazenas**

7' ♀♀ and ♂♂: mid and hind legs mostly reddish yellow, flagellum mostly reddish yellow. ♀♀: ventral margin of mandible with slightly developed tooth. ♂♂: fore trochanter with stout tooth (Fig. 19). (Distribution: Algeria, Egypt, Tunisia, Kazakhstan, United Arab Emirates) .... ***D. dentipes* Saunders**

8 ♀♀ and ♂♂: hind femur black basally (Fig. 21). ♀♀ Clypeal margin ventrally with 2 triangular teeth, scape basoventrally dark brown. ♂♂ fore trochanter without tooth (Fig. 23), fore femur with ventral tooth just apical to middle of femur. (Distribution: Kazakhstan, China (Inner Mongolia)) .... ***D. arenarius* Kazenas**

8' ♀♀ and ♂♂: hind femur red basally (Fig. 22). ♀♀ Clypeal margin ventrally with two rounded teeth, scape basoventrally yellow. ♂♂ fore trochanter with tooth (Fig. 24), fore femur with tooth just basal to middle of femur. (Distribution: Kazakhstan) .... ***D. wojciechi* Kazenas**

9 Propodeal lateral face with silvery pubescence (Figs. 27, 28) **10**

9' Propodeal lateral face without silvery pubescence (Figs. 33, 34, 36, 37) **16**

10 Females **11**

10' Males **14**

11 Fore femur slender, about 4 × as long as wide (cf. Fig. 25), longest ventral setae longer than width of femur. (Distribution: United Arab Emirates) .... ***D. hameri* sp.n.**

11' Fore femur stout, about 3 × as long as wide (cf. Fig. 26), longest ventral setae shorter than width of femur. (Distribution: North Africa) **12**

12 Propodeal dorsum coriaceous, dull (Fig. 27). A3 dorsally whitish, only slightly longer than scape (excluding radicle). (Distribution: Morocco) .... ***D. venustus* de Beaumont**

12' Propodeal dorsum with fine transverse striation, shining (Fig. 28). A3 dorsally reddish brown or dark brown, clearly longer than scape (excluding radicle). **13**

13 Body predominantly brownish with black and white marks (Distribution: Morocco) .... ***D. pulawskii* de Beaumont**

13' Body predominantly black with white and yellow marks (Distribution: Morocco, Tunisia) .... ***D. tunisiensis* Mokrousov & Khedher**

14 Propodeal dorsum coriaceous, dull (cf. Fig. 27). Fore trochanter with small tooth ventrally, fore femur with small tooth basoventrally. (Distribution: Morocco) .... ***D. venustus*** **de Beaumont**

14' Propodeal dorsum with fine transverse striation (cf. Fig. 28). Fore trochanter without tooth ventrally, fore femur with small tubercle basoventrally **15**

15 Frons sparsely punctured, punctures about 4 × diameters apart; vertex punctate/coriaceous, dull (Fig. 29); ocular ocellar length about 1.0 – 1.2 × smallest diameter of hind ocellus. (Distribution: Morocco) .... ***D. pulawskii*** **de Beaumont**

15' Frons more closely punctured, punctures about one diameter apart, vertex punctate, shining (Fig. 30); ocular ocellar length about 1.6 × smallest diameter of hind ocellus. (Distribution: Morocco, Tunisia) .... ***D. tunisiensis*** **Khedher & Mokrousov**

16 Dorsal corner of mesopleuron without setae (Fig. 32); dorsal surface of hind coxa with sparse setae; propodeum with lateral face dull, coriaceous (Fig. 32); propodeal dorsum with short but conspicuous carinae basally and medially (Fig. 33); antennae yellow. ♂♂ unknown. (Distribution: Egypt) .... ***D. cereolus*** **Morice**

16' Dorsal corner of mesopleuron with dense appressed, silvery setae (Fig. 31); dorsal surface of hind coxa with dense appressed silvery setae; propodeum with lateral face smooth, shiny, sometimes carinate (Fig. 31); propodeal dorsum with less conspicuous carinae or striations (Figs. 34, 36, 37); antennae usually darkened apically **17**

17 ♀♀ and ♂♂: body mostly black (Fig. 39). T2 laterally with dense patch of silvery appressed pubescence. A3 shorter than scape (excluding radicle); propodeum with fine reticulate sculpture (Fig. 34). ♂♂ A13 longer, about 2.5 × as long as wide, less strongly flattened. (Distribution: Oman) .... ***D. porcellaneus*** **Guichard**

17' ♀♀ and ♂♂: body mostly dark yellow (Figs. 35, 38). T2 laterally with at most a small patch of sparse, appressed pubescence. A3 as long as scape (excluding radicle); propodeum with fine transverse striations (Figs. 36, 37). ♂♂ A13 less elongate, about 1.8 × as long as wide, strongly flattened **18**

18 ♀♀: vertex and most of mesoscutum dark yellow. Propodeum, lateral face without conspicuous carinae near dorsal margin (cf. Fig. 32). Pygidial plate wider with oblong furrows. (♂♂ known) (Distribution: Egypt, Israel, Jordan, Oman, United Arab Emirates) .... ***D. nabataeus*** **de Beaumont**

18' ♀♀: vertex and mesoscutum black. Propodeum, lateral face with some conspicuous carinae near dorsal margin (Fig. 31). Pygidial plate narrow. (♂♂ unknown) (Distribution: India) ..... ***D. politus*** **Turner**

4. Phylogenetic analysis

The data set for phylogenetic analysis is entirely new and consists of an ingroup comprising all fifteen previously described species of *Dinetus*, plus one new species of *Dinetus* described in this paper, and three outgroup taxa (*Oxybelus uniglumis* (Linnaeus, 1758), *Mellinus arvensis* (Linnaeus, 1758) and *Stangeella cyaniventris* (Guérin-Méneville, 1831)). The outgroup taxa, representing Crabronidae s.str., Mellinidae and Sphecidae respectively, were selected from the three most closely related major clades to *Dinetus*, as shown in the most recent analysis of Apoidea higher taxa (Sann et al. 2018), which provided a reclassification of Crabronidae s.l. placing *Dinetus* in the monogeneric Dinetinae, as sister group to a much reduced Crabronidae s.str., with Crabronidae + Dinetinae being sister group to Mellinidae + Sphecidae. The data set comprised 49 morphological characters coded from adult specimens in the collections of NHMUK, OUMNH and NCU (244 specimens in total). Both sexes were coded where possible, except for *D. rakhimovi* (♂), *D. hameri* sp.n. (♂), *D. cereolus* (♂) and *D. politus* (♂), which are unknown; *D. tunisiensis* (♀) was unknown to us at the time of the analysis; and *D. simplicipes* (♀) and *D. wojciechi* (♀), which were unavailable to us but for which some characters were coded by reference to de Beaumont (1960) and Kazenas (1998). Character definitions follow the principles proposed by Sereno (2007). Characters were chosen first from the generic diagnosis of *Dinetus* provided by Bohart & Menke (1976), so as to test the monophyly of the genus *Dinetus* (we did not assume *Dinetus* to be monophyletic, although it is regarded as highly apomorphic and morphologically isolated (Bohart & Menke 1976) and placed in its own subfamily Dinetinae following the analysis of Sann et al. 2018); and second to inform on the topology within the *Dinetus* clade by adapting characters provided by de Beaumont (1960) and supplementing these with new characters we discovered. Missing data were indicated by '?'; characters that could not be scored due to absence of homologous structures were indicated by '–'. Polymorphic characters were explicitly coded as such, and enclosed in {} in the matrix (for ease of type-setting {12} has been replaced by 'Y' in Table 1).

Parsimony analyses were implemented with WinClada ver. 1.00.08 (Nixon 1999 – 2002) using equal weighting. Heuristic searches were conducted using the traditional search option with the following settings: multistate characters were treated as unordered; maximum number of trees held was set to 10,000; number of replicates set to 10,000; and starting trees per replicate set to 10. All other search parameters were left at their default settings. Cladograms were rooted between the first outgroup, *Stangeella cyaniventris*, and the remaining taxa. The relative support for each node was assessed using the jackknife, as implemented in WinClada. Resampling was undertaken with the following settings: replicates = 1,000; maximum number of trees = 10,000. All other parameters remained at their default settings. Cladograms were prepared using WinClada.

4.1. Characters used for phylogenetic analysis

1 Male, apical sternites, setae: without a fringe and tuft (0); with a dense fringe on S6 and tuft on S7 (1).
2 Male, A12 and A13, proportions and shape relative to A11: similar (0); much narrower and longer (1).
3 Male, fore tarsus, rake spines: not obviously flattened (similar to larger setae on fore tarsus) (0); flattened (clearly different from larger setae on fore tarsus) (1).
4 Female, clypeal margin, projections: two (0); three (1); four (2).
5 Male, fore femur, ventrally: rounded (0); with strong carina running all the way to base (1); with any carina weak or flattened basally (2).
6 Female, ocular ocellar length, relative to hind ocellar diameter: greater (0); equal or less (1).
7 Female, clypeus, medial convexity, size relative to clypeal width: 1/3 (0); 1/5 (1).
8 Mesosoma, setae, shape and reflection: not flattened, without strong silver reflection (0); all flattened, with strong silver reflection (1).
9 Female, fore leg, telotarsus: triangular, basally tapered (0); oblong, parallel sided (1).
10 Scutellum, punctures, density: dense, interspaces mostly < diameter of puncture (0); moderate, with interspaces mostly 1 – 1.5 × diameter of puncture (1); sparse, interspaces mostly > 3 × diameter of puncture (2).
11 Vein cu-a, joining after fork of M and Cu by: at least 5 × width of cu-a (0); 2 – 4 × width of cu-a (1); cu-a joining very close to fork of M and Cu, or before it (2).
12 Propodeum, lateral surface, sculpture: finely striate, dull (0); finely granular, dull (1); weakly coriaceous, smooth and shiny (2).
13 Hind femur, colour: predominantly black (0); predominantly yellow or red (1).
14 Frons, setae: undifferentiated (0); both appressed and erect (1).
15 Mesopleuron, setae, shape: all straight or evenly curved (0); some crimped (wavy) (1).
16 Male, fore trochanter, ventrally, shape: rounded (0); angled (1); with large blunt tooth (2); with small sharp tooth (3).
17 Subdiscoidal cell, apex, shape: subrectangular (0); oblique (1).
18 Female, face, setae above toruli: present (0); largely absent (1).
19 Male, scape, apical foramen, size relative to scape: < 0.5 (0); > 0.5 (1).
20 Mesopleuron, setae, posteriorly: present (0); absent (1).
21 Mesoscutum, setae: present (0); largely absent (1).
22 Female, pronotum, setae: present (0); absent (1).
23 Propodeum, laterally surface, setae: present all over (0); present posteriorly (1); largely absent (2).
24 Propodeum, dorsal surface, lateral margins: black (0); yellow (1).
25 Mesosoma, ground colour: predominantly black (0); predominantly yellow or reddish (1).
26 Clypeus, flattened silvery setae: present (0); absent (1).
27 Male, fore femur: unmodified (0); with a large tooth ventrally, near middle of femur (1); with several small teeth ventrally (2); with a blunt tubercle basoventrally (3); with a small tooth basoventrally (4).
28 Male, antenna, flagellar spiral segments: more basal with broad pad like tyloids present on A4 and A5 (0); more apical, A4 and A5 more elongate with tyloids indistinct (1).
29 Male, A3, length to width ratio: < 1.3 × (0); 1.5 – 2.5 × (1); > 3.5 × (2).
30 Torulus, shape: rounded (0); comma-shaped with basal projection (1).
31 Male, antennal flagellum, spiralled towards apex: no (0); yes (1).
32 Mandible, externoventral notch: absent (0); present (1).
33 Episternal sulcus, extent: reaching anteroventral margin of mesothorax (0); ending opposite fore coxal cavity but not turning forwards (1).
34 Male, mid tibial spurs, number: two (0); one (1); none (2).
35 Fore wing, submarginal cells, number: three (0); two (1); one (2).
36 Upper metapleural area, setae: present (0); absent (1).
37 Female, tegula, colour: black to brown (0); yellow (1).
38 Male, basal half of mandible, shape: flat (0); strongly concave (1).
39 Radial cell, apex: pointed (0); rounded (1); truncate (2).
40 Female, tergum 1, white marks: absent (0); two spots (1); a narrow band (2); a broad mark (3).
41 Male, tergum 1, white marks: absent (0); two spots (1); a broad mark (2).
42 Female, tergum 2, white marks: absent (0); two spots (1); a narrow band (2); a broad mark (3).
43 Male, tergum 2, white marks: absent (0); two spots (1); a narrow band (2); a broad mark (3).
44 Female, mid tibia, with ivory mark: absent (0); present (1).
45 Male, mid tibia, with ivory mark: absent (0); present (1).
46 Female, frons, colour: black (0); black with yellow stripe mark next to compound eye (1); mostly yellow with black extending downwards from ocellar triangle (2); all yellow (3).
47 Male, frons, colour: black (0); black with yellow stripe mark next to compound eye (1); mostly yellow with black extending downwards from ocellar triangle (2); all yellow (3).

Table 1. Data matrix of 49 adult morphological characters and 19 taxa. The first two lines read vertically provide the character number. Data matrix; **Y** = polymorphic with both states 1 and 2.

Character:	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	444444444 123456789
Taxon:					
Stangeella cyaniventris	0000000000	2101001000	0000000-20	0000000010	000000000
Mellinus arvensis	000100-000	0010000000	0000010-10	0011211000	033001100
Oxybelus uniglumis	0001000001	2000001000	0020000-10	0000011021	111000000
Dinetus pictus	1111100000	0000000000	0020000011	1112101021	213110200
Dinetus simplicipes	111?1?00?0	0000000000	0?20000011	111210?02?	0?0?0?2?0
Dinetus psammophilus	0000211111	1111120000	0000100011	1112111023	222113311
Dinetus rakhimovi	???0?11111	11101?00?0	000000???1	?11?101?23	?2?1?2???
Dinetus arenarius	0000211111	1111100000	0000001001	1112111023	212111211
Dinetus wojciechi	000?2?11?1	111130?00	0?00001001	111211?12?	2??2?1?2?1
Dinetus dentipes	0000211111	1111110000	0001000001	1112111122	222111311
Dinetus turanicus	0000211111	1111110000	0001000001	1112111122	222111311
Dinetus porcellaneus	0000211112	2200031111	1120004111	1112100020	100010121
Dinetus venustus	000021111**Y**	2200031111	1110002121	1112100020	011110221
Dinetus pulawskii	0000211112	2200001111	1110013121	1112101020	010002221
Dinetus tunisiensis	000?2?11?2	2200001?11	1?10013121	111210?02?	0?0?1?2?1
***Dinetus hameri* sp.n.**	???0?11112	22100?11?1	101110???1	?11?101?22	?0?1?3?2?
Dinetus cereolus	???0?11?12	21100?11?1	112111???1	?11?101?2?	???1?3?2?
Dinetus nabataeus	0000211112	2210?01111	1121110011	1112101020	000113311
Dinetus politus	???0?11112	2210??11?1	112111???1	?11?101?20	??2?0?2???

48 Female, intertegular distance: > 1.1 mm (0); 0.9–1.1 mm (1); < 0.9 mm (2).

49 Male, intertegular distance ≥ 0.8 mm (0); < 0.8 mm (1).

4.2. Results of phylogenetic analysis

Our analysis produced a single fully resolved most parsimonious cladogram of 125 steps, with consistency index = 0.60 and retention index = 0.76 (Fig. 1). Three strongly supported clades were found within *Dinetus* (jackknife values > 80%) (Fig. 2), corresponding to the three enlarged species groups that we recognised morphologically above, and consequently these groups are formally named as follows: *pictus* group is now subgenus *Dinetus*; *dentipes* group is now *Dentidinetus* subgen.n.; and *cereolus* group is now *Venustidinetus* subgen.n. We also found a strongly supported clade that placed subgenus *Dentidinetus* and subgenus *Venustidinetus* as sister groups (jackknife support = 95%). The *Dinetus* clade has surprisingly low support (75%) despite being supported by five characters in this analysis. The most likely reasons for this are: a) the large amount of missing data, due to some species being only represented by one sex; and b) because many of the characters chosen to be informative within the *Dinetus* clade are also variable within the outgroup taxa and this homoplasy lowers the jackknife support. This result might be improved by selecting more characters that informed the relationship between the *Dinetus* clade and the outgroup taxa. The character states that support each of these four main clades within *Dinetus* are as follows. Subgenus *Dinetus*: 1. Male with setae of apical sternites forming a dense fringe on S6 and tuft on S7; 2. Male with A12 and A13 much narrower and longer than A11; 3. Male fore tarsus with rake spines flattened and clearly different from larger setae on fore tarsus. Subgenus *Dentidinetus* + subgenus *Venustidinetus*: 5. Male fore femur ventrally with any carina weak; 6. Female ocular ocellar length, equal to or less than hind ocellar diameter; 7. Female clypeus with medial convexity 1/5 of clypeal width; 8. Mesosomal setae all flattened and with strong silver reflection; 9. Female fore leg with telotarsus oblong, parallel sided. Subgenus *Dentidinetus*: 10. Scutellum with punctures moderately dense with interspaces mostly mostly 1–1.5 × diameter of puncture; 11. Vein cu-a joining after fork of M and Cu by 2–4 × width of cu-a; 12. Lateral surface of propodeum with sculpture finely granular and dull; 13. Hind femur predominantly yellow or red; 14. Frons with setae both appressed and erect; 15. Mesopleuron with some setae crimped (wavy). Subgenus *Venustidinetus*: 10. Scutellum with punctures sparse, interspaces mostly > 3 × diameter of puncture; 11. Vein cu-a joining very close to fork of M and Cu, or before it; 12. Propodeum with sculpture of lateral surface weakly coriaceous, smooth and shiny; 17. Subdiscoidal cell with apex oblique; 18. Female, face with setae above toruli largely absent; 19. Male scape with length of apical foramen > 0.5 length of scape; 20. Mesopleural setae posteriorly absent; 21. Mesoscutal setae largely absent; Female pronotal setae absent. The character states that support the *Dinetus* clade are as follows: 30. Torulus comma-shaped with basal projection; 31. Male antennal flagellum, spiralled towards apex; 32. Mandible with externoventral notch present; 34. Male with two mid tibial spurs; 35. Fore wing with two submarginal cells.

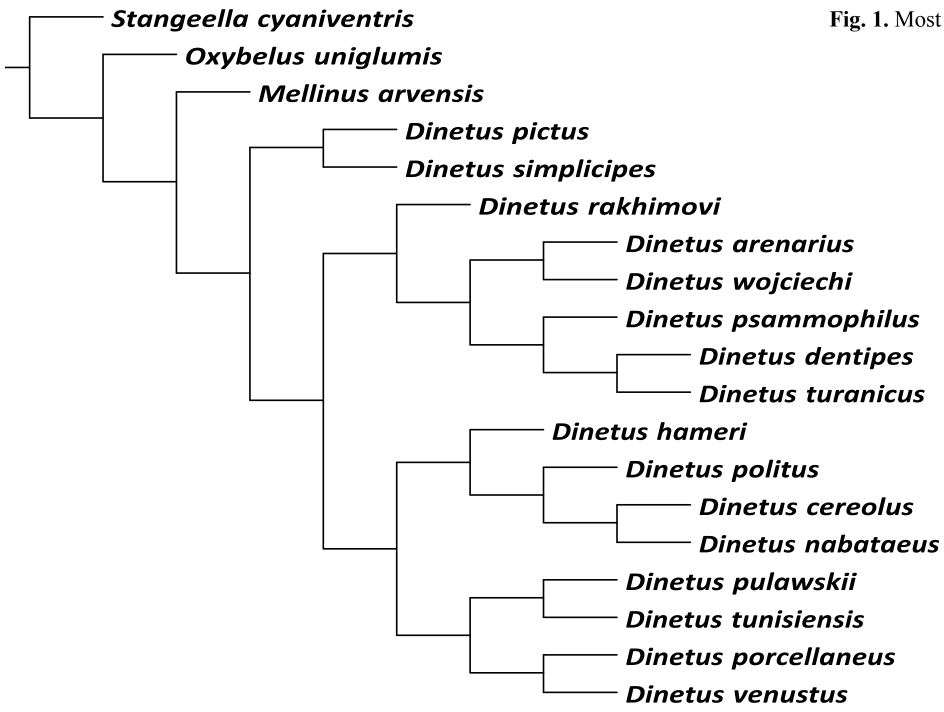


Fig. 1. Most parsimonious cladogram.

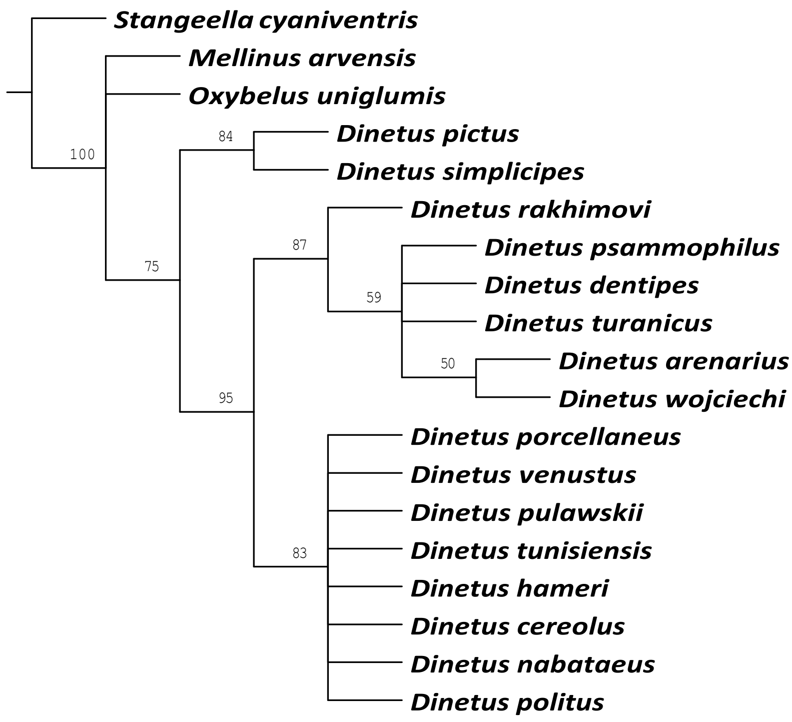
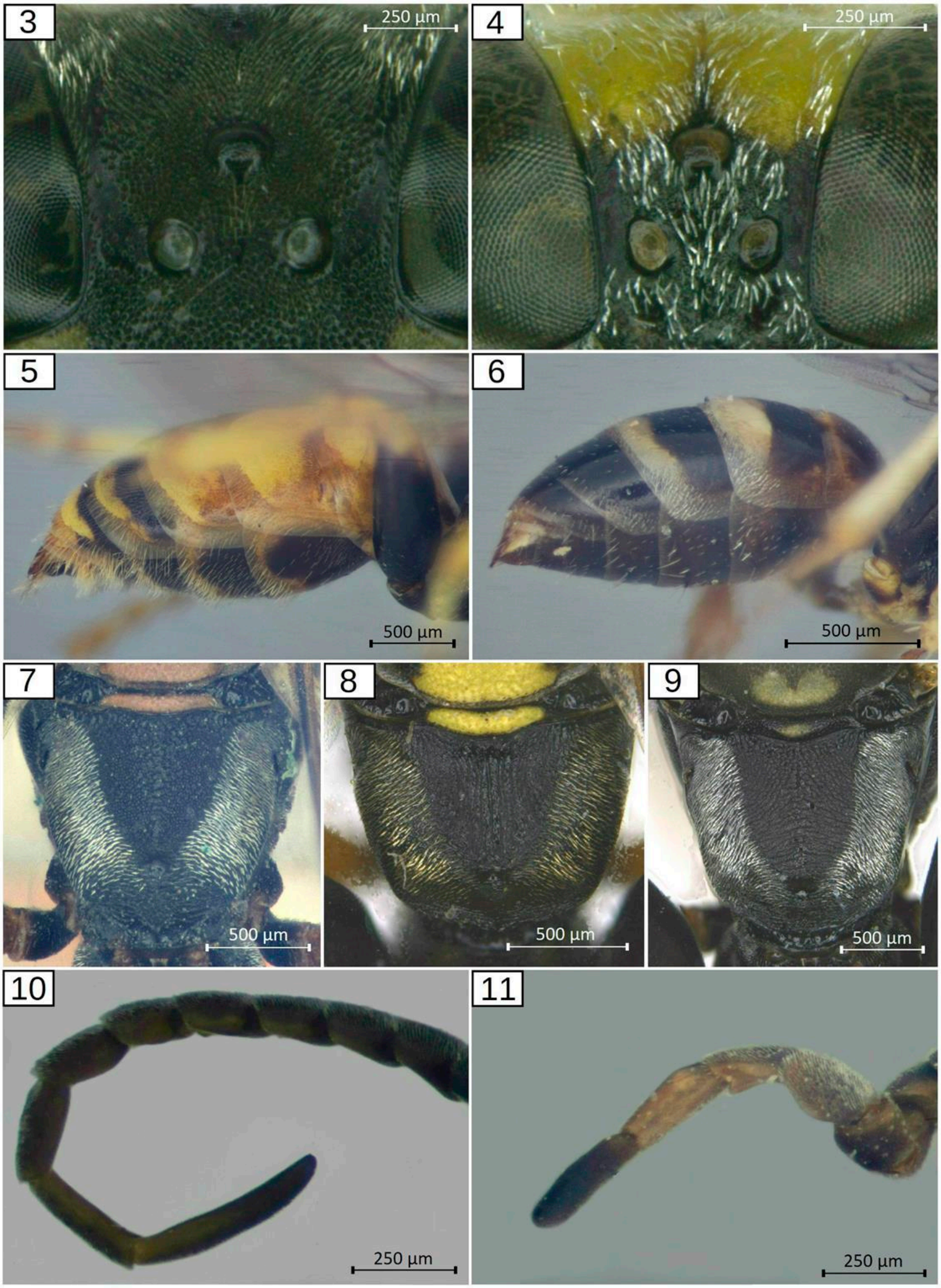


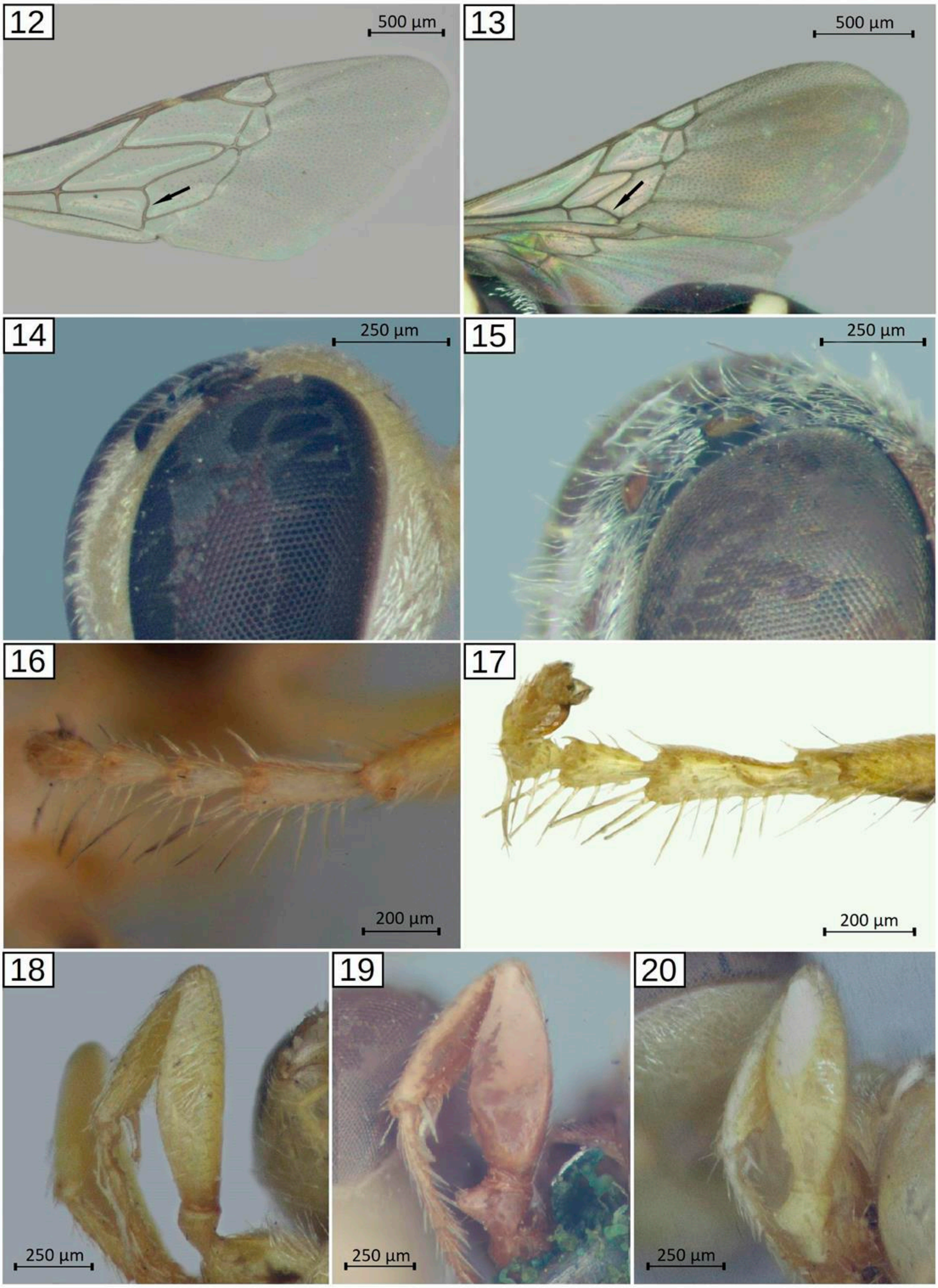
Fig. 2. Resampled tree with jackknife values, nodes with < 50% support are collapsed.

5. Discussion

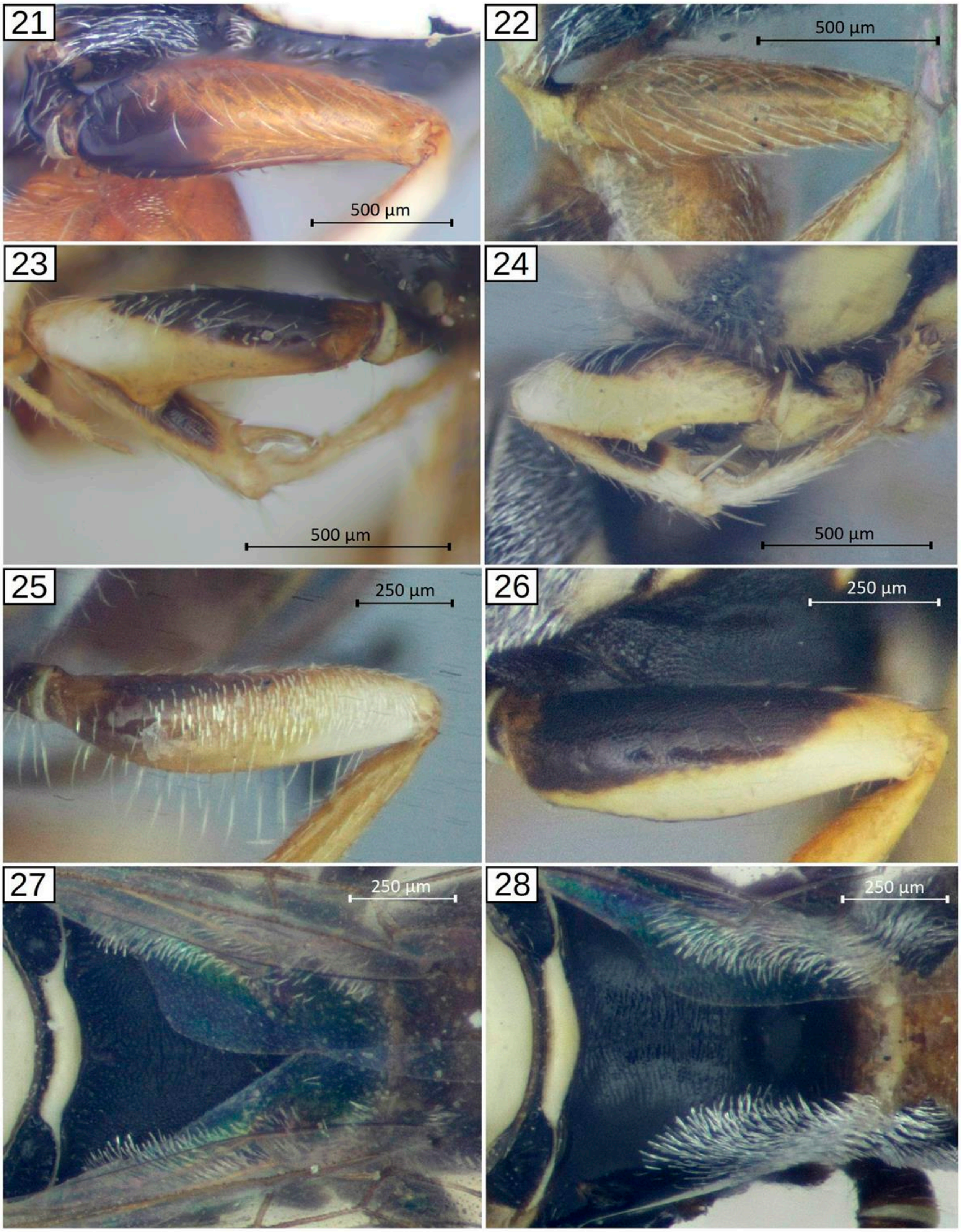
Although the phylogenetic hypothesis that we present in this paper provides strong support for four major clades, it must nevertheless be regarded as preliminary for a number of reasons. We only used three outgroup taxa and inclusion of further taxa could affect the outcome. The study is also based solely on morphological characters; DNA evidence should be sought to test the patterns of relationship found here. For many taxa one sex is missing and missing data can have unforeseen and deleterious consequences for a phylogenetic analysis (Nixon & Wheeler 1992; Novacek 1992). Finally, for various reasons (small body size, many species so far represented by only a small number of specimens, and some potential collecting areas being historically hard to access) we believe that the genus is still under-collected and more



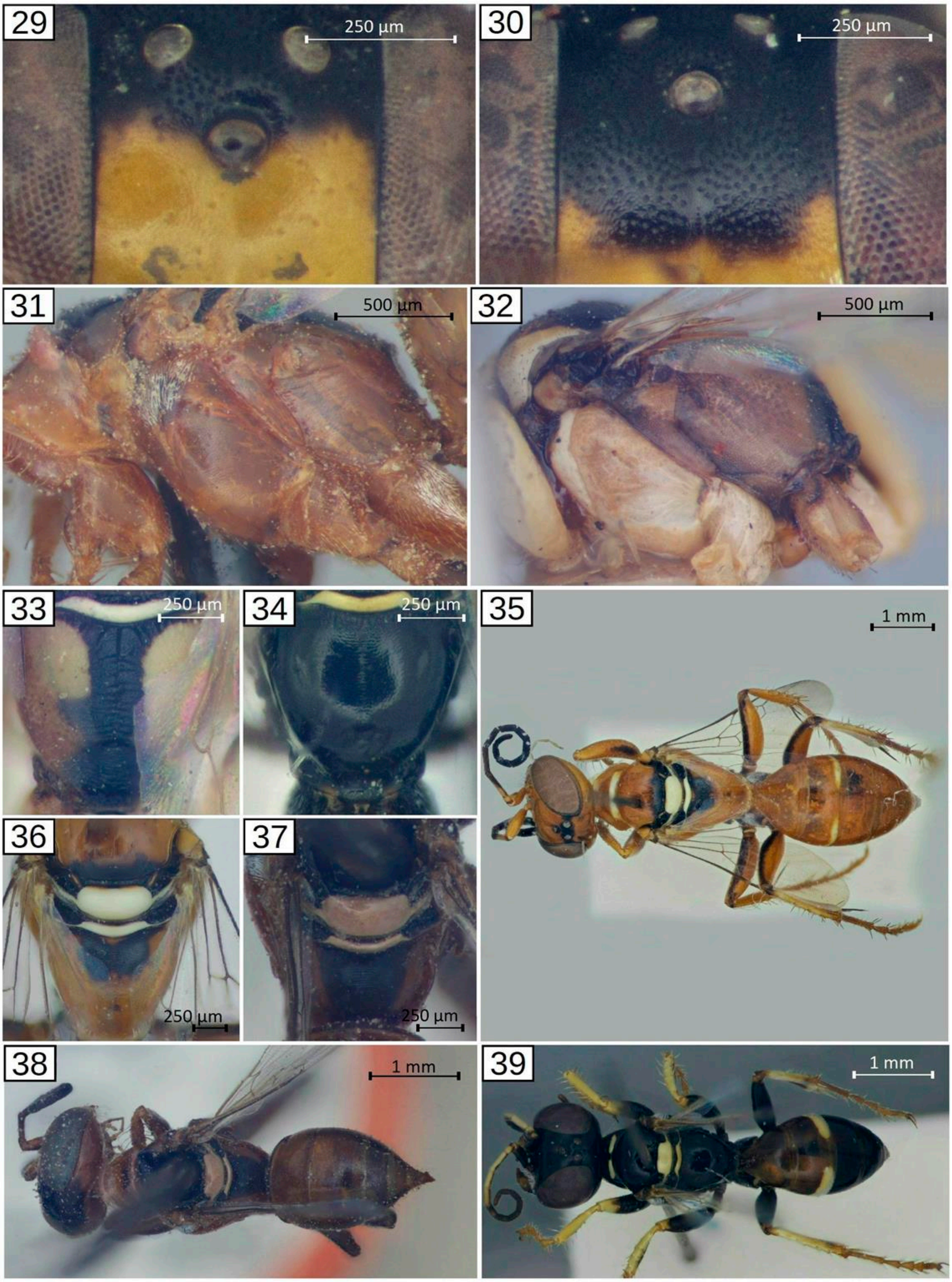
Figs. 3–11. *Dinetus* spp.: **3**: *D. pictus* ♀, frons and vertex, dorsal view, NHMUK013379442; **4**: *D. rakhimovi* ♀, frons and vertex, dorsal view; **5**: *D. pictus* ♂, metasoma, lateral view, NHMUK013379443; **6**: *D. venustus* ♂, metasoma, lateral view, NHMUK013379453; **7**: *D. simplicipes* ♂, propodeum, dorsal view, NHMUK013379449; **8**: *D. pictus* ♂, propodeum, dorsal view; **9**: *D. pictus* ♀, propodeum, dorsal view; **10**: *D. pictus* ♂, A10 and A11 antennomeres, NHMUK013379443; **11**: *D. simplicipes* ♂, A10 and A11 antennomeres, NHMUK013379449. — ***Picture credits***: all NHMUK specimens – David G. Notton (NHMUK); NCU specimen – Piotr Olszewski (NCU).



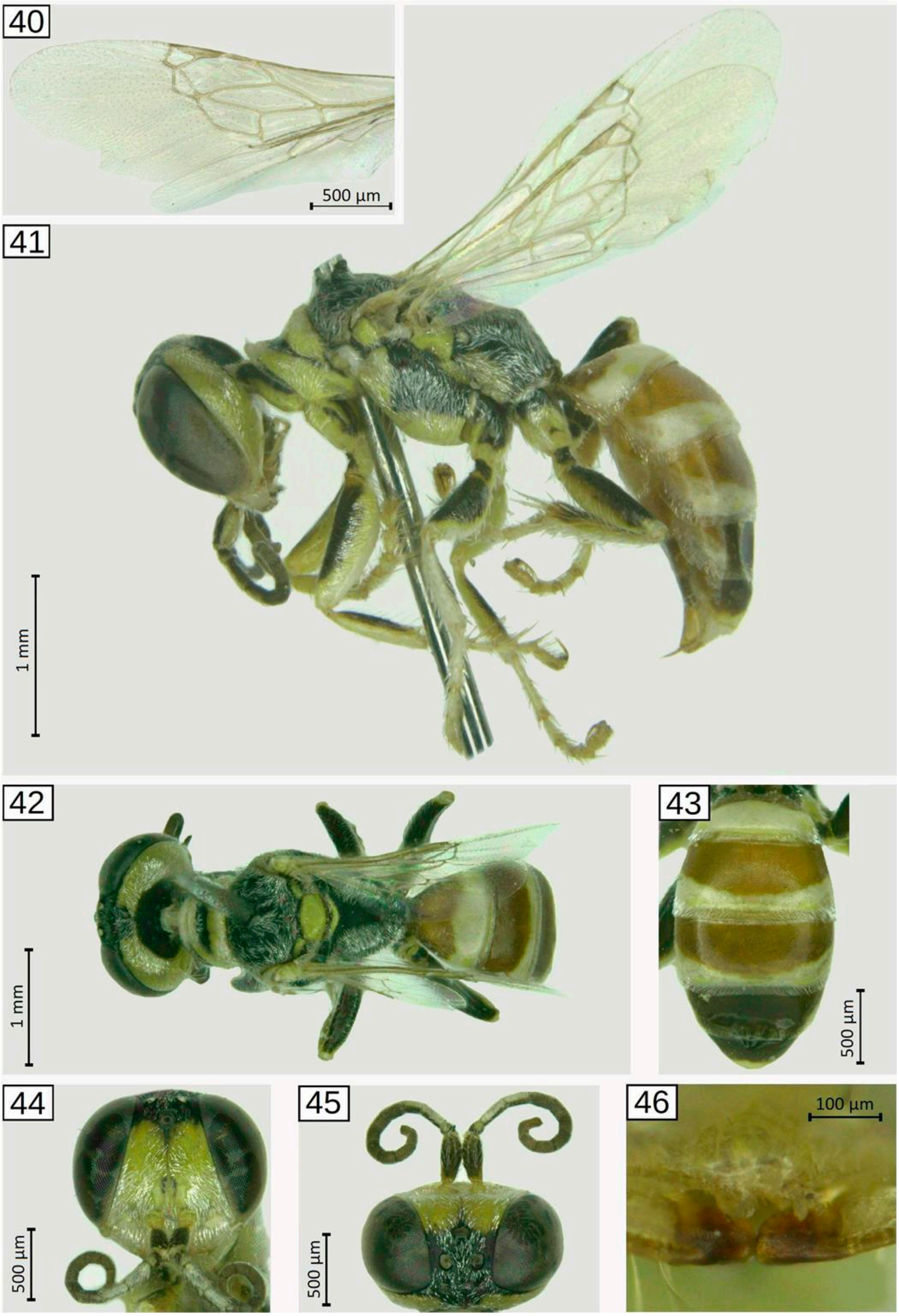
Figs. 12–20. *Dinetus* spp.: **12**: *D. arenarius* ♀, fore wing, dorsal view, NHMUK010812208; **13**: *D. tunisiensis* ♂, fore wing, dorsal view, NHMUK010812654; **14**: *D. psammophilus* ♀, frons, lateral view, NHMUK010812206; **15**: *D. dentipes* ♀, frons, lateral view, NHMUK013379426; **16**: *D. psammophilus* ♀, fore basitarsus, NHMUK010812206; **17**: *D. rakhimovi* ♀, fore basitarsus; **18**: *D. turanicus* ♂, fore leg, NHMUK 013379450; **19**: *D. dentipes* ♂, fore leg, NHMUK013379439; **20**: *D. psammophilus* ♂, fore leg, NHMUK013379446. — ***Picture credits***: all NHMUK specimens – David G. Notton (NHMUK); NCU specimen – Piotr Olszewski (NCU). — ***Arrow*** in 12, 13 pointing to apex of subdiscoidal cell.



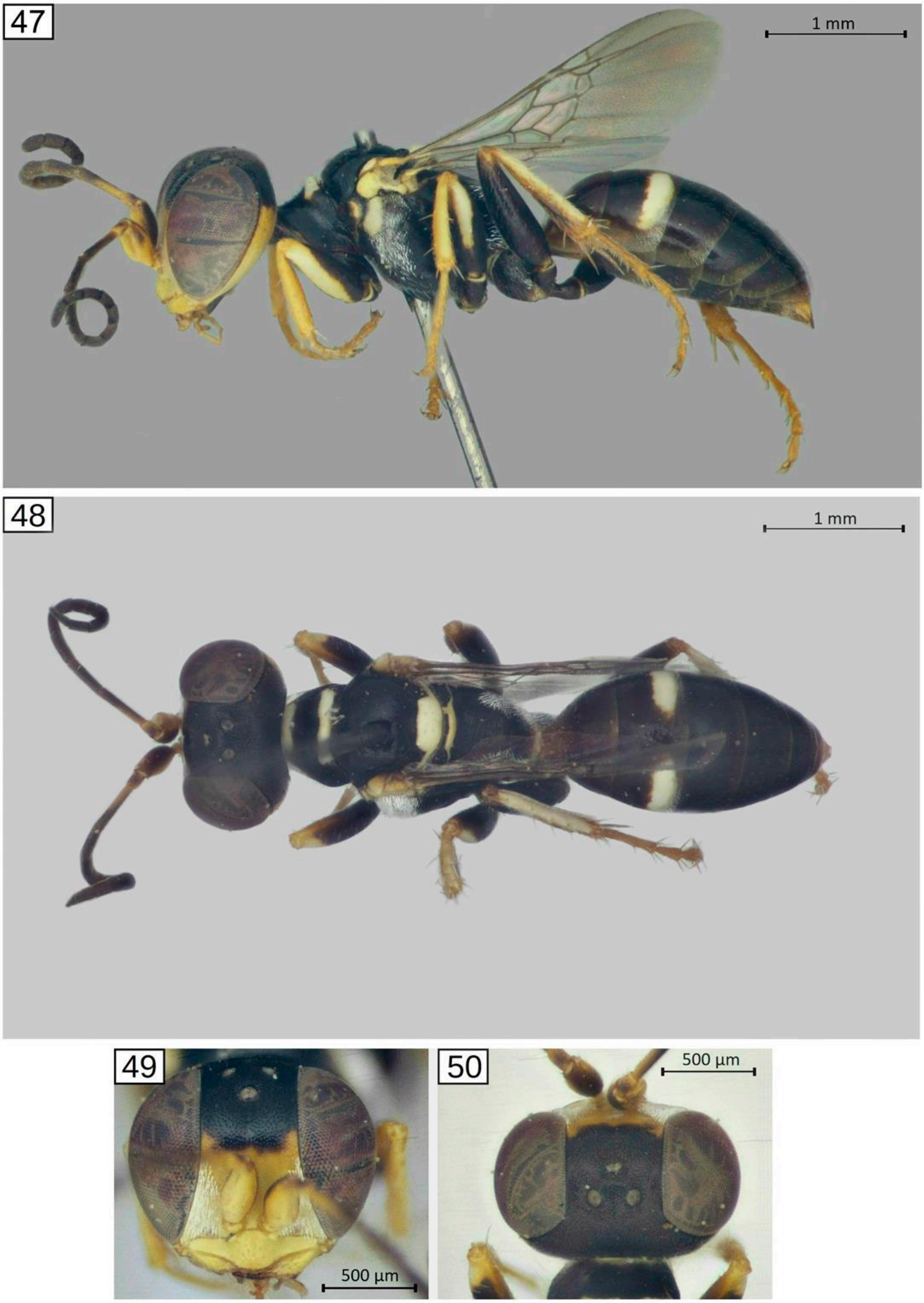
Figs. 21–28. *Dinetus* spp: **21**: *D. arenarius* ♀, hind femur, NHMUK013379438; **22**: *D. wojciechi* ♂, hind femur, NHMUK010812209; **23**: *D. arenarius* ♂, fore leg, NHMUK013379438; **24**: *D. wojciechi* ♂, fore leg, NHMUK010812209; **25**: *D. hameri* ♀, fore femur, NHMUK010812655; **26**: *D. tunisiensis* ♂, fore femur, NHMUK010812654; **27**: *D. venustus* ♀, propodeum, dorsal view, NHMUK 013379452; **28**: *D. pulawskii* ♀, propodeum, dorsal view, NHMUK013379447. — ***Picture credits***: all NHMUK specimens – David G. Notton (NHMUK).



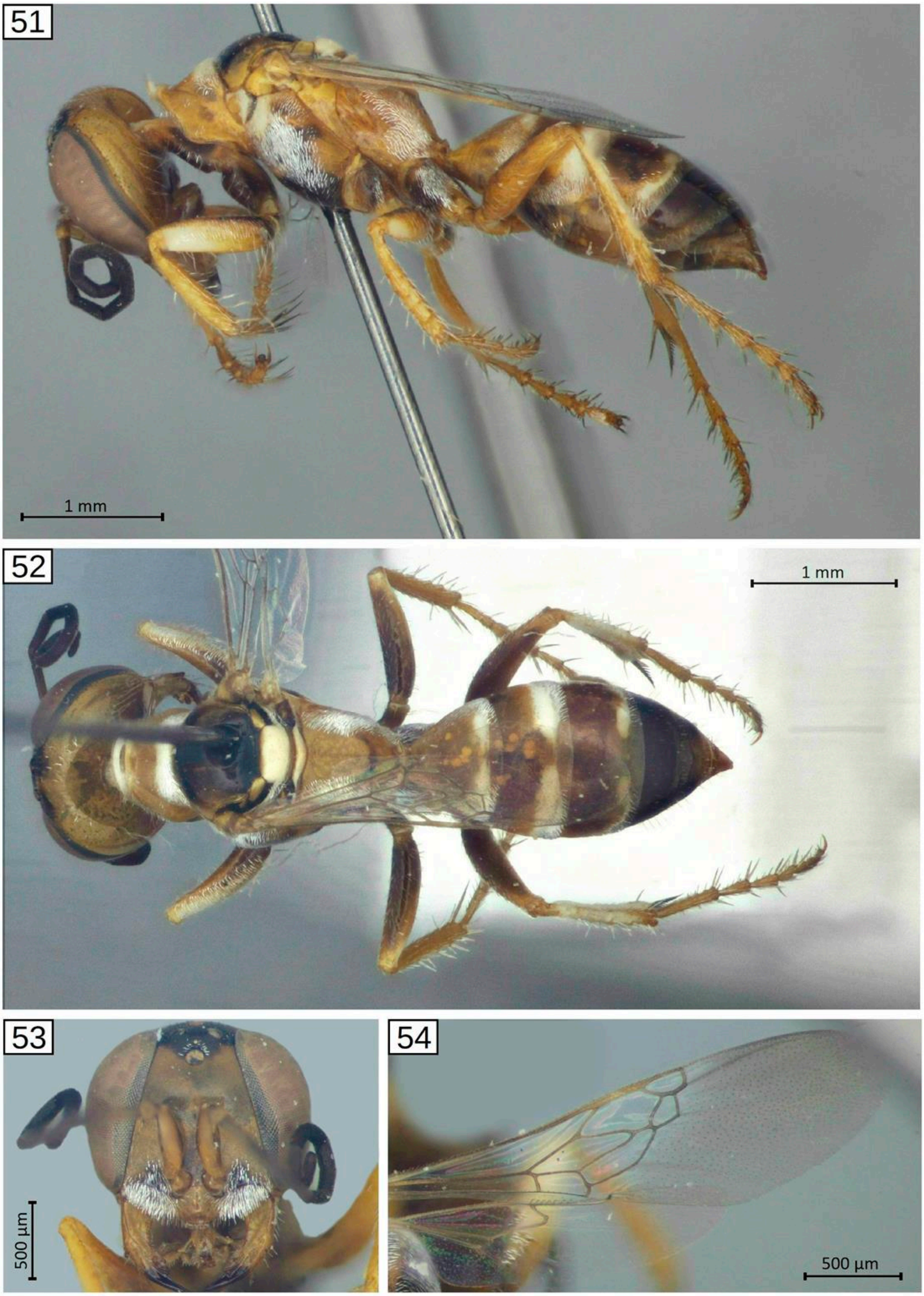
Figs. 29–39. *Dinetus* spp.: **29**: *D. pulawskii* ♂, frons, frontal view, NHMUK013379448; **30**: *D. tunisiensis* ♂, frons, frontal view, NHMUK010812654; **31**: *D. politus* ♀, mesosoma, lateral view, NHMUK013379444; **32**: *D. cereolus* ♀, mesosoma, lateral view, OUMNH; **33**: *D. cereolus* ♀, propodeum, dorsal view, OUMNH; **34**: *D. porcellaneus* ♀, propodeum, dorsal view, NHMUK013379454; **35**: *D. nabataeus* ♀, habitus, dorsal view, NHMUK013379440; **36**: *D. nabataeus* ♀, propodeum, dorsal view, NHMUK013379440; **37**: *D. politus* ♀, propodeum, dorsal view, NHMUK013379444; **38**: *D. politus* ♀, habitus, dorsal view, NHMUK013379444; **39**: *D. porcellaneus* ♀, habitus, dorsal view, NHMUK013379454. — ***Picture credits***: all NHMUK & OUMNH specimens – David G. Notton (NHMUK).



Figs. 40–46. *Dinetus rakhimovi* ♀: **40**: Fore and hind wings, dorsal view; **41**: Habitus, lateral view; **42**: Habitus, dorsal view; **43**: Metasoma, dorsal view; **44**: Head, frontal view; **45**: Head, dorsal view; **46**: Clypeal margin, frontal view. — ***Picture credits***: NCU specimen – Piotr Olszewski (NCU).



Figs. 47–50. *Dinetus tunisiensis* ♂, NHMUK010812654: **47**: Habitus, lateral view; **48**: Habitus, dorsal view; **49**: Head, frontal view; **50**: Head, dorsal view. — ***Picture credits***: NHMUK specimen – David G. Notton (NHMUK).



Figs. 51–54. *Dinetus hameri* ♀, holotype, NHMUK010812655: **51**: Habitus, lateral view; **52**: Habitus, dorsal view; **53**: Head, frontal view; **55**: Fore and hind wings, dorsal view. — ***Picture credits***: NHMUK specimen – David G. Notton (NHMUK).

species are likely to be found. A recent analysis of COI DNA barcodes of spheciform wasps by Schmid-Egger et al. (2018) is of interest because it includes four species of *Dinetus*, i.e., *D. pictus*, *D. dentipes*, *D. nabataeus*, and *D. venustus*. Although this analysis recovered *Dinetus* as a clade, and also recovered a sister group relationship between *D. nabataeus* and *D. venustus* (which are both in subgenus *Venustidinetus*), it did not root the *Dinetus* clade in the same place as in the analysis presented here.

However, we consider it premature to draw any firm conclusions from a comparison with this analysis because it only used a short section of a single mitochondrial gene and four (of the 16) species of *Dinetus.* A very interesting feature of the phylogeny of *Dinetus* that we found in the present study is that the three subgenera have quite different geographic distributions: subgenus *Dinetus* – Europe, Kazakhstan and north Africa, including the only species in Europe; subgenus *Dentidinetus* – all species are found in central Asian desert regions of Iran, Kazakhstan, Mongolia, Turkmenistan and Uzbekistan, with the widespread *D. dentipe*s extending out of this region into north Africa; subgenus *Venustidinetus* – all species except one found in north Africa and the Middle East, the exception being *D. politus* in India. This supports the result of the phylogenetic analysis, that is to say there are three clades with independent evolutionary histories in different biogeographical regions, and suggests that the genus could be a suitable subject for a more extensive biogeographical study. The extensive development of flattened silvery setae with differentiated crimped setae seen in subgenus *Dentidinetus* suggests a specific adaptation to desert conditions, by analogy with the extensive white or pale setae seen in other deserticolous aculeate Hymenoptera. Subgenus *Venustidinetus* by contrast appears to have undergone extensive loss of body setation and reduction in puncturation resulting in an overall very smooth shiny appearance. We would also note that the modifications of the male fore trochanter and femur (characters 16 & 27) appear to be very variable across the clade (subgenus *Dentidinetus* + Subgenus *Venustidinetus*) and should be studied in more detail. We suggest that these structures are used in specific courtship behaviours and have evolved rapidly as a part of behavioural mechanisms to ensure interspecific reproductive isolation

6. Conclusion

In conclusion, our analysis provided evidence for four strongly supported clades within *Dinetus*; three of the clades corresponded to the three enlarged species groups that we recognised morphologically above, and consequently these groups are formally named as follows: *pictus* group is now subgenus *Dinetus*; *dentipes* group is now *Dentidinetus* subgen.n.; and *cereolus* group is now *Venustidinetus* subgen.n. The fourth strongly supported clade placed subgenus *Dentidinetus* and subgenus *Venustidinetus* as sister groups. We also found some supporting biogeographic evidence that the three subgenera have independent evolutionary histories in different biogeographic regions. Although our study should be regarded as preliminary, other studies that touch on the phylogeny of *Dinetus* are very limited in scope and none provides any strongly supported conclusions that contradict our result.

7. Acknowledgements

The authors wish to thank James Hogan and Darren Mann (OUMNH) for kindly making the type of *D. cereolus* available. We also owe a special debt of gratitude to Prof. K. Szpila (Nicolaus Copernicus University, Toruń) for providing a specimen of *Dinetus rakhimovi* and we are grateful to Dr Abbas Aghaei Afshar (Kerman University of Medical Sciences, Iran) and Dr Kamran Akbarzadeh (Tehran University of Medical Sciences, Iran) for excellent help in organizing collecting trips. We thank also PD Dr. Michael Ohl and one other anonymous referee for providing useful reviews of the manuscript.

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Zeitschrift/Journal: Arthropod Systematics and Phylogeny

Jahr/Year: 2020

Band/Volume: 78

Autor(en)/Author(s): Olszewski Piotr, Notton David G., Kitching Ian J.

Artikel/Article: Review of the genus Dinetus Panzer, 1806 (Hymenoptera: Crabronidae: Dinetinae) with descriptions of new subgenera and new species 361-377