

Geometric morphometric analysis of a new Miocene bumble bee from the Randeck Maar of southwestern Germany (Hymenoptera: Apidae)

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Abstract. The first fossil bumble bee (Apinae: Bombini) from the Miocene Randeck Maar of southwestern Germany is described and illustrated. The specimen is subjected to a geometric morphometric analysis along with a diversity of other bumble bee species representing most major extant lineages, and particularly the subgenus *Bombus* s.s. The morphometric analysis supports the placement of the Randeck Maar species within *Bombus* s.s., as a species distinct from all others in the subgenus. It shows that extant subgenera of bumblebees were already derived in the early/middle Miocene. The Randeck Maar fossil is formally described as *Bombus (Bombus) randeckensis* Wappler & Engel **sp. n.**

Introduction

The bumble bees (Bombini: *Bombus* Latreille) are some of the most charismatic and beloved of all insects. Their robust form, relatively small colonies and distinctive colour patterns have made them a favourite of entomologists and laymen alike. Not surprisingly, this fascination has translated into an intensity of study, including fine-scale taxonomic investigations into the world's fauna (e.g. Williams, 1991, 1998; Bertsch *et al.*, 2005; Rasmont *et al.*, 2005, 2008; Murray *et al.*, 2008; Williams *et al.*, 2008, 2009, 2011, 2012; Bertsch, 2010; Kozmus *et al.*, 2011). *Bombus* presently comprises about 250 valid species (Williams *et al.*, 2008), although various subspecies may require elevation to specific status. The bumble bees can boast perhaps more critical study than any other lineage of bees except of course the ubiquitous honey bees (Apini: *Apis* Linnaeus). In addition, considerable cladistic work has been invested into recovering a stable set of relationships among and within the numerous subgenera (e.g. Ito, 1985; Williams, 1985, 1994; Pederson, 2002; Cameron & Williams, 2003; Kawakita

et al., 2003, 2004; Hines *et al.*, 2006; Cameron *et al.*, 2007; Hines, 2008; Bertsch, 2010; Bertsch *et al.*, 2010a, b).

Unfortunately, the fossil record of bumble bees is remarkably sparse, much like that of the remainder of the Apoidea (e.g. Michez *et al.*, 2012). Indeed, only 11 fossil bee species have been documented that putatively can be assigned to Bombini (Table 1), and most of these are poorly documented or described and their placement within *Bombus* s.l. is uncertain. The oldest bumble bee fossil, *Probombus hirsutus* Piton, 1940, was described from the deposit of Menat (France, Paleocene) as a close relative of the bumble bees, but is in fact a megachiline (Nel & Petrulėvičius, 2003) and may belong to the genus *Ctenoplectrella* Cockerell (Megachilinae: Ctenoplectrellini). Other bumble bee fossils were described from Oligocene or Miocene deposits. Certainly a detailed revision of the fossil Bombini is desperately needed, as the study of such taxa has not kept up with the same intensity as the modern fauna has inspired.

Herein we provide the description and analysis of a newly recognized fossil bumble bee from the early / middle Miocene (Burdigalian/Karpatian) Randeck Maar. The species is represented by an exquisitely preserved forewing (Fig. 1). In order to distinguish the fossil species from its close congeners as well as to determine its overall affinities with

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Table 1. Previously described fossil bumble bees and possible bombines.

Taxon	Age (Ma)	Epoch	Locality
<i>Bombus anacolus</i> Zhang <i>et al.</i> , 1994	17.0–15.2 ^a	Miocene	Shandong, China
<i>Bombus?</i> <i>crassipes</i> Novak, 1877	18.0–17.0 ^b	late early Miocene	Krottensee, Czech Republic
<i>Bombus dilectus</i> Zhang <i>et al.</i> , 1994	17.0–15.2 ^a	Miocene	Shandong, China
<i>Bombus luianus</i> Zhang, 1990	17.0–15.2 ^a	Miocene	Shandong, China
<i>Bombus?</i> <i>pristinus</i> Unger, 1867	11.2–7.1 ^c	late Miocene	Euboea, Greece
<i>Bombus proavus</i> Cockerell, 1931	21.3–12.1 ^d	middle to upper Miocene	Latah, USA
<i>Bombus vetustus</i> Rasnitsyn & Michener, 1991	11.2–7.1 ^e	late Miocene	Botchi River, Russia
<i>Bombus</i> sp.	~20.0 ^f	Oligocene	Bilina Mine, Czech Republic
<i>Calyptapis</i> ^g <i>florissantensis</i> Cockerell, 1906	37.0–33.9 ^h	Eocene–Oligocene	Florissant, USA
<i>Oligoapis</i> ⁱ <i>beskonakensis</i> Nel & Petrulevičius, 2003	22.5 ^j	Oligocene–Miocene	Bes-Konak, Turkey
<i>Parelectrobombus</i> ⁱ <i>patriciae</i> Nel & Petrulevičius, 2003	22.5 ^j	Oligocene–Miocene	Bes-Konak, Turkey

^afor summary see Yang *et al.* (2007).

^bRNDr. J. Prokop, personal communication.

^cBachmayer *et al.* (1971).

^dGray & Kittleman (1967).

^eAkhmetjev (1973).

^ffor summary see Knor *et al.* (2012).

^g*Calyptapis* Cockerell, originally described as being near *Melissodes* (Cockerell, 1906), was moved to the Bombini by Cockerell (1908). If Cockerell (1908) is correct in his placement, then *Calyptapis* is assuredly a junior synonym of *Bombus* s.l. and may take priority over a subgeneric name currently used for Recent taxa alone.

^hEvanoff *et al.* (2001).

ⁱLikely synonyms of *Bombus* s.l.

^jPaicheler *et al.* (1978).

other bombines, we subjected the specimen to a geometric morphometric analysis following that employed elsewhere for living and fossil bees (e.g. Aytekin *et al.*, 2007; Tofilski, 2008; Francoy *et al.*, 2008, 2009; Michez *et al.*, 2009; De Meulemeester *et al.*, 2012).

Materials and methods

Terminology and repositories

Morphological terminology for the description of the bombine wing follows that of Engel (2001), while the subgeneric classification of Williams *et al.* (2008) was adopted for Bombini. The Randeck Maar specimen is deposited in the Staatliches Museum für Naturkunde, Stuttgart (SMNS), Germany, while representative Bombini, Centridini and Anthophorini used in the analysis were sampled from the following collections: Department of Entomology, Natural History Museum, UK; Morphometrics Lab, Hacettepe University, Turkey; Laboratory of Zoology, University of Mons, Belgium; Laboratory of Paleontology, Muséum national d'Histoire naturelle, Paris, France; Cornell University Insect Collection, Ithaca, New York, USA; and Division of Entomology; University of Kansas Natural History Museum, Lawrence, Kansas, USA.

Geological setting

The geological setting, stratigraphy, depositional environment and age of the early/middle Miocene of the Randeck Maar area is reviewed in detail elsewhere (e.g. Schweigert,

1998; Lutz *et al.*, 2000). The Randeck Maar is located in southwest Germany, southeast of Stuttgart at the escarpment of the Swabian Alb (48°71'N, 9°31.8'E, 750 m elevation) and is the largest ancient maar in that region. During the early Miocene, the Mesozoic rocks of the Swabian Alb were penetrated by numerous volcanic dykes leading to phreatomagmatic eruptions when the rising nepheline-melilithic magma contacted groundwater (Bleich, 1988). The Maar deposits consist of volcanoclastic limestones overlain by Miocene sediments (Krautter & Schweigert, 1991), which are dated as early/middle Miocene (Burdigalian, Karpatian, MN 5, *c.* 16–18 Ma) after the mammal fauna (Heizmann, 1983). In one phase of sedimentation, bituminous laminites ('dysodiles') and laminated, varve-like limestones were deposited. These limestones contain exceptionally well-preserved fossil insects and plants (e.g. Armbruster, 1938, 1939; Schawaller, 1986; Gregor, 1986; Ansorge & Kohring, 1995; Kotthoff, 2005; Kotthoff & Schmid, 2005; Kotthoff *et al.*, 2011). Paleobotanical data place the Randeck Maar flora within the Central European middle Miocene mixed mesophytic forests, growing in a Cfa climate (warm temperate-humid-hot summer, Cfa classification: Köppen & Geiger, 1928; Kottek *et al.*, 2006) with mean annual temperature (MAT) from 14–15 °C, and an estimated mean annual precipitation (MAP) from 600–2000 mm (Gregor, 1986; Krautter & Schweigert, 1991).

Shape analysis

Geometric morphometrics

Geometric morphometrics is a recent core of methods which aim at quantifying and analysing the overall shape of a



Fig. 1. Photograph of holotype (SMNS 68000/28) forewing of *Bombus* (*Bombus*) *randeckensis* sp. n., from the Miocene Randeck Maar of southwestern Germany: (A) detail of wing (scale bar = 1 mm); (B) entire rock fragment on slide as prepared by L. Armbruster.

structure (Bookstein, 1991; Rohlf & Marcus, 1993). When fossil specimens are not easily assigned to modern groups because they are fragmentary, damaged, or because important morphological details are obscured, this technique can provide a powerful tool in palaeontology for discriminating taxa at different levels, and for discussing the taxonomic affinities between fossils and extant taxa (e.g. Roberts *et al.*, 2008; Michez *et al.*, 2009; De Meulemeester *et al.*, 2012). However, taxonomic affinities calculated based on the shape analysis of a structure should not be mistaken with phylogenetic affinities. Cladistic methods including geometric morphometrics still face different challenges: (i) shapes are continuous data, (ii) character polarity is still difficult, and (iii) in shape analysis, landmark coordinates are not independent variables. Furthermore, morphoclustering can differ from phylogeny because of divergent rates of evolution (e.g. Cardini, 2003).

Validation of shape discrimination

In order to study wing shapes of close relatives of the Randeck Maar bee fossil, we sampled 328 bee specimens from three apid tribes [Bombini ($n = 316$), Centridini ($n = 3$), and Anthophorini ($n = 9$)] (Table S1). As the Randeck Maar bee fossil was determined as close to extant Bombini in preliminary principal component (PCA) and linear discriminant (LDA) analyses based on a smaller sample (see details below for PCA and LDA analyses), additional specimens were chosen to represent the morphological diversity of bumble bees by including all the 15 extant subgenera and 125 species (50% of world diversity).

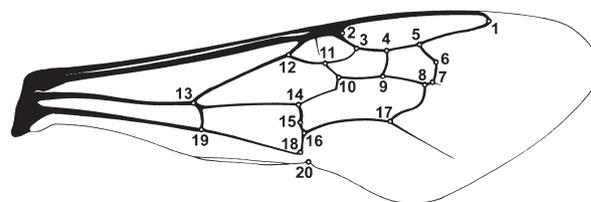


Fig. 2. Right forewing of a generalized bumble bee depicting the 18 landmarks used in the analyses (adapted from Aytekin *et al.*, 2007).

Caste attribution of the Randeck Maar bee fossil was not possible based on its wing size only because many specimens are needed to evaluate intraspecific polymorphism. However, even if the sex is unknown, we hypothesized that the specimen is a worker, given that bumble bee workers are more common than sexual castes. Therefore, all extant sampled specimens were females to avoid the likely effect of sexual dimorphism (Pretorius, 2005; Rattanawanee *et al.*, 2010).

The right forewings of the 328 specimens were analysed using geometric morphometric procedures (Bookstein, 1991; Rohlf & Marcus, 1993). Wing shape was captured from photographs by digitizing 2D Cartesian coordinates of 18 landmarks placed on the wing veins (Fig. 2). Two-dimensional Cartesian coordinates of the landmarks were digitized on the wing photographs with tps-DIG v2.16 (Rohlf, 2010a). The landmark configurations were scaled, translated and rotated against the consensus configuration using the GLS Procrustes superimposition method to remove all nonshape differences and to separate the size and shape components

of the form (Rohlf & Slice, 1990; Adams *et al.*, 2004). The superimposition was performed with tps-RELW (Rohlf, 2010b). The aligned landmark configurations were projected into the Euclidean space tangent to the curved Kendall's shape space to aid further statistical analyses. The closeness of the tangent space to the curved shape space was tested by calculating the least-squares regression slope and the correlation coefficient between the Procrustes distances in the shape space with the Euclidean distances in the tangent space (Rohlf, 1999). This variation amplitude of our dataset was calculated with tps-SMALL v1.20 (Rohlf, 2003).

Shape variation was assessed by PCA based on the superimposed landmark coordinates. The PCA was calculated with tps-RELW v1.49 (Rohlf, 2010b). Shape discrimination within the dataset was also assessed by linear discriminant analysis (LDA) performed in R version v2.9.1 (R Development Core Team, Vienna, Austria). Specimens were grouped *a priori* by tribe and genus (Centridini, Anthophorini) or subgenus (Bombini). The subgeneric classification of *Bombus* was based on the system advocated by Williams *et al.* (2008). The effectiveness of the discriminant analysis for separating groups was tested by the percentages of individuals correctly classified to their original group (hit ratios, HR) in an assignment procedure based on the Mahalanobis Distance (MD) between specimens and the centroid of the groups in the LDA space. We employed the 'leave-one-out' approach to assess the performance of the assignment procedure (Table S2).

Assignment of the Randeck Maar fossil

Taxonomic affinities of two fossil specimens were examined: the Randeck Maar specimen and the *Paleohabropoda oudardi* specimen. Placement of *Paleohabropoda oudardi* has been demonstrated elsewhere (Michez *et al.*, 2009) and was used only as a practical example and for purposes of comparison. The fossils were assigned to extant tribes based on unsupervised (PCA) and supervised methods (LDA).

A PCA was calculated based on the superimposed landmark coordinates of both fossils and extant species (Fig. 3). Morphological proximities of the fossil with the bee tribes were assessed based on the scores of the fossils in the PC space. Taxonomic affinities of the fossils were also examined by using LDA based on recent species wing shape. The two fossil specimens were included *a posteriori* in the computed discriminant space as 'unknown' specimens. Assignment of the fossils was estimated by calculating the MD between these 'unknowns' and a group mean for a contemporary genus and subgenus (Table S3).

In order to assess the placement of the Randeck Maar fossil, the MD between the fossil and the centroids of *Bombus* subgenera were compared to the distances observed among centroids of all the subgenera (Table S3). The distances between the fossil and the centroids of *Bombus* subgenera were also compared to the ranges of distances observed (i) between subgeneric centroids and their consubgeneric specimens, (ii) among consubgeneric specimens, and (iii) between subgeneric centroids and the non-consubgeneric specimens (Table S4).

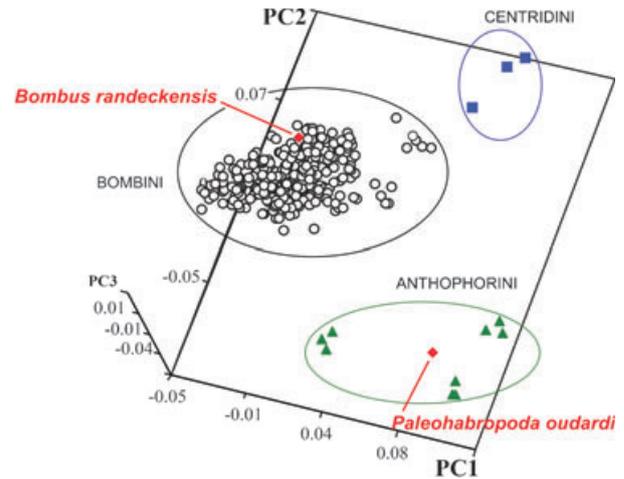


Fig. 3. Distribution of the 330 examined specimens of modern and fossil bee specimens, along the first three RWs. RWA of tangent space coordinates derived from GPA of the original coordinates digitized from the wing.

Species assignment of the Randeck Maar fossil and sexual dimorphism of wing shape

In order to assess the potential effect of the sexual dimorphism on subgeneric assignment, a new dataset of 395 male specimens of the subgenus *Bombus* was considered: *Bombus affinis* Cresson ($n = 19$), *B. canariensis* Pérez ($n = 15$), *B. cryptarum* (Fabricius) ($n = 30$), *B. florilegus* Panfilov ($n = 7$), *B. franklini* (Frison) ($n = 3$), *B. hypocrita* Pérez ($n = 21$), *B. ignitus* Smith ($n = 20$), *B. jacobsoni* Skorikov ($n = 50$), *B. lucorum* (Linnaeus) ($n = 30$), *B. magnus* Vogt ($n = 30$), *B. moderatus* Cresson ($n = 5$), *B. occidentalis* Greene ($n = 26$), *B. patagiatus* Nylander ($n = 30$), *B. sporadicus* Nylander ($n = 27$), *B. terrestris* (Linnaeus) ($n = 30$), *B. terricola* Kirby ($n = 30$) and *B. tunicatus* Smith ($n = 22$). Subgeneric assignment of each male specimen was estimated by calculating the MD between these 'unknowns' and the centroid of groups of contemporary genera and subgenera based on the previous female dataset.

Moreover species assignment of the Randeck Maar fossil was not developed because preliminary analyses showed that interspecific variation of bumble bee wing shape is lower than intraspecific sexual dimorphism (T. De Meulemeester, unpublished data). If species attribution of unknown specimens depends on sex, and as the sex of the fossil is unknown, then species attribution for the fossil is too speculative.

Results

The regression coefficient between the Procrustes distances and the Euclidean distances is close to 1 (0.9983) and a high correlation coefficient (0.9999) between these two distances is obtained. This means that the linear tangent space closely approximates the shape space, thereby permitting us to be confident in the variation amplitude of our dataset.

In the morphometrics space defined by the PCA, all three tribes are well isolated from each other (Fig. 3). Tribe discrimination in the PC space is therefore truly effective. Based on this unsupervised approach the Randeck Maar specimen is clustered with the Bombini. In agreement with Michez *et al.* (2009), *Paleohabropoda oudardi* is clustered with the Anthophorini.

As observed in the PCA, tribes were greatly isolated from each other in the LDA (Tables S2, S3). Moreover, discrimination of most bombine subgenera were clearly recognized (Table S2). Only three subgenera (*Cullumanobombus* Vogt, *Melanobombus* Dalla Torre, *Pyrobombus* Dalla Torre) were less well discriminated (HR 62, 61 and 58%, respectively). A *posteriori* assignment of the two fossil shows that the Randeck Maar specimen is morphologically close to the subgenus *Bombus* s.s. (MD = 5.85) among Bombini while *Paleohabropoda oudardi* is close to *Habropoda* Smith among the Anthophorini (MD = 15.92) (Table S3).

The MD distance between the Randeck Maar fossil and the centroid of the subgenus *Bombus* s.s. (MD = 5.85) was compared to the intrasubgeneric range of MD between *Bombus* s.s. specimens and *Bombus* s.s. centroid (min = 2.16; median = 3.34; max = 5.09), and between *Bombus* s.s. specimens themselves (min = 2.65; median = 4.88; max = 7.36). These ranges were compared to the range of MD between *Bombus* s.s. centroid and specimens of the other subgenera (min = 4.31; median = 7.23; max = 12.15). The comparison to the intra- and intergroup MD demonstrates that the Randeck Maar fossil is very close to *Bombus* s.s. and is best assigned therein (Tables S3, S4). The MD between the fossil and the centroid of the assigned subgenus is smaller than the maximum distance observed between two specimens of *Bombus* s.s. in the discriminant space (MD = 7.36).

Most of the *Bombus* s.s. males (83%) are attributed in the group of *Bombus* s.s. females. This result is quite similar to that from the assignment procedure including only females (Table S3). Subgeneric assignment therefore seems to be independent of the sex of a specimen.

Systematics

Genus *Bombus* Latreille
Subgenus *Bombus* Latreille

Bombus (Bombus) randeckensis Wappler & Engel sp. n.

Bombini: Joachim, 2008: 52, fig. 9, pl. 5 (fig. 8).
Bombini: Joachim, 2010: 39, fig. 9, pl. 5 (fig. 8).

Diagnosis. The new species differs from species such as *B. sporadicus*, *B. tunicatus*, *B. lucorum* and *B. jacobsoni* in the more extensively infuscated area in the marginal cell. In the latter series of species this darkened area is restricted to the apical half of the anterior half of the marginal cell, while in the new species it extends the entire length of the anterior half of the marginal cell (Fig. 1).

Description. (Fig. 1). *Forewing*: Total length 14.34 mm; maximum width 5.03 mm; marginal cell length 3.88; length of first submarginal cell (as measured from origin of Rs + M to juncture of r-rs and Rs) 1.69 mm; height of first submarginal cell (measured from Rs + M to pterostigma) 0.82 mm; height of second submarginal cell (measured from midpoint on M between 1m-cu and 1rs-m to juncture of r-rs and Rs) 0.74 mm; height of second medial cell (as measured from Cu1 to juncture of 1m-cu and M) 1.13 mm; maximum diagonal length of second medial cell (as measured from origin of Cu1 to juncture of 2m-cu and M) 3.20 mm; first free abscissa of Cu offset from M + Cu by vein width (*i.e.*, posterior border M + Cu in line with anterior border Cu at cu-a); cu-a nearly confluent with basal vein (first free abscissa of M) (Milliron, 1971).

Holotype. Forewing; SMNS 68000/28 (old Armbruster collection No. A5119); Randeck Maar, southeast of Stuttgart, Swabian Alb (48°71'N, 9°31.8'E, 750 m elevation); early Miocene, 16–18 Ma (Burdigalian, Karpatian, MN 5); deposited in the Staatliches Museum für Naturkunde, Stuttgart.

Etymology. The specific epithet is based on the type locality of the Randeck Maar.

Discussion

Despite the holotype of *Bombus randeckensis* only being a wing, its identity and affinities among other bumble bees could be determined with reasonable robustness. The geometric morphometric procedures employed herein permit a comparatively robust identification of the present fossil as well as recognition of its close relatives, and reveals it as distinct from any of the extant members of its subgenus. The potential for such methodology is great, not only for the discrimination of taxa and recognition and characterization of cryptic forms, but also for more rigorous means of associating otherwise fragmentary fossils or potentially even living species known from poorly preserved or incomplete type series.

The recognition of a species of *Bombus* s.s. in the early Miocene of Germany has broad implications for the dating of cladogenetic events among bumble bees. For example, crown-group *Bombus* s.s. have been dated using molecular techniques alone (Hines, 2008) to having arisen merely 7–8 Ma (*i.e.* late Miocene: late Tortonian–early Messinian) and having diverged from its sister group, *Alpinobombus*, 13–14 Ma. Obviously, these dates must be considered with scepticism given the presence of *B. randeckensis* 10 Ma earlier than crown-group *Bombus* s.s. and at least 2–3 Ma earlier than the *Bombus* s.s.–*Alpinobombus* divergence. Naturally, if *B. randeckensis* was sister to the remainder of the subgenus (*i.e.* if the living species of *Bombus* s.s. form a monophylum), then this conflict in terms of ages can be partially explained by noting that the Randeck Maar fossil was a stem group to the subgenus *Bombus*. Alternatively, if *B. randeckensis* was more closely related to one or more of the putatively primitive

species (e.g. *B. sporadicus*, *B. jacobsoni* or *B. tunicatus*), and thereby placed in the crown group, then the age of this clade would have to be pushed back considerably. By considering *B. randeckensis* as close to *Bombus* s.s., regardless of whether it should be placed in a stem group or in the crown group, the purported age of divergence between *Bombus* s.s. and *Alpinobombus* must be pushed back to earlier than 16–18 Ma. A phylogenetic analysis of the species of *Bombus* s.s., including *B. randeckensis*, based on morphometric data of the forewings is not possible at the moment because cladistic methods including (geometric) morphometrics data are still in the beginning of their development (e.g. Catalano *et al.*, 2010; Goloboff & Catalano, 2011; Clouse *et al.*, 2011). When such methods are developed further, they will almost certainly permit a more rigorous phylogenetic placement for the Randeck Maar bumble bee as well as an elaboration on the aforementioned hypotheses regarding possible dates for the clades, among others.

The Randeck Maar fauna and flora lived in an environment similar to the tropical areas of Southeast Asia (Wang, 1961; Wolfe, 1979) or even Florida in USA (Braun, 1950). If *B. randeckensis* was a stem group to *Bombus* s.s., then it highlights either a unique habitat shift for this extinct species, or a dramatically different ecological niche primitively for the subgenus. Given that most *Alpinobombus* – the sister group to *Bombus* s.s. – share the colder temperate ecology of their extant sisters, it seems more likely that *B. randeckensis* simply reflects a deviation from the norm otherwise characteristic for the combined clade. Certainly many bumble bees can be quite broad in their ecological tolerances. A classic example of this is *B. terrestris* which is found natively from Fennoscandia to Morocco (Rasmont *et al.*, 2008). However, within *Bombus* s.s. such species are more derived while the putatively basal recent species are more restricted ecologically, much like *Alpinobombus*.

It is hoped that additional and more complete material of *B. randeckensis* will be discovered. Nonetheless, we believe that the techniques employed for this particular fossil will prove invaluable for the critical evaluation of additional fossil *Bombus* as well as other bees, and might spur a modern reappraisal of the described species elaborated in Table 1.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2012.00642.x

Table S1. List of bombyine, centridine and anthophorine bee species sampled for higher-level (i.e. above *Bombus* s.s.) geometric morphometric analyses. Numbers of individuals sampled listed alongside names.

Table S2. Specimen assignment using the “Leave-One-Out” procedure in the LDA of wing shape. Original groups are along the rows, predicted groups are along the columns. The hit ratio (HR%) is also given for each species.

Table S3. Mahalanobis distances (MD) between centroids in the discriminant space. The MD distances between the Randeck Maar (RM) fossil and *Paleohabropoda oudardi* and the centroids are also shown. Based on MD, the RM fossil is assigned to the subgenus *Bombus* s.s. (closest centroid), while *Paleohabropoda oudardi* is assigned to the genus *Habropoda*.

Table S4. Mahalanobis distances (MD):(i) between the Randeck Maar (RM) fossil and the *Bombus* subgenus centroid (Centr.); (ii) between *Bombus* subgenus centroids and consubgeneric specimens, (iii) among consubgeneric specimens, and (iv) between *Bombus* subgenus centroids and the non-consubgeneric specimens.

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