

Subgeneric classification and biology of the leafcutter and dauber bees (genus *Megachile* Latreille) of the western Palearctic (Hymenoptera, Apoidea, Megachilidae)

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Abstract

A new identification key is presented for the western Palearctic subgenera of the bee genus *Megachile*. In addition, the species composition of each subgenus is discussed, and for large subgenera, species groups are delineated to facilitate future taxonomic treatment. The nesting biology and floral associations of each subgenus are briefly reviewed. Lectotypes are designated for *Megachile albocincta* Radoszkowski, *M. genalis* Morawitz, *M. hirsuta* Morawitz, *M. inornata* Walker, *M. luteipennis* Friese, *M. mandibularis* Morawitz, *M. melanogaster* Eversmann, *M. orientalis* Morawitz, *M. picicornis* Morawitz, *M. pilicrus* Morawitz, *M. sedilloti* Pérez, *M. thevestensis* Ferton, *M. vestita* Giraud (= *M. giraudi* Gerstäcker) and *M. villipes* Morawitz. In addition, the following taxonomic changes are proposed: the subgenus *Paracella* is synonymized with the subgenus *Anodontetricharaea* (**syn. n.**); three species, *Megachile breviceps* Friese, *M. luteipennis* and *M. algira* Radoszkowski are excluded from the Palearctic fauna as they were likely based on mislabeled specimens; *M. luteipennis* is newly placed in synonymy with *M. dimidiata* Smith (**syn. n.**), and *M. algira* with *M. opposita* Smith (**syn. n.**); *M. punctatissima* Spinola is considered an incorrect spelling of *Stelis punctulatissima* (Kirby) and not a valid species-group name. *Heriades sinuata* Spinola is newly placed in synonymy with *H. truncorum* (Linnaeus) (**syn. n.**); *M. boops* Friese is transferred to the genus *Hoplitis* (**comb. n.**) and placed in synonymy with *Hoplitis tigrina* (Morawitz) (**syn. n.**); *M. pyrsa* Vachal is transferred to the genus *Prodoxys* (**comb. n.**) and placed in synonymy with *Prodoxys carnea* (Gribodo) (**syn. n.**); *Stelis megachiloides* Alfken is transferred to the genus *Megachile* (**comb. n.**) and placed

in synonymy with *M. marginata* Smith (**syn. n.**); *M. larochei* Tkalčú and *M. lanigera* Alfken are placed in synonymy with *M. albobirta* (Brullé), *M. albocincta* Radoszkowski with *cyanipennis* Guérin-Ménéville, *M. rhodosiaca* Rebmann and *M. heinrichi* (Tkalčú) with *M. doriae* Magretti, *M. vicina* Morawitz with *M. giraudi*, *M. picicornis* Morawitz and *M. albocincta* Pérez with *M. marginata*, *M. essenensis* (Pasteels) with *M. maxillosa* Guérin-Ménéville, *M. sexmaculata* Alfken, *M. sexmaculata thracia* Tkalčú and *M. pilicrus flavida* Zanden with *M. melanogaster*, *M. transitoria* Benoist with *M. parietina* (Geoffroy), *M. judaea* (Tkalčú) with *M. pasteelsi* (Zanden), *M. cyrenaica* Schulthess, *M. fumosa* Alfken and *M. fulvocrinita* Alfken with *M. sedilloti*, *M. insignis* Zanden with *M. soikai* Benoist, *M. mavromoustakisi* Zanden with *M. troodica* Mavromoustakis and *M. semiplea* Cockerell with *M. versicolor* Smith (**syn. n.**). *Megachile rhodoleucura* Cockerell is reestablished as a valid species (**stat. rev.**). *Megachile posti* Mavromoustakis is considered as a valid species (**stat. n.**) and not as a subspecies of *M. basilaris* Morawitz. *Megachile calloleuca* Cockerell is newly placed into the subgenus *Megachile*, *M. inornata*, *M. thevestensis*, *M. troodica* into the subgenus *Anodontetricharaea*, and *M. hirsuta*, *M. pasteelsi* into the subgenus *Chalicodoma*.

Keywords

Megachile, classification, nesting biology, oligolecty, solitary bees

Introduction

The bee genus *Megachile* Latreille, 1802 accounts for a significant proportion of most bee faunas (Michener 2007). In its current delineation, this genus includes more than 1400 species (Ascher and Pickering 2016) in 55 subgenera (Michener 2007, Trunz et al. 2016, and references therein). These subgenera are distributed in two groups based on nesting biology: the leafcutter species (or group 1 subgenera), which cut leaf discs to line their brood cells; and the dauber bees (or group 2 subgenera), which use resin or mud to build their cells (Michener 2007, Trunz et al. 2016). The subgenus *Creightonella* Cockerell, 1908, the lone member of a third group according to Michener (2007), is considered to be a member of group 1 (Trunz et al. 2016). The dauber bees have sometimes been placed in a separate genus, *Chalicodoma* Lepelletier, 1841 (e.g. Michener 1965, Pasteels 1965, Tkalčú 1969); Trunz et al. (2016) recently showed that the dauber lineages constitute a paraphyletic assemblage from which the leafcutters evolved, and the separation of the dauber bees into one (*Chalicodoma*) or a few well-delineated, monophyletic genera did not appear practical. Consequently, Trunz et al. (2016) advocated the use of a classification close to Michener's generic classification, with a large genus *Megachile* that includes both leafcutter and dauber lineages with the exception of three comparatively small tropical groups segregated as separate genera: *Gronoceras* Cockerell, 1907, *Heriadopsis* Cockerell, 1931 and *Matangapis* Baker & Engel, 2006 (Trunz et al. 2016). This classification is adopted here, placing all Palearctic species into one large genus *Megachile* that includes, among others, *Chalicodoma*, *Creightonella* and *Pseudomegachile* Friese, 1898 as subgenera. With respect to the Palearctic fauna, the following further changes were also made to Michener's classification by Trunz et al. (2016): the subgenus *Parachalicodoma* Pasteels, 1966 was merged with the subgenus *Pseudomegachile*; its species are considered here to form a species

group of *Pseudomegachile*, referred to as the *incana* group; *Eumegachile* Friese, 1899 (with only one species, *Megachile bombycina* Radoszkowski, 1874) was merged into the subgenus *Megachile*; *Eurymella* Pasteels, 1965 was recognized as a valid subgenus of the genus *Megachile* and not as a synonym of *Eutricharaea* Thomson, 1872. Lastly, the morphologically unusual species *M. giraudi* Gerstäcker, 1869, placed alternately in the subgenera *Eutricharaea* (e.g. Tkalců 1974) and *Xanthosarus* Robertson, 1903 (e.g. Özbek and Zanden 1994, Ornos et al. 2007) is included here in *Eutricharaea* based on its phylogenetic position (Trunz et al. 2016). All these classificatory changes were based on highly supported topologies (100% bootstrap support in all maximum likelihood analyses) and are adopted here. Trunz et al. (2016) further considered *Anodonteutricharaea* Tkalců, 1993 and *Paracella* Michener, 1997 to be synonymous. *Paracella* was first described in 1965 (Pasteels 1965), although this description is not valid because no type species was designated. Michener (1997) used the same name to reestablish the subgenus. Consequently *Anodonteutricharaea* has priority and *Paracella* is placed here as a synonym of *Anodonteutricharaea* (syn. n.), and not the other way around as suggested by Trunz et al. (2016).

Palearctic leafcutter and dauber bees have not been recently revised, with the exception of the central European species for which identification keys are available (e.g., Benoist 1940, Dorn and Weber 1988, Banaszak and Romasenko 2001, Amiet et al. 2004, Scheuchl 2006). At the European scale no revision exists except that of Friese (1911); according to Nieto et al. (2014), 81 species are present in Europe but the taxonomic status of approximately a quarter of them remains in doubt. Most subgenera are in urgent need of revision in the Palearctic, and these taxonomic revisions are hampered by the uncertain subgeneric placement of several Palearctic species. Moreover, no practical key to the subgenera exists (see comments on the key in Michener 2007: 565) and the classificatory changes mentioned above need to be implemented in identification keys.

As a first step towards a better taxonomic treatment of this important group of bees, a new key to the western Palearctic subgenera is proposed here; when needed, I delineate species groups within large subgenera. For some subgenera, I briefly comment on the species composition and highlight taxonomic problems associated with some species. For large subgenera such as *Eutricharaea*, the number of unpublished synonymies is so large that presenting a list of species, even tentative, does not seem appropriate at this point. I also verify and change if necessary the subgeneric placement of each of the western Palearctic species (Ascher and Pickering 2016, Kuhlmann et al. 2016), based on the examination of the type material of most species. A few lectotypes are designated, mostly when the identity of the species is currently unclear, and a few new synonymies are also proposed to avoid using names that will be placed in synonymy in the near future. I decided not to give distribution data for each species; such data will be presented in the online Checklist of the Western Palearctic Bees (Kuhlmann et al. 2016) and on the Discover Life website (Ascher and Pickering 2016). Last but not least, what is known about the nesting biology and floral associations of each subgenus is summarized.

Materials and methods

Terminology and abbreviations

Terminology follows Michener (2007). In the key, the morphological characters are given in order of importance, with the most distinctive characters first. For simplicity, metasomal terga and sterna are commonly abbreviated as T and S, respectively, when they are numbered (e.g., T1 for metasomal tergum 1, S1 for metasomal sternum 1). When part of the integument is orange or red, I simply mention that the particular body part is orange or red; thus “front basitarsus yellowish-white” or “mandible orange” means that the cuticula of these body parts is yellowish-white or orange. For convenience I often refer to a subgenus simply with its subgeneric name [e.g. *Eutricharaea* and not *Megachile* (*Eutricharaea*)]; thus throughout the manuscript, *Chalicodoma* refers to the subgenus *Chalicodoma* and not to the genus *Chalicodoma* of some authors; when the subgenus *Megachile* is meant, *Megachile s. str* is used.

Collections studied with abbreviations

BMNH	Natural History Museum, London, UK
CSE	Private collection of Christian Schmid-Egger, Berlin, Germany
DAAN	Department of Agriculture, Ministry of Agriculture and Natural Resources, Nicosia, Cyprus
ETHZ	Eidgenössische Technische Hochschule, Entomologische Sammlung, Zürich, Switzerland
ISZP	Polish Academy of Sciences, Institute of Systematic Zoology, Krakow, Poland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MSCA	Maximilian Schwarz Collection, Ansfelden, Austria
NMPC	National Museum (Natural History), Prague, Czech Republic
NMW	Naturhistorisches Museum, Wien, Austria
OLML	Oberösterreichisches Landesmuseum, Linz, Austria
OUMNH	University Museum of Natural History, Oxford, UK
RMNH	Nationaal Natuurhistorisch Museum Naturalis, Leiden, Holland
SEMC	University of Kansas, Snow Entomological Museum, Lawrence, USA
SMFD	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
ZIN	Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia
ZMHB	Museum für Naturkunde, Berlin, Germany

Geographic coverage of the key

The keys presented by Michener (2007) for the Palearctic subgenera of *Megachile* cover both the Palearctic and Oriental regions. They are difficult to use for non-specialists as they rely on few characters; moreover, several Palearctic species do not run properly through the key. For this reason, the present key relies on numerous alternative characters; some of these characters will be useful in other geographic regions, while others will not. This key covers all species known to me from the western Palearctic region. It also covers the faunas of Iran, central Asia and Siberia, which are essentially similar to the Western Palearctic fauna, but will progressively become less practical towards the Oriental zone (e.g. in Pakistan or in the Himalayas). It will not be useful in India, China and Japan: other, distinctive subgenera occur there (e.g., *Aethomegachile* Engel & Baker, 2006, *Chelostomoda* Michener, 1962 and *Megella* Pasteels, 1965) while some distinct Palearctic groups do not (e.g., the *incana* group of *Pseudomegachile*, or the *montenegrensis* group of *Chalicodoma*). Moreover Oriental members of some subgenera (notably *Anodontetricharaea* or *Pseudomegachile*) are distinct from the Palearctic species and will not run properly through the present key.

As mentioned above, the key covers the northern parts of the Arabian Peninsula (Saudi Arabia north of Jeddah) as well as the United Arab Emirates but not the southern part (Yemen, Oman, southern parts of Saudi Arabia). The fauna of the southern part of the Arabian Peninsula is poorly known and rather distinct from the Palearctic fauna: temperate subgenera such as *Xanthosarus* or *Megachile s. str.* do not appear to occur there, while several taxa with Afrotropical affinities are found (e.g., *Amegachile* Friese, 1909, the *eurimera* group of *Eurymella*; and *Stenomegachile* Pasteels, 1965). These three lineages are not included in the key but are briefly described below; their inclusion would render this key less practical for the vast majority of its users.

Delineation of species groups within large subgenera

Informal “species groups” are particularly convenient for referring to groups of presumably related taxa sharing distinctive morphological features; such informal groups are not regulated by the code of zoological nomenclature and do not have to be monophyletic. Furthermore, it does not matter if the recognition of such groups renders the rest of the subgenus paraphyletic. I use species groups to facilitate the taxonomic treatment of large, diverse subgenera. Such subgenera typically appear in different couplets of the key and I find it useful to have a name to refer to these groups. Often, such groups have been given subgeneric rank in the past, for example “*Neoeutrigharaea* Rebmann, 1967”. This group could be referred to as the *Neoeutrigharaea* group of *Eutrigharaea*. I prefer to refer to this group as the *rotundata* group of *Eutrigharaea*, as most people will be familiar with species names and not necessarily with subgenus names. For clarity, I list existing but not currently valid, subgeneric names for each species group.

Results

Taxa excluded from the Palearctic fauna or from the genus *Megachile*

The following three species descriptions were likely based on mislabeled specimens. First, *Megachile breviceps* Friese, 1898, described from a single specimen putatively collected in Spain and preserved in ZMHB, does not appear to belong to any known Palearctic taxon. Pasteels (1966) noted the peculiar morphology of *M. breviceps* and tentatively placed it into the subgenus *Callomegachile* Michener, 1962 due to its similarity to the *disjuncta* group of species. I consider *M. breviceps* as a member of *Callomegachile* with unclear geographic origin; its vestiture pattern (vestiture grey on head and mesosoma, orange-brown on metasoma) is reminiscent of some Australian taxa. In the same article *Megachile luteipennis* Friese, 1898 is described, supposedly from Algeria. A female preserved in ZMHB is designated here as a lectotype; it is labeled as follows: 1. “Algeria 1890”; 2. “*Megachile luteipennis* det. Friese 1897”; 3. “Lectotype *Megachile luteipennis* des. Zanden 1992”; this designation has not been published and is accepted here. Both the original description and the lectotype agree perfectly with the Oriental species *M. (Lophanthedon) dimidiata* Smith, 1853. I place *M. luteipennis* as a junior synonym of *M. dimidiata* (syn. n.) and consider its type locality to be an error. Lastly, several syntypes of *Megachile algira* Radoszkowski, 1874, supposedly from Algeria, are preserved in different institutions (ZMHB, ISZP, as well as BMNH according to Baker 2004). I have examined three syntypes (ZMHB and ISZP), which agree with Radoszkowski’s original description. As noted by Baker (2004: 240), *M. algira* is not a Palearctic species but probably originates from Java; Baker (2004) further writes under *M. algira* “= *Chalicodoma (Callomegachile) florale oppositum* (Sm. 1853)”. *M. floralis* (Fabricius, 1804) and *M. opposita* Smith, 1853 were considered as two distinct species by Gonzalez and Engel (2012) and I place *M. algira* as a junior synonym of *M. opposita* (syn. n). Note that *M. opposita* is not a member of *Callomegachile* but is considered here to be a member of the *semivestita* group of *Pseudomegachile* (*Largella* Pasteels, 1965).

The type of *Megachile boops* Friese, 1921, described from “Jaribaschi im Amanusgebirge” (Nur Mountains, Hatay Province, Turkey) could not be located in ZMHB or SMFD. The description does not match any known species of the genus *Megachile* but points to *Hoplitis (Megahoplitis) tigrina* (Morawitz, 1872). John Ascher and Eli Wyman (pers. comm., July 2014) located a specimen of *H. tigrina* (det. John Ascher) identified as *M. boops* by Friese, labeled “Amanusgeb., Jaribasch” (AMNH). Given that the original description mentions only one specimen, this specimen is probably the holotype of *M. boops*, which is here placed as a junior synonym of *Hoplitis tigrina* (syn. n). Similarly, the description of *Megachile pyrsea* Vachal, 1910, of which I was unable to locate the type, does not appear to match any existing species of the genus *Megachile*; rather, several features point to a Dioxyine bee: absence of pulvillus, first submarginal cell larger than second, T6 with apical margin simple (thus without preapical carina), T7 small, hidden under T6. Based on the original description, in

particular the color of the integument, Maximilian Schwarz (pers. comm., May 2014) suggests placing *M. pyrsa* as a junior synonym of *Prodiioxys carnea* (Gribodo, 1894), which I formally do here (syn. n.). *Megachile punctatissima* Spinola, 1806 has been mentioned as a valid species of the genus *Megachile* (e.g. Nieto et al. 2014, Ascher and Pickering 2016). The entry in Spinola (1806: 135) under *M. punctatissima* is “3. MEGACHILE PUNCTATISSIMA. Latr. hist. des. inst. [SIC] 14. p. 54. n. 5” and was not meant as a species description. “*M. punctatissima* Latreille” is likely an incorrect spelling of “*Apis punctulatissima* Kirby, 1802, [= *Stelis punctulatissima* (Kirby, 1802)]”, given that the entry in Latreille (1805) was “*Apis punctatissima*. Kirby, tab. 16, fig. 9”, thus precisely referring to Kirby’s species. Lastly, *Heriades pusilla* Spinola, 1808 and *Heriades sinuata* Spinola, 1808 have been included in the genus *Megachile* (Schletterer 1889, Ungricht et al. 2008); based on their original descriptions (no existing syntype is known: Casolari and Casolari-Moreno 1980) both are considered to belong to the Osmiini (see further details in Suppl. material 1). Based on its original description (axillae with spine) and especially on the account of its nesting biology (nests in *Rubus* stems, partitions made of masticated leaf material), *H. pusilla* likely refers to a species of the genus *Osmia* Panzer, 1806 subgenus *Hoplosmia* Thomson, 1872. *Heriades pusilla* is probably best placed in synonymy with *Osmia* (*Hoplosmia*) *ligurica* Morawitz, 1868 and treated as a *nomen oblitum*; however I do not formally transfer this species into *Osmia* for now as this would create a homonymy with the valid species *Osmia pusilla* Cresson, 1864. To resolve this case study of the Spinola collection and the designation of a lectotype or neotype appear to be necessary. The original description of the male of *H. sinuata* precisely refers to a species of *Heriades* (see details in Suppl. material 1; the identity of the female is unclear and may refer to either *Hoplosmia* or *Heriades*). Spinola apparently did not know the male of *Heriades truncorum* (Linnaeus, 1758): the entry in Spinola (1806) under “*Megachile truncorum*” was “Mas. [male]- *Megachile campanularum* Latr.”. Consequently *H. sinuata* is placed as a junior synonym of *H. truncorum* (syn. n.).

New lectotype designations

A likely syntype of *Megachile inornata* Walker, 1871 could be located and examined (BMNH), a female labeled as follows: 1. “Garden around Mt Sinai [printed]”; 2. “F. Sm. Coll. 79 22”; 3. “*Megachile* sp f: ex Lord Colln and possibly a syntype of *inornata* Walker 1871: 48” [handwritten by D. Baker]; 4. “Lectotype *Megachile inornata* des. C. Praz 2015”. This specimen agrees with Walker’s short original description of the female; the species is valid and newly placed into the subgenus *Anodontetricharaea*. A lectotype is also designated for *Megachile mandibularis* Morawitz, 1875 (ZIN); it is a male in good condition bearing the following labels: 1. “14” [printed]; 2. “ЗАРВИШ. ДОЛ” [abbreviation for the Zeravshan Valley; both localities given in the original description are in present-day Uzbekistan according to Appendix B of Baker (2004)]; 3. “*Megachile mandibularis* F. Morawitz”; 4. “Lectotype *Megachile mandibularis* des. C. Praz 2015”.

A lectotype is also designated for *Megachile villipes* Morawitz, 1875 (ZIN); it is a well-preserved male labeled as follows: 1. “КИЗИЛЬ КУМ” [Kyzylkum (Desert); localities in the original description are in present-day Kazakhstan according to Appendix B of Baker (2004)]; 2. “*villipes* F. Morawitz”; 3. “Syntypus”. 4. “Lectotype *M. villipes* des Tkalců”. This designation has not been published and it is accepted here. As suggested by Tkalců (1993), both *M. mandibularis* and *M. villipes* are valid species of the subgenus *Anodontetricharaea*. A lectotype is designated for *Megachile thevestensis* Ferton, 1908, a well-preserved female labeled as follows: 1. “voisine de *flabellipes* nouvelle? *thevestensis*” [handwritten by Ferton: “near *flabellipes*, new?” The word “*thevestensis*”, written vertically, was probably added later by Ferton]; 2. “Tebessa 12/7 06 n sp?” [Tébessa, Algeria, 12 July 1906]; 3. “Mus. Paris Coll. Ferton”; 4. “Lectotype *Megachile thevestensis* des. C. Praz 2016”. *M. thevestensis* is newly placed here into the subgenus *Anodontetricharaea*. A lectotype is designated for *Megachile hirsuta* Morawitz, 1893, a male from “Masar-Boschara” bearing the additional label “Lectotype *Megachile hirsuta* des. B. Tkalců”; this designation is not published and is accepted here. The type locality cannot be located with precision, although it is in the “Sarawschan” region (Zeravshan valley) according to Becker (1917: 399); a locality named “Mazar” appears on old maps some 30 km westwards of the Zeravshan glacier in Tadjikistan. Given that *M. hirsuta* is a high-altitude species throughout its range, the lectotype was probably collected in the upper Zeravshan valley in the Sughd Region of Tadjikistan. *M. hirsuta* is newly placed into the subgenus *Chalicodoma*. A lectotype is also designated for *Megachile melanogaster* Eversmann, 1852 (ISZP), a well preserved female labeled as follows: 1. “*melanogaster* mihi”; 2. [a rounded, gold label]; 3. “Orenburg” [printed on pink label; Orenburg Region, Russia]; 4. “Lectotype *Megachile melanogaster* des. C. Praz 2013”. A lectotype is designated for *Megachile picicornis* Morawitz, 1877, a well-preserved female labeled as follows: 1. “Kurgulutschaiskaja” [handwritten, black ink; in present-day Azerbaijan according to Astafurova and Pesenko 2006: 78]; 2. “*picicornis* Mor. Type”; 3. “Lectotype *Megachile picicornis* des. C. Praz 2015”. A conspecific male from the same locality is designated as a paralectotype (des. C. Praz 2015). The original description of *Megachile orientalis* Morawitz, 1895 suggests that the female and male were not conspecific. The study of two syntypes (ZIN) confirms that the female is a *Eutricharaea* while the male belongs to the subgenus *Pseudomegachile*. I designate here the female specimen as the lectotype; it is a well-preserved specimen labeled as follows: 1. “Copet. D.” [Kopet Dag, or Turkmen-Khorasan Mountain Range, Turkmenistan and Iran]; 2. “Nerduali (...)” [date not readable. I could not find this locality on maps; Volkovitsh and Kalashian (2002) cited it as the “Nerduali River” in the Khorasan Province, Iran]; 3. “*Megachile orientalis* f F. Moraw.”; 4. “Lectotype *Megachile orientalis* des. C. Praz 2016” (ZIN). A lectotype is further designated here for *Megachile sedilloti* Pérez, 1895, a female from “Kairouan v. 1884” [Kairouan, Tunisia, May 1884] bearing the following label: “Lectotype *Megachile sedilloti* des. Baker 1990”; this designation has not been published and is accepted here. A further female from the same locality is designated as a paralectotype (it bears a label “Paralectotype *M. sedilloti* des Baker 1990”). A lectotype (MNHN) is also designated for *Megachile vestita* Giraud, 1863 (not *vestita* Smith

1853; the name *Megachile giraudi* has been proposed as a replacement name), a female labeled as follows: 1. “Suse [Susa, Italy]”; 2. “Lectotype *Megachile vestita* Giraud des. C. Praz 2010”. Three further females (two from “Suse” and one from “Vall.”, likely Vallouise, France) are designated as paralectotypes (des. C. Praz 2010). As indicated by Benoist (1940), the male described by Giraud (preserved in MNHN) is not conspecific. A well-preserved female originating from Egypt is designated as a lectotype for *Megachile albocincta* Radoszkowski, 1874; it bears the following label “Lectotype *Megachile albocincta* des. C. Praz 2013” (ISZP); an additional female (ISZP) is designated as a paralectotype. Lastly, lectotypes are designated for *Megachile genalis* Morawitz, 1880: a well-preserved female (both antennae are partly broken) labeled as follows: 1. [rounded, silver disc]; 2. “114506”. 3. “*genalis* Mor.”. 4. “Syntypus”. 5. “Mor. 1880: 380 Tjan Shan (...)” [Tian Shan Mountains; according to the original description, which mentions “Im Tjan-Shan auf dem Plateau des kleinen Juldus”, this is likely the Yulduz Valley, Xinjian autonomous region, China]. 6. “Lectotype *Megachile genalis* des. C. Praz 2015” (ZIN); and for *Megachile pilicrus* Morawitz, 1877: a well-preserved female labeled as follows: 1. “Borshom Siewers” [Borjomi, Georgia; leg. G. Sievers]; 2. “Lectotype *Megachile pilicrus* des. C. Praz 2015” (ZIN).

New synonymies, new taxonomic status and new subgeneric placement

The following new synonymies are proposed based on the examination of the type material, or if the type material could not be obtained or examined, on the original descriptions. Rationale and details on each of these synonymies are given in Suppl. material 1. *Megachile larochei* Tkalců, 1993 and *M. lanigera* Alfken, 1933 are placed in synonymy with *M. albohirta* (Brullé, 1839) (syn. n), which is newly placed into the subgenus *Anodontetricharaea*. *Megachile mavromoustakisi* Zanden, 1992 is placed in synonymy with *M. troodica* Mavromoustakis, 1953 (syn. n), which is newly placed into the subgenus *Anodontetricharaea*. *Megachile judaea* (Tkalců, 1999) is considered as a junior synonym of *Chalicodoma pasteelsi* Zanden, 1998 (syn. n), which is newly placed into the subgenus *Chalicodoma*. *Megachile transitoria* Benoist, 1934, of which the type appears to be lost (MNHN), is considered to have been based on an intersex specimen of *M. parietina* (Geoffroy, 1785) and is placed in synonymy with that species (syn. n). *Megachile rhodosiaca* Rebmann, 1972 and *M. heinrichi* (Tkalců, 1979) are placed in synonymy with *M. doriae* Magretti, 1890 (syn. n). *Megachile picicornis* and *M. albocincta* Pérez, 1879 (not *M. albocincta* Radoszkowski, 1874; *M. perezii* Mocsáry, 1887 and *M. provincialis* Pérez, 1890 are replacement names) are placed in synonymy with *M. marginata* Smith, 1853 (syn. n) (the holotype of *M. marginata* is in OUMNH); the holotype (NMPC) and paratype (ZMHB) of *Stelis megachiloides* Alfken, 1942 are likely intersex specimens of *M. marginata*, and this species is transferred into the genus *Megachile* (comb. n.) and placed in synonymy with *M. marginata* (syn. n.). *Megachile sexmaculata* Alfken, 1942, *M. sexmaculata thracia* Tkalců, 1979 and *M. (Megachile) pilicrus flavida* Zanden, 1998, are placed in synonymy with *M. melanogaster* (syn. n).

Megachile cyrenaica Schulthess, 1924, *M. fumosa* Alfken, 1934 and *M. fulvocrinita* Alfken, 1934 are placed in synonymy with *M. sedilloti* (syn. n). *Megachile insignis* Zanden, 1996 is placed in synonymy with *M. soikai* Benoist, 1961 (syn. n), and *M. vicina* Morawitz, 1894 [not *M. vicina* Mocsáry, 1879; *Chalicodoma* (*Pseudomegachile*) *atropyga* Zanden, 1995 was suggested as a replacement name] is placed as a junior synonym of *M. giraudi*. *Megachile semipleta* Cockerell, 1921 is placed in synonymy with *M. versicolor* Smith, 1844. *Megachile albocincta* Radoszkowski, 1874 is placed in synonymy with *M. cyanipennis* Guérin-Ménéville, 1845.

The subgeneric placement of *Megachile rhodoleucura* Cockerell, 1937, described from Zimbabwe and known only in the female sex has varied; Pasteels (1965) placed it in *Pseudomegachile*, while Eardley (2013) recently placed it in synonymy with *M. (Euryrmella) eurimera* Smith, 1853. I examined the holotype of *M. rhodoleucura* (BMNH) and confirm that it is a member of *Pseudomegachile*, distinct from *M. eurimera* and thus *M. rhodoleucura* is reestablished as a valid species here (stat. rev.). The holotype female is sculpturally identical with *Megachile riyadhensis* (Alqarni, Hannan, Gonzalez and Engel, 2012) and both species may well be conspecific as they only differ in the coloration of the metasomal vestiture (it is fulvous in *M. rhodoleucura* and snow white in *M. riyadhensis*). I do not formally place *M. riyadhensis* as a synonym of *M. rhodoleucura* as the male of the latter is unknown; however given that many African *Megachile* reach the Arabian Peninsula I consider likely that both taxa are conspecific. *Megachile calloleuca* Cockerell, 1931 is newly placed into the subgenus *Megachile* based on the examination of the holotype (BMNH). Lastly, the examination of paratypes of *Megachile basilaris posti* Mavromoustakis, 1952 (MSCA) and of a syntype of *M. basilaris* Morawitz, 1875 (ZIN) indicates that both are not conspecific and *M. posti* is considered as a valid species (stat. n.).

Notes on important morphological characters

Females: Detailed descriptions of important morphological characters can be found elsewhere (Pasteels 1965, Mitchell 1980, Michener 2007) and only a few new or particularly important characters are presented here. The subgenera have mostly been defined on the base of female mandibular characters, especially the conformation of the teeth along the apical margin of the mandible (Michener 2007). Following Michener (2007), the mandibular teeth are numbered from apical-most, or “lowest” tooth (tooth 1), to basal-most, or “upper” tooth (Fig. 1). Often, determining the precise number of teeth is difficult; the upper tooth may be acute, truncate, or more or less divided into two teeth (as in Fig. 1), and even within a given subgenus a continuum may exist between these states. The concave space between teeth is named “interspace”; interspaces are also numbered from apical-most (or lowest) to basal-most (or upper) interspace (Fig. 1). Of central importance for the recognition of the leafcutter subgenera is the presence and location of cutting edges, blade-like edges that are located in the interspaces (Fig. 1). Cutting edges are entirely absent in dauber bees (or group 2 subgen-

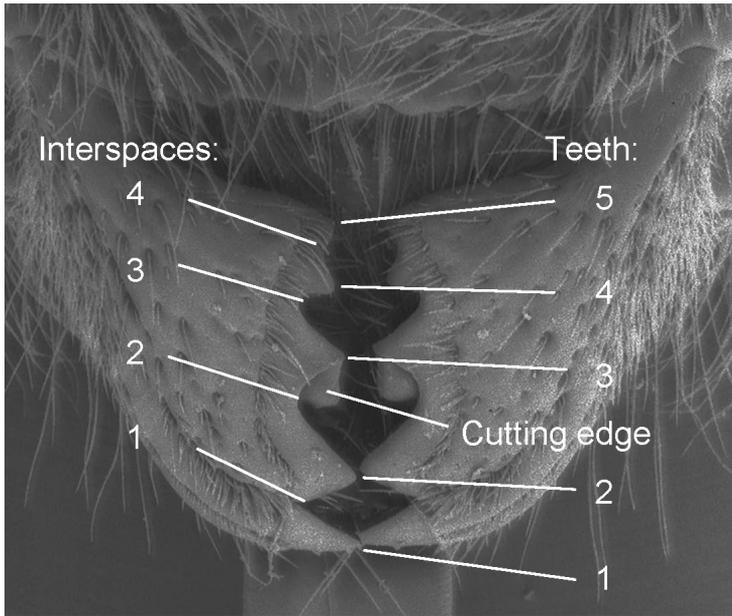
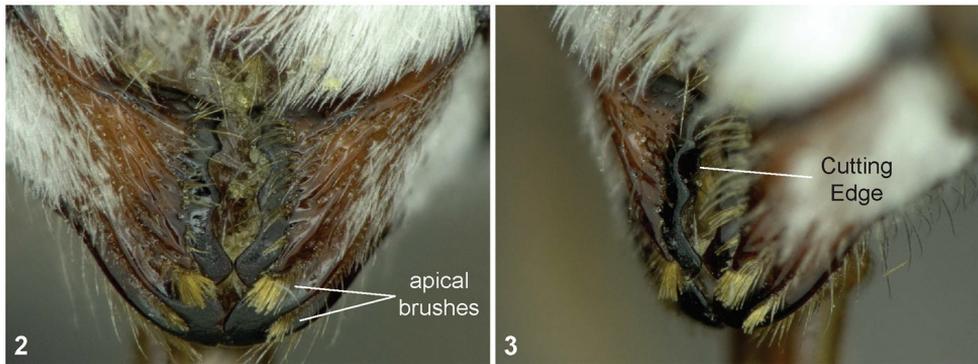


Figure 1. Female mandible of *Megachile (Megachile) centuncularis*; the white lines and the numbers indicate the five teeth (numbers on the right) and the four interspaces (numbers on the left); in this species, there is a partial cutting edge in the second interspace and, in front view, no visible cutting edge in the other interspaces. Picture by Andreas Müller (Müller et al. 1997).

era), and mostly present in the leafcutter subgenera (group 1 subgenera). Often, the cutting edges are partial (Fig. 1), thus not filling the entire length of the interspace; in addition, they may be recessed, partially hidden behind the margin of the mandible, and thus invisible or little visible in front view (Fig. 2). When determining whether a cutting edge is present or absent, it is therefore important to rotate the specimen so that the inner margin of the mandible can be seen in lateral view (Fig. 3). However, if a couplet of the key asks whether a cutting edge is visible or invisible *in front view*, such recessed cutting edges are considered invisible. Michener (2007) considered new world taxa such as *Megachile (Megachile) montivaga* Cresson, 1878 (see Sheffield et al. 2011: Fig. 26a), or the subgenus *Chryosarus* Mitchell, 1943 to lack cutting edges; here species with similar mandibular structure are considered to have cutting edges, although strongly recessed and invisible in front view.

For the separation of the different leafcutter subgenera of Africa, Pasteels (1965) put particular emphasis on the presence or absence of small brushes of orange hairs in the grooves located below and above the outer ridge near the base of tooth 1 in the female mandible (Fig. 2). Species with robust mandibles with tooth 1 particularly broad tend to have reduced brushes of hairs in these grooves, for example *Xanthosarus* and *Eurymella* (see Figs 35, 38, 40, below), while in species of the subgenera *Megachile s. str.*, *Anodonteutricharaea* and most *Eutricharaea*, the mandibular tooth 1 is less developed and these brushes are present (Fig. 2; see also Figs 30–33, 39, 41, below).



Figures 2–3. Female mandible of *Megachile (Eutricharaea) orientalis*. **2** Front view; the white lines indicate the brushes of hairs in the grooves near the base of tooth 1 **3** Lateral view; the cutting edge is continuous and spans the interspaces 2–4, although it is completely recessed behind the mandibular margin and thus not visible in front view.

Another useful character for the separation of the subgenera is the conformation of the two setae on the basal part of the claws (Pasteels 1965, Tkalců 1993), although this character has so far not been included in identification keys. In the key I refer to the setae of the claws of the hind legs, but the condition described is similar on all claws. In group 2 subgenera, the two setae are more or less similar in thickness; the length of the basal seta is equal to approximately a third of the length of the apical seta (Fig. 4); the condition is unclear in some *Callomegachile*. In most group 1 subgenera (*Eutricharaea*, *Megachile s. str.*, *Xanthosarus*), the basal seta is modified to a short, thick process (Fig. 5); this process is less than three times as long as its basal width and visibly thicker than the apical seta. *Eurymella* (Fig. 6) and especially *Anodonteutricharaea* (Fig. 7) are distinct among the leafcutter subgenera in that the basal seta is thin and of similar appearance to the apical seta, although considerably shorter; its length is more than four times its basal width. In *Creightonella*, only one long seta is present (presumably this seta corresponds to the apical seta of other subgenera). This character is not always easy to evaluate, and in old specimens the thin setae may be broken; however, in many cases I find it to be a useful character, especially for the recognition of *Anodonteutricharaea*.

Males: Michener's key (Michener 2007) to the males for the Palearctic and Oriental subgenera of *Megachile* is problematic because it largely relies on the presence or absence of hairs laterally on S8. Most group 2 subgenera have numerous hairs laterally on S8, while most group 1 subgenera lack such hairs (for exceptions see Michener 2007: 556–557). This morphological trait is not visible when the abdomen is in repose. The key presented here is based on alternative criteria and as a result it does not segregate the dauber from the leafcutter subgenera in a dichotomous way.

Many male *Megachile* bear numerous, conspicuous modifications of their legs; Wittmann and Blochstein (1995) have illustrated these structures and provided a detailed presentation of their possible functions during mating. These structures, which include among others the front coxal spine and the modified front tarsi, are



Figures 4–7. Claw of hind leg of females; the white lines show the basal seta; the seta is considered elongate in **4**, **6** and **7** and modified to a thick process in **5**. **4** *Megachile* (*Pseudomegachile*) *ericetorum* **5** *M.* (*Eutricharaea*) *deceptoria* **6** *M.* (*Eurymella*) *patellimana* **7** *M.* (*Anodonteutricharaea*) *thevestensis*.

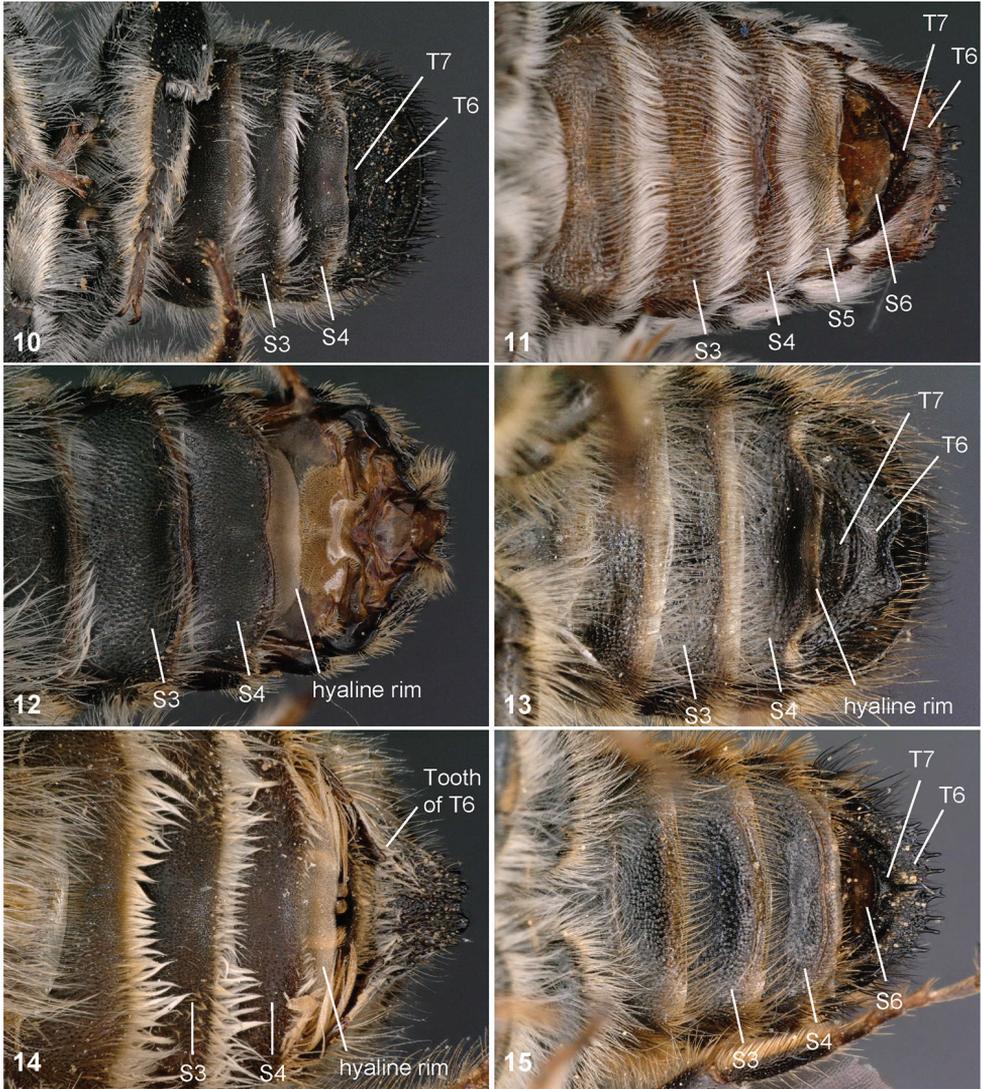
not presented in detail here (see Mitchell 1980, Wittmann and Blochstein 1995 and Michener 2007 for further details). In the present key to males, the first couplet is based on the presence or absence of a front coxal spine. In the vast majority of the Palearctic species, this character is unambiguous: the tooth is either entirely missing, or clearly present. In some species of the subgenus *Megachile* [e.g., *Megachile ligniseca* (Kirby, 1802)], the spine is considered absent in keeping with central European keys (Benoist 1940, Amiet et al. 2004, Scheuchl 2006) although the surface of the coxa is angulate. In *M.* (*Eutricharaea*) *soikai*, the condition is ambiguous because there is a minute tooth hidden in hairs. Pasteels (1965) considered similar species to have a front coxal tooth. I included *M. soikai* in the first alternative of couplet 1 (front coxa without tooth) because the tooth is nearly impossible to see unless the hairs are removed; however choosing the other alternative for this species would also lead to the correct subgenus. In a few other species [*M. lanata* (Fabricius, 1775), *M. villipes*] the tooth is small although much more developed than in *M. soikai*; such species are included in the second alternative (front coxa with tooth) because the tooth is conspicuous and bears a patch of modified, orange hairs that contrasts with the white hairs of the surface of the front coxa. Another, important diagnostic character is the



Figure 8–9. Inferior projection of male mandible. **8** *Megachile (Eutricharaea) leachella*, inferior projection pointed and projecting posteriorly **9** *M. (Creightonella) albisecta*, inferior projection rounded and directed ventrally.

inferior projection of the mandible (Figs 8–9), which may be present or absent; this projection is sometimes difficult to see, especially if the mandibles are closed; moreover, the projection is often heavily covered by dense vestiture, especially in group 2 subgenera. The shape of this projection is important: in group 1 subgenera (except, for the Palearctic fauna, in *Creightonella*) having such projection, the projection is pointed posteriorly and rests in repose along the gena (Fig. 8), whereas in those group 2 subgenera with inferior projection, as well as in *Creightonella*, the projection is truncate, rounded or quadrate and not pointed posteriorly (Fig. 9). The subgenera *Chalicodoma* and *Anodonteutricharaea*, as well as some species in the subgenera *Pseudomegachile* and *Megachile* lack this inferior projection and the inferior margin is straight, although sometimes swollen medially (e.g. *M. ericetorum* Lepelletier, 1841) or with dense vestiture (e.g. species of *Anodonteutricharaea*).

Lastly, other useful characters to separate the subgenera of Michener's group 1 are found on the metasomal sterna (Figs 10–15). S5 and S6 are commonly hidden in *Megachile* and often bear important diagnostic traits at the specific level; when hidden, these sterna are visibly less sclerotized, punctate and hairy than S4; in this case, the genital opening is closed in repose by the margin of S4 and the apical margin of either T6 or T7 (Fig. 10). In some groups, however, S5 and sometimes S6 are partly exposed and slightly less sclerotized than S4. In the subgenus *Creightonella*, the apical half of S5 is exposed and S6 forms a rounded, weakly sclerotized projection apically (Fig. 11); this projection of S6 covers the concave apical margin of T7 and closes the genital opening in repose. In the *incana* group of *Pseudomegachile*, S5 but not S6 is partly exposed in repose, and in most species of the *montenegrensis* group of *Chalicodoma* (Fig. 15), S6 forms a hyaline, rounded projection that covers the genital opening, approaching the condition found in *Creightonella*. Lastly, the structure of the apical margin of S4 is important to tell apart the subgenera of group 1: in *Anodonteutricharaea*, *Megachile s. str.*, *Amegachile* as well as most *Eurymella* (including the Palearctic species), the apical rim



Figures 10–15. Male metasoma, ventral view. **10** *Megachile (Eutricharaea) giraudi*, metasoma with four exposed sterna, S4 without hyaline rim, T7 small, unmodified **11** *M. (Creightonella) amabilis*, metasoma with six exposed sterna, S6 with rounded, weakly sclerotized projection **12** *M. (Anodonteutricharaea) sp. aff. inornata*, metasoma with four exposed sterna, S4 with apical, hyaline rim (note that S5–S8 are visible in this specimen because the metasoma has been stretched) **13** *M. (Megachile) ligniseca*, condition as in Fig. 12 **14** *M. (Eurymella) patellimana*, condition as in Fig. 12 **15** *M. (Chalicodoma) montenegrensis*, S6 partly exposed, with rounded, weakly sclerotized projection.

of S4 is slightly depressed, hyaline, glabrous and visibly less sclerotized than the disc of S4 (Figs 12–14). In *Eutricharaea*, the hyaline rim is entirely lacking, the apical margin is sclerotized (Fig. 10) and often covered by numerous hairs (not clearly so in Fig. 10).

Key to the Palearctic subgenera of *Megachile*

- 1 **Females:** scopa present, metasoma with 6 terga, antenna with 12 segments .. **2**
 – **Males:** scopa absent, metasoma with 7 terga (although T7 is often small and little visible, e.g. Fig. 10), antenna with 13 segments **11**
- 2 Mandible (Fig. 16) 5- or 6-toothed (upper teeth often small and little visible), apices of all teeth and interspace 2–4 similar in shape and gradually becoming smaller from tooth 1 upwards; interspace 2 with incomplete cutting edge well-visible in front view; interspaces 3 and sometimes 4 with a small, incomplete cutting edge little visible in front view; surface of mandible regularly convex, not forming two plane surfaces, with few ridges but numerous elongate punctures, covered by numerous hairs (Fig. 16). Vertex long, ocelloccipital distance mostly longer than interocular distance [subequal to interocular distance in *Megachile arabica*]. Hind basitarsus comparatively slender, length more than three times its maximal width (as in Fig. 26); claws of hind legs basally with only one elongate seta.....**Subgenus *Creightonella***
- Mandible not as above: tooth 1 often not larger than other teeth; or teeth or interspaces above tooth 1 of different shapes or not becoming gradually smaller (Figs 17–25, 32–41, although see Figs 2, 22); surface of mandible different, not covered by numerous hairs. Length of vertex and shape of hind basitarsus variable, but in forms with cutting edges, vertex shorter and hind basitarsus usually broad (Figs 28–29). Claws of hind legs basally with two setae (Figs 4, 6–7), although basal seta often modified to short, thickened process (Fig. 5) **3**
- 3 Mandible without cutting edges between the teeth (Figs 17–25). First submarginal cell longer than second. Metasoma more or less parallel-sided, tapering apically only beyond T4. Hind basitarsus comparatively slender, length more than three times (3.3–3.5 x) its maximal width (Fig. 26) [except in the *incana* group of *Pseudomegachile* (Fig. 27)]. Basal hair on claws of hind legs not conspicuously thickened, elongate, its length at least a third of the length of apical seta (Fig. 4) [character unclear in some *Callomegachile*]..... **4**
- Mandible with cutting edges in at least one interspace (Fig. 1), although cutting edges sometimes incomplete, not entirely filling the interspace, or recessed and partly hidden under margin of interspace so that they are not visible in front view (Figs 2–3). First submarginal cell subequal in length to second. Metasoma often triangular in dorsal view, its maximal width at level of T2 or T3, and then tapering apically. Hind basitarsus usually comparatively broad, its length less than three times (2.2–2.7) its maximal width (Figs 28–29) [except in a few species of the subgenus *Megachile* (see Scheuchl 2006: 111)]. Basal hair on claws of hind legs variable, mostly modified to a short, thickened process (Fig. 5) **7**
- 4 Large species, body length above 14 mm. Vestiture predominantly black except snow white on posterior parts of mesosoma and on T1 and T2. Clypeus

- very short, truncate apically, with truncation forming a nearly vertical, shiny surface (Fig. 17). Mandible elongate, more or less parallel-sided or narrowest preapically, with three blunt teeth (Fig. 17); mandibular ridges shiny, not dulled by microsculpturing (Fig. 17). Hypostomal area with a strong posterior tooth (Fig. 17). Ocelloccipital distance nearly twice the interocellar distance.....**Subgenus *Maximegachile***
- Body length variable. Vestiture different. Character combination not as above: clypeus modified or not; if modified, then mandible surface dulled by microsculpturing (Fig. 18). Hypostomal area without strong posterior tooth. Ocelloccipital distance variable **5**
- 5 Clypeus modified, with either a broad, vertical, shiny truncation (Fig. 18), or emarginate apically. Mandible with few shiny ridges, surface dulled by microsculpturing (Fig. 18). Preoccipital carina always present laterally
.....**Subgenus *Callomegachile***
- Clypeus with apical margin convex (Fig. 19) or straight (Figs 20–22, 24–25; although see also Fig. 23). Mandible surface variable, often with numerous shiny ridges. Preoccipital carina absent, or weak [e.g. in *M. foersteri*] **6**
- 6 Clypeus with apical margin convex and produced over base of labrum, denticulate or at least with 3–4 blunt, impunctate tubercles (Fig. 19). Mandible elongate (Fig. 19), with outer margin nearly straight and apical margin long, with tooth 3 very small or absent, thus with two apical teeth and a nearly straight margin above. Head little developed posteriorly, ocelloccipital distance usually shorter than interocellar distance, rarely subequal to interocellar distance [e.g. in *M. nasidens*]..... **subgenus *Chalicodoma***
- Clypeus with apical margin straight or weakly convex, usually not produced over base of labrum (Figs 20–25); if weakly crenulate and produced medially to small tubercle [*M. ericetorum* (Fig. 20)], then ocelloccipital distance much longer than interocellar distance; if apical margin sometimes convex and produced over base of labrum, or swollen medially (Fig. 22), then mandible not as above, less elongate, with outer margin regularly rounded and inner margin with four teeth or more (*incana* and *rhodoleucura* groups; Fig 22 and Fig. 4 in Alqarni et al. 2012). Mandible commonly less elongate, with outer margin rounded (Figs 24–25), although sometimes approaching the condition found in *Chalicodoma* [e. g., *M. ericetorum* (Fig. 20) or *M. lanata*]. Ocelloccipital distance shorter or longer than interocellar distance
.....**Subgenus *Pseudomegachile***
- 7 Basal hair on claws of all legs comparatively long, length more than 4 times its basal width, in appearance and color similar to apical hair, although shorter (Fig. 7). Mandible either 4-toothed with upper tooth broad and truncate, approaching the 5-toothed condition (Fig. 30) or 5-toothed (Fig. 31); mandible with a partial cutting edge in second interspace (Fig. 30) (cutting edge often small, recessed and difficult to see; Fig. 31), and either a strongly reduced cutting edge or no visible cutting edge in third interspace (Figs 30–31). Scopa usu-

- ally white to yellowish-white on S2-S4 [light orange in *M. albohirta*] and sterna without apical fasciae beneath the scopa.....**Subgenus *Anodonteutricharaea***
- Basal hair on claws of all legs modified to a thickened process, length at most 4 times its basal width (Fig. 5) [except in *Eurymella* (Fig. 6), which has a very different mandible (Fig. 38)]. Shape of mandible variable, with 4 or 5 teeth, position of the cutting edges variable. Color of scopa variable, but if scopa white or yellowish-white (as in most species of the subgenus *Eutricharaea*) then sterna usually with apical fasciae beneath the scopa.....**8**
- 8 Mandible in front view (Figs 1, 32–34) with a conspicuous, partial cutting edge in second interspace [little visible in *M. genalis*] and no visible cutting edge in third interspace (a partial, recessed cutting edge is present but not visible in front view). Mandible mostly with upper tooth subdivided in two teeth, thus 5-toothed (Figs 1, 32), although sometimes not clearly so (Fig. 33) [except 4-toothed in *M. bombycina* (Fig. 34)]. Clypeus usually without median, impunctate line; apical half flat or slightly concave in lateral view, with punctuation sparse and with shiny interspaces up to 2–3 punctures wide (Fig. 32) [except in *M. lapponica*, with clypeus densely punctured (Fig. 33), and in *M. bombycina*, with clypeus modified (Fig. 34)]. Scopa mostly orange-red at least basally, rarely white; sterna without apical fasciae beneath scopa.....**Subgenus *Megachile***
- Mandible not as above, either with a complete cutting edge in third interspace (Fig. 35); or all cutting edges recessed and invisible in front view (Figs 2, 36, 39); mandible 4- or 5-toothed. Clypeus different, either densely punctured or with median impunctate line, and without depressed or flat zone in apical third (Figs 35–41). Color of scopa variable; sterna with or without apical fasciae beneath scopa.....**9**
- 9 Scopa usually orange at least on S2-S4, sometimes entirely dark or yellow white on S2-S3 [e.g. in *M. maritima*], rarely entirely yellow-white; sterna always without apical fasciae beneath scopa. Mandible with small, partial cutting edge visible in front view in second interspace (Figs 35–37); third interspace at least as deep as long, mostly with well-visible cutting edge in front view (Fig. 35) [except in *M. nigriventris* (Fig. 36); unclear in *M. willughbiella* (Fig. 37)]; mandible robust, tooth one broader than other teeth [unclear in *M. nigriventris*]**Subgenus *Xanthosarus***
- Scopa often white on S2-S4 or S2-S5, dark on S6 or on S5 and S6, sometimes entirely dark or orange, but if orange, sterna usually with conspicuous apical fasciae beneath scopa. Mandible with second interspace mostly without visible cutting edge in front view (Figs 38–41); if small cutting edge present in second interspace, then cutting edge usually recessed and hidden behind margin; shape of third interspace variable, mostly longer than deep (Figs 39–41; but see Fig. 38); mandible often less robust**10**
10. Mandible robust (Fig. 38), tooth 1 markedly larger than teeth 2–4; mandible apically without tuft of orange hairs near the base of tooth 1; third interspace

- as deep as long, with conspicuous, complete cutting edge. Hind basitarsus comparatively broad, length approximately 2.2 times its maximal width (Fig. 29). Claw of hind leg with basal seta elongate, its length at least four times its basal width (Fig. 6) **Subgenus *Eurymella***
- Mandible less robust (Figs 2, 39, 41), tooth 1 usually not markedly larger than teeth 2–4 [except in *M. deceptoria* and a few other species (Fig. 40)]; mandible apically with tufts of orange hairs in the grooves below and above the outer ridge near the base of tooth 1 (Figs 2, 39, 41) [except in *M. deceptoria* and a few other species (Fig. 40)]; third interspace longer than deep, usually with cutting edge little-visible (Fig. 39). Hind basitarsus comparatively elongate (Fig. 28), length more than 2.5 times its maximal width [except in *M. marginata*]. Claw of hind leg with basal seta modified to a short, thick process (Fig. 5) **Subgenus *Eutricharaea***

Males:

- 11 Coxa 1 without tooth or projection, although surface sometimes angulate [e.g. in *Megachile (Megachile) ligniseca*], or tooth minute and little visible [*apostolica* group of *Eutricharaea*; this group is included under both alternatives] **12**
- Coxa 1 with tooth or projection, projection sometimes short but well visible [in *M. (Pseudomegachile) lanata*, *M. (Pseudomegachile) riyadhensis* and *M. (Anodonteutricharaea) villipes*] **16**
- 12 Large species (i.e. body length above 13 mm) with vestiture predominantly black except snow-white on posterior parts of mesosoma, on T1 and basal part of T2. Preoccipital carina present laterally. Preapical carina of T6 bilobed, without teeth **Subgenus *Maximegachile***
- Body length variable. Combination of characters not as described above, especially vestiture. Preoccipital carina absent laterally. Preapical carina of T6 variable **13**
- 13 Small species (i.e. body size 7–9 mm) with mid and hind legs orange-red and front tarsi yellow-orange. Mandible with inferior projection. T6 with preapical carina denticulate, with area above carina densely covered with white vestiture **Subgenus *Eutricharaea, apostolica* group**
- Combination of characters not as described above; mostly larger species ≥ 10 mm; if body length less than 10 mm, then preapical carina of T6 rounded, vestiture of T6 different. Mandible with or without inferior projection **14**
- 14 Preapical carina of T6 bilobed or rounded, without well-delimited teeth (Fig. 42). Mandible usually with inferior projection (as in Fig. 8) [except in *M. pilicrus* and *M. armenia*]. First submarginal cell not visibly longer than second..
..... **Subgenus *Megachile***

- Preapical carina of T6 with at least four well-delimited teeth, usually with 6–10 teeth. Mandible always without inferior projection. First submarginal cell longer than second..... **15**
- 15 T7 produced to a long spine medially (Fig. 43). S5 partly exposed in repose, slightly less sclerotized than S4. Mandible 4-toothed
..... **Subgenus *Pseudomegachile, incana* group**
- T7 not produced to a long spine medially (Figs 44–45). S5 retracted under S4 in repose, much less sclerotized than S4. Mandible 3-toothed.....
..... **Subgenus *Chalicodoma, lefebvrei* and *parietina* groups**
- 16 T7 large and exposed, either pointed or triangular in dorsal view with a strong longitudinal carina dorsally (Fig. 46); or rounded, without longitudinal carina but with a spine basally on disc directed ventrally [*M. doriae*; in this species, disc of T6 with small tooth (Fig. 47)]. Apical margin of S5 and S6 visible in repose, S6 apically convex, margin resting on apical margin of T7 and closing the genital opening (Fig. 11)..... **Subgenus *Creightonella***
- T7 not as above; if produced to a tooth or a spine, then tooth rounded and without longitudinal carina dorsally [*montenegrensis* group of *Chalicodoma* (Figs 15, 48)]; or tooth smaller, compressed laterally [as in numerous *Pseudomegachile*, for example *M. ericetorum* (Fig. 51)] and T7 thus not triangular in dorsal view; if T7 rounded or truncate apically (Fig. 45), then disc always without basal spine. S5 and S6 mostly retracted under S4 in repose [except in the *montenegrensis* group of *Chalicodoma* (Fig. 15), where the condition of S6 is approaching that seen in *Creightonella*] **17**
- 17 Mandible with inferior process produced posteriorly to a triangular spine resting on hypostomal area in repose (Fig. 8). First submarginal cell not visibly longer than second..... **18**
- Mandible either without inferior process; or with inferior process truncate, quadrate, not projecting posteriorly, often covered by hairs (as in Fig. 9), then first submarginal cell longer than second..... **19**
- 18 T7 large, well-visible, either produced apically to a small tooth medially, or weakly trifold, or broadly truncate. Disc of T6 above carina mostly without light vestiture, surface of integument visible. Front tarsi always white or yellow-orange, often larger than front tibia. Mandible commonly 4-toothed [except in large species such as *M. maritima* and *M. lagopoda*, both of which have a 3-toothed mandible]. S4 apically mostly with hyaline apical margin (as in Figs 12–14) **Subgenus *Xanthosarus***
- T7 little visible, never produced to a small tooth. Disc of T6 mostly with dense, light vestiture [except sometimes in *M. giraudi*] entirely hiding integument surface. Front tarsi variable. Mandible always 3-toothed. S4 apically without hyaline apical margin (Fig. 10) **Subgenus *Eutricharaea***
- 19 Front coxal tooth long, at least twice as long as basal width *and* front coxa with an impunctate, shiny, glabrous area anteriorly to the tooth. T7 medially produced to a tooth (Fig. 15), sometimes trifold *and* T6 laterally with con-

- spicuous tooth (Fig. 48). Mandible without inferior projection
 **Subgenus *Chalicodoma, montenegrensis* group**
- Front coxal tooth not particularly long, *or* front coxa without impunctate, shiny and glabrous area anteriorly to the spine. T7 variable, if produced to median tooth, then T6 laterally without tooth [except with a short tooth in *M. albohirta* and *M. saussurei*, both with short front coxal tooth]. Mandible with or without quadrate inferior projection..... **20**
- 20 T6 with preapical carina narrow, restricted to less than a third of tergal width, strongly produced posteriorly (Fig. 49). T6 apically (beneath the preapical carina) with two median teeth (Fig. 14). Mandible yellow without inferior projection **Subgenus *Eurymella, patellimana* group**
- T6 not as above, if preapical carina denticulate, then carina wider than third of tergal width; apical margin of T6 variable. Integument of mandible mostly brown, mandible with or without inferior projection..... **21**
- 21 Preoccipital carina present laterally. Preapical carina of T6 bilobed, never denticulate. Clypeus often glabrous basally and with dense fringe of hairs apically. Mandible with quadrate inferior projection, often covered by numerous hairs **Subgenus *Callomegachile***
- Preoccipital carina absent laterally or very weak. Preapical carina of T6 mostly denticulate [except in a few *Pseudomegachile*, e.g. *M. lanata*]. Vestiture of clypeus different, usually entirely covered by dense vestiture. Mandible with or without quadrate inferior projection..... **22**
- 22 Mandible always without inferior projection and T6 with a small lateral tooth (often hidden under hairs) (Fig. 50). T7 usually small, little visible and unmodified (Fig. 50), not produced to a tooth apically [except in *M. albohirta*, in which T7 is small, apically produced to a truncate, median process]. First submarginal cell not visibly longer than second. Gonostylus apically broaden and with numerous hairs on external surface (Fig. 50) **Subgenus *Anodonteutricharaea***
- Mandible with or without quadrate inferior projection, but if projection absent, then T6 without lateral tooth (Fig. 51). T7 either produced to a triangular tooth that is compressed laterally [*M. ericetorum*; *flavipes* group (Fig. 51)]; or large and exposed and of variable shape [*rhodoleucura* and *cyanipennis* groups (Fig. 52); *M. foersteri* (Fig. 53)], rarely small and hidden [*M. lanata*]. First submarginal cell longer than second. Gonostylus different, apex with a dense fringe of hairs along interior margin (Figs 51–52) **Subgenus *Pseudomegachile***

Species groups, species composition and biology of the Western Palearctic subgenera

Subgenus *Anodonteutricharaea*

Diagnosis and description. This subgenus is widely distributed in the Old World (Trunz et al. 2016). Of the criteria given here, not all will apply to *Anodonteutricharaea*

outside the Palearctic; characters that appear constant in this subgenus throughout its range are the elongate basal seta on the claws in the female (Fig. 7), which is the most salient diagnostic trait to identify the females of *Anodonteutricharaea*; and the absence of an inferior projection on the mandible and the characteristic shape of the gonostylus in the male (Fig. 50). **Females:** Palearctic females of *Anodonteutricharaea* agree with *Eutricharaea* in their small to medium size, mostly white or yellowish white scopa (although it is orange in *Megachile albobirta*). The sterna do not have continuous, apical fasciae beneath the scopa. In contrast to *Eutricharaea*, the mandible is similar to that of the subgenus *Megachile s. str.* (Figs 30–31), with a partial cutting edge in the second interspace and no visible cutting edge in the third interspace in the Palearctic species; often in *Anodonteutricharaea*, the cutting edges are entirely recessed and invisible in front view (Fig. 31). Also as in *Megachile s. str.*, the mandible is 5-toothed, or if 4-toothed, the upper tooth is truncate and weakly divided into two teeth, thus approaching the 5-toothed condition (Fig. 30). In some species, there is a straight, carinate ridge in the middle of the interacetabular interspace; this ridge is placed above the outer ridge (see Gonzalez and Engel 2012: Fig. 5) and extends from the mandibular base to the middle of interspace 1 (Figs 30–31). In most other group 1 subgenera, this ridge is less visible, less carinate or regularly curved. **Males:** Males of *Anodonteutricharaea* can be diagnosed by the absence of projection along the inferior margin of the mandible, unlike most other group 1 subgenera; the mandible is either 3- or 4-toothed. The gonostylus is distinct and diagnostic (Fig. 50): it is broadened apically, with numerous hairs on the external surface. In the Palearctic, the few known species are superficially similar to *Eutricharaea* in the light body vestiture, the presence of a front coxal spine (spine short in *M. villipes*), the T6 with disc covered by dense, white tomentum and multidentate preapical carina, and the small, unmodified T7 (except in *M. albobirta*, where T7 is produced to a short median tooth). In most Palearctic species, the front tarsi are slightly enlarged, yellowish-white or yellowish-brown and have a black macula ventrally on tarsal segments 2 (most species) or 1 and 2 (*M. albobirta*). Palearctic *Anodonteutricharaea* are readily distinguished from *Eutricharaea* in the hyaline apical margin of S4 (Fig. 12).

Species composition. The Palearctic species of *Anodonteutricharaea* form a rather homogenous group; how this group relates to the eight species groups recognized by Pasteels (1965) for the African fauna remains to be investigated. The following western Palearctic species belong to this subgenus: *Megachile albobirta*, *M. inornata*, *M. thevestensis*, and *M. troodica*. *M. mandibularis* and *M. villipes* are probably restricted to Central Asia and records of the latter from the western Palearctic (Schulthess 1924, Zanden 1989, Özbek and Zanden 1994) likely refer to other species. I have seen at least three additional, undescribed species in the western Palearctic.

Biology. Very little is known on the biology of this subgenus. Ferton (1920) described nests of *Megachile thevestensis*. The cells were placed individually or in groups of two in existing cavities between rocks or in burrows in the soil; it was unclear whether the female had dug the burrow or used a preexisting burrow. All cells investigated consisted of an external, rigid layer of leaf fragments (not circularly cut as in most other group 1 subgenera) and a layer of petals inside. I have captured *M. villipes* on *Alhagi*

(Fabaceae) in Uzbekistan, while *M. inornata* and a closely related, undescribed species appear oligolectic on Lamiaceae. *M. troodica* also appears to have a distinct or exclusive preference for Lamiaceae (Mavromoustakis 1953), and in *M. thevestensis* and another, undescribed species from Morocco, the hairs on the median parts of the clypeus are short and simple, suggesting pollen collection from nototribic flowers such as Lamiaceae (see comments under the subgenus *Pseudomegachile*).

Subgenus *Callomegachile*

Diagnosis and description. In the few species present in the Palearctic, the preoccipital carina is always well developed and constitutes a good diagnostic trait. **Females:** Females can be recognized by the mandible without cutting edges and by the dull mandibular surface with comparatively few punctures or ridges [the mandible is also dull in some *Chalicodoma* of the *montenegrensis* group, and to some extent in *Megachile* (*Pseudomegachile*) *foersteri* Gerstäcker, 1869 (Fig. 23)]. The clypeus is always modified in the species of *Callomegachile* present in the Palearctic, either broadly truncate, with truncation wide, shiny, vertical or overhanging the base of the labrum (Fig. 18). **Males:** Males of the species present in the Palearctic always have a front coxal tooth and a quadrate projection along the inferior margin of the mandible. In many *Callomegachile* (but not in *M. sculpturalis* Smith, 1853), the first segment of the front tarsi forms a ventral concavity. The preapical carina of T6 is entire, without denticulation. The clypeus is mostly glabrous basally and with a dense fringe of hairs apically; in most other Palearctic *Megachile*, the clypeus is entirely covered by hairs.

Species composition. *Megachile sculpturalis*, an Oriental species, has recently been introduced to western Europe (Vereecken and Barbier 2009, Amiet 2012, Quaranta et al. 2014, Westrich et al. 2015); otherwise, only a few species of *Callomegachile* occur on the Arabian Peninsula, including *M. simonyi* Friese, 1903 and *M. cephalotes* Smith, 1853 among others. At least two further species occur on the Arabian Peninsula; they probably belong to previously described African species. As mentioned above, *M. breviceps* likely does not belong to the Palearctic fauna.

Biology. Most species of the subgenus *Callomegachile* investigated so far predominantly use resin to build their nests (Michener 2007), although other materials (wood chips, mud or even leaf fragments) are sometimes used (Piel 1930). *Megachile sculpturalis* nests in existing cavities in wood and uses resin to separate the cells; the nest plug is also built with resin but sometimes covered with a thin layer of mud (Quaranta et al. 2014, Westrich et al. 2015). Whether mud is also used for the cell partitions is unclear. In contrast, *M. cephalotes* appears to build entire cells with mud; the cells are placed in hollow stems (Gupta et al. 2004). Apparently, a “brown-colored detachable membranous layer” (Gupta et al. 2004: 58) lines the inside of the mud walls, but it is unclear what this layer refers to as it exhibits a nipple-shaped projection apically, which seems to refer to the cocoon. The floral choices of the widely polylectic species *M. sculpturalis* have been studied using pollen analyses (Quaranta et al. 2014, Westrich et al. 2015).



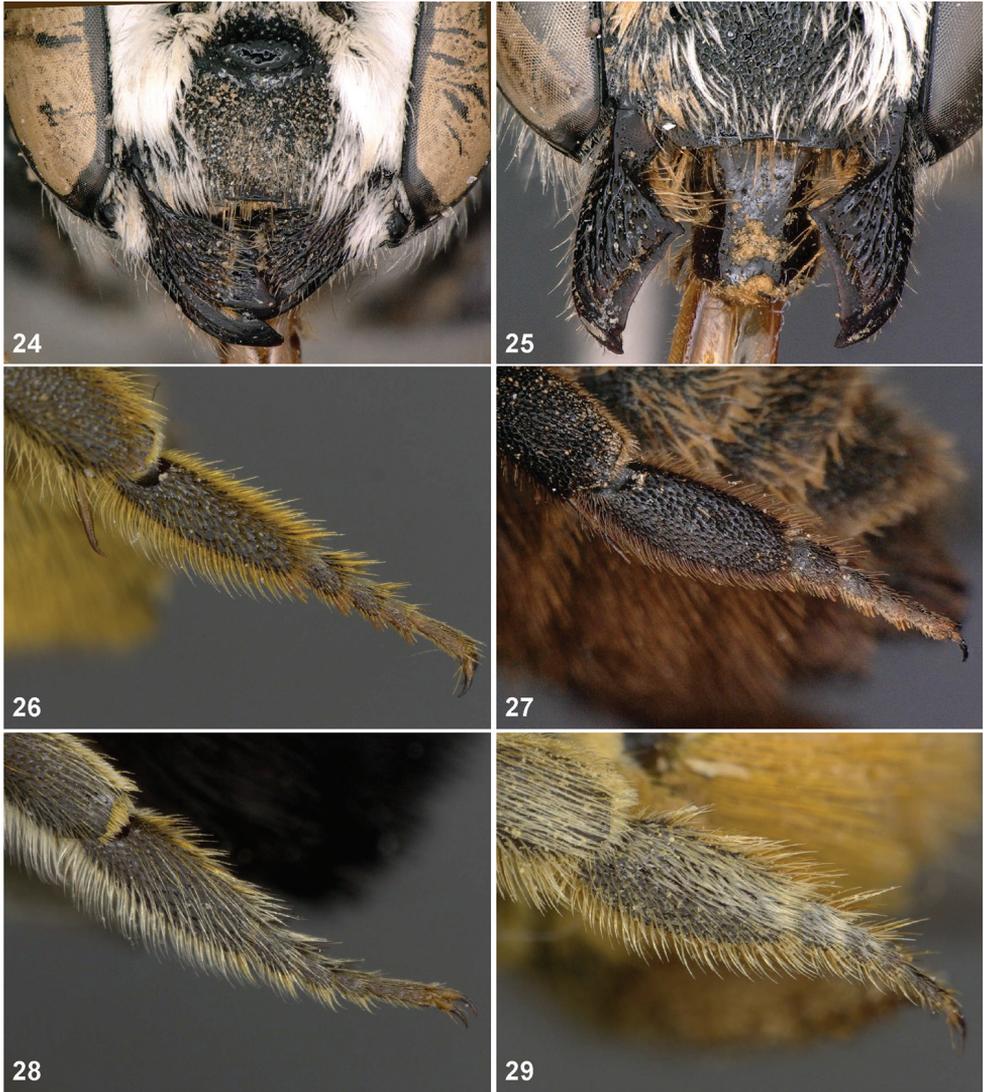
Figures 16–23. Female clypeus and mandibles, front view. **16** *Megachile* (*Creightonella*) *amabilis* **17** *M.* (*Maximegachile*) *maxillosa*; the white line indicates the hypostomal tooth **18** *M.* (*Callomegachile*) *sculpturalis* **19** *M.* (*Chalicodoma*) *hungarica* **20** *M.* (*Pseudomegachile*) *ericetorum* **21** *M.* (*Pseudomegachile*) *incana* **22** *M.* (*Pseudomegachile*) sp. aff. *incana* **23** *M.* (*Pseudomegachile*) *foersteri*.

Subgenus *Chalicodoma*

Diagnosis and description. Females: Females can be recognized by the combination of the convex, denticulate apical margin of the clypeus and the elongate mandible with a straight margin above the two apical teeth (Fig. 19) (rarely with minute tooth 3, e.g., in the *montenegrensis* group). Only some species of *Pseudomegachile* have similarly elongate mandibles, for example *Megachile ericetorum* (Fig. 20) and *M. lanata*. The former can easily be separated from *Chalicodoma* by the different apical margin of the clypeus (Fig. 20) and the long ocellocipital distance, which is markedly longer than the interocellar distance; *M. lanata* has a short clypeus with apical margin entire (as in Fig. 24), not denticulate. In some species of the *cyanipennis* group of *Pseudomegachile*, notably *M. saussurei* Radoszkowski, 1874, the apical margin of the mandible is nearly straight, with reduced teeth (Fig. 25), thus approaching the condition found in *Chalicodoma*. In such species however, the mandible is less elongate, with the outer margin strongly convex. In *M. (Pseudomegachile) incana* Friese, 1898, the mandible is 5 to 6 toothed (Fig. 21), and in old specimens the teeth may be little visible and the condition thus similar to that seen in *Chalicodoma*; as in *Chalicodoma*, the ocellocipital distance is shorter than the interocellar distance in *M. incana*. All species of the *incana* group can easily be diagnosed by the large body size, the light-grey metasomal vestiture without dense tergal fasciae and the comparatively broad hind basitarsus (Fig. 27). **Males:** Males *Chalicodoma* fall into three distinct species groups and there are few diagnostic characters common to all. In all species the mandible is comparatively elongate, 3-toothed and without inferior projection, and the preapical carina of T6 is denticulate.

Species groups. Tkalčú (1969) and Rebmann (1970) have independently divided the subgenus *Chalicodoma* into the same four groups, to which they gave subgeneric rank. I recognize three groups, not four, because *Megachile hirsuta*, unknown to both Tkalčú and Rebmann at that time, renders the distinction between two of their groups difficult in the female sex. Recognizing these groups as subgenera appears little useful for species identification in the Palearctic and I recognize them as species groups.

1. montenegrensis group (*Euchalicodoma* Tkalčú, 1969; *Xenochalicodoma* Tkalčú, 1971; *Allomegachile* Rebmann, 1970; *Katamegachile* Rebmann, 1970). **Males:** Front coxa with large, spatulate tooth. T6 with lateral tooth (Fig. 48) [small in *Megachile rufitarsis* (Lepelletier, 1841)]. T7 mostly produced to large, rounded, median tooth (Figs 15, 48) (tooth small in *M. rufitarsis*), or trifold. Gonostylus simple, slightly broaden apically (Fig. 48). In this species group, the front tarsi are variously modified. Unusual characters of males of some or all species of this group are the partly exposed S5 (character not visible in Fig. 15), the apically strongly convex margin of S6 (Fig. 15), as in *Creightonella*, and, in some species, in the lack of hairs laterally on S8, unlike other group 2 subgenera. **Females:** Surface of mandible mostly dull, with few shiny ridges or punctures, except in *M. rufitarsis*, in which the mandible is as in the *parietina* group. S6 with depressed apical zone, with strong preapical carina separating the elevated, basal part from the depressed apical zone, except in *M. montenegrensis* Dours, 1873



Figures 24–29. Female clypeus and mandibles, front view. **24.** *Megachile (Pseudomegachile) seraxensis* **25** *M. (Pseudomegachile) saussurei* **26–29** Female hind basitarsus, lateral view **26** *M. (Pseudomegachile) ericetorum* **27** *M. (Pseudomegachile) incana* **28** *M. (Eutricharaea) giraudi* **29** *M. (Eurymella) patellimana*.

and *M. hirsuta*, both of which have dull mandibles. In *M. montenegrensis*, the vertex is slightly concave laterally, a unique feature in Palearctic *Chalicodoma* (see Tkalcù 1969).

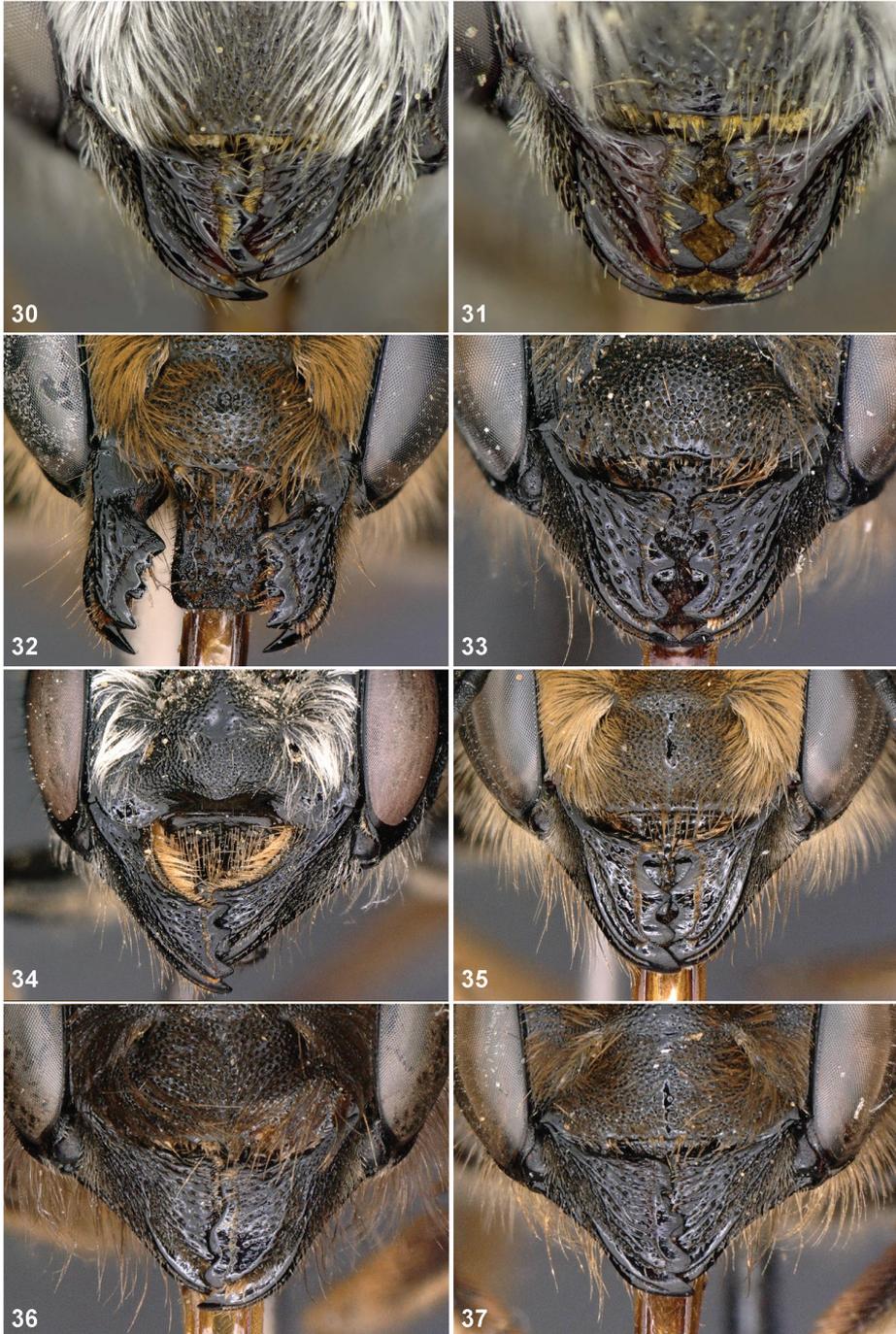
2. lefebvrei group (*Allochalicodoma* Tkalcù, 1969; *Heteromegachile* Rebmann, 1970). **Males:** Front coxa without tooth. T6 with a small lateral tooth (sometimes reduced to a mere angle, as in Fig. 45). T7 rounded apically, unmodified. Gonostylus tapering apically, thickened preapically and without preapical, projecting lobe

(Fig. 45). **Females:** Surface of the mandible covered with numerous shiny ridges and punctures (Fig. 19), as in the *parietina* group. S6 with depressed apical zone; carina separating the elevated part from the depressed marginal area interrupted medially and only visible laterally. In addition, all females of the *lefebvrei* group have conspicuously modified vestiture on the clypeus (Fig. 19) and the frons: the hairs are short, simple and bent apically (Müller 1996). Such modified hairs are not found in the *montenegrensis* group and only rarely found in the *parietina* group.

3. *parietina* group. Males: Front coxa without tooth. T6 without lateral tooth. T7 rounded or truncate. Gonostylus with preapical lobe (Fig. 44). **Females:** S6 mostly not divided in two zones (weakly so in some species, such as *Megachile nasidens* Friese, 1898), without preapical carina. Hairs on clypeus mostly branched, except in some rare species [e.g. *M. marina* Friese, 1911 and *M. palaestina* (Tkalců, 1988)].

Species composition. Females of this subgenus are sculpturally uniform and frequently exhibit mimetic color evolution; hidden sternites of males are mostly diagnostic but these structures have only been described for few species (e.g. Tkalců 1969, 1974). Consequently, the taxonomic status of numerous “geographic” forms within *Chalicodoma* remains unclear and a complete species list is not given here. In the West Palearctic, there are at least five species in the *montenegrensis* group [*Megachile hirsuta*, *M. manicata* Giraud, 1861, *M. mauritaniae* (Tkalců, 1992), *M. montenegrensis* and *M. rufitarsis*], two to five species in the *lefebvrei* group [*M. heinii* Kohl, 1906, known only in the female sex; and depending on the species concept adopted one to four additional, parapatric species: *M. albocristata* Smith, 1853, *M. hungarica* Mocsáry, 1877, *M. lefebvrei* (Lepelletier, 1841) and *M. roeweri* (Alfken, 1927)]; and approximately 20 species in the *parietina* group, of which three are undescribed.

Biology. The nesting biology of *Megachile parietina* has been described in detail (reviewed in Westrich 1989 and Müller et al. 1997). This species builds exposed nests made of hard mud in rock crevices, more rarely on twigs (Rebmann 1969, Vereecken et al. 2010). These exposed nests are particularly hard and resistant; Kronenberg and Hefetz (1984) have demonstrated that females of *M. sicula* (Rossi, 1794) add labial gland secretions to the mud; these secretions rapidly harden and render the nest hydrophobic. Accounts of the nesting biology of the few species of the *parietina* group investigated so far indicate that the cells are built in a similar way: in *M. pyrenaica* Lepelletier, 1841, the cells are often hidden in holes in walls or under stones (Le Goff 2007), or placed in existing holes in steep, hard soil slopes, under overhanging rocks (Müller et al. 1997), or as described by Fabre (1879, 1882) under the roof tiles of old barns; sometimes the nests are exposed on stones as in *M. parietina* (Le Goff, 2007); in *M. rufescens* (Pérez, 1879) the nests appear to be mostly placed on twigs (Fabre 1882). *M. sicula* builds nests both on twigs and on rock surfaces (Kronenberg and Hefetz 1984, Vereecken et al. 2010). Few studies have documented the nesting biology of species of the other species groups: *M. manicata* appears to nest exclusively in existing holes in rocks (Le Goff 2012, Gogala 2014, C. Praz, unpublished data); Le Goff (2012) described one nest containing two cells made of hard mud mixed with pebbles; the nests observed were closed with hard mud. Nests of *M. lefebvrei* have been described in detail by Ferton (1908, 1920); the



Figures 30–37. Female clypeus and mandibles, front view. **30** *Megachile (Anodontetricharaea) albobirta* **31** *M. (Anodontetricharaea) thevestensis* **32** *M. (Megachile) versicolor* **33** *M. (Megachile) lapponica* **34** *M. (Megachile) bombycina* **35** *M. (Xanthosarus) lagopoda* **36** *M. (Xanthosarus) nigriventris* **37** *M. (Xanthosarus) willughbiella*.

biology of this species slightly deviates from the typical nesting biology seen in the subgenus. Females build 2–4 cells in holes in rocks; these cells have the general appearance of those built by *M. parietina*, thus they consist of mud mixed with “salivary secretions” (Ferton 1908: 545), without pebbles. Once several cells are built, they are covered with a thin (1 mm), concave layer of hardened mud; this layer is located inside the hole of the rock and its outer surface is a few millimeters beneath the external surface of the rock. Subsequently, the female fills the space above the thin mud layer with a mix of pebbles and masticated plant material. According to Ferton, the masticated plant material contains salivary secretions (but no resin), and it hardens quickly. Ferton (1920) reports a nest of *M. lefebvrei* from southern France; the nest structure and the material used were similar but the nest had been built in an empty snail shell.

Many species of *Chalicodoma*, including *Megachile hirsuta*, *M. montenegrensis*, *M. manicata*, *M. parietina*, and *M. pyrenaica* have a distinct or exclusive preference for Fabaceae (Westrich 1989, Müller et al. 1997, Gogala 2014, C. Praz, unpublished data). All species of the *lefebvrei* group are likely polylectic with a preference for Lamiaceae (Müller 1996; C. Praz, unpublished data). The pollen spectrum of the other species remains poorly investigated.

Subgenus *Creightonella*

Diagnosis and description. The subgenus *Creightonella* is in many ways intermediate between the leafcutter and the dauber bees. **Females:** Females can easily be diagnosed by the shape and structure of the mandible (Fig. 16): the mandibular surface is distinct, with numerous, elongate punctures but comparatively few long ridges, and is covered by numerous hairs. The apical margin has 5 or 6 teeth, with tooth 1 broad and larger than the other teeth, and the teeth 2–5 (-6) becoming progressively smaller. There is a conspicuous, partial cutting edge in the second interspace and a small, little visible cutting edge in the third and sometimes fourth. In spite of being a leafcutter, *Creightonella* does not have the typical tapering metasoma of most other group 1 members and the hind basitarsus is slender (as in Fig. 26). The hind claw has only one elongate seta, a unique condition in Palearctic *Megachile*. **Males:** Males of *Creightonella* have a strong front coxal tooth and a rounded projection along the inferior margin of the mandible (Fig. 9). The front tarsi are unmodified although in *Megachile albisecta* (Klug, 1817) they are yellowish-brown (Fig. 9) and the second tarsal segment has a dark spot on the ventral side. The preapical carina of T6 is mostly denticulate (weakly so in *M. arabica* Friese, 1901) and laterally the carina extends at right angle towards the base of the tergum. T7 is mostly triangular in dorsal view, with a strong longitudinal carina (Fig. 46), except in *M. doriae*, where T7 is truncate, but with a spine on the basal part of the disc (Fig. 47). The apical margin of S5 is exposed in repose and the apical margin of S6 is convex and rests on the apical margin of T7 in repose (Fig. 11).

Species composition. Most Palearctic species fall into a rather homogenous group of species referred to here as the *albisecta* group (*Metamegachile* Tkalců, 1967), even if

the structure of T7 is rather different in *Megachile doriae*; there are at least four valid species in this group: *M. albisecta*, *M. amabilis* Cockerell, 1933, *M. doriae* and *M. morawitzi* Radoszkowski, 1876; a fifth is undescribed (A. Monfared and C. Praz, in prep). The status of *M. ghigii* Gribodo, 1924, described from Libya, and *M. aurantiaca* Rebmann, 1972 from Iran (a junior homonym of *M. aurantiaca* Friese, 1905) as well as of numerous Central Asian taxa related to *M. albisecta* remains unclear. On the Arabian Peninsula, additional species with Afrotropical affinities occur: Pasteels (1979) placed *M. arabica* in the *aurivilli* group (see Pasteels 1965) and *M. felix* (Pasteels, 1979), known only in the female sex, in the *angulata* group. Mentions of *M. sudanica* Magretti, 1898 from Jordan (Zanden 1989) possibly refer to *M. arabica*, and both species may be conspecific (Pasteels 1965: 26). In addition, I have seen a single specimen putatively from Yemen (BMNH) of an African species with a modified clypeus, possibly either *M. bicornuta* Friese, 1903 or *M. cornigera* Friese, 1904, both in the African *cornigera* group.

Biology. The nesting biology of *Megachile albisecta* has been described in detail (Ferton 1901). This species nests in burrows in the ground; whether the females dig their own burrows or rent existing cavities as suggested by Ferton is not clear, although a brief description of a nest by Grandi (1961) mentions a nest “excavated in very hard soil” [the Oriental species *M. frontalis* (Fabricius, 1804) consistently digs its own burrows in hard, heavy soils (Michener and Szent-Ivany 1960, Willmer and Stone 1989)]. Reports of nests in dead wood (Benoist 1940) and in stems (Banaszak and Romasenko 2001) are likely identification errors. Unlike the circular leaf discs cut by *M. frontalis* (see Michener and Szent-Ivany 1960: Plate 1), the leaf fragments used by *M. albisecta* are irregular; in *M. frontalis*, the leaf fragments used for the outer layer of the cells are also irregular (Michener and Szent-Ivany 1960: 31 and Plate 3; Willmer and Stone 1989). In *M. albisecta* the fragments are stuck together by masticated leaf material, and the entire cell rests on a solid plug of masticated leaf pulp mixed with pebbles. The nest plug consists of circular leaf fragments and pebbles cemented together by masticated leaf pulp. Nests of *M. albisecta* do not appear to include resin according to the description by Ferton (1901), although Ferton’s subsequent articles (Ferton 1908: 547) suggest that resin was included in the nest. Possibly the leaf pulp is hardened with secretions but not resin. Resin was not found in the nests of *M. frontalis* (Michener and Szent-Ivany 1960; Willmer and Stone 1989) but was reported from the nest of the African *M. cornigera* (Michener 1968). *M. arabica* has been observed cutting leaf discs (H. Priesner, cited in Alfken 1934). *M. albisecta* (and possibly all species of the *albisecta* group) is oligolectic on Asteraceae, with a preference for Carduoideae (C. Praz, unpublished data).

Subgenus *Eurymella*

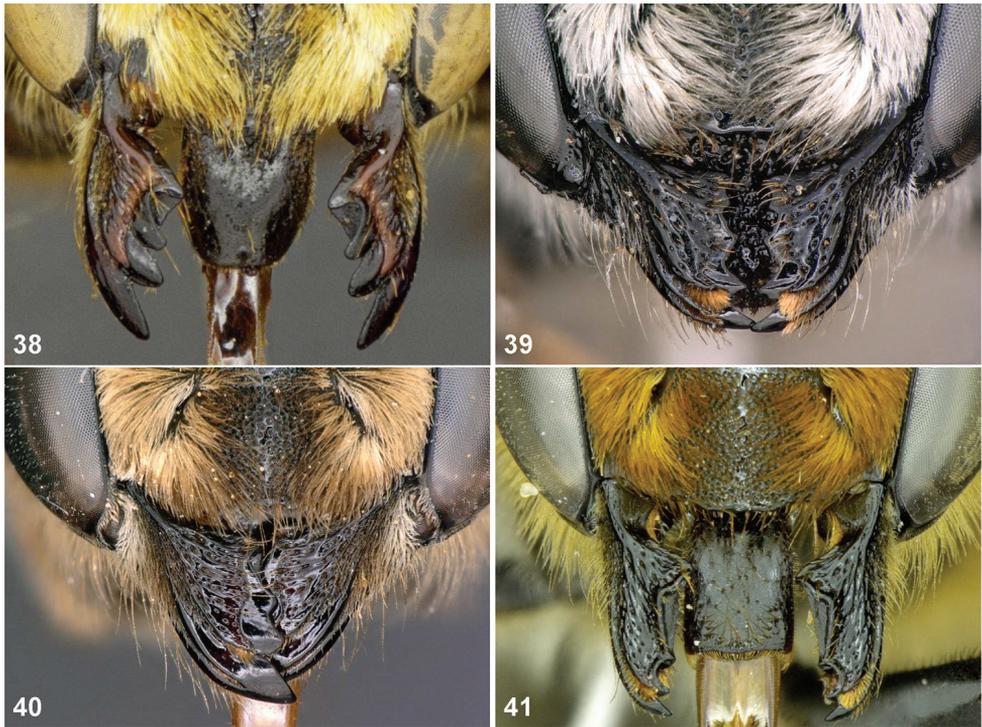
Diagnosis and description. Females: The females of most *Eurymella* have a distinct, robust mandible (Fig. 38), with tooth one markedly larger than the other teeth; the

mandible is 4-toothed in Palearctic and Arabian species and divided into two plane surfaces by the outer ridge; the brushes of orange hairs in the grooves near the base of tooth one are lacking or reduced (Fig. 38). A complete, well-visible cutting edge is present in the third interspace (Fig. 38). Some *Eutricharaea* (*Megachile deceptor* Pérez, 1890 and a few related species; see under the subgenus *Eutricharaea*) also have a robust mandible, with tooth one comparatively large, and reduced brushes of hairs near the base of tooth one (Fig. 40). In *Eurymella*, the hind basitarsus is comparatively broad, its length approximately 2.3 times its maximal width (Fig. 29). In *Eutricharaea*, the hind basitarsus is usually less broad (Fig. 28) (length approximately 2.7 times its maximal width), except in a few species such as *M. marginata*. In *Eurymella* the claw of the hind leg bears two thin setae (Fig. 6); the condition is not as clear as in *Anodonteutricharaea* because the basal seta is short in *Eurymella*. As in *Eutricharaea* but unlike most other group 1 subgenera, the sterna have conspicuous apical fasciae beneath the scopa in the Palearctic species. **Males:** Males of *M. patellimana* Spinola, 1838, the only Palearctic species outside the Arabian Peninsula, are easy to diagnose using the criteria mentioned in the key, especially the uniquely shaped T6 (Fig. 49) and the absence of inferior mandibular tooth (see below for the males of other species from the Arabian Peninsula).

Species composition. This subgenus is diverse in Africa, where it forms numerous, morphologically distinct species groups (Pasteels 1965); very few morphological features characterize all males of *Eurymella*, while the females are more homogeneous. In the Palearctic, *Eurymella* is probably represented by only one distinctive species, *Megachile patellimana*, included in the *patellimana* group (Pasteels 1965). Pasteels (1979) mentions two species of the *eurimera* group (see Pasteels 1965) from the southern parts of the Arabian Peninsula: *M. gibboclypearis* Pasteels, 1979 and “*M. aff. eurimera* Smith, 1854”.

Note. Both Arabian species of the *eurimera* group are known only in the female sex, although the male of the widely distributed Afrotropical species *Megachile eurimera* is well known (Pasteels 1965, Eardley 2013). The males of the *eurimera* group differ from those of the *patellimana* group in the pointed, inferior projection of the mandible and the simple T6 with preapical carina not produced posteriorly. In the present key, males of *M. eurimera* would run to couplet 18 (*Eutricharaea* and *Xanthosarus*); they differ from *Eutricharaea* in the strikingly different genitalia (see Pasteels 1965: p. 83), the presence of a wide, hyaline margin apically on S4 (as in Fig. 14), and the apical margin of T6 (beneath the preapical carina) with two teeth (as in Fig. 14). *Xanthosarus* is presumably absent from the Arabian Peninsula.

Biology. Little is known on the biology of *Eurymella*; only a brief account is given by Pasteels (1965: 127) for *Megachile semifulva* Friese, 1922: the nests of this species are placed in burrows in the ground and consist of leaf discs. Gess and Roosenschoon (2017) described nests of *M. patellimana* in the United Arab Emirates. The nests were placed in excavated burrows in compacted sand; it was not clear whether the burrows had been dug by *M. patellimana* or were pre-existing. A female was captured carrying a cut leaf piece, while another was captured carrying a piece of tough green plastic.



Figures 38–41. Female clypeus and mandibles, front view. **38** *Megachile* (*Eurymella*) *patellimana* **39** *M.* (*Eutricharaea*) *rotundata* **40** *M.* (*Eutricharaea*) *deceptoria* **41** *M.* (*Eutricharaea*) *giraudi*.

Subgenus *Eutricharaea*

Diagnosis and description. Females: In females the scopa is mostly white at least basally (often dark apically) and the sterna have distinct apical fasciae beneath the scopa (lacking in *Megachile giraudi* and *M. hohmanni* Tkalčú, 1993). In a few rare cases, the scopa is orange or entirely black (some populations of *M. melanogaster*, *M. hohmanni*). The upper mandibular tooth is usually truncate (e.g. *M. leachella* Curtis, 1828), although it is sometimes acute (e.g. *M. deceptoria*; Fig. 40) or conversely clearly divided into two teeth [e.g. *M. rotundata* (Fabricius, 1787); Fig. 39]. In some species, such as *M. orientalis*, the mandible is clearly 5-toothed (Fig. 2). There is no visible cutting edge in the second interspace (Figs 39–41), in contrast to the subgenera *Xanthosarus*, *Megachile* or *Anodonteutricharaea* (in the latter all cutting edges are often strongly reduced); even in the third interspace, the cutting edge is often small and partly hidden behind the margin in many *Eutricharaea*. **Males:** In the Palearctic, males of this subgenus can be recognized by the following criteria: the preapical carina of T6 is mostly denticulate (weakly so in some species such as *M. rotundata*) and the disc of T6 covered with dense, light vestiture entirely hiding cuticula (except in some populations of *M. giraudi*). T7 is small and little visible. The mandible is 3-toothed, always with triangular inferior projection. In contrast to the subgenera *Anodonteutricharaea* and

Megachile and to most *Xanthosarus* and *Eurymella*, S4 does not have a hyaline rim apically (Fig. 10). The front tarsi may be modified or not, and the front coxal tooth is present (although minute in the *apostolica* group).

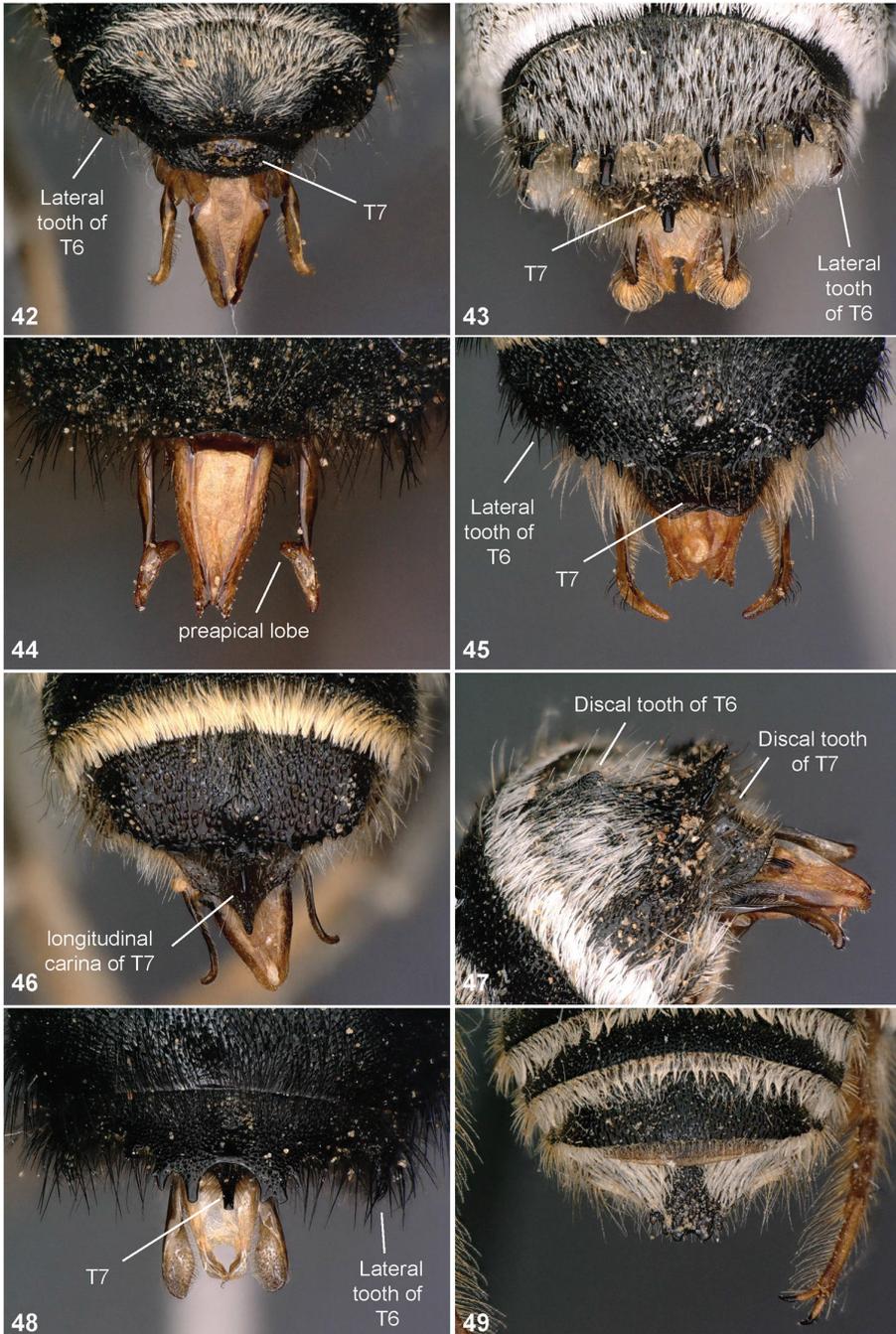
Species groups.

1. *rotundata* group (*Neoeutricharaea* Rebmann 1967). **Males:** Gonostylus simple, not bifid apically, s-shaped in lateral view (Fig. 54). Front coxa with tooth. T2 and sometimes T3 with fovea laterally. Apical margin of S4 unmodified, medially without tubercle or spot of dense, golden hairs (Fig. 10). Pretarsal claws of all legs with two similar, thin setae (as on Fig. 4). Front legs modified or not. **Females:** T2 and sometimes T3 with fovea laterally. Ocelloccipital distance often larger than diameter of lateral ocellus. Clypeus apically with comparatively wide, impunctate margin. Scopa usually white, black on S6, sometimes also S5, rarely entirely black.

Note. This group is particularly diverse and additional species groups may be recognized for isolated, divergent species: *Megachile giraudi*, with a particularly long interspace 3 in the female sex (Fig. 41) and front basitarsus modified, with a long apical projection in the male sex; *M. orientalis*, with the female mandible 5-toothed with cutting edges hidden behind the mandibular margin (Figs 2–3) (the male is a regular member of the *rotundata* group); and *M. hohmanni*, included in a distinct, monotypic subgenus by Tkalců (1993). Another group includes species with robust, 4-toothed mandible (Fig. 40), with tooth one larger than the other teeth and with reduced tufts of hairs apically, approaching the condition seen in *Eurymella*; males of this group are mostly characterized by the strongly convex and medially produced apical margin of T5. In the Palearctic, this group includes *M. communis* Morawitz, 1875, *M. deceptoria*, *M. dohrandti* Morawitz, 1880, *M. sedilloti*, *M. jakesi* Tkalců, 1988, probably *M. arachosiana* Gonzalez, Engel and Hinojosa-Díaz, 2010 as well as at least one undescribed species. Because all these species do not have particularly distinct gonostylus, I do not recognize separate species groups for them. Of note, the *rotundata* group also occurs in Africa; Pasteels (1965) referred to it as the *malangensis* group. I have examined the type material of *M. malangensis* Friese, 1904 (ZMHB); this species is a member of *Eutricharaea* and not of *Paracella* (= *Anodonteutricharaea*) as suggested by Eardley (2013).

2. *naevia* group. **Males:** Similar to males of the *rotundata* group, but gonostylus apically shortly bifid (Fig. 55). Front tarsi modified, yellowish-white. T2 with a weak fovea laterally. **Females:** As in the *rotundata* group, but mandible always red. Apical margin of clypeus straight with comparatively wide impunctate area. Ocelloccipital distance shorter than diameter of lateral ocellus. T2 but not T3 with fovea laterally.

3. *leachella* group. **Males:** Gonostylus either bifid (Fig. 56) with long (e.g. *Megachile leachella*) or short (e.g. *M. walkeri* Dalla Torre, 1896) preapical process, or simple (e.g. *M. concinna* Smith, 1879), in all cases apically with rounded emargination (Fig. 56). Front coxa with tooth. T2 and T3 without fovea laterally (although the corresponding area on T2 is often finely punctured and covered with brown hairs which contrast with white hairs on rest of the tergum). Apical margin of S4 either with a patch of yellow hairs medially, or a minute tubercle covered with numerous short, white hairs. Pretarsal claw with basal hair short, thickened, as in the female (as in Fig. 5), and api-



Figures 42–49. Apex of male metasoma; **42–46, 48** T5-T7 and apex of genital capsule, dorsal view **47** T5-T7 and apex of genital capsule, lateral view **49** T4-T6, dorsal view **42** *Megachile* (*Megachile*) *melanopyga* **43** *M.* (*Pseudomegachile*) *sp. aff. incana* **44** *M.* (*Chalicodoma*) *parietina* **45** *M.* (*Chalicodoma*) *hungarica* **46** *M.* (*Creightonella*) *albisecta* **47** *M.* (*Creightonella*) *doriae* **48** *M.* (*Chalicodoma*) *manicata* **49** *M.* (*Eurymella*) *patellimana*.

cal hair long. Front legs not modified although front tarsi sometimes yellowish brown. **Females:** T2 and T3 without fovea laterally (although the corresponding area on T2 is often finely punctured and covered with brown hairs which contrast with white hairs on rest of the tergum). Ocellocipital distance commonly equal to the diameter of the lateral ocellus. Clypeus apically with narrow impunctate zone. Scopa white on S1-S5, black on S6, sometimes partly or entirely orange-red, never black on S5.

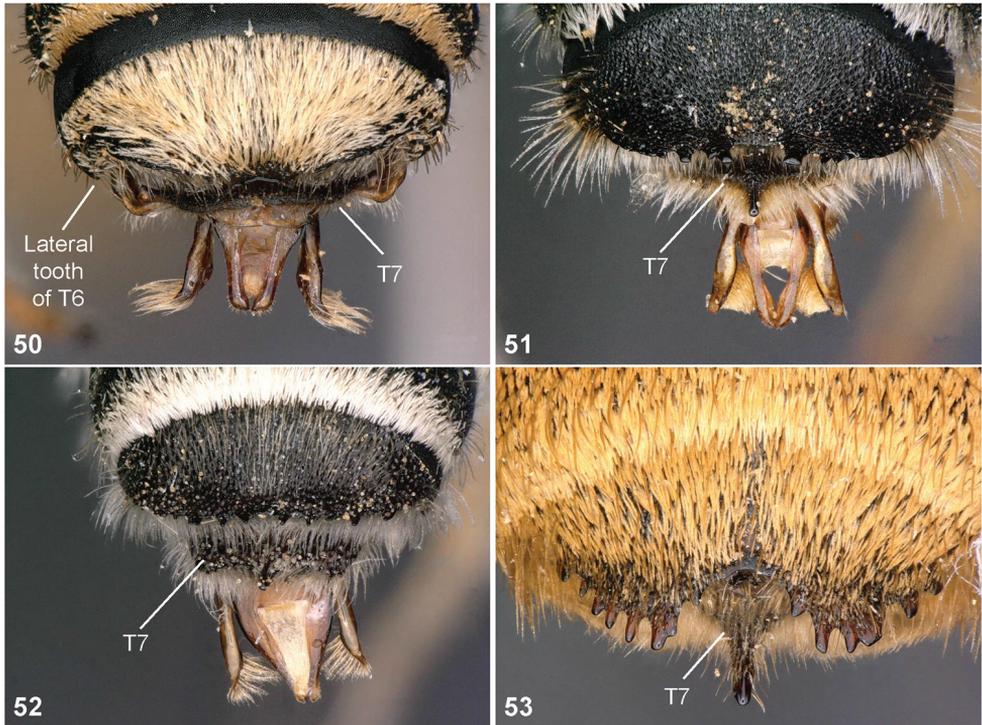
Note. *Megachile ventrisi* Engel, 2008, from Saudi Arabia, Yemen (Engel and Schwarz 2011) and at least Kenya (C. Praz and L. Packer, unpublished) belongs to another African and Oriental group in which the male front tarsi are modified (the ventral surface of the first tarsal segment is concave) and the gonostylus simple but differently shaped, without apical emargination. This group was included in the *leachella* group (as the “*argentata*” group) by Pasteels (1965); it includes the African species known as *M. frontalis* Smith, 1853, which is a junior homonym of *M. frontalis* (Fabricius, 1804); “*M. frontalis* Smith” is a member of *Eutricharaea* and not of *Paracella* (= *Anodonteutricharaea*) as suggested by Eardley (2013).

4. *apostolica* group. Males: As *leachella* group, with the following exceptions: gonostylus bifid apically (as in *Megachile pilidens* Alfken, 1924), but apex conspicuously slender and preapical process long. Front coxa with minute tooth (see comments above). Front tarsi yellowish-white. **Females:** As *leachella* group, with the following exceptions: all legs predominantly orange; terga brown; hairs on ventral side of mid and hind femora modified, short, apically thickened. *M. walkeri* (included in the *leachella* group) also has similarly modified hairs (Engel 2008), but in *M. walkeri* the cuticula of T1 and T2 is orange.

5. *leucomalla* group. Males: Male gonostylus as in *rotundata* group, but bent apex longer (Fig. 57). Front tarsi greatly enlarged, yellowish-white. S2 and S3 (but not S4) medio-apically with dense patch of yellow hairs. T2 and T3 without clearly delimited fovea. Pretarsal claw of all legs with two similar hairs. **Females:** Body length above 13 mm; punctuation of mesonotum coarse and sparse, interspaces shiny and nearly as large as puncture diameters. Apical clypeal margin truncate, premarginal, impunctate zone comparatively narrow. T2 and T3 without clearly delimited fovea.

Species composition. This is a large and taxonomically complex subgenus in need of revision. The number of unpublished synonymies is large and a list of species is not given here. There is only one species in the *leucomalla* group, *M. leucomalla* Gerstäcker, 1869. I know one Palearctic species in the *apostolica* group, *Megachile soikai*; this species is possibly conspecific with one of the African species related to *M. apostolica* Cockerell, 1937 and listed by Gonzalez et al. (2010: 65). In the *naevia* group, I know two species: *M. naevia* Kohl, 1906 from the Socotra Archipelago and an undescribed species from the Arabian Peninsula, North to Israel. There are more species in the *leachella* group [possibly seven; see Soltani et al. (in press) for a treatment of the taxa allied to *M. concinna*], and a large number of species, a few of which undescribed, in the *rotundata* group, for a possible total of 29 species in the western Palearctic.

Biology. *Megachile rotundata*, a European species introduced into North America for the pollination of alfalfa, has been studied in detail (reviewed in Pitts-Singer and



Figures 50–53. Apex of male metasoma, dorsal view. **50** *Megachile* (*Anodonteutricharaea*) sp. aff. *inornata* **51** *M. (Pseudomegachile) ericetorum* **52** *M. (Pseudomegachile) saussurei* **53** *M. (Pseudomegachile) foersteri*.

Cane 2011). All species of *Eutricharaea* use leaf discs to build their brood cells, although *M. rotundata* (and *M. giraudi*, see below) sometimes use petal fragments and not leaves (Westrich 1989, and references therein). In *M. minutissima* Radoszkowski, 1876, the cell walls are sometimes omitted when the nest is located in cavities of small diameters, so that leaf discs are only used to build the cell partitions (Krombein 1969). The outer nest plug of *M. marginata* consists of a series of leaf discs covered by a layer of mud, possibly mixed with “saliva” (Ferton 1914). Nests of *Eutricharaea* are mostly built in existing cavities such as stems or beetle burrows (e.g. *M. rotundata*), under stones or in existing cavities in the ground (e.g. *M. pilidens*: Müller et al. 1997; *M. marginata*: Ferton, 1914; *M. minutissima*: Alqarni et al. 2014), or more rarely in burrows dug by the bee in sandy soil (*M. leachella*: Westrich 1989; note that this species may accept trap nests under artificial conditions: Holm and Skou 1972) or in hard soil (*M. deceptoria*: Benoist 1940, Grandi 1961, Zettel et al. 2005, Mazzucco and Mazzucco 2007). *M. giraudi* appears to nest specifically in holes in rocks and to use petals for cell construction (Maneval 1939, Banaszak and Romasenko 2001; C. Praz and A. Müller, unpublished). The description of nesting aggregations in the soil for *M. leucomalla* in Central Asia (Marikovsakya 1968; see also Banaszak and Romasenko 2001) likely refers to another species, probably *M. communis*, based on Fig. 1 in Marikovsakya (1968).

The pollen preferences of species included in the subgenus *Eutricharaea* are varied; most species are probably polylectic with a preference for Fabaceae (e.g. *Megachile ro-*

tundata and *M. pilidens*: Westrich 1989; see also O'Neill et al. 2004; *M. minutissima*: Alqarni et al. 2014); Müller and Bansac (2004) have shown that some species have a distinct (e.g. *M. apicalis*) or exclusive preference for Carduoideae (*M. marginata*, *M. melanogaster* and *M. flabellipes* Pérez, 1895), and in these species a modified pollen collecting device is found under the hind trochanter and femur. Soltani et al. (in press) analyzed the pollen preferences of the taxa allied to *M. concinna*; all taxa were polylectic, although *M. leucostoma* Pérez, 1907 and *M. anatolica* Rebmann, 1969 showed a preference for Plantaginaceae (*Linaria*-type) and Lamiaceae, respectively. Two species have long and conspicuous hairs on the galea, *M. dolosa* Alfken, 1936 and *M. posti*; all known specimens of *M. posti* from Cyprus were collected on *Noaea mucronata* (Forssk.) Asch. & Schweinf. (Chenopodiaceae) (Mavromoustakis 1952). Strikingly similar hairs are found on the galea and first labial palpi of some *Hoplitis* [e.g. *H. karakalensis* (Popov 1936); A. Müller, pers. comm., January 2016]; this pollen collecting apparatus likely constitutes an adaptation for collecting pollen from small flowers of Chenopodiaceae (Müller 2016).

Subgenus *Maximegachile* Guiglia and Pasteels, 1961

Diagnosis and description. This species-poor, group 2 subgenus is probably represented in the Palearctic by one conspicuous species that is well characterized in the key. In both sexes, *Maximegachile* consists of large, elongate bees with a typical vestiture pattern: hairs are predominantly black except snow white on the propodeum, on T1 and the basal part of T2. No other Palearctic species has such a vestiture pattern. **Females:** In addition, females have an elongate, 3-toothed mandible, a modified clypeus and a strong hypostomal tooth (Fig. 17). **Males:** The males are characterized by the absence of both front coxal spine and inferior mandibular projection, by the bilobed carina of T6 and the strong preoccipital carina (see additional comments to the male morphology below).

Species composition. Two species have been mentioned for the Palearctic region and for the Arabian Peninsula: Pasteels (1979) mentions *Megachile maxillosa* Guérin-Méneville, 1845 from the Arabian Peninsula and describes *M. essenensis* (Pasteels, 1979) from a single male collected in Southern Israel. Based on the examination of numerous specimens of *M. maxillosa* from Africa, it seems that *M. maxillosa* occurs as two distinct morphs in the male sex: a large morph (body length approximately 20 mm) with clypeus entirely glabrous and covered by coarse punctures on its disc; and a smaller morph (body length approximately 15 mm) with clypeus covered by dense vestiture at least apically and with finer punctures. A similar conclusion seems to have been reached by Eardley (2012: 26), who mentions that the lower clypeus is “densely pubescent (naked in very large specimens)”. I have seen both morphs from the Arabian Peninsula but the limited material that I have seen from Israel were of the small morph, which corresponds to the description of *M. essenensis*. For now, I thus place *M. essenensis* as a junior synonym of *M. maxillosa* (syn. n.), in line with the treatment of *M. maxillosa* in Africa, and consequently I recognize only one species in the Palearctic region.



Figures 54–57. Genital capsule, lateral view. **54** *Megachile (Eutricharaea) apicalis* **55** *M. (Eutricharaea) sp. aff. naevia* **56** *M. (Eutricharaea) leachella* **57** *M. (Eutricharaea) leucomalla*.

Biology. Gess and Roosenschoon (2017) provide a description of the nesting biology of *Megachile maxillosa* in the United Arab Emirates. Nests of this species were found in trap nests. Entire cells were built using a mixture of sand and resin and the completed nests were closed with a plug of sand and resin. According to Gess and Gess (2003), the same species visits plants from various families but shows a preference for the Fabaceae, notably *Crotalaria*, in South Africa and Namibia.

Subgenus *Megachile*

Diagnosis and description. Females: In females of this subgenus, the mandible always has a conspicuous, partial cutting edge in the second interspace (reduced in *Megachile genalis*, which is easy to diagnose due to the thickened buldge at the base of the mandible: Amiet et al. 2004, Scheuchl 2006), and no visible cutting edge in the third interspace (Figs 32–34). The mandible is mostly 5-toothed with the distance between both upper teeth subequal to the distance between the other teeth (not clearly so in *M. genalis*) (Figs 1, 32); in some species teeth 4 and 5 are poorly separated (Fig. 33). In *M. bombycina*, the mandible is elongate and 4-toothed but the partial cutting edge in the second interspace

is well visible (Fig. 34). In most species, the clypeus is flat or slightly depressed preapically, and there the punctures are coarse and the interspaces wide, shiny (Fig. 32); this condition is not found in *M. lapponica* Thomson, 1872, in which the clypeus is densely punctured (Fig. 33), and in *M. bombycina*, in which the clypeus is modified, short, laterally truncate and medially produced to a blunt triangular process, and with its apical margin forming a wide, smooth and slightly concave area (Fig. 34). In the female sex, many species of *Megachile s. str.* are sculpturally similar to *Anodontetricharaea*; in the former, the scopa is mostly orange basally and rarely white, while in *Anodontetricharaea* the scopa is mostly white to yellowish white; and *Anodontetricharaea* can be distinguished by the presence of two unmodified setae on the pretarsal claws; in *Megachile s. str.*, the basal seta is modified to a thicken process, as in *Eutricharaea* or *Xanthosarus* (as in Fig. 5). **Males:** Males of the subgenus *Megachile s. str.* are rather homogenous both in their sculpture and in genitalic structures, and often difficult to identify. All males of the subgenus *Megachile s. str.* lack a front coxal spine, although in some species (*M. ligniseica*, *M. melanopyga* Costa, 1863), the front coxa forms a weak angle. The mandible is always 3-toothed, mostly with inferior projection (lacking in *M. pilicrus* and *M. armenia* Tkalčú, 1992). In most species the disc of T6 is devoid of white or light pubescence (except in *M. pyrenaica* Pérez, 1890, *M. armenia*, *M. pilicrus* and *M. melanopyga*), the preapical carina of T6 is never denticulate, although there is a lateral tooth at the lateral margin of T6 (Fig. 42). T7 is either small or exposed, but mostly unmodified (without tooth apically). The gonostylus is always simple, never bifid apically (Fig. 42).

Species composition. There are at least 14 valid species in the Western Palearctic: *Megachile alpicola* Alfken, 1924, *M. armenia*, *M. bombycina*, *M. calloleuca*, *M. centuncularis* (Linnaeus, 1758), *M. genalis*, *M. lapponica*, *M. ligniseica*, *M. melanopyga*, *M. melanota* Pérez, 1895, *M. octosignata* Nylander, 1852, *M. pilicrus*, *M. pyrenaica* and *M. versicolor*. I have not been able to locate the type of *M. dacica* Mocsáry, 1879; Schwarz et al. (1996) and Westrich (2011) recognized this species as valid; in contrast, according to identified material in his collection (OLML), B. Tkalčú considered *dacica* as a valid subspecies of *M. lapponica*. The status of *M. melanota* is unclear, as it may represent a dark color form of *M. octosignata*.

Biology. All species are leafcutters and build brood cells made of leaf fragments (e.g. Malysheva 1958, Westrich 1989, Ruhnke 2000); no Palearctic species appears to use petals as documented in the Nearctic *Megachile montivaga* (Michener, 2007, and references therein; Orr et al. 2015). The nests are mostly located in existing, above-ground cavities; some species such as *M. centuncularis* are flexible and nest both in above-ground cavities and in the soil (Westrich 1989, and references therein). Nests of *M. pyrenaica* and *M. octosignata* are placed under stones or in the soil (Ferton 1909, Grandi 1961, Westrich 1989), and a nest of *M. melanopyga* was found “loose in the grass” (Friese 1898). *M. genalis* exclusively nests in standing stems, favoring fresh stems, thus from plants of the same year; the female digs an opening and places the brood cells vertically above or below the entrance (Ruhnke 2000, and references therein). According to a brief account by Friese (1898), *M. pilicrus* nests in dry stems of thistles.

Most species of the subgenus *Megachile* are polylectic, often with a preference for Fabaceae and Asteraceae (Westrich 1989). *Megachile lapponica* is an oligolectic on *Epilobium* (Westrich 1989, Kühn et al. 2006), while *M. genalis* is possibly oligolectic on Asteraceae (Westrich 1989); *M. pilicrus* is oligolectic on Carduoideae and its hind trochanter and femur are covered by modified, stiff hairs, as observed in some *Eutricharaea* species specialized on these plants (Müller and Bansac 2004).

Subgenus *Pseudomegachile*

Diagnosis and description. This subgenus is morphologically diverse and in both sexes few diagnostic traits are common to the entire subgenus. The description is given for the each species group. The rather distinct *incana* group has previously been recognized as a distinct subgenus, *Parachalicodoma*, but in Trunz et al.'s phylogeny (Trunz et al. 2016), this group was nested within *Pseudomegachile*, with *Megachile foersteri* being sister to a clade formed by the *cyanipennis* and the *incana* groups. Based on its morphology, the *rhodoleucura* group (not included in Trunz et al. 2016) appears to build a transition between the *incana* and the *cyanipennis* groups. Similarly, the Oriental group of species previously known as *Largella* (considered here to form the *semivestita* group) is rather distinctive, although *M. lanata* is intermediate between the *semivestita* group and other, regular looking *Pseudomegachile*. Thus although *Pseudomegachile* could be split into several subgenera, numerous species are intermediate and the recognition of several subgenera does not seem practical or necessary: the number of species is not particularly large in the Palearctic or in the Oriental region, and having numerous subgenera would not be of much utility.

Species groups.

1. *foersteri* group: Males: Large species (body size above 15 mm) with metasoma densely covered by grey to yellow-brown vestiture. Front coxal spine present. Front tarsi modified, first tarsal segment concave inferiorly, segment 2 and 3 brownish-yellow and with black maculae on ventral surface. Mandible 4-toothed with quadrate inferior projection. Preapical carina of T6 multidentate and T7 produced into a long median tooth (Fig. 53). **Females:** Large (body size above 17 mm) and robust species with metasoma entirely covered by grey to yellow-brown vestiture. Mandibular surface comparatively dull (Fig. 23); mandible slightly elongate (condition intermediate between that seen in the *cyanipennis* and *ericetorum* groups), with apical margin weakly 4-toothed. Apical margin of clypeus truncate, laterally with a blunt tooth (Fig. 23). Ocellocipital particularly long, nearly three times longer than the interocellar distance.

2. *cyanipennis* group (*Xenomegachile* Rebmann, 1970): Males: Front coxal tooth present. Mandible 4-toothed (teeth sometimes blunt or small), with quadrate inferior projection. Front tarsi slightly enlarged, brownish-yellow to yellowish-white, first segment with one dark spot on ventral surface (except in *Megachile cyanipennis*). Preapical carina of T6 multidentate, laterally mostly without tooth (a small tooth is present in *M. saussurei*). T7 large, well visible from above, produced to a short spine (Fig. 52), or

trifid, or broadly truncate. **Females:** Mandible comparatively short, external margin strongly rounded, apical margin 4-toothed (Fig. 24), although sometimes teeth nearly absent and margin almost straight (Fig. 25); impunctate, premarginal area along apical margin comparatively wide (Fig. 24). Scutellum elevated medially. Ocelloccipital distance shorter than interocellar distance.

3. *rhodoleucura* group: **Males:** As in *cyanipennis* group, with the following differences: front coxal tooth small; mandible without inferior projection; front tarsi unmodified although first segment with dark spot on ventral surface; T7 with apical margin emarginate medially (Alqarni et al. 2012: Fig 12). **Females:** As in *cyanipennis* group, but apical clypeal margin apically swollen, projected over base of labrum (Alqarni et al. 2012: Figs 3–4); modified vestiture consisting of simple, short hairs on clypeus, supra-clypeal area and frons; scutellum not elevated medially.

4. *incana* group (*Parachalicodoma* Pasteels, 1966): **Males:** Medium to large species (body length above 12 mm) with pale metasomal vestiture not forming distinct tergal fasciae. Front coxa without tooth. Front tarsi unmodified. Mandible 4-toothed, without inferior projection. Preapical carina of T6 multidentate, laterally with strong tooth (Fig. 43). T7 produced to rounded or truncate spine (Fig. 43). S5 partly exposed in repose (in all other groups of *Pseudomegachile*, S5 is hidden under S4). **Females:** Large, robust species (body length above 13 mm) with pale metasomal vestiture not forming distinct tergal fasciae. Mandible 5 to 6 toothed, teeth either blunt (Fig. 21) or acute (Fig. 22); width of impunctate, premarginal area along apical margin intermediate between *cyanipennis* and *ericetorum* groups. Ocelloccipital distance shorter than interocellar distance. Hind basitarsus broad, 2.7 times as long as wide (Fig. 27). Scutellum not elevated medially. In one species the facial vestiture is modified as in the *rhodoleucura* group.

4. *ericetorum* group: **Males:** Front coxa with tooth. Mandible 3-toothed, without inferior projection, although inferior margin swollen medially. Front tarsi not particularly modified although partly yellow-brown, second segment ventrally with weak, black spot. Preapical carina of T6 multidentate (Fig. 51). T7 produced to a median tooth that is compressed laterally (Fig. 51). **Females:** Mandible long and slender, almost as in *Chalicodoma*, weakly 4-toothed, impunctate area along apical margin narrow (Fig. 20). Scutellum not elevated medially. Clypeus flat in profile, medially produced to a small tooth (Fig. 20), laterally weakly denticulate. Ocelloccipital distance longer than interocellar distance.

5. *flavipes* group (*Archimegachile* Alfken, 1933): **Males:** As in *ericetorum* group, but front tarsal segments 1–3 or 1–4 maculated ventrally, maculations sometimes reduced to thin lines. **Females:** As in *ericetorum* group, with following differences: clypeus apically without median tooth, or tooth minute; ocelloccipital distance either subequal to or shorter than interocellar distance.

6. *lanata* group: **Males:** Front coxal spine short; front tarsi unmodified. Mandible weakly 4-toothed, without inferior projection although the inferior margin is swollen medially. Preapical carina of T6 bilobed, not denticulate. T7 small, little visible. **Females:** Mandible as in *ericetorum* group, 4-toothed and comparatively elongate, im-

punctate area along apical margin narrow. Clypeus short, apical margin straight, without medial tooth. Ocellocipital distance slightly shorter than interocellar distance.

Species composition. There is only one Western Palearctic species each in the *foersteri*, *rhodoleucura*, *ericetorum* and *lanata* groups (*Megachile foersteri*, *M. riyadhensis*, *M. ericetorum* and *M. lanata*; see above for comments on the taxonomic status of *M. riyadhensis*); three species in the *incana* group, of which two are undescribed (Dorchin and Praz, in prep.). At least *M. cinnamomea* Alken, 1926, *M. farinosa* Smith, 1853, *M. flavipes* Spinola, 1838, *M. sanguinipes* Morawitz, 1875 and *M. tecta* Radoszkowski, 1888 are valid species of the *flavipes* group; the status of *M. rubripes* is unclear: both *M. flavipes* and *M. rubripes* are parapatric and sculpturally very similar and have been considered as two subspecies of the same species by some authors (e. g., Özbek and Zanden 1994). At least *M. cyannipennis*, *M. nigripes* Spinola, 1838, *M. saussurei*, *M. schmabli* Radoszkowski, 1893 and *M. seraxensis* Radoszkowski, 1893 are valid species within the *saussurei* group, which includes at least three undescribed species (Dorchin and Praz, in prep.).

Biology. The nesting biology of *Megachile ericetorum* has been described in detail (references in Westrich 1989). Ferton (1895) provides a description of the nests, which are located in existing cavities such as existing holes in soil or clay banks, or in reed stems. The cells are arranged linearly and consist of mud; Ferton observed females gathering moist soil close to streams, a behavior not observed in bees of the subgenus *Chalicodoma*, which add secretions to dry mud to build their nests (see under that subgenus). The outside of the cell is coarse and irregular, while the inner wall is lined with a thin (up to 0.5 mm) layer of resin. The cell is closed with a plug of soil; the cell cap is not lined with resin on the inside of the cell, although resin is found on the outer surface, which constitutes the base of the nest cell. The nest closure consists of a layer of mud covered by a thin layer of resin, with sometimes an additional layer (2 mm) of mud. Rozen and Kamel (2007) described the biology of *M. nigripes*, a member of the *saussurei* group. The species nests in tunnels dug by the females in “adobe”, i. e., hard, dry, mud walls. The cells, oriented almost vertically in the oblique tunnels, are elongate and not arranged linearly. The cell walls probably consist of the excavated mud wall and the inside of the cell is uneven but appears to have been lined with dark coating that is “water retardant but not truly waterproof”. The authors conclude that it may consist of “very fine soil particles bound together by partly dried nectar”. The nests of species of the *flavipes* group have been briefly described several times (Gutbier 1914, Alfken 1934, Mavromoustakis 1939, Krombein 1969). The most precise account describes the nests of *M. rubripes* in Turkmenistan (Ponomareva 1958). Nests of this species were found in reed stems. Two cells were arranged linearly and made of mud “moistened with water, apparently without using secretions (...); the dry cells instantly disintegrate on submergence in water”. As in *M. ericetorum*, the outside of the cell is irregular, but the inside is smooth; in *M. rubripes* resin or secretions were apparently not used to line the inner wall.

Megachile ericetorum is likely oligolectic on Fabaceae (Westrich 1989, Müller et al. 1997), although according to Westrich (1989) Lamiaceae pollen is very occasionally

also used (see also Gogala 2014). Limited evidence based on floral records suggests that *M. foersteri* has a preference for Carduoideae (Asteraceae) (C. Praz, unpublished data). According to Rozen and Kamel (2007), the main host of *M. nigripes* in Egypt is *Trifolium alexandrinum* L. I observed *M. saussurei* on *Medicago* in Uzbekistan and in Iran (see also Popov 1946), *M. flavipes* and the closely related *M. rubripes* only on Fabaceae. As indicated by Alqarni et al. (2012), many unrelated species of *Pseudomegachile* have conspicuously modified facial hairs; these modified hairs are always found on the clypeus but may also be found on the supraclypeal area and the frons. In the species associated with Fabaceae listed above, the hairs on the face are plumose at least in fresh specimens, while in species with modified hairs, the hairs are short, simple and often bent downwards apically, or wavy (see Müller 1996). Alqarni et al. (2012) listed several species of *Pseudomegachile* with such modification; among the Palearctic species, they cite the following species. *M. riyadhensis*, which they collected exclusively on *Blepharis* (Acanthaceae); I examined the pollen present in the scopa of the holotype of *M. rhodoleucura* (with identical facial vestiture as *M. riyadhensis*; see comments above) and the pollen also belongs to Acanthaceae. *M. farinosa* and *M. cinnamomea* (the condition is not clear in the latter species), both in the *flavipes* group also have modified facial hairs; according to my field observations, *M. farinosa* has a preference for the flowers of *Vitex* (Lamiaceae), while *M. cinnamomea* is likely polylectic. In the *saussurei* group, Alqarni et al. (2012) cite *M. transgrediens* Rebmann, 1970 as having modified facial hairs; this mention likely refers to one of two undescribed species from Turkey and Iran with modified hairs (*M. transgrediens* is probably a junior synonym of *M. saussurei*; C. Praz, unpublished); these two undescribed species are sculpturally close to *M. saussurei*, in fact differing from the latter in the female sex mostly by the modified facial vestiture. Host plants of these two species are unknown. *M. seraxensis* also has modified facial hairs; I collected one female of this species visiting *Blepharis*. Lastly, I collected in Israel several specimens of an undescribed species of the *incana* group collecting the pollen from *Blepharis*; this species has modified hairs on the clypeus, supraclypeal area and frons, exactly as in *M. riyadhensis*. Another closely related species from the *incana* group from Oman and the UAE has branched hairs on the clypeus; it was observed foraging on *Crotalaria* (Fabaceae; Sarah Gess, pers. comm., September 2016).

Subgenus *Xanthosarus*

Diagnosis and description. Females: Most females of *Xanthosarus* have a typical, broad mandible (Fig. 35) with tooth 1 larger than other teeth, without apical brush of hairs in the grooves around the base of tooth 1. In such females there is a well-visible, continuous cutting edge in the third interspace and a partial cutting edge in the second interspace (Fig. 35), the third interspace is deeper than the other interspaces, and the two upper teeth close together or poorly separated, so that the mandible is not clearly 5-toothed. Such females will be easy to identify using the present key. The mandible of *Megachile nigriventris* Schenck, 1868 (Fig. 36) [and to some extent of *M. willughbiella*

(Kirby, 1802): Fig. 37] is different, less robust, with the cutting edges little visible in front view; the upper tooth is broadly truncate and the condition is intermediate between the 4-toothed and the 5-toothed conditions. In all Palearctic species of *Xanthosarus*, the clypeus is finely and densely punctured, regularly convex (Figs 35–37) unlike the condition found in most females of *Megachile s. str.* The scopa is mostly orange-red basally, sometimes nearly entirely black (*M. nigriventris*) or yellow-white on sternites 2 and 3 [e.g. *M. maritima* (Kirby, 1802)], rarely entirely yellowish-white. The sterna lack the apical fringe of hairs beneath the scopa, unlike in most *Eutricharaea* or in *M. (Eurymella) patellimana*. **Males:** In males of *Xanthosarus* the front coxal spine is always well developed; often there is a field of modified, short, orange bristles on the surface anteriorly to the spine, but such field may be lacking (e.g. in *M. analis* Nylander, 1852). The front tarsi are always yellow or white, from relatively narrow [e.g. *M. analis*, *M. circumcincta* (Kirby, 1802)] to conspicuously enlarged [e.g. *M. lagopoda* (Linnaeus, 1761), *M. maritima*]; the first tarsal segment is mostly strongly concave interiorly, except in *M. analis*. The mandible is either 3-toothed (*M. lagopoda*, *M. maritima*) or more commonly 4-toothed; the inferior margin always has a pointed process directed posteriorly; in some large species, this process is particularly large and glabrous, except for some orange hairs apically. The disc of T6 is mostly not covered by white vestiture; the preapical carina of T6 is bilobed or weakly denticulate. The apical margin of T6 often lacks a lateral tooth (a small tooth is sometimes present, e.g. in *M. maritima*). The apex of T7 is usually produced to a small tooth medially, although the tooth is small in some species; in other species T7 is weakly trifid. The gonostylus is variable, either simple or strongly bifid, but this character does not clearly segregate groups.

Species composition. There are at least seven species in the western Palearctic: *Megachile analis*, *M. circumcincta*, *M. diabolica* Friese, 1898, *M. lagopoda*, *M. maritima*, *M. nigriventris* and *M. willughbiella*. *M. fulvimana* Eversmann, 1852 has been mentioned from Southeastern Europe (Banaszak and Romasenko 2001); this species is known to me only from Central Asia. *M. mguildensis* Benoist, 1940, from Algeria and Morocco, apparently closely related to *M. nigriventris*, may either represent a distinct species or merely a color morph of *M. nigriventris*. Özbek and Zanden (1994) further cite *M. metatarsalis* Morawitz, 1894 from Turkey; this species is unknown to me. The status of *M. fulvescens* Smith, 1853 from Sicily is unclear; it is unlikely to represent a species distinct from those listed above; its description (“the pollen brush is of golden hue towards the base, becoming bright fulvous at the apex”) suggests *M. maritima*. Similarly, the status of *M. maacki* Radoszkowski, 1874 remains in doubt; Scheuchl (2006) provides a description of the male and the female and differentiates this species from *M. nigriventris*. However, no lectotype has been designated. Of the possible syntypes that I could examine (ISZP), one male agrees with the original description and does not appear specifically distinct from *M. nigriventris*. Possibly, *M. maacki* represents an Eastern Palearctic, geographic form of *M. nigriventris*. *Xanthosarus* appears particularly diverse in the mountains of Central Asia and in Mongolia, where several additional species occur.

Biology. Most species of the subgenus *Xanthosarus* place their brood cells made of cut leaves in underground burrows or more rarely under stones; the females appear

to dig the burrows themselves (Westrich 1989, and references therein; Hartmann and Arens 1998). *Megachile nigriventris* digs burrows only in decaying wood (Westrich 1989, Dubitzky 2000, Reichholf 2002), while *M. willughbiella* either digs burrows in decaying wood or uses existing cavities such as vacant *Anthophora* cells (Westrich 1989, and references therein; Müller et al. 1997). *Megachile analis* is unusual in that it uses thin bark fragments and not leaves for the construction of the cells (Westrich 1989, and references therein); leaf discs are also used by this species.

Megachile nigriventris is likely oligolectic on Fabaceae (Westrich 1989, Müller et al. 1997) and *M. diabolica* possibly on Campanulaceae (Hartmann and Arens 1998); *M. analis* and *M. willughbiella* are polylectic but show a preference for Fabaceae and Campanulaceae, as well as for the genus *Epilobium* by *M. willughbiella* (Westrich 1989, Müller et al. 1997). *Megachile lagopoda* and *M. maritima* are likely polylectic with a preference for Fabaceae and Asteraceae.

Additional Arabian subgenera not present in the Palearctic

Amegachile

This subgenus is widespread in Africa and in the Oriental zone. I have seen two specimens from Yemen, one male and one female, presumably from two different species: the female is sculpturally similar to *Megachile fimbriata* Smith, 1853, thus belonging to the *fimbriata* group (Pasteels 1965) while the male is a member of the *bituberculata* group (possibly *M. melanops* Cockerell, 1937), with unmodified front tarsi. Both sexes of the African members of *Amegachile* have been well characterized by Pasteels (1965).

Chelostomoda

This subgenus is distributed in the tropical regions of Southeast Asia, from India to northern Australia; in China and Japan, it enters the East Palearctic region. I have examined one female (possibly *Megachile spissula* Cockerell, 1911; Stephan Risch, pers. comm., May 2014) of this subgenus from Hamburg, Germany (CSE). It is assumed here that this female represents an isolated record, possibly from nests that have been carried overseas, and that populations of this species are not currently established in Europe. For this reason, this subgenus is not included in the key.

Stenomegachile

I have seen one single female from Yemen (BMNH; likely *Megachile chelostomoides* Gribodo, 1894) belonging to this African, group 2 subgenus. This characteristic subgenus has been precisely described elsewhere (Pasteels 1965, Michener 2007).

Discussion

The review of the nesting biology of western Palearctic *Megachile* bees suggests that the morphology of the female mandible, which has largely provided the basis for the sub-generic classification of the genus, appears to be associated with nesting biology. First, the reduction of the cutting edges in some group 1 members appears to be associated with reduced leafcutting activities: in the Palearctic, cutting edges are reduced in some *Eutricharaea* (Fig. 2) and *Anodonteutricharaea*, such as *Megachile* (*Anodonteutricharaea*) *thevestensis* (Fig. 31); the latter species is peculiar in using irregularly cut leaf fragments and petals in its nest (Ferton 1911) instead of the circular leaf discs used by most other group 1 subgenera. In the New World, group 1 species in which the cutting edges are reduced use petals or chewed leaves and no leaf discs in their nests [e.g. in some species of the Neotropical subgenera *Chryosarus* and *Schrottkyapis* Mitchell, 1980; Zillikens and Steiner 2004, Martins and Almeida 1994; or in the Nearctic *M.* (*Megachile*) *montivaga*: Orr et al. 2015, and references therein]. Second, the shape of the mandible varies with nesting substrate. Subgenera that are predominantly cavity nesters, such as most members of *Eutricharaea* and of *Megachile s. str.*, have a less robust mandible with tooth one smaller or subequal to the other teeth. In these species, the apical brushes of hairs near the base of tooth 1 are present (Figs 2, 32–33, 39, 41). Ground-nesting species digging their own burrows (e.g. *Xanthosarus*, possibly *Eurymella* and *Creightonella*) tend to have broad mandibles with tooth one larger than the other teeth; these species also lack or have a reduced brush of hairs in the grooves near the base of tooth 1 (Figs 35, 38). A similarly shaped mandible is found in some species of the subgenus *Eutricharaea*, such as *M. deceptoria* (Fig. 40); unlike most other species of *Eutricharaea*, this species probably digs its own burrows (see references above). Lastly, the mandibular structure of *M. nigriventris* (Fig. 36) and *M. willughbiella* (Fig. 37), both in the subgenus *Xanthosarus*, differs from the structure seen in other species of the same subgenus (Fig. 35); both species are exceptions in *Xanthosarus* in that they do not dig their burrows in the soil, but in wood (*M. willughbiella* also uses existing cavities). The taxonomic lesson to draw from these observations is that the mandibular structure is generally conserved within subgenera as long as the nesting biology is uniform; changes in nesting habits may induce changes in morphology. In nearly all subgenera of *Megachile*, some unusual species are found with strongly modified mandibular morphologies (for example *M. genalis* and *M. bombycina* in the subgenus *Megachile*; *M. deceptoria*, *M. orientalis* and *M. giraudi* in *Eutricharaea*; *M. nigriventris* in *Xanthosarus*; the *incana* group of species in *Pseudomegachile*). Such species render the morphological delineation of these subgenera difficult. Conversely, similar nesting habits found in distantly related lineages lead to convergent evolution in the mandibular structure, as observed between *M.* (*Eurymella*) *patellimana* (Fig. 38) and *M.* (*Eutricharaea*) *deceptoria* (Fig. 40), and between *M.* (*Pseudomegachile*) *ericetorum* (Fig. 20) and the species of *Chalicodoma* (Fig. 19). These convergences in female morphology, as well as the repeated losses and, possibly, reappearance of specialized male structures have contributed to the confusing systematics of the genus *Megachile*.

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Supplementary material I

Additional notes on the new synonymies

Authors: Christophe J. Praz

Data type: species data

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