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Discovery of the Bee Tribe Tarsaliini in Arabia (Hymenoptera: Apidae), with the Description of a New Species

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ABSTRACT

The uncommonly encountered bee tribe Tarsaliini (Apinae) is recorded from the Arabian Peninsula for the first time, and based on a new species of the genus *Tarsalia* Morawitz. The tribes Ancylaini and Tarsaliini are diagnosed and their differences highlighted. *Tarsalia kindahensis* Engel, new species, is described and figured from the eastern portion of the Najd of central-eastern Saudi Arabia (Qassim and Riyadh regions). The new species is most similar to *T. mimetes* (Cockerell), known only from Egypt and Sudan, as well as the larger *T. persica* (Warncke) from Iran. These three species are morphologically and largely geographically distinct from the remainder of the genus, and are segregated into a new subgenus, *Astibomelissa* Engel. An updated and corrected checklist of the genera and subgenera of bees recorded from Saudi Arabia is appended.

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INTRODUCTION

The bee species of *Tarsalia* Morawitz are some of the more uncommonly encountered and little studied among Eurasian and northeastern African Anthophila. The genus was first described by Morawitz (1895) from material collected by explorer naturalist Dmitry K. Glazunov (1869–1913) in Razavi Khorasan Province, Iran (at the time a southern part of “Greater Khorasan” of Persia), and near the present-day borders of Turkmenistan and Afghanistan. Subsequently, Popov (1935) described a related species from southern Tajikistan (eastern Khatlon Province), and Baker (1971) a species from southern India (Karaikal), while subspecific forms of Morawitz’s and Popov’s species were documented from the eastern Mediterranean (Pittioni, 1950; Mavromoustakis, 1952). Popov (1935) also noted a similarity between *Tarsalia* and the genus *Ancyla* Lepeletier de Saint Fargeau, considering that some species of the latter may eventually prove to belong within the former. Nearly a half century later, Warncke (1977) took this similarity a step further and united *Ancyla* and *Tarsalia* as subgenera within a single genus, and subsequently provided a revision for the combined group (Warncke, 1979). Baker (1998) corrected some errors of previous authors when describing another Indian species (Konkan), as well as transferring a further two overlooked taxa described in other genera, and thereby bringing the known fauna at the time to seven species (table 1). For nearly the last 20 years no further taxonomic treatments have considered species of the genus in any detail, nor has considerable material improved our impoverished understanding of the distribution or biology of *Tarsalia*.

The general placement of *Tarsalia* among other groups of Apidae has also been challenging for several reasons, not the least of which is a dearth of material. Subsequent to Morawitz’s (1895) description, *Tarsalia* were rarely considered by melittologists, usually overlooked (e.g., Ashmead, 1899) or mentioned only in passing as a genus of anthophorines (e.g., Friese, 1896: under his concept of “Podaliriinae”). Cockerell (1933) noted a general similarity between a species of *Tarsalia* and the New World tribe Exomalopsini, although he did not recognize his species as congeneric with Morawitz’s genus and instead placed the Sudanese taxon in *Tetralonia* Spinola (Eucerini). This same author again noted a similarity between *Tarsalia* and the Exomalopsini, as well as Emphorini, when describing a species of *Ancyla* from Algeria, but again wrongly attributed its genus—this time to *Ancyloscelis* Latreille. It was Popov (1935) who first drew clearer attention to the affinities between *Tarsalia* and *Ancyla*, and documented the peculiar asymmetry in the male seventh metasomal sternum of the former. In his world classification of bees, Michener (1944) brought *Tarsalia* and *Ancyla* together formally into a tribe Ancylaini⁴ (Michener, 1944), although the characters purportedly shared between these genera were problematic and applied only to one or the other of the two (Baker, 1998). Michener (1944) did not have material from which to base his character assessments, relying on generally inadequate published descriptions, and even excluded the tribe from his final phylogenetic scheme due to the dearth of substantive information. Popov (1949) subsequently suggested a relationship between Ancylaini and Exomalopsini (echoing the notion of Cockerell, 1933), as

⁴ The tribe was originally established as Ancylini (Michener, 1944), but was emended to Ancylaini to remove homonymy with a family group among the Gastropoda (Engel et al., 2008; ICZN, 2010).

TABLE 1. Hierarchical classification of tribes Tarsaliini and Ancyilaini, with summaries of species distributions and synonyms (see also Baker, 1998).

Tribe TARSALIINI Engel, 2015	
Genus <i>Tarsalia</i> Morawitz, 1895	
Subgenus <i>Astibomelissa</i> Engel, n. subgen.	
<i>T. kindahensis</i> Engel, n. sp.	Saudi Arabia: Najd
<i>T. mimetes</i> (Cockerell, 1933)	Egypt, Sudan
<i>T. persica</i> (Warncke, 1979)	Iran: Khuzestan, Fars
Subgenus <i>Tarsalia s.str.</i>	
<i>T. ancyliformis</i> Popov, 1935	Turkey, Israel, Turkmenistan, Uzbekistan, Tajikistan
= <i>T. ancyliformis mediterranea</i> Pittioni, 1950	Cyprus, Sardinia
<i>T. cellularis</i> (Cameron, 1898)	India: Deccan Plateau
<i>T. deccana</i> Baker, 1971 [1972]	India: Eastern and Western ghats
<i>T. hirtipes</i> Morawitz, 1895	Turkey, Uzbekistan, Iran: Razavi Khorasan, Fars, Khuzestan
= <i>T. hirtipes cyriaca</i> Mavromoustakis, 1952	Cyprus
<i>T. strobilanthae</i> Baker, 1998	India: Konkan Coast
Tribe ANCYLAINI Michener, 1944	
Genus <i>Ancyla</i> Lepeletier de Saint Fargeau, 1841	
<i>A. asiatica</i> Friese, 1922	Lebanon, Turkey
<i>A. brevis</i> Dours, 1873	Algeria
= <i>A. punica</i> Friese, 1922	Tunisia
<i>A. cretensis</i> Friese, 1902	Crete
= <i>A. cretensis kilikia</i> Warncke, 1979	Turkey
<i>A. holtzi</i> Friese, 1902	Bulgaria, Cyprus, Greece, Iraq, Iran: Fars
= <i>A. holtzi anatolica</i> Warncke, 1979	Turkey
<i>A. nitida</i> Friese, 1902	Armenia, Azerbaijan, Greece, Turkey
= <i>A. nitida nigricornis</i> Friese, 1902	
<i>A. oraniensis</i> Lepeletier de Saint Fargeau, 1841	Algeria, Morocco, Tunisia
= <i>A. flavilabris</i> (Lucas, 1849)	
= <i>A. heterodoxa</i> (Cockerell, 1937)	
<i>A. orientalis</i> Warncke, 1979	Greece, Iraq, Syria, Turkey
<i>A. stollii</i> Friese, 1922	Iran: Fars, Lebanon, Syria, Turkey

well as Eucerini. The tribe has remained little understood (e.g., Michener and Moure, 1957), and attempts to place Ancyilaini among other apine bees have given varied results but consistently place *Ancyla* and *Tarsalia* near Eucerini, though they are not always as a monophyletic group (Roig-Alsina and Michener, 1993; Silveira, 1993a, 1995; Baker, 1998; Praz and Packer, 2014; Plant and Paulus, 2016). Baker (1998) went so far as to constrain Ancyilaini to only its type genus, removing *Tarsalia* as a basal branch within Eucerini and noting the birecurved gradulus on the female second metasomal sternum in both. Nonetheless, Michener (2000, 2007) retained Ancyilaini in its traditional sense, correctly noting that several of Baker's (1998) characters were questionably defined or coded. Recently, the genus *Tarsalia* was again removed from Ancyilaini, although this time placed within its own tribe, Tarsaliini, and as a putative sister group to Eucerini (Engel, 2015).

Including a species established herein, the Tarsaliini and Ancyilaini each consist of eight, uncommonly encountered species (table 1), the latter occurring in Mediterranean Europe, Western Asia, and northern Africa, while the former encompasses roughly the same area although

more restricted in northeastern Africa and extending into Central Asia and India. The known records of *Tarsalia* reveal a rather disjunct distribution—the European/Western and Central Asian occurrences, the Indian species, and those species in northeastern Africa. Here we report the discovery of the tribe Tarsaliini for the first time from the Arabian Peninsula, expanding the distribution of this lineage into the region and closing the otherwise purported gap between those taxa in northeastern Africa and the Asiatic fauna. In addition, we provide revised diagnoses of the tribes Ancylini and Tarsaliini, highlighting their distinctive traits. An initial survey of the supraspecific groups of bees occurring in Saudi Arabia was outlined by Engel et al. (2013) with the intention of encouraging further collecting throughout the peninsula. Subsequently, several genera have been newly recorded for the country, or even the entire peninsula, much as is done here with *Tarsalia*, and we accordingly append an updated list (appendix).

MATERIAL AND METHODS

Specimens of *Tarsalia* were taken at two localities in central Saudi Arabia during the 2011 and 2013 field seasons, while other attempts to locate individuals and nests were unsuccessful. The available material is deposited in the Division of Entomology (Snow Entomological Collections), University of Kansas Natural History Museum, Lawrence, Kansas (SEMC), and the King Saud University Museum of Arthropods, Plant Protection Department, College of Food and Agriculture Sciences, King Saud University, Riyadh, Saudi Arabia (KSMA). Comparative material of all other species of *Tarsalia*, with the exception of *Tarsalia cellularis* (Cameron), and diverse *Ancyla* and Eucerini were examined from the collections of SEMC.

Descriptions are provided in the context of improving identifications of and species-level treatments of bees (Engel, 2011; Gonzalez et al., 2013). For the descriptive sections, the morphological terminology is largely adapted from Michener (2007) and Engel (2001), and from Snelling (1981) in terms of setal orientation. However, we have used a slightly revised terminology for tibial spurs, particularly the protibial calcar (= “fibula” sensu Snodgrass, 1956). Following Engel (2009) we use the term *rachis* for the main, longitudinal body of the spur along its entire length, and as commonly employed in biology for any spine or shaft forming the principle axis. For the protibial calcar, which forms a portion of the foreleg strigilis or “antenna cleaner,” we restrict the term *malus*⁵ (in Latin referring to a mast) to that apical portion of the rachis beyond the primary velum (and, when present, the secondary, anterior velum: Schönitzer and Renner, 1980; Schönitzer, 1986). The anterior velum is often lacking, but variably represented among different lineages by a carina, thin lamella, or a reduced, lamellate lobe (Schönitzer, 1986).

Microphotographs were prepared through the combination of consecutive images at successive focal plans, all shot using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens. Measurements of specimens relied upon an ocular micrometer and an Olympus SZX-12 stereomicroscope, those of the paratype male in parentheses.

⁵ The term *malus* as used by Michener (1944, 2007), Eickwort (1969), and Engel (2000, 2001) is equivalent to *rachis*, but the latter term is more broadly applicable to the axial length of all tibial spurs.

SYSTEMATICS

Subfamily Apinae Latreille, 1802

Tribe Ancyilaini Michener, 1944

Ancyilini Michener, 1944: 273. Type genus: *Ancyla* Lepeletier de Saint Fargeau, 1841.
Ancyilaini Michener, nomen emendatum; Engel et al., 2008: 199; ICZN, 2011: 116.

DIAGNOSIS: Bees of small to moderate size (5–10 mm in length); head about as wide as long to wider than long and face comparatively narrow, interocular distance less than compound eye length; vertex comparatively straight, not uniformly convex nor excavated between compound eyes and ocelli in facial view. Lower face often without maculation (see sexes below); clypeus flat to weakly protuberant in profile, scarcely bent back at side of labrum. Labrum broader than long. Malar space linear, nearly lacking with mandibular base abutting lower compound eye margin. Mandible simple, without distinct subapical tooth; articulations equidistant from compound eye, posterior articulation behind mediolongitudinal axis of compound eye. Postpalpal portion of galea broad proximally, then attenuate and with weakly sclerotized strip extending to apex; maxillary palpus with six palpomeres. Glossa and labial palpus much shorter than prementum; submental spine present; paraglossa short; labial palpus with four palpomeres, first two palpomeres similar in shape to apical two palpomeres, not flattened; submental spine absent. Pronotum without transverse carina. Propodeum basally declivitous, basal area impunctate, not covered by setae. Protibial calcar of strigilis with anterior carina or thin lamella on rachis bordering primary velum but lacking anterior, secondary velum; primary velum rectangular with inner margin rounded, with inner apical corner projected as acutely pointed process; malus short, often shorter than velum, with apex straight, inner margin minutely ciliate. Mesotibial spur long, serrate, apex slightly incurved; mesobasitarsal comb absent. Metabasitibial plate short, wider than long, apically weakly and broadly rounded; metatibial spurs long, serrate, apices straight or slightly incurved. Pretarsal arolium present. Forewing with pterostigma small, longer than wide, scarcely wider than prestigma; pterostigmal margin inside marginal cell convex, sometimes weakly so; marginal cell apex not truncate, bent away from anterior wing margin; three submarginal cells present; membrane with setae throughout. Hind wing with 2M+Cu about one-half as long as M, or slightly more; cu-a transverse, one-half length or more of M; jugal lobe short, slightly less than one-half length of vannal lobe. Metasomal tergum I without carina at angle of anterior- and dorsal-facing surfaces, at most sharply angulate in some males.

FEMALE: Face without maculation; probasitarsus without anterior or posterior combs; metatibial and metabasitarsal scopa large, dense, composed of long, plumose setae, without oil-collecting structures; metabasitibial plate surface bare and smooth; pretarsal claws with small basal tooth; metasomal tergum VI with narrow pygidial plate; gradulus of metasomal sternum II simple; sterna II–V with scattered long, subdecumbent setae apically, but not forming scopa.

MALE: Clypeus, supraclypeal area, paraocular area, and antennal scape with maculation; apical margin of clypeus with linear patch of distinctive setae; ventral surface of mandible and

usually postgena near mandibular base with characteristic patch of dense setae; flagellum crenulate; mesobasitarsus, metatibia, metabasitarsus, and metatibial spurs frequently greatly modified (e.g., mesobasitarsus swollen with dense setae; metatibia swollen, with modified setae; metabasitarsus thickened and arched, with concave inner surface and modified; metatibial spurs elongate and broadly curved); metabasitibial plate covered with appressed setae; pretarsal claws deeply cleft; tergum VII setose, with pygidial plate present; sternum V with subapical, paramedial setal patches and apical, paramedial, thumblike processes bordering medial concavity; sternum VI with medial tubercle extending between processes of sternum V, and variously with broadly concave areas laterally and medially, with mediolongitudinal ridge or carina and medioapical margin variously modified; sternum VII with lateral and apical lobes; sternum VIII with apical lobes; gonostylus without setigerous parapepial lobe; spatha present.

COMMENTS: The presently included species, all in the genus *Ancyla* (= *Plistotrichia* Morawitz, 1874), and their distributions are summarized in table 1. The nesting biology and immature stages have been reported for two species of *Ancyla* (Straka and Rozen, 2012), and the species are generally considered specialists of Apiaceae and has mouthparts similar to short-tongued bees (Silveira, 1993b; Straka and Rozen, 2012).

Tribe Tarsaliini Engel, 2015

Tarsaliini Engel, 2015: 4. Type genus: *Tarsalia* Morawitz, 1895.

DIAGNOSIS (modified and expanded from Engel, 2015): Bees of small to moderate size (5.5–13 mm in length); head wider than long, but face comparatively narrow, interocular distance less than compound eye length; vertex comparatively straight, not uniformly convex nor excavated between compound eyes and ocelli in facial view (fig. 1D). Lower face often with maculation (see sexes below); clypeus weakly to moderately protuberant in profile, strongly bent back at side of labrum. Labrum broader than long. Malar space linear, nearly lacking with mandibular base abutting lower compound eye margin. Mandible simple, without distinct subapical tooth; articulations equidistant from compound eye, posterior articulation behind mediolongitudinal axis of compound eye. Postpalpal portion of galea broad proximally, then attenuate and with weakly sclerotized strip extending to apex; maxillary palpus with six palpomeres. Glossa and labial palpus longer than prementum; submental spine present; paraglossa short, not exceeding first labial palpomere; labial palpus with four palpomeres, first two palpomeres long, sheathlike (contrasting with condition in Ancylaini where first two palpomeres are similar in shape to apical two palpomeres); submental spine present. Pronotum without transverse carina. Propodeum basally with subhorizontal area, subhorizontal area punctate and setose. Protibial calcar of strigilis with anterior carina or thin lamella on rachis bordering primary velum but lacking anterior, secondary velum; primary velum rectangular with inner margin blunt, straight, with inner apical corner projected as acutely pointed process (as in most Eucerini, Ancylaini, Exomalopsini, and Emphorini: Schönitzer, 1986); malus elongate, as long as or longer than velum, with apex straight or slightly incurved, inner margin minutely ciliate. Mesotibial spur long, serrate, apex slightly

incurved; mesobasitarsal comb absent. Metabasitibial plate short, wider than long, apically weakly and broadly rounded; metatibial spurs long, serrate, apices slightly incurved. Pretarsal arolium present. Forewing with pterostigma small (fig. 1A), as long as wide, scarcely wider than prestigma; pterostigmal margin inside marginal cell weakly or not convex; marginal cell apex not truncate, bent away from anterior wing margin; three submarginal cells present; membrane with setae throughout. Hind wing with $2M+Cu$ one-half as long as M or less; $cu-a$ transverse, more than one-half length of M ; jugal lobe short, slightly less than one-half length of vannal lobe. Metasomal tergum I with or without carina at angle of anterior- and dorsal-facing surfaces (absent in two species).

FEMALE: Labrum, clypeus, and supraclypeal area usually with maculation (fig. 1D) (absent in one species); paraocular area usually without maculation (present in one species); antennal scape usually without maculation (present in one species); probasitarsus without anterior or posterior combs; metatibial and metabasitarsal scopa large, dense, composed of long, plumose setae, without oil-collecting structures; metabasitibial plate surface bare and smooth; pretarsal claws with minute basal tooth; metasomal tergum VI with narrow pygidial plate; gradulus of metasomal sternum II weakly birecurved (similar to condition in some *Thygater* Holmberg); sterna II–V with scopa composed of long, dense setae, such setae often apically wavy or sinuous (similar to type IV of Pasteels and Pasteels, 1974).

MALE: Labrum with maculation (reduced to a medioapical spot in one species); clypeus and supraclypeal area usually with maculation (absent in one species); paraocular area with maculation; antennal scape usually without maculation (absent in one species), flagellum not crenulate nor elongate; metabasitibial plate often shorter than in female, covered with appressed setae; pretarsal claws deeply cleft; tergum VII setose, with true pygidial plate absent (no raised pygidial plate, instead surface continuous with disc and uniformly covered with setae), instead with distinct lateral carina and apicomediaally produced and truncate to weakly bilobate (broadly and shallowly emarginate), medial projected area rounded and deflexed in two species; apical margin sternum V straight to medially lobate; sternum VI narrowed apically, apical margin usually characteristic (truncate, rounded, or medially emarginate), with lateral marginal areas broadly concave and typically smooth, producing narrow medial area usually bearing a medial tubercle or carina; sternum VII with lateral and apical lobes; sternum VIII with apical lobes; gonostylus with parapenial lobe bearing thickened setae; spatha present (absent in one species); hidden sterna and genitalia asymmetrical (sternum VII usually strongly asymmetrical; sternum VIII less dramatically so; sometimes with penis valves strongly asymmetrical).

COMMENTS: Recently, the tribe was proposed as “new” again in Plant and Paulus (2016), despite having already been made available a year prior to this. The name as employed by these authors has no nomenclatural standing.

Baker (1998) speculated that the characteristic sternal setae functioned as a scopa. However, conclusive evidence demonstrating the use of the sternal setae for pollen transport is lacking, and both Michener (2007) and Plant and Paulus (2016) indicated that specimens with copious pollen in the hind-leg scopae lacked pollen on the sterna. However, we’ve followed Baker (1998) in considering the sternal setae as a metasomal scopa as

the female of the new species described below has appreciable pollen in only two places on the body: the hind-leg scopae and the sternal setae. It is hoped that biological studies will someday be possible to permit an evaluation of the true functional significance of the dense sternal setae of *Tarsalia*.

The chiral form of the male terminalia is unique among bees. The asymmetry of the male sternum VII, and to a lesser degree sternum VIII, along with the sometimes hypertrophy of one penis valve, is immediately distinctive and peculiar. The purpose for this consistent chirality is unclear and, as noted by Baker (1998), does not correspond to any asymmetry in the female terminal sclerites. Until such time as the mating behavior of these bees is discovered, the function of these asymmetries shall remain a mystery, but in the meantime they represent a strong synapomorphy for the tribe.

We have considered the males of *Tarsalia* to lack a true pygidial plate. It is definitive that a pygidial plate as traditionally defined (Michener, 1944) is lacking in males of *Tarsalia*. However, the seventh tergum is medioapically produced with the tergal apical margin carinate, suggestive of a plate, and leading some to speculate that the majority of the tergal apical dorsum is equivalent to a pygidial plate (Michener, 2007). However, this apical surface is continuous on all sides with the remainder of the tergal disc, as well as identically sculptured and uniformly covered with setae, in stark contrast to the distinctly raised surface of a pygidial plate which also almost invariably differently sculptured and either lacking in setae or with such setae distinctly differing from those of the surrounding disc. Thus, from a strictly morphological standpoint we do not consider a true pygidial plate to be present in *Tarsalia*, and the form of the seventh tergum in these bees should not be confused with those lineages in which such a plate is present (e.g., Ancyloini). Even if the apical protrusion of the seventh tergum of male *Tarsalia* should be shown later to be developmentally homologous to the pygidial plate, it still remains a fundamentally different structure of uncertain function and such a character state should not be equated or confused with the pygidial plate in other bees. Referring to the present character state as a "pygidial plate" obscures the uniqueness of the condition found among *Tarsalia*, as well as misleads others, we believe, as to its morphological identity (i.e., that a true pygidial plate is lacking).

Genus *Tarsalia* Morawitz, 1895

Tarsalia Morawitz, 1895: 9. Type species: *Tarsalia hirtipes* Morawitz, 1895, by monotypy. Friese, 1896: 211; Baker, 1998: 837; Michener, 2000: 666; Michener, 2007: 686.
Ancyla (*Tarsalia*) Morawitz; Warncke, 1977: 58; Warncke, 1979: 192.

DIAGNOSIS: As for tribe (above).

COMMENTS: The genus currently includes two rather distinct groups, one with three species in northeastern Africa, Arabia, and Iran, while the other has five species in Western and Central Asia, south into India, and west on the Mediterranean islands of Cyprus and Sardinia (table 1).

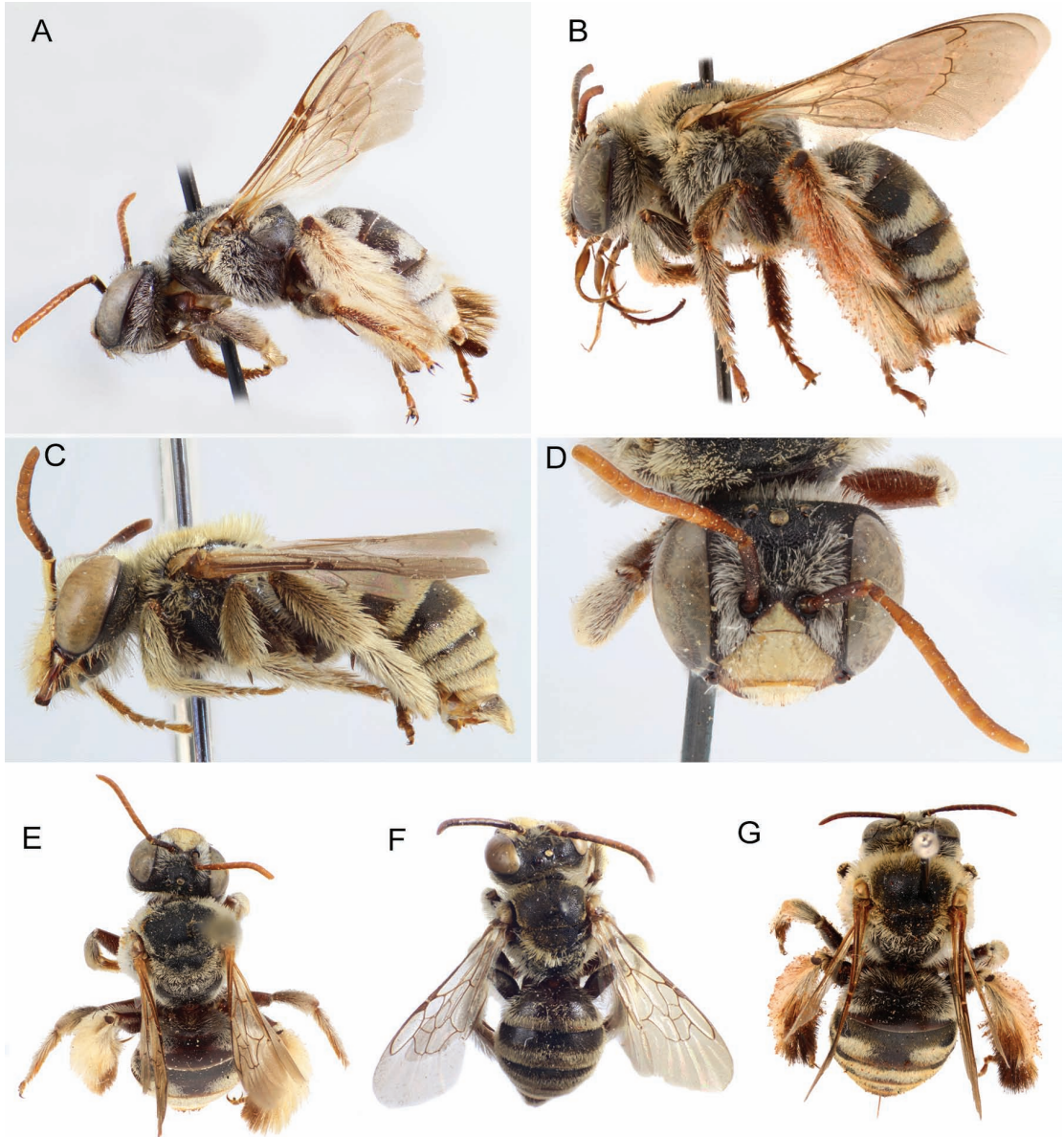


FIGURE 1. Representative species of *Tarsalia* Morawitz, subgenus *Tarsalia* s. str. **A.** *Tarsalia (Tarsalia) ancyliformis* Popov, lateral habitus of female. **B.** *T. (T.) hirtipes* Morawitz, lateral habitus of female. **C.** *T. (T.) deccana* Baker, lateral habitus of male holotype. **D.** Facial view of female *T. ancyliformis*. **E.** Dorsal habitus of female *T. ancyliformis*. **F.** Dorsal habitus of male *T. deccana*. **G.** Dorsal habitus of female *T. hirtipes*.



FIGURE 2. Posterior view of metatibial and metabasitarsal scopae of species of *Tarsalia* Morawitz. **A.** Open scopal form of *Tarsalia* (*Tarsalia*) *ancyliformis* Popov. **B.** Dense, closed scopal form of *T.* (*Astibomelissa*) *persica* (Warncke).

Key to Subgenera of *Tarsalia*

1. Metasoma and mesosoma dark reddish brown to black (fig. 1); metatibial scopa open (fig. 2A); subtriangular patch of distinctive, squamiform setae on outer surface of metatibia apical to metabasitibial plate (Sardinia, Cyprus, Western and Central Asia, India) *Tarsalia s. str.*
- Metasoma and majority of mesosoma light castaneous to testaceous (figs. 3, 4); metatibial scopa densely closed (fig. 2B); outer surface of metatibia apical to metabasitibial plate without patch of distinctive setae, area similar to remainder of scopal setae (northeastern Africa, Arabia, Iran) *Astibomelissa*, n. subgen.

Astibomelissa Engel, new subgenus

TYPE SPECIES: *Tarsalia kindahensis* Engel, new species.

DIAGNOSIS: Body length approximately 5.5–9.0 mm; integument pale castaneous to testaceous on metasoma and majority of mesosoma (figs. 3–5, 6). Female metatibial scopa densely

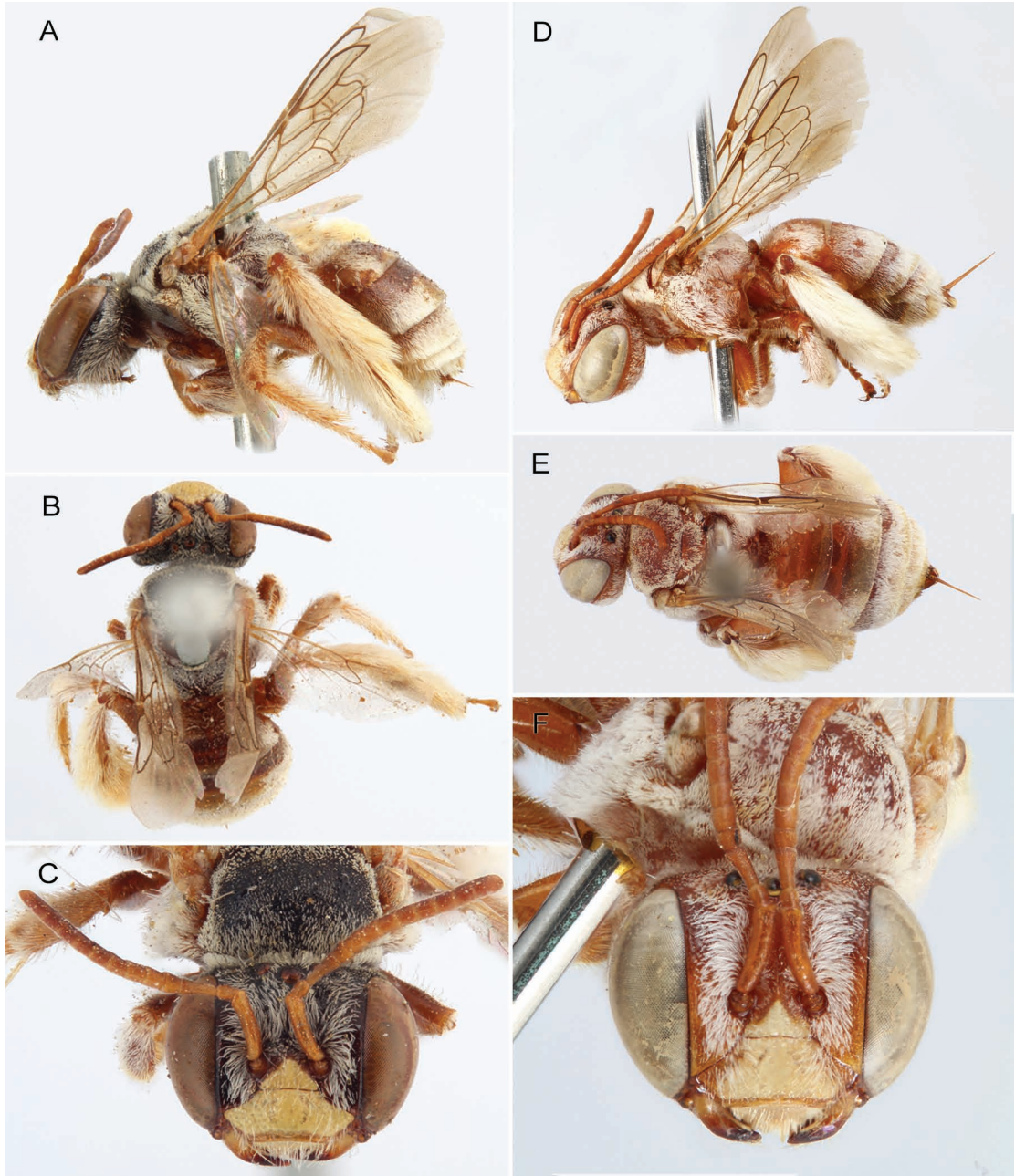


FIGURE 3. Representative species of *Tarsalia* Morawitz, subgenus *Astibomelissa*, new subgenus. **A.** *Tarsalia (Astibomelissa) mimetes* (Cockerell), lateral habitus of female. **B.** Dorsal habitus of female *T. mimetes*. **C.** Facial view of female *T. mimetes*. **D.** *T. (A.) persica* (Warncke), lateral habitus of female. **E.** Dorsal habitus of female *T. persica*. **F.** Facial view of female *T. persica*.

closed (fig. 2B); outer surface of metatibia apical to metabasitibial plate without patch of distinctive setae, area similar to remainder of scopal setae. Metasomal tergum I with or without carina at angle of anterior- and dorsal-facing surfaces (all species of *Tarsalia* s. str. with carina, albeit sometimes weakly so).

ETYMOLOGY: The new subgeneric name is a combination of the Greek *astibes* (meaning, “untrodden,” hence “desert”) and *melissa* (meaning, “bee”). The gender of the name is considered feminine.

INCLUDED SPECIES: The subgenus presently includes three species: *T. persica* (Warncke) from forest steppes and semidesert regions of Iran to either side of the Zagros Mountains (Warncke, 1979; Baker, 1998); *T. mimetes* (Cockerell) from Upper Egypt and the Sudan (Cockerell, 1933; Baker, 1998); and *T. kindahensis*, n. sp., from the Najd Plateau of Saudi Arabia (east of the Hejaz and immediately west of the ad-Dahna Erg or Desert), with records from near Unayzah and separated by the Thuwayrat dunes from the others southeast near al-‘Amāriah on the Tuwayq escarpment, Riyadh.

Key to Species of *Astibomelissa*

1. Mesoscutum with numerous appressed to decumbent, plumose setae (usually missing on central disc, presumably due to abrasion), setae longer, not squamiform; outer surface of probasitarsus with fine, erect to suberect setae with distinctly sinuate or wavy apices (= type IV of Pasteels and Pasteels, 1974); inner setae of metabasitarsus white to pale yellow and similar to setae of scopa; metasomal tergum I without transverse carina at angle of anterior- and dorsal-facing surfaces; smaller species, 5.5–7.5 mm in total length (Saudi Arabia; northeastern Africa) 2
- Mesoscutum tomentose, with dense covering of appressed, minute (typically about 0.50× ocellar diameter), squamiform setae; outer surface of probasitarsus with fine, subdecumbent setae tapering to straight apices; inner setae of metabasitarsus fuscous, contrasting with surrounding white to pale yellow setae of scopa; metasomal tergum I with transverse carina at angle of anterior- and dorsal-facing surfaces; larger species, 7.9–8.8 mm in length [Iran] *T. persica* (Warncke)
2. Female with yellow facial maculation confined to labrum, clypeus, and supraclypeal area (fig. 3C); metasomal scopa dense, with setae greatly elongate and subdecumbent to suberect; small species, approximately 5.5–6.5 mm in length (male unknown) [Egypt, Sudan] *T. mimetes* (Cockerell)
- Female with yellow facial maculation extending to paraocular area and scape (fig. 6C); metasomal scopa not so dense, with setae long and largely decumbent to subdecumbent; moderate-sized species, approximately 6.7–7.5 mm in length (central Saudi Arabia). *T. kindahensis* Engel, n. sp.



FIGURE 4. Holotype male of *Tarsalia (Astibomelissa) kindahensis* Engel, new species, from central Saudi Arabia. A. Lateral habitus. B. Dorsal habitus. C. Facial view.

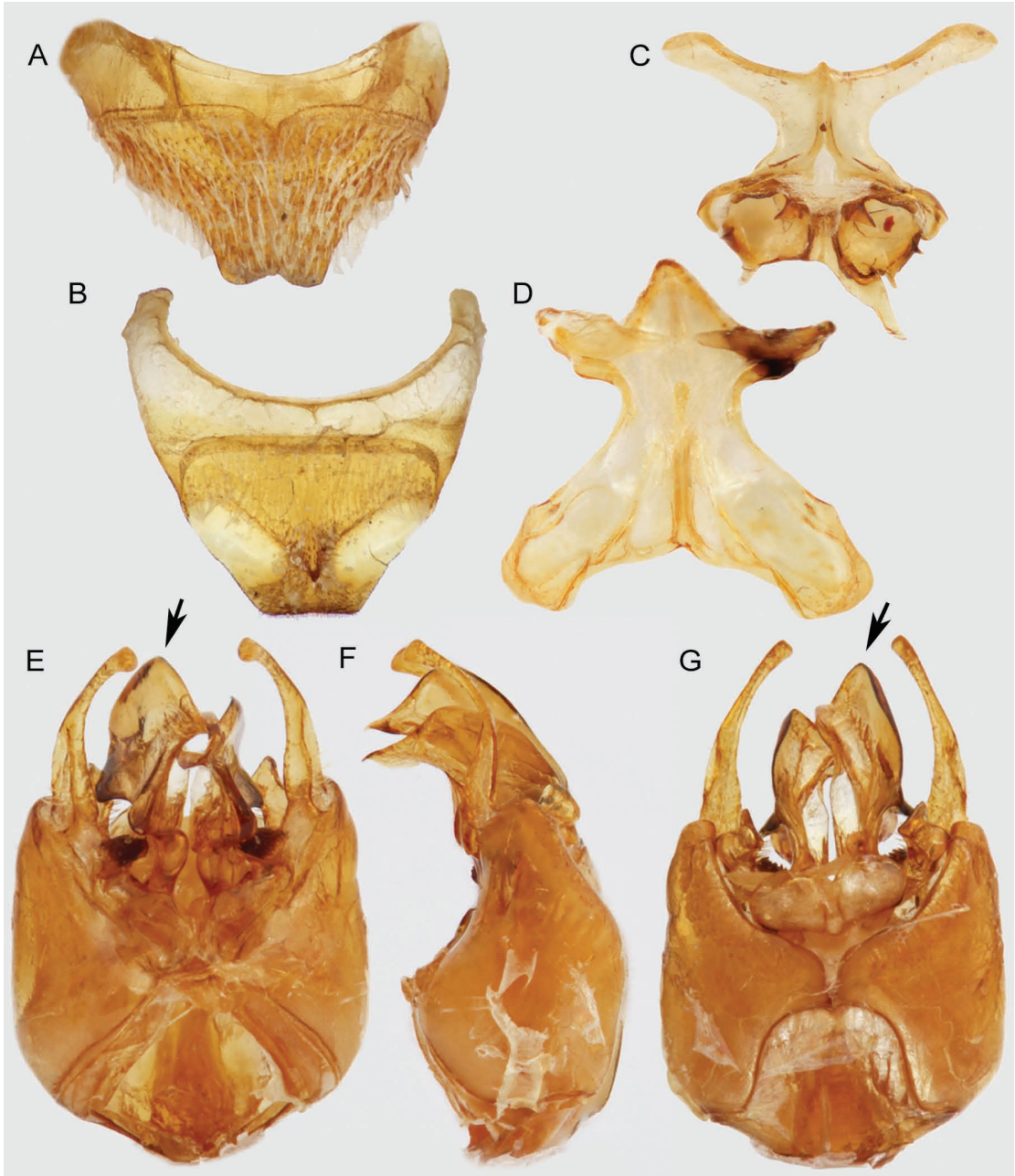


FIGURE 5. Male terminalia of *Tarsalia (Astibomelissa) kindahensis* Engel, new species, from central Saudi Arabia; note the pronounced asymmetry of the penis valves (arrows). **A.** Dorsal view of metasomal tergum VII. **B.** Ventral view of metasomal sternum VI. **C.** Ventral view of metasomal sternum VII. **D.** Ventral view of metasomal sternum VIII. **E.** Genital capsule, ventral view. **F.** Genital capsule, lateral view. **G.** Genital capsule, dorsal view.

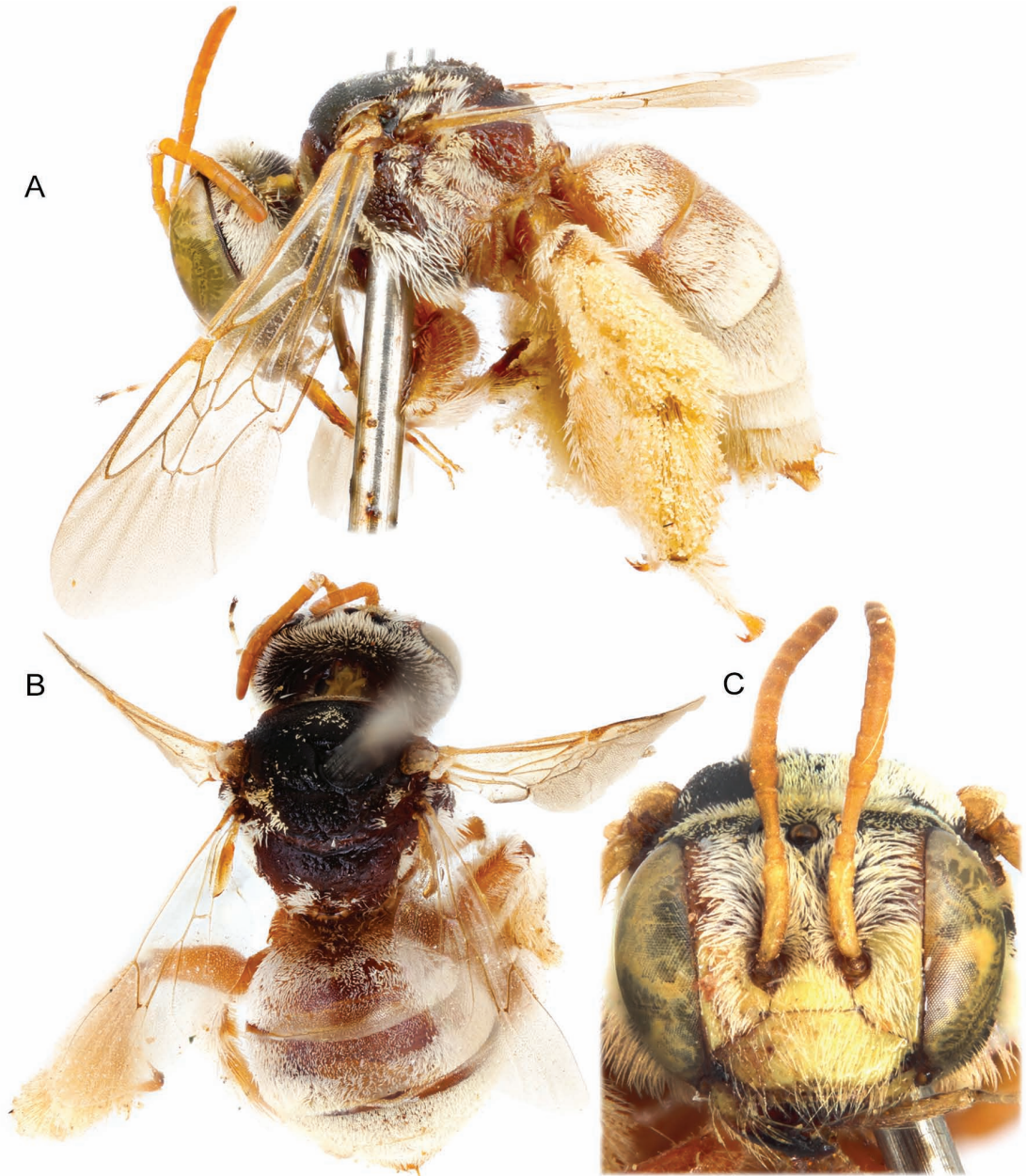


FIGURE 6. Paratype female of *Tarsalia (Astibomelissa) kindahensis* Engel, new species, from central Saudi Arabia. A. Lateral habitus. B. Dorsal habitus. C. Facial view.

Tarsalia (Astibomelissa) kindahensis Engel, new species

Figures 4–6

DIAGNOSIS: *Tarsalia kindahensis* can be recognized by combination of largely pale castaneous to light testaceous integument on metasoma, legs, and sometimes large portions of mesosoma although nota and much of pleura darker (figs. 4, 6); outer surface of female probasitarsus with dense, long, suberect setae with sinuate or wavy apices; metasomal tergum I without transverse dorsal carina; female metasomal scopa with long, subdecumbant setae with sinuate or wavy apices; male tergum VII with medioapical produced margin weakly bilobate (fig. 5A); male sternum VI apically truncate and with medial tubercle (fig. 5B); male hidden sterna asymmetrical and of characteristic form (fig. 5C); left penis valve hypertrophied (figs. 5E, 5G); and unique possession of yellow facial maculation on female paraocular area and scape, in addition to labrum, clypeus, and supraclypeal area (fig. 6C).

DESCRIPTION: MALE: Total body length 6.72 mm (7.14 mm); forewing length 4.70 mm (5.18 mm). Head wider than long, length 1.69 mm (1.94 mm), width 2.28 mm (2.34 mm); inner margins of compound eyes comparatively straight, parallel in lower two-thirds, slightly diverging in upper third, upper interorbital distance 1.31 mm (1.37 mm), lower interorbital distance 1.16 mm (1.22 mm); apex of clypeus slightly below lower tangent of compound eyes; clypeus weakly protuberant and convex; ocelli at upper tangent of compound eyes; lateral ocelli separated from median ocellus by about one-half median ocellar diameter; lateral ocellus separated from eye by about 1.6× lateral ocellar diameter; lateral ocellus separated from posterior of head by about its diameter; scape short, extending at most to lower border of median ocellus; FI slightly longer than apical width, longer than FII. Intertegular distance 1.41 mm (1.53 mm). Basal area of propodeum weakly defined, about as long as metanotum. Legs without special modifications; mesobasitarsus elongate, straight, spur extending to slightly basad basitarsal midlength; metafemur slightly thicker than mesofemur; metabasitarsus elongate. Forewing with basal vein basad cu-a by 2–3 times vein width; 1m-cu entering second submarginal cell; second submarginal cell shortest, narrowed toward anterior wing margin; 2rs-m arcuate. Hind wing with nine distal hamuli. Metasomal tergum I without carina at angle of anterior- and dorsal-facing surfaces (similar to *T. mimetes*); tergum VII gradulus medially pointed posteriorly, without lateral gradular teeth (sensu Baker, 1998), but lateral area instead angulate, apical margin projected, deflexed medially, margin shallowly and broadly emarginate (fig. 5A); sternum V with medioapical margin produced with broad, apically blunt lobe; sternum VI narrowed apically, medioapical margin truncate, with broadly concave, smooth ovoid areas laterally along margin producing narrow medial disc bearing a medial tubercle (fig. 5B); hidden sterna VII and VIII asymmetrical and as in figures 5C and 5D; genitalia as in figures 5E–G, with penis valves markedly asymmetrical (figs. 5E, 5G).

Integument somewhat shining. Labrum with coarse, shallow, contiguous punctures, otherwise smooth. Clypeus with coarse, faint, shallow punctures separated by less than a puncture width, except slightly more spaced along borders and more oblique, approximately separated by a puncture width or sometimes slightly more, integument between punctures smooth. Supr-

aclypeal area with smaller, more well-defined punctures, separated by a puncture width, except medially slightly more separated, integument otherwise smooth. Face below level of antennae with small, faint, scattered punctures, separated by less than a puncture width along border with clypeus and subantennal sulcus, then becoming sparser toward inner margin of compound eye such that paraocular margin impunctate, integument between punctures smooth. Face above level of antennae with small, well-defined punctures separated by less than a puncture width, integument between punctures faintly imbricate; punctures sparse in short, broad triangular patch immediate anterior to median ocellus and absent in paraocular margin where integument is strongly imbricate; ocellocular space medially as on upper face but with punctures absent along outer border of lateral ocellus and in paraocular margin bordering compound eye, former patch smooth, latter strongly imbricate; vertex as on upper face; gena as on upper face except punctures smaller and becoming gradually more widely spaced ventrally such that on lower gena punctures separated by 2–3 times a puncture width, integument between punctures smooth; postgena with minute punctures similar to those on lower gena except sparse, integument otherwise smooth. Pronotum with sparse, minute punctures, integument otherwise smooth. Mesoscutum with small, well-defined punctures separated by less than a puncture width, with some posteromedially separated by about a puncture width, integument between punctures; tegula generally smooth to faintly imbricate, with sparse, minute punctures; mesoscutellum with punctures as on mesoscutum except somewhat larger and coarser. Metanotum finely imbricate with scattered, shallow, faint punctures. Pleura with small, well-defined punctures, integument otherwise smooth except more imbricate in area of mesepisternal border with metepisternum; punctures on hypoepimeral area becoming oblique ventrally, nearly contiguous, except sparse along scrobal sulcus; punctures on preepisternal area smaller, becoming shallower, fainter, and oblique toward anterior margin; punctures on mesepisternum below scrobal sulcus becoming fainter along posterior border and on ventral-facing surface; metepisternum imbricate with sparse punctures. Basal area of propodeum largely obscured by setae, integument apparently imbricate and coarsely punctate; posterior and lateral surfaces of propodeum faintly imbricate to smooth, with scattered, small punctures. Metasomal terga with minute, well-defined punctures separated by less than a puncture width, except anterior-facing depression of tergum I largely smooth and narrow apical margins of terga smooth, integument between punctures smooth; sterna as on terga except punctures coarser and integument otherwise more imbricate.

Coloration of head generally testaceous to black (lighter in holotype male, darker in paratype male), except labrum entirely yellow; mandible largely yellow except dark reddish brown to black apically; clypeus and supraclypeal area entirely yellow; paraocular area yellow below level of antennae and broadly along compound eye in lower half of upper face; paraocular area in upper half of face above antennae dark brown to testaceous; scape yellow, pedicel and flagellomeres I and II yellowish brown; remainder of flagellum orange. Pronotum dark reddish brown to testaceous (testaceous in holotype male, dark testaceous along borders blending to dark reddish brown posteriorly in paratype male). Mesoscutum and mesoscutellum dark testaceous to black; tegula semitranslucent; metanotum testaceous to dark reddish brown; pleura

testaceous to dark reddish brown; basal area of propodeum dark testaceous to black, remainder of propodeum testaceous to dark reddish brown. Legs testaceous. Wing membranes hyaline, faintly parchment colored; veins yellowish brown to dark brown. Metasoma testaceous.

Pubescence white and often obscuring integument on frons, vertex, gena, mesosoma, tibiae, tarsi, and metasomal terga where such setae usually appressed to decumbent and plumose (setae with numerous, minute branches along length of rachis, giving feathered appearance: similar to short-branched setal forms described by Saunders, 1878, and Braue, 1913), setae of mesoscutum not squamiform, typically as long as or slightly longer than ocellar diameter (setae abraded from large areas of mesosoma and anterior metasomal terga on paratype male, allowing view of integumental sculpture); labrum with transverse, medial patch of short, erect, branched setae; setae below level of antennae typically sparse, suberect to erect, long, and minutely branched, similar setae on postgena; mesosoma with setae less prominent on preepisternal area and posteroventrally on mesepisternum and anteroventrally on lateral propodeal surface; tergal setae largely short and appressed; sternal setae longer, suberect, and posteriorly directed.

FEMALE: As described for male, except as follows: total body length 7.50 mm; forewing length 5.00 mm. Head wider than long, length 1.81 mm, width 2.44 mm; inner margins of compound eyes comparatively straight, slightly convergent below, upper interorbital distance 1.51 mm, lower interorbital distance 1.33 mm; lateral ocelli separated from median ocellus by about one-half median ocellar diameter; lateral ocellus separated from eye by about 2.0× lateral ocellar diameter; lateral ocellus separated from posterior of head by about its diameter; scape short, extending to slightly less than distance to lower border of median ocellus; FI elongate, length about twice apical width, about twice as long as FII. Intertegular distance 1.56 mm.

Coloration as in darker male (above) (fig. 6).

Pubescence as in male except for sex differences: probasitarsus with fine, erect to suberect setae with distinctly sinuate or wavy apices; metatibial and metabasitarsal scopa composed of dense, elongate, plumose setae; metasomal sterna II–V with rows of elongate, subdecumbent setae with sinuate or wavy apices, forming distinct scopa; sternum VI with medioapical patch of dense, short, erect setae.

HOLOTYPE: ♂, Saudi Arabia: Riyadh, al-Amariah [al-‘Amāriah, a locality about 12 km west of Riyadh], Majra [Mazra‘ah] al-Gasim [al-Qasim, farm], 23.v.2011 [23 May 2011], M.A. Hannan (KSMA).

PARATYPES: 1 ♀, Saudi Arabia: Riyadh, al-Amariah [al-‘Amāriah], Majra [Mazra‘ah] al-Gasim [al-Qasim, farm], 19.vi.2011 [19 June 2011], M.A. Hannan & I. Naser (SEMC); 1 ♂, Saudi Arabia: Qassim [al-Qassim], Unizah [Unayzah], al-Watania Farm, Rowdah, 29.v.2013 [29 May 2013], M.A. Hannan; *Pulicaria undulate* [sic] [*Pulicaria undulata*] (SEMC).

FLORAL RECORD: The paratype male was taken while visiting flowers of *Pulicaria undulata* (L.) C.A. Mey (Asteraceae: Asteroideae: Helianthodea: Inuleae), a rather common annual herb in the region, known as false fleabane or regionally as “Jethjath” and used in medicinal tea. Regional beekeepers consider *P. undulata* as a good source for pollen and nectar during the spring.

ETYMOLOGY: The specific epithet refers to the ancient kingdom of Kindah, which occupied, among other areas, large portions of the Najd, encompassing the type localities.

COMMENTS: There is variation in color of the head and mesosoma between the two males, the one from Qassim being darker and similar to the female from al-‘Amāriah, while the male from al-‘Amāriah is distinctly lighter. The lighter male is more testaceous in those areas where the Qassim male is dark testaceous to dark reddish brown, and dark testaceous to reddish brown in those places where the female and male from Qassim are dark reddish brown to black. However, despite these color differences, the integumental, structural, and genitalic traits are identical between the males. The male of *T. kindahensis* superficially resembles to some degree the male of the sympatric *Tetraloniella* (*Tetraloniella*) *persiciformis* Alqarni et al. (2012), a eucerine that has also been taken visiting flowers of *P. undulata*.

DISCUSSION

The new species described here is most similar to the African *T. mimetes*, a rare species known only at present from the female. *Tarsalia mimetes* and *T. kindahensis* are both smaller species that lack the characteristic matt of mesoscutal tomentum of *T. persica*, and also share distinctive setae on the outer surface of the probasitarsi, have fully concolorous white to pale yellow scopal setae, and lack a dorsal carina on the first metasomal tergum. Aside from the aforementioned characters, *T. kindahensis* also differs from *T. persica* in the form of the male terminalia, particularly noticeable in the more dramatically hypertrophied left penis valve, and from all other species in the genus by the unique presence of yellow maculation on the female scape and paraocular area. The specialized setae on the probasitarsus of *T. mimetes* and *T. kindahensis* suggest some kind of interesting association or use, either in preparing the nest or for collecting pollen, although anterior and posterior probasitarsal combs are lacking in *Tarsalia*. In the female of *T. kindahensis*, although there is abundant pollen in the scopa, there are no grains within the setae of the probasitarsi. It would be revealing to discover more about the pollen-collecting behavior of these species. Unfortunately, nothing is known of the biology of *Tarsalia*, although several floral records have been documented across a wide range of families but principally among the Asteraceae (table 2).

The two groups of *Tarsalia*, considered here as subgenera, are as distinctive as many genera among the closely related Eucerini (e.g., Moure and Michener, 1955; Michener et al., 1955; LaBerge, 1957, 1970; Pesenko and Sitdikov, 1988; Baker, 1998, 2003; Michener, 2007), and could therefore be considered as such. We have retained them as subgenera for the time being as considerable sampling of these rare bees is needed in order to more fully understand their diversity, distribution, and unique characters. In particular, extensive biological data are needed from the various groups in order to ascertain their floral associations and the significance of differences in the scopal setae and patches bordering the metabasitibial plates, to say nothing about their nesting biology and the anatomy of their developmental stages. There are also great gaps in the available occurrence data for many species, particularly throughout Egypt, Sudan, and the Arabian Peninsula, and bordering areas where seemingly similar and suitable habitat occurs, not to overlook the similar gaps across Central Asia, South Asia, and the Mashriq (Levant + Iraq). As presently understood, the two subgenera overlap only within Iran.

TABLE 2. Floral records for species of *Tarsalia* Morawitz. Records are summarized from Popov (1935, 1944, 1967), Baker (1998), and from the new floral associate reported herein. All floral species are eudicots (a.k.a. tricolpates) of the pentapetalate clade (Eudicots: Core Eudicots: Pentapetalae) and divided among the “superrosids” and “superasterids” (Soltis et al., 2005; Moore et al., 2010).

	CLADE ROSIDS	
	ORDER CUCURBITALES	
Family Cucurbitaceae		
<i>Citrullus vulgaris</i> Schrad.		<i>T. hirtipes</i>
	ORDER FABALES	
Family Fabaceae		
<i>Alhagi kirghisorum</i> Schrenk		<i>T. ancyliformis</i> , <i>T. hirtipes</i>
<i>Cullen drupaceum</i> (Bunge) C.H. Stirt.		<i>T. ancyliformis</i>
	ORDER MALPIGHIALES	
Family Euphorbiaceae		
<i>Chrosophora tinctoria</i> (L.) A. Juss.		<i>T. hirtipes</i>
	CLADE ASTERIDS	
	ORDER APIALES	
Family Apiaceae		
<i>Carum carvi</i> L.		<i>T. ancyliformis</i>
<i>Eryngium caucasicum</i> Trautv. ¹		<i>T. ancyliformis</i>
	ORDER ASTERALES	
Family Asteraceae		
<i>Blumea</i> sp.		<i>T. deccana</i>
<i>Centaurea iberica</i> Trevir. & Spreng.		<i>T. ancyliformis</i>
<i>C. solstitialis</i> L.		<i>T. ancyliformis</i>
<i>C. triumfettii</i> All. ²		<i>T. ancyliformis</i> , <i>T. hirtipes</i>
<i>C.</i> sp.		<i>T. ancyliformis</i>
<i>Cynara scolymus</i> L.		<i>T. ancyliformis</i>
<i>Onopordon acanthium</i> L.		<i>T. hirtipes</i>
<i>Pulicaria undulata</i> (L.) C.A. Mey		<i>T. kindahensis</i>
	ORDER DIPSACALES	
Family Caprifoliaceae		
<i>Dipsacus laciniatus</i> L.		<i>T. ancyliformis</i>
	ORDER LAMIALES	
Family Acanthaceae		
<i>Strobilanthes</i> sp.		<i>T. strobilanthae</i>
Family Verbenaceae		
<i>Vitex agnus-castus</i> L.		<i>T. ancyliformis</i>

¹ Reported by Popov (1967) under the junior synonym *E. caeruleum* M. Bieb.

² Reported by Popov (1967) under the junior synonym *C. squarrosa* Willd.

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REFERENCES

- Alqarni, A.S., M.A. Hannan, and M.S. Engel. 2012. A new wild, pollinating bee species of the genus *Tetraloniella* from the Arabian Peninsula (Hymenoptera, Apidae). *ZooKeys* 172: 89–96.
- Alqarni, A.S., M.A. Hannan, I.A. Hinojosa-Díaz, and M.S. Engel. 2013. First record of *Chiasmognathus* from the Kingdom of Saudi Arabia (Hymenoptera, Apidae). *Journal of Hymenoptera Research* 35: 83–89.
- Alqarni, A.S., M.A. Hannan, and M.S. Engel. 2014a. New records of nomiine and halictine bees in the Kingdom of Saudi Arabia (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* 87 (3): 312–317.
- Alqarni, A.S., M.A. Hannan, and M.S. Engel. 2014b. First record of the bee genus *Compsomelissa* in the Kingdom of Saudi Arabia (Hymenoptera: Apidae). *Pan-Pacific Entomologist* 90 (1): 37–39.
- Ashmead, W.H. 1899. Classification of the bees, or the superfamily Apoidea. *Transactions of the American Entomological Society* 26: 49–100.
- Baker, D.B. 1971 [1972]. A new *Tarsalia* (Hym., Apoidea) from southern India. *Entomologist's Monthly Magazine* 107 (1289–1291): 246–248.
- Baker, D.B. 1994. The date of the Hymenoptera section of the *Exploration scientifique de l'Algérie*. *Archives of Natural History* 21 (3): 345–350.
- Baker, D.B. 1998. Taxonomic and phylogenetic problems in Old World eucerine bees, with special reference to the genus *Tarsalia* Morawitz, 1895 (Hymenoptera: Apoidea: Anthophoridae). *Journal of Natural History* 32 (6): 823–860.
- Baker, D.B. 2003. *Ulugombakia*, a new eucerine bee from Malaya (Hymenoptera: Apoidea: Apidae). *Beiträge zur Entomologie* 53 (1): 123–129.
- Braue, A. 1913. Die Pollensammelapparate der beinsammelnden Bienen. *Jenaische Zeitschrift für Naturwissenschaft* 50 (1): 1–96, +4 pls.
- Cameron, P. 1898. Hymenoptera Orientalia, or contributions to a knowledge of the Hymenoptera of the Oriental Zoological Region. Part VII. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society* 42 (11): 1–84, +1 pl.
- Cockerell, T.D.A. 1933. Descriptions and records of bees — CXLV. *Annals and Magazine of Natural History, Tenth Series* 12 (67): 126–136.
- Cockerell, T.D.A. 1937. Descriptions and records of bees — CLXIV. *Annals and Magazine of Natural History, Tenth Series* 20 (117): 280–286.
- Dours, J.A. 1873. Hyménoptères du bassin Méditerranéen / *Andrena* (suite). *Revue et Magasin de Zoologie Pure et Appliquée* 1 (3): 274–325.

- Eickwort, G.C. 1969. A comparative morphological study and generic revision of the augochlorine bees (Hymenoptera: Halictidae). *University of Kansas Science Bulletin* 48 (13): 325–524.
- Engel, M.S. 2000. Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). *Bulletin of the American Museum of Natural History* 250: 1–89.
- Engel, M.S. 2001. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History* 259: 1–192.
- Engel, M.S. 2005. Family-group names for bees (Hymenoptera: Apoidea). *American Museum Novitates* 3476: 1–33.
- Engel, M.S. 2009. Revision of the bee genus *Chlerogella* (Hymenoptera, Halictidae), Part I: Central American species. *ZooKeys* 23: 47–75.
- Engel, M.S. 2011. Systematic melittology: where to from here? *Systematic Entomology* 36 (1): 2–15.
- Engel, M.S. 2015. Notes on family-group names for bees (Hymenoptera: Apoidea). *Journal of Melittology* 46: 1–7.
- Engel, M.S., J.S. Ascher, and D.A. Yanega. 2008. Ancylini Michener, 1944 (Insecta, Hymenoptera): proposed emendation of spelling to Ancylaini, to remove homonymy with Ancylini Rafinesque, 1815 (Mollusca, Gastropoda) [Case 3461]. *Bulletin of Zoological Nomenclature* 65 (3): 198–201.
- Engel, M.S., M.A. Hannan, and A.S. Alqarni. 2012. *Systropha androsthene*s in Saudi Arabia (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* 85 (1): 62–64.
- Engel, M.S., A.S. Alqarni, and M.A. Hannan. 2013. A preliminary list of bee genera in the Kingdom of Saudi Arabia (Hymenoptera: Apoidea). *Journal of the Saudi Society of Agricultural Sciences* 12 (1): 85–89.
- Engel, M.S., A.S. Alqarni, M.A. Hannan, I.A. Hinojosa-Díaz, and C.D. Michener. 2014. Allodapine bees in the Arabian Peninsula (Hymenoptera: Apidae): a new species of *Braunsapis* from the Sarawat Mountains, with an overview of the Arabian fauna. *American Museum Novitates* 3801: 1–15.
- Friese, H. 1896. Die Bienen Europa's (Apidae europaeae) nach ihren Gattungen, Arten und Varietäten auf vergleichend morphologisch-biologischer Grundlage. Teil II. Solitäre Apiden. Genus *Eucera*. Berlin: Friedländer & Sohn, 216 pp.
- Friese, H. 1902. Neue Bienen-Arten aus Griechenland. (Hym.). *Zeitschrift für Systematische Hymenopterologie und Dipterologie* 2 (2): 105–108.
- Friese, H. 1922. Neue Arten der Anthophorinae (Hym.). *Konowia* 1 (1–2): 59–66.
- Gonzalez, V.H., T. Griswold, and M.S. Engel. 2013. Obtaining a better taxonomic understanding of native bees: where do we start? *Systematic Entomology* 38 (4): 645–653.
- Griswold, T.L. 2013. New Palearctic bee species of *Protosmia* subgenus *Nanosmia* (Hymenoptera: Megachilidae). *Journal of Melittology* 20: 1–9.
- Hinojosa-Díaz, I.A., A.S. Alqarni, A. Lira-Noriega, and M.S. Engel. 2016. Ecological niche modeling of the rare bee *Promelitta alboclypeata* reveals possible cryptic differentiation across northern Africa and Arabia (Hymenoptera: Melittidae). *Apidologie* 47 (4): 509–514.
- ICZN [International Commission on Zoological Nomenclature]. 2010. Ancylini Michener, 1944 (Insecta, Hymenoptera): spelling emended to Ancylaini to remove homonymy with Ancylini Rafinesque, 1815 (Mollusca, Gastropoda) [Opinion 2246 (Case 3461)]. *Bulletin of Zoological Nomenclature* 67 (1): 116–117.
- LaBerge, W.E. 1957. The genera of bees of the tribe Eucerini in North and Central America (Hymenoptera, Apoidea). *American Museum Novitates* 1837: 1–44.
- LaBerge, W.E. 1970. A new genus with three new species of eucerine bees from Mexico (Hymenoptera: Anthophoridae). *Journal of the Kansas Entomological Society* 43 (3): 321–328.

- Latreille, P.A. 1802. Histoire naturelle des fourmis, et recueil de memoires et d'observations sur les abeilles, les araignées, les faucheurs, et autres insectes. Paris: Crapelet, xvi + 445 pp.
- Lepelletier de Saint Fargeau, A.L.M. 1841. Histoire naturelle des insectes — Hyménoptères, vol. 2. Paris: Roret, 680 pp.
- Lucas, P.H. 1849. Cinquième classe.—Insectes. Cinquième ordre. Les Hyménoptères. *In* Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842 publiée par ordre du gouvernement et avec le concours d'une commission académique. Sciences physiques. Zoologie, histoire naturelle des animaux articulés [troisième partie: insectes (suite)]: 141–344, +1 pl. [pl. 19]. Paris: Imprimerie Royale, 527 pp. [Refer to Baker (1994) for details on the dating of livraisons comprising the third part of Lucas' work on the arthropods; all 122 arthropod plates were also issued as a separate quarto Atlas in June 1849.]
- Mavromoustakis, G.A. 1952. On the bees (Hymenoptera, Apoidea) of Cyprus.—Part III. *Annals and Magazine of Natural History* (12) 5 (57): 814–843.
- Michener, C.D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bulletin of the American Museum of Natural History* 82 (6): 151–326.
- Michener, C.D. 1999. Genus-group names of bees and supplemental family-group names. *Scientific Papers, Natural History Museum, University of Kansas* 1: 1–81.
- Michener, C.D. 2000. *The bees of the world*. Baltimore: Johns Hopkins University Press, xiv+[i]+913 pp., +16 pls.
- Michener, C.D. 2007. *The bees of the world*, 2nd ed. Baltimore: Johns Hopkins University Press, xvi+[i]+953 pp., +20 pls.
- Michener, C.D., and J.S. Moure. 1957. A study of the classification of the more primitive non-parasitic anthophorine bees (Hymenoptera, Apoidea). *Bulletin of the American Museum of Natural History* 112 (5): 395–451.
- Michener, C.D., W.E. LaBerge, and J.S. Moure. 1955. Some American Eucerini bees. *Dusenian* 6 (6): 213–230.
- Moore, M.J., P.S. Soltis, C.D. Bell, J.G. Burleigh, and D.E. Soltis. 2010. Phylogenetic analysis of 83 plastid genes further resolves the early diversification of eudicots. *Proceedings of the National Academy of Sciences of the United States of America* 107 (10): 4623–4628.
- Morawitz, F.F. 1874. Die Bienen Daghestans. *Horae Societatis Entomologicae Rossicae* 10 (2–4): 129–189.
- Morawitz, F.F. 1895. Beitrag zur Bienenfauna Turkmeniens. *Horae Societatis Entomologicae Rossicae* 29: 1–76.
- Moure, J.S., and C.D. Michener. 1955. A contribution toward the classification of neotropical Eucerini (Hymenoptera, Apoidea). *Dusenian* 6 (6): 239–331.
- Pasteels, J.J., and J.M. Pasteels. 1974. Étude au microscope électronique à balayage des scopas abdominales chez de nombreuses espèces d'abeilles (Apoidea, Megachilidae). *Tissue and Cell* 6 (1): 65–83.
- Pesenko, Y.A., and A.A. Sitdikov. 1988. Classification and phylogenetic relations of the genera of the tribe Eucerini (Hymenoptera, Anthophoridae) with two submarginal cells. *Entomologicheskoe Obozrenie* 67 (4): 846–860. [in Russian, with English translation in *Entomological Review* (1990) 69 (1): 88–104.]
- Pittioni, B. 1950. On the insect fauna of Cyprus. Results of the expedition of 1938 by Harald, Håkan and P.H. Lindberg. V. Hymenoptera Aculeata I. Diptera, Fossores und Apoidea der Insel Cypern. *Commentationes Biologicae* 10 (12): 1–94.
- Plant, J.D., and H. Paulus. 2016. Evolution and phylogeny of bees: review and cladistic analysis in light of morphological evidence (Hymenoptera, Apoidea). *Zoologica* 161: 1–364.

- Popov, V.V. 1935. Beiträge zur Bienenfauna von Tadjikistan (Hymenoptera, Apoidea [sic]). Travaux de la Filiale de l'Académie des Sciences de l'URSS au Tadjikistan 5: 351–408. [in Russian, with German summary]
- Popov, V.V. 1944. *Tarsalia ancyliformis* Popov as an oligolectic bee. Travaux de la Filiale de l'Académie des Sciences de l'URSS au Tadjikistan 5: 155–160. [in Russian]
- Popov, V.V. 1949. Tribe Pararhophitini (Hymenoptera, Anthophorinae) as an Early Tertiary element of the contemporary fauna of the desert of Central Asia and Egypt. Doklady Akademii Nauk SSSR 66 (3): 507–510. [in Russian]
- Popov, V.V. 1967. Bees (Hymenoptera, Apoidea) of Central Asia and their distribution on flowering plants. Trudy Zoologicheskogo Instituta Akademii Nauk SSSR 38: 11–381. [in Russian]
- Praz, C.J., and L. Packer. 2014. Phylogenetic position of the bee genera *Ancyla* and *Tarsalia* (Hymenoptera: Apidae): a remarkable base compositional bias and an early Paleogene geodispersal from North America to the Old World. Molecular Phylogenetics and Evolution 81: 258–270.
- Roig-Alsina, A., and C.D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). University of Kansas Science Bulletin 55 (4): 123–162.
- Saunders, E. 1878. Remarks on the hairs of some of our British Hymenoptera. Transactions of the Entomological Society of London 1878 (2): 169–172, +1 pl.
- Schönitzer, K. 1986. Comparative morphology of the antenna cleaner in bees (Apoidea). Zeitschrift für Zoologische Systematik und Evolutionsforschung 24 (1): 35–51.
- Schönitzer, K., and M. Renner. 1980. Morphologie der Antennenputzapparate bei Apoidea. Apidologie 11 (2): 113–120.
- Shebl, M.A., A.S. Alqarni, and M.S. Engel. 2016. First record of the bee genus *Melitta* from the Arabian Peninsula (Hymenoptera: Apoidea: Melittidae). Zoology in the Middle East 62 (4): 352–357.
- Silveira, F.A. 1993a. Phylogenetic relationships of the Exomalopsini and Ancylini (Hymenoptera: Apoidea). University of Kansas Science Bulletin 55 (5): 163–173.
- Silveira, F.A. 1993b. The mouthparts of *Ancyla* and the reduction of the labiomaxillary complex among long-tongued bees (Hymenoptera: Apoidea). Entomologica Scandinavica 24 (3): 293–300.
- Silveira, F.A. 1995. Phylogenetic relationships and classification of Exomalopsini with a new tribe Teraognathini (Hymenoptera: Apoidea). University of Kansas Science Bulletin 55 (12): 425–454.
- Snelling, R.R. 1981. Systematics of social Hymenoptera. In H.R. Hermann (editor), Social insects, vol. 2: 369–453. New York: Academic Press, xiii + 491 pp.
- Snodgrass, R.E. 1956. Anatomy of the honey bee. Ithaca: Cornell University Press, xiv + [i] + 334 pp.
- Soltis, D.E., P.S. Soltis, P.K. Endress, and M.W. Chase. 2005. Phylogeny and evolution of angiosperms. Sunderland: Sinauer, x + 370 pp.
- Straka, J., and J.G. Rozen, Jr. 2012. First observations on nesting and immatures of the bee genus *Ancyla* (Apoidea: Apidae: Apinae: Ancyilaini). American Museum Novitates 3749: 1–24.
- Warncke, K. 1977. Ideen zum natürlichen System der Bienen (Hymenoptera, Apoidea). Mitteilungen der Münchner Entomologischen Gesellschaft 67: 39–63.
- Warncke, K. 1979. Beiträge zur Bienenfauna des Iran: 10. Die Gattung *Ancyla* Lep., mit einer revision der Bienengattung *Ancyla* Lep. Bolletino del Museo Civico di Storia Naturale di Venezia 30: 183–195.

APPENDIX

HIERARCHICAL CHECKLIST OF BEE GENERA AND SUBGENERA
IN SAUDI ARABIA

The following builds upon our earlier list (Engel et al., 2013), from which we are developing a guide to the Arabian bee fauna (Engel and Alqarni, in prep.). As in our earlier list, clepto-parasitic groups are denoted with an asterisk. Dates and citations for family- and genus-groups names within this list can be found in Engel (2005, 2015) and Michener (1999, 2007), respectively, and are not included here. Citations for recent records are appended.

-
- Family COLLETIDAE Lepeletier de Saint Fargeau
 - Subfamily COLLETINAE Lepeletier de Saint Fargeau
 - Genus *Colletes* Latreille
 - Subfamily HYLAEINAE Viereck
 - Genus *Hylaeus* Fabricius
 - Subgenus *Hylaeus* s. str. (Engel, unpubl. data)
 - Subgenus *Nothylaeus* Bridwell (Engel, unpubl. data)
 - Subgenus *Paraprosopis* Popov

 - Family ANDRENIDAE Latreille
 - Subfamily ANDRENINAE Latreille
 - Genus *Andrena* Fabricius
 - Subgenus *Chrysandrena* Hedicke
 - Subgenus *Graecandrena* Warncke
 - Subgenus *Melanapis* Cameron
 - Subgenus *Suandrena* Warncke
 - Subfamily PANURGINAE Leach
 - Tribe Melitturgini Newman
 - Genus *Borgatomelissa* Patiny
 - Tribe Meliturgulini Engel
 - Genus *Meliturgula* Friese
 - Tribe Panurgini Leach
 - Genus *Panurginus* Nylander (Shebl and Engel, unpubl. data)
 - Genus *Panurgus* Panzer
 - Subgenus *Panurgus* s. str.

Family HALICTIDAE Thomson

Subfamily ROPHITINAE Schenck

Tribe Rophitini Schenck

Genus *Dufourea* Lepeletier de Saint FargeauSubgenus *Dufourea* s. str.Genus *Systropha* Illiger (Engel et al., 2012)

Subfamily NOMIINAE Robertson

Tribe Nomiini Robertson

Genus *Lipotriches* GerstaeckerSubgenus *Rhopalomelissa* Alfken (Alqarni et al., 2014a)Genus *Nomia* LatreilleSubgenus *Crocisaspidia* AshmeadGenus *Pseudapis* KirbySubgenus *Pseudapis* s. str.

Subfamily HALICTINAE Thomson

Tribe Nomioidini Börner

Genus *Ceylalicthus* StrandSubgenus *Ceylalicthus* s. str.Genus *Nomioides* SchenckSubgenus *Nomioides* s. str.

Tribe Halictini Thomson

Genus *Halictus* LatreilleSubgenus *Argalictus* Pesenko (Alqarni et al., 2014a)Subgenus *Seladonia* RobertsonSubgenus *Vestitohalictus* BlüthgenGenus *Lasioglossum* CurtisSubgenus *Afrodialictus* PaulySubgenus *Ctenonomia* CameronSubgenus *Evylaeus* RobertsonSubgenus *Lasioglossum* s. str.Genus *Sphecodes* Latreille (Engel, unpubl. data)

Family MELITTIDAE Kawall

Subfamily MELITTINAE Kawall

Tribe Melittini Kawall

Genus *Melitta* Kirby (Shebl et al., 2016)

Subfamily DASYPODAINAE Börner

Tribe Promelittini Michener

Genus *Promelitta* Warncke (Hinojosa-Díaz et al., 2016)

Tribe Dasypodaini Börner

Genus *Dasypoda* Latreille

Family MEGACHILIDAE Latreille

Subfamily MEGACHILINAE Latreille

Tribe Anthidiini Ashmead

Genus *Afranthidium* MichenerSubgenus *Mesanthidium* PopovGenus *Anthidium* FabriciusSubgenus *Anthidium* s. str.Subgenus *Proanthidium* FrieseGenus *Icteranthidium* MichenerGenus *Pachyanthidium* FrieseSubgenus *Trichanthidiodes* Michener and GriswoldGenus *Pseudoanthidium* FrieseSubgenus *Pseudoanthidium* s. str.

Tribe Osmiini Newman

Genus *Osmia* PanzerSubgenus *Helicosmia* ThomsonGenus *Protosmia* DuckeSubgenus *Nanosmia* Griswold (Griswold, 2013)Genus *Pseudoheriades* Peters

Tribe Megachilini Latreille

Genus *Chalicodoma* Lepeletier de Saint FargeauSubgenus *Chalicodoma* s. str.Subgenus *Pseudomegachile* FrieseGenus *Coelioxys* Latreille*Subgenus *Allocoelioxys* Tkalců*Genus *Megachile* LatreilleSubgenus *Creightonella* CockerellSubgenus *Eutricharaea* Thomson

Family APIDAE Latreille

Subfamily XYLOCOPINAE Latreille

Tribe Xylocopini Latreille

Genus *Xylocopa* LatreilleSubgenus *Koptortosoma* GribodoSubgenus *Ctenoxylocopa* Michener

Tribe Ceratinini Latreille

Genus *Ceratina* LatreilleSubgenus *Dalyatina* Terzo et al.Subgenus *Euceratina* Hirashima et al.Subgenus *Pithitis* Klug

Tribe Allodapini Cockerell

Genus *Compsomelissa* Alfken (Alqarni et al., 2014b)Genus *Braunsapis* Michener (Engel et al., 2014)

Subfamily NOMADINAE Latreille*

Tribe Ammobatini Handlirsch*

Genus *Ammobates* Latreille*Subgenus *Ammobates* s. str.*Genus *Chiasmognathus* Engel* (Alqarni et al., 2013)

Subfamily APINAE Latreille

Tribe Eucerini Latreille

Genus *Eucera* ScopoliSubgenus *Synhalonia* PattonGenus *Tetraloniella* AshmeadSubgenus *Tetraloniella* s. str. (Alqarni et al., 2012)

Tribe Tarsaliini Engel

Genus *Tarsalia* Morawitz (reported herein)Subgenus *Astibomelissa* Engel

Tribe Anthophorini Dahlbom

Genus *Amegilla* FrieseSubgenus *Amegilla* s. str.Subgenus *Micramegilla* BrooksSubgenus *Zebramegilla* BrooksGenus *Anthophora* LatreilleSubgenus *Heliophila* KlugSubgenus *Paramegilla* FrieseSubgenus *Petalosternon* BrooksSubgenus *Pyganthophora* Brooks

Tribe Melectini Westwood*

Genus *Melecta* Latreille*Subgenus *Paracrocisa* Alfken*Genus *Thyreus* Panzer*

Tribe Apini Latreille

Genus *Apis* LinnaeusSubgenus *Micrapis* AshmeadSubgenus *Apis* s. str.

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