

Allodapine Bees in the Arabian Peninsula (Hymenoptera: Apidae): A New Species of *Braunsapis* from the Sarawat Mountains, with an Overview of the Arabian Fauna

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ABSTRACT

An interesting new species of allodapine bee (Xylocopinae: Allodapini: Allodapina) is described and figured from males and females captured in the Sarawat Mountains near al-Baha, representing the first records of the tribe for Saudi Arabia. *Braunsapis alqarnii* Engel and Michener, new species, is similar to the small species of the genus known from Africa and Madagascar but is distinguished on the basis of several features, most notably the male hind legs and terminalia. Notes are provided on the known allodapine fauna of the Arabian Peninsula, with a key to the species.

INTRODUCTION

The bees of the tribe Allodapini are usually slender, soft bodied, and most similar to the tribe Ceratinini of the apid subfamily Xylocopinae but entirely different in general appearance from the large bodied, robust species of the tribe Xylocopini. The Allodapini differ from the

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Ceratinini in many characters (Michener, 2007), the most easily seen and appreciated of which is the presence of two, rather than three, submarginal cells in the forewing. Allodapini are found in the tropical and subtropical parts of the Old World, from Africa at the west to Taiwan and the Philippines in the east, from Turkey and southeastern China in the north south to Australia and South Africa. The new species described below is a member of the genus *Braunsapis* Michener, which is the largest genus of the tribe and almost as widespread as the tribe. Like the tribe, this genus is most abundant and diversified in southern Africa (Michener, 1975a), but is the only allodapine genus found across southern Asia and nearby islands from Yemen and India to China and the Philippines. Since the Saudi Arabian species described below is a *Braunsapis*, most of the comparative commentary relates to that genus.

The Allodapini are almost unique among bees in that the larvae are not reared in individual cells made by adult females. Instead, in most allodapine genera, eggs are laid in a nest burrow and developing larvae are often in contact with one another. The immature stages (eggs to pupae) of *Braunsapis* are free in the lower part of the nest burrow, where the larvae are fed progressively by adult females. In this genus the older immatures are usually kept above younger ones in the burrow; an adult has to pass pupae and large larvae to feed young larvae. In the few other bees whose larvae may contact one another (many *Bombus* Latreille, a few megachilids), larvae spin at least cocoons so that pupae are isolated. Allodapines do not spin cocoons.

Many allodapine nests are occupied by two to several adult females. There is commonly division of labor among such females, one (often mated, i.e., with sperm cells in the spermatheca) being the principal egg layer, another (often unmated) being the principal forager. In most if not all species, however, many nests contain only one adult female. Thus, the social behavior associated with multiple females is facultative. Some papers dealing with life cycles and nesting behavior of *Braunsapis* species are by Michener (1971), Maeta et al. (1985), and Aenmeay et al. (2006).

Most bee larvae are grubs, the kinds differentiated by mostly microscopic features. Perhaps because they are usually free to contact one another, possibly to compete for food or to promote removal of feces, allodapine larvae have evolved the greatest diversity of distinctive characters found in any group of bees (Michener, 2007: 622). These often include setae and projections that extend forward from the head, setae and tubercles that presumably support the larvae in sometimes vertical burrows, and projections that support pollen provided by adult bees. Most of the genera are differentiated in part, often most conspicuously, by larval characters (e.g., Michener, 1975b, 1975c, 1975d, 1976, 1977a; Chenoweth et al., 2008), and differences among species are also commonly evident.

The great majority of allodapine nests are simple burrows in pith of dead, dry stems (or twigs) of plants, usually entering where a stem has been broken or cut (Michener, 1970). Some species, however, regularly or occasionally occupy burrows in galls, seed pods, thorns, or emergence burrows of other insects in wood. Thus they use preexisting burrows as well as new burrows in pith. Brauns (1926) in his work on African allodapines, reported nesting in earth or banks, but such behavior has not been verified by later studies. Brauns, however, was a good observer and the possibility of soil nests must be considered.

During recent fieldwork in southwestern Saudi Arabia, three of us (M.S.E., A.S.A., M.A.H.) found and collected a series of a new species of small *Braunsapis* visiting a variety of flowers in a vegetated area surrounding the outflow of a natural spring near the ancient village of Thy 'Ain as well as fresh flowers in nearby cultivated areas. Both localities are not far from the city of al-Baha and are along highway 246 as it descends to the Tihamah. A search of the area for nests in stems or twigs yielded nothing; a search for nests in soil or banks would be desirable. It was, however, rather late in the flowering season. This is the first record of the genus *Braunsapis* for Saudi Arabia, and indeed of the entire tribe Allodapini, and the genus can be added to the growing checklist of genera for the Kingdom (Engel et al., 2013; Alqarni et al., in press).

The new species is quite distinctive among the various species groups of *Braunsapis* previously recognized (table 1), and is described and illustrated herein. In addition we provide a brief overview of the known allodapine fauna of the Arabian Peninsula, with a key to the species. We hope that this work will inspire regional entomologists and pollination workers to seek nests, specimens, and information on the biology of these minute bees.

MATERIAL AND METHODS

Material considered herein is deposited in the Division of Entomology (Snow Entomological Collections), University of Kansas Natural History Museum, Lawrence, Kansas (**SEMC**); the King Saud University Museum of Arthropods, Plant Protection Department, College of Food and Agriculture Sciences, King Saud University, Riyadh, Kingdom of Saudi Arabia (**KSMA**); and the Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York, New York (**AMNH**). Morphological terminology generally follows that of Engel (2001) and Michener (1975a, 2007), while the format for the description follows that employed elsewhere for allodapine bees (e.g., Michener, 1975a, 1977b; Reyes, 1991a, 1991b, 1993; Engel and Dathe, 2011; Engel, 2013). Photomicrographs were prepared using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens, while measurements were taken using an ocular micrometer on an Olympus SZX-12 stereomicroscope. Measurements of the holotype are provided, with the range observed among paratypes presented in parentheses.

SYSTEMATICS

Genus *Braunsapis* Michener

Braunsapis alqarnii Engel and Michener, new species

Figures 1–12

DIAGNOSIS: The new species stands out immediately among other *Braunsapis* in the form of the male hind leg (fig. 4) and the genital capsule (figs. 7–9), particularly the presence of an elongate lateral apical process and pronounced medioventral apical process on the gonocoxa.

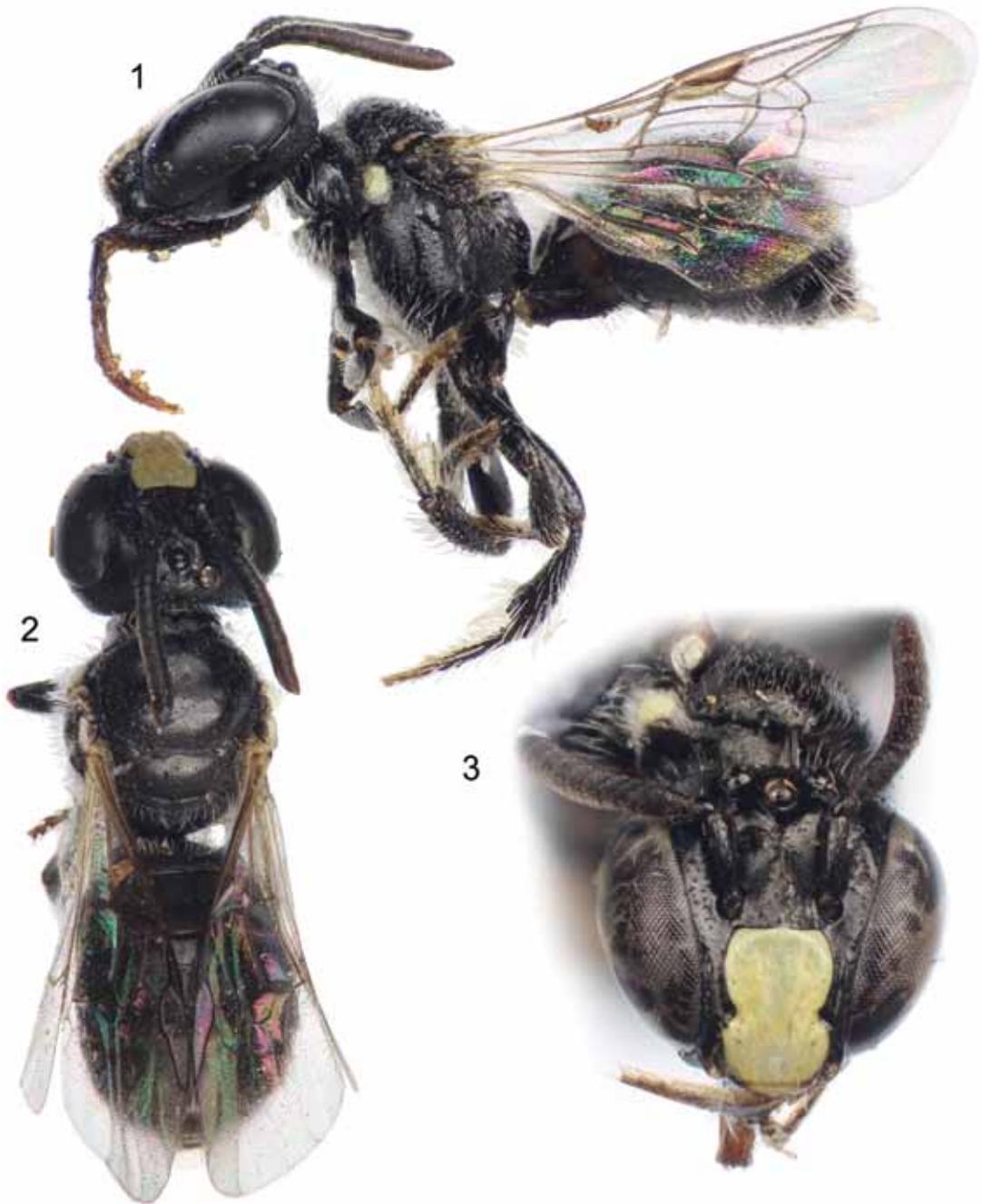
DESCRIPTION: Male. Total length 3.65 mm (3.10–3.90 mm); forewing length 2.65 mm (2.50–2.70 mm); head slightly broader than long, length 1.02 mm (1.02–1.06 mm), width

TABLE 1. Diversity of species recognized in the genus *Braunsapis* Michener¹ (Allodapini: Allodapina). Species groups after Michener (1975a, 1977b) and Reyes (1991a, 1991b, 1993).

Species Group	Region	Included Species
<i>diminuta</i>	Australian	[6 spp.] <i>B. anthracina</i> Reyes, <i>B. clarissima</i> (Cockerell), <i>B. diminuta</i> (Cockerell), <i>B. diminutoides</i> Reyes, <i>B. plebeia</i> (Cockerell), <i>B. plumosa</i> Reyes
<i>verticalis</i>	Australian	[1 sp.] <i>B. verticalis</i> Reyes
<i>simillima</i>	Australian	[6 spp.] <i>B. biroi</i> (Friese), <i>B. boharti</i> (Krombein), <i>B. nitida</i> (Smith), <i>B. protuberans</i> Reyes, <i>B. simillima</i> (Smith), <i>B. unicolor</i> (Smith)
<i>associata</i>	Australian	[6 spp.] <i>B. associata</i> (Michener), <i>B. praesumptiosa</i> (Michener), <i>B. eximia</i> Reyes, <i>B. falcata</i> Reyes, <i>B. platyura</i> Reyes, <i>B. hirsuta</i> Reyes
<i>minor</i>	Australian	[4 spp.] <i>B. occidentalis</i> (Michener and Syed), <i>B. minor</i> (Michener and Syed), <i>B. dolichocephala</i> Reyes, <i>B. hyalina</i> Reyes
<i>breviceps</i>	Oriental	[3 spp.] <i>B. bislensis</i> Michener and Borges, <i>B. breviceps</i> (Cockerell), <i>B. kaliago</i> Reyes and Sakagami
<i>mixta</i>	Oriental and Arabian	[8 spp.] <i>B. mixta</i> (Smith), <i>B. picitarsis</i> (Cameron), <i>B. philippinensis</i> (Ashmead), <i>B. hewitti</i> (Cameron), <i>B. flaviventris</i> Reyes, <i>B. palavanica</i> (Cockerell), <i>B. malliki</i> Reyes, <i>B. arabica</i> Engel and Dathe
<i>puangensis</i>	Oriental	[1 sp.] <i>B. puangensis</i> (Cockerell)
<i>cupulifera</i>	Oriental	[10 spp.] <i>B. cupulifera</i> (Vachal), <i>B. clarihirta</i> Reyes, <i>B. apicalis</i> Reyes, <i>B. lateralis</i> Reyes, <i>B. reducta</i> (Cockerell), <i>B. reversa</i> (Cockerell), <i>B. signata</i> Reyes, <i>B. aurantipes</i> Reyes ² , <i>B. indica</i> Reyes, <i>B. engeli</i> Jobiraj
<i>alqarnii</i>	Arabian	[1 sp.] <i>B. alqarnii</i> Engel and Michener, n. sp.
<i>madecassa</i>	Malagasy	[4 spp.] <i>B. antandroy</i> Brooks and Pauly, <i>B. maculata</i> Reyes, <i>B. madecassa</i> (Benoist), <i>B. madecassella</i> Michener
<i>bouyssoui</i>	African	[4 spp.] <i>B. bouyssoui</i> (Vachal), <i>B. nautica</i> (Cockerell), <i>B. rolini</i> (Vachal), <i>B. strandi</i> (Masi)
<i>minutula</i>	African	[4 spp.] <i>B. rugosella</i> (Cockerell), <i>B. minutula</i> (Friese), <i>B. longula</i> (Friese), <i>B. ghanae</i> Michener
<i>paradoxa</i>	African	[4 spp.] <i>B. acuticauda</i> Michener, <i>B. elizabethana</i> (Strand), <i>B. maxschwarzi</i> Engel, <i>B. paradoxa</i> (Strand)
<i>vitrea</i>	African	[4 spp.] <i>B. albipennis</i> (Friese), <i>B. fuscinervis</i> (Cameron), <i>B. otavica</i> (Cockerell), <i>B. vitrea</i> (Vachal)
Not placed as to group	African	[27 spp.] <i>B. foveata</i> (Smith), <i>B. flavitarsis</i> (Gerstaecker), <i>B. angolensis</i> (Cockerell), <i>B. calidula</i> (Cockerell), <i>B. lyrata</i> (Cockerell), <i>B. neavei</i> (Vachal), <i>B. aureoscopa</i> Michener, <i>B. somatotheca</i> (Strand), <i>B. trochanterata</i> (Gerstaecker), <i>B. virilipicta</i> (Strand), <i>B. affinissima</i> (Gribodo), <i>B. facialis</i> (Gerstaecker), <i>B. natalica</i> Michener, <i>B. gorillarum</i> (Cockerell), <i>B. simplicipes</i> Michener, <i>B. rubicundula</i> (Strand), <i>B. pallida</i> Michener, <i>B. debilis</i> (Cockerell), <i>B. leptozonia</i> (Vachal), <i>B. albitarsis</i> (Friese), <i>B. luapulana</i> (Cockerell), <i>B. rhodesi</i> (Cockerell), <i>B. draconis</i> Michener, <i>B. stuckenbergorum</i> Michener, <i>B. liliputana</i> (Strand), <i>B. langenburgensis</i> (Strand), <i>B. albolineata</i> (Cockerell)

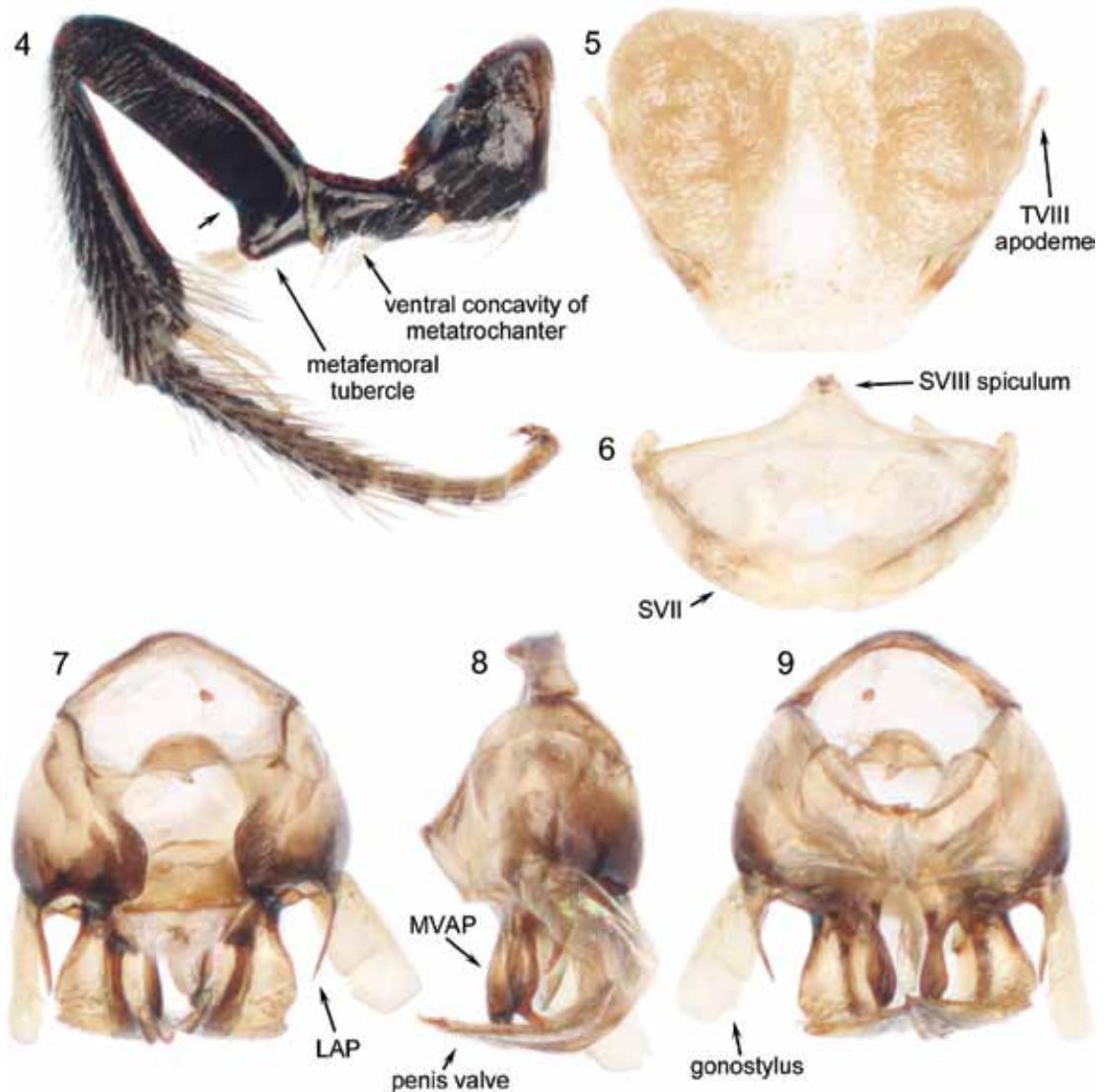
¹ Some authors have considered *Effractapis* Michener (Malagasy) and *Nasutapis* Michener (African) to be synonyms of *Braunsapis* and thereby transfer *Effractapis furax* Michener and *Nasutapis straussorum* Michener to the latter genus (e.g., Fuller et al., 2005). These taxa are considered generically distinct herein, following Michener (2007).

² We consider *B. aurantipes narendrani* Jobiraj to be a synonym (n. syn.) of the nominate subspecies and thereby eliminate subspecies within this taxon.



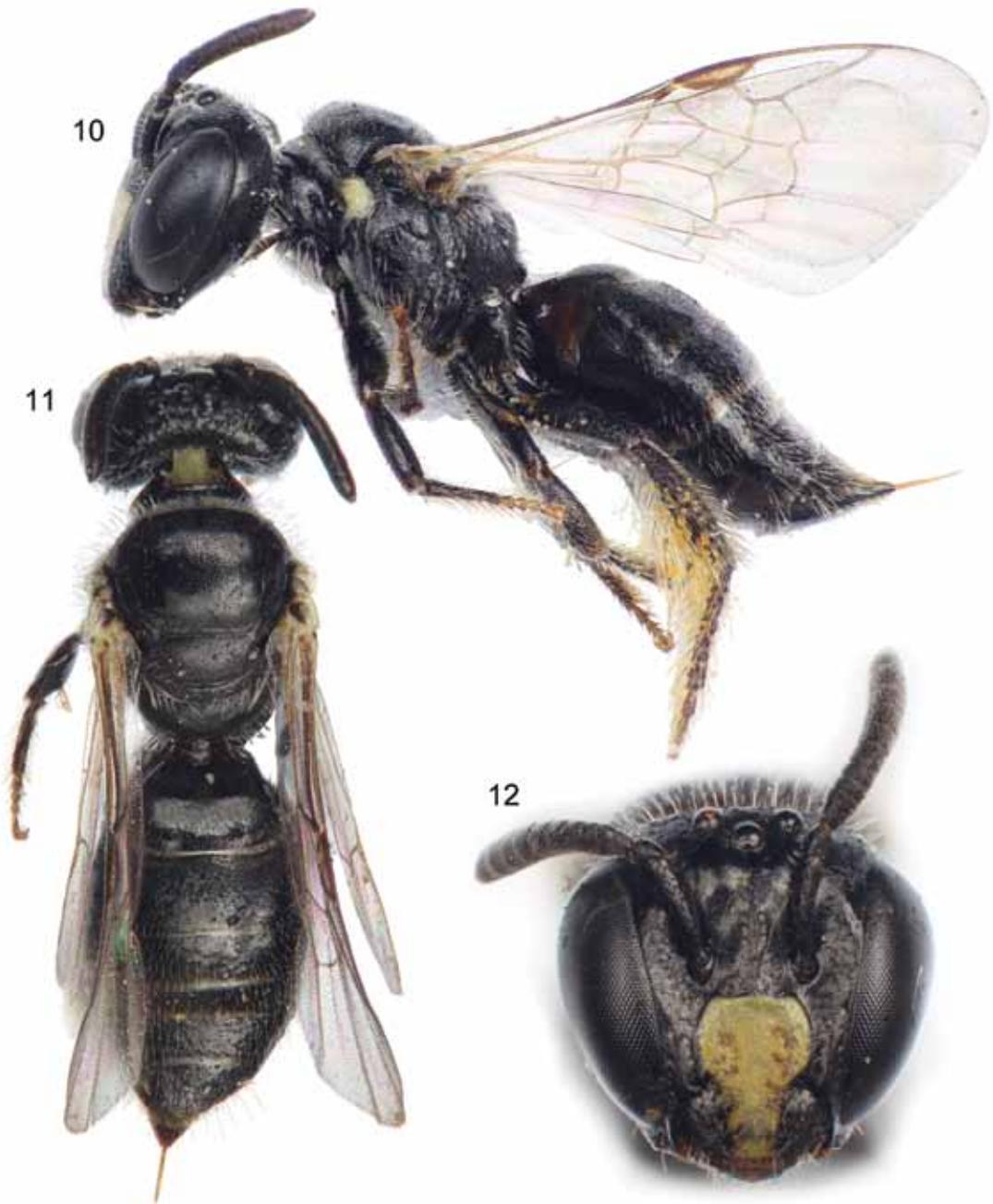
FIGURES 1–3. Male paratype of *Braunsapis alqarnii* Engel and Michener, new species. 1. Lateral habitus. 2. Dorsal habitus. 3. Facial aspect.

1.14 (1.14–1.17 mm); compound eyes with inner margins relatively straight, converging below, upper interorbital distance 0.73 mm (0.63–0.75 mm), lower interorbital distance 0.47 mm (0.47–0.49 mm). Mandible tridentate, median tooth largest. Scape short, extending to



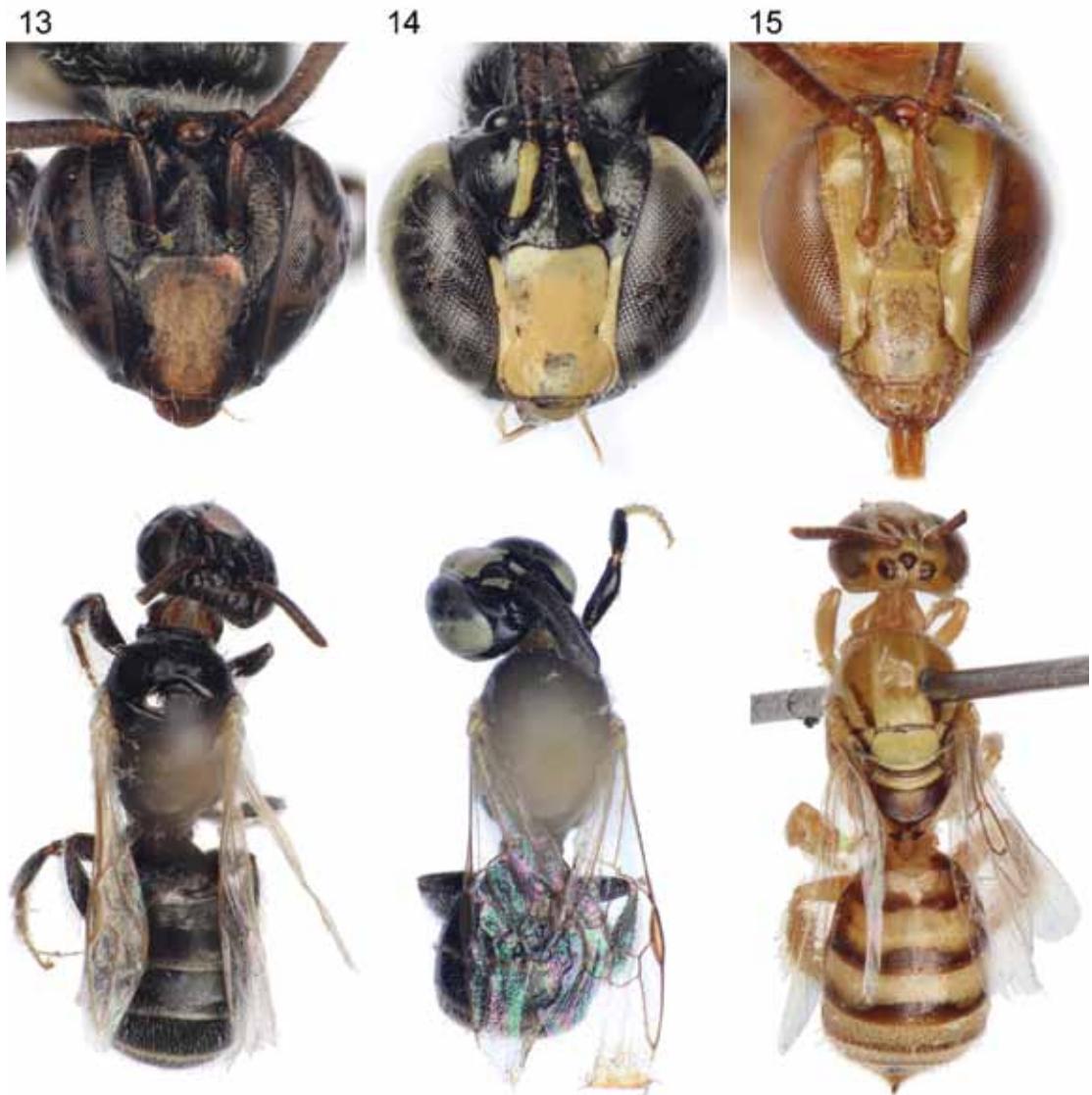
FIGURES 4–9. Male terminalia of *Braunsapis alqarnii* Engel and Michener, new species. 4. Hind leg, small arrow indicates weakly concave, polished, asetose area just apical of metafemoral tubercle. 5. Eighth metasomal tergum (genital chamber roof). 6. Fused and hidden seventh and eighth metasomal sterna. 7. Genital capsule, dorsal view. 8. Genital capsule, lateral view. 9. Genital capsule, ventral view. LAP = lateral apical process of gonocoxite; MVAP = medioventral apical process of gonocoxite.

just below level of lower margin of median ocellus, about five times as long as broad; malar space much shorter than one-third basal mandibular width, anteriorly about one-third as long as maximum scape width, posteriorly nearly as long as scape width; minimum distance from clypeus to compound eye margin slightly greater than scape width; first flagellomere slightly broader than long, second about twice as broad as long, following flagellomeres progressively longer, so that penultimate flagellomere is about as long as broad; epistomal sulcus straight at base of clypeus (fig. 3); genal area wider than compound eye in lateral view,



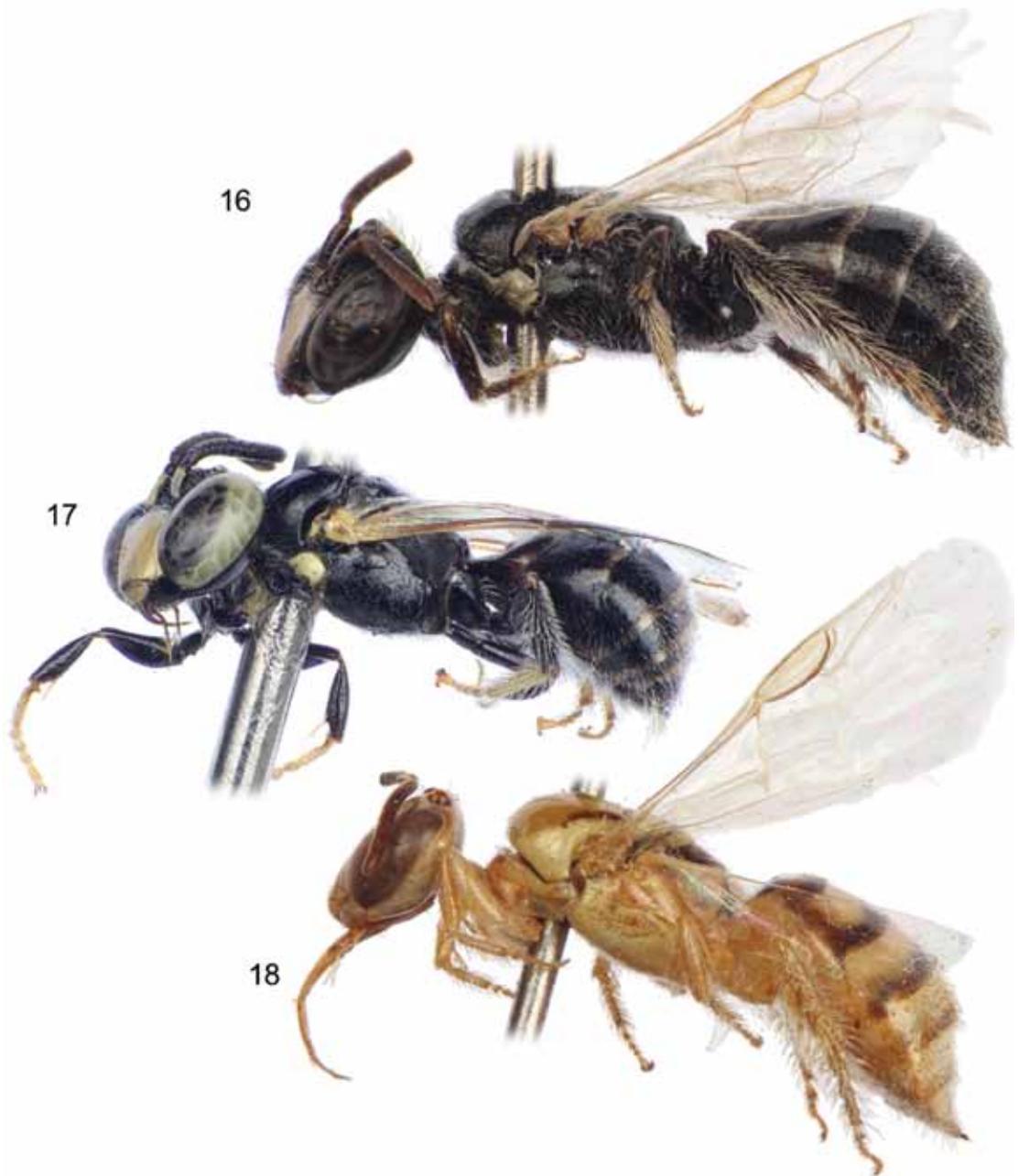
FIGURES 10–12. Female paratype of *Braunsapis alqarnii* Engel and Michener, new species. **10.** Lateral habitus. **11.** Dorsal habitus. **12.** Facial aspect.

slightly wider below middle than elsewhere (fig. 1). Forewing venation as shown in figure 1 and as in *Braunsapis leptozonia* (Vachal). Metatrochanter midventrally with broad concavity (fig. 4); metafemur not swollen, ventral surface flattened or weakly concave basally except for large basal tubercle about as wide as femur and tapering conically to rounded apex (fig.



FIGURES 13–15. Representative species of Arabian Allodapini. 13. (top) *Braunsapis arabica* Engel and Dathe, 2011, female, facial view; (bottom) *B. arabica*, female, dorsal view. 14. (top) *B. arabica*, male, facial view; (bottom) *B. arabica*, male, dorsal view. 15. (top) *Compsomelissa boernerii* Alfken, female, facial view; (bottom) *C. boernerii*, female, dorsal view (Note: specimen is considerably faded and so many of the darkened areas of the head and mesosoma are light chestnut brown or paler).

4), this tubercle not shining and concave on proximal surface. Genital chamber with roof (eighth metasomal tergum) as in figure 5, with surface wrinkled (as in Oriental, Australian, and some African species of *Braunsapis*); terminalia as in figures 6–9; genitalia quite different from those of other species such as *B. leptozonia* (vide Michener, 1975a: fig. 107), lacking peglike setae; ventroapical plate of gonocoxite short (a transverse band with membranous area between it and rest of gonocoxite) with inner apical projection large, dark, almost as



FIGURES 16–18. Representative species of Arabian Allodapini. **16.** *Braunsapis arabica* Engel and Dathe, 2011, female, lateral aspect. **17.** *B. arabica*, male, ventrolateral oblique aspect. **18.** *Compsomelissa boernerii* Alfken, female, lateral aspect (Note: specimen is considerably faded and so many of the darkened areas of the head and mesosoma are light chestnut brown or paler).

long as width of plate, enlarged apically so that projection is clublike, apex of projection with two (possibly three) adjacent, stout, slightly curved, tapering setae that together form a claw-like process directed upward; outer apical projection shorter than inner projection, slender,

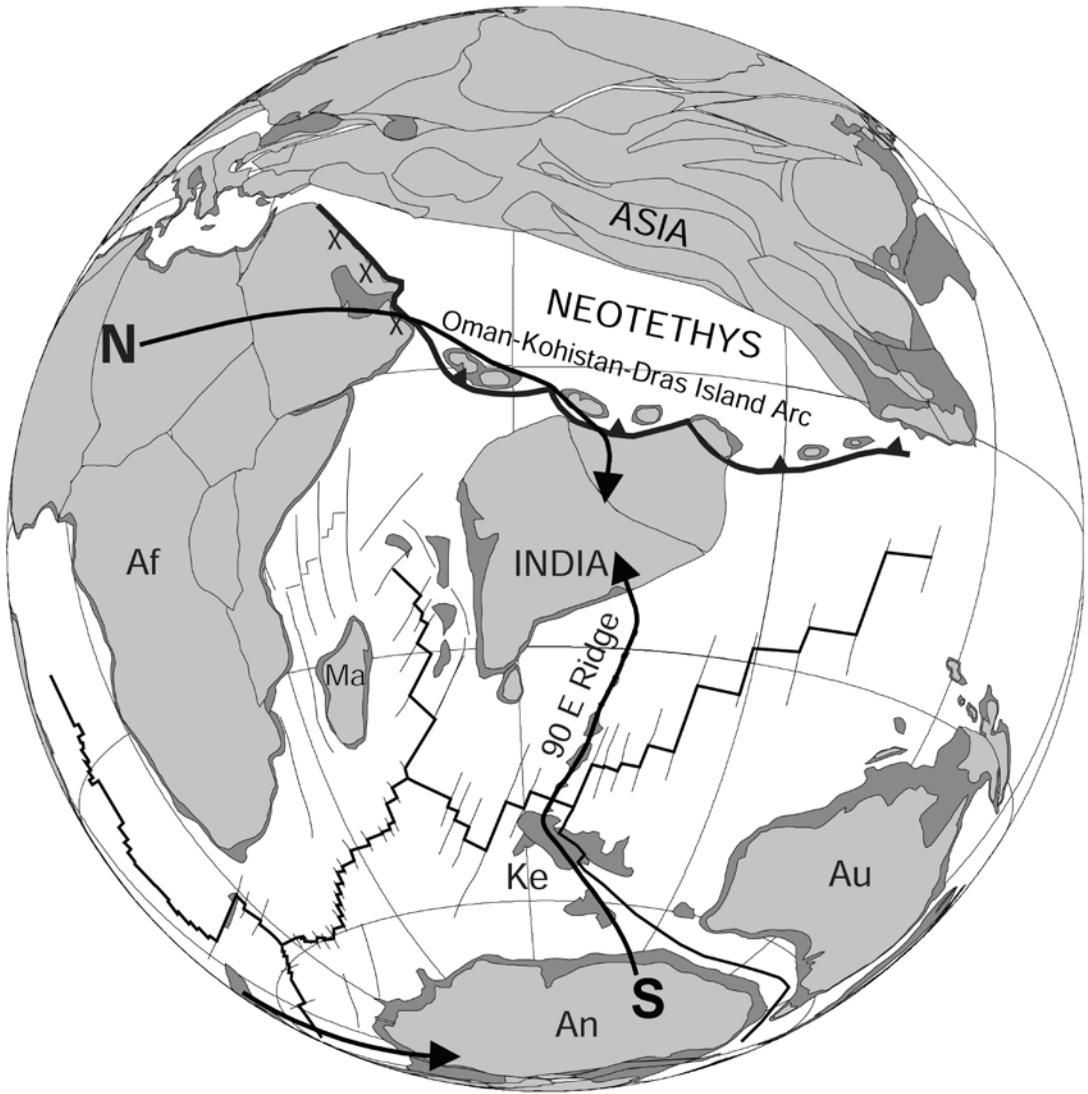


FIGURE 19. K-T boundary (65 Ma) geography showing biogeographic connections between the Indian subcontinent and surrounding regions including the Arabian Plate. The Oman-Kohistan-Dras archipelago persisted in one form or another into at least the late Eocene and close to the time of contact between India and Asia (map reproduced with permission from Chatterjee and Scotese, 2010). Such physical connections permitted plants and animals to move between these biogeographic realms and perhaps permitted ancestral species of the *mixta* species group to disperse from India into eastern Arabia, while ancestors of the *sarawatisis* species group would have come from the connection between Africa and western Arabia. Abbreviations: Af = Africa; An = Antarctica; Au = Australia; Ke = Kerguelen Plateau; Ma = Madagascar.

tapering to point, adjacent to gonostylus; intermediate apical projection entirely absent; gonostylus entirely membranous, about twice as long as wide.

Labrum minutely roughened and surface coarsely irregular, shining; clypeus shining, minutely imbricate, with scattered inconspicuous punctures giving rise to small setae;

remainder of face with irregular smooth areas and areas of small punctures often separated by less than a puncture width; vertex more strongly punctate, mostly with punctures separated by much less than a puncture width; genal area shining, minutely lineolate especially posteriorly, with punctures mostly separated by more than a puncture width, with no contrast between punctuation of upper and lower parts (thus unlike *B. leptozonia* in this respect). Mesoscutum shining, imbricate, with small punctures separated by a puncture width or more; punctures in many places indistinct; mesoscutellar punctuation similar to that of mesoscutum although on anterior border of mesoscutellum slightly more closely spaced; metanotum coarsely imbricate; pleural punctuation similar to that of mesoscutum; propodeum coarsely imbricate except for lateral surface which is rather dull with strong, dense punctuation, these punctures, unlike those elsewhere, not giving rise to setae and so dense that surface could well be described as finely reticulate; legs finely imbricate except smooth on much of under surface of metafemur; metabasitibial plate not recognizable, not defined by carinae; metasomal terga and sterna finely lineolate, with punctures in most areas coarser than those of mesoscutum and in some areas also closer, but posterior margins smooth although less evident on posterior segments; posterior margin of seventh tergum broadly rounded.

Integument mostly black; labrum pale yellow with distal and lateral margins dark. Clypeus pale yellow except for black ventrolateral corners; pronotal lobe pale yellow; under side of flagellum dark brown, especially toward antennal apex; tegula transparent with inner border brown and a yellowish spot anteriorly, but often appearing black or nearly so because of black background; basal sclerites of forewing largely pale yellowish; wings hyaline, veins dark to light brown; metasomal terga with apical margins narrowly semitranslucent.

Pubescence sparse, whitish translucent or slightly yellowish, sparse as is typical for the genus, not forming tergal pale bands; metatrochanter with long, branched setae ventrally; metafemur with large bare area ventrally and with tuft of dense setae on apex of ventral tubercle; metatibia with patch of long setae on inner apex; dorsal metasomal setae slightly curved, almost decumbent, apices blunt; seventh metasomal tergum with fringe of incurved setae (longest setae laterally).

Female. As described for the male except for typical sex differences and as follows: Total length 3.65–4.35 mm; forewing length 2.45–2.90 mm; head about as long as wide, length 1.02–1.14 mm, width 1.12–1.20 mm; compound eyes with inner margins relatively straight, converging below, upper interorbital distance 0.73–0.80 mm, lower interorbital distance 0.51–0.61 mm. Sixth metasomal tergum nearly straight in profile, without lateral projections. Labrum brownish black; lower half of clypeus (i.e., below tentorial pits) with yellow tapering to middle third of apical margin of clypeus, so that lower lateral clypeal areas are black and yellow area is much narrower than on upper half of clypeus (fig. 12).

HOLOTYPE: ♂, Saudi Arabia: al-Baha, Thy Ein [‘Ain] village, 690 m, 19°55′59.61″N, 41°26′41.41″E, 24-v-2012 [24 May 2012], M.S. Engel (KSMA).

PARATYPES: 5 ♀ ♀, 14 ♂ ♂, Saudi Arabia: Al-Baha, Thy Ein [‘Ain] village, 690 m, 19°55′59.61″N, 41°26′41.41″E, 24-v-2012 [24 May 2012], M.S. Engel (SEMC); 22 ♀ ♀, 17 ♂ ♂,

Saudi Arabia: Al-Baha, Thy Ein [‘Ain] village, 690 m, 19°55′59.61″N, 41°26′41.41″E, 25-v-2012 [25 May 2012], M.S. Engel (SEMC, one of each sex in AMNH and KSMA); 6 ♂♂, Saudi Arabia: Baha [al-Baha], Thee Ain [Thy ‘Ain] village, 690 m, 19°55′59.61″N, 41°26′41.41″E, 24-v-2012 [24 May 2012], M.A. Hannan (KSMA); 3 ♀♀, 11 ♂♂, Saudi Arabia: Baha [al-Baha], Thee Ain [Thy ‘Ain] village, 690 m, 19°55′59.61″N, 41°26′41.41″E, 25-v-2012 [25 May 2012], M.A. Hannan (KSMA).

ETYMOLOGY: The specific epithet is a patronym honoring Abdulaziz S. Alqarni for his numerous contributions to the study of Saudi bees and his promotion of melittological systematics in Saudi Arabia.

KEY TO THE ALLODAPINI OF THE ARABIAN PENINSULA

Four species are presently recognized in the fauna: *Braunsapis arabica* Engel and Dathe, *B. alqarnii* n. sp., *Compsomelissa ocellata* (Michener), and *C. boernerii* Alfken (Michener, 1966, 1975a; Engel, 2011; Engel and Dathe, 2011; Alqarni et al., in press). Here we provide a key to this fauna as an aid to regional melittologists.

1. Forewing 2m-cu present (figs. 1, 10); body black, commonly with yellow areas on face and pronotum (figs. 1–3, 10–14, 16, 17) (genus *Braunsapis* Michener)2
- Forewing 2m-cu absent (fig. 18); all tagmata with extensive yellow areas (figs. 15, 18) (genus *Compsomelissa* Alfken) 3
2. Male scape black and paraocular areas bordering epistomal sulcus black (fig. 3); male metafemur as in figure 4; genitalia with pronounced medioventral apical process on gonocoxite; smaller species, total length 3.10–3.90 mm in males, 3.65–4.35 mm in females, head width 1.14–1.17 mm in males, 1.12–1.20 mm in females (Saudi Arabia: Sarawat Mts.)
..... *B. alqarnii* Engel and Michener, n. sp.
- Male scape with conspicuous yellow mark ventrally and paraocular areas border epistomal sulcus yellow (fig. 14); male metafemur unmodified; genitalia without medioventral apical process; larger species, total length 4.40–4.50 mm in males, 4.80–5.50 mm in females, head width 1.33–1.35 mm in males, 1.33–1.47 mm in females (United Arab Emirates)
..... *B. arabica* Engel and Dathe
3. Vertex yellow; ocelli enlarged so that ocellocular distance about half of ocellar diameter (Yemen, Saudi Arabia: Jazan) *C. ocellata* (Michener)
- Vertex with black band between summits of compound eyes including ocelli (sometimes faded in older specimens such that area is more brownish in ocellocular area); ocelli not greatly enlarged, ocellocular distance about equal to ocellar diameter (Yemen)
..... *C. boernerii* Alfken

DISCUSSION

Braunsapis alqarnii is truly a distinctive species within the genus and is rightfully placed in its own species group among such groupings previously recognized in the genus

(e.g., Michener, 1975a, 1977b; Reyes, 1991a, 1991b, 1993). The enormous medioventral apical process of the gonocoxite and the prominent basal metafemoral tubercle bearing a dense tuft of setae at its apex are entirely unlike anything previously known within the genus. Similarly, the form of the male hind leg is unique. The metatrochanter bearing a midventral concavity is known in many other species, but the metafemur with a broadly smooth ventral surface in the basal half and bearing a large basal tubercle, itself with an apical tuft of setae, is unknown elsewhere in the genus. Together these features serve to distinguish *B. alqarnii* and give it, at least morphologically, a relatively isolated position among *Braunsapis* species groups.

Nonetheless, in many other respects *B. alqarnii* is similar in small size and general appearance to various small African species, such as *B. leptozonia*, likely indicating a relationship between subsets of the African fauna and the southwestern Arabian species. Even the modifications of the hind legs are similar, although in *B. leptozonia* the basal femoral projection is more toothlike, farther from the base of the femur, concave and shiny on the anterior surface, and lacks a terminal tuft of setae (vide Michener, 1975a: fig. 104). In addition, the bare area on the under surface of the metafemur is less extensive in *B. leptozonia*. Despite these similarities, the genitalia of *B. alqarnii* remain unique within the genus.

It is interesting to note that the allodapines of the western borders of the Arabian Peninsula have distinct African affinities, while the single species presently known from the eastern boundaries of the peninsula is clearly of Oriental origin and remarkably similar to *B. mixta* (Smith), a species living in India and Sri Lanka. Naturally, a comprehensive phylogeny of *Braunsapis* including *B. alqarnii* and *B. arabica* would shed considerable light on the historical biogeography of this region, particularly if *B. arabica* clustered among or basal to the Asian or Asian + Australian clade recovered by Fuller et al. (2005: see also Schwarz et al., 2004), and *B. alqarnii* among the other generally African taxa. Considerable biogeographic connections are known between the Indian and Arabian subcontinents (e.g., Conti et al., 2002; Chatterjee and Scotese, 2010), and these are hypothesized to have been supported by temporary connections through archipelagos existing during the latest Cretaceous and Early Tertiary, perhaps continuing as late as the later Eocene (Chatterjee and Scotese, 2010; Chatterjee et al., 2013) (fig. 19). It is likely that these connections permitted progenitors of the Arabian lineages to independently move into the peninsula from Africa and from India during the Early Tertiary, and suggesting that the genus is older than implied by some molecular-only estimates. Indeed, paleontological evidence has highlighted that in some cases fossils of clades predate that of such estimates by many millions of years (e.g., Wappler et al., 2012). Unfortunately, no fossils are known of true Allodapini, but a related tribe, the Boreallodapini, was present at least in the fauna of Europe during the mid-Eocene (Engel, 2001). The presence of boreallodapines, and thus Allodapini, by this time period indicates that perhaps even the genus *Braunsapis* or early stem groups were well established and sufficiently widespread to permit such migrations to take place. Naturally, continued phylogenetic work on *Braunsapis* is needed in conjunction with further surveys of both the living and any future discovered fossil faunas.

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REFERENCES

- Aenmay, T.K., S.M. Tierney, N. Pillay, and M.P. Schwarz. 2006. Nesting biology of an African allodapine bee *Braunsapis vitrea*: female biased sex allocation in the absence of worker-like behavioural castes. *Ethology, Ecology, and Evolution* 18 (3): 205–220.
- Alqarni, A.S., M.A. Hannan, and M.S. Engel. In press. First record of the bee genus *Compsomelissa* in the Kingdom of Saudi Arabia (Hymenoptera: Apidae). *Pan-Pacific Entomologist*.
- Brauns, H. 1926. A contribution to the knowledge of the genus *Allodape*, St. Farg. & Serv. Order Hymenoptera; Section Apidae (Anthophila). *Annals of the South African Museum* 23 (3): 417–434.
- Chatterjee, S., and C. Scotese. 2010. The wandering Indian plate and its changing biogeography during the Late Cretaceous–Early Tertiary period. In S. Bandyopadhyay (editor), *New aspects of Mesozoic biodiversity*: 105–126. Berlin: Springer Verlag, xiv+134 pp.
- Chatterjee, S., A. Goswami, and C.R. Scotese. 2013. The longest voyage: tectonic, magmatic, and paleoclimatic evolution of the Indian plate during its northward flight from Gondwana to Asia. *Gondwana Research* 23 (1): 238–267.
- Chenoweth, L.B., S. Fuller, S.M. Tierney, Y.C. Park, and M.P. Schwarz. 2008. *Hasinamelissa*: A new genus of allodapine bee from Madagascar revealed by larval morphology and DNA sequence data. *Systematic Entomology* 33 (4): 700–710.
- Conti, E., T. Eriksson, J. Schönenberger, K.J. Sytsma, and D.A. Baum. 2002. Early Tertiary out-of-India dispersal of Crypteroniaceae: Evidence from phylogeny and molecular dating. *Evolution* 56 (10): 1931–1942.
- 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. 2011. A note on the bee genus *Compsomelissa* Alfken 1924 in Yemen (Hymenoptera: Apidae). *Entomofauna* 32 (10): 209–212.
- Engel, M.S. 2013. A new species of the allodapine bee genus *Braunsapis* from the Central African Republic (Hymenoptera: Apidae). *Journal of Melittology* 21: 1–7.
- Engel, M.S., and H.H. Dathe. 2011. Order Hymenoptera, family Apidae: tribe Allodapini, genus *Braunsapis*. *Arthropod Fauna of the UAE* 4: 630–635.
- 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.
- Fuller, S., M. Schwarz, and S. Tierney. 2005. Phylogenetics of the allodapine bee genus *Braunsapis*: Historical biogeography and long-range dispersal over water. *Journal of Biogeography* 32 (12): 2135–2144.
- Maeta, Y., S.F. Sakagami, and C.D. Michener. 1985. Laboratory studies of the life cycle and nesting biology of *Braunsapis sauteriella*, a social allodapine bee (Hymenoptera, Apidae). *Sociobiology* 10 (1): 17–41.

- Michener, C.D. 1966. A new genus of ceratinine bees from the Red Sea area (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society* 39 (4): 572–576.
- Michener, C.D. 1970. Nest sites of stem and twig inhabiting African bees (Hymenoptera: Apoidea). *Journal of the Entomological Society of Southern Africa* 33 (1): 1–22.
- Michener, C.D. 1971. Biologies of African allodapine bees. *Bulletin of the American Museum of Natural History* 145 (3): 219–305.
- Michener, C.D. 1975a. A taxonomic study of African allodapine bees (Hymenoptera, Anthophoridae, Ceratinini). *Bulletin of the American Museum of Natural History* 155 (2): 67–240.
- Michener, C.D. 1975b. Larvae of African allodapine bees. 1. The genus *Allodape* (Hymenoptera: Xylocopinae). *Journal of the Entomological Society of Southern Africa* 38 (1): 1–12.
- Michener, C.D. 1975c. Larvae of African allodapine bees. 2. *Braunsapis* and *Nasutapis* (Hymenoptera: Xylocopinae). *Journal of the Entomological Society of Southern Africa* 38(2): 223–242.
- Michener, C.D. 1975d. Larvae of African allodapine bees. 3. The genera *Allodapula* and *Eucondylops*. *Journal of the Entomological Society of Southern Africa* 38 (2): 243–250.
- Michener, C.D. 1976. Larvae of African allodapine bees. 4. *Halterapis*, *Compsomelissa*, *Macrogalea*, and a key to African genera. *Journal of the Entomological Society of Southern Africa* 39 (1): 33–37.
- Michener, C.D. 1977a. Discordant evolution and the classification of allodapine bees. *Systematic Zoology* 26 (1): 32–56.
- Michener, C.D. 1977b. Allodapine bees of Madagascar (Hymenoptera, Apoidea). *American Museum Novitates* 2622: 1–18.
- Michener, C.D. 2007. *The bees of the world*, 2nd ed. Baltimore, MD: Johns Hopkins University Press, xvi+[i]+953 pp., +20 pls.
- Reyes, S.G. 1991a. Revision of the bee genus *Braunsapis* in the Oriental Region (Apoidea: Xylocopinae: Allodapini). *University of Kansas Science Bulletin* 54 (6): 179–207.
- Reyes, S.G. 1991b. A review of the bee genus *Braunsapis* in Madagascar (Hymenoptera: Anthophoridae). *Journal of African Zoology* 105 (2): 125–130.
- Reyes, S.G. 1993. Revision of the bee genus *Braunsapis* in the Australian Region (Hymenoptera: Xylocopinae: Allodapini). *University of Kansas Science Bulletin* 55 (3): 97–122.
- Schwarz, M.P., S.M. Tierney, S.J.B. Cooper, and N.J. Bull. 2004. Molecular phylogenetics of the allodapine bee genus *Braunsapis*: A-T bias and heterogenous substitution parameters. *Molecular Phylogenetics and Evolution* 32 (1): 110–122.
- Wappler, T., T. De Meulemeester, A.M. Aytakin, D. Michez, and M.S. Engel. 2012. Geometric morphometric analysis of a new Miocene bumble bee from the Randeck Maar of southwestern Germany (Hymenoptera: Apidae). *Systematic Entomology* 37 (4): 784–792.

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