

**THE CLEPTOPARASITIC BEE GENUS *CHIASMognathus*
(HYMENOPTERA: APIDAE) IN KENYA, WITH THE DESCRIPTION
OF TWO NEW SPECIES**

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ABSTRACT

The minute, cleptoparasitic bee genus *Chiasmognathus* (Nomadinae: Ammobatini) is documented from western Kenya, representing the southernmost records of the lineage. Two species are recognized from the Great Rift Valley—*Chiasmognathus aturksvenicus*, from the southwestern side of Lake Turkana, and the other, *C. riftensis*, from further south near Lake Bogoria. The former was captured in association with its host, *Nomioides (Nomioides) turanicus* (Halictinae: Nomioidini). *Chiasmognathus sahelensis* is considered a new junior synonym of *Pasites gnomus*, and the latter epithet is transferred to *Chiasmognathus: C. gnomus*. We illustrate and discuss intraspecific variation in some morphological features of these tiny bees.

Keywords: Apoidea, taxonomy, Nomadinae, Halictidae, Kenya, Turkana, Bogoria

INTRODUCTION

As is often the case, it is the smaller things in our world that are the most easily overlooked or ignored, even when they may be of profound importance. Such has been true for the study of insects in general, usually pushed aside while biologists chase after the charismatic megafauna of our world. Nonetheless, the legions of insects with whom we share the planet are the modern-day descendants of a lineage stretching back over 400 million years (Grimaldi & Engel, 2005; Engel, 2015). It is the ancestors of these smaller inhabitants who quite truthfully shaped every terrestrial ecosystem, and who remain vital to the functioning of

those same environments today (Grimaldi & Engel, 2005). Even within a group as critical to ecosystem health as the bees (Apoidea: Anthophila), there are biases toward the study of the social lineages, and particularly the honey bees (Smith & Saunders, 2016) and their relatives, as well as species commanding an impressive and large habitus. Diminutive bees are common, and these species are of considerable importance for pollination, floral diversity, and ecological processes more broadly. The diversity of the Apoidea's more Lilliputian residents is impressive, and, not surprisingly, lesser known in comparison to the more conspicuous elements. Nonetheless, when focused attention is applied many new species can be discovered. One such example is the genus *Chiasmognathus* Engel, a group of tiny cleptoparasitic bees found widely, albeit uncommonly, across the Eastern Hemisphere (Engel, 2006, 2009; Alqarni *et al.*, 2013). Where known, species of *Chiasmognathus* are cleptoparasites in the nests of nomioidine bees (Rozen, 2008), principally *Nomioides* Schenck but also *Ceylalicetus* Strand (Engel 2008b; Straka & Engel, 2012). Although only four of the current 15 species were known before 2007 (see table 1), further material and additional taxa have steadily accumulated (table 1), especially from nomioidine nesting aggregations, and it is likely that wherever nomioidines are found so too shall be their cleptoparasites.

Chiasmognathus are among the smallest of all bees, ranging in size from nearly 2 mm up to 'giants' around 3.6–4.2 mm, and within the Ammobatini the genus is most similar to *Parammobatodes* Popov. *Chiasmognathus* have the long axes of the closed mandibles crossing along the labral margins (the feature that gave the genus its name), a slightly swollen pedicel tightly adjoined to the scape, the antenna in both sexes with 10 flagellomeres [a rather uncommonly encountered character among bees (*e.g.* Brooks & Engel, 1999), but when present most often found in cleptoparasitic genera (*e.g.* Linsley, 1943; Hurd & Linsley, 1972; Engel & Michener, 2012), including elsewhere among Ammobatini such as *Pasites* Jurine and *Melanempis* Saussure (Michener, 2007)], the pronotum dorsally concealed by the mesoscutum, metasomal tergum I dorsally broader than long, and a rather proximally contracted forewing venation with only two submarginal cells and a broadly truncate and weakly appendiculate marginal cell (Engel, 2006, 2009). Most interestingly, *Chiasmognathus* lack a jugal lobe in the hind wing (Engel, 2006), a trait elsewhere in the Ammobatini known only in *Melanempis*, which in the tribe represents the opposing end of the body size spectrum: 15–22mm in length (Michener, 2007). Hitherto the genus included 13 species that may be found from the windward islands of Cape Verde in the far west (Straka & Engel, 2012), within the Sahel Belt (Engel, 2010) and northeastern Africa (Warncke, 1983); the southeastern portion of the Balkans, western Anatolia, and the Levant (Warncke, 1983; Engel, 2008b); across Arabia (Engel, 2009, unpubl. data; Alqarni *et al.*, 2013; Engel & Straka, 2016); and from there extending through southern Asia as far south as Sri Lanka (Engel, 2006, 2008a), and northward in Central Asia as far as the Ili Depression in Kazakhstan (Engel, 2006, 2008a; Engel & Packer, 2013) (table 1).

Within *Chiasmognathus*, only three species have been documented as occurring in Africa. *Chiasmognathus aegyptiacus* (Warncke) in northeastern Egypt (Warncke, 1983), *C. batelkai* Straka & Engel in the two most westerly islands of the windward Barlavento portion of the Cape Verde archipelago (Straka & Engel, 2012), and *C. gnomus* (Eardley) in Niger (Eardley & Brothers, 1997; Engel, 2010) (table 1). Despite these few occurrences for *Chiasmognathus*, its hosts, nomioidines, are diverse, with almost 100 species (Pesenko, 1983; Michener, 2007), and widespread throughout the Old World including over 30 species in Africa (Pesenko & Pauly, 2005), suggesting the possibility that the cleptoparasites may approach them in geographic scope and species diversity. It is therefore intuitively pleasing that *Chiasmognathus* were subsequently discovered in Kenya (Martins, 2012), representing for the moment the southernmost record of the genus. Here we provide descriptions for the species reported by Martins (2012), as well as another from the Rift Valley region of Kenya.

Table 1. List of the 15 described species of *Chiasmognathus* Engel (*Ammobatini*), along with information on distribution, sexes known, and host species (*N* = *Nomioides* Schenck; *C* = *Ceylalictus* Strand).

Species, authority & sexes known	Distribution	Host
<i>C. aegyptiacus</i> (Warncke, 1983), ♂♀	Egypt, Israel	unknown
<i>C. aturksvenicus</i> , n. sp., ♂♀	Kenya: Turkana	<i>N. turanicus</i> Morawitz
<i>C. aurantiacus</i> Engel (2009), ♀	UAE	unknown
<i>C. batelkai</i> Straka & Engel (2012), ♂♀	Cape Verde	<i>C. capverdensis</i> Pesenko <i>et al.</i>
<i>C. gnomus</i> (Eardley, 1997) ¹ , ♂♀	Niger	unknown
<i>C. gussakovskii</i> (Popov, 1937), ♂♀	Tajikistan, Kyrgyzstan	unknown
<i>C. himyarensis</i> Engel (2009), ♀	Yemen	unknown
<i>C. nearchus</i> Engel (2009), ♂♀	UAE, Oman, Saudi Arabia	<i>N. rotundiceps</i> Handlirsch
<i>C. orientanus</i> (Warncke, 1983), ♂♀	Turkey, Cyprus, Crete, Israel, Bulgaria	<i>N. minutissima</i> (Rossi)
<i>C. pashupati</i> Engel (2008b), ♂♀	Pakistan: Sindh	<i>N. patruelis</i> Cockerell
<i>C. rhagae</i> Engel (2008a), ♀	Iran: Tehran	unknown
<i>C. riftensis</i> , n. sp., ♀	Kenya: Bogoria	unknown
<i>C. sabaicus</i> Engel & Straka (2016), ♂	Yemen	unknown
<i>C. scythicus</i> Engel & Packer (2013), ♂♀	Kazakhstan: Almaty	unknown
<i>C. taprobanicola</i> Engel (2008b), ♂♀	Sri Lanka	<i>Ceylalictus</i> spp.

¹ *Chiasmognathus sahelensis* Engel is a new junior synonym of *Pasites gnomus* Eardley (in Eardley & Brothers, 1997), and the latter epithet is transferred to *Chiasmognathus*: *C. gnomus* (Eardley), new combination.

MATERIAL AND METHODS

Material is deposited in the following repositories: **AMNH** American Museum of Natural History; **NMK** National Museums of Kenya, Nairobi, Kenya; **PCYU**, Packer Collection, Department of Biology, York University, Toronto, Canada; **SEMC**, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA and **TBI** Turkana Basin Institute, Turkana, Kenya. Morphological terminology generally follows that of Engel (2001) and Michener (2007), with the descriptions modeled after those used elsewhere for *Chiasmognathus* (e.g. Engel, 2007; Engel & Packer, 2013). Descriptions are provided here in the context of furthering information on character and species diversity for future systematic work among bees (Engel, 2011), for modern hypotheses of specific circumscription for bees (Gonzalez *et al.*, 2013), and as an ultimate foundation for the illumination of general evolutionary patterns (Grimaldi & Engel, 2007).

An ocular micrometer on an Olympus SZX-12 stereomicroscope was used to take measurements of individual specimens. Microphotographs were prepared either with a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens, illuminated by a Xenon flash (head, habitus and genitalia images) or a Visionary Digital BK Plus imaging system with a Canon EOS 5D digital SLR camera (details of morphological variation in *C. aturksvenicus* and views of tergum VI of both species). Environmental scanning electron micrographs (ESEM) were taken with a Thermofisher Quanta 3D FEG DualBeam microscope with no coating and with Low Vacuum and Gaseous Sensory Electron Detectors.

DNA barcodes (Hebert *et al.*, 2003) were obtained from a single right midleg placed in a well-plate for processing at the Biodiversity Institute of Ontario. The methods described by

Ivanova et al. (2006; <http://www.ccdb.ca/resources.php>) were followed with the primers LepF1 and LepR1 (Hebert *et al.*, 2004). The online BOLD platform was used for data analysis and barcode index numbers (BINs) (Ratnasingham & Hebert, 2013) obtained from the resulting sequences.

TAXONOMIC TREATMENT

Genus *Chiasmognathus* Engel

Chiasmognathus aturksvenicus Engel, Packer & Martins, new species
(figures 1–18)

DIAGNOSIS: The new species can be distinguished most easily from its regional congener (*vide infra*) by the virtually impunctate mesoscutal central disc (figures 2, 12, 15) (punctures mostly sparse but distinct throughout in *C. riftensis*, figures 20, 24), tergum VI yellow-orange, setae seemingly concolourous with background and difficult to see with light microscope, sides strongly concave and apex convex (figures 14, 16) (integument pale brown in *C. riftensis* with pale setae easy to see against darker background, sides convex and apex concave, figures 23, 25) and the distinctly tubular appendiculate vein of the marginal cell that (except in one individual) is at least as long as its basal width (figures 4, 5) (absent as a tubular vein in *C. riftensis* Fig. 22).

DESCRIPTION: Male. Total body length 2.82 mm (2.82–3.07 mm); forewing length 2.10 mm (2.10–2.40 mm). Head wider than long, width 0.94 mm (0.94–0.96 mm), length 0.72 mm (0.72–0.75 mm); inner margins of compound eyes straight, convergent below, upper interorbital distance 0.67 mm (0.67–0.70 mm), lower interorbital distance 0.46 mm (0.46–0.48 mm); apex of clypeus at lower tangent of compound eyes; paraocular carina strongly produced below, tangential to inner margin of compound eye; vertexal area strongly convex in frontal view, ocelli above upper tangent of compound eyes, ocellar triangle slightly prominent; clypeus nearly flat, surface faintly convex, apicolateral corners with small patches of tightly packed, elongate, erect, curved setae (characteristic of males of *Chiasmognathus*); labrum longer than wide, lateral margins tapering in apical half to acutely rounded apex; malar space vestigial posteriorly, 0.4 times basal mandibular width anteriorly; frontal line distinct from just below lower tangent of antennal toruli to median ocellus, carinate in lower half, impressed in upper half. Mesoscutum with parapsidal lines narrow, more distinct than broader, shallow median line, median line extending to about mesoscutal midlength; intertegular distance (*i.e.* distance between inner margins of tegulae) 0.56 mm (0.56–0.61 mm); mesoscutellum weakly bigibbous (varying from moderately bigibbous to weakly convex). Forewing marginal cell broadly truncate, appendiculate vein tubular at least as long as its basal width (reduced to a strong angulation in one specimen); two submarginal cells (owing to absence of 1rs-m: note that the holotype retains 1rs-m in the right forewing only; 1rs-m is straight, anteriorly separated from 2rs-m by about vein width and posteriorly nearly touching 2rs-m, and demarcates an exceptionally narrow, nearly linear medial submarginal cell), second submarginal cell less than half as long as first; 2rs-m arched to form convex apex to second submarginal cell; both m-cu crossveins entering second submarginal cell. Hindwing with 4 distal hamuli; Rs short, perpendicular to costal margin; without defined rs-m, instead M runs straight to Rs apex; M+Cu elongate, longer than M and Rs combined. Terminalia as depicted in figures 6–10.



Figures 1–3. Photographs of holotype male of *Chiasmognathus aturksvenicus*, new species, from Turkana. 1. Lateral habitus. 2. Dorsal habitus. 3. Facial view.

Integument generally shining (figures 1, 2). Labrum with larger punctures intermingled with smaller punctures, smaller punctures more numerous along basal margin, separated by 1–2 times a puncture width, otherwise punctures separated by 2–5 times a puncture width, becoming particularly sparse along lateral borders and medioapically, integument between punctures nearly smooth; clypeus with small punctures separated by 0.5–2 times a puncture width centrally, apical margin narrowly impunctate; face and vertex with small punctures separated by 0.5–2 times a puncture width, integument between punctures smooth, punctures become sparser toward paraocular carina with nearly impunctate area bordering carina, malar space impunctate, punctures on vertex posterior to ocelli somewhat weaker than those elsewhere on face and vertex, small impunctate area along outer border of lateral ocellus; punctures on gena and



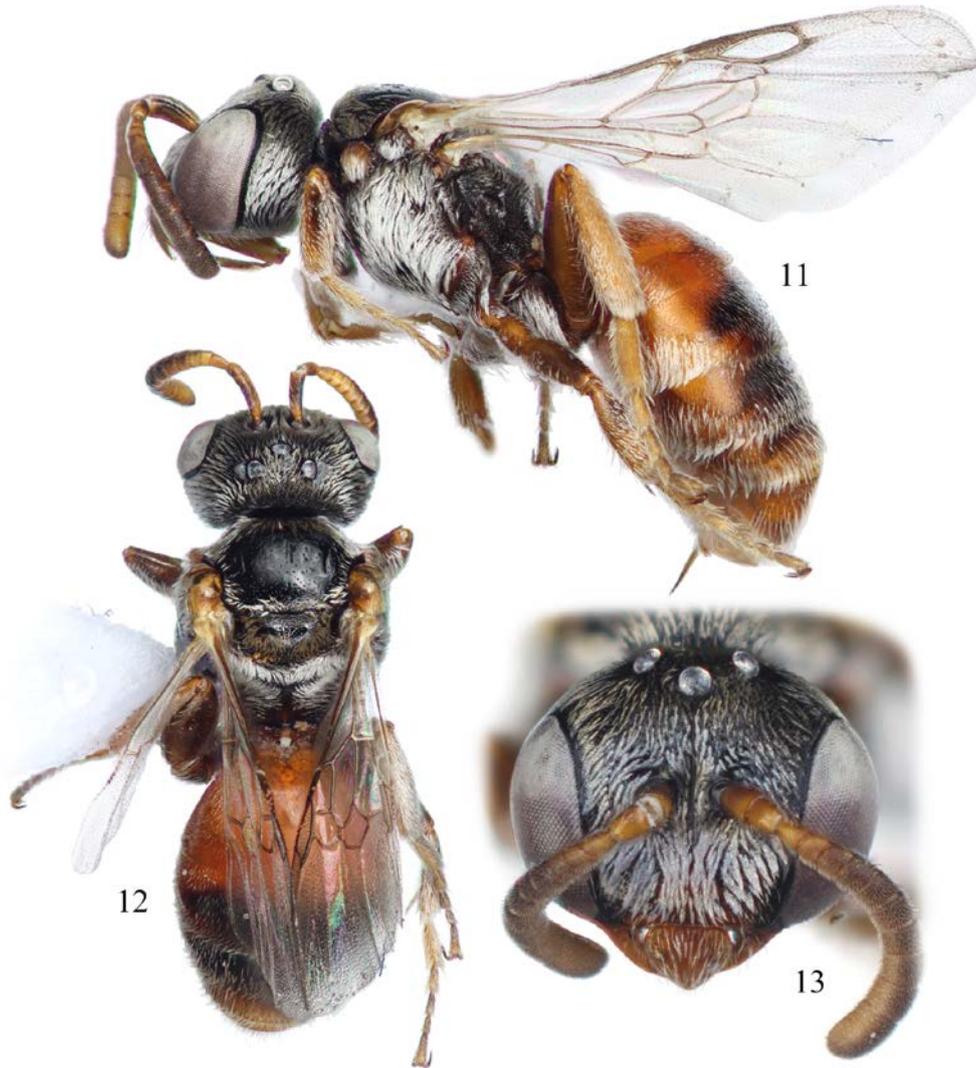
Figures 4–5. Photographs of forewings of holotype male of *Chiasmognathus aturksvenicus*, new species. 4. Left forewing with typical condition of two submarginal cells. 5. Right forewing showing aberrant presence of 1rs-m and three submarginal cells.

postgena separated by 1–2 times a puncture width, with small, well-defined punctures, punctures slightly larger than those of face, integument otherwise smooth. Mesoscutum punctures separated by 1–4 times a puncture width outside parapsidal lines and in posterior quarter, over majority of disc punctures distinctly more sparse, separated by 2–8 times a puncture width and variable in size, extreme centre of disc virtually impunctate, integument otherwise smooth and shining; tegula with a few sparse punctures in anterior half, otherwise smooth; mesoscutellum with punctures denser, slightly larger, and more well-defined than on mesoscutum, separated by up to 1.5 times a puncture width medially, more sparse laterally, integument otherwise smooth; metanotum with punctures separated by a puncture width or frequently less; mesepisternum with well-defined punctures separated by 0.5–2 times a puncture width, those posteriorly along border with metepisternum almost uniformly separated by less than a puncture width, those of hypopimeral area slightly more widely spaced, integument otherwise smooth; metepisternum impunctate in ventral half, upper portion weakly and irregularly strigose;

lateral surface of propodeum weakly strigose, more strongly so around propodeal spiracle; posterior surface with punctures separated by 0.5–3 times a puncture width except sparser along medial pit, integument otherwise smooth; basal area of propodeum short, obscured by plumose setae, integument shiny and strigose beneath dense setation. Metasomal terga and sterna finely imbricate, faintly on terga, imbrication more prominent on sterna, except tergum I almost devoid of microsculpture; tergum I with exceptionally fine, minute punctures, on disc separated by 1–3 times a puncture width, with a few scattered larger punctures, punctures sparser elsewhere; remaining terga with punctures more defined, slightly larger, and scattered, punctures separated by 3–5 times a puncture width, punctures weaker and sparser apically; sterna impunctate except at setal bases.

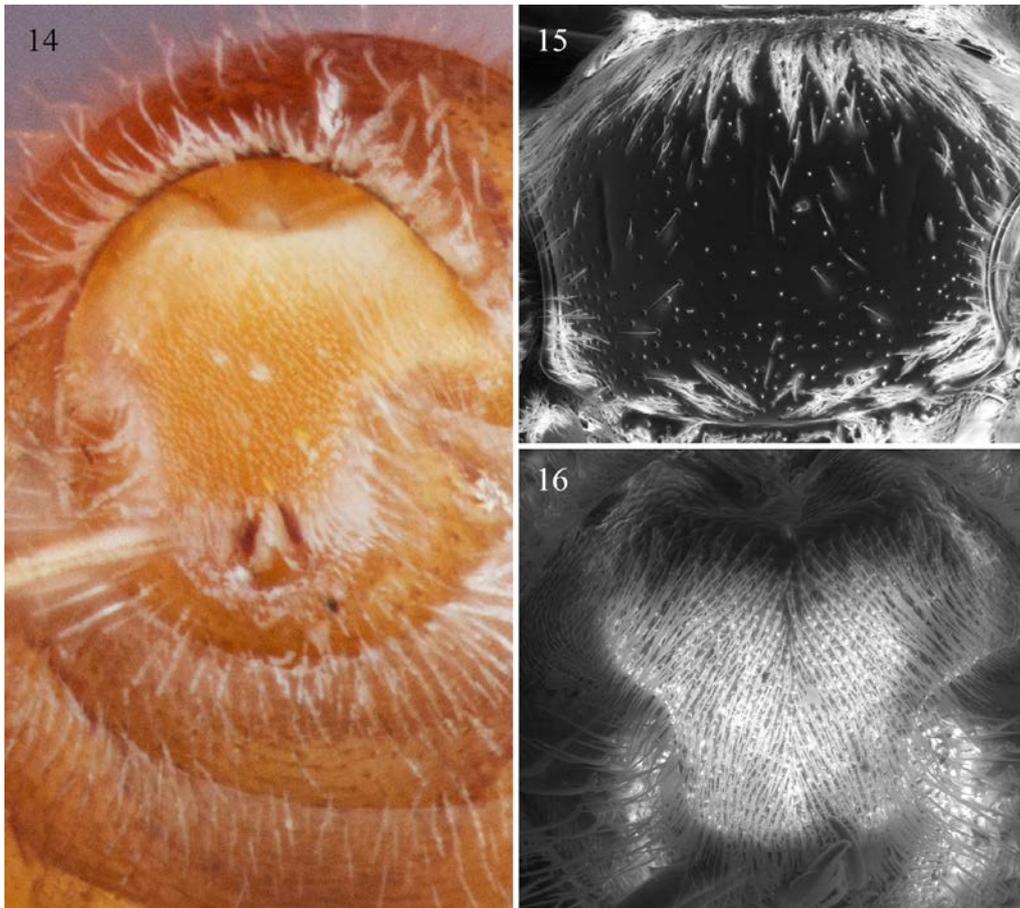


Figures 6–10. Male terminalia of *Chiasmognathus aturksvenicus*, new species, from Turkana. 6. Metasomal sternum VII. 7. Metasomal sternum VIII. 8. Genital capsule, dorsal view. 9. Genital capsule, lateral view. 10. Genital capsule, ventral view.



Figures 11–13. Photographs of female of *Chiasmognathus aturksvenicus*, new species, from Turkana. 11. Lateral habitus. 12. Dorsal habitus. 13. Facial view.

Integument of head and mesosoma black to dark brown (nearly black) and shining except labrum brown (sometimes darker medially); mandible dark brown at base, yellow brown over most of length, with reddish apex; labiomaxillary complex light brown to yellow brown; scape brown (often lighter basally); pedicel and flagellum light brown to yellow brown; pronotal lobe brown to light brown; tegula translucent light brown; legs dark brown to chestnut brown except tarsi, tibial apices, and femorotibial joints lighter (often yellow brown to more yellow). Wing veins pale brown to light yellow brown, those around costal and marginal cells and pterostigma darker; membranes clear hyaline. Metasomal terga dark brown (sometimes somewhat reddish brown on first and less often second terga), tergum VII yellow margined with brown, pregradular areas of terga



Figures 14–16. Photographs and ESEM images of female of *Chiasmognathus aturksvenicus*, new species. 14. Tergum VI. 15. ESEM of mesoscutum. 16. ESEM detail of tergum VI.

beyond tergum I light brown to light yellow brown (often covered by overlapping terga and therefore not visible in specimens unless metasoma is outstretched), apical impressed areas pale brown; sterna somewhat paler brown than terga with apical impressed areas lighter in colour.

Pubescence silvery white. Head with numerous, fine, appressed to subappressed plumose setae, such setae nearly obscuring integument of clypeus and face below level of antennal toruli, such setae intermingled with a few suberect to erect finer, simple setae; appressed plumose setae present on gena, particularly in lower half. Mesosoma with appressed to subappressed, plumose setae along dorsal border of pronotum and on pronotal lobe, anterior one third and lateral and posterior borders of mesoscutum, and largely obscuring integument of mesepisternum, metanotum, and dorsal area of metapostnotum; such plumose setae slightly longer and more suberect on mesoscutellum, setae dense but not obscuring integument. Metasoma with sparse, suberect to subappressed, short, simple to minutely branched setae, and with more abundant, longer, plumose setae, such setae most abundant laterally and apically on terga II–VI, forming

loose apical fasciae, broadly interrupted medially on TII and sparse medially on TIII; sterna with scattered subappressed, simple to minutely branched setae.

Female. As described for male except in usual gender differences and as follows: Total body length 2.86–3.62 mm; forewing length 2.10–2.85 mm. Head wider than long, width 0.88–1.20 mm, length 0.69–1.05 mm; upper interorbital distance 0.64–0.82 mm, lower interorbital distance 0.44–0.58 mm; lacking tight, elongate, curved setae at extreme apicolateral corners of clypeus. Intertegular distance 0.50–0.80 mm. Second submarginal cell more than half as long as first. Tergum VI sides concave, apex weakly convex.

Sculpturing as in male except punctures of metasomal tergum V denser than on preceding terga, punctures separated by about a puncture width except apically.

Colouration as in male except head and mesosoma sometimes approximating dark brown on areas where male is black, and light brown to yellow brown on labrum, apicolateral corner of clypeus, basal and apical rings of scape (remainder of scape brown), pedicel, entirety of first and second flagellomeres and anterior surface of remainder of flagellum (posterior surface brown), pronotal lobe, and tarsi and tibiae except sometimes tibiae as in male. Metasoma dark brown except tergum I entirely reddish orange (reddish brown in one female), tergum II in basal half and entirety of sides reddish orange except reddish brown subapically (in one female largely reddish brown), terga III and IV basally and laterally reddish orange (in one female largely reddish brown), tergum V entirely reddish orange except for reddish brown anterolateral patches; tergum VI flat portion yellow.

Pubescence silvery white (except tinged golden in some individuals on mesoscutum and mesoscutellum); appressed plumose setae of mesoscutum sometimes occupying wider portion of anterior portion; erect to suberect, simple setae of metasomal terga longer subapically and more numerous on more apical terga; loose apical fasciae of tergum IV sparse medially; tergum VI flat portion with two distinct setal types, long and bent at the apex and short and forked.



Figures 17–18. Photographs of living *Chiasmognathus aturksvenicus*, on flowers of *Euphorbia hirta*. 17. Female. 18. Male.

HOLOTYPE: ♂; Kenya: Turkana, Turkana Basin Institute, Nachekichok, 2-iii-2012, Dino J. Martins (TBI).

PARATYPES (6♂♂, 9♀♀): 1♂, 2♀♀, Kenya: Turkana, Turkana Basin Institute, Nachekichok, 2-iii-2012, Dino J. Martins (PCYU); 2♂♂, 2♀♀, Kenya: Turkana, Turkana Basin Institute, 2-iii-2012, Dino J. Martins (PCYU, SEMC, TBI); 3♂♂, 4♀♀, Kenya: Turkana, South Turkwel, Turkana Basin Institute, 14-iv-2012, Dino J. Martins, on *Euphorbia hirta* L. [Euphorbiaceae] (AMNH, NMK, PCYU, SEMC), 1♀, Kenya: Turkana, South Turkwel, Turkana Basin Institute, 14.iii.2012, P. Lomosingo & D.J. Martins, on *Euphorbia hirta*, TBI-BEE-00122 (PCYU).

HOST PLANT: The species has been found at inflorescences of *Euphorbia hirta* L. (Euphorbiaceae), which is a common weed of disturbed ground in East Africa, especially in dry/seasonal areas.

HOST BEE: *Nomioides (Nomioides) turanicus* Morawitz; 1♀, Kenya: Turkana, Turkana Basin Institute, Nachekichok, 2-iii-2012, Dino J. Martins (TBI).

ETYMOLOGY: The specific epithet is taken from the general name for the Turkana region in the Turkana language—Aturksven.

VARIATION: The smallest female is distinctly darker than the others. The metrics for this individual are: total body length 2.73 mm, forewing length 1.97 mm; head width 0.91 mm, length 0.74 mm; upper interorbital distance 0.65 mm, lower interorbital distance 0.44 mm; intertegular distance 0.53 mm. At the other extreme, there is one female with the metapostnotum and propodeum orange-brown and the mesoscutellum red-brown. There is much variation in puncture density on the disc of the mesoscutum, particularly in females, with the punctures denser and more distinct in larger individuals. Some mesoscutal punctures are separated by scarcely more than their widths in the largest female specimens but they remain sparse on the disc. The weak bigibbosity of the mesoscutellum is absent in some individuals. As noted in the description, the holotype male has three submarginal cells on the right forewing (owing to the presence of 1rs-m), all other individuals have two submarginal cells on both forewings.

The appendiculation of the marginal cell is at least as long as its basal width except in one female in which it is a distinct angulation, in another female it is more than four times longer than wide. Even the weakest appendiculate vein in *C. aturksvenicus* is stronger than the same structure in any of the *C. riftensis* in which even the angulation of the marginal cell is non-tubular.

COMMENTS: The habitat of this species is dry acacia and palm riverine woodland (see for example Packer & Martins, 2015, figure 6). The vegetation is dominated by large *Acacia tortilis* (Forssk.) Hayne (syn: *Vachellia tortilis* (Forssk.) Galasso & Banfi) trees and Doum palms (*Hyphaene coriacea* Gaertn.). The sparse understory consists of scattered *Salvadora persica* L. and *Maerua* sp. bushes with herbaceous *Tribulus terrestris* L. and *Blepharis* sp. flowering. Very low-growing herbaceous plants include the common weed *Euphorbia hirta* L. where grazing by goats was limited. Rainfall had been experienced in the weeks preceding the capture of the bees and this had induced flowering in this typically dry site.

Both male and female *C. aturksvenicus* were observed on flowers of *E. hirta* (figures 17, 18) in the vicinity of a shallow depression in bare soil where both *Nomioides turanicus* and *Ceylaliectus* sp. were abundant. Males were observed at this site 'ambushing' females who were trying to enter host nests in the ground. Both sexes were collected at flowers by placing a Ziploc bag over the flower after the bee landed on it and sealing the bee into the bag as netting the low vegetation proved difficult.

The nature of the setation on the flat portion of tergum VI of the female is notable for its mix of bent and forked setae. This is in distinct contrast to the next species, which has simple, robust, and tapering straight setae, and also in comparison to *C. rhagae* Engel in which these setae are uniformly strongly hooked, apically recurved.

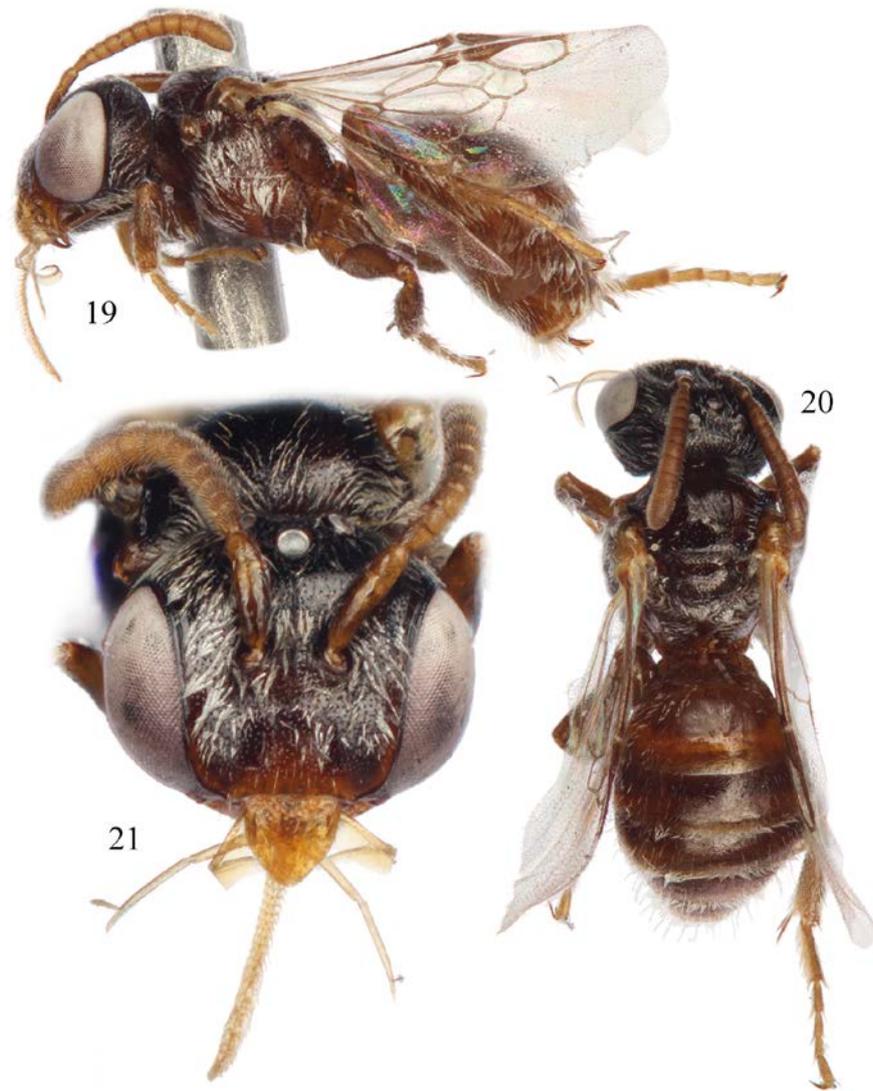
Chiasmognathus riftensis Engel, Packer & Martins, new species
(figures 19–25)

DIAGNOSIS: The new species is diagnosed by differential characters in the account of *C. aturksvenicus* (*vide supra*). The male remains unknown but given the general similarity between the two Kenyan species it is likely to have similar differences to *C. aturksvenicus* in terms of punctation and absence of the appendiculate vein as for the female.

DESCRIPTION: Female. Total body length 2.62 mm (2.60–2.76 mm); forewing length 1.93 mm (1.90–2.03 mm). Head wider than long, width 0.89 mm (0.87–0.97 mm), length 0.70 mm (0.68–0.76 mm); inner margins of compound eyes straight, convergent below, upper interorbital distance 0.65 mm (0.63–0.75 mm), lower interorbital distance 0.47 mm (0.44–0.53 mm); apex of clypeus at lower tangent of compound eyes; paraocular carina strongly produced below; ocelli above upper tangent of compound eyes, ocellar triangle slightly prominent; clypeus faintly convex; labrum longer than wide, lateral margins tapering in apical half to acutely rounded apex; malar space vestigial posteriorly, 0.4 times basal mandibular width anteriorly; mandibles simple, crossing in repose but not covering labrum; frontal line distinct from just below lower tangent of antennal toruli to near median ocellus, carinate over entire length. Mesoscutum with median and parapsidal lines impressed, median line extending to slightly before mesoscutal midlength; intertegular distance 0.51 mm (0.56 mm); mesoscutellar surface even, not bigibbous. Forewing marginal cell broadly truncate, appendiculate vein absent; two submarginal cells, second submarginal cell shorter, but more than one-half length of first; 2rs-m arched to form convex apex to second submarginal cell; both m-cu crossveins entering second submarginal cell. Hind wing with 5 distal hamuli; Rs short, perpendicular to costal margin; without defined rs-m, instead M runs nearly straight to Rs apex (presence of bulla marking a fenestra in the wing may indicate the position of where M and rs-m traditionally met, although no spectral trace of apical abscissa of M evident (spectral trace of apical abscissa of Rs present, as well as that of Cu); M+Cu elongate, much longer than M and Rs combined. Tergum VI with sides weakly convex, apex distinctly concave.

Integument generally shining. Labrum with a few large punctures intermingled with more numerous smaller punctures, separated by 1–2 times a puncture width, punctures particularly sparse medioapically, integument between punctures smooth; clypeus with small punctures mostly separated by 1–2 times a puncture width, apical margin narrowly impunctate; face and vertex with small punctures separated by 1–3 times a puncture width, integument between punctures smooth, punctures become sparser toward paraocular carina, malar space impunctate, small impunctate area along outer border of lateral ocellus; punctures on gena and postgena separated by 1–2 times a puncture width, integument otherwise smooth. Mesoscutum with small, well-defined punctures, punctures separated by 1–4 times a puncture width, punctures distinctly present across central disc, integument otherwise smooth and shining; tegula impunctate and smooth; mesoscutellum with punctures as on mesoscutum, except punctures exceedingly sparse laterally, integument otherwise smooth; metanotum with punctures as on mesoscutum;

mesepisternum with well-defined punctures separated by 0.5–2 times a puncture width, those posteriorly along border with metepisternum more closely spaced, integument otherwise smooth; metepisternum impunctate in ventral portion, upper portion weakly and irregularly strigose; lateral surface of propodeum weakly strigose, more strongly so around propodeal spiracle; posterior surface with punctures separated by 1–2 times a puncture width except sparse along medial pit, integument otherwise smooth; narrow basal area of propodeum short, integument coarsely imbricate. Metasomal terga and sterna finely imbricate, faintly on terga, imbrication more prominent on sterna, except tergum I almost devoid of microsculpture; terga with sparse, minute punctures except tergum I virtually impunctate; sterna impunctate except at setal bases.



Figures 19–21. Photographs of holotype female of *Chiasmognathus riftensis*, new species, from Bogoria. 19. Lateral habitus. 20. Dorsal habitus. 21. Facial view.

Integument of head black to dark brown, mesosoma dark reddish brown, shining except labrum yellow brown; mandible yellow brown with reddish apex; labiomaxillary complex light yellow brown; clypeus apically, lower paraocular area, and malar space yellow brown; anterior surface of antenna yellow brown (remainder brown); pronotal lobe yellow brown; tegula translucent yellow brown; legs chestnut brown except lighter ventrally and yellow brown on tarsi and tibial apices. Wing veins brown to light brown; membranes clear hyaline. Metasomal terga dark reddish brown except more prominently orange to light reddish brown on tergum I, subapically and laterally on tergum II, and basally on tergum III; sterna yellow brown. Tergum VI pale brown.

Pubescence silvery white. Head with numerous, appressed to subappressed plumose setae, such setae most abundant along compound eyes and below level of antennal toruli, intermingled with a few suberect to erect finer, simple setae; appressed plumose setae present on gena, particularly in lower half, and postgena. Mesosoma with appressed to subappressed, plumose setae along dorsal border of pronotum and on pronotal lobe; anteriorly, anterolaterally, and posterolaterally on mesoscutum; laterally on mesoscutum and metanotum; and largely obscuring integument of mesepisternum and basal area of propodeum; otherwise with fine, subappressed to suberect, simpler setae. Metasoma with scattered, minute, subappressed setae on tergal discs, longer erect, simple setae subapically; terga I and II with small, apicolateral patches of appressed plumose setae; terga III–V with thin, weak apical fasciae of appressed plumose setae, interrupted medially on terga III and IV; broad; flat surface of tergum VI with fine, simple, subappressed to suberect setae gradually tapering from base to apex; sterna with scattered, subappressed, simple setae.

Male. Unknown.

HOLOTYPE: 1♀, Kenya: Rift Valley, Lake Bogoria, 0.322339 36.070175 [0°19'20.4"N, 36°04'12.6"E], 1004 m, 10.ix.2011, Packer, Mutiso, Martins (NMK).

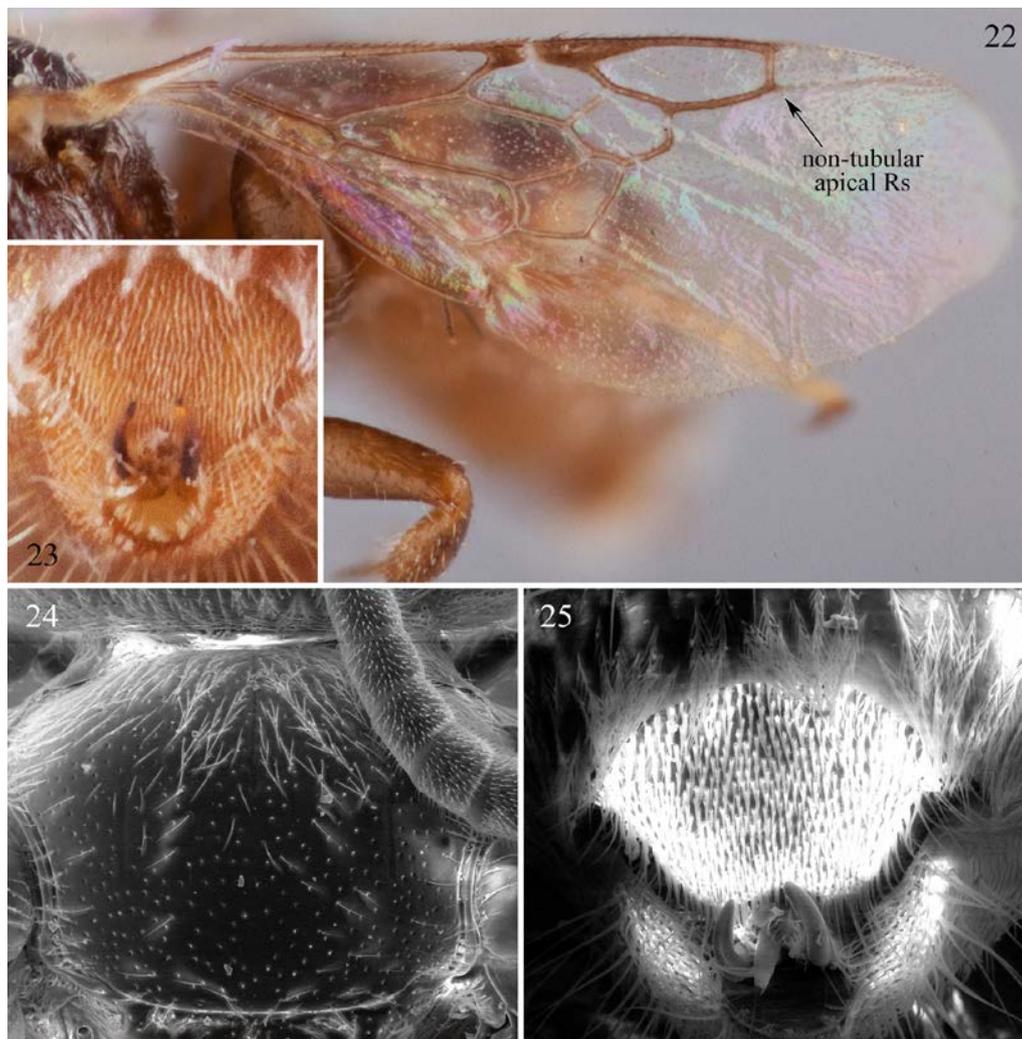
PARATYPES: 2♀♀, Kenya: Rift Valley, Lake Bogoria, 0.322339 36.070175 [0°19'20.4"N, 36°04'12.6"E], 1004 m, 10.ix.2011, Packer, Mutiso, Martins (PCYU, SEMC).

ETYMOLOGY: The specific epithet refers to the occurrence of the species in the Great Rift Valley of Kenya.

HOST PLANT: One specimen of this species was collected on flowers of *Portulaca quadrifida* L. (Portulacaceae) a common low-growing weed.

VARIATION: One paratype is somewhat more distinctly bicolourous than the holotype with a darker mesosoma but with metasomal terga largely orange brown, II especially brightly so.

COMMENTS: The habitat of this species is Acacia woodland along the western shore of Lake Bogoria. The vegetation at this site is dominated by acacia trees, mainly *Acacia tortilis* with an understory of *Acacia brevispica* Harms (syn: *Senegalia brevispica* (Harms) Seigler & Ebinger) and *Grewia tenax* (Forssk.) Fiori and herbaceous plants including *Ocimum* sp., *Commelina* sp., *Commicarpus* sp., *Orthosiphon* sp., and *Portulaca* sp. The bee was collected in Kenya in August 2011. Larger-than typical amounts of rainfall had been experienced that year as part of the 'long-rains' when the Inter-Tropical Convergence Zone (ITCZ) crossed the equator going northward, which had induced an above average flowering and an associated peak of bee activity. The site has a mixture of lateritic soils with sand and the bee was found along the raised edge of a road running along the western shore of Lake Bogoria. Numbers of the host bee *Nomioides* sp. were observed entering/exiting nest holes in the ground along the shallow road bank at this site and the cleptoparasites were found inspecting the host nest aggregation.



Figures 22–25. Photographs (except where otherwise stated) of holotype female of *Chiasmognathus riftensis*, new species. 22. Right forewing. 23. Tergum VI. 24. ESEM of mesoscutum. 25. ESEM detail of tergum VI.

One of the paratypes has three mites on the anterior declivitous surface of TI. These belong to the family Neopygmephoridae (Trombidiformes: Heterostigmata), probably to the genus *Parapygmephorus* Cross some of which are known to attack halictids (Eickwort, 1990), the bee family to which the host of *C. riftensis* belongs. This family of mites has also been found on cleptoparasitic bees with halictids as hosts (Kurosa, 2001).

DNA Barcodes

DNA barcode sequences were obtained from four *C. aturksvenicus* and two *C. riftensis* paratypes, their BOLD BIN numbers are AAW3683 and ABA3972, respectively. The maximum sequence divergence within each species was 0.15% and 0.31%, respectively,

while the minimum distance between them was 9.46. The individuals of *C. aturksvenicus* sequenced included the small dark one mentioned in the variation section (*vide supra*), and also one of the largest and more brightly coloured ones.

DISCUSSION

Cleptoparasitic bees are important components of the melittofauna especially considering their potential for indicating healthy populations of their hosts and bee communities in general (Sheffield *et al.*, 2013). However, their taxonomy is often difficult (Magnacca & Brown, 2012), lagging behind that of their hosts. For example, while there are keys for the identification of all species of *Lasioglossum* Curtis in eastern North America (Gibbs, 2011; Gibbs *et al.*, 2013; McGinley, 1986), the only source for identification of their cleptoparasites, in the genus *Sphecodes* Latreille (Mitchell, 1960) is both out-of-date and often not up to the task. Identification is particularly difficult for the smaller species and it is not surprising, perhaps, that *Chiasmognathus* is undergoing a rapid increase in species descriptions, now that its hosts are known, and their nest sites can be searched for the cleptoparasites. Indeed, since the genus was first described little more than ten years ago (Engel, 2006), on average, one species a year has been described (table 1). It is too early to determine what association there is, if any, between hosts, host shifts, and speciation among *Chiasmognathus* given the insufficient nature of our basic natural history data for these tiny bees. The most thorough study has been that of Rozen (2008) for *C. pashupati* in Pakistan, while for more than half of the known species hosts remain to be discovered and relationships within the genus are murky. Moreover, as already noted above, the genus is likely far more diverse and exploration of nesting aggregations across Asia and elsewhere in Africa will certainly reveal further taxa. For the moment we peer through a glass darkly, with perhaps the greater proportion of the extant diversity remaining to be uncovered. In this paper we describe two more species of the genus, the first from tropical East Africa, we also describe substantial morphological variation within one of them.

Given this difficulty with species-level taxonomy of cleptoparasitic bees, the degree of intraspecific variation we have documented in *C. aturksvenicus* might be considered indicative of there being more than one species. However, the DNA barcode data support conspecificity of both the smallest and the larger individuals. While identical sequences do not necessarily always mean conspecificity in cases where there are discrete morphological differences among related species (Gibbs, 2018), in this instance the morphological variation observed in colouration, density of punctation of the mesoscutum, degree of bigibbosity of the mesoscutellum, and length of the appendicular vein are all continuous and, with the exception of mesoscutal punctation, are not clearly allometric in nature. For example, the individual with the most weakly developed appendicular vein is the third smallest individual and one of the smaller individuals has this vein more than twice as long as its basal width. While the palest individual is the smallest, the second smallest individual is one of the darkest specimens. Pale colouration is well known among bees of hot deserts and even more extreme intraspecific variation has been documented for an unrelated, non-cleptoparasitic bee species also from the Turkana Basin (Packer & Martins, 2015). Degree of bigibbosity of the mesoscutellum is often noted as a character separating cleptoparasitic bee species (*e.g.* Mitchell, 1962) or as a character useful in the reconstruction of their phylogenetic relationships (*e.g.* Rightmyer, 2004), however we found continuous variation between

moderately bigibbous and weakly convex conditions within *C. aturksvenicus*. Thus, we are confident that our samples are indicative of one species of *Chiasmognathus* currently known from the Turkana Basin.

The BIN for *C. aturksvenicus* – AAW3683 – is also shared by a single specimen of *C. orientanus* (Warncke), although the divergence between its sequence and those of *C. aturksvenicus* averages more than 1.5%. This is a level not uncommonly found in comparisons of closely related bee species (Gibbs, 2009) and we do not doubt that the two are heterospecific.

Variation in submarginal cell number is well known among the bees and the subject has recently been reviewed by Scarpulla (2018). Our holotype male *C. aturksvenicus* with three submarginal cells on one forewing and two on the other (all other specimens of *Chiasmognathus* known have just the two submarginal cells), represents the first example of intraspecific variation in submarginal cell number in the Nomadinae outside of the genus *Nomada* Scopoli.

We found marked differences in the setation of the flat portion of tergum VI of the females in our two species and also between them and *C. rhagae*. The latter has these setae strongly hooked with their apices recurved. In contrast, the same area is covered in simple setae in *C. riftensis*, but a mixture of short forked and long less strongly hooked ones in *C. aturksvenicus*. Further comparisons of these structures among species of *Chiasmognathus* is warranted as the size, shape, colour, and structure of the setae of similar patches on the dorsum of apical terga are commonly used in keys and diagnoses for female cleptoparasitic bees (e.g. Onuferko, 2018; Rightmyer, 2008).

We have recorded *Chiasmognathus* from East Africa for the first time. The genus is quite widespread (table 1) but is not known from South Africa, which has been more thoroughly searched for bees than any other country on the continent. It is interesting to consider the biogeographic relations among the bees of Kenya with those of the nearby arid areas around the Sahara and those of South Africa and Namibia. While a formal analysis of African bee biogeography is well beyond the scope of this paper, we can perform some simple analyses that prove illustrative. There are 64 genera of bees known from Kenya, five are not found in either of the other areas under discussion while 46 are found in all three. Eleven are shared between Kenya and southern Africa but seemingly not from the Sahel (*Scrapter* Lepageletier and Serville in the Colletidae, *Mermiglossa* Friese in the Andrenidae, the halictids *Eupetersia* Blüthgen, *Patellapis* Friese, and *Thrinchostoma* Blüthgen, melittids *Meganomia* Cockerell and *Samba* Friese, the megachilid *Othinosmia* Michener, and *Afromelecta* Lieftinck, *Axestotrigona* Moure, and *Pachymelus* Smith in the Apidae), but only two are found in the Sahel and Kenya but not southern Africa, the melittid *Uromonia* Michener and the megachilid *Haetosmia* Popov. While perfunctory, these data do seem to suggest greater affinities between the Kenyan melittofauna and that of southern Africa than to the Sahel.

ACKNOWLEDGMENTS

We are grateful to Sheila Dumesh for couriering specimens between Toronto and Lawrence; to P. Lomosingo, L. Kabui, and M. Mutiso for assistance with fieldwork; to Ismael A. Hinojosa-Díaz, Sheila Dumesh, and Liam Graham for assistance with photography; and to Thomas Onuferko for useful discussion. Liam Graham's contribution was funded by a generous donation by Robert and Cecily Bradshaw. We thank Magdalena Jaklewicz for assistance with taking the ESEM images that were made possible through the Advanced Light

and Electronic Microscopy Facility at York University. We also thank Barry M. O'Connor for identifying the mite associated with *C. riftensis*. LP's fieldwork in Kenya was made possible by a research grant from the Natural Sciences and Engineering Research Council of Canada. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum. DJM's research is supported by the National Geographic Society, Whitley Fund for Nature, and Princeton University.

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The nomenclatural acts established within the present work are registered under the following LSIDs:

Article: urn:lsid:zoobank.org:pub:DB135818-52EA-4551-ACA8-3A55226C353E
Chiasmognathus aturksvenicus: urn:lsid:zoobank.org:act:45CCE4C9-97D6-4473-BA4A-28E94DFEC5D6
Chiasmognathus riftensis: urn:lsid:zoobank.org:act:F8F8989A-7712-4F7A-9498-59C61DA6E94E

Periodical: urn:lsid:zoobank.org:pub:B62B8B9A-D679-4C59-8C2D-9C021CD93285