Discoscapidae fam. nov. (Hymenoptera: Apoidea), a new family of stem lineage bees with associated beetle triungulins in mid-Cretaceous Burmese amber

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Source: Palaeodiversity, 13(1) : 1-9

Published By: Stuttgart State Museum of Natural History

URL: https://doi.org/10.18476/pale.v13.a1

Discoscapidae fam. nov. (Hymenoptera: Apoidea), a new family of stem lineage bees with associated beetle triungulins in mid-Cretaceous Burmese amber

George Poinar Jr.

Abstract

A new family, genus and species of minute, stem lineage, pollen-collecting bee is described from mid-Cretaceous Burmese amber. The female specimen of *Discoscapa apicula* gen. et sp. nov. in the new family Discoscapidae (Hymenoptera: Apoidea) shares with modern bees, plumose hairs, a rounded pronotal lobe, middle and hind leg scopae containing pollen grains and a pair of spurs on the hind tibia. But its narrow hind basitarsi, extremely low placed antennal sockets and some wing vein features are those of apoid wasps. A unique diagnostic character of the new family not found on any extant or extinct lineage of apoid wasps or bees is a bifurcated scape. Pollen grains in scopae on the femur and tibia of the middle and hind legs and on the claw and tarsus of the middle leg show that the bee had recently visited one or more flowers. Further evidence of this action is the presence of 21 beetle triungulins in the amber, five of which are in direct contact with the bee.

Keywords: Apoidea; Burmese amber; stem lineage bee; mid-Cretaceous.

1. Introduction

Bees are an important component in the evolutionary history and diversification of the angiosperms. The great majority of bees depend on pollen, nectar, oils, waxes, scents and resins from flowering plants for adult and larval nutrition, sexual attractants and nest construction (Renner 2006; Michener 2007). Various morphological adaptations have evolved in bees to enable them to recognize, collect and utilize these plant products (Danforth et al. 2006). The still unanswered question is what basic morphological modifications apoid wasps underwent to change their habits from carnivory to palynivory. And what, if any, additional morphological and physiological alterations in both adults and developmental stages, accompanied this dietary change.

While the fossil record of bees is quite extensive, the great majority are from Cenozoic deposits and have features very similar to extant generic lineages (Zeuner & Manning 1976; Michener 2007). However, amber fossils from the mid-Cretaceous can tell us what morphological changes certain lineages of apoid wasps underwent as they became palynivores.

While floral elements in the mid-Cretaceous Myanmar amber tropical forest were mostly conifers, ginkgos, ferns, liverworts, lycopods, cycads and horsetails, a diverse selection of small flowered angiosperms, many of which are in extinct families, had made their appearance (Poinar 2018a). In this amber forest, as angiosperms were diversifying, primitive bees were evolving from apoid wasps (Danforth & Poinar 2011).

One such stem lineage bee in Burmese amber was a female, described below as *Discoscapa apicula* gen. et sp. nov. in the new family Discoscapidae (Hymenoptera: Apoidea). This fossil displays both Antophila bee as well as apoid wasp features. Based on its habitus and morphology, including plumose hairs, a rounded pronotal lobe, middle and hind leg scopae and a pair of spurs on the hind tibia, the female bee falls within the monophyletic group that currently includes all living bees that utilize pollen for development of their brood (Michener 2007). Along with these bee characters are narrow hind basitarsi, low placed antennal sockets and wing venation patterns that are characteristic of apoid wasps.

A unique diagnostic character of the new genus not found in either apoid wasps or bees is a bifurcated antennal scape. Pollen grains in scopae on the femur and tibia of the middle and hind legs and on the claw and tarsus of the middle leg show that *Discoscapa* had recently visited one or more flowers in anthesis. A list of small flowers described from Burmese amber that *Discocapa* could have visited is presented (Table 1). Additional evidence that the fossil bee had visited flowers is the presence of twenty-one beetle triungulins in the same piece of amber. It is possible that the large number of triungulins caused the bee to accidently fly into the resin.

2. Material and methods

The single female specimen of *Discoscapa apicula* is positioned at the edge of a small piece of amber. The specimen was obtained from a mine first excavated in 2001, in the Hukawng

Valley, southwest of Maingkhwan in Kachin State (26º20′N, 96º36′E) in Burma (Myanmar). This amber site, known as the Noije Bum 2001 Summit Site, was recently assigned to the mid-Cretaceous on the basis of paleontological evidence, placing the age at 97 to 110 Mya (Cruickshank & Ko 2003). A more recent study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Ma, at the Albian/Cenomanian boundary (Shi et al. 2012). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit site indicate an araucarian (possibly *Agathis*) tree source for the amber (Poinar et al. 2007b). Observations and photographs were made with a Nikon SMZ-10 stereoscopic microscope and Nikon Optiphot optical microscope (with magnifications up to 650x). Helicon Focus Pro X64 was used to stack photos for better overall clarity and depth of field.

3. Systematic palaeontology

Some portions of the specimen are damaged, missing or concealed. Part of the face beneath the ocelli had been scraped away, along with the left antenna. Other than the mandibles, the mouthparts are concealed. The terminal tarsal segments of the right hind leg are missing. Wing venation nomenclature and other terminology used in the present work are based on formats displayed in Michener at al. (1994).

Order Hymenoptera Linnaeus, 1758

Superfamily Apoidea Latreille, 1802

Family Discoscapidae nov.

L S I D f o r f a m i l y : urn:lsid:zoobank.org:act:6415DB B8-BB33-47EC-94E5-28CB7B2116E5

T y p e g e n u s : *Discoscapa* gen. nov.

G e n e r a i n c l u d e d : Type genus only.

D i a g n o s i s : Small, black, mostly hairless, pollen-collecting female bee with large bifurcated scape; trifid mandible; antennal insertions positioned beneath lower margin of eyes; wing with large stigma, large marginal cell and three submarginal cells; first recurrent vein received by first submarginal cell; scopae with branched, pollen collecting hairs on mid and hind femora and tibia; midtibia with single spur; hind tibia with two spurs; claws bifid; arolium large, bifid; pygidial plate present; hind leg strigil and cerci absent.

Genus *Discoscapa* nov.

L S I D f o r g e n u s : urn:lsid:zoobank.org:act:7741683E-206C-4556-B3AF-D3B8AAB864E8

E t y m o l o g y : The generic name is from the Latin “disco” = different and the Latin “scapa” = stem, in regards the modified antennal scape of the fossil.

T y p e s p e c i e s : *Discoscapa apicula* gen. et sp. nov.

I n c l u d e d s p e c i e s : Type species only.

D i a g n o s i s : As for family (by monotypy)

Discoscapa apicula sp. nov.
Figs. 1–9, 10A

L S I D f o r s p e c i e s : urn:lsid:zoobank.org:act:CF429 E0D-AE81-4037-9473-3C0F1E37D38B

E t y m o l o g y : The specific epithet “apicula” is Latin for small bee.

H o l o t y p e : Female specimen No. B-Hy-20 deposited in the Poinar amber collection maintained at Oregon State University.

T y p e l o c a l i t y : Amber mine in the Hukawng Valley, southwest of Maingkhwan in the state of Kachin (26º20′N, 96º36′E), northern Myanmar (Burma).

Table 1. Size of flowers described from Burmese amber

Flower	Size (in mm)	Reference
Antiquifloris latifibris	5.0	Poinar et al. (2016)
Dispariflora robertae	0.5–1.8	Poinar & Chambers (2019c)
Endobeuthos paleosum	3.2–4.6	Poinar & Chambers (2018a)
Eoepigynia burmensis	1.5	Poinar et al. (2007a)
Exalloanthum burmense	2.1	Poinar (2018a)
Lachnociona terriae	5.0	Poinar et al. (2008)
Micropetasos burmensis	0.8	Poinar et al. (2013)
Palaeoanthella huangii	1.0	Poinar & Chambers (2005)
Setitheca lativalva	4.9	Poinar & Chambers (2018b)
Strombothelya monostyla	2.3	Poinar & Chambers (2019b)
Strombothelya grammogyna	4.2	Poinar & Chambers (2019b)
Tropidogyne lobodisca	3.4	Poinar & Chambers (2019a)
Tropidogyne pentaptera	3.4–5.0	Poinar & Chambers (2017)
Tropidogyne pikei	5.1	Chambers et al. (2010)
Zygadelphus aetheus	1.1	Poinar & Chambers (2019d)

D i a g n o s i s : As for family (by monotypy).

L S I D f o r p u b l i c a t i o n : urn:lsid:zoobank.org:pub:5E9C2F14-56B2-4E01-B25F-E54256035BDC

D e s c r i p t i o n : Body small, dark, 3.0 mm in length, nearly hairless except for scopae on mid and hind legs; head proportionally large (Fig. 1A, B).

Head (Figs. 1A, B, 2A, 4C–E). Large in proportion to body, length 1.3 mm; width 1.2 mm; eyes bare, white (black discoloration occurred where amber surface was polished too close to eyes); eyes slightly concave on inner surface; three ocelli; vertex slightly convex; remaining portion of lower face with erect setae; clypeus impunctate, transverse, upper margin flat, only slightly longer than labrum, length clypeus 126 mm, width clypeus 190 mm; space between clypeus and antennal sockets approximately equal to one socket diameter; labrum broader than long; length labrum 108 mm; mandible tri-dentate; malar space unknown since base of mandibles obscured; galea, max-

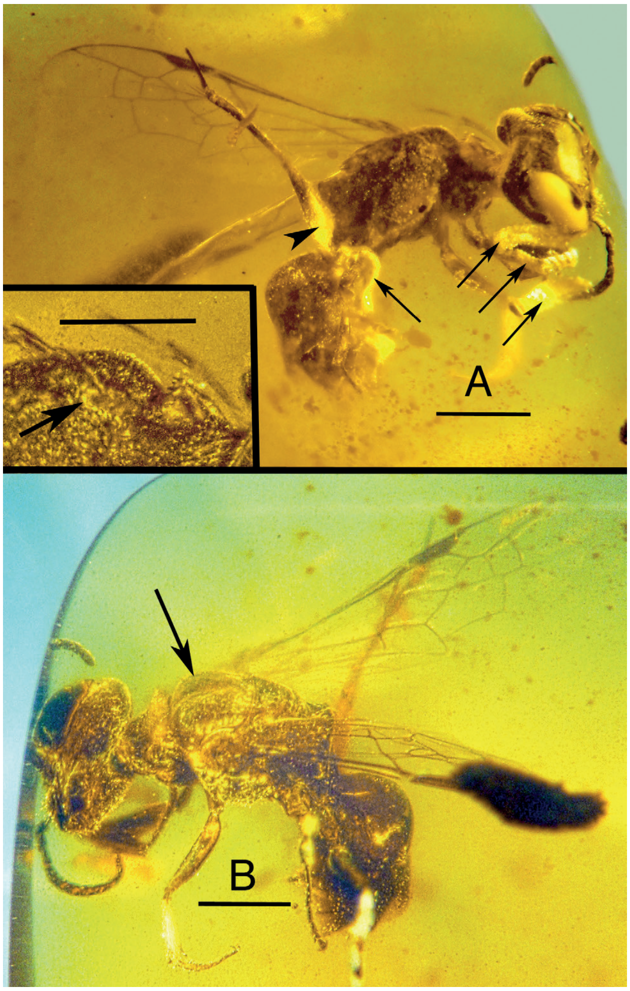

Fig. 1. *Discoscapa apicula* gen. et sp. nov. in Burmese amber. **A** – Right lateral view of body. Arrows show four associated beetle triungulins. Arrowhead shows scopae on hind leg femur. Bar = 0.65 mm. Insert shows rounded pronotal lobe (arrow). Bar = 0.70 mm. **B** – Left lateral view of body. Arrow shows scutum. Bar = 0.62 mm.

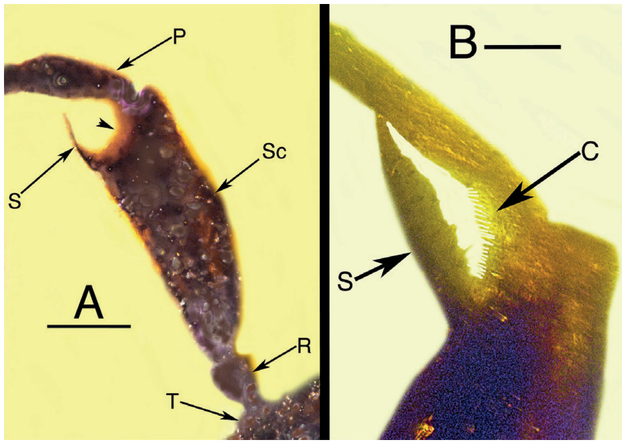

Fig. 2. *Discoscapa apicula* gen. et sp. nov. in Burmese amber. **A** – Bifurcated scape. T= torulus; R = radicle; Sc = scape; P = pedicle; S = spur. Arrowhead shows velum with wax-like deposit lining curvature. Bar =106 µm. **B** – Foreleg strigilis. S = spur, C = comb with velum. Bar = 60 µm.

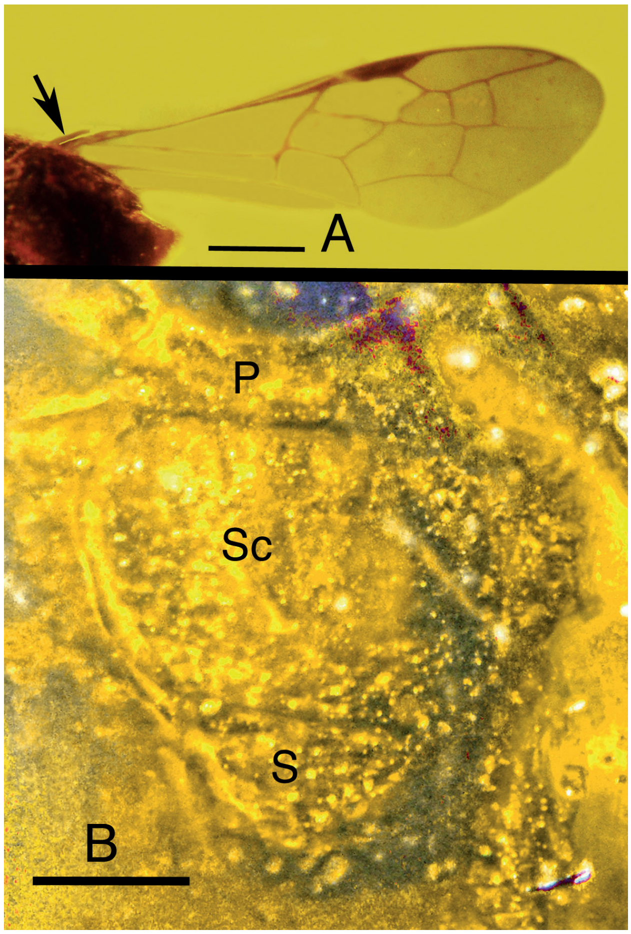

Fig. 3. *Discoscapa apicula* gen. et sp. nov. in Burmese amber. **A** – Forewing. Arrow shows tegula. Bar = 440 µm. **B** – Dorsal view of mesosoma. P = pronotum, Sc = scutum, S = scutellum. Bar = 320 µm.

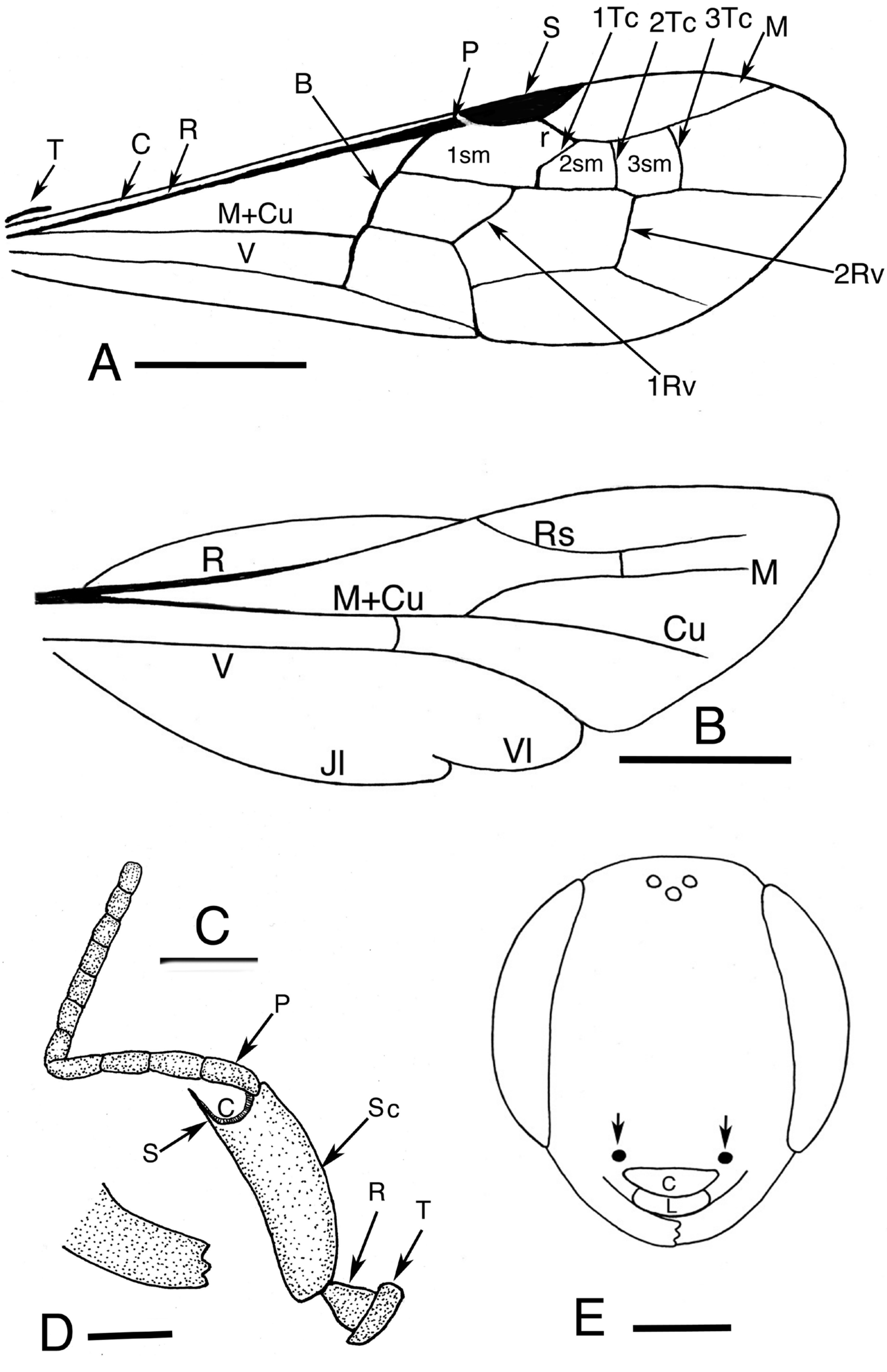

Fig. 4. *Discoscapa apicula* gen. et sp. nov. in Burmese amber. **A** – Forewing. B = Basal vein, C = costa, P = prestigma, R= radius, S= stigma, V= v vein, 1Tc = first transverse cubital vein, 2Tc = second transverse cubital vein, 3Tc = third transverse cubital vein, 1sm = first submarginal cell, 2sm = second submarginal cell, 3sm = third submarginal cell, 1Rv = first recurrent vein, 2Rv = second recurrent vein, r = r vein. Bar = 520 µm. **B** – Hind wing. R = radius vein, Rs = radial sector, M = medial vein, Cu = cubitus vein, V = V vein, Jl = jugal lobe, Vl = vannal lobe. Bar = 420 µm. **C** – Right antenna. T = torulus; R = radicle; Sc = scape; P = pedicle; S = spur; C = area of curvature with wax-like deposit on velum. Bar = 146 µm. **D** – Mandible. Bar = 125 µm. **E** – Frontal view of head. Arrows show low positioned antennal sockets. C = clypeus; L = labrum. Bar = 300 µm.

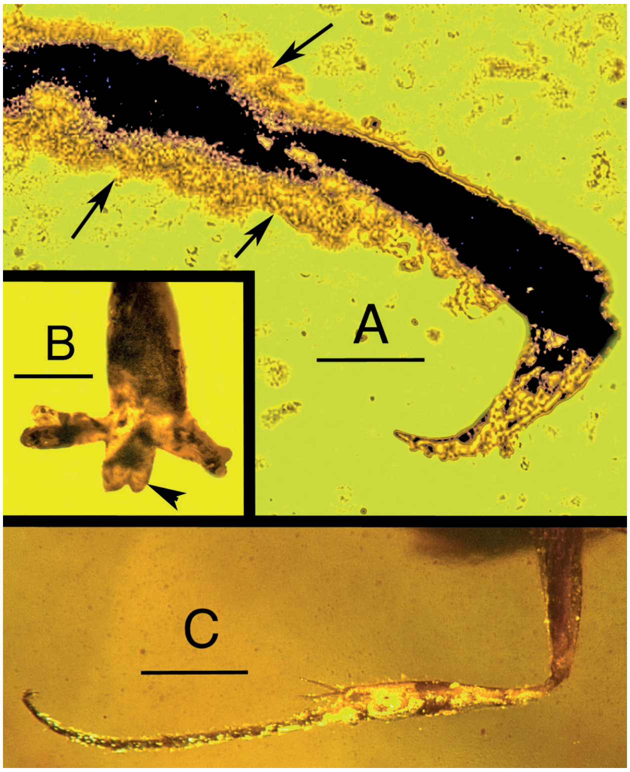

Fig. 5. *Discoscapa apicula* gen. et sp. nov. in Burmese amber. **A** – Lateral view of terminal tarsal segments and claw. Arrows show pollen clusters attached to tarsomeres. Bar = 93 µm. **B** – Ventral view of claws. Arrowhead shows bi-lobed arolium. Bar = 62 µm. **C** – Hind leg. Bar = 400 µm.

illary palps and labial palps concealed; antennal sockets widely separated, positioned beneath basal margin of compound eyes; subantennal sutures obscured; torulus slightly erumpent, radicle distinct, length radicle, 80 mm; scape enlarged, bifurcated at apex; length scape 370 mm (without radicle), width scape 140 mm; antenna with 10 flagellomeres; pedicel slightly longer than first flagellomere.

Mesosoma (Figs. 1A, B, 2B, 3A, B, 4 A, B, 5A–C, 6A, B, 7A, B, 8A, B; 9, 10A). Length mesosoma, 1.1 mm, length pronotum, 180 mm, rounded pronotal lobe present; scutum rounded, length scutum, 600 mm; scutellum flat, length scutellum, 230 mm; length forewing, 2.6 mm; stigma wider and broader than prestigma; marginal cell on wing margin, with pointed apex extending beyond third submarginal cell; marginal cell longer than distance from its apex to wing tip; basal vein gently and uniformly curved; first recurrent vein entering first submarginal cell well before first transverse cubital vein, which is sharply bent at lower third. First submarginal cell more than twice length of third submarginal cell when measured along posterior margin. Second transverse cubital vein meeting marginal cell near its basal third. M and Cu veins extending, although somewhat fading, nearly to wing margin. V vein extends to the fold in lower wing margin. Tegula present. Hind wing 2.0 mm in length, with jugal lobe about 0.77 times length of vannal lobe; hamuli not observed. Fore tibia with strigilis, mid-tibia with single spur, a pair of short brushes present on underside of middle leg tibia; short basitibial plate on outer side of mid tibia; hind tibia with two spurs; hind basitarsus slender; scopae with branched hairs located on femur and tibia of mid and hind legs (Figs. 7B, 8A, B, 9 insert); angle of branches varies from 110 degrees to 90 degrees (perpendicular) from main axis with up to 12 branches occurring on some setae. Tarsal claws slightly cleft at tip; arolium large, bifid; hind leg strigilis absent.

Metasoma (Figs. 1A, B, 7C). Length, 945 mm, not petiolate, with six visible segments; dorsal hair bands not noted; propodeum with borders angled, length propodeum, 270 mm; pygidium possessing sting on T7. Cerci absent.

Comments: The following major characters place *Discoscapa* among the apoid bees: (1) ventral extension of the pronotum with the presence of a rounded pronotal lobe (Fig. 1A, insert); (2) presence of plumose hairs (Figs. 7B, 8A, B, 9 insert); (3) scopae on femur and tibia of middle and hind legs (Figs. 7A, 8A, B, 9); (4) midtibia with single spur (Fig. 6A); (5) hind tibia with two spurs (Figs. 5C, 6B); (6) absence of posterior strigil; (7) presence of mid-femoral brush; (8) bifid tarsal claws (Michener et al. 1994; Michener 2007).

Discoscapa shares some features with representatives of the bee family Colletidae. These include the marginal cell longer than the stigma, with the apical portion positioned on the wing margin, the second submarginal cell little more than half as long as the first, the stigma longer than the prestigma, vein r arising near the middle of the stigma, the basal vein only feebly arcuate (Figs. 3A, 4A), scopae located on the mid and hind legs (Figs. 7A, 8A, B, 9) and the presence of both basitibial and pygidial plates (Stephen et al. 1969; Michener et al. 1994; Michener 2007).

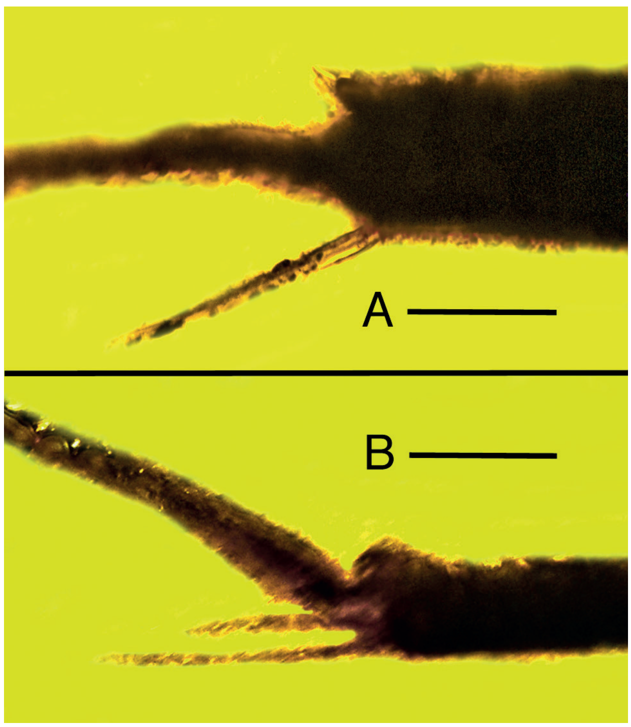

Fig. 6. Tibial spurs of *Discoscapa apicula* gen. et sp. nov. in Burmese amber. **A** – Single spur on mesotibia. Bar = 108 µm. **B** – Paired spurs on metatibia. Bar = 84 µm.

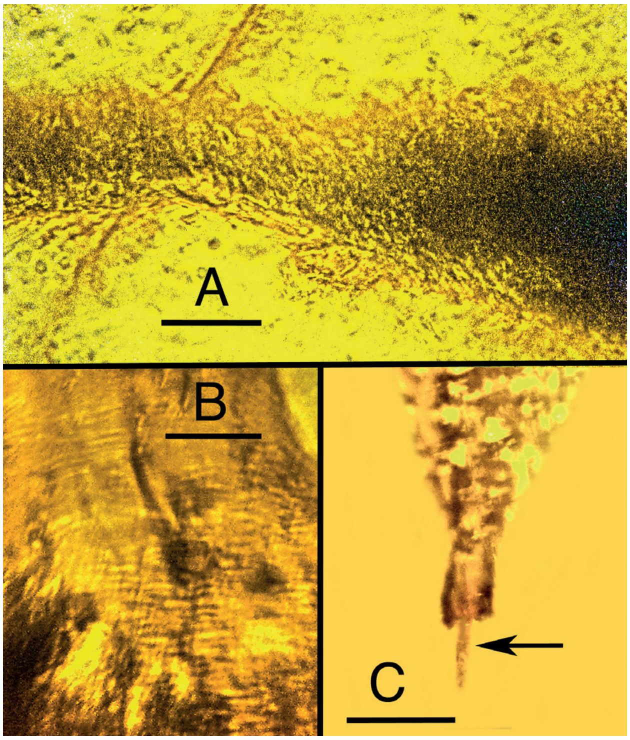

Fig. 7. *Discoscapa apicula* gen. et sp. nov. in Burmese amber. **A** – Scopa at femur-tibial junction of midleg. Bar = 130. **B** – Plumose hairs on midleg femur. Bar = 55 µm. **C** – Pygidium. Arrow shows sting. Bar = 95 µm.

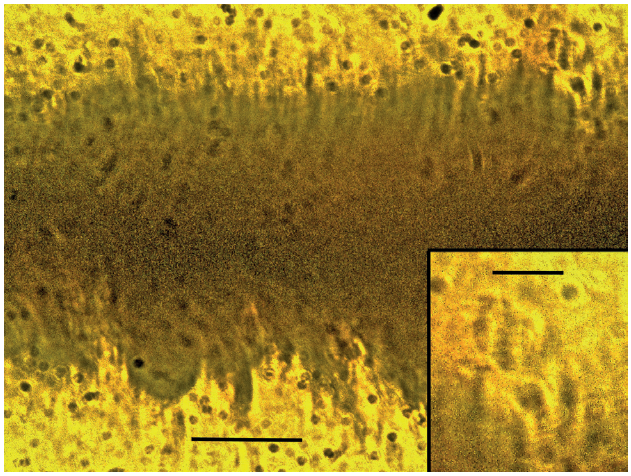

Fig. 9. Pollen catching hairs with surrounding pollen grains on the hind leg femur of *Discoscapa apicula* gen. et sp. nov. in Burmese amber. Bar = 213 µm. Insert shows branches on hairs. Bar = 50 µm.

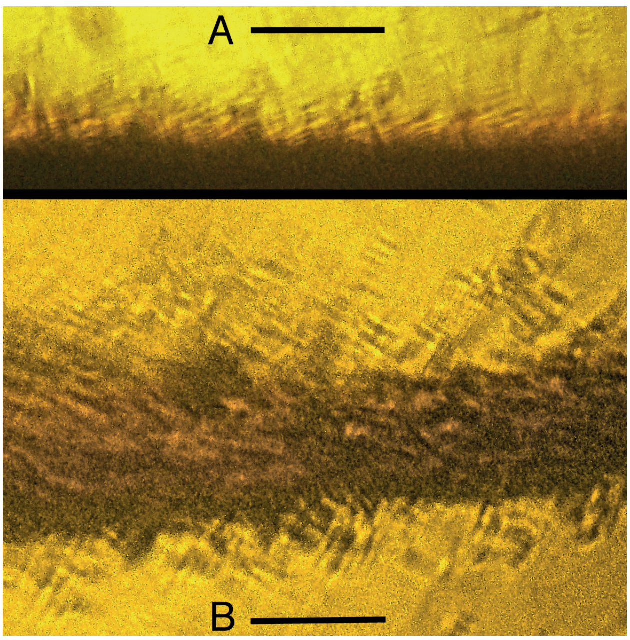

Fig. 8. *Discoscapa apicula* gen. et sp. nov. in Burmese amber. **A** – Plumose hairs on hind leg basitarsus. Bar = 45 µm. **B** – Plumose hairs on hind leg tibia. Bar = 35 µm.

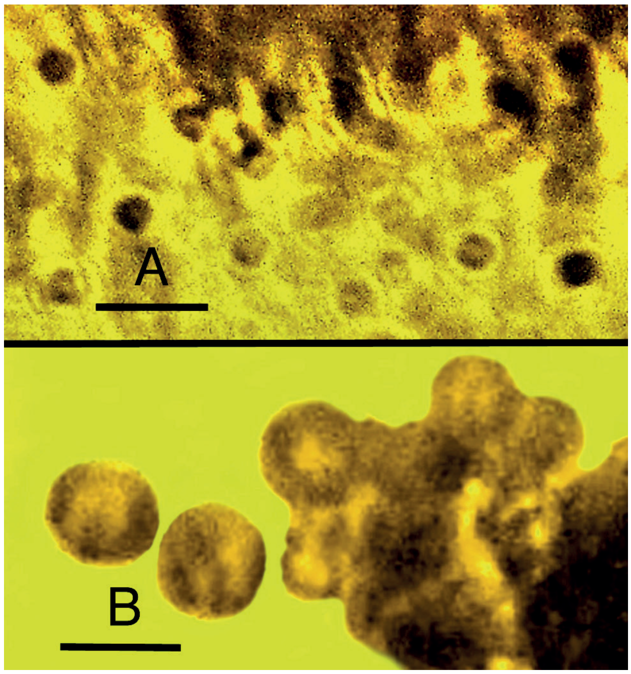

Fig. 10. A – Pollen grains associated with pollen catching hairs of *Discoscapa apicula* gen. et sp. nov. in Burmese amber. Bar = 38 µm. **B** – Pollen grains of the Burmese amber angiosperm flower *Dispariflora robertae*. Bar = 16 µm.

Discoscapa also contains some features of apoid wasps. One is the narrow basitarsus that is not broader than the subsequent tarsal segments (Fig. 5C). Another is the extremely low position of the antennal insertions that are placed beneath a horizontal line connecting the lower eye margins (Fig. 4E). While members of the subfamily Dufourinae (Halictidae) have antennal sockets with the upper margins below the middle of the face, it is rare for bees to have the antennal sockets positioned below the level of the eyes (Stephen et al. 1969; Michener et al. 1994; Michener 2007). However, low antennal insertions can be found in representatives of the wasp subfamily Crabroninae and tribes Pemphredonini and Astatini.

Discoscapa also shares some venational features with apoid wasps. On the forewing of *Discoscapa*, the first recurrent vein is received by the first submarginal cell (Figs. 3A; 4A). This feature occurs in bees with two submarginal cells but is rare in bees with three submarginal cells. However it occurs in representatives of the apoid wasp subfamilies Ampulicinae, Eremiasphecinae, Sphecinae, Xenosphecinae, Nyssoninae and Larrinae (Bohart & Menke 1976; Goulet & Huber 1993; Prentice 1998; Michener 2007).

There appears to be no record of a bee or apoid wasp with a large bifurcated scape (Figs. 2A, 4C) (Bohart & Menke 1976; Zeuner & Manning 1976; Schönitzer 1986; Michener et al. 1994; Prentice 1998; Michener 2007), which is considered a unique diagnostic character of *Discoscapa*. The opening of the bifurcation is wider than the width of the flagellomeres and it is possible that the flagellomeres of the opposite antennae were passed through the opening, which served as a type of strigilis. While a very short ring of cuticular protrusions surround the outer rim of the opening, the concave surface of the bifurcation is coated with a wax-like deposit.

While the major morphological characters, as well as biological features discussed below, align *Discoscapa* with the Anthophila, the unique structure of the scape and combination of apoid bee and wasp characters prohibit placement of the fossil in any present extinct or extant family of apoid bees or wasps (Bohart & Menke 1976; Zeuner & Manning 1976; Michener et al. 1994; Prentice 1998; Michener 2007).

4. Discussion

Discoscapa is the second primitive, stem lineage bee to be described from Burmese amber. The first, *Melittosphex burmensis* Poinar & Danforth (2006), also retained some wasp features and was placed in a separate family, the Melittosphecidae. The three submarginal cells of *Discoscapa*, as well as the bifurcated scape and low antennal insertions, distinguish it from *Melittosphex* (Poinar & Danforth 2006; Danforth & Poinar 2011).

Considering the morphological variation present today among the various bee genera, it is likely that many of these lineages evolved independently from different lineages of apoid wasps. Another early bee lineage, based on a phylogenomic analysis of the Apoidea, is thought to have evolved from the apoid wasp lineage, Ammoplanina (Crabronidae), which is considered by Sann et al. (2018) as the closest extant relative of bees.

While it may not fit within the crown group of modern bees, *Discoscapa apicula* was obviously a pollen-collecting species based on the presence of large amounts of pollen in the plumose hairs on the hind femur (Figs. 9, 10A). *Melittosphex* and *Discoscapa* are now the oldest known stem lineages of pollen collecting Apoidea and provide insights into morphological features that existed during the transition from predatory wasps to pollen collecting bees. The small size of *Discoscapa* and *Melittosphex* place them among the so-called "minute" bees, which are well adapted for visiting correspondingly small flowers since large bees have difficulty obtaining nectar and pollen from small solitary flowers (Stephen et al. 1969).

Pollen in branched hairs on the hind leg femur (Fig. 9) shows that *Discoscapa* had recently visited one or more flowers in anthesis. Pollen grains attached to the mid-leg tarsi and claws (Fig. 5A) could have arrived there when the bee was visiting the flowers or was cleaning its dorsum since many bees are known to clean their backs with their middle legs (Jander 1976).

A number of very small angiosperm flowers, ranging in size from 0.8 mm to 5.1 mm, have been described from Burmese amber (Table 1). Pollen grains on the hind femur of *Discoscapa* (Fig. 9) range from 10 µm to 15 µm in diameter, which fall within the size range of pollen grains from the following Burmese amber flowers: *Dispariflora robertae* Poinar & Chambers 2019c, *Eoepigynia burmensis* Poinar et al. 2007a, *Antiquifloris latifibris* Poinar et al. 2016, *Micropetasos burmensis* Poinar et al. 2013. and *Exalloanthum burmense* Poinar 2018a. Of the above flowers, the pollen on *Discoscapa* most closely resembled the size, shape and configuration of pollen grains from *Dispariflora robertae* Poinar & Chambers 2019c (Fig. 10A, B).

Other evidence that *Discoscapa* had recently visited flowers before it was captured in resin is the presence of 21 beetle triungulins in the same amber piece, some of which are still in contact with *Discoscapa* (Fig. 1A). It is well known that active first stage beetle triungulins of the families Meloidae, Rhipiphoridae and Cleridae gather in flowers and attach themselves to visiting bees. The triungulins are then carried back to the nest where they feed on the developing stages of the bees and stored provisions (nectar and pollen) (Clausen 1962, 1976; Falin et al. 2000). These triungulins will be described in a separate study.

In their molecular study on early bee diversification (Danforth et al. 2006), the results suggested an African origin for bees since the earliest branches included predominantly African lineages. This implies that bees may have evolved in Gondwana. Since it has been proposed that Burmese amber originated in Gondwana along the northern part of what is now Australia (Poinar 2018b), it is possible that bees in Burmese amber represent the earliest known lineages of these pollinators. Danforth et al. (2006) also concluded that their results showed that the earliest bee lineages were narrow host-plant specialists, which suggests that *Melittosphex* and *Discoscapa* may have specialized on one or two species or genera of the Burmese amber angiosperms listed in Table 1.

Acknowledgments

The author thanks Alex Brown for donating the specimen to the Poinar amber collection, Dr. André Nel and Dr. David Roubik for their constructive comments on earlier versions of the manuscript and Roberta Poinar for general comments on the topic.

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Manuscript received: 30 October 2019, revised version accepted: 25 November 2019.