

The first Late Cretaceous ants (Hymenoptera: Formicidae) from southern Africa, with comments on the origin of the Myrmicinae

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Ants (10 specimens) comprise 12% of the hymenopteran Armaniid-Kind assemblage collected from the Turonian deposits at Orapa, Botswana. The taxa *Orapia* Dlussky, Brothers & Rasnitsyn, gen. n. (Armaniinae), *Orapia rayneri* Dlussky, Brothers & Rasnitsyn, sp. n., *Orapia minor* Dlussky, Brothers & Rasnitsyn, sp. n., *Afropone* Dlussky, Brothers & Rasnitsyn, gen. n. (Ponerinae), *Afropone oculata* Dlussky, Brothers & Rasnitsyn, sp. n., *Afropone orapa* Dlussky, Brothers & Rasnitsyn, sp. n., *Afromyrma* Dlussky, Brothers & Rasnitsyn, gen. n. (oldest known Myrmicinae), and *Afromyrma petrosa* Dlussky, Brothers & Rasnitsyn, sp. n. are described. The significance of these findings is discussed in the context of observed faunal changes in Cretaceous ants, evolutionary changes in the Ponerinae, and time and mode of origin of Myrmicinae.

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Introduction

There are very few major insect fossil assemblages in the southern hemisphere. Of these, one of the most important, although perhaps the least well studied, is that from Orapa, Botswana. Although these deposits have been known for about 20 years, only elementary information has been published about the diversity of insects there and a few papers have dealt with some of the more striking fossils (McKay & Rayner 1986; Rayner 1993, Rayner et al. 1998 and references therein). An estimate of the insect and hymenopteran composition and diversity has recently been done (Brothers & Rasnitsyn in press). The detailed results relating to the ants in that material are presented below. The presence of 10 ant specimens out of 86 hymenopterans identified at least to superfamily (12%), including 6 basal Armaniinae, 3 intermediate Ponerinae and 1 advanced Myrmicinae, is in agreement with the attribution of the entire hymenopter-

an assemblage to the Armaniid Kind. The ants are of particular interest because of the presence of the oldest known myrmicine, which provides new clues on the probable early evolution of the ants.

An overview of the geology and general palaeontology of the Orapa deposits, which were excavated during diamond-mining operations in central Botswana, has been given by Rayner et al. (1998). A comment needs to be made about the aging of the fossils, however. The eruption which created the crater has been dated by four different analyses using zircon crystals to an average date of 91 Mya (Brothers & Rasnitsyn in press), which places the eruption clearly as Turonian (89.0 ± 0.5 to 93.5 ± 0.2 Mya: International Commission on Stratigraphy 2002) (rather than Cenomanian as stated by Rayner et al. 1998). The fossiliferous sediments were apparently deposited very soon after the eruption (Rayner et al. 1998), so a Turonian date for the fossils themselves is also likely.

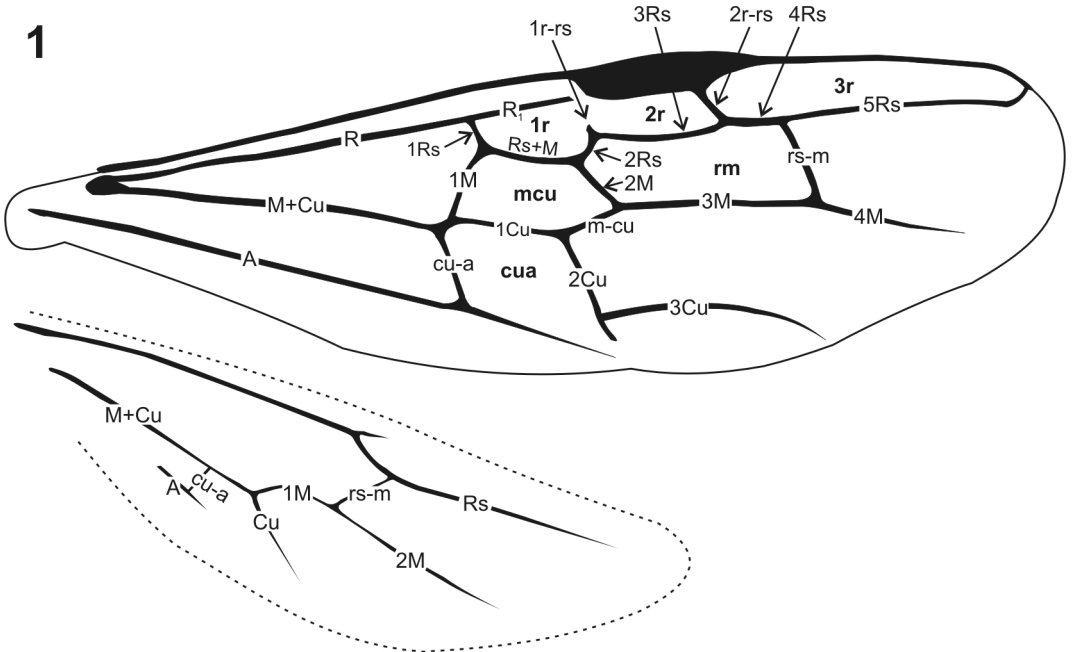


Figure 1. Ant wing venation, based on holotype of *Orapia rayneri* Dlussky, Brothers & Rasnitsyn, sp. n. Fore wing based on part (BP/2/26924), hind wing on counterpart (BP/2/25935).

Materials and methods

Material examined. – Material from Orapa is housed in the Bernard Price Institute of Palaeontology (BPI) at the University of the Witwatersrand, Johannesburg, and also in the National Museum of Botswana, Gaborone. DJB and APR examined all blocks with insects in the BPI and identified all Hymenoptera. APR prepared drawings using a stereo microscope and drawing tube, and DJB photographed them using a Zeiss digital photomicroscope with crossed polarising filters to enhance contrast. The descriptions and final drawings were prepared using CorelDraw© by reference to the original drawings and photographs. On a subsequent visit to Gaborone, DJB and I. J. McKay established the existence of about 220 rock pieces with insect fossils in that collection, but found only 9 with possible hymenopterans, and no ants.

Family Formicidae Latreille, 1802

Subfamily Armaniinae Dlussky, 1983

Genus *Orapia* Dlussky, Brothers & Rasnitsyn, **gen. n.**

(Figs 1-9)

Etymology. – The name *Orapia* is derived from that of the only locality at which it has been found. The gender is feminine.

Type species. – *Orapia rayneri* Dlussky, Brothers & Rasnitsyn, sp. n.

Description. – Winged female. Head with occipital margin smoothly rounded. Eyes rather small, ovate, placed above head midlength. Mandibles without teeth, linear, short, evenly curved. Antenna filiform with scape very short. Waist one-segmented, petiole (2nd abdominal segment) broadly attached to 1st gastral segment, slightly widened caudally, longer than wide. 1st and 2nd gastral (3rd and 4th abdominal) segments with no constriction at junction. Sting short.

Fore wing (see Fig. 1 for lettering) with cells 1+2r, 3r, rm and mcu closed, cua almost so. Cell 1+2r subdivided by rudiment of 1r-rs, rs-m meeting Rs distal to 2r-rs, so making cell rm hexagonal. Vein 1Rs forming acute angle with R₁, directed posteroapically. Cell mcu pentagonal. Crossvein cu-a originating near or from cell m-cu. Pterostigma entirely margined by veins. Hind wing with Rs, M and Cu free, section 1M arched, about as long as rs-m.

Comparison. – Differs from all Armaniinae except

Khetania Dlussky, 1999 in the wide head with mandibular bases far apart, and from *Khetania* in the form of the petiole which is not much tapered anteriorly and not transverse. Additionally, it differs from all Armaniinae with known hind wing venation (*Armania robusta* Dlussky, 1983, *A. curiosa* (Dlussky, 1983, *Pseudarmania rasnitsyni* Dlussky, 1983) in having rs-m about as long as, and not much shorter than, 1M.

Remarks. – The placement of *Orapia* within the subfamily Armaniinae is certain despite the fact that some of the diagnostic features of the subfamily (detached trochantellus, two hind tibial spurs) cannot be seen on any available fossil. The observed archaic characters, such as petiolar form and very short female scape, are known only in Armaniinae, and reliably imply the inclusion of *Orapia* in this paraphyletic subfamily. Two other archaic characters, the apically directed base of 1Rs and the permanent presence of a rudiment of 1r-rs, are also characteristic of Armaniinae, but the first is also known in some Ponerinae and the second in Sphecomyrminae (*Baikuris mandibularis* Dlussky, 1987, *B. mirabilis* Dlussky, 1987) and as individual aberrations in some basally placed extant ants in the subfamilies Myrmeciinae and Ponerinae.

Included species. – *Orapia rayneri* Dlussky, Brothers & Rasnitsyn, sp. n.; *O. (?) minor* Dlussky, Brothers & Rasnitsyn, sp. n.

***Orapia rayneri* Dlussky, Brothers & Rasnitsyn, sp. n.**

(Figs 1-8)

Etymology. – The species name is in honour of Dr Richard Rayner, erstwhile palaeobotanist at the BPI, who was primarily responsible for assembling the material from Orapa and assisted DJB greatly in providing initial access to it.

Type material. – Holotype ♀. BOTSWANA: Orapa; Upper Cretaceous, Turonian, BP/2/26924, BP/2/25935 (part and counterpart, lateral view, well preserved, lacking pronotum and upper part of petiole). Paratypes. BOTSWANA: Both Orapa; Upper Cretaceous, Turonian: ♀ BP/2/25238 (dorsal view); ♀ BP/2/26991/1 (lateral view, incomplete, only head with antennal base, fore wing and partial mesosoma preserved).

Additional material. – BOTSWANA: Orapa; Upper Cretaceous, Turonian: ♂ BP/2/18220 (dorsal view, mesosoma, fore wing, petiole and gaster); BP/2/26210 and BP/2/28068a (fore-wing fragments). (Based on size and available morphology, these poorly preserved specimens may also belong here.)

Description ♀. – Winged, body length ca. 14 mm. Head nearly as long as wide. Eye about 0.25 times as long as head, with longer diameter about 1.5 times as long as shorter. Anterior margin of clypeus possibly with broad rectangular lobe, or latter may be labrum extending from beneath straight clypeal margin. Mandible saber-like and evenly curved, lacking masticatory margin, preapical tooth not apparent (absent or not preserved). Antenna filiform, of sphecooid type, with scape short and thick (about 1.8 times as long as wide and 0.2 times as long as head), flagellomeres 3-6 longer than scape, 2.2 times as long as wide, following flagellomeres gradually shorter. Scutum transverse, flat, not hiding pronotum. Fore wing rather wide (about 3 times as long as wide), with apex of cell 3r rounded, vein 1M 2.5 to 3.5 times as long as 1Rs, vein cu-a meeting M+Cu before 1M by a little more than vein width. Petiole widely attached to gaster, lacking distinct node and cylindrical base, 1.3 times as long as wide. Gaster ovate. Sting short.

Measurements, mm: Holotype: body length 13.8; mesosoma length 5.7; head length 2.7, width 2.7; longer eye diameter 0.64; scape length 0.55, width 0.30; fore-wing length 10.0, length to apex of cell 3r 9.7; petiole length 1.57. Paratype BP/2/25238: body length 14.3; mesosoma length 4.1; head length 2.7, width 2.5; longer eye diameter 0.67; fore-wing length to apex of cell 3r 9.0; petiole length 1.47, width 1.13. Paratype BP/2/26991/1: head length 2.5; longer eye diameter 0.65; fore-wing length to apex of cell 3r 10.4.

♂. Not known with any certainty, therefore no description provided.

Comparison. – Differs from *O. (?) minor* in its larger size and the more proximal position of cu-a with respect to 1M.

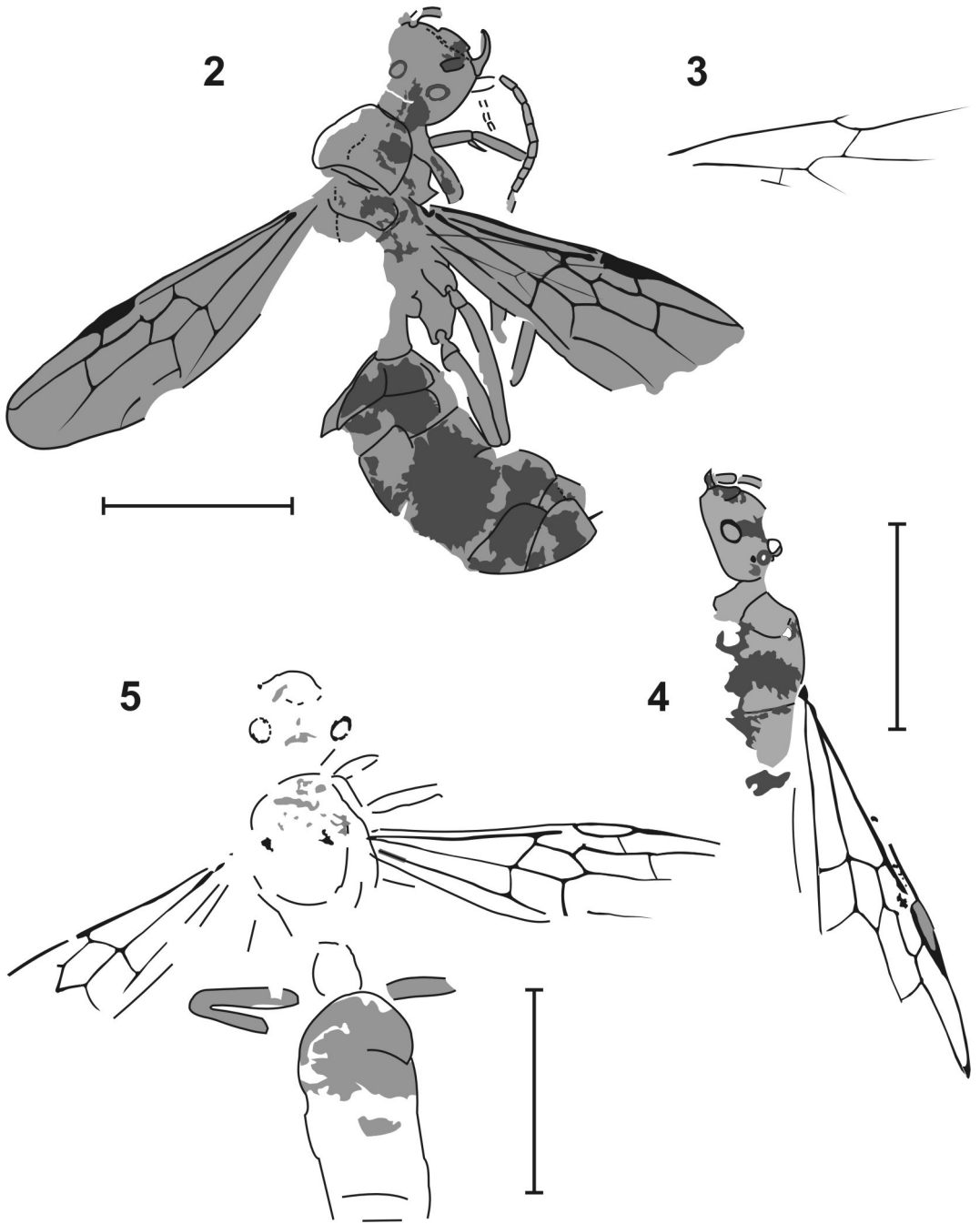
***Orapia (?) minor* Dlussky, Brothers & Rasnitsyn, sp. n.**

(Fig. 9)

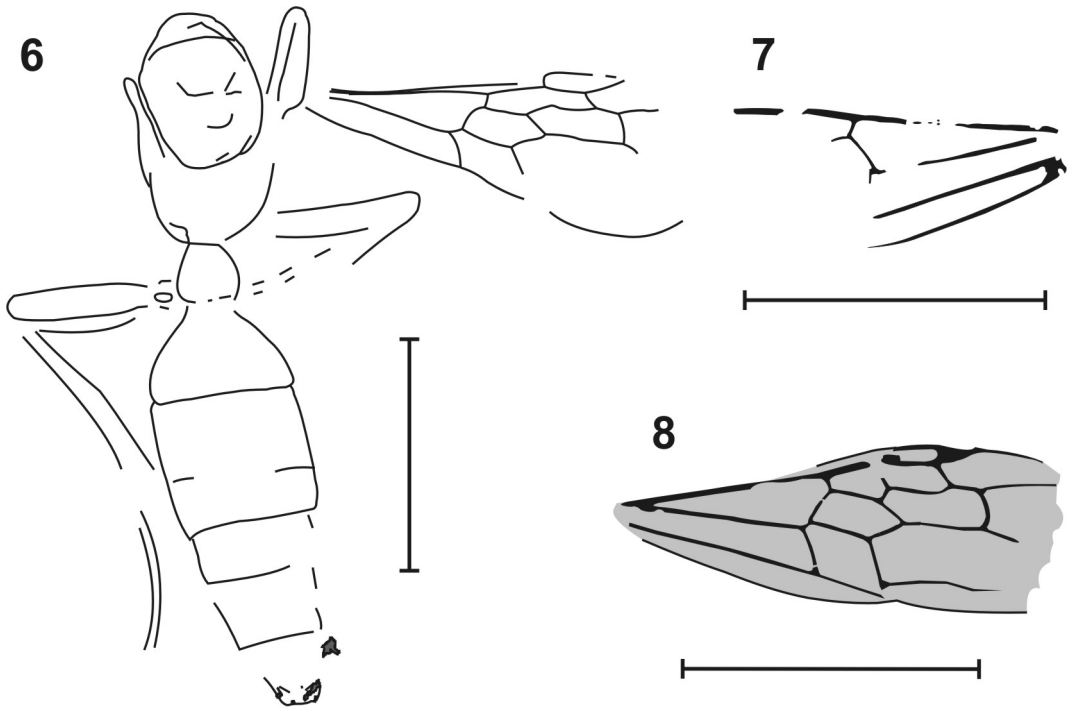
Etymology. – The species name refers to its smaller size when compared with the type species of *Orapia* (“minor” is Latin for “smaller”).

Type material. – Holotype ♀. BOTSWANA: Orapa; Upper Cretaceous, Turonian, BP/2/25845/2 (partially preserved, lacking most of head and mesosoma, oblique lateral view).

Description ♀. – Winged, body length ca. 9 mm. Scape apparently short. Mid flagellomeres longer



Figures 2-5. *Orapia rayneri* Dlussky, Brothers & Rasnitsyn, sp. n. 2, holotype ♀, based mainly on part (BP/2/26924), left wing and some thoracic details added from counterpart (BP/2/25935). 3, venation of hind wing of counterpart (BP/2/25935). 4, paratype ♀ (BP/2/26991/1). 5, paratype ♀ (BP/2/25238). (Lines = visible sclerite boundaries; paler fill = areas of colour differing from that of matrix; dark fill = preserved coalified organic material; scales = 5 mm.)



Figures 6-8. Specimens tentatively attributed to *Orapia rayneri* Dlussky, Brothers & Rasnitsyn, sp. n. 6, ♂ (BP/2/18220, dorsal view, mesosoma, fore wing, petiole and gaster). 7, 8, fore-wing fragments: 7 (BP/2/26210); 8 (BP/2/28068a). (Lines = visible sclerite boundaries; paler fill = areas of colour differing from that of matrix; dark fill = preserved coalified organic material; scales = 5 mm.)

than scape, 2.2 times as long as wide. Fore wing rather wide (3.3 times as long as wide), with apex of cell 3r subacute, vein 1M 1.4 times as long as 1Rs, cu-a meeting Cu distal to base of vein 1M. Gaster ovate. Sting short, thin.

Measurements, mm: body length 9.1; mesosoma length 2.9; head width 1.6; fore-wing full length 6.0, length to apex of cell 3r 5.5.

♂. Unknown.

Comparison. – Differs from *O. rayneri* in its smaller size and the more distal position of cu-a with respect to 1M.

Remarks. – Since the head and petiole are not preserved in the sole specimen available, the diagnostic characters of *Orapia* cannot be identified in it. At the same time, the wing venation and particularly the presence of the 1r-rs rudiment and the obliquely distal orientation of 1Rs indicate inclusion of the fossil within Armaniinae. Its similarity with *O. rayneri* in general appearance is great

enough, while the differences in size and venational details are small enough, to justify including both species under one generic name.

Subfamily **Ponerinae** Lepeletier, 1835.

Genus ***Afropone*** Dlussky, Brothers & Rasnitsyn, *gen. n.*

(Fig. 10-12)

Etymology. – The name *Afropone* is derived from that of Africa, the continent on which it was found, and *Ponera*, the type genus of its subfamily. The gender is feminine.

Type species. – *Afropone oculata* Dlussky, Brothers & Rasnitsyn, sp. n.

Description. – Head with occipital margin rounded. Eyes well developed. Female mandible short, evenly curved, lacking masticatory margin. Scutum flat. Propodeum rounded or weakly angular in side view, with no spines or teeth. Hind tibia with two spurs. Fore wing with cells 1+2r, 3r, mcu,

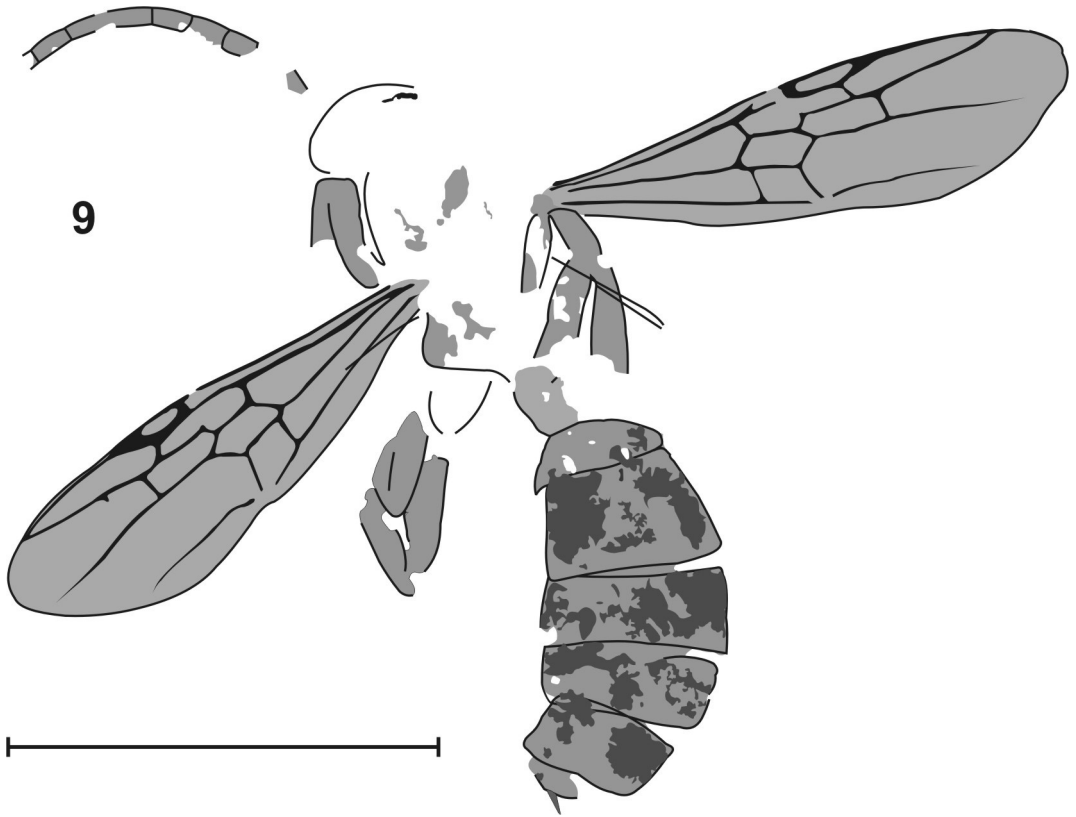


Figure 9. *Orapia minor* Dlussky, Brothers & Rasnitsyn, sp. n., holotype ♀ (BP/2/25845/2). (Lines = visible sclerite boundaries; paler fill = areas of colour differing from that of matrix; dark fill = preserved coalified organic material; scale = 5 mm.)

and possibly *rm* closed (*3r* is inferred as closed based on the thickened *R* at its junction with *Rs* which is not preserved; *rm* is inferred as closed because of the general plesiomorphy of the venation). Pterostigma rather small, elongate, margined by veins. Vein *1Rs* directed obliquely apically, meeting *R*₁ at an acute angle. Crossvein *cu-a* joining *M+Cu* slightly proximal to *1M*. Petiole with moderately developed node, clearly constricted at junction with gaster. 1st and 2nd gastral (3rd and 4th abdominal) segments separated by distinct constriction.

Comparison. – A similar petiolar structure is known in extant (*Myrmecia* Fabricius, 1804) and extinct Myrmeciinae (*Prionomyrmex* Mayr, 1868; *Archimyrmex* Cockerell, 1923), which differ in having long mandibles with a toothed molar mar-

gin, and also in some Ponerinae like *Canapone* Dlussky, 1999 from the Late Cretaceous Canadian amber (Dlussky 1999; Dlussky & Perfilieva 2003). *Afropone* differs from all known fossil Ponerinae in having unusually large eyes. In general appearance, the female of *Afropone* is similar to some extant Pseudomyrmecinae, which differ in organisation of their cranio-mandibular system, however: all extant Pseudomyrmecinae have strong triangular mandibles with a well developed mola and, correspondingly, well developed occipital angles of the head capsule. Pseudomyrmecinae additionally differ in having a well separated postpetiole and a distinctly more proximal position of *cu-a*.

Remarks. – A well separated 3rd abdominal segment is known in Myrmeciinae, Ponerinae, Cerapachyinae, Pseudomyrmecinae, Myrmicinae,

Leptanillinae, Aenictinae and some Ecitoninae (the little known subfamilies Aenictogitoninae, Apomyrminae and Leptanilloidinae, each with one genus and 1-7 species based either only on males (Aenictogitonini) or workers, are excluded from consideration). (However, unlike *Afropone*, female Leptanillinae (except *Anomalomyrma* Taylor, 1990), Aenictinae and Ecitoninae are always wingless.) Most Ponerinae and Cerapachyinae have abdominal segments 3 and 4 weakly constricted at their junction, so that the 3rd segment is a part of the gaster (functional abdomen). By contrast, in most Myrmicinae and all Pseudomyrmecinae that segment is deeply separated as the 2nd waist segment, the postpetiole. Only the Myrmeciinae, some Ponerinae, Cerapachyinae and Myrmicinae are similar to female *Afropone* in having an intermediate state of postpetiolar separation, with a moderately deep constriction. Of these subfamilies, female and worker Myrmeciinae differ from *Afropone* in having elongated mandibles with a toothed apical margin, female and worker Pseudomyrmecinae, and Cerapachyinae, most Ponerinae and Myrmicinae in having triangular mandibles with a dentate masticatory margin. However, some Ponerinae and Myrmicinae have sickle-shaped mandibles with a smooth inner margin, as in *Afropone*. Another important character is the position of crossvein cu-a which is distal in the more basal subfamilies, including Myrmeciinae and Ponerinae, and proximal in more advanced ones, including Pseudomyrmecinae and Myrmicinae (Dlussky 1981). The combination of characters shows that *Afropone* can best be attributed to Ponerinae.

Included species. – *Afropone oculata* Dlussky, Brothers & Rasnitsyn, sp. n.; *Afropone* (?) *orapa* Dlussky, Brothers & Rasnitsyn, sp. n.

Afropone oculata Dlussky, Brothers & Rasnitsyn, **sp. n.**

(Figs 10, 11)

Etymology. – The species name refers to its large eyes (“oculus” is Latin for “eye”).

Type material. – Holotype ♀. BOTSWANA: Orapa; Upper Cretaceous, Turonian, BP/2/28072a/2 (dorsal view).

Additional material. BOTSWANA: Orapa; Upper Cretaceous, Turonian, ♀ BP/2/26631-17. (lateral view, faint traces of head, leg and wing fragments, propodeum, petiole and deformed postpetiole). (As in the

holotype of *A. oculata*, this specimen shows the eye in an anterior position; the petiole in side view has its maximum height near its midlength. The sizes of the preserved parts are practically the same as in the holotype of *A. oculata*. Because of its poor preservation, this specimen is not included in the type series.)

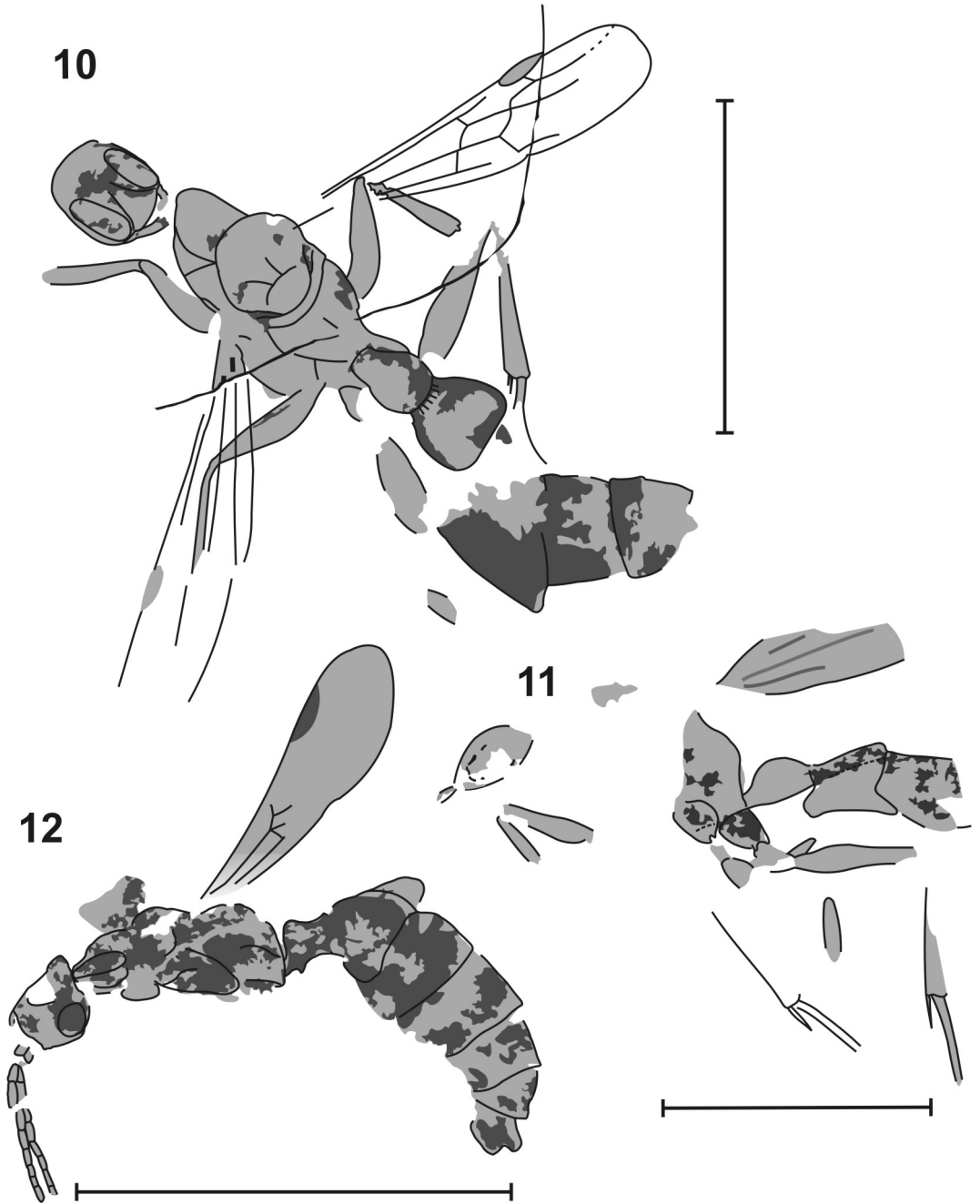
Description ♀. – Winged, body length about 12 mm. Body elongate. Head ovate with near parallel sides and smoothly rounded occipital margin, 1.4 times as long as wide. Fore clypeal margin smoothly rounded. Antennal bases widely separated. Eye ovate, shifted far forward, occupying a considerable part of side of head, with longer diameter 2.5 times as long as shorter and 0.7 times as long as head. Mandible short, weakly curved, lacking well developed masticatory margin, no teeth preserved. Mesosoma rather narrow (twice as long as wide). Scutum flat, 0.7 times as long as wide (with scutellum, as long as wide). Fore wing rather narrow (4.5 times as long as wide), with vein 1M twice as long as 1Rs, vein 2+3Rs sharply angled at position of 1r-rs which is apparently lost. Veins 2+3Rs and 2+3M diverging at junction with m-cu, making cell m-cu quadrangular and cell rm triangular or absent (because of a crack in the matrix where rs-m crossvein would occur, the true form of cell rm cannot be ascertained). Crossvein cu-a meeting M+Cu before base of 1M by slightly more than vein width. Petiole with node and narrowed anterior and posterior regions, 1.4 times as long as wide, widest at posterior third, clearly separated from postpetiole (3rd abdominal segment). In turn, postpetiole separated from 1st gastral (4th abdominal) segment by deep constriction, its length 0.85 times width and 0.9 times length of petiole. Postpetiole anteriorly with short longitudinal rugae.

Measurements, mm: Holotype: body length 11.6; head length 1.6, width 1.4; eye longer diameter 1.0; mesosoma length 3.7; scutum length 1.1, width 1.5; scutellum length 0.5; full wing length 6.2; petiole length 1.23, width 0.9; postpetiole length 1.13, width 1.40. (Non-type specimen BP/2/26631-17: petiole length 1.32, height 0.75.)

♂. Unknown.

Comparison. – Differs from *A.* (?) *orapa* in its larger size and more anterior eye position.

Remarks. – Although it is possible that *A.* (?) *orapa* represents the male of this species, this is unlikely, the differences in eye position and size being greater than observed in other species of primitive ants.



Figures 10-12. Species of *Afropona* Dlussky, Brothers & Rasnitsyn, gen. n. 10, *Afropona oculata* Dlussky, Brothers & Rasnitsyn, sp. n., holotype ♀ (BP/2/28072a/2). 11, *Afropona oculata* (?) poorly preserved specimen (BP/2/26631-17). 12, *Afropona orapa* Dlussky, Brothers & Rasnitsyn, sp. n., holotype ♂ (BP/2/26628/1). (Lines = visible sclerite boundaries; paler fill = areas of colour differing from that of matrix; dark fill = preserved coalified organic material; scales = 5 mm.)

Afropone* (?) *orapa Dlussky, Brothers & Rasnitsyn, **sp. n.**

(Fig. 12)

Etymology. – The species name is a noun in apposition derived from the locality.*Type material.* – Holotype ♂. BOTSWANA: Orapa; Upper Cretaceous, Turonian, BP/2/26628/1 (lateral view).*Description* ♂. – Body length ca. 7 mm. Head deformed, probably as long as or a little shorter than wide. Eye round, positioned posteriorly so that malar space only slightly shorter than eye. Judging from preserved fragments, mandible short, curved, without well developed masticatory margin. Antenna filiform with scape short and flagellomeres twice as long as wide. Mesosoma elongate. Propodeum smoothly rounded in side view. Fore wing moderately narrow (3.7 times as long as wide). Petiole with node rather high and rounded in side view, well developed short cylindrical region anteriorly, constricted behind and well separated from 3rd abdominal segment, with ventral tooth. 3rd and 4th abdominal segments separated by distinct but shallow constriction. 7th abdominal tergum with subapical transverse impression. Genitalia exposed (not covered by pygidium).

Measurements, mm: mesosoma length 2.4; head length 0.8; longer eye diameter 0.4; fore wing length 3.8; petiole length 0.60, height 0.37.

♀. Unknown.

Comparison. – Differs from *Afropone oculata* in its smaller size and eye position (shifted backward rather than forward). Other Late Cretaceous male Ponerinae are not known, and the only Palaeocene ones are the huge male *Pachycondyla rebekkae* Rust and Andersen, 1999, nearly 17 mm long.*Remarks.* – This species can be included in *Afropone*, although the characters available are insufficient for completely reliable attribution. Some differences from *A. oculata* (form of head and abdominal base) may merely be sexual, but the differences in size and in eye position are unlikely to be so. In modern primitive ants, male and female sizes never differ as much as in the present case, and the eyes never differ so much in their position on the head.Subfamily **Myrmicinae** Lepeletier, 1835.***Afromyrma*** Dlussky, Brothers & Rasnitsyn, **gen. n.**

(Fig. 13)

Etymology. – The name *Afromyrma* is derived from Africa and “myrmex”, Greek for “ant”. The gender is feminine.*Type species.* – *Afromyrma petrosa* Dlussky, Brothers & Rasnitsyn, sp. n.*Description.* – Head with clear occipital angles. Eye well developed. Mandible stout, triangular, with well developed chewing margin. Propodeum lacking spines or teeth. Waist distinctly two-segmented; petiole with weak node, distinctly narrowed anteriorly; postpetiole with convex sides, narrower than gaster.*Comparison.* – *Afromyrma* differs from all known Cretaceous ants in combining a well developed two-segmented waist and triangular mandibles with well developed masticatory margin. Among the Cretaceous ants, only *Kyromyrma neffi* Grimaldi and Agosti, 2000 has mandibles with a well developed masticatory margin, but its waist is one-segmented. Comparison with more advanced Myrmicinae known since the Eocene is scarcely possible because of the inadequate preservation of the unique fossil.*Remarks.* – In spite of the condition of the fossil, with many important characters not determinable, we consider the well formed postpetiole and triangular mandible with a well developed masticatory margin sufficient to attribute *Afromyrma petrosa* to Myrmicinae.***Afromyrma petrosa*** Dlussky, Brothers & Rasnitsyn, **sp. n.**

(Fig. 13)

Etymology. – The species name is an adjective from the Latin word “petra” meaning “rock”, with reference to the fossil nature of the species.*Type material.* – Holotype ♀ (?). BOTSWANA: Orapa; Upper Cretaceous, Turonian, BP/2/26501 (dorsal view, poorly preserved).*Description* ♀ (?). – Body elongate, about 10 mm long. Head slightly wider than long. Eye ovate, somewhat shifted posteriorly, with longer diameter 1.4 times as long as shorter. Mesosoma twice as long as wide. Petiole widest at midlength.

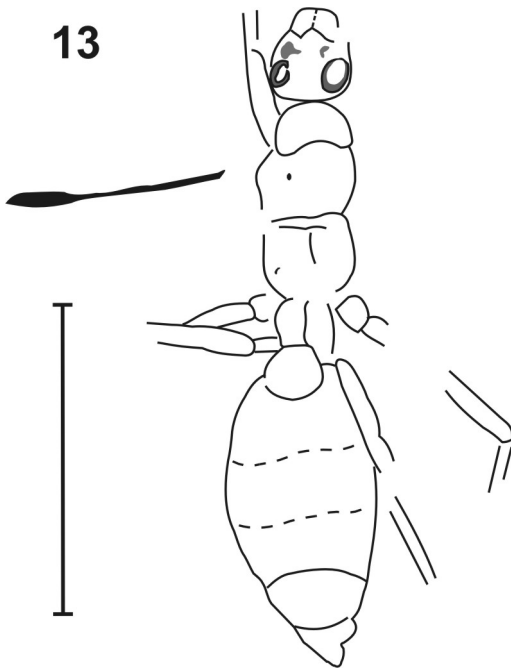


Figure 13. *Afromyrma petrosa* Dlussky, Brothers & Rasnitsyn, sp. n., holotype ♀ (BP/2/26501). (Lines = visible sclerite boundaries; paler fill = areas of colour differing from that of matrix; dark fill = preserved coalified organic material; scale = 5 mm.)

Postpetiole much narrower than following segments, about as long as wide and 1.1 times as long as petiole, 0.4 times as wide as gaster.

Measurements, mm: Holotype: body length 10.3; mesosoma length 3.2; head length 1.2, width 1.3; petiole length 0.80; postpetiole length 0.87, width 0.93.

♂. Probably unknown.

Remarks. – There is uncertainty about the sex of the holotype. Its head is typically female in form, while the apparent number of abdominal segments and the form of the abdominal apex look rather male-like. However, where preservation is poor, head characters are usually more easily interpretable than the number of abdominal segments and structure of the abdominal apex (regions not as well sclerotized and therefore more subject to deformation). This is why the fossil is tentatively identified as a female.

Discussion

The most striking feature of the mid-Cretaceous ant fauna is its synchronous change in composition in the Turonian of Eurasia, North America and southern Africa. In the earlier Albian and Cenomanian deposits, only Armaniinae are found. The absence of ants in the Cenomanian resins of Agapa in North Siberia is also indicative, because earlier Armaniinae with their usual body length of over 10 mm would have a low probability of being enclosed in the small pieces of that resin, but the smaller Sphecomyrminae, if present, would probably have been captured there.

Burmese amber, which is now dated, not very precisely, as Cenomanian or possibly Turonian (Shedrin et al. 2001; Grimaldy & Engel 2002) may be somewhat different. Found there are a specialised sphecomyrmine ant, *Haidomyrmex cerberus* Dlussky, 1996, and the enigmatic *Burmo-myрма rossi* Dlussky, 1996 that possesses a sting and one-segmented petiole like in Sphecomyrminae, Nothomyrmecinae, Aneuretinae and Falsiformicidae, but combined with a wing entirely devoid of any venation, a condition found in no other fossil ants or “Scolioidea”, although it is known in a few extant ants (unfortunately, the unique fossil has lost the head and much of the mesosoma).

Turonian resins of New Jersey, USA, have yielded several sphecomyrmine ants, and also the oldest Ponerinae (*Brownimecia clavata* Grimaldi, Agosti & Carpenter 1997) and Formicinae (*Kyromyrma neffi*). In the Turonian of Kazakhstan (Kzyl Dzhar), besides several armaniine ants, *Petropone petiolata* Dlussky, 1975 and *Cretopone magna* Dlussky, 1975, which most probably represent Ponerinae, have been found. From the southern African Turonian, we have described two species of Armaniinae, two of Ponerinae and one of Myrmicinae (above).

No Armaniinae are found in post-Turonian deposits. Instead, Sphecomyrminae are not uncommon in the Santonian of Yantardakh in North Siberia, in Campanian Canadian amber, and in Baikura in North Siberia (Maastrichtian?). The Canadian amber also includes the extant ant subfamilies Ponerinae (*Canapone dentata* Dlussky, 1999) and Dolichoderinae (*Eotapinoma macalpini* Dlussky, 1999).

The present information on the southern African Turonian ants, coupled with the new data on the

age of Burmese amber, agrees well with, and updates, the inferences by Grimaldi & Agosti (2000) on the timing of early ant evolution, with the subfamilies diverging mainly since the Albian through the Turonian. If the Burmese amber is accepted as of Cenomanian age, the specialised Sphecomyrminae found there would date the origin of this subfamily as not later than the end of the Albian. The presence of Ponerinae in the Turonian of southern Africa and central Asia indicates their near worldwide distribution by that time. If our attribution of *Afromyrma* to Myrmicinae is correct, the known age of that subfamily is the same as of Ponerinae and Formicinae, and even earlier than the Campanian origin suggested by Grimaldi & Agosti (2000); until now its earliest occurrence was in the Middle Eocene (Wilson 1985; Dlussky & Rasnitsyn in press). It is worth mentioning that already in the Turonian *Afromyrma* and *Kyromyrma* Grimaldi et Agosti, 2000 both possessed triangular mandibles with a well developed masticatory margin that are characteristic of the overwhelming majority of post-Cretaceous ants, but not of any Armaniinae, Sphecomyrminae or Cretaceous Ponerinae (*Brownimecia* Grimaldi, Agosti & Carpenter 1997, *Afropone*).

However, *Afropone* is the most interesting from an evolutionary point of view. It has the abdomen much more differentiated than in the Late Cretaceous North American *Brownimecia* and in many post-Cretaceous Ponerinae. On the other hand, its mandibles and the entire cranio-mandibular system (as defined by Dlussky & Fedoseeva 1988) are very primitive (as is true for *Brownimecia*). There are a few extant Ponerinae with similar sabre-like mandibles lacking teeth (some *Leptogenys* Roger, 1861), but they have evidently lost the teeth (morphocline reduction in tooth number is evident in the *L. processionalis* group: Bolton pers. com.) and their head capsule is clearly specialised.

Afropone also demonstrates a mixture of plesio- and apomorphic characters in its wing venation, as follows:

Position of crossvein cu-a. Its position near cell mcu is evidently plesiomorphic, as in all Armaniinae, Sphecomyrminae, Myrmeciinae, Nothomyrmeciinae and Ponerinae, as well as in the vast majority of other hymenopterans including all sawflies. In more advanced ant subfamilies

(Pseudomyrmecinae, Myrmicinae, Formicinae, Dolichoderinae) cu-a is roughly midway between the wing base and cell mcu.

Crossvein 1r-rs. In ants, cells 1r and 2r, completely separated by vein 1r-rs, are found only in *Armania robusta* and *Pseudarmania rasnitsyni* (Armaniinae), where additionally veins 2Rs and 3Rs meet at a distinct angle. In *Baikuris mandibularis*, *B. mirabilis* (Sphecomyrminae), *Armania curiosa* and *Orapia* (Armaniinae), 1r-rs is present but does not reach the pterostigma, and so cells 1r and 2r are incompletely separated; veins 2Rs and 3Rs still meet at an angle. In *Myrmecia* (Myrmeciinae), *Paltothyreus* Mayr, 1862, *Platythyrea* Roger, 1863 and *Afropone* (Ponerinae) cell 1+2r is usually entire and vein 1r-rs is absent, but 2+3Rs is still angular, thus indicating the former position of 1r-rs (only atavistic individuals display a rudiment of 1r-rs, seen in a species of *Myrmecia* and *Platythyrea cribrinodis* Gerstäcker, 1859). The remaining ants, including known species of *Sphecomyrma* Wilson & Brown, 1967, *Dlusskyidris* Bolton, 1994 (Sphecomyrminae), *Archimyrmex* (Myrmeciinae), *Nothomyrmecia* Clark, 1934 (Nothomyrmeciinae) and *Aneuretus* Emery, 1893 (Aneuretinae), have vein 2+3Rs curved and not angular, with no clear signs of the former separation of cells 1r and 2r. In Apocrita other than ants, a complete or nearly complete 1r-rs is an uncommon feature, but it is not rare in the more plesiomorphic wings of various aculeate wasps (Sphecidae s.l.: various Angarosphecinae, most Astatinae and Ampulicinae; various Tiphidae; etc.).

Form of cell rm. A quadrangular or, in the case of an angular 2+3Rs, pentagonal to hexagonal cell rm, with 2Rs and 2M diverging basal to crossvein m-cu, veins 2Rs and 3M thus leaving cell mcu separately, is plesiomorphic for ants. This state is characteristic of all Armaniinae, Ectoninae, Sphecomyrminae, Myrmeciinae and Nothomyrmeciinae, the vast majority of Ponerinae and Pseudomyrmecinae, of those Cerapachyinae with relatively complete venation, and of the least advanced Dolichoderinae; it is not found in any studied Myrmicinae, Formicinae, Dorylinae, Aenictinae, or Leptanillinae. The apomorphic state is a triangular cell rm, resulting from loss of vein 2M, so that veins 2Rs and 3M have a common junction with cell mcu, a condition observed in

Aneuretus simoni Emery, 1893 (the only living aneuretine ant), some Pseudomyrmecinae (species of *Tetraponera* Smith F., 1852 with smaller body size) and some Ponerinae, Dolichoderinae and Myrmicinae. Pseudomyrmecinae, Ponerinae and Dolichoderinae display smooth transitions between a quadrangular and triangular cell rm, while within Myrmicinae a triangular rm is probably plesiomorphic. However, as a rule those myrmecines with the most complete venation (*Messor* Forel, 1890, *Pheidole* Westwood, 1839, *Aphaenogaster* Mayr, 1853, *Anisopheidole* Forel, 1914, *Pogonomyrmex* Mayr, 1868) have cell rm both triangular and petiolate basally, an apomorphic condition as compared with a non-petiolate triangular cell.

Thus *Afropone* combines deeply plesiomorphic characters characteristic of Armaniinae (structure of the cranio-mandibular system, proclinate base of vein Rs, angular 2+3Rs) with apomorphies characteristic of advanced Ponerinae and basal Myrmicinae (triangular or absent cell rm).

The last observation, in conjunction with our find of the earliest myrmecine ant (*Afromyrma*) in the Turonian of southern Africa, can shed some light on the problem of the origin of the Myrmicinae. The most popular hypothesis claims the basal Ectatommini (Ponerinae) to be the myrmecine ancestors (Emery 1911, 1922; Wilson 1971, and others). Extant non-specialised Ectatommini are *Ectatomma* Smith F., 1858, in South America, and *Rhytidoponera* Mayr, 1862, mainly in Australia but also in the Oriental Region. Their similarity with Myrmicinae in head structure (curved frontal carinae, widely separated antennal bases, clypeus of unmodified form and tibial-spur number 1:1:1) is really striking. However, more detailed analysis reveals significant contrary evidence, as follows (Dlussky & Fedoseeva 1988):

In some myrmecine workers (*Manica* Jurine, 1807) the mesosomal structure (e.g., retained scutellum remnants, see Rasnitsyn 1980: fig. 210b) is plesiomorphic when compared with all known Ponerinae, specially Ectatommini, and in those respects when compared with all other wingless females (workers) of ants except Sphecomyrminae (wingless Armaniinae are unknown).

Abdominal morphology, including the structure of the musculature, indicates that the myrmecine form cannot be derived from the ectatommine condition and probably originated even before the ponerine structure was fully developed.

There are two sets of observations which indirectly imply an Afrotropical origin for Myrmicinae:

In the vast majority of contemporary biocenoses, Myrmicinae are either the dominant ant group, or the second most abundant after Formicinae. Practically all Cretaceous and Palaeogene ants have so far been found in Eurasia and North America, and they suggested delayed development of Myrmicinae. The oldest myrmecine ant before the present find was *Eocenidris crassa* Wilson, 1985 from the Eocene Arkansas amber, and before the Miocene their incidence was low (not above 2% of all ants in the Eocene of Grube Messel, Green River, and Baltic amber, and 4.8% in the Early Oligocene of Florissant). Only in the Miocene did their participation reach 40% (Middle Miocene of Vishnevaya Balka in North Caucasus; Dlussky 1981b). A notable exception is the Sicilian amber, which is now dated as the Early Eocene and attributed to the Afrotropical rather than the Palaearctic region (Skalski & Veggiani 1990) with Myrmicinae about 50% of the ants (Emery 1891).

There are important reasons to consider specialised desert-ant assemblages as having originated independently in five arid regions (in North America, the Palaearctic, South America, Australia, and southern Africa) from pre-existent humid faunas (Dlussky 1981a). Because of their characteristic pre-adaptation, viz. the presence of a proventricular valve which permits storage of liquid food in the crop, the adaptive zone of diurnal zoonecrophagy is usually occupied in deserts by Formicinae and Dolichoderinae. Unlike them, Myrmicinae have the proventriculus closed by a sphincter, which is why they cannot store much food in the crop and so are usually carpophagous, storing seeds in the nest. This holds true for all deserts except the southern African ones, where species of *Ocymyrmex* Emery, 1886 (Myrmicinae) occupy the niche of larger diurnal zoonecrophages. This could be interpreted as an indication that when the southern African desert-ant assemblage was being formed, the ants better pre-adapted for this niche elsewhere (larger Formicinae and Dolichoderinae) were absent, thus enabling local Myrmicinae to occupy this adaptive zone. Only later did some species of *Cataglyphis* Foerster, 1850 (Formicinae), larger diurnal zoonecrophages of Palaearctic deserts, reach there via dunes along the coast, but this adaptive zone had already been

occupied by the highly specialised *Ocymyrmex*, so *Cataglyphis* was restricted to semiarid biotopes (Dlussky 1981).

Finding *Afropone* and *Afromyrma* in the southern African Turonian is additional indirect evidence of the Afrotropical origin of Myrmicinae. This is not to say that *Afropone oculata* is a direct myrmicine ancestor; it is too specialised (e.g., in its huge eyes), and it co-existed with Myrmicinae (*Afromyrma*). However, an unknown relative that combined plesiomorphic character states of Armaniinae with characters of advanced Ponerinae and basal Myrmicinae might well be such an ancestor.

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