

Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: a preliminary review

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The kimberlitic eruption that formed the crater at Orapa occurred about 91 Mya, and its fossiliferous sediments were deposited shortly thereafter. The pieces of rock from Orapa which contain insect fossils, approximately 2000 currently housed in the Bernard Price Institute of Palaeontology at the University of the Witwatersrand and about 220 in the National Museum of Botswana in Gaborone, were screened for Hymenoptera, and all arthropods on the 68 pieces so selected were identified to the lowest level possible. After adjusting for the prior selection of Hymenoptera, the ordinal composition of the arthropods was calculated. The major components, based on number of specimens, are: Coleoptera (29 %), Homoptera (18 %), Blattodea (17 %), Diptera (13 %), Thysanoptera (7 %), and Hymenoptera and Orthoptera (6 % each). The major components of the 108 specimens (at least 68 species) of Hymenoptera are approximately: Chalcidoidea (20 %), Formicidae and Sphecidae *s.l.* (12 % each), Megalynidae, Braconidae and Bethyloidea (9 % each), Scelionidae (7 %), Gasteruptionidae (6 %) and Ichneumonidae (5 %). Comparison with hymenopteran assemblages from other Cretaceous localities, shows that the Orapa assemblage conforms with the Armaniid Kind, but with an unusually high number of Chalcidoidea (exceeding Scelionidae), and is essentially concordant with expectations based on other Turonian assemblages of Hymenoptera.

Key words: fossils, fossil assemblages.

INTRODUCTION

The fossil history of insects is fragmentary, although there are very many localities scattered around the world of different ages from which insect fossils have been collected (Rasnitsyn & Quicke 2002). Most localities have produced only a few specimens, however, which means that opportunities for assessing changes in faunal composition over time and space are limited to consideration of the relatively few rich assemblages or *Lagerstätten*. These are mainly found in the northern hemisphere, so the discovery of such an assemblage in the southern hemisphere is of particular importance. Although the deposits at Orapa, Botswana, 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; Brothers 1992; Rayner 1993; Rayner *et al.* 1998 and references therein; Dlussky *et al.*, in press). A recent

opportunity for us to examine the material from Orapa presently housed in the Bernard Price Institute of Palaeontology (BPI) at the University of the Witwatersrand and in the National Museum of Botswana (NMB), has enabled us to make better estimates of the composition of the insect fauna at the ordinal level, and also of the hymenopteran diversity. These results are presented below.

Overviews of the geology, general palaeontology and palaeoenvironment of the Orapa deposits, which were excavated during diamond-mining operations in central Botswana, have been given by Rayner *et al.* (1991, 1998), so we will not deal with these aspects. A comment needs to be made about the aging of the fossils, however. The eruption which created the crater has been dated by various means as 93.1 ± 1.4 Mya (U/Pb of zircons; Davis 1977), 87.4 ± 5.7 and 92.4 ± 6.1 Mya (fission tracks in whole zircon crystals; Haggerty *et al.* 1983), 90.29 Mya (isochron from linear regression of fission tracks in two uranium zones of a zircon crystal; Haggerty *et al.* 1983) and 75–100 Mya

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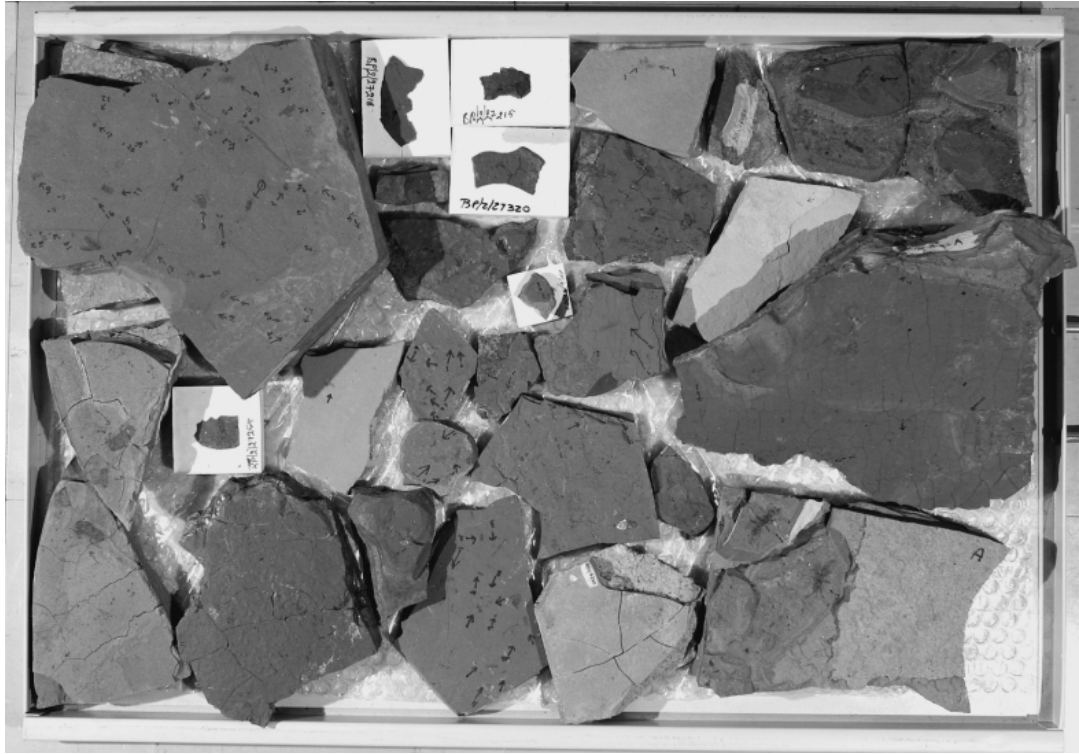


Fig. 1. Example of tray of rock pieces with Hymenoptera and other specimens in the Bernard Price Institute of Palaeontology (tray length = 600 mm).

(palynology; Scholtz in Rayner *et al.* 1991). The average of 91 Mya (from the zircon analyses) 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.

We estimate that there are about 2000 pieces of rock with insect fossils from Orapa presently housed in the BPI, and that these could contain about 5000 insect specimens. In addition, there are about 220 similar pieces in the NMB, with about 600 insect specimens and one spider. The insect ordinal composition of the Orapa fossil assemblage has not yet been calculated, so we have used the results of this study of the hymenopterans to make a preliminary assessment of the ordinal structure of the assemblage. This was possible because insect fossils are abundant in the material, so that one piece of rock may display several (exceptionally up to 70) fossils (Fig. 1). In July 2001

all the material kept in the BPI was screened (by D.J.B.) for hymenopteran fossils, and all the rock pieces so selected were screened (by A.P.R.) for all arthropod fossils (only a single spider was found in addition to insects). In January 2003 the specimens in the NMB were similarly screened by D.J.B., assisted by Ian McKay of BPI. The insects were generally identified to order level (Table 1), and the hymenopterans to the lowermost level possible (mainly to family), recognizing that the state of preservation of some specimens made identifications somewhat uncertain. The minimal number of hymenopteran species (number of morphotypes discernible without proper taxonomic study) was also evaluated (Table 2).

Special provision was made while calculating the ordinal composition to compensate for the prior selection in favour of the hymenopterans. Sixty-eight blocks were found to have hymenopteran fossils (part and counterpart, including partial counterparts and, when so identifiable, pieces broken off a particular block, were all considered as single blocks). Given one hymenopteran

Table 1. Composition of the Orapa insect fauna by order (%), based on the intensively studied part of the collection in the Bernard Price Institute of Palaeontology and the National Museum of Botswana (68 blocks selected for the presence of Hymenoptera – see text), excluding fossils not identified to order.

Taxa	<i>n</i>	Percentage
Spiders (Araneae)	1	0.2
Dragonflies, damselflies (Odonata: small zygopteran)	1	0.2
Cockroaches (Blattodea)	112	17.5
Earwigs (Dermaptera: Forficulina)	3	0.5
Crickets, etc. (Orthoptera)	38	5.9
Bark-lice (Psocoptera)	2	0.3
Thrips (Thysanoptera)	45	7.0
Leaf hoppers, etc. (Hemiptera: Homoptera)	115	17.9
True bugs (Hemiptera: Heteroptera)	17	2.6
Beetles (Coleoptera)	183	28.6
Moths (Lepidoptera)	3	0.5
Flies, etc. (Diptera)	81	12.6
Wasps, etc. (Hymenoptera) (total 108) ¹	40	6.2
Total	641	100

1: to counteract the effect of prior selection in favour of hymenopterans, 68 hymenopteran fossils are excluded from the calculations (see text).

per block to be the result of the prior selection, it seems reasonable to consider the additional specimen(s) as randomly collected. Therefore, when the number of blocks (68) is subtracted from the number of hymenopterans recorded (108), the

result (40) can be taken as an approximation of the number of hymenopterans in a random sample of that size. This method would exaggerate the numbers of hymenopterans were there to be a tendency for them to be buried in groups, but we

Table 2. Composition of the Orapa hymenopteran assemblage.

Taxon	<i>n</i>	Percentage ¹	Minimum no. of spp.
Gasteruptionidae (Kotujellitinae)	5	5.8	4
Evaniidae	3	3.5	3
Megalyridae (Cleistogastrinae gen. n.)	8	9.3	1
Scelionidae (three may actually be Chalcidoidea and one Diapriidae)	6	7.0	6
New family? (sister to Chalcidoidea?)	1	1.2	1
Chalcidoidea (not identified to family, mainly because of poor preservation)	17	19.8	13
Ichneumonidae (cf. <i>Tanychorella</i> Rasnitsyn and advanced forms)	4	4.6	4
Braconidae	8	9.3	8
?Bethyloynymidae	1	1.2	1
?Embolemyidae (cf. <i>Baissobius</i>)	1	1.2	1
?Chrysididae (cf. <i>Hypocleptes</i>)	1	1.2	1
Bethylidae	8	9.3	7
Sphecidae <i>s.l.</i> (Angarosphecinae, Ampulicinae, several Pemphredoninae)	10	11.6	10
?Sierolomorphidae (more advanced than <i>Loreisomorpha</i> Rasnitsyn)	1	1.2	1
Formicidae (six Armaniinae, three Ponerinae, one Myrmicinae)	10	11.6	5
Vespidae (<i>Curiosivespa orapa</i> & <i>C. sp. n.</i>)	2	2.3	2
Subtotal (for 16 'families')	86	100	68
Parasitica indet.	2		
Aculeata indet.	7		
Apocrita indet.	13		
Total	108		

1: percentage of specimens identified to superfamily level at least.

Note: unless otherwise stated, fossils identified with and without question marks have been included equally in the calculations.

have the impression that this is not often the case (a cluster of three megalyrids being exceptional), so the estimate should be fairly accurate. Detailed analysis of the ordinal composition of the Orapa insect assemblage is beyond the scope of this paper because that requires comparison with data on various other Mesozoic and Cainozoic insect assemblages. This will be dealt with in another paper. However, it should be noted that the proportional representation of the various taxa is rather different from previous estimates, such as by McKay (1990) (who categorized 40.4 % of the insect fossils as unidentifiable, 38.7 % as Coleoptera, 9.9 % as Blattodea, 3.9 % as Hymenoptera, 3.3 % as Diptera, 3.2 % as Hemiptera, and 1.5 % as Orthoptera, plus four specimens of Dermaptera and one of Odonata), and Rayner (1993) and Rayner *et al.* (1998) (who gave pie charts, purportedly based on McKay (1990), showing the identified insects as about 64 % Coleoptera, 17 % Blattodea, 6 % Hymenoptera, 5 % Diptera, 4 % Hemiptera, and 1 % each Orthoptera and Dermaptera).

The emphasis in this paper is on the hymenopterans, so the only figure in Table 1 of particular relevance is the hymenopteran share of 6.2 %. It is similar to, although somewhat above, the later Mesozoic values, generally 2 % to 5 %, given by Rasnitsyn (1980: Table 4, excluding the taphonomically deviant localities) for other assemblages of impression fossils (as opposed to inclusions in fossil resins). The hymenopteran share in the Orapa insect assemblage thus seems not to differ appreciably from that usually found in other later Mesozoic assemblages (from the Middle Jurassic till at least the Turonian; no reliable data are yet available for later Late Cretaceous assemblages of impression fossils). Rasnitsyn (1980, 1990, Rasnitsyn *et al.* 1998; Rasnitsyn & Martínez-Delclòs 2000) has identified several kinds of Mesozoic assemblages of hymenopteran impression fossils. Taxon-orientated rather than age- or stratigraphy-orientated names are used for the assemblage kinds because the time boundaries between succeeding kinds do not necessarily coincide with those of stratigraphical and geochronological units.

The oldest known Mesozoic assemblages of Hymenoptera are of Late (in part possibly Middle) Triassic age and consist only of Archexyelinae (Xyelidae). They come from both Gondwana and Laurasia, namely from Australia (*Archexyela crosbyi*

Riek; Riek 1955), South Africa (*Moltenia rieki* Schlüter; Schlüter 2000) and Central Asia (some two dozen species; Rasnitsyn 1969). Archexyelinae are found only in the Triassic deposits, so these assemblages will be referred to as belonging to the Archexyelinae Kind.

Jurassic assemblages are known from Eurasia only (Rasnitsyn 1980, 1990 and references therein). They are diverse but not in ways enabling further grouping. These assemblages can be characterized by the absence of several taxa typical of the Cretaceous and Cainozoic rather than the presence or general dominance of ones particularly characteristic of the Jurassic. In fact, there are several taxa endemic to the Jurassic, but they are either at most of subfamily rank (*e.g.* Praeaulacinae, Protohelorinae) or rare and local (Gigasiricidae, Jurapriidae). Dominant groups are often Xyelidae, Ephialtitidae or, sometimes, Sepulcidae, which are also not particularly rare in the Cretaceous, where they sometimes even dominate (especially Xyelidae in the temperate Cretaceous). Higher taxa that are absent in the Jurassic but widespread in the Cretaceous are much better indicators. These are Tenthredinidae, higher Ceraphronoidea (particularly Megaspilidae), Proctotrupoidea (Cynipoidea, Platyastroidea, Chalcidoidea, and Proctotrupoidea except Mesoserphidae, Roproniidae *s.l.* and Heloridae *s.l.*), Ichneumonoidea and Aculeata (Bethyloymidae belong to the Vespomorphia but not to the Aculeata). This is why the assemblages of the Jurassic jointly have been referred to as the Aculeate-free Kind.

Characteristic of the Cretaceous are assemblages of two kinds, the Baissine (with Proctotrupid and Angarosphecine Subkinds) and Armaniid Kinds. The first is characterized by an abundance of basal Gasteruptiidae (mainly *Manlaya* Rasnitsyn), with (in the Angarosphecine Subkind) or without (in the Proctotrupid Subkind) a particular abundance of the archaic digger wasps of the subfamily Angarosphecinae (*Sphecidae s.l.*). The Armaniid Kind is based on the appearance of the least advanced ant subfamily Armaniinae, and can additionally be characterized by the decline or absence of various archaic groups, including Baissinae, Proctotrupidae and Angarosphecinae. Unfortunately, the post-Turonian part of the Cretaceous is practically free of hymenopteran impression fossils. Instead, there are many assemblages of inclusions in various fossil resins extending from the mid-Early to the latest Late Cretaceous

ages. This is of little help in the present context, though, because the taxonomic composition of various inclusion assemblages changes gradually and demonstrates no clear-cut time-delimited boundaries (Rasnitsyn 1990; Rasnitsyn & Kulicka 1990). Because of prevailing taphonomic influences, even the Early Cretaceous inclusion assemblages have much more in common with the latest Cretaceous ones than with the chronologically closer Early Cretaceous assemblages of impression fossils. This is why we have no idea when in the Cretaceous the assemblages of the Armaniid Kind went extinct.

Comparison of the above information with that in Table 2 makes it evident that the Orapa assemblage belongs to the Armaniid Kind of hymenopteran assemblage, because it includes Armaniinae, Baissinae are absent, and Angarosphecinae are subordinate to more advanced Sphecidae *s.l.* There is an additional important feature of the Orapa assemblage in common with another of the Armaniid-Kind assemblages, that of the Turonian at Kzyl Zhar in Kazakhstan. This is the presence of two species of *Curiosivespa* Rasnitsyn. This genus is also known from the Early Cretaceous (from Baissa in Siberia and Bon Tsagan in Mongolia; Carpenter & Rasnitsyn 1990) but is subordinate there to the more basal genus *Priorvespa* Carpenter & Rasnitsyn. Otherwise, *Curiosivespa* is found only in Kzyl Zhar and Orapa; at both localities no other vespid wasps have yet been found.

The Orapa assemblage also shows some unique features. The most striking is the abundance of Chalcidoidea. It is of little significance that chalcidoids have not been recorded with any certainty in any other assemblages of the Armaniid Kind; all of them were taphonomically selected in favour of larger insects, so the absence of chalcidoids is not unexpected. Of importance, though, is that even in assemblages of inclusions in fossil resins, the chalcidoid share rarely approaches that of Orapa. In the Cretaceous, this is the case only in the Medicine Hat and Baikura assem-

blages, which are both much later in the Late Cretaceous (Rasnitsyn & Kulicka 1990). Particularly striking is that the Orapa chalcidoids considerably outnumber scelionids, something not observed elsewhere in the Cretaceous. Other features unusual for Cretaceous impression assemblages and rather to be expected in inclusion assemblages are the relative abundance of Evaniidae (*cf.* Basibuyuk, Fitton *et al.* 2000; Basibuyuk, Rasnitsyn *et al.* 2000), Braconidae and Bethyloidea, and the rarity of Ichneumonidae. Some other hymenopteran taxa at Orapa (Megalyridae: Cleistogastrinae and Bethyloidea) are otherwise characteristic of the Jurassic and, to a much lesser extent, the Early Cretaceous, and so represent unexpected elements in the Late Cretaceous. These archaic taxa counterbalance the 'young'-appearing impression which the abundant chalcidoids might give to the Orapa assemblage. Another notable feature is the presence of the oldest known myrmicine ant (Dlussky *et al.*, in press).

In general, the composition of the Orapa hymenopteran assemblage conforms with the Armaniid Kind, which is consistent with the suggested mid-Cretaceous and particularly Turonian age. At the same time, the composition is somewhat deviant compared to other assemblages of the Armaniid Kind, which may result from its geographic origin. However, this inference cannot be tested until we have other comparable African fossil assemblages.

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