A Preliminary Paleoecological Analysis of Fossil Insects from a Cretaceous Crater Lake at Orapa Diamond Mine in Botswana[1]

Sandiso Mnguni[2,3], Ian James McKay[6], Lelethu Unathi-Nkosi Peter Heshula[4], Simon Kamande Kuria[5], and Shaw Badenhorst

Evolutionary Studies Institute (ESI), School of Geosciences (GEOS), University of the Witwatersrand, Private Bag 3, Braamfontein, Johannesburg, 2050, South Africa.

J. Entomol. Sci. 61(1): 000–000 (Month 2025)
DOI: 10.18474/JES25-09

Abstract Taphonomy is a field that explores the intricate processes through which organisms decay and ultimately become fossilized within the geologic record. Since the Devonian period, a diverse array of fossil insects have been uncovered in various ancient environments. In Africa, a particularly noteworthy site is the large Cretaceous volcanic crater lake found inside the Orapa Diamond Mine in Botswana, which was created by an eruption of diamond-rich epiclastic kimberlites. The deposit bears fossil plants and insects that have been studied in the past by many researchers. This work investigated the taphonomy of fossil insects from this deposit through a preliminary analysis of two sediment types, which included 40 brown-red blocks and 20 olive-green blocks. We measured and compared relative abundances of insect taxa, insect body parts, insect size, plant stems, and plant fragments found in brown-red blocks and olive-green blocks. The brown-red blocks contained more complete faunal specimens and had a higher abundance of Diptera, Hymenoptera, and Blattodea, whereas olive-green blocks contained more disarticulated wings, elytra, and abdomen and had a higher abundance of Coleoptera and Hemiptera despite having a smaller sample size. In addition, olive-green blocks had more slabs with a high abundance of plant fragments and stems. Both sediment types contained an equal number of small- to medium-sized insects. The results suggest that the two sediment types represent different environments. However, color alone is not a reliable criterion for separating rock facies. More studies are needed to consolidate our findings.

Key Words paleoentomology, biostratinomy, diagenesis, biosphere, lithosphere

Taphonomy is a study of how biological remains transition from the biosphere to the lithosphere (Martin 1999), focusing on various factors that influence the accumulation and preservation of specimens (Smith 2012, Smith and Moe-Hoffman 2007). This complex process unfolds at different stages that cover the period from death to burial (biostratinomy) and from burial to excavation (diagenesis). Abiotic (e.g., wind and

[1]Received 5 February 2025; accepted for publication 4 March 2025.
[2]Corresponding author (email: msandiso@gmail.com).
[3]Entomology Unit, Biosystematics Division, Agricultural Research Council—Plant Health and Protection (ARC-PHP), Private Bag X134, Queenswood, Roodeplaat, Pretoria, 0121, South Africa.
[4]Department of Biotechnology and Biological Science, Faculty of Agricultural Sciences, University of Fort Hare, Alice, 5700, South Africa.
[5]Department of Biological and Environmental Sciences, Faculty of Natural Sciences, Walter Sisulu University (Nelson Mandela Drive campus), Private Bag X1, Mthatha, 5117, South Africa.
[6]Dr. McKay died in July 2022 but nonetheless played an important role to this work.

water currents, energy, photoperiod, light intensity, oxygen, temperature, salinity, substrate, nutrients, etc.) and biotic factors (e.g., intra- and interspecific competition, grazing, predation, symbiosis, etc.) play crucial roles (Cohen 2003). Other factors like ecology (e.g., habitat, diet type, feeding preference, population dynamics, phenology, etc.), behavior, morphology and chemical composition also affect the fossilization potential of living organisms (Smith 1986, 2012; Smith et al. 2006). Once a living organism dies, postmortem alterations caused by changes in biological, physical, anatomical, and chemical processes subsequently affect the information preserved on the fossil record (Lyman 2010). When thoroughly studied, dead organisms with distinct ontogenetic stages, habits, and sizes can potentially provide valuable paleoenvironmental reconstructions (Martínez-Delclòs and Martinell 1993). Differing deposition environments is another possible factor to consider, as it results in different assemblages that can potentially lead to misinterpretations.

Insects are keystone species in both terrestrial and aquatic ecosystems as pollinators, recyclers, detritivores, predators, scavengers, and food sources for other animals (Penney and Jepson 2014). They are the most speciose animal clade in the history of life on Earth (Clapham et al. 2016). Paleontologists and entomologists thought that fossil insects were rare, unreliable, and generally not well preserved to be studied and subsequently result in paleoenvironmental reconstructions (Nel et al. 2010). However, since the Carboniferous, fossil insects can be found in marine, fluvial, palustrine, and lacustrine deposits, as well as in tree resin (Smith and Moe-Hoffman 2007). Most fossil insects are found in ancient lakes. In modern times, fossil insects are readily used as models to understand their evolution, from the Devonian to the Quaternary age (Nel et al. 2010). Smith (2012) used actualistic studies to provide a valuable schematic diagram that outlines taphonomic controls within insect assemblages preserved across various lacustrine environments. The schematic diagram distinguishes between proximal and distal environments. Lacustrine environments accumulate at the bottom of lakes and consist of layers of clay, silt, sand, and organic material. They are formed when rivers or streams carry sediments into a lake basin. They can be small or large, ephemeral or long lived, and open or closed systems (Smith 2012). Moreover, they can be saline or freshwater; with variable nutrient contents, temperature measures, and other physicochemical properties, and are known to be an important reference for ecological and conservation studies (Cohen 2003).

There are significant differences in geological structures (see Gernon et al. 2009a, b), sequences, and inclusions between proximal and distal environments in lake systems. Distal environments produce fine-grained blocks, whereas proximal environments yield coarse-grained ones. It is thought that insects that were slowly buried in fine-grained blocks (i.e., distal environments), which would have been found in anoxic conditions, may be better preserved than those that were rapidly buried in coarse-grained blocks, which would have been found in proximal environments that offered oxic conditions (McKay 1990, Smith 2012, Wilson 1988). Despite anoxic conditions, fossil assemblages preserved in distal environments have less exposure to any form of damage. As such, the paleoentomofauna encountered in distal environments usually contain more winged insects with varying body sizes and more articulated specimens. In contrast, assemblages preserved in proximal environments predominantly record smaller insects and more disarticulated body parts (Smith 2012).

As a result, water depth and distance from the shore are important factors in insect preservation (Smith 2012), and numerous studies have explored this notion. The type of lake, its associated sedimentary rocks, water chemistry, and sampling region within the lake influence the quality of the insect assemblages (Smith 1986, 2000, 2012; Smith et al. 2006; Wilson 1980, 1982, 1988). Wilson (1988) investigated the taphonomy of insects in lacustrine Eocene deposits in western North America by comparing insect assemblages found in proximal and distal environments. Smith (2000) studied the taphonomy of insects found in Willcox Playa, an ephemeral lake in southeastern Arizona, by comparing dead and live insect assemblages that were preserved in shallow and subsurface blocks along the shoreline of the lake. Smith and Moe-Hoffman (2007) also studied the taphonomy of Diptera preserved in blocks collected from the Eocene Florissant Fossil Beds in Colorado by comparing insect assemblages found in proximal and distal environments. Smith (2000) and Wilson (1988) state that past lacustrine environments can be reconstructed using empirical evidence from several fields such as sedimentology, geochemistry, stratigraphy, taphonomy, and taxonomy, and that such reconstructions are feasible through the process of uniformitarianism. Similar studies that investigated the taphonomy of insects of Cretaceous age were done by Bezerra and Mendes (2024), Bezerra et al. (2020, 2021, 2023), Kopylov et al. (2020), Pan et al. (2012), Smith (1986), and Wang et al. (2012). However, no study has used fossil insects preserved in lacustrine blocks of Cretaceous age from Africa.

The Orapa Diamond Mine in Botswana exists within the Kalahari Desert, about 35 km south of the Makgadikgadi Pans, 250 km due west of Francistown, and approximately 824 km from Johannesburg in South Africa. It is the largest conventional open-pit diamond mine producer by carats in the world (Brook 2019). It has a length of 1,600 m and a width of 1,000 m. It is 960 m above sea level, has a semiarid climate, an average temperature range of 21–32°C, an annual rainfall of 500 mm, with mopane tree (*Colophospermum mopane* [Bentham] Leonard) being the most dominant vegetation (McKay 1990, Mnguni 2022). It has a large Cretaceous volcanic crater lake (Fig. 1), which was formed by an eruption of adjoining diamondiferous epiclastic kimberlites. The kimberlite predominantly consisted of fragments from the mantle that were transported in calcite-rich fluids, which included large amounts of gaseous carbon dioxide and water. The mine has talus, fluvial, debris flow, granular flow, and fine-to-coarse-grained blocks that have been gradually exposed by mining operations since the 1960s (Gernon et al. 2009a, b). The deposit was dated by radioactive low-uranium zircons ^{238}U into ^{206}Pb to be between 92.4 $\pm$ 6.1 and 87.4 $\pm$ 5.7 Ma, with a rapid rate of geological deposition of approximately half a million years (Dobbs 1978).

The early infilling of the crater was caused primarily by gravity-driven catastrophic processes that consisted of kimberlitic material and chunks of surrounding country rock that the kimberlite possibly collected on its journey to the surface of the lake (McKay 1990). The debris and granular flows consisting of large chunks transported by mud were found inside the crater, flowing from the periphery toward the center (McKay 1990). The movement of debris and granular flows into the lake resulted in the deposition of sandstone in a form of coarse-grained blocks mixed with fine-grained blocks, which were formed by the slow settling of the finer-grained blocks in the water column (McKay 1990). Debris and granular flows also stirred up mud that had settled slowly, resulting in the formation of thick layers of unlaminated

Fig. 1. Top view of the Orapa Diamond Mine showing the open pit left after removal of crater lake facies and kimberlite (S 21°18.465′, E 25°22.177′). Photo by I.J.M., June 2018.

mudstone (McKay 1990). The result of these processes was a thick layer of lacustrine sediments consisting of interbedded fine-grained and coarser-grained blocks. They have varves, mud, or desiccation cracks and calcite layers, and are presently different colors (e.g., brown-red, olive-green, pink, and yellow). The varves are thin layers light in color that produce pairs of laminations usually under 0.5 mm thick. They have light and dark layers; the light layer was formed by coarse silt and fine sand that would have been deposited in spring and summer, whereas the dark layer was formed by clay and fine silt that would have accumulated during the winter season (Greenwalt et al. 2014). The fibrous coarse calcite crystals were deposited during dry periods after the lacustrine sediments had lithified (Smith 1986). These different-colored lacustrine blocks preserve fossil plants and insects that have already been studied by many researchers in the past (e.g., Bamford 1990; McKay 1990; Mnguni 2022; Rayner 1993; Rayner et al. 1991, 1997; Waters 1990). There remains considerable work to be done on the collection from this deposit.

Fossil plants include angiosperm leaves, seeds, stems, flowers, and spores belonging to five plant orders: Magnoliales, Laurales, Hamamelidales, Violales, and Typhales (Bamford 1990). Fossil insects include insect orders such as the Coleoptera, Diptera, Hymenoptera, Hemiptera, Orthoptera, Thysanoptera, Blattodea, and several other groups (Brothers and Rasnitsyn 2003). The paleoenvironment of the deposit was reconstructed as strongly seasonal with warm, high-humidity wet summers and cold, dry winters. The presence of phytophagous and predaceous insect groups suggests that there was continuous vegetation cover in and around the crater lake. It also suggests that there would have been trees not far from it. Many of the fossil insects are preserved complete, indicating that there was slow settling of finer-grained blocks and mud in the water column. The complete preservation also suggests that there were few natural enemies in the lake. More important, an inference can be drawn that the Orapa paleolake likely experienced a low-energy deposition.

This study aimed to compare relative abundances of faunal and floral inclusions to investigate the possibility that brown-red blocks represent distal environments, whereas olive-green blocks represent proximal environments. The broad and overarching aim of this study was to use taphonomy to understand the environmental conditions of the paleolake and understand how environmental conditions controlled the taphonomy of the sediments and their faunal and floral inclusions. Therefore, the main objective of the study was to compare the paleoentomofauna and paleoflora preserved in the two different deposition environments.

Materials and Methods

The sedimentary sequence in the lacustrine sediments, in general, includes interbedded mudflows, sandstones, and massive mudstone. Some of the unlaminated mudstones are covered with tiny pits that look like raindrop impressions left behind in soft mud. Some of them have mud or desiccation cracks, which are indicative of sunny or shady environments. Calcite layers run diagonally over the bedding planes. The fossil material was collected by researchers in several visits from 18 sites within the Orapa Diamond Mine in Botswana in the 1980s. It is housed in the Herbarium of the Evolutionary Studies Institute at the University of the Witwatersrand, Braamfontein, Johannesburg, South Africa.

A total of 100 lacustrine blocks were randomly selected (Table 1). These were divided as follows: 20 brown, 20 red, 20 olive-green, 20 pink, and 20 yellow (Fig. 2). Results from brown and red blocks were combined as it was established that they were probably deposited in the same environment (McKay 1990). The different shades of these two colors were almost always difficult to distinguish with the naked eye. The combination meant that 40 brown-red blocks were compared with 20 olive-green blocks. The pink and yellow blocks were omitted in the final analysis as they were interpreted as being affected by postdepositional processes (McKay 1990). Therefore, they did not form part of the scope of the study. More important, we have confirmed that their exclusion does not significantly change the merit of the study. Being Despite consistent with other findings, we consider this to be preliminary work.

The relative abundances of insect taxa, insect body parts, insect size, plant stems, and plant fragments were recorded in each of the colored blocks. All the recorded variables were measured and recorded as count data. The count data for all the blocks used for this work are recorded and presented in Table 2. The brown and red blocks were combined (Fig. 3) and compared against olive-green blocks (Fig. 4) as presented in Table 3. Moreover, plant stems and plant fragments were categorized as either low, medium, or high abundance as presented in Table 4.

The blocks with a high relative abundance of plant stems and plant fragments were estimated to have >50% of the surface covered, a medium relative abundance was between 25 and 50% coverage, and a low relative abundance was <25% coverage. The term "none" means that there were no insect taxa, insect body parts, insect sizes, plant stems, and plant fragments recorded on the block.

Table 1. Specimen numbers of the different-colored mudstone blocks that have been discovered from Orapa Diamond Mine in Botswana (n = 100).

Block Color	Specimen Numbers
Brown	BP/2/18498, BP/2/27191, BP/2/25912, BP/2/26713, BP/2/25579, BP/2/26806, BP/2/26711, BP/2/25888, BP/2/26968, BP/2/18522, BP/2/25859, BP/2/25234, BP/2/26239, BP/2/26822, BP/2/18536, BP/2/25251, BP/2/26503, BP/2/18683, BP/2/26430, BP/2/26632.
Red	BP/2/27462, BP/2/27585, BP/2/25842, BP/2/27767, BP/2/26863/B, BP/2/28020, BP/2/28047, BP/2/22447/B, BP/2/25553, BP/2/26837, BP/2/25648, BP/2/28233, BP/2/27023, BP/2/27232, BP/2/27863, BP/2/25997, BP/2/25306, BP/2/26209, BP/2/27604, BP/2/27617.
Olive-Green	BP/2/28033/A, BP/2/25765, BP/2/18597, BP/2/28198/B, BP/2/28213, BP/2/22091, BP/2/27696, BP/2/18547, BP/2/25803/A, BP/2/25324/A, BP/2/21919/B, BP/2/24398, BP/2/25339, BP/2/25757, BP/2/21922, BP/2/18601, BP/2/25565, BP/2/22070, BP/2/25502, BP/2/24267.
Pink	BP/2/23674, BP/2/22466/B, BP/2/23892, BP/2/23677, BP/2/22540, BP/2/27480, BP/2/27389, BP/2/26576, BP/2//26342/B, BP/2/18177, BP/2/26409/B, BP/2/27445/C, BP/2/26411, BP/2/22543, BP/2/27375/A, BP/2/26581, BP/2/26585, BP/2/26490, BP/2/27358, BP/2/27355.
Yellow	BP/2/17910, BP/2/17562, BP/2/18018, BP/2/17900, BP/2/17994, BP/2/18142, BP/2/17658, BP/2/18282, BP/2/17844, BP/2/17873, BP/2/18370, BP/2/17955, BP/2/18026, BP/2/17402, BP/2/18416, BP/2/18220, BP/2/18312, BP/2/17245, BP/2/18054, BP/2/18333.

For insect taxa, insect body parts, insect size, plant stems, and plant fragments, each category was divided by the total number summarized vertically. The horizontal summation is only for reference. These were then presented as percentages that were used to construct the graphs. For example, for unknown specimens it was 148/238. For whole-bodied specimens it was 110/219. The same procedure was followed as denoted in Tables 3 and 4.

All observations were conducted using an Olympus SZX7 binocular microscope with an Olympus U-TV0.36XC camera. Insect sizes were measured randomly using the insect body parts, either vertically or horizontally, depending on the orientation of the specimen, using a line drawing embedded in the Olympus SZX7 binocular microscope.

A model by Smith (2012) that depicts taphonomic controls of insects in lacustrine settings (Fig. 5) was used to understand the environmental conditions of the paleolake, and how environmental conditions controlled the taphonomy of

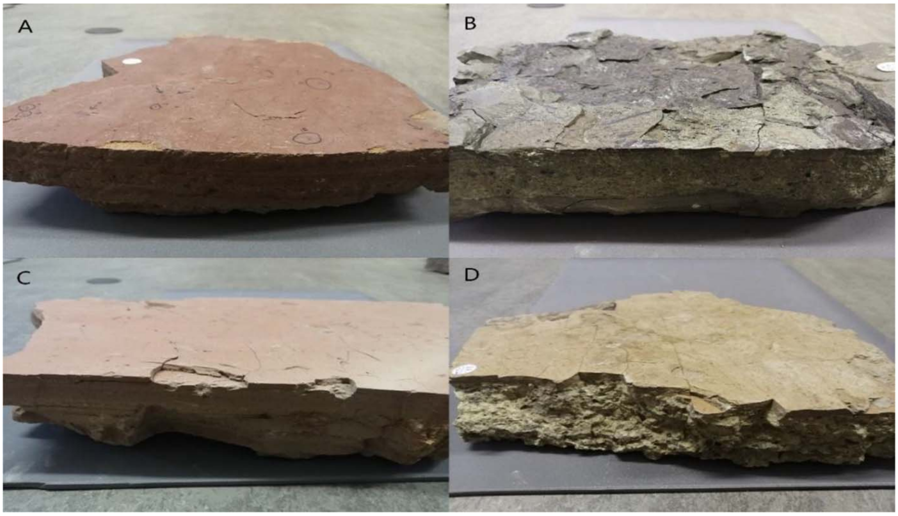

Fig. 2. Lacustrine blocks consisting of interbedded fine-grained with coarse-grained material from Orapa Diamond Mine in Botswana: (a) brown-red (BP/2/28058), (b) olive-green (BP/2/18544), (c) pink (BP/2/26533), and (d) yellow (BP/2/17890a).

the sediments and their plant and insect inclusions at the Orapa Diamond Mine in Botswana.

All the statistical analyses were conducted using PAST4PROJECT Statistical Software (https://folk.uio.no/ohammer/past/). The data were checked for normality and were nonparametric. Therefore, they were analyzed using a 95% confidence interval of the Chi-Square contingency analysis test. This is accepted as a suitable test for assessing a relationship between two categorical variables (Smith 2000). Our study met this condition.

Measures that recorded 0 were excluded in the statistical analyses. Traditionally, Chi-Square contingency analysis tests are said not to work well with recorded frequencies that are <5 (Smith 2000). As a solution to this, Zar (1996), cited in Smith (2000), strongly suggested combining or completely removing rows and columns that have extremely low frequencies. Even with this removal of the measures with low frequencies, in the end, a significant number of measures was still included in the statistical analysis of this study.

Results

Insect orders. Most insects could not be identified to any order because of poor or incomplete preservation in both brown-red blocks and olive-green blocks. Overall, although not statistically significant, brown-red blocks had more unknown insects than olive-green blocks. For those that could be identified, Coleoptera generally had the biggest contribution, with olive-green blocks having a greater representation than brown-red blocks. The results observed for Hemiptera were identical to those of

Table 2. Actual numbers showing the relative abundances of the insect taxa (orders), body parts, and sizes of fossil insects preserved in different-colored mudstone blocks from Orapa Diamond Mine in Botswana (*n* = 100).

Mudstone Blocks	Brown	Red	Green	Pink	Yellow	Total
Insect Orders						
Unknown	100	48	29	13	23	213
Coleoptera	25	20	17	16	6	84
Diptera	10	5	2	1	0	18
Hymenoptera	7	0	1	1	2	11
Hemiptera	4	3	3	3	0	13
Blattodea	4	4	1	2	1	12
Orthoptera	3	0	1	1	0	5
None	2	3	5	5	8	23
Total	155	83	59	42	40	379
Insect Body Parts						
Whole Body	61	49	24	26	24	184
¾ Body	14	6	1	0	1	22
Wing	13	1	9	2	1	26
Antennae	7	3	2	1	2	15
Abdomen	6	6	4	1	3	20
Elytra	11	2	9	3	3	28
Pair of Elytra	7	0	2	0	0	9
Leg	12	1	3	1	1	18
Fragment	11	7	0	2	1	21
Total	142	75	54	36	36	343
Insect Size (mm)						
0.0—0.9	5	0	0	1	2	8
1.0–4.9	78	45	22	30	17	192
5.0–9.9	27	18	8	9	10	72
10.0–14.9	5	5	2	3	3	18
15.0–19.9	1	2	1	3	1	8
Total	116	70	33	46	33	298

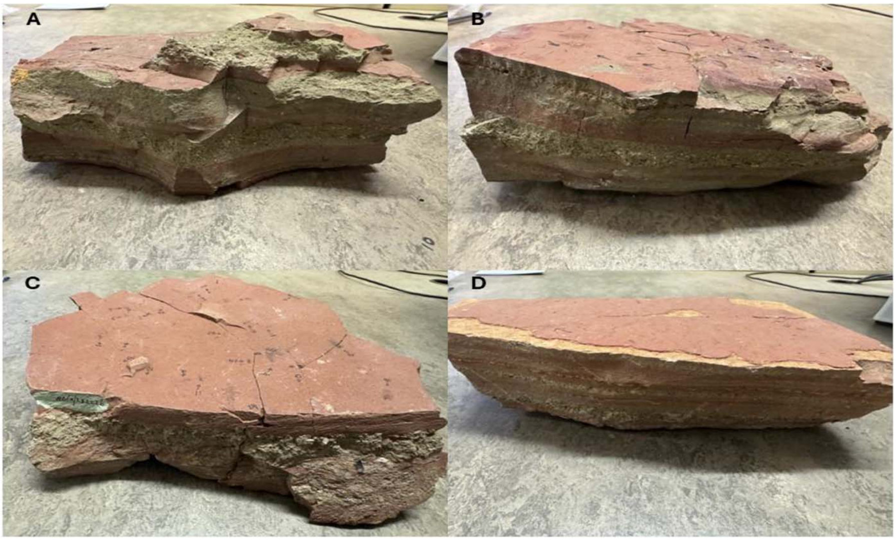

Fig. 3. Representatives of brown-red blocks consisting of interbedded fine-grained with coarse-grained material from Orapa Diamond Mine.

Coleoptera. The olive-green blocks also had a greater proportion of slabs with no insects than brown-red blocks. Although in small amounts, brown-red blocks contained a slightly larger proportion of Diptera, Hymenoptera, and Blattodea than olive-green blocks ($\chi^2 = 10.92$, df $= 7$, $P = 0.1288$; Fig. 6).

Fig. 4. Representatives of olive-green blocks consisting of interbedded fine-grained with coarse-grained material from Orapa Diamond Mine.

Table 3. Actual numbers showing the relative abundances of insect taxa (orders), body parts, and sizes of fossil insects preserved in 40 brown-red and 20 olive-green blocks from Orapa Diamond Mine in Botswana (*n* = 60).

Mudstone Blocks	Brown-Red	Olive-Green	Total
Insect Orders			
Unknown	148	29	177
Coleoptera	45	17	62
Diptera	15	2	17
Hymenoptera	7	1	8
Hemiptera	7	3	10
Blattodea	8	1	9
Orthoptera	3	1	4
None	5	5	10
Total	238	59	297
Insect Body Parts			
Whole body	110	24	134
¾ Body	20	1	21
Fragment	20	0	20
Wing	14	9	23
Antennae	10	2	12
Abdomen	12	4	16
Elytra	13	9	22
Leg	13	3	16
Pair of Elytra	7	2	9
Total	219	54	273
Insect Size (mm)			
0.0–0.9	5	0	5
1.0–4.9	123	22	145
5.0–9.9	45	8	53
10.0–14.9	11	2	13
15.0–19.9	3	1	4
Total	187	33	220

Table 4. Actual numbers showing the relative abundances of plant fragments and plant stems preserved in 40 brown-red and 20 olive-green blocks from Orapa Diamond Mine in Botswana (*n* = 60).

Mudstone Blocks	Brown-Red	Olive-Green	Total
Plant Fragments			
Low	148	29	177
Medium	45	17	62
High	15	2	17
None	5	5	10
Total	238	59	297
Plant Stems			
Low	110	24	134
Medium	20	1	21
High	20	0	20
None	14	9	23
Total	219	54	273

Insect body parts (disarticulation). Most insects were intact in both brown-red blocks and olive-green blocks (Table 2). The brown-red blocks contained slightly more ¾ bodies and other fragments, which were either nonexistent or minimal in olive-green blocks. The olive-green blocks had slightly more disarticulated wings, abdomens, and elytra compared with brown-red blocks. There was an equal number of antennae, legs, and paired elytra in both brown-red and olive-green blocks ($\chi^2 = 26.56$, df $= 8$, $P = 0.0004$; Fig. 7).

Insect size. Although not significant, most insects were small, ranging between 1 and 4.9 mm in both brown-red blocks and olive-green blocks (Table 3). There was also a smaller number of medium-sized insects, ranging between 5 and 9.9 mm in both brown-red blocks and olive-green blocks. A few large insects ranging between 10 and 14.9 mm and 15 and 19.9 mm were also found in both brown-red blocks and olive-green blocks. The relative abundances of insects was equal in 1- to 4.9-mm, 5- to 9.9-mm, and 10- to 14.9-mm size ranges in both brown-red blocks and olive-green blocks ($\chi^2 = 3.07$, df $= 4$, $P = 0.6114$; Fig. 8).

Plant fragments. Despite the summation, olive-green blocks had significantly more slabs with a high amount of plant fragments compared with brown-red blocks (Table 4). The brown-red blocks had significantly more slabs with none, low, and medium amounts of plant fragments compared with olive-green blocks. Most slabs had a significantly low amount of plant fragments in both brown-red blocks and olive-green blocks. Notably, both brown-red blocks and olive-green blocks had >50% of rocks with a low amount of plant fragments. Approximately 35% of brown-red blocks had no plant fragments whatsoever, compared with only 10% of olive-green blocks ($\chi^2 = 33.16$, df $= 3$, $P = 0.0001$; Fig. 9).

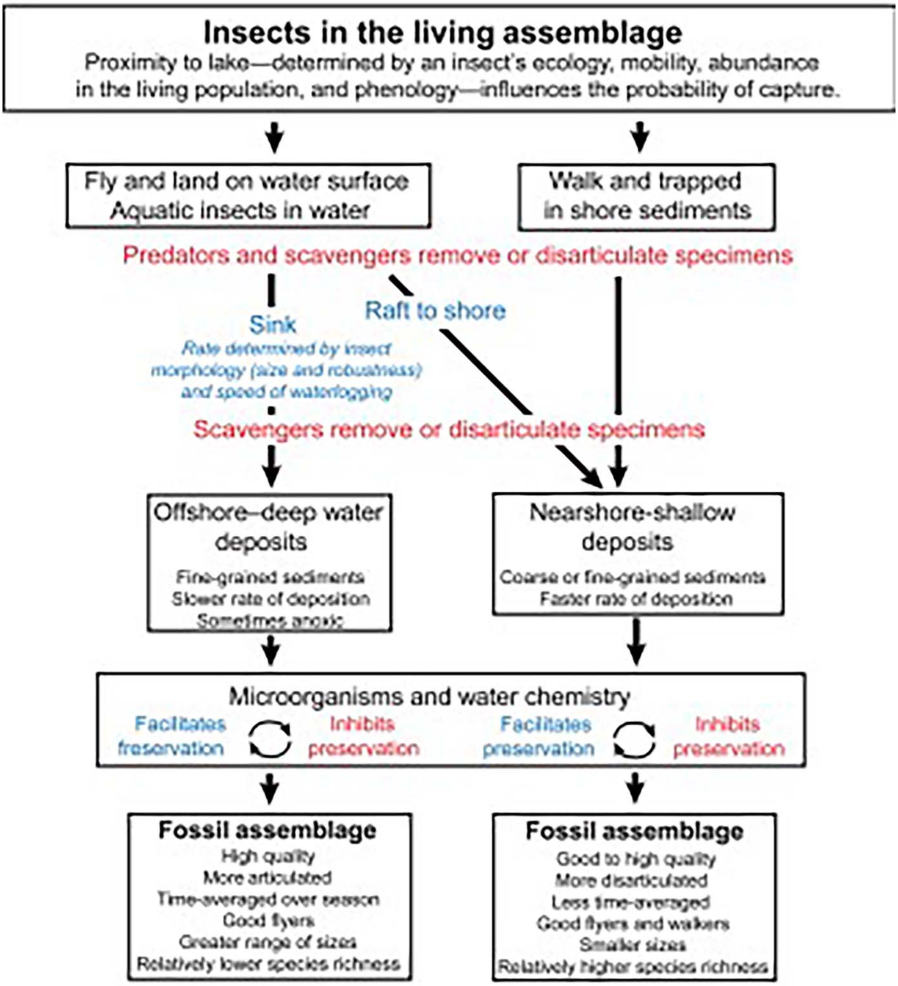

Fig. 5. Model that depicts the main taphonomic controls concerning insect preservation in lacustrine settings. Taken from Smith (2012, p. 349).

Plant stems. Despite the summation, olive-green blocks had significantly more slabs with low, medium, and high amounts of plant stems compared with brown-red blocks (Table 4). In total, brown-red blocks had significantly far fewer plant stems than olive-green blocks. Instead, brown-red blocks had significantly more slabs with no amount of plant fragments compared with olive-green blocks. Over 70% of brown-red blocks contained no plant stems at all ($\chi^2 = 33.16$, df $= 3$, $P = 0.0001$; Fig. 10).

Discussion

The olive-green blocks had a greater proportion of Coleoptera, Hemiptera, and slabs with no fossil insects on them. They also had a greater proportion of disarticulated

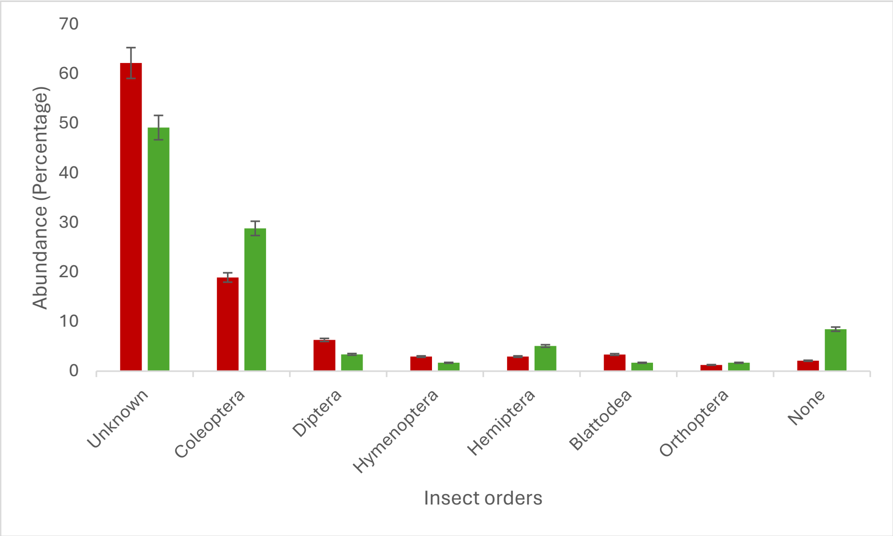

Fig. 6. Relative abundance of insect orders and unknown specimens in percentages (n = 60; χ^2 = 10.92, df = 7, P = 0.1288). Brown-red bars indicate brown-red blocks; olive-green bars indicate olive-green blocks. "Unknown" means unidentified specimens; "none" means an absence of any specimen on the blocks.

wings, abdomens, and elytra. In addition, olive-green blocks had more slabs with high numbers of plant fragments and plant stems. Astonishingly, this pattern is observed despite having fewer slabs than brown-red blocks. This is rather surprising, since brown-red blocks were expected to represent a proximal environment, whereas olive-green blocks represent a distal environment. However, the results of this preliminary study suggest that brown-red blocks represent a distal environment and olive-green blocks characterize a proximal environment. Perhaps there were some unknown mechanisms or factors such as wind, water currents, debris flow, and granular flow that carried the plant material to the center of the paleolake (Bezerra et al. 2021). The notable differences involving the insect orders were generally insignificant. The results need to be confirmed by a larger sample size in the future.

Notably, although the difference is small and insignificant, there were more strong fliers in brown-red blocks than in olive-green blocks (which had a higher proportion of Coleoptera and Hemiptera). The strong fliers include Diptera (e.g., Rayner 1987; Rayner and Waters 1990; Waters 1989a, b, 1990), Hymenoptera (e.g., Brothers 1992; Brothers and Rasnitsyn 2003, 2008; Kopylov et al. 2010; Rasnitsyn and Brothers 2007, 2009), Blattodea (e.g., Rayner and McKay 1986), Orthoptera (e.g., Brothers and Rasnitsyn 2003), and others. The presence of Diptera, Hymenoptera, Blattodea, and Coleoptera (e.g., Kuschel et al. 1994; McKay 1990, 1991; Mnguni 2022; Mnguni et al. 2022, 2023, 2024a, b, c; Woolley 2016) in brown-red blocks supports the postulation that these were from a distal environment. This is largely because the strong fliers

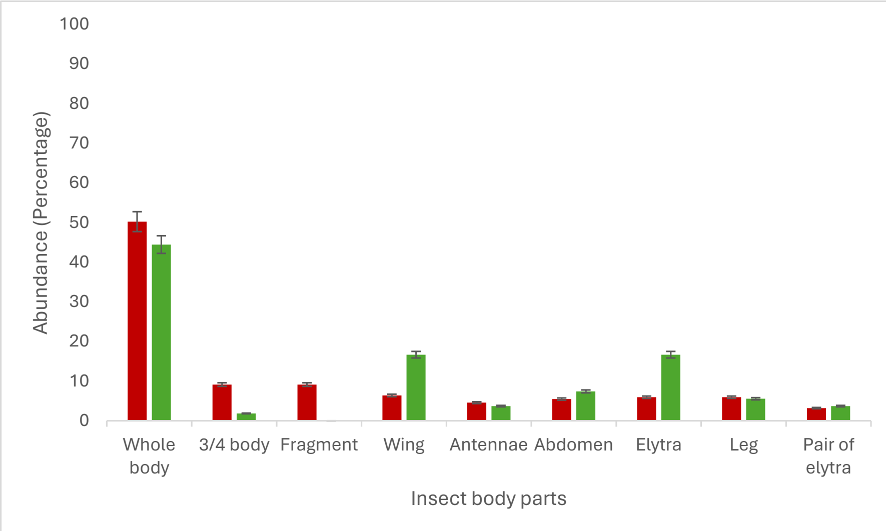

Fig. 7. Relative abundance of insect body parts in percentages (*n* = 60; χ^2 = 26.56, df = 8, *P* = 0.0004). Brown-red bars indicate brown-red blocks; olive-green bars indicate olive-green blocks.

in these insect orders may have possibly flown and landed in the water, spread their wings, and sunk to the bottom of the lake (Smith et al. 2006). Otherwise, an alternative action would have been to break the surface tension of the water and then sink to the bottom of the crater lake. Perhaps some of these insects were carried by rain or floods when already dead from farther afield.

When insects land on the water surface and are not fed upon or scavenged, they may either sink to the bottom of the lake (depending on factors such as size, robustness, and waterlogging) or be rafted to the side of the lake and become trapped on the periphery. At Orapa Diamond Mine, those that sank to the bottom of the lake are preserved in brown-red blocks, whereas those that became rafted to the shore are preserved in olive-green blocks. Alternatively, insects landing on the water surface may experience decay or decomposition, which will completely remove them from the record. If they are trapped on the periphery of the lake, then that is where they will be preserved, if they are not predated or scavenged upon (Smith 2012). Most insects float on the surface of the water. The length of the floating duration of an insect usually depends on its density, wing size, body size (subsequent tracheal system size), and whether the insect entered the surface of the water alive or dead (Smith 2012). Small insects tend to outnumber large insects on the surface of the water (Smith 2012), and denser insects tend to break the water surface tension faster than less dense insects (Martínez-Delclòs and Martinell 1993). The Orapa Diamond Mine has yielded consistent results of preserving a higher number of small-sized insects, suggesting that many of the insects had a longer flotation duration and took longer to break the water surface tension.

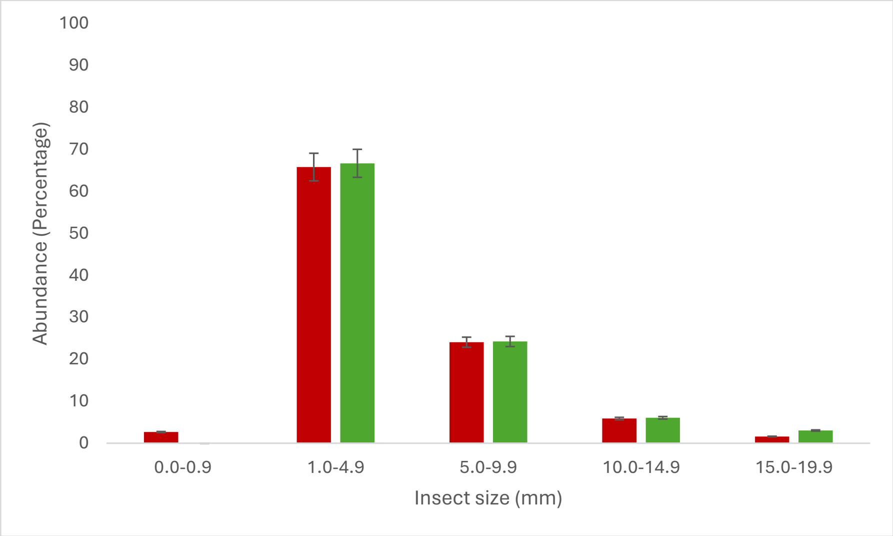

Fig. 8. Relative abundance of insect sizes in percentages (n = 60; χ^2 = 3.07, df = 4, P = 0.6114). Brown-red bars indicate brown-red blocks; olive-green bars indicate olive-green blocks.

Insects that enter the surface of the water alive actively take in water through their tracheal system and drown or sink to the bottom of the lake, and this inevitably increases their density, reducing their flotation duration. Larger and more complex tracheal systems result in faster flooding, rapid density increase, and an even shorter flotation duration. There were very few large insects in the Orapa paleolake that would have experienced faster flooding, a rapid density increase, and an even shorter flotation duration. In addition, it has been shown that any incident that destabilizes the surface tension of the water surface (e.g., heavy rain) causes all insects to quickly sink to the bottom (Martínez-Delclòs and Martinell 1993). It is possible that insects that spent extended periods of time in the water experienced decay that removed them from the record (Smith 2000, 2012).

Decay and decomposition are usually hindered by environmental factors such as hypersalinity or low temperatures, which slow down the metabolic processes of the decomposition bacteria (Martínez-Delclòs and Martinell 1993). This suggests that the deposit would have been hypersaline, as previously suggested by McKay (1990). Alternatively, when insects experience longer flotation durations, they may become surrounded by microbial biofilms that protect them from most physical damage (Smith 2000, 2012). This could explain why many of the insects from this deposit are complete and well-preserved with organic matter.

Once an insect has broken the tension of the water surface, it sinks to the bottom vertically and slowly; and the time of descent depends on its density and water depth (Martínez-Delclòs and Martinell 1993). It is at this stage that insects may be fragmented by natural enemies (i.e., predators, parasites, parasitoids, and scavengers; Duncan et al. 2003). Finally, insects reach the sediment surface and become buried,

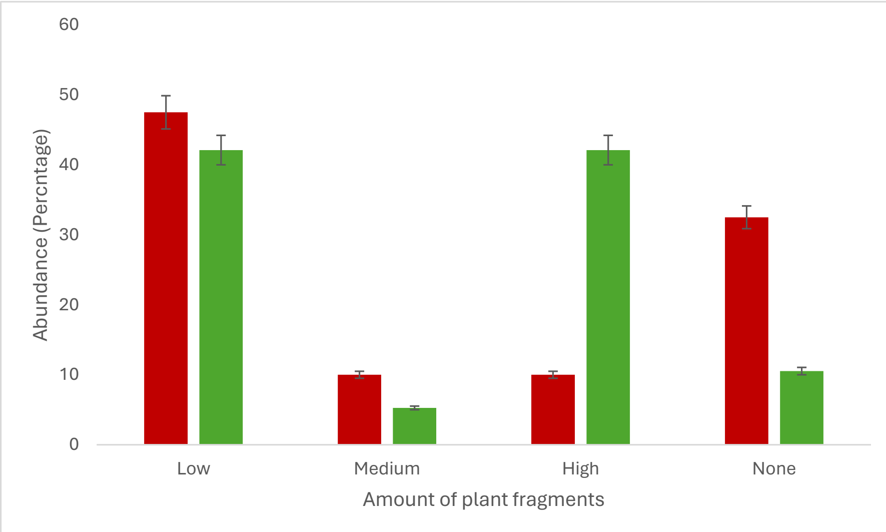

Fig. 9. Relative abundance of plant fragments in percentages (*n* = 60; χ^2 = 33.16, df = 3, *P* = 0.0001). Brown-red bars indicate brown-red blocks; olive-green bars indicate olive-green blocks. "None" means an absence of any specimen on the blocks.

and this is where the depositional environment (e.g., salinity, oxygen levels, sediment composition, and rates of sedimentation) as well as the robustness of an insect come into play (Martínez-Delclòs and Martinell 1993). During this stage, the absence of predators, benthic scavengers, and bioturbators results in a completely articulated specimen (Martínez-Delclòs and Martinell 1993). A rapid burial was once considered to be pivotal and necessary for exceptional preservation, but new findings suggest that early mineralization is the most important factor (Smith 2000, 2012). Moreover, complete and articulated insects of the same taxa typically fall, rest, and become buried close to each other (Álvarez-Parra et al. 2024).

Insects may be deposited in fine-grained blocks that had a slow rate of deposition, or they may be deposited in coarser blocks that had a faster rate of deposition (Smith 2012). At the Orapa Diamond Mine, both sediment types were present (McKay 1990). Sediment types influence the preservation quality of specimens, disarticulation, and time averaging in fossil assemblages (Smith 2012). The most common disarticulation parts are between the (a) head and thorax, (b) head and base of antennae, (c) antennal segments, (d) thoracic segments and legs, (e) articulated parts of the leg, (f) prothorax and wings, and (g) metathorax and abdomen (Rasnitsyn and Quicke 2002). Although most insects were preserved intact, disarticulation parts were all recorded in this study (Table 3, Figs. 2–4). Furthermore, actualistic studies similar to our work that have been conducted elsewhere (Martínez-Delclòs and Martinell 1993; Smith 2000, 2012; Wilson 1980, 1982, 1988) have provided more insights that disarticulation varies significantly with the following patterns: (a) antennae disarticulate fast and remain on the surface; (b) legs disarticulate from the coxae or trochanter; (c) wings are the last appendages

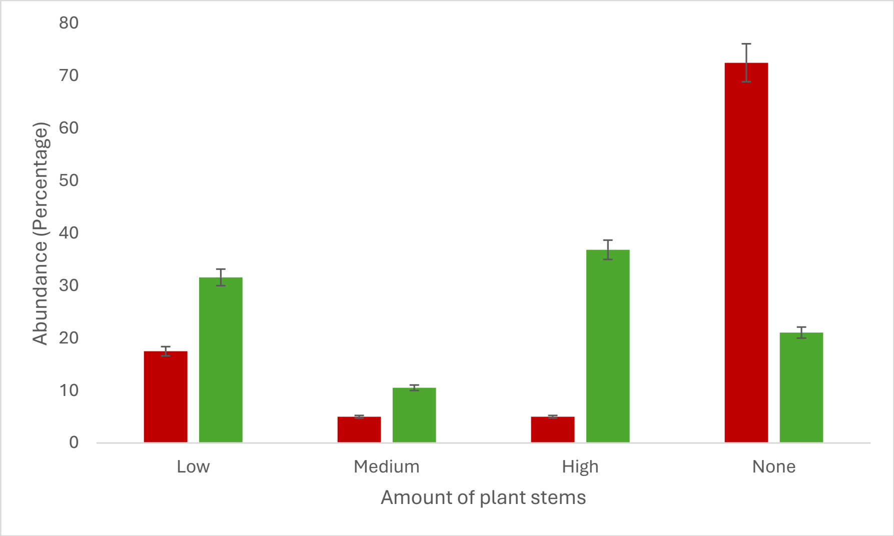

Fig. 10. Relative abundance of plant stems in percentages (n = 60; χ^2 = 57.15, df = 3, P = 0.0001). Brown-red bars indicate brown-red blocks; olive-green bars indicate olive-green blocks. "None" means an absence of any specimen on the blocks.

to detach, even when the other parts of the body have disarticulated; (d) heads almost always disarticulate at a later stage; and (e) thorax is the last part of the body to disarticulate (Carpenter et al. 1992). All these inferences are supported by the data of this study. The results also prove that taphonomy can be used to understand the environmental conditions of the lake, and to understand how the environmental conditions controlled the taphonomy of the sediments, and their plant and insect inclusions. Therefore, it is evident that taphonomy remains an important tool in reconstructing ancient ecosystems.

In conclusion, the Orapa Diamond Mine offers another example of an ancient ecosystem reconstructed using taphonomy. Factors such as wind, water currents, debris flow, and granular flow carried plant and insect material to proximal and distal environments. Strong fliers and intact specimens are prominent in distal environments, whereas weak fliers, small size, and disarticulated individuals are more common in proximal environments. The small insects had a longer flotation duration and took longer to break the water surface tension. The insects did not experience decay, suggesting that the water was hypersaline (confirmed by calcite layers running across bedding planes), or perhaps the insects were surrounded by microbial biofilms that protected them from physical damage. More important, the presence or absence of surface mats can potentially have a crucial impact on these findings, and may strongly affect the conclusions drawn in this study. In the future, more robust or comprehensive studies of this nature are needed to consolidate the findings of this study.

Acknowledgments

We thank The Office of the President of Botswana, Botswana National Museum, and De Beers Botswana Mining Company for the invitation and permission to collect and work on the fossil material. We acknowledge Mr. J. Claase from Wirsam Scientific and Precision Equipment (Pty) Ltd. (Johannesburg, South Africa) for maintaining the Olympus SZX7 binocular microscope. This work is based on research supported by the National Research Foundation of South Africa (Grant UID: 113518 and 131055), the Palaeontological Scientific Trust, Johannesburg, and the GENUS (Department for Science, Innovation, and Technology [DSIT]–National Research Foundation [NRF] Centre of Excellence in Palaeosciences [DSIT–NRF CoE–Pal] Top–Up [Reference: COE2018–16PHD, COE2019–D11, COEPH2020–11 and COE2021–SM]). Salary funding for I.J.M. came from the GENUS (DSIT–NRF CoE–Pal). In addition, the support of the GENUS (DSIT–NRF Centre of Excellence in Palaeosciences [DSIT–NRF CoE–Pal], Grant UID: 86073) toward this research is also hereby acknowledged. Opinions expressed and conclusions arrived at in this publication are those of the authors and are not necessarily to be attributed to the sources of funding and support.

The authors declare that there are no potential conflicts of interest in the form of competing financial funding sources, owning of shares, and other payments. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

S.M. dedicates this work to his late supervisor, I.J.M. (1963–2022) and former colleague, Ms. Lumka Anita Mdodana (1988–2023). The original contributions presented in the study are all included in the article or supplementary material; further inquiries can be directed to the corresponding author/s.

References Cited

Álvarez-Parra, S., C.A. Bueno-Cebollada, E. Barrón, J. Pérez-Cano, M.V. Paredes-Aliaga, C. Rubio, A. Rodrigo, N. Meléndez, X. Delclòs and E. Peñalver. 2024. Taphonomy and palaeoenvironmental interpretation of a new amber-bearing outcrop from the mid-Cretaceous of the Maestrazgo Basin (E Iberian Peninsula). Span. J. Palaeontol. 39. https://doi.org/10.7203/sjp.28426.

Bamford, M.K. 1990. The angiosperm palaeoflora from the Orapa pipe, Botswana. PhD Dissertation. Univ. Witwatersrand, Johannesburg, South Africa.

Bezerra, F.I., J.H. da Silva, E.V.H. Agressot, P.T.C. Freire, B.C. Viana and M. Mendes. 2023. Effects of chemical weathering on the exceptional preservation of mineralized insects from the Crato Formation, Cretaceous of Brazil: Implications for late diagenesis of fine-grained Lagerstätten deposits. Geol. Mag. 160(5): 911–926. https://doi.org/10.1017/S0016756823000043.

Bezerra, F.I., J.H. da Silva, E.D.C. Miguel, A.R. Paschoal, D.R. Nascimento, P.T. Freire, B.C. Viana and M. Mendes. 2020. Chemical and mineral comparison of fossil insect cuticles from Crato Konservat Lagerstätte, Lower Cretaceous of Brazil. J. Iber. Geol. 46: 61–76. https://doi.org/10.1007/s41513-020-00119-y.

Bezerra, F.I. and M. Mendes. 2024. A palaeoecological analysis of the Cretaceous (Aptian) insect fauna of the Crato Formation, Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 641: 112134. https://doi.org/10.1016/j.palaeo.2024.112134.

Bezerra, F.I., M.M. Solórzano-Kraemer and M. Mendes. 2021. Distinct preservational pathways of insects from the Crato Formation, Lower Cretaceous of the Araripe Basin, Brazil. Cretac. Res. 118: 104631. https://doi.org/10.1016/j.cretres.2020.104631.

Brook, M.C. 2019. From prospecting to jewellery: The story of the Botswana Diamond Pipeline. Bots. Notes Rec. 51: 144–159. https://www.jstor.org/stable/27010845.

Brothers, D.J. 1992. The first Mesozoic Vespidae (Hymenoptera) from the Southern Hemisphere, Botswana. J. Hymenopt. Res. 1(1): 119–124.

Brothers, D.J. and A.P. Rasnitsyn. 2003. Diversity of Hymenoptera and other insects in the Late Cretaceous (Turonian) deposits at Orapa, Botswana: A preliminary review. Afr. Entomol. 11(2): 221–226. https://hdl.handle.net/10520/EJC32559.

Brothers, D.J. and A.P. Rasnitsyn. 2008. A new genus and species of Euparagiinae from the Late Cretaceous of Southern Africa (Hymenoptera: Vespidae). Alavesia 2: 73–76.

Carpenter, S.R., K.L. Cottingham and D.E. Schindler. 1992. Biotic feedbacks in lake phosphorus cycles. Trends Ecol. Evol. 7(10): 332–336. https://doi.org/10.1016/0169-5347(92)90125-U.

Clapham, M.E., J.A. Karr, D.B. Nicholson, A.J. Ross and P.J. Mayhew. 2016. Ancient origin of high taxonomic richness among insects. Proc. Royal Soc. B Biol. Sci. 283(1824): 20152476. https://doi.org/10.1098/rspb.2015.2476.

Cohen, A.S. 2003. Paleoecological archives in lake deposits: Records from important groups. Ch. 11. *In* Paleolimnology. Oxford Univ. Press, New York.

Dobbs, P., **1978.** The distribution of kimberlitic mass flow sediments in the Orapa crater 2125 AK1. DeBeers (Botswana) Mining Company Limited. Internal Report 105(17): 15–16.

Duncan, I.J., F. Titchener and D.E. Briggs. 2003. Decay and disarticulation of the cockroach: Implications for preservation of the blattoids of Writhlington (Upper Carboniferous), UK. Palaios 18(3): 256–265. https://doi.org/10.1669/0883-1351(2003)018%3C0256:DADOTC%3E2.0.CO;2.

Gernon, T.M., M. Field and R.S.J. Sparks. 2009b. Depositional processes in a kimberlite crater: The Upper Cretaceous Orapa South Pipe (Botswana). Sedimentology 56(3): 623–643. https://doi.org/10.1111/j.1365-3091.2008.00989.x.

Gernon, T.M., G. Fontana, M. Field, R.S.J. Sparks, R.J. Brown and C. Mac Niocaill. 2009a. Pyroclastic flow deposits from a kimberlite eruption: The Orapa South Crater, Botswana. Lithos 112: 566–578. https://doi.org/10.1016/j.lithos.2009.04.016.

Greenwalt, D.E., T.R. Rose, S.M. Siljestrom, Y.S. Goreva, K.N. Constenius and J.G. Wingerath. 2014. Taphonomy of the fossil insects of the middle Eocene Kishenehn Formation. Acta Palaeontol. Polon. 60(4): 931–947. https://doi.org/10.4202/app.00071.2014.

Kopylov, D.S., D.J. Brothers and A.P. Rasnitsyn. 2010. Two new labenopimpline ichneumonids (Hymenoptera: Ichneumonidae) from the Upper Cretaceous of southern Africa. Afr. Invert. 51(2): 423–430. https://hdl.handle.net/10520/EJC84670.

Kopylov, D.S., A.P. Rasnitsyn, D.S. Aristov, A.S. Bashkuev, N.V. Bazhenova, V.Y. Dmitriev, A.V. Gorochov, M.S. Ignatov, V.D. Ivanov, A.V. Khramov and A.A. Legalov. 2020. The Khasurty fossil insect lagerstätte. Paleontol. J. 54: 1221–1394. https://doi.org/10.1134/S0031030120110027.

Kuschel, G., R.I. Oberprieler and R.J. Rayner. 1994. Cretaceous weevils from southern Africa, with description of a new genus and species and phylogenetic and zoogeographical comments (Coleoptera, Curculionoidea). Entomol. Scand. 25(2): 137–149. https://doi.org/10.1163/187631294X00261.

Lyman, R.L. 2010. What taphonomy is, what it isn't, and why taphonomists should care about the difference. J. Taphon. 8(1): 1–16.

Martin, R.E. 1999. Taphonomy: A Process Approach. Cambridge Paleobiology Series 4. Cambridge Univ. Press, Cambridge, United Kingdom.

Martínez-Delclòs, X. and J. Martinell. 1993. Insect taphonomy experiments. Their application to the Cretaceous outcrops of lithographic limestones from Spain. Kaupia 2: 133–144.

McKay, I.J. 1990. Cretaceous Carabidae (Coleoptera) from Orapa, Botswana. PhD Dissertation, Univ. Witwatersrand, Johannesburg, South Africa.

McKay, I.J. 1991. Cretaceous Promecognathinae (Coleoptera: Carabidae): A new genus, phylogenetic reconstruction and zoogeography. Biol. J. Linn. Soc. 44(1): 1–12. https://doi.org/10.1111/j.1095-8312.1991.tb00603.x.

Mnguni, S. 2022. Upper Cretaceous Staphylinidae from Orapa Diamond Mine in Botswana. PhD Dissertation, Univ. Witwatersrand, Johannesburg, South Africa.

Mnguni, S., S. Badenhorst and M.K. Bamford. 2024a. *Paleothius mckayi* sp. n.: A new species of Staphylininae (Arthropoda: Insecta: Coleoptera: Staphylinidae) from Orapa in Botswana. J. Entomol. Sci. 59(3): 275–288. https://doi.org/10.18474/JES23-53.

Mnguni, S., I.J. McKay and S. Badenhorst. 2022. *Afrinophilina orapa*: A new genus and species of Paederinae (Coleoptera: Staphylinidae) from Cretaceous lacustrine deposits at Orapa Diamond Mine, Botswana. *Authorea* Preprints. December 25.

Mnguni, S., I.J. McKay and S. Badenhorst. 2023. *Afristenus orapensis*: A new genus and species of Steninae (Coleoptera: Staphylinidae) with "harpoon-like" mouthparts from the Upper Cretaceous lacustrine deposits at Orapa Diamond Mine, Botswana. Cretac. Res. 142: 105398. https://doi.org/10.1016/j.cretres.2022.105398.

Mnguni, S., I.J. McKay and S. Badenhorst. 2024b. *Cretafrica orapensis*: A new genus and species of Mycetoporinae (Coleoptera: Staphylinidae) from lacustrine deposits at Orapa Diamond Mine, Botswana. Insect Syst. Evol. 55(4): 437–450. https://doi.org/10.1163/1876312X-bja10061.

Mnguni, S., I.J. McKay and S. Badenhorst. 2024c. A fossil Paederinae from a lacustrine deposit at Orapa Diamond Mine in Botswana. J. Entomol. Sci. 59(4): 433–447. https://doi.org/10.18474/JES23-99.

Nel, A., J.F. Petrulevičius and D. Azar. 2010. Palaeoentomology, a young old field of science. Ann. Soc. Entomol. France 46(1–2): 1–3. https://doi.org/10.1080/00379271.2010.10697635.

Pan, Y., J. Sha, F.T. Fürsich, Y. Wang, X. Zhang and X. Yao. 2012. Dynamics of the lacustrine fauna from the Early Cretaceous Yixian Formation, China: Implications of volcanic and climatic factors. Lethaia 45(3): 299–314. https://doi.org/10.1111/j.1502-3931.2011.00284.x.

Penney, D. and J.E. Jepson. 2014. Fossil insects: An introduction to Palaeoentomology. Siri Scientific Press, Rochdale, Greater Manchester, United Kingdom.

Rasnitsyn, A.P. and D.J. Brothers. 2007. Two new hymenopteran fossils from the mid-Cretaceous of southern Africa (Hymenoptera: Jurapriidae, Evaniidae). Afr. Invert. 48(1): 193–202. https://hdl.handle.net/10520/EJC84581.

Rasnitsyn, A.P. and D.J. Brothers. 2009. New genera and species of Maimetshidae (Hymenoptera: Stephanoidea sl.) from the Turonian of Botswana, with comments on the status of the family. Afr. Invert. 50(1): 191–204. https://hdl.handle.net/10520/EJC84637.

Rasnitsyn, A.P. and D.L. Quicke. eds. 2002. History of Insects. Springer Science and Business Media. Kluwer Academic Publishers, Dordrecht, the Netherlands, 517 pp.

Rayner, R.J. 1987. March flies from an African Cretaceous springtime. Lethaia 20: 123–127. https://doi.org/10.1111/j.1502-3931.1987.tb02029.x.

Rayner, R.J. 1993. The fossils from the Orapa Diamond Mine: A review. Bots. Notes Rec. 25(1): 1–17. https://hdl.handle.net/10520/AJA052550590_225.

Rayner, R.J., M.K. Bamford, D.J. Brothers, A.S. Dippenaar–Schoeman, I.J. McKay, R.G. Oberprieler and S.B. Waters. 1997. Cretaceous fossils from the Orapa Diamond Mine. Palaeontol. Afr. 33: 55–65. http://hdl.handle.net/10539/16400.

Rayner, R.J. and I.J. McKay. 1986. The treasure chest of the Orapa diamond mine. Bots. Notes Rec. 18(1): 55–61. https://journals.co.za/doi/pdf/10.10520/AJA052550590_803.

Rayner, R.J. and S.B. Waters. 1990. A Cretaceous crane-fly (Diptera: Tipulidae): 93 million years of stasis. Zool. J. Linn. Soc. 99(4): 309–318. https://doi.org/10.1111/j.1096-3642.1990.tb00557.x.

Rayner, R.J., S.B. Waters, I.J. McKay, P.N. Dobbs and A.L. Shaw. 1991. The mid–Cretaceous palaeoenvironment of central Southern Africa (Orapa, Botswana). Palaeogeogr. Palaeoclimatol. Palaeoecol. 88: 147–156. https://doi.org/10.1016/0031-0182(91)90020-R.

Smith, D.M. 2000. Beetle taphonomy in a recent ephemeral lake, southeastern Arizona. Palaios 15(2): 152–160. https://doi.org/10.1669/0883-1351(2000)015%3C0152:BTIARE%3E2.0.CO;2.

Smith, D.M. 2012. Exceptional preservation of insects in lacustrine environments. Palaios 27(5): 346–353. https://doi.org/10.2110/palo.2011.p11-107r.

Smith, D.M., A. Cook and C.R. Nufio. 2006. How physical characteristics of beetles affect their fossil preservation. Palaios 21(3): 305–310. https://doi.org/10.2110/palo.2004.p04-91.

Smith, D.M. and A.P. Moe-Hoffman. 2007. Taphonomy of Diptera in lacustrine environments: A case study from Florissant Fossil Beds, Colorado. Palaios 22(6): 623–629. https://doi.org/10.2110/palo.2006.p06-119r.

Smith, R.M.H. 1986. Sedimentation and palaeoenvironments of Late Cretaceous crater-lake deposits in Bushmanland, South Africa. Sedimentology 33(3): 369–386. https://doi.org/10.1111/j.1365-3091.1986.tb00542.x.

Wang, B.O., F. Zhao, H. Zhang, Y.A.N. Fang and D. Zheng. 2012. Widespread pyritization of insects in the Early Cretaceous Jehol Biota. Palaios 27(10): 707–711. https://doi.org/10.2110/palo.2012.p12-029r.

Waters, S.B. 1989a. A new hybotine dipteran from the Cretaceous of Botswana. Palaeontology 32(3): 657–667.

Waters, S.B. 1989b. A Cretaceous dance fly (Diptera: Empididae) from Botswana. Syst. Entomol. 14(2): 233–241. https://doi.org/10.1111/j.1365-3113.1989.tb00280.x.

Waters, S.B. 1990. Cretaceous Diptera from Orapa, Botswana. PhD Dissertation, Univ. Witwatersrand, Johannesburg, South Africa.

Wilson, M.V.H. 1980. Eocene lake environments: Depth and distance-from-shore variation in fish, insect, and plant assemblages. Palaeogeogr. Palaeoclimatol. Palaeoecol. 32: 21–44. https://doi.org/10.1016/0031-0182(80)90029-2.

Wilson, M.V.H. 1982. Early Cenozoic insects: Paleoenvironmental biases and evolution of the North American insect fauna. Proc. Third N. Am. Paleontol. Conv. 2: 585–588.

Wilson, M.V.H. 1988. Reconstruction of ancient lake environments using both autochthonous and allochthonous fossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 62(1–4): 609–623. https://doi.org/10.1016/0031-0182(88)90074-0.

Woolley, C. 2016. The first scarabaeid beetle (Coleoptera, Scarabaeidae, Melolonthinae) described from the Mesozoic (Late-Cretaceous) of Africa. Afr. Invert. 57(1): 53–66. https://doi.org/10.3897/AfrInvertebr.57.8416.

Zar, J.H. 1996. Biostatistical Analysis, 3rd Ed. Prentice Hall, Englewood, New Jersey, 502 pp.