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ON SOME FOSSIL ARTHROPODA FROM THE LIMEWORKS, MAKAPANSGAT, POTGIETERSRUS

by

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ABSTRACT

The fossil arthropod remains from the Limeworks deposit consist of puparial and dung ball casts from the Lower Phase I (Member 3) through to the Upper Phase I (Member 4) breccias. The puparial stages are represented in two gross sizes; cuticular remains and segmentation are evident in a few. Possible palaeoenvironmental implications based on the puparial remains and their state of preservation are briefly discussed.

A remarkably well preserved fossilised juvenile centipede from the Lower Phase I (Member 3) breccia is placed on record for the first time.

INTRODUCTION

The Limeworks quarry, Makapansgat, needs no introduction; the site is already famous for its large variety of fossil remains, including cercopithecids, hyaenas, sabre-toothed cats and an abundant bovid assemblage accompanied by *Australopithecus africanus* (*A. prometheus* Dart 1948).

Since 1947 during the preparation of the bone rich breccias, fossil puparial casts have frequently been found in close association with fragmentary fossil mammalian remains. This was first recorded by Kitching (1959) with the discovery of an undistorted, well preserved puparium with cuticle from what was then known as the grey breccia. This specimen was assigned to the blow-fly family Calliphoridae.

Thousands of blow-fly and a fair number of larger puparial casts have either been recovered from or observed in the deposit to date. They are less abundant in the Lower Phase I (Member 3) than in the Upper Phase I (Member 4) breccia. In a block of Member 4 breccia a large number of blow-fly puparial casts were found in close association with dung ball casts; the blow-fly eggs were in all probability deposited in the dung prior to its use by the dung beetles. In a few instances long bone shafts and flakes have been recovered from Member 3 breccia showing insect-bored holes or burrows which in some instances have penetrated the solid shafts into the marrow cavity.

An interesting discovery among the arthropod remains from the Limeworks is a fossilised juvenile centipede embedded in a lens of almost pure calcite.

The complete lack of references on fossil Arthropoda of Plio-Pleistocene age and the paucity of descriptions and illustration of puparial stages of extant forms has greatly hampered identification of the fossil remains. Where comments on present day puparial stages are available, they usually refer to colour and gross size which are both variable and unreliable. Zumpt (1965) summarises what is known of the puparia of a variety of blow-fly species, but his comments are not detailed enough for comparative purposes.

DESCRIPTION

Blow-fly puparia

The blow-fly family Calliphoridae is very rich in species and is sub-divided into a number of subfamilies and tribes. A great number of species develop in carrion and other organic matter (Zumpt 1965). In the fossil puparium assigned to the family Calliphoridae (Kitching 1959) the cuticle is well preserved; segmentation and the remains of the anterior and posterior spiracles are clearly visible, but the majority of specimens examined consist of undistorted casts, and only in a few are there traces of cuticle or segmentation (fig. 1: A and B.)

There are slight size variations in the fossil puparial casts ranging from 10,5 to 12 mm in greatest length with a maximum diameter of between 5,5 and 6 mm. Where gross sizes are quoted for extant blow-fly puparial stages, the fossil remains compare favourably in size with those of some species of *Chrysomya* and *Sarcophaga*, but with the lack of diagnostic morphological features and the paucity of comparative material the fossil forms are best assigned to the sub-order Brachycera, family Calliphoridae.

Notwithstanding their state of preservation, it is estimated that between 50 and 60 % of the adult flies were able to complete their life cycle. This conclusion is based on the presence of openings at the apical ends of the puparia with small burrows leading from the openings; the imago, or adult flies, were able to emerge from the puparia and burrow out of the then soft soil of the deposit.

In a small block of bone rich Member 3 breccia the majority of preserved puparia have been replaced by a calcite infill, and only in a few instances is there evidence that the adult flies had emerged.

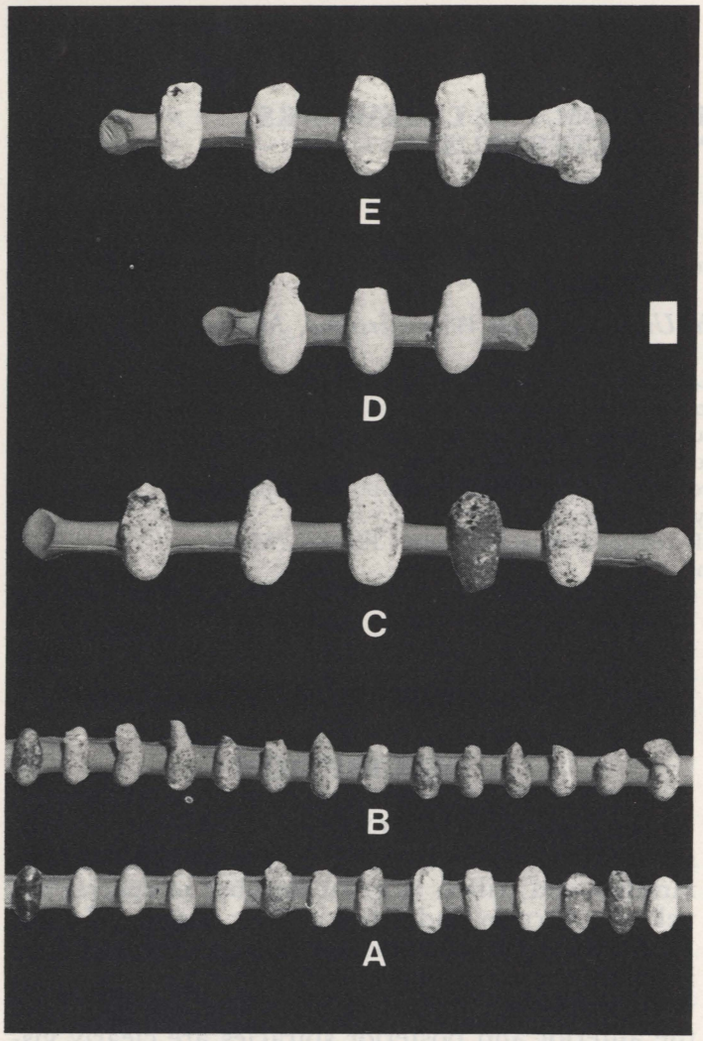

Figure 1. Fossil puparial casts: A, blow-fly from Member 3; B, blow-fly from Member 4; C, carrion beetle from Member 3; D, carrion beetle from Oligocene deposits, Badlands of South Dakota, U.S.A.; E, carrion beetle from Member 4.
(Note: all photographic scales in cm)

Carrion-beetle puparia

An even greater lack of descriptive and comparative material exists for carrion-beetle remains. Based on the expert advice of Dr. Endrödy-Younga, the author's own observations on extant carrion beetles, and deductions from the occurrence of the puparial casts within the deposit, they are here tentatively assigned to the family Trogidae.

The casts are less abundant in the bone rich breccia of Member 3 than in Member 4 where they are found in fair numbers in bone rich areas within the deposit, especially among rodent bone accumulations which can be attributed to heaped up owl pellets. The puparial casts are undistorted but show slight gross size variation from between 15 to 20 mm in length and 8 to 10 mm in diameter, but this is an unreliable feature (fig. 1: C and E). It is appropriate to note here that casts similar in shape and size have been collected by the present author from a tortoise of Oligocene age near the town of Scenic, in the Badlands of South Dakota, U.S.A. (fig. 1–C).

With the openings at the apical ends and the burrows leading from the opening of the casts it seems evident, as in the case of the fossil blow-fly, that here, too, a large percentage of the adults emerged from the puparia prior to their fossilisation.

In a block of Member 4 breccia, measuring approximately 26 × 22 × 15 cm and rich in rodent skeletal remains, at least 30 specimens with casts and burrows were exposed during preparation (fig. 2).

Dermestid bored and scarred bones

In a number of fossilised long bones and flakes recovered from Member 3 the sub-periosteum of the bones has a "moth-eaten" appearance. In others this feature occurs together with holes or burrows bored into the bone. These burrows are between 4 and 5 mm in diameter and penetrate the solid shafts of metacarpal, radial, tibial and metatarsal bones at varying angles; in a few instances they penetrate into the marrow cavities (fig. 3). Up to now this damage has only been observed on long bones and flakes from Member 3 breccia and not in any specimens from Member 4.

Skaife (1953) comments that the fully grown larva of some species has the habit of boring into anything at hand to make sheltered tunnels for itself as a place for pupation. Wood in infested store rooms may be badly damaged, and mortar between bricks may be honeycombed with burrows.

From what could be deduced from the brief descriptions in the literature the "moth-eaten" appearance of the specimens and the size of the burrows, it seems that the damage can be attributed to one of the species assigned to the family Dermestidae.

Fossil dung ball casts

In Africa there are over 1 800 species of dung beetles south of the Sahara with some 800 different species south of the Zambezi and Kunene rivers (Bornemissza 1979). In view of this diversity and the lack of adequate descriptive and comparative material the fossil dung ball casts are simply assigned to the family Scarabaeidae, tribe Coprini.

Three undistorted almost spherical casts with a maximum diameter of 35 mm and the impression of a fourth were found in close association with blow-fly puparial casts embedded in a block of Member 4 breccia. Fairly clear burrows containing secondary infill lead from the dung ball casts, and they indicate that the adult beetles emerged from the remains of the dung balls, probably by way of the original tunnels or burrows made by the parents (fig. 4).

One of the casts was completely removed from the matrix and sectioned. The internal structure is less compact than that of the surrounding matrix. Rodent skeletal elements are present in the infill, and small calcite filled cavities are not common.

Figure 2. Carrion beetle puparial casts from Member 4. Arrows indicate burrows.

Figure 3. Dermestid bored bovine long bones from Member 3. From left to right, tibial shaft, proximal end of metacarpal and distal end of metatarsal.

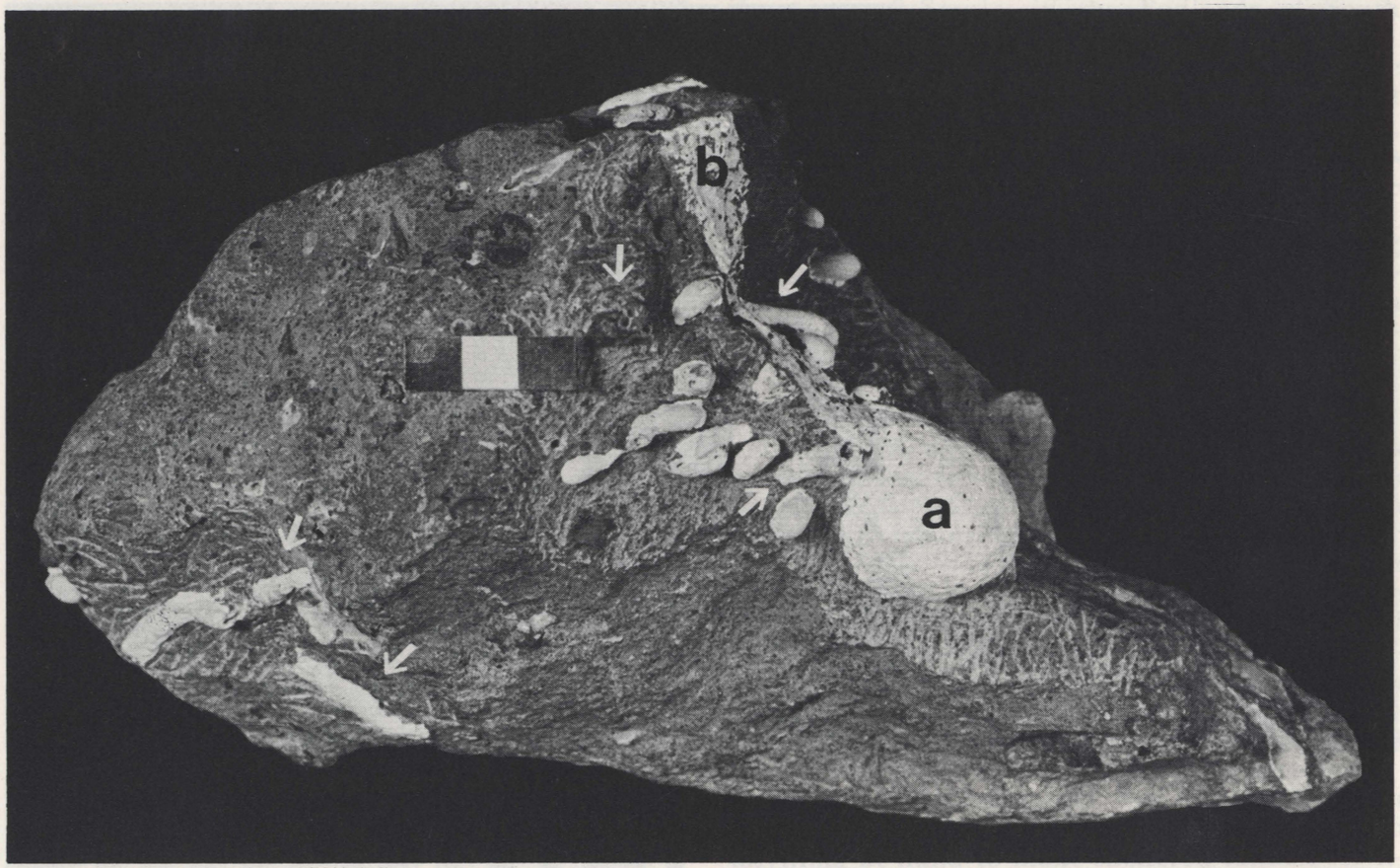

Figure 4. Dung ball together with blow-fly puparial casts from Member 4: A, dung ball; B, part of dung beetle burrow. Arrows indicate blow-fly burrows.

The infill must have filtered down the tunnels or burrows into the remains of the original dung balls left by the adults. A 3 mm thick, fairly soft layer of matrix immediately surrounding the casts could represent the space previously occupied by the original dung.

Fossilised juvenile centipede

During December 1974, a visitor to the Limeworks, Laura Graves, recovered a small piece of Member 3 breccia containing a fossil from one of the sorted and stacked rows of material in the breccia camp. The specimen was handed to the author and identified as a centipede. On the basis of descriptions and illustrations of extant centipedes (Chilopoda) (Attems 1928, 1934, Grobbelaar 1921, Lawrence 1935–1938, 1953, 1955 a, b, Manton 1965, Pocock 1891 and others) the fossil specimen could be identified as *Scolopendra* cf. *morsitans* Linn.

The specimen is a juvenile with a maximum length of 30 mm and it is exposed in ventral view. It is remarkably well preserved in a thin lens of almost pure calcite within the grey breccia Member 3. The specimen is somewhat flattened, giving it an elongate appearance (fig. 5).

Because of its small size the specimen was carefully examined microscopically. There are 21 somites, or segments, each bearing a pair of light creamy coloured legs. The claws, tarsals, prefemurs, and femurs are clearly distinguishable. The first tarsus of each is longer than the second, and the remains of minute protrusions near the distal end on some of the first tarsal segments may indicate the position of the tarsal spurs. The right anal leg is lost; the left is long and slender with faint traces of minute spines on the prefemur (fig. 5). The anterior part of the head was damaged, most probably during excavation, but the remains of the two rounded and segmented maxillipes can be distinguished. The dorsal head plate seems to extend over the anterior margin of the first tergite. Dark crossbands near the anterior end of each tergite, or dorsal plate, can be clearly seen, especially in the posterior segments; this is a typical feature in some of our South African *Scolopendra morsitans* Linn. (R.F. Lawrence pers. comm.). An interesting feature in the specimen is the position of some of the legs forming waves which could be the result of leg movement at the time of death.

DISCUSSION

Brain (1958: 115–118) and Partridge (1979: 485–487) give differing climatic interpretations for the accumulation of the Limeworks deposit. Brain suggests a deposition controlled by seasonal fluctuations in the level of the water table in the cavern for the Lower Phase I (Member 3) breccia, and Partridge concludes that this deposit was laid

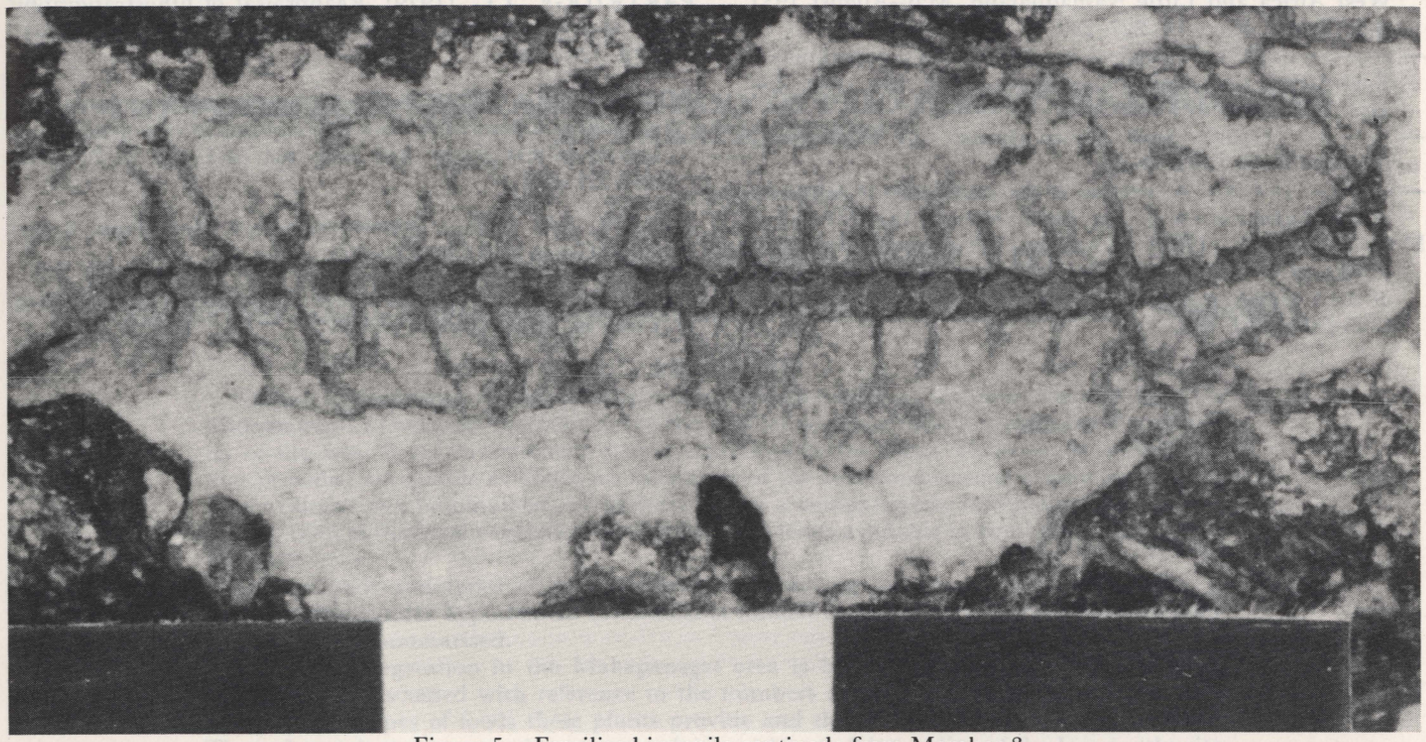

Figure 5. Fossilised juvenile centipede from Member 3.

down during vigorous flows and sheetfloods. For the Upper Phase I (Member 4) Brain envisaged a more open cavern and drier conditions, but Partridge mentions episodic sheetfloods and fairly wet conditions at times.

It has been observed that extant blow-fly will not enter dark recesses readily and will not deposit their eggs on carrion partially submerged in water or where the larval and puparial stages could be prone to drowning. Furthermore, it is well known that carrion beetles prefer to feed on dried-out carcasses and bone.

Puparial cases dropped into water float on top for some time and drift to the edge of the pool or stream where they accumulate in numbers, eventually sinking to the bottom after being saturated and filled with water. The cuticle normally softens considerably, and the cases become easily distorted. This feature is not evident in the fossil puparial casts.

The presence of the fossil puparial casts as well as the undistorted dung ball casts and the dermestid burrows thus pose some palaeoenvironmental implications. Although the arthropod remains here described are less abundant in the bone rich Member 3 than in Member 4, they occur persistently throughout the approximately two metres of the former phase, and, as already mentioned, it seems evident that a large number of adults were able to emerge from the puparial stages. Therefore, it seems most probable that drier climatic conditions than previously envisaged existed in the cavern when the Lower Phase I (Member 3) was deposited and a more open cavern and seasonal, almost arid conditions existed during the deposition of the Upper Phase I (Member 4) breccia. The latter conclusion is supported by the more abundant blow-fly and carrion beetle remains and from what can be generally deduced from the less abundant mammalian fauna when it is considered as a whole.

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