A new fossil terrestrial isopod with implications for the East African Miocene land form

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Synopsis

A new species of fossil terrestrial isopod *Eubelum rusingaense* sp. nov. is described from the Lower Miocene of Rusinga Island, Lake Victoria, Kenya. It is suggested that the animal lived at about 2500 m within the montane forest litter. The invalid family group names Atracheata and Pseudotracheata (Vandel 1960) are replaced by Oniscacea and Porcellionoidea.

Introduction

The British-Kenya Miocene Expedition of 1947 (Leakey 1953, Leakey & Clark, 1955) collected a large quantity of fossil material from Rusinga Island, Lake Victoria, Kenya. A selection of arthropod fossils from this area has been figured, but without description, by Leakey (1953*a* : 445). Amongst the 'myriapod' specimens deposited in the British Museum (Natural History), London, were 46 specimens of a pseudotracheate terrestrial isopod of the family Eubelidae. This is the first recorded occurrence of the family as a fossil. This family, with the Armadillidae and Armadillidiidae, represent the most highly evolved group of conglobating forms within the Oniscoidea. Forms described from an older horizon, the Eocene-Oligocene Baltic Amber, all belong to the more primitive families Oniscidae, Porcellionidae and Trichoniscidae. The Armadillidiidae represented by *Armadillidium molassicum* (Heer, 1865) is found in the Miocene of Oeningen. The family Eubelidae is now essentially a family with a tropical distribution. The sole exception is *Sphaerobathytropa ribauti* Verhoeff, found in the central Pyrenees, but Vandel (1943) considered this species to represent a pre-glacial remnant fauna.

Fossil terrestrial isopods are rarely found and the handful of species so far described hardly allows a phylogeny to be erected which is backed up by fossil evidence. Edney (1960), however, supposed that the marine isopods left the sea via the littoral in the middle Mesozoic, whilst Vandel (1943 : table 2) proposed that the terrestrial forms were developed from the marine Cirolanidae. The latter are well represented in the fossil record (Jurassic-Recent) if the genus *Palaega* is accepted within this family, as suggested by Rathbun (1935) and Imaizumi (1953). Considering the world-wide tropical distribution of the Eubelidae and especially their occurrence in the Americas, Africa and southern India, the latest date for the establishment of the family is Albian, since it was at about this time that the Guinea-Brazil areas became separated (Maack 1969). Edney (1954, 1968) and Warburg (1968) have dealt in detail with the morphological and behavioural adaptations required to survive on land.

Systematic description

Order ISOPODA Latreille, 1817

Suborder ONISCOIDEA Latreille, 1803

Superfamily **PORCELLIONOIDEA** Verhoeff, 1918 [nom. transl. Morris herein, ex Porcellionidae Verhoeff, 1918] (=Pseudotracheata Vandel, 1960).

Vandel (1960:95) formalized the classification of the Oniscoidea. Unfortunately in the tribe Crinocheta the two family group names that he chose, Atracheata and Pseudotracheata, were not based on an included nominate genus and are therefore invalid names under the Rules

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(Art. 11(e)). The replacement name for the Atracheata must be Oniscacea [nom. transl. Morris herein, ex Oniscia Rafinesque-Schmaltz, 1815: 101]. The new names are used in exactly the same sense as Vandel's (1960) replaced names and with the same included families.

Family EUBELIDAE Budde-Lund, 1899

Genus EUBELUM Budde-Lund, 1885

TYPE SPECIES. Eubelum lubricum Budde-Lund, 1885 by monotypy.

RANGE. Lower Miocene to Recent.

Eubelum rusingaense sp. nov. (Figs 1-11)

DIAGNOSIS. *Eubelum* with three-jointed antennal flagellum. Eyes with 17–19 ommatidia. Profrons folded onto vertex. Triangular escutcheon present. Shallow groove on coxopodite ridge of first pereion segment. *Schisma* and *sulcus arcuatus* present. Telson not divisible into two parts. Uropod protopodite almost completely fills space between the fifth pleonite and telson. Distal part of telson converging posteriorly.

LOCALITY AND HORIZON. Clark & Leakey (1951 : 9) locality R.1a from between Hiwegi Hill and the east coast of Rusinga Island, Lake Victoria, Kenya. The beds are of Lower Hiwegi Series, Lower Miocene age.

HOLOTYPE. BM(NH) In.61025

PARATYPES. In.61026–In.61070.

DESCRIPTION. Cephalon with convex profrons pushed up over the vertex and extending as a ridge along the frontal line. The frons is prominent with shallow lateral antennal grooves. Antennary tubercle raised into ridge; clypeus convex. There is a prominent median spine of the frontal lamina. Labrum strongly convex, rounded, triangular with the ventral portion bearing two strong laterally-directed ridges. A triangular escutcheon is developed. The mandibles are quadrate.

The anterior margin of the first pereion has a moderately sulcate margin and a straight posterior margin. The thickened coxopodite ridge of the epimeron of the first pereionite has a shallow ventrolateral groove. The epimeron is contiguous with the segment but the junction is marked by a deep *sulcus arcuatus* running parallel to and all the way along the lateral margin. A *schisma* is present and the internal lobe is the largest. The marginal edges of the second to fourth pereionites are rounded and thinned for their combined insertion into the *schisma* during enrollment. The fifth to seventh pereionite margins are squared off with a gentle lateral curvature. The pleonite segments are similarly squared off.

The telson is not divisible into two parts, having arcuate lateral margins and a gently rounded posterior margin. The uropod protopodite fills the space between the telson and the fifth pleonite. The body is capable of complete or nearly complete conglobation. There are sparse minute pits on the thoracic segments especially along the posterior bands of the segments. The abdominal segments are smooth. A few random granules may be present on the anterior part of the telson.

Figs 1–11. Eubelum rusingaense sp. nov. Lower Hiwegi Series, Lower Miocene of Rusinga Island, Kenya; all $\times 5$. 1, 2, anterior and left lateral views of holotype, In.61025. 3–11, paratypes. 3, ventral view of In.61026, to show triarticulate flagellum of left second antenna. 4, ventral view of In.61027, to show leg bases. 5, dorsolateral view of In.61028, to show ommatidia of right eye. 6, left lateral view of In.61029. 7, ventral view of In.61030, to show clypeus and schisma. 8, ventral view of In.61031, to show coxopodite ridge. 9, ventral view of In.61032, showing imperfect preservation of legs. 10, anterolateral view of In.61033, to show ommatidia of right eye. 11, anterolateral view of In.61034, to show partial enrollment.

Fig. 12. Eubelum ignavum Budde-Lund, 1899. Recent; 8000–9000 ft (2460–2775 m), Djem-Djem Forest, Ethiopia. Anterior view of BM(NH) Zool. Dept. no. 1949.2.2.235, ×5.





























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DISCUSSION. The isopods are preserved in the round in a semi-transparent calcite. They occur with other, as yet undescribed, arthropods especially insects and myriapods. The nearest relations to the fossil species are *Eubelum ignavum* Budde-Lund, 1899 and *E. dollfusii* Budde-Lund, 1899. *E. rusingaense* differs from *E. dollfusii* by its continuous frontal line across the cephalon. *E. ignavum*, which has a continuous frontal line, differs because the posterior part of its profrons is not pushed up onto the vertex and its eye has only 14–15 ommatidia. The distal portion of the telson of both the Recent species has parallel sides and is relatively wider than the fossil species. *E. rusingaense* does have some similarities with the type species *E. lubricum* Budde-Lund from Zaïre, Congo Republic and Cabinda (Angola) (Ferrara & Schmalfuss 1976) but the telson is not so convergent, the larger eyes have 23–24 ommatidia, the escutcheon is much less prominent but broader, and it differs in the shape of the supra-antennal line. Van Name (1920 : 85) compared *E. asperius* with *E. ignavum*, but Arcangeli (1950) made *E. asperius* the type species of a new subgenus *Pseudethelum*, based on the two-jointed flagellum of the second antenna. Ferrara & Schmalfuss (1976) went further and suggested that after a thorough revision of the genus the *asperius* group would warrant generic separation from *Eubelum* s.s.

Enrollment. The specimens from Rusinga are found in many degrees of enrollment, from a flat to a relaxed arched condition; six specimens show a nearly complete enrollment with only a slight gape between the frontal line and the pleotelson. The coxopodite ridge of the first pereionite is ventrally grooved but, although complete closure would seem possible, none of the specimens show contact between the groove and the squared-off margins of the epimera of the fifth to seventh pereionites and first to fifth pleonites. The face is flattened and the escutcheon is well developed. The method and order of enrollment appears to be as in Vandel (1943 : fig. 10). When straight, the specimens can protrude the cephalon by a hinged movement along the posterior margin of the cephalon.

REMARKS. Although terrestrial isopods are not dependent on an aquatic environment, they are poorly adapted to resist desiccation and super-saturation. Their habits are governed by the need to avoid excesses, although they will move along a hydrocline towards the saturation point. Since their transpiration rate is greater than their normal uptake of water, the difference between the two rates has to be made up from moist substances taken up by mouth or by water taken directly through the body wall (Edney 1954). Their moisture requirements can be satisfied by a number of habitats, consequently isopods are not indicative of any particular one. E. rusingaense probably lived in a damp montane forest litter, but could have lived in moist open grassland, under stones or near a water margin. The genus Eubelum in East Africa is, today, confined to montane forest at fairly high altitudes, certainly above 2000 m, where there is a relatively high annual precipitation rate. The nearest modern relatives of E. rusingaense, E. ignavum and E. dollfusii, have so far only been found in the Ethiopian highlands between 7000 ft (c. 2150 m) and 9000 ft (c. 2775 m) in montane forest litter near water margins (Barnard 1940: 365). Rusinga Island lay, before the Miocene, within the Kavirondo rift valley system at about 4000-4500 ft (1300-1350 m) (Shackleton 1951, Pulfrey 1960, Bishop & Trendall 1967). Andrews & Van Couvering (1975) deduced that the pre-uplift elevation of the sub-Miocene remnant surface was at about 1500 m. They further note that this is the lower limit of the montane forest. Their analysis of the fauna showed no clear predominance of any vegetational type, but indicated that large tracts of forest occurred in the immediate vicinity. If the distribution of the East African isopods was climatically controlled in the Miocene as it is now then the surface would have been at a somewhat higher altitude than has been previously suggested, i.e. within the montane forest belt at about 2500 m. Eubelum is not confined to the highlands of East and central Africa but occurs in the lowlands of West Africa. However, these largely belong to the asperius group, that is now thought to be generically separable from Eubelum s.s. Furthermore, Vandel (1945: 226) considered that lowland species represented recent immigrants, whilst highland species were those that remained near the autochthon. This suggestion is supported by the close relationship between the new species and the Recent indigenous species.

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