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The Biogeography of Somalia

Stygobitic Isopods of East Africa (*)

GIUSEPPE MESSANA
«Centro di Studio per la Faunistica ed Ecologia Tropicali», via Romana 17, 50125, Florence Italy

SUMMARY

In Africa, and in East Africa in particular, freshwater isopods are exclusively subterranean. The fauna of subterranean waters from this region, although not as rich and varied in isopod species as temperate areas, includes a good number of strictly stygobitic isopods from karst environments, no riverine interstitial species, and is well represented by marine interstitial forms.

From the beginning of the century to date, 6 species of 2 genera of the family Stenasellidae, *Stenasellus* and *Acanthastenasellus*, and 3 species of 2 genera of Cirolanidae, *Skotobaena* and *Haptolana*, have been discovered in the karst environment of Somalia, Kenya, Ethiopia and Tanzania. Marine interstitial isopods are represented by 2 species, one from the family Microcerberidae and the other from the Janiropsidae. Stygophilic and stygoxene isopods are completely absent from continental waters, and are present only in some coastal caves of Kenya with one cirolanid species of the widely distributed marine genus *Annina*.

The author discusses the present distribution of the isopod families Cirolanidae and Stenasellidae in the subterranean waters of East Africa and offers some considerations on the colonization and zoogeographic connections with isopods from other regions. The presence of species of Stenasellidae which have undergone a different morphological evolution from the other species of the family in the region is explained by the presence of stygobic fishes living in the same phreatic layer. The cohabitation of cirolanids and stenasellids in the same localities, together with a distribution which matches the coast-line of ancient seas, leads to the hypothesis of a simultaneous invasion of subterranean waters directly from the sea.

In tropical Africa, particularly in the eastern areas, aquatic isopods occur exclusively in subterranean waters. The limited amount of information on isopods from superficial waters all refers to marine isopods, usually sphaeromatids (e.g. *Dynamenella*) which ascend the River Congo estuary (Brian & Dartevelle, 1949), and to cymothoids of the genera *Ichthyoxenus* and *Lironeca*, both parasites of characid and cichlid fish (Fryer, 1956; Trilles, 1976, 1979; Avdeev, 1984), but nothing exists on fresh water, free-living forms. This situation seems to be the rule for most tropical regions. Moreover, the few limnic species to be found in temperate regions can almost be considered as accidental, restricted as they are to a few genera of Asellidae in Europe and North America, and to a few reported species of the Janiridae family in South America and South Africa (Bowman et al., 1987; Grindley, 1963).

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No satisfactory explanation has yet been offered as to why isopods or amphipods (Ruffo, personal communication; Williams, 1986) have failed to colonize the inland waters of Africa. Their absence from these areas is rather strange, considering that the Sahara, Somalia and Ethiopia were submerged during the Cretaceous, although the hydro-geological situation in the rest of Africa has remained fairly stable since Pre-Cambrian times, with vast sedimentary basins periodically connected to each other and with the sea. Only East Africa, once emerged, has been shaped from the Miocene onwards by tectonic movements, whilst moderate orogenic compressions have affected South and North Africa (Beadle, 1974).

The discovery of isopods in the underground waters in East Africa is not new — in 1914 Alluaud and Jeannel had already reported numerous specimens of a species of cirolanid isopod, *Annina lacustris* Budde Lund, 1908, in coastal caves of Kenya and Tanzania. In this case the isopods were not true stygobites, but marine forms which, favoured by the tidal patterns of the Indian Ocean and their ability to adapt to the environment, had begun to colonize a new habitat. In 1932, the «Mission scientifique à l'Omo» led by Arambourg (Arambourg et al., 1935) reported a number of other isopods, but unfortunately all trace of these specimens is lost. Nothing more was heard about stygobitic isopods of East Africa until 1966, with the publication of the description of *Stenasellus pardii* Lanza, a species from water-holes in south-central Somalia. Since then, 12 other species of isopods from subterranean waters have been described, belonging to 7 genera of the Cirolanidae, Stenasellidae, Microparasellidae and Microcerberidae families. The last two families are interstitial marine and will not be treated in detail in the present paper (for a list of the species and their distribution see Messana & Chelazzi, 1986).

CIROLANIDAE

This family comprises approximately 40 genera, 17 of which are stygobitic. In spite of considerable contributions from several authors over the last few years (Botosaneanu et al., 1986; Bowman, 1975; Bruce, 1981, 1986), the taxonomy of the family is still much confused. The stygobitic forms have colonized subterranean waters in Mediterranean and Caribbean regions and in tropical East Africa (Fig. 1). In East Africa itself the family is represented by one marine genus, *Annina* Budde-Lund, 1908 (sub-family Eurydicinae), which in this context can be considered as stygoxene, and by two strictly stygobitic genera, *Haptolana* Bowman, 1966 and *Skotobaena* Ferrara & Monod, 1972, belonging to two distinct groups of the Cirolaninae sub-family (the Cirolana and Faucheria groups respectively).

Annina lacustris (Fig. 2c), is a marine form which generally lives under drift wood in the intertidal zone. Its presence in the underground world is limited to a few coastal caves of Kenya and Zanzibar, and is a good example of active colonization of a subterranean habitat. Morphologically, *A. lacustris*

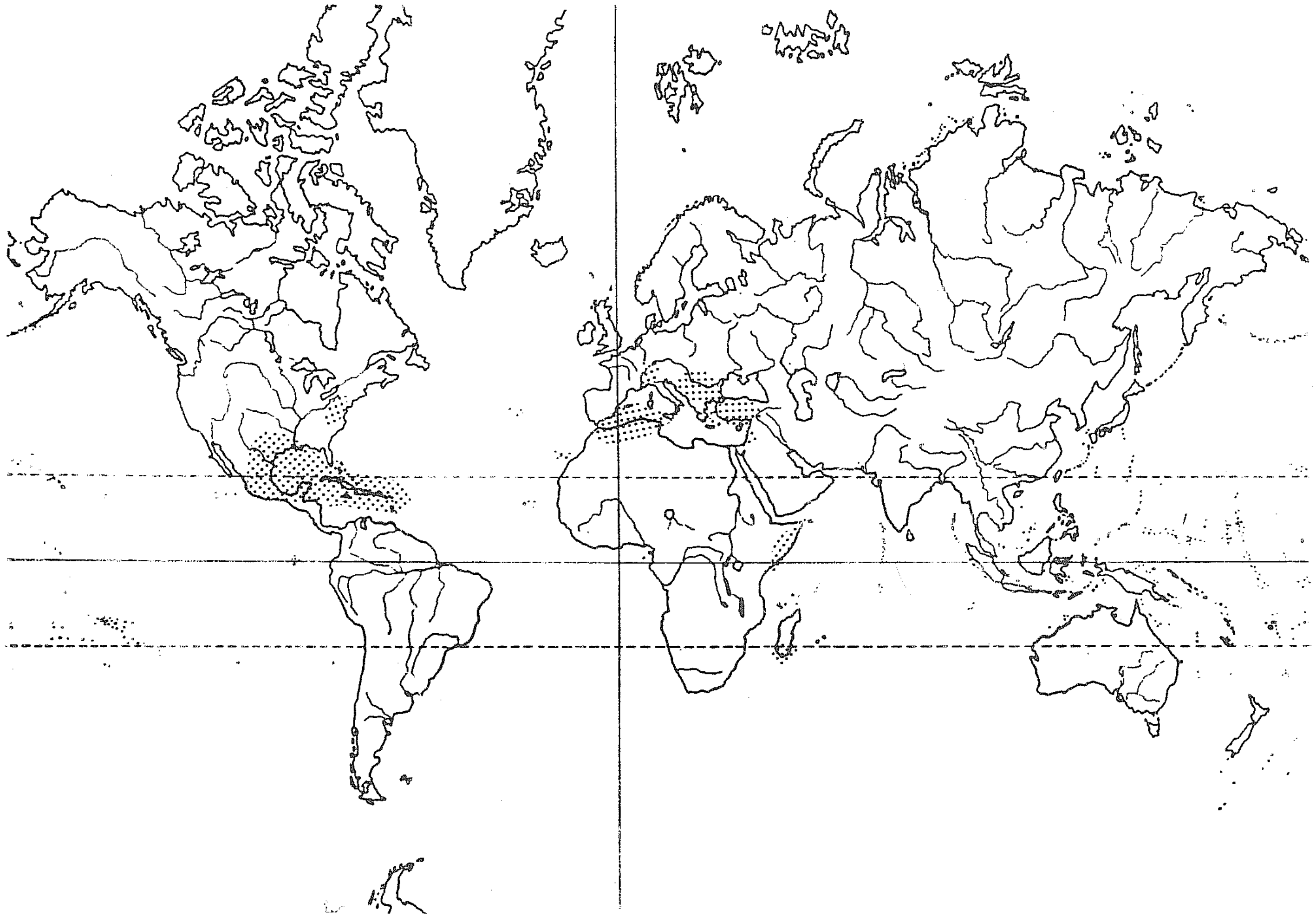

FIG. 1 - Distribution of the Cirolanidae in continental subterranean waters.

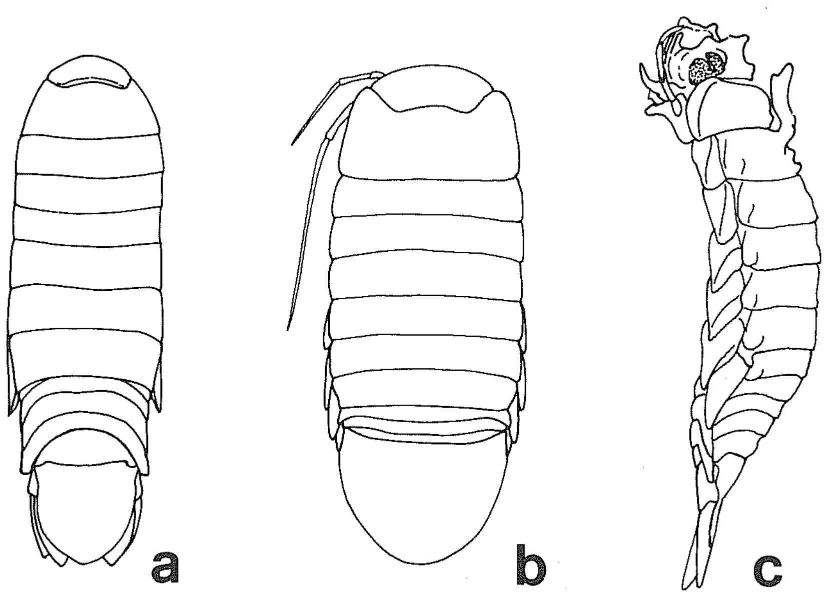

FIG. 2 - Subterranean Cirolanidae of East Africa: a) *Haptolana somala*; b) *Skotobaena monodi*; c) *Annina lacustris* (side view).

is not particularly adapted to the subterranean environment — but it is ovoviviparous, which is of prime importance. Ovoviviparity has only been reported in this genus (Klapow, 1970; Bowman, 1971; Messana 1984) and perhaps evolved as a protection for the offspring of intertidal species against their harsh environment. This characteristic is obviously of great advantage in conquering habitats where the salinity, different from the original, is liable to change dramatically over short periods of time.

Only two species of the genus *Haptolana* have been described, one from Somalia (*H. somala* Messana & Chelazzi, 1984) and the other from Cuba (*H. trichostoma* Bowman, 1966), both subterranean and which in all probability could be attributed to two different genera (Messana & Chelazzi, 1984). *Skotobaena*, on the other hand, is a genus endemic to the Horn of Africa, and comprises two species, *S. mortoni* Monod, 1972 and *S. monodi* Ferrara & Lanza, 1978. Morphologically, the two genera are quite different. *Haptolana somala* (Fig. 2a) has five free pleonites, a long, sharp mandible, seven pairs of subchelate legs and a glabrous endopodite on pleopods 3-5, a very hairy exopodite, and it closes itself up like a pen-knife, not into a ball. Its seven prehensile peraeopods give the impression that this species feeds by micropredation — a common characteristic in Cirolanidae species (Bruce, 1986) — on the fish *Barbopsis devecchii* Di Caporiacco, 1926 (Cyprinidae) or the decapod Athyidae *Caridina lanzana* Holthuis, 1980, with which it shares the same water-holes in the Wadi Nougal valley of North Somalia. The two *Sko-*

tobaena (Fig. 2b) have only three free pleonites, and a strong, stout mandible. The last four pairs of legs are walking legs, and the pleopods have only a few short setae. Observations in the field and on live animals kept in the laboratory suggest it is a grazing species (probably feeding on microorganisms it finds on the rocks and in the mud), and a highly specialised detritivore adapted to hypogean life, capable of moderate volvation, but a poor swimmer. *S. monodi* can be found in many localities throughout central and southern Somalia, and *S. mortoni* in one locality in Ethiopia. The fact that two distinct species of *Skotobaena* exist in Eastern Africa – inhabiting zones among the first to emerge in that area – which both have highly specialised characteristics (massive reduction of pleopod setae, reduced number of free pleonites, volvation etc.) suggests that this genus may well have colonized subterranean waters long before *Haptolana* did.

STENASELLIDAE

The strictly stygobitic Stenasellidae family lives in Central America, the Mediterranean and Balkan areas, and in the Oriental and Afrotropical regions (Fig. 3). Two genera of the family can be found in the Horn of Africa, *Stenasellus* Dollfus, 1987 and *Acanthastenasellus* Chelazzi & Messana, 1987 (Fig. 4 a-f).

The monospecific genus *Acanthastenasellus* (Fig. 4 f), endemic to Somalia, shows remarkable modifications of peraeonites I-VII. It is an extremely spiny looking genus, due to lateral expansion of the tergites, and at the same time is very hard and strong on account of heavy calcification of the sternites. Modification of the appendices, however, has resulted in reduction of the endopodite and in longer uropod expodites, and has affected the size of the basipodite of pereiopods II-VII and the number of spines on the dactylopodite of pereiopods II-VII. As far as the other characteristics are concerned, *Acanthastenasellus* does not differ much from the genus *Stenasellus*, although it should be remembered that differential analysis was conducted on female characteristics, since no male specimen was available.

The genus *Stenasellus*, with 25 species described in the world, is represented by five species in the Horn of Africa (*S. agiuranicus* Chelazzi & Messana, 1987; *S. costai* Lanza, Chelazzi & Messana, 1970; *S. kenyensis* Magniez, 1974/75; *S. migiurtinicus* Messana, Chelazzi & Lanza, 1974; *S. pardii* Lanza, 1966), which are all similar (Fig. 4 a-e). One of the species, however, *S. pardii* (Fig. 4 e), differs markedly from the rest by having the peculiar characteristics of a species adapted more to an interstitial habitat than to a karst environment like the others. It is extremely small with short antennae and uropods and with only a few sternal spines on the dactylus of the ambulacral peraeopods. As mentioned above, this last character is also present in *Acanthastenasellus*, and according to Magniez (1985) is apomorphous in the family.

It is interesting to note that the two species of Somalian Stenasellidae

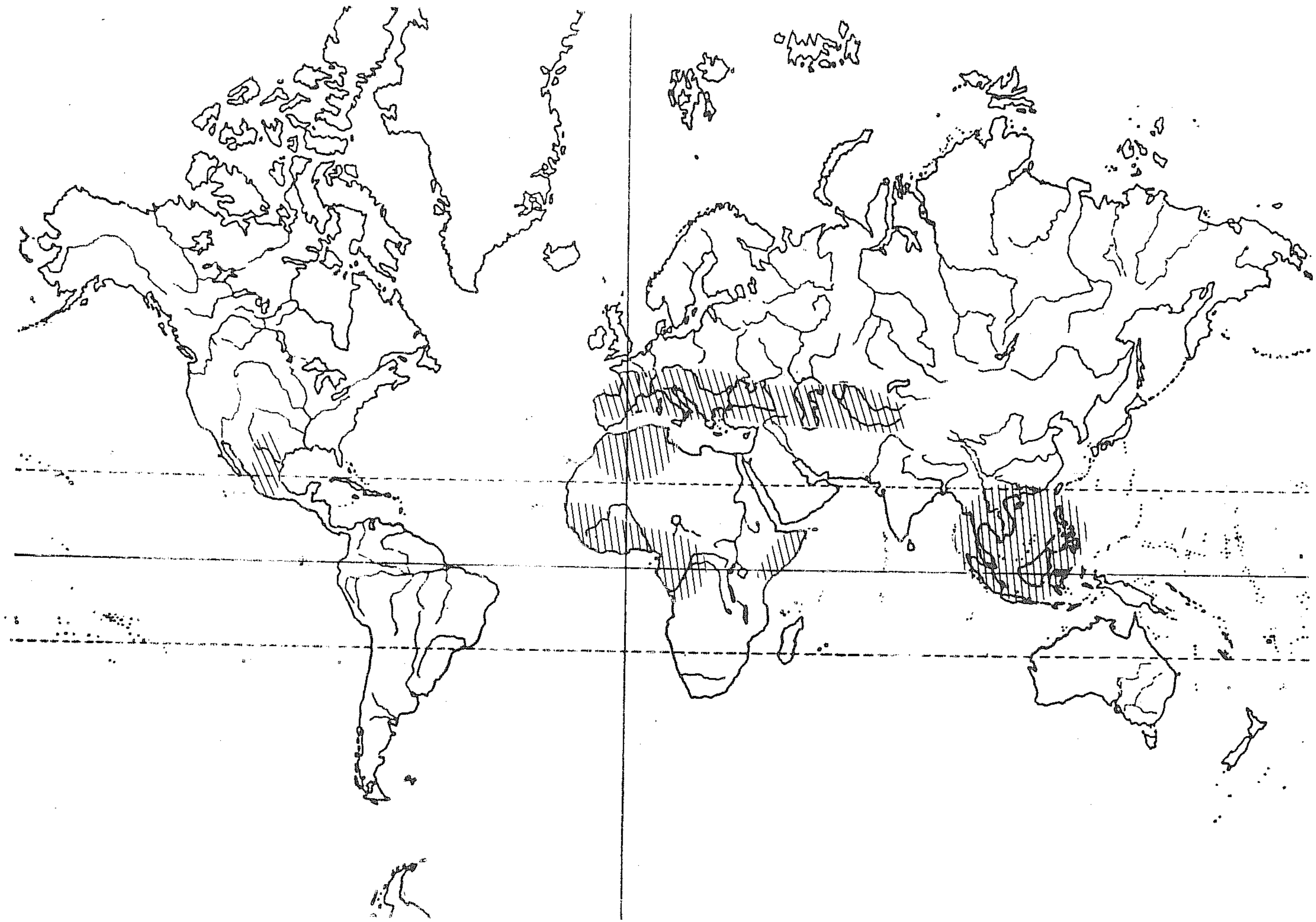

FIG. 3 - Geographical distribution of the Stenasellidae.

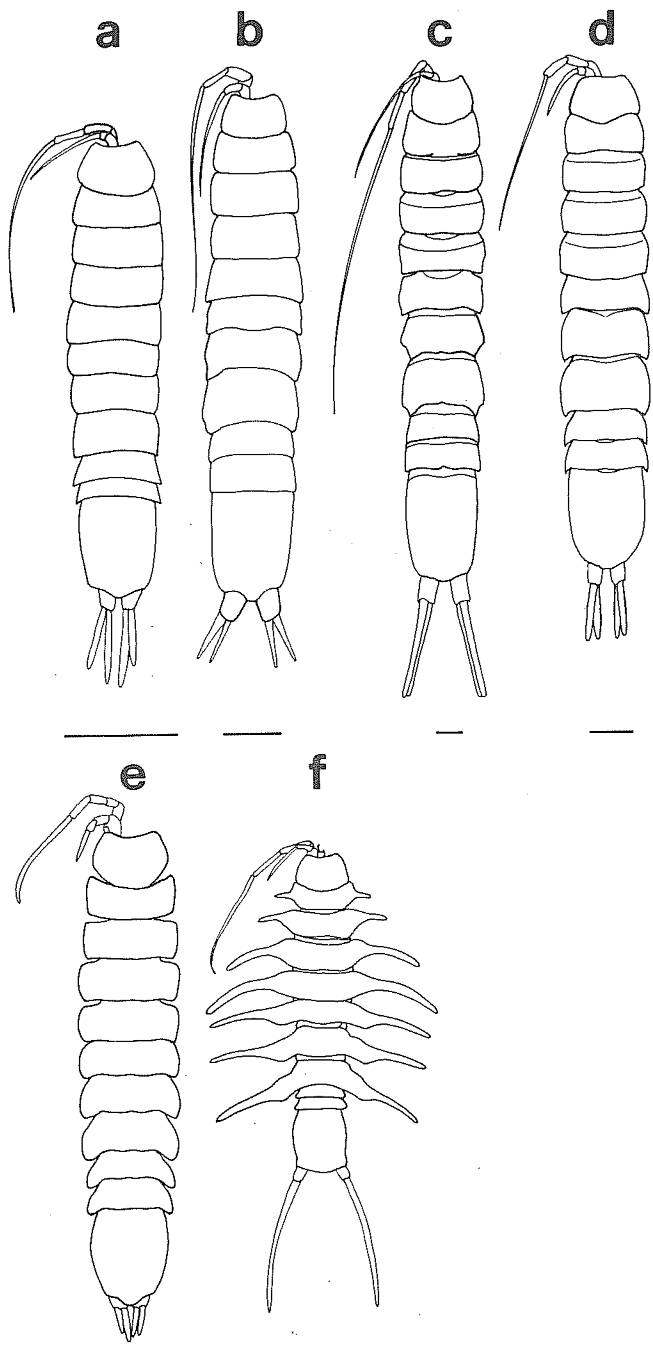

FIG. 4 - East African Stenasellidae: a) *Stenasellus kenyensis*; b) *S. agiuranicus*; c) *S. costai*; d) *S. migiurtinicus*; e) *S. pardii*; f) *Acanthastenasellus forficuloides*. Each line represents 1 mm.

whose characteristics easily distinguish them from the others, and which are the most evolved stygobitically (*Acanthastenasellus forficuloides* and *Stenasellus pardii*), are found in the same strata as two of the three species of Somalian stygobitic fish (*Phreatichtys andruzzii* and *Uegitglanis zammaranoi*). As none of the other stenasellid from karst formations in the area show any special adaptations, it seems reasonable to suppose that these two species evolved after the arrival of the ancestors of modern stygobitic fish in Somalian underground waters, by choosing two different defence strategies to cope with the pressure: behavioural in *S. pardii*, by assuming or reverting to interstitial life, and morphological in *A. forficuloides*, by protecting itself with a fearful armour.

The arrival of fishes coming from the Oriental regions — at least the Clariidae — in African waters dates back to the Pleistocene (Thinès, 1969), and consequently *S. pardii* must have begun its evolutionary differentiation during this period, which demonstrates the capability of rapid evolution of the Stenasellidae. The history of colonization of underground waters by the family has been outlined by Magniez (1966, 1974, 1981, 1983), who claims it derived from a common ancestor which inhabited the epicontinental seas of the Lower Cretaceous (Fig. 5a) and followed an interstitial route to colonize the subterranean waters, first occupying underground river systems and then finally reaching the karst waters of adjacent areas. Certainly the tropical and sub-tropical species of Stenasellidae all seem to exhibit the characteristics of forms adapted more to a karst environment than to an interstitial one. Especially in East Africa, almost all the species are to be found in a karst environment, with the exception of *Stenasellus pardii* which probably occupied the interstitial habitat after the arrival of predators. From a preliminary analysis, the interstitial species in the rest of the world seem to be restricted to the temperate zones.

As the present distribution of the Stenasellidae matches the coast-line of late Cretaceous marine ingressions (Beadle, 1964; Furon, 1968; Merla et al., 1979), and as no isopod or amphipod species — as stated before — is to be found in continental waters of regions never submerged by the sea, it would appear that the various species of Stenasellidae from the Horn of Africa, and perhaps from elsewhere too, colonized the karst waters of the continent, together with other crustaceans, directly from the ancient seas (Fig. 5b). Only later, under various types of pressure (predation in the case of East African species), did they colonize the waters of interstitial aquifers.

This view is supported by the simultaneous presence in the underground waters of continental East Africa of the two Cirolanidae and Stenasellidae families, whose world wide distribution have many features in common (Fig. 1 and 3). In East Africa in particular, distribution of the various species of the two families is very similiar, *Stenasellus, Skotobaena* and *Haptolana* can often be found in the same phreatic layer (Fig. 6). Thus strenghtening the hypothesis that the Stenasellidae and at least the more «stygobitically evolved» Cirolanidae, such as *Skotobaena*, colonized the subterranean waters during the same period.

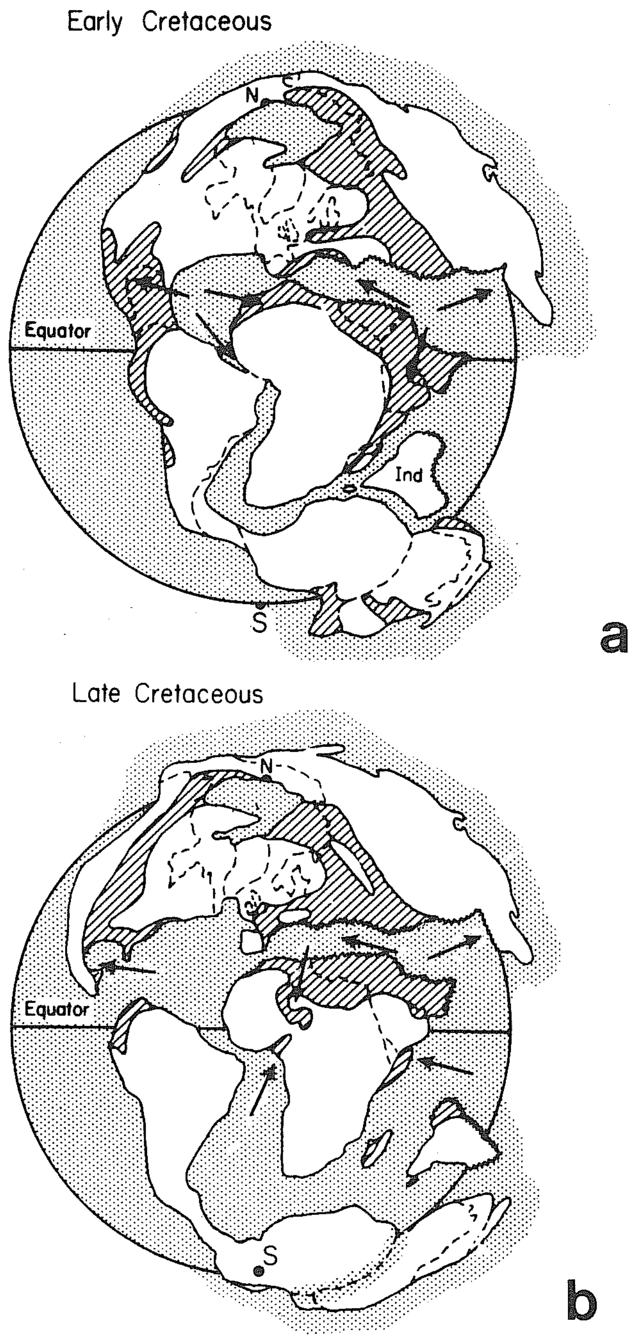

FIG. 5 - Probable colonization routes taken by ancestors of present day Stenasellidae. Hypothesis of origin in Lower Cretaceous (a), or Upper Cretaceous (b).

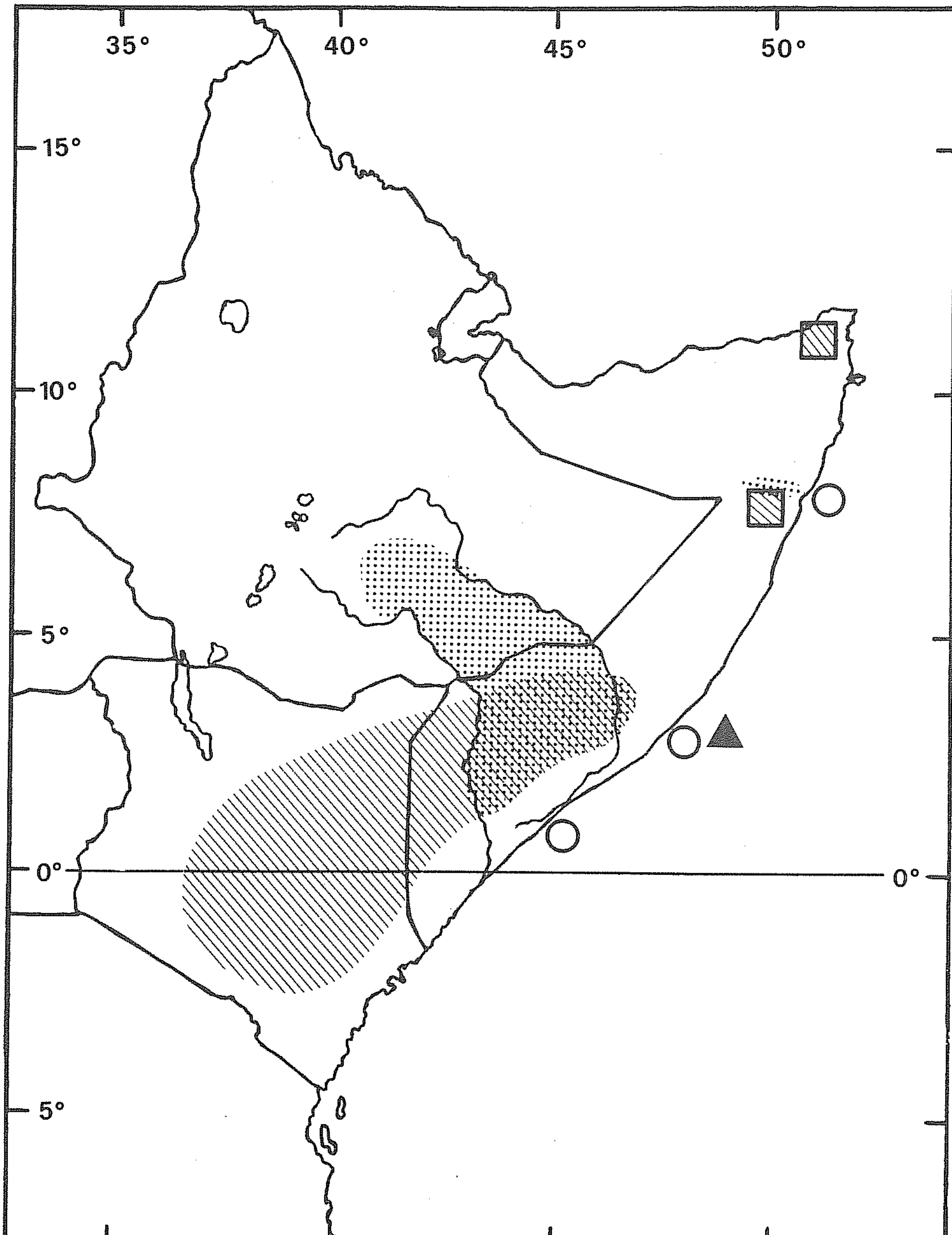

FIG. 6 - Distribution of stygobitic isopods in East Africa. Dotted areas: *Skotobaena*; hatched areas: Stenasellidae, white circles *Angeliera* sp.; black triangles: *Microcerberus anfindicus*.

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