PALEOBIOLOGY OF MESSEL ERINACEOMORPHS

by

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CONTENTS

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Key-words: Lipotyphla, Erinaceomorpha, Middle Eocene (MP 11), Grube Messel, Germany, Paleobiology.

Mots-clés: Lipotyphla, Erinaceomorpha, Eocène moyen (MP 11), Grube Messel, Allemagne, Paléobiologie.

Palaeovertebrata, Montpellier, Vol. jubil. D.E. Russell (M. Godinot & P.D. Gingerich Eds.), **25** (2-4): 215–224, 2 pl.
(Reçu le 25 Février 1994, accepté le 12 Octobre 1994, publié le 16 Décembre 1996)

ABSTRACT

Three erinaceomorph species are known from the early Middle Eocene of Grube Messel near Darmstadt, Germany, which are referred to the family Amphilemuridae. *Pholidocercus hassiacus*, *Macrocranion tupaiodon*, and *Macrocranion tenerum* showed extraordinary adaptations to their different life strategies, and several of their specializations are unknown among living insectivores. *Pholidocercus* was a well-defended robust animal with an opportunistic feeding strategy. *Macrocranion tupaiodon* was a slender forest floor-dweller with saltatorial specializations to escape from predators; fishes were the preferred component of its omnivorous diet. *Macrocranion tenerum* exhibited a combination of both survival strategies, extremely elongated hind limbs for rapid and even ricochetal flight and a spiny exterior as an effective protective device; it was probably specialized for feeding on ants. Thus, closely related, omnivorous-insectivorous forest floor-dwellers could exploit the Messel ecosystem.

ZUSAMMENFASSUNG

Aus dem unteren Mitteleozän der Grube Messel bei Darmstadt, Deutschland, sind 3 Erinaceomorphen-Arten bekannt, die zur Familie Amphilemuridae gestellt werden. *Pholidocercus hassiacus*, *Macrocranion tupaiodon* und *Macrocranion tenerum* lassen außergewöhnliche Anpassungen an unterschiedliche Lebensstrategien erkennen, und manche der Spezialisationen sind von heutigen Insektenfressern nicht bekannt. *P. hassiacus* war ein gutgeschütztes, robustes Tier mit einer opportunistischen Ernährungsweise. *M. tupaiodon* war ein schlankes Tier mit saltatorischen Spezialisationen für rasche Flucht vor Räubern; Fische machten einen herausragenden Anteil der omnivoren Nahrung aus. *M. tenerum* verfügte über eine Kombination der Überlebensstrategien der beiden anderen Arten: extrem verlängerte Hinterbeine für schnelle und wendige, gelegentlich wohl auch biped-hüpfende Flucht und ein Stachelkleid als wirkungsvolle Schutzeinrichtung; wahrscheinlich ernährte sich die Art von Ameisen. Nahverwandte, omnivor-insectivore Waldboden-Bewohner konnten so das Messeler Ökosystem ausnutzen.

RESUME

De l'Eocène Moyen de la fosse de Messel près de Darmstadt, Allemagne, trois espèces d'érinacéomorphes sont connues. Elles sont placées dans la famille des Amphilemuridae. *Pholidocercus hassiacus, Macrocranion tupaiodon* et *Macrocranion tenerum* montrent des adaptations extraordinaires à leurs différents modes de vies, et plusieurs de leurs spécialisations sont inconnues chez les insectivores actuels. *Pholidocercus* était un animal robuste, bien protégé, et présentant un régime alimentaire opportuniste. *M. tupaiodon* était un animal léger, avec une spécialisation au saut pour échapper aux prédateurs; des poissons constituaient une large part de son régime alimentaire omnivore. *M. tenerum* présentait une combinaison de ces deux stratégies de survie: des membres postérieurs extrêmement allongés pour une fuite rapide, vraisemblablement bipède, et une couverture de piquants comme protection efficace; il se nourrissait probablement de fourmis. Ainsi, ces habitants du sol forestier, étroitement apparentés et omnivores-insectivores, pouvaient exploiter l'écosystème de Messel.

INTRODUCTION

Erinaceomorpha is a suborder of the Lipotyphla or Insectivora sensu stricto. Aside from hedgehogs, living lipotyphlan insectivores include shrews, moles, golden moles, tenrecs, and solenodons. The radiation of lipotyphlans was well underway by early Paleogene time and probably began in the Late Cretaceous. Whether a taxon like *Paranyctoides* FOX, 1979 from the Upper Cretaceous of North America was a member of an already definable order Lipotyphla or even represents the earliest known member of the lipotyphlan suborder Erinaceomorpha (see Fox 1984, Carroll 1988) has yet to be established. *Adunator* RUSSELL, 1964 is considered the most primitive and most generalized known genus of the Erinaceomorpha by Butler (1988). This genus was first described by D.E. Russell (1964) from the Paleocene of Walbeck in Germany and Cernay-lès-Reims in France, and the very closely related genera *Mckennatherium* VAN VALEN, 1965 and *Diacocherus* GINGERICH, 1983 from the Paleocene of North America probably can be included in *Adunator* (Bown & Schankler 1982, Novacek *et al.* 1985).

Erinaceomorphs are a critical group for our understanding of insectivore and eutherian phylogeny. They take a basal position within Lipotyphla and hedgehogs (Erinaceidae) as the only extant family have retained a suite of primitive eutherian characters. Erinaceomorphs were frequently considered as either ancestors or close relatives of various major groups of eutherians, including bats, primates, tupaiids, dermopterans, and condylarths. Early Paleogene erinaceomorphs, in particular, show many features that suggest potential relationships with a wide variety of taxa. The suggestion that primates took their origin from Erinaceomorpha has been repeatedly raised by paleontologists (cf. Novacek 1985, MacPhee *et al.* 1988). Most of these discussions on erinaceomorph relationships are based exclusively on dental morphology, however, for the simple reason that most early Paleogene taxa are known only from isolated teeth or dental fragments. Their fossil record is rich compared to most other insectivore families, and erinaceomorphs are rather abundant in most early Tertiary European, Central and East Asian, and North American faunas. Despite this, the number of available morphological characters is limited and they are restricted to only one functional system, the masticatory apparatus. Thus convergent traits to other eutherian groups are sometimes hard to judge. Further problems in assession relationships arise from the subtle differences in tooth characters in many early Paleogene insectivores and other eutherian mammals. In my opinion, reliable phylogenetic conclusions require the assessment of a wide variety of biological adaptations and therefore an extraordinary preservation of fossils. Grube Messel near Darmstadt, Germany, is reknowned for the diversity and completeness of its mammalian fossils, and it seems worthwhile, then, to report on the paleobiology of its erinaceomorphs. Reliable systematic allocations and paleobiological reconstructions of the Messel animals and plants will ultimately contribute to the reconstruction of an early Paleogene terrestrial ecosystem.

The site is a former opencast oilshale mine. The fossiliferous sediments were deposited about 50 my ago — during the early Middle Eocene (= MP 11) — into a freshwater lake of tectonic origin. For some hundreds of thousands of years the lake acted as a depository for a rich fauna and flora flourishing under tropical to subtropical climatic conditions. Complete mammalian carcasses sank to the lake bottom where anoxic conditions and very weak water currents prevented them from being disintegrated and dispersed. As a result, mammalian fossils are largely complete and articulated, and many of them even have the outlines of the soft body and the gut contents preserved (see Schaal & Ziegler 1992 for synopsis).

THE MESSEL ERINACEOMORPHS

Three erinaceomorph species are known from Messel: *Macrocranion tupaiodon* WEITZEL, 1949, *Macrocranion tenerum* (TOBIEN, 1962), and *Pholidocercus hassiacus* KOENIGSWALD & STORCH, 1983. *Macrocranion* is currently referred to the family Dormaaliidae QUINET, 1964 (= essentially the adapisoricids of former classifications) and *Pholidocercus* to the Amphilemuridae HELLER, 1935 (Koenigswald & Storch 1983, Novacek *et al.* 1985, MacPhee *et al.* 1988). Dormaaliids and amphilemurids are, however, probably closely related (see also Novacek 1985, Hooker 1986) and I now prefer to assign all Messel species to a single family, to which the name Amphilemuridae has to be applied. In any case, the allocations involve several issues, since Butler (1988) recently questioned the inclusion of *Macrocranion* and amphilemurids among erinaceomorphs and lipotyphlan insectivores on the whole. Moreover, amphilemurids have been frequently classified in the past as primates. The complete Messel specimens thus have an important bearing on these contrasting views about systematics and classification, too.

PALEOBIOLOGICAL RECONSTRUCTIONS

I will consider mainly defence and feeding strategies, including defensive structures, modes of locomotion, specializations for the handling and ingestion of food items, and analyses of gut contents.

Dixon (1982) made a prediction about the protective adaptations of living erinaceine hedgehogs 50 my in the future. The spiny cover would develop into more effective rims and would become perfectly arranged to roll up. If we would follow these adaptive trends back in time in general, an erinaceomorph 50 my ago — the period when the Messel mammals were thriving — would show only incipiently particular defensive devices. This illustrates frequently held views on mammalian phylogeny: The continuous improvement of particular adaptations known from living, more or less closely related animals is assumed, and from the primitive dental characters of many early eutherian groups a primitive general bauplan of the animals is concluded. We should consider, however, that erinaceomorphs in general had time enough for adaptive radiations prior to the early Middle Eocene, that the tropical-subtropical Messel ecosystem comprised a vast variety of niches, and that adaptations known from living mammals are not necessarily the best and only ones possible.

Pholidocercus hassiacus

(Plate 1, fig. 1; Plate 2, fig. 2)

Pholidocercus hassiacus, the scaly-tail, was originally described on the basis of 5 specimens (Koenigswald & Storch 1983). Of particular interest regarding alleged primate-erinaceomorph relationships was the basicranium of an isolated skull, a type of preservation that is rarely found at Messel (MacPhee *et al.* 1988).

Pholidocercus, like living erinaceines, trusted in defense and protection from predators. It is a robust animal of about 19 cm head and body length and 16-20 cm tail length. The legs are relatively short. The tail is surrounded by a tube of dermal ossifications which overlap like tiles. Dermal ossifications forming a protective cover are unknown from living insectivores. The nasal and frontal bones show a sharply delimited field of deep vessel indentations which suggests a cover by a horny plate or leathery callus on the forehead. These features, too, are probably part of the defensive strategy of *Pholidocercus*, but similar structures can also be found in mammals which dig with their nose and forehead for food. The outline of the pelage on the back exhibits relatively long and possibly rather stiff bristles. The large terminal phalanges of hands and feet are deeply cleft and they obviously were equipped with strong horny claws. We can thus conclude a well-defended, ground-dwelling animal which moved on all fours and was an able scratch-digger (Koenigswald & Storch 1983, Koenigswald *et al.* 1992).

The dentition clearly indicates an omnivorous diet. The decidedly bunodont and inflated molars and fourth premolars suggest a large proportion of rather soft food items like various insects and fruit pulp. I^1, C^1, and P_1 are slightly enlarged and otherwise the antemolar dentition shows only little differentiation. This would also indicate insects or other small invertebrates as the preferred animal food component. Seizing and killing larger or hard-scaled prey items would require a much more differentiated antemolar dentition.

The gut contents of three specimens are preserved and confirm these conclusions. In two specimens thin insect cuticles predominate, while in the third plant remains prevail. In all of the investigated specimens, the plant remains consist of lumps of large cells with very thin walls, probably of pulpy fruits, and of leaf tissue. Most of the insect chitin cuticles are thin, packed in thick layers, and bear a surface pattern of delicate scales. Some coarser cuticle fragments are obviously from beetles but most of the insect remains are not yet determined. *Pholidocercus* thus shows an opportunistic feeding strategy, similar to living hedgehogs.

Macrocranion tupaiodon

(Plate 1, fig. 2; Plate 2, fig. 3)

Weitzel (1949) described *Macrocranion tupaiodon* on the basis of a few poorly preserved specimens. At that time no suitable preparation techniques for the Messel fossils were known. Tobien (1962) considerably increased our knowledge about tooth morphology and the systematic context. Maier (1977, 1979) studied several virtually complete specimens and concluded essential biological adaptations of the animals. *M. tupaiodon* is among the most abundant Messel mammals, apart from bats.

Macrocranion tupaiodon represents a different adaptive type than *Pholidocercus*, and may best correspond with living hairy hedgehogs (Hylomyinae = Echinosoricinae). It is a slender animal of about 16 cm head and body length and 12-15 cm tail length. It shows cursorial adaptations for rapid flight from predators. The hind limbs, in particular the tibia and metatarsals, are conspicuously elongated and bear strong muscle attachments. In both hands and feet the first and fifth digits are much shortened and all terminal phalanges are short and blunt. Metatarsals II-IV are long. The shape of the terminal phalanges and the closely joined metatarsals suggest strictly ground-dwelling habits. The skull is rather pointed and most likely was equipped with a fairly short and mobile muzzle, due to attachments of facial muscles just in front of the orbit. The orbits are very small. In some specimens the soft body outlines reveal relatively large ears and in one case even long tactile hairs on the muzzle. The pelage on the back is short and wooly (see Wuttke 1992) and the tail is naked. *M. tupaiodon* can thus be characterized as a swift nocturnal forest floor-dweller. It was a fast quadrupedal cursor and could escape from predators by a jumping mode of locomotion. The animal had very acute tactile, olfactory, and acoustic senses to assess its orientation (Maier 1977, 1979, Koenigswald *et al.* 1992).

From the dentition we can conclude omnivory as in *Pholidocercus*. However, the bunodont specializations of the molars are somewhat less distinct and the upper canines are somewhat more enlarged than in *Pholidocercus*. This would indicate a larger animal component of the diet.

Quite a large number of preserved gut contents reveal fish as a favorite dish. Some gut contents consist exclusively of fish remains (ribs, fin rays, vertebrae, skull fragments) and thus the animals must have foraged along the edge of the former Messel lake — which may explain their abundance in the mammalian fauna. All other specimens contain relatively small amounts of insect cuticles. Besides, plant remains play an important role in the gut contents. They consist mainly of fragments of seed shells and lumps of tissues, probably from fruits. Seeds predominate among vegetable matters, but actually they may constitute only parts of ingested pulpy fruits. The gut contents of one specimen consists only of seeds, probably of *Rutaspermum* sp. (Rutaceae) (see Collinson & Gregor 1988). Remains of leaves, stalks, and fungus are very rare. *M. tupaiodon* thus was an omnivore with an emphasis on animal food and a particular specialization for fish. The lack of obvious swimming adaptations suggests that it did not dive for fish in the open water, but rather hunted along the lakeside and pools or else simply scavenged fish carcasses.

Macrocranion tenerum

(Plate 2, fig. 1 and fig. 4)

The third erinaceomorph species from Messel was originally described by Tobien (1962) as *Messelina tenera* on the basis of incomplete dental remains and the very poorly and incompletely preserved skeleton of the type specimen only. Later, it was transferred by Russell *et al.* (1975) to *Macrocranion* and this new allocation has been widely accepted. Recently, a virtually complete skeleton turned up which is extraordinarily well preserved; only the tail is lacking. This specimen was described by Storch (1993).

Macrocranion tenerum is a small and gracile animal of almost 9 cm head and body length with striking specializations. The skeleton shows basically a generalized bauplan including many plesiomorphic features. The hind limbs, however, exhibit various remarkable saltatorial adaptations. The hind-legs, in particular metatarsals II-IV, are extremely elongated, much more so than in *M. tupaiodon*. For example, the relative lengths of the hind limb segments (as a percentage of the thoraco-lumbar vertebral length) are clearly above the values for the elephant shrew *Rhynchocyon*, which escapes from predators by a rapid halfbound gait. They are below the values for various desert-dwelling gerbils, which are able quadrupedal saltators. But unlike these gerbils, the foot of *M. tenerum* is the longest hind limb segment, as in such ricochetal mammals as the jerboa *Allactaga* (Storch 1993). In a plot of the crural index (tibia:femur) against the brachial index (radius:humerus), *M. tenerum* and the springhare *Pedetes* coincide; *Pedetes* is also a ricochetal mammal. Morphological saltatorial adaptations include the long ilium with the strong spina anterior inferior, the long and well-developed third trochanter on the femur, the long and sharply defined groove for the patella, the extensively fused tibia and fibula, the large antero-lateral tibial crest, the extremely elongated metatarsals II-IV and reduced metatarsals I and V, the very short and blunt terminal phalanges, the long tuber calcanei, and the closely crowded digits. On the skull, the long infraorbital canal, the large infraorbital foramen, and a depression in front of the orbit suggest a mobile proboscis. The orbits are small. Smell was the predominant sense used for locating food, assisted by acute tactile and acoustic senses.

We thus can conclude a ground-dwelling, swift, and highly manueverable animal. It probably gathered food from the forest-floor rather than chase its prey, and thus a bounding gait likely served as a means of escaping from predators. Therefore, in its basic adaptations it seems to correspond with the larger *M. tupaiodon*. The well-preserved outline of the integument, however, reveals a major difference: The body of *M. tenerum* is covered with spines (or very strong bristles) similar to extant erinaceine hedgehogs. Such a combination of survival strategies — rapid flight and an efficient protective device — is unknown in any other living or fossil insectivore and is extraordinary for any mammal. *Macrocranion tenerum*, then, was a well-defended speedy animal with a jumping — and occasionally even ricochetal — mode of locomotion.

The dentition consists of only two major functional segments. The antemolar region in front of the fourth premolars is strikingly homodont and thus departs markedly from the primitive lipotyphlan condition. The simple, and with the exception of P^3, single-rooted teeth form continuous shearing edges on the upper and lower jaws. The posterior section includes the bunodont molars and fourth premolars and here grinding action certainly predominated over pure cutting action. The configuration of the dentition suggests the ingestion of preferably small and soft animal prey. Foraging on larger or hard-shelled food items would require the differentiation of the anterior dentition, for example the enlargement and sharpening of particular teeth for enhanced puncturing functions.

The rich gut contents of the single available specimen consist of small pieces of thin insect cuticles, which all have the same scaly surface design. Most probably these cuticles come from small social insects such as ants. There are no chitin scales and cuticles with a cover of false hairs. Therefore, we can exclude particular insect groups with aquatic larval states like caddis flies, may flies, and mosquitoes (Richter 1987, 1993). Thus, the gut contents suggest that *M. tenerum* visited the edge of the Messel lake only by chance. Plant remains are extremely rare. This individual lived exclusively on insects and we can predict an insectivorous diet for the species *Macrocranion tenerum* in general.

CONCLUSIONS

The extraordinary preservation of mammalian fossils from Messel, including articulated skeletons, soft body outlines, and gut contents, allows reliable biological reconstructions. Messel erinaceomorphs are represented by three highly specialized amphilemurid species. Some of the adaptations to their feeding and survival strategies are not matched by living insectivores and others, for example dermal ossifications of *Pholidocercus*, look rather bizarre. Erinaceomorphs from the early Paleogene are primitive regarding particular characters of their dentition or skeleton. However, their adaptations to varied life strategies are refined and even extravagant.

ACKNOWLEDGMENTS

Percy M. Butler and Chris Beard provided helpful comments on an earlier version of this paper. I thank Gotthard Richter for the SEM photos of gut contents.

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LEGENDS OF PLATES

PLATE 1

Erinaceomorphs from the middle Eocene of Grube Messel near Darmstadt, Germany.

Fig. 1.— *Pholidocercus hassiacus* KOENIGSWALD & STORCH.
a: Holotype, specimen Hess. Landesmus. Darmstadt Me 7577. The larger distal part of the tail is missing.
b: Paratype, specimen Senckenberg-Mus. Frankfurt ME 758. Detail of the soft body outline above the spine, showing the long bristly hair.

Fig. 2.— *Macrocranion tupaiodon* WEITZEL.
a: specimen Senckenberg-Mus. Frankfurt ME 2400. Distal parts of the forelimbs and tail are not preserved.
b: detail from the same specimen. The soft body outline above the lumbar and pelvic regions shows a short and woolly pelage.

PLATE 2

Fig. 1.— *Macrocranion tenerum* (TOBIEN).
a: specimen of private collection Behnke. The tail is broken off, only a few proximal vertebrae being preserved.
b: detail from the same specimen. The soft body outline above the lumbar and pelvic regions shows a cover with strong bristles and spines.

Fig. 2.— *Pholidocercus hassiacus* KOENIGSWALD & STORCH.
a, b: insect cuticle and leaf tissues from the gut contents.

Fig. 3.— *Macrocranion tupaiodon* WEITZEL.
a, b: fragment of a fish vertebra and plant tissues (probably of a pulpy fruit) from the gut contents.

Fig. 4.— *Macrocranion tenerum* (TOBIEN).
a, b: dense layers of thin insect cuticles and single cuticle fragments (presumably of ants) from the gut contents.

PLATE 1

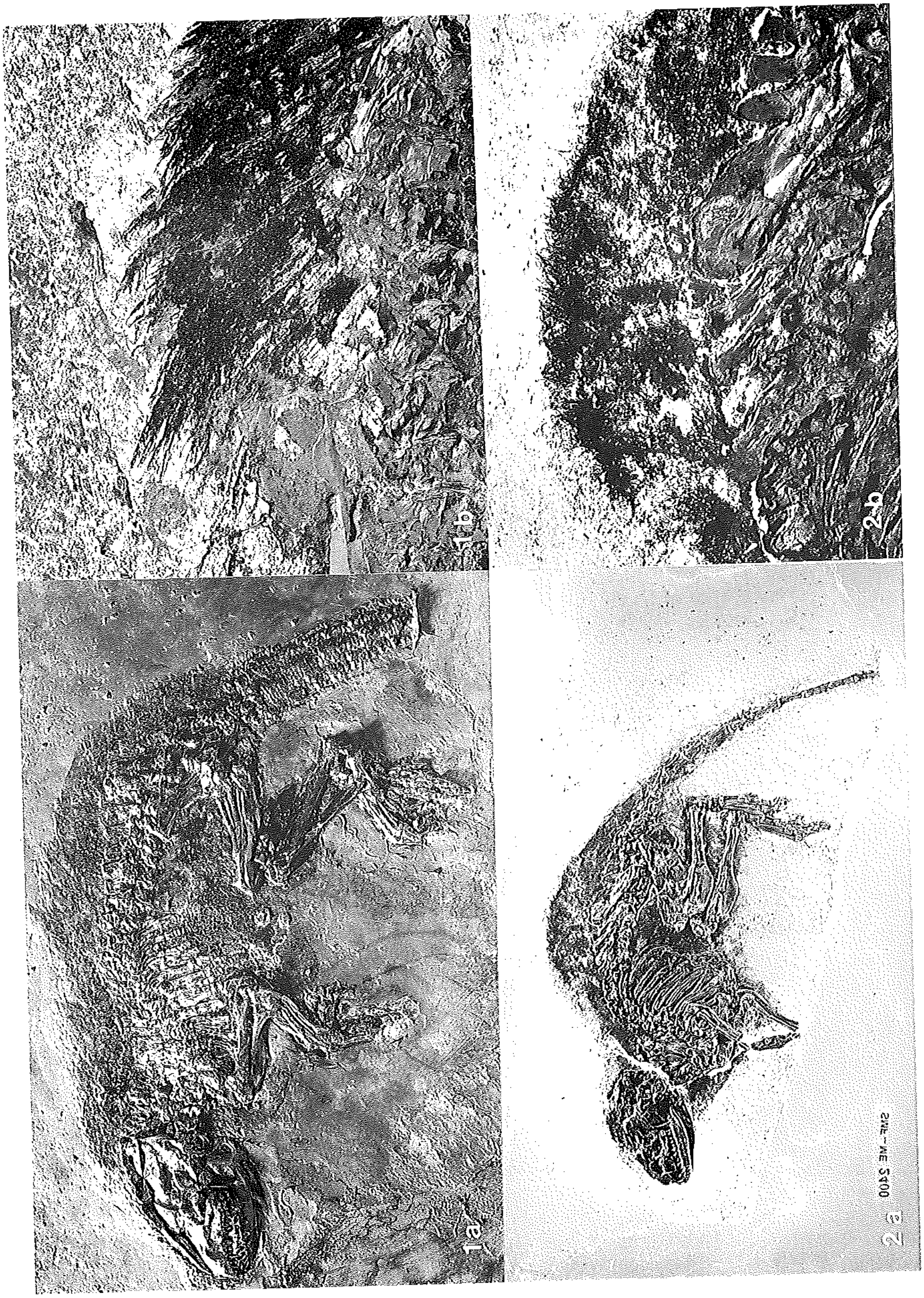

PLATE 2