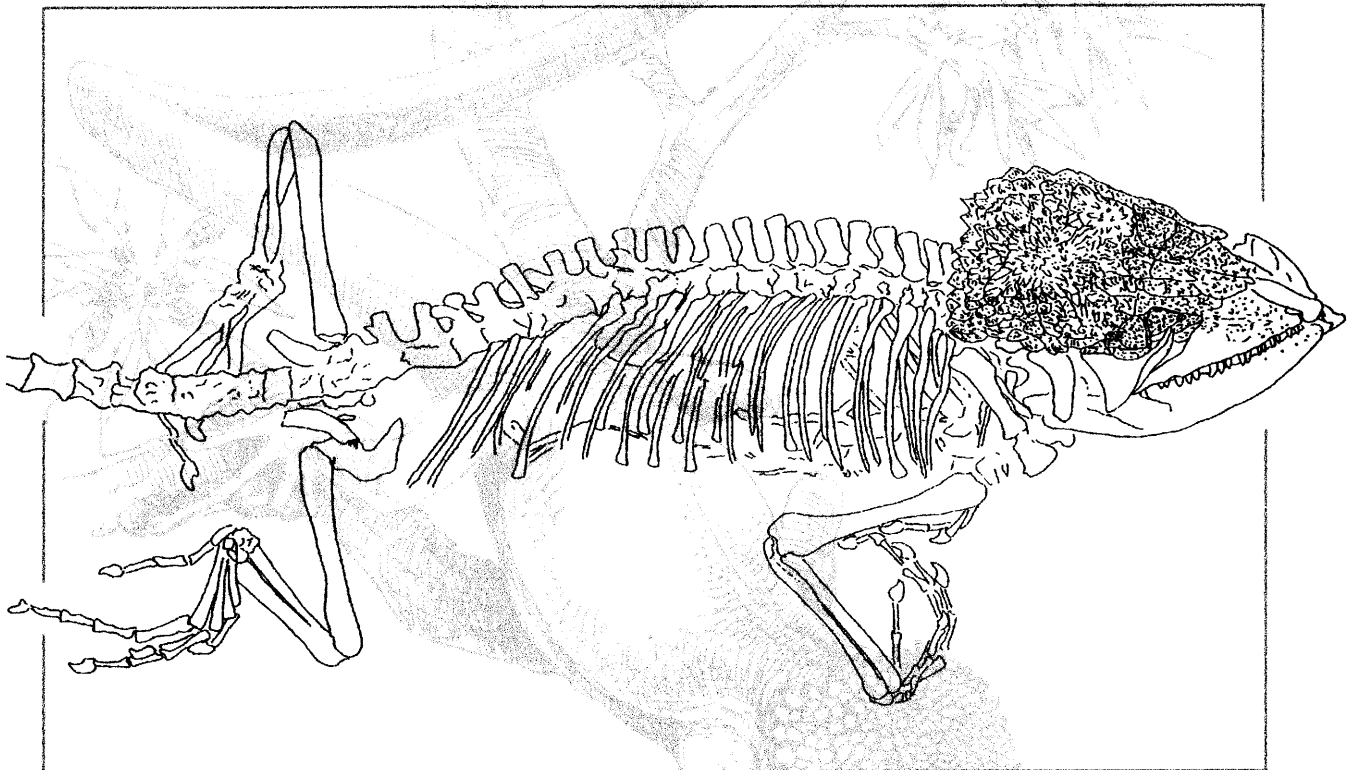


**Taxonomy and Paleobiology of a basal Scincoid Lizard
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from the Messel Formation
(Middle Eocene: basal Lutetian, Geiseltalium), Germany**

by

SINJE WEBER



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Zusammenfassung

Aus dem Weltnatuerbe Grube Messel bei Darmstadt (Mittleres Eozän, basales Lutetium oder Geiseltalium) wurde eine bisher noch nicht beschriebene Echsenart untersucht. Ihre systematische Einordnung, phylogenetische Position und die Rekonstruktion ihrer Lebensweise war Ziel dieser Arbeit. Dazu wurden u. a. vergleichende anatomische Untersuchungen an rezenten Echsen durchgeführt. Die systematische Einordnung innerhalb der Echsen (Lacertilia) erweist sich als problematisch, und es ist nicht möglich das neue Taxon fossilen oder rezenten Formen eindeutig zuzuordnen. Es handelt es sich um eine neue Echsen-gattung und Art der Infraordnung Scincomorpha (Skinkartige). Sie wird in die Überfamilie der Scincoidea als familia incertae sedis gestellt. In dieselbe Überfamilie gehören die Scincidae (Skinke), Cordyliformes (Gürtelschweife) und die bereits in der Unteren Kreide ausgestorbenen Paramacellodidae. Auffallende Merkmale sind zunächst der verhältnismäßig große, skulpturierte Kopf sowie der außerordentlich lange Schwanz. Zur Bearbeitung liegen sechs überwiegend gut erhaltene Exemplare und ein Abguß des neuen Taxons vor, das bisher aus keiner anderen Fundstelle bekannt ist. Die Fossilien sind fast vollständig artikuliert, Magen-/Darminhalt ist bei drei Exemplaren erhalten und epidermale Schuppen an manchen Phalangen liegen bei zwei Exemplaren vor. Dies ist ein für Messel typischer, aber ansonsten außergewöhnlicher Erhaltungszustand. Die Messeler Fossilien liegen in einem kerogenen Tonstein, der weithin als „Messeler Ölschiefer“ bekannt ist und in einem (sub-) tropischen See abgelagert wurde. Die Mächtigkeit der Messel Formation beträgt ca. 200m und hat eine Ausdehnung von 1000 x 700m. Die Knochenelemente in Messel sind oft flachgedrückt, verformt oder von anderen Elementen verdeckt. Aus anderen Fossilienfundstätten sind von Lacertiliern oftmals nur Zähne, Kieferfragmente oder Frontoparietalkomplexe erhalten. Die charakteristische Skulptur auf dem Schädeldach des neuen Taxons kommt durch Hautverknöcherungen (Osteoderme) zustande. Über den Hinterrand des Kopfes ragen kleine occipitale Knochenstacheln hervor. Ähnliche Osteoderm-Anordnungen kommen auch bei Skinken und Gürtlechsen vor. Die Anordnung der über den Augen liegenden (supraorbitalen) Osteoderme entspricht derjenigen bei Lacertiden, jedoch fehlt die für das neue Taxon typische Skulpturierung bei Lacertiden. Durch die Schädelosteoderme werden die für die Taxonomie wichtigen Schädelsturen verdeckt. Einige wenige dieser Sturen konnten aber durch konventionelles Röntgen sichtbar gemacht werden. Das neue Taxon besitzt stumpfkönische Zähne, die Zahnkrone hat laterale Schneidekanten, ist lingual leicht zurückgebogen und trägt ebenfalls lingual parallele Striationen. Diese Zahnmerkmale sind typisch für die Überfamilie der Scincoidea, ebenso ein auf dem Retroartikularfortsatz befindliches Tuberkel. Ein weiteres besonderes Merkmal des neuen Taxons ist der prominente posteriore Processus des Jugale (Processus zygomaticus). Er reicht bis zur Hälfte des hinteren Schläfenfensters zurück. Hierbei handelt es sich um ein sehr primitives Merkmal, das bei den Lacertiliern als weitgehend reduziert oder abwesend gilt und in dieser speziellen Ausprägung bei anderen Echsen sonst nicht vorkommt. Dieses Merkmal wurde offenbar parallel in den verschiedenen Infraordnungen reduziert. Diese Ausprägung scheint ein Übergangsstadium in der evolutionären Reduktion des unteren Schläfenbogens darzustellen.

Kladistische Untersuchungen lieferten verschiedene phylogenetische Hypothesen. Zu ihrer Berechnung wurden die Matrizen von vier verschiedenen Autoren verwendet bzw. die Anzahl der Merkmale und Taxa nach bestimmten Kriterien reduziert. Eine Diskussion der Ergebnisse im Zusammenhang mit den vergleichenden anatomischen Untersuchungen schließt sich an. Letztere haben hier einen höheren Stellenwert. Die kladistischen Untersuchungen bieten zum Teil widersprüchliche Ergebnisse und bestätigen die problematische Position der neuen Gattung und Art. Möglicherweise handelt es sich um den Nachfahren eines Stammgruppenvertreter der Scincoidea oder das neue Taxon stellt eine interessante Verbindung zwischen den Scincidae und Cordyliformes dar. Die genaue Stellung im System der Lacertilia bleibt jedoch ungeklärt.

Als Holotyp wurde das am besten erhaltene Exemplar gewählt (SMF ME 3516). Es zeigt u.a. einen außerordentlich langen Schwanz, der am distalen Ende ventral eingerollt ist. Er ist etwa dreieinhalb mal länger als Kopf und Rumpf zusammen. Bei einer Gesamtlänge des Individuums von etwas über 90 cm entfallen etwa 70 cm auf den Schwanz. Aller Wahrscheinlichkeit nach handelt es sich um einen Greifschwanz, ein Hinweis auf eine baumbewohnende (arboricole) Lebensweise. Die Krallen (bzw. die Ungualphalangen) sind stark gekrümmt, eine typische Ausprägung für kletternde Echsen. Im Gegensatz dazu zeigen bodenlebende Echsen kaum gekrümmte, gestreckte Krallen. Vorder- und Hinterbeine sind nahezu gleich lang, auch das ist typisch für kletternde Echsen und spricht ebenfalls für eine arboricole Lebensweise. Bodenlebende Echsen haben dagegen in der Regel längere Hinter- als Vorderbeine. Bei Formen, die auf den Hinterbeinen rennen können, wird der Schub durch die relative Verlängerung der Hinterbeine sogar noch vergrößert. Insgesamt sind die Beine bei kletternden Echsen kürzer als bei bodenlebenden Echsen. Dies trägt zur Beweglichkeit bei und optimiert die Kraftübertragung und der Körperschwerpunkt liegt tiefer. Die Vorderbeine spielen beim Klettern eine wichtige Rolle zur effektiven Lokomotion. Lange Hinterbeine sind beim Klettern dagegen eher hinderlich. Auch die Proportionen von Tibia zu Femur bei der neuen Gattung und Art sprechen für eine kletternde Lebensweise. Vertreter der Scincoidea tragen oft nicht nur Osteoderme auf dem Kopf, sondern auch der Körper ist bedeckt mit ihnen. Das ist bei dem neuen Taxon nicht der Fall. Die Reduktion dieser Körperosteoderme kann funktionsmorphologische Gründe haben: Bei *Abronia taeniata* (Anguidae) sind die Körperosteoderme im Zusammenhang mit der arboricolen Lebensweise reduziert, um eine höhere Beweglichkeit im dreidimensionalen Habitat zu gewährleisten. Zusammenfassend spricht also der Greifschwanz, die gekrümmten Krallen, die Beinproportionen und das Fehlen der Körperosteoderme für eine arboricole Lebensweise des neuen Taxons.

Um die Ernährungsweise zu rekonstruieren, wurde der bei drei Individuen vorhandene Magen-/Darminhalt untersucht. Er ist als kohlige, schwarze Masse im abdominalen Bereich erhalten. Untersuchungen mit dem Rasterelektronenmikroskop ergaben hauptsächlich Pflanzenreste und einige wenige Insektenreste. Allerdings muß man mit Rückschlüssen auf die Ernährung vorsichtig sein. Nur die widerstandsfähigsten Nahrungsreste können überliefert werden. Damit spiegelt der Magen-/Darminhalt natürlich nicht das gesamte Spektrum der Ernährung wider. Jedoch ist die große Menge der Pflanzenreste in allen drei Exemplaren auffällig. Den größten Teil der Pflanzenreste machen Fragmente von Rinde und Stengeln aus, eine ungewöhnliche Nahrung für eine Echse. Bei einem Individuum wurden auch Reste von Samen- oder Frucht-schalen gefunden. Die Fragmente von Insektencuticula, die in zwei der drei Exemplare nachgewiesen wurden, können einerseits unbeabsichtigt mitgeschluckt worden sein oder eine zusätzliche Nahrungsquelle darstellen. Möglicherweise handelt es sich zum Teil um Käfercuticula, eine genaue Bestimmung ist zur Zeit nicht möglich. Obwohl es sich bei der neuen Gattung und Art um einen spezialisierten Pflanzenfresser zu handeln scheint, sind die Zähne relativ unspezialisiert und zeigen nicht den für Pflanzenfresser oft vorkommenden mehrspitzigen Zahntyp. Offenbar waren die konischen, mit lateralen Schneidekanten versehenen Zähne ausreichend für das Abbeißen von Rinde und Zweigen. Um diese schwerverdaulichen Pflanzenreste mehr oder weniger effizient aufzuschließen, besaß das neue Taxon möglicherweise Modifikationen im Verdauungstrakt die bei spezialisierten Pflanzenfressern vorkommen können. Die dicht aneinanderliegenden Knochenschuppen auf dem Schädeldach schränken die Beweglichkeit des Schädels ein, die aber bei Predatoren wichtig ist. Die neue Gattung und Art war eher ein Pflanzen- und evtl. auch ein Insektenfresser als ein effektiver und flinker Jäger. Sein robuster größtenteils akinetischer Schädel und das vermutete Vorhandensein eines sog. jugomandibularen Ligamentes läßt auf eine große Beißkraft schließen. Nach den gewonnenen Hinweisen zur Paläobiologie besetzt das neue Taxon die „Paläo-Nische“ eines relativ großen, überwiegend herbivoren und arboricolen Scincoiden mit guten Kletterfähigkeiten.

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by

SINJE WEBER

Abstract. – A new lizard genus and species is described from the World Heritage Messel Pit Fossil Site (Middle Eocene: basal Lutetian, Geiseltalium) near Darmstadt, Germany. It is placed within the Scincoidea (Scincidae, Cordyliformes + Paramacellodidae), but no attribution to a distinct family can be made. Its phylogenetic position is problematic as it probably represents the descendant of a stem group taxon of the Scincoidea or an interesting „link“ between Scincidae and Cordyliformes. Extensive phylogenetic analyses using numerical taxonomy are undertaken. Unaltered and modified matrices from different authors are analysed in order to generate a variety of phylogenetic hypotheses. These are discussed with the results of comparative anatomy, the latter having a higher impact on the final classification. Key characters of the new taxon are as follows: The dorsal aspect of the skull is covered with a characteristic osteodermal pattern, the jugal has a huge posterior process, the retroarticular process and teeth show a typical scincoid morphology. Six well preserved specimens can safely be attributed to the new species which is not yet known from any other fossil site. The very long prehensile tail of the new genus and species, its curved claws, limb proportions and missing body osteoderms strongly suggest an arboreal mode of life. The long tail could secure support by grabbing branches, but probably was too fragile to hold the entire body weight. The locomotion and microhabitat exploitation of the new taxon can best be compared to the arboreal emerald monitors *Varanus prasinus* and *Varanus beccarii* with their long tails and strongly curved claws. In three of the fossil specimens intestinal contents are still preserved. They contain plant remains and a few fragments of insect cuticula. Due to its cover of osteoderms, the skull was largely akinetic, suggesting the new taxon not to be an effective and agile predator, but a rather large herbivore and occasional insectivore, which was probably capable of strenuous biting. Its presence in the Lower Middle Eocene of Messel neither supports nor contradicts the current opinions of Scincoid Paleobiogeography.

Keywords: Lacertilia, Scincomorpha, Scincoidea, Numerical Taxonomy, Cladistics, Palaeobiology, Intestinal Contents, Eocene, Messel

1 Introduction

1.1 Aims of this study

A lizard of uncertain taxonomical position from the Messel Pit Fossil Site, which is unknown from the fossil record and from extant specimens, will be described. The taxonomical position and phylogeny of the new taxon will be discussed by comparing morphological information with the results of numerical taxonomy. A palaeobiological reconstruction of the appearance, mode of life and feeding habits of the new taxon will be based on comparative morphology, morphometry and on gut content analysis. The paleobiogeography of the new taxon will be discussed in context with related taxa.

1.2 The Messel Pit Fossil Site

1.2.1 Geology

The Messel Pit Fossil Site is situated 8 km Northeast of Darmstadt and 20 km Southeast of Frankfurt (Fig. 1). The pit has an extent of 700 by 1000 meters (Fig. 2), a central depth of 70 meters and is surrounded by a ridge called Sprendlinger Horst. The latter represents the northern extension of the so-called crystalline Odenwald. The central core of the ridge contains rocks of Palaeozoic age and is covered by sediments and vulcanites from the Lower Permian (Rotliegend). To date it is unclear how the depression was formed which allowed the accumulation of water, representing the Eocene lake Messel. In Eocene times, the Upper Rhine Graben sank down over 2000 meters and simultaneously the Sprendlinger Horst shield shifted upwards. A plausible model connects these tectonic events with the origin of the depression that later formed Lake Messel (e.g. WAGNER 1950, MATTHESS 1966, HARMS 2001). In total, six oil shale localities in vicinity of Messel are situated on a rough line running from Southwest to Northeast (SCHAAL 1992). This would be consistent with the appearance of a Graben structure during these strong tectonic events that took place during the Early Eocene (MATTHESS 1966, JACOBY 1997). Another widely discussed model shapes Lake Messel as a crater that originated from a crater lake explosion (RIETSCHER 1994). An unlikely, but not yet falsified explanation for the depressions on the Sprendlinger Horst is asteroid impact (MÜLLER, M. 1995, PIRRUNG 1998). It is also possible that tectonic and volcanic processes both contributed to the genesis of the depression (HARMS 2001). To further investigate this question a Messel Drilling Projekt is currently carried out.

During the Lower Middle Eocene (Lutetium or better Geiseltalium after FRANZEN & HAUBOLD 1985) a freshwater lake produced sediments which today represent the Messel Formation. In the centre of the pit, the so called oil shale rock is still more than 200 m in thickness and the deposition period was estimated to about one million (GOTH 1990) to two million (IRION 1977) years. Both authors calculated a sedimentation rate of 0.1 to 0.15 mm / year, a measurement which is consistent with modern tropical lakes. However, IRION (1977) points out that these measurements were taken from the central, well laminated sediments only. Other members of the formation are less well laminated and may therefore have been sedimented in much shorter periods of time. The depositional period of the Messel Lake is a topic of current research (Messel Drilling Project 2001). The age of the Messel sediments has been estimated to +/- 49 Mill. years, which corresponds to the MP11 zone and is based on volcanic material (LIPPOLT et al. 1975, WEBER & ZIMMERLE 1985) and mammal biostratigraphy (HAUPT 1911, TOBIEN

1968). According to FRANZEN (1992a) the evolutionary advancement of the early horses, the artiodactyl *Messelobunodon* (FRANZEN 1981, FRANZEN & KRUMBIEGEL 1980), the rodent *Ailuravus* (TOBIEN 1968) and the primate *Europolemur* (FRANZEN 1987) support a correlation of the Messel Formation to the Lower Middle Eocene (basal Lutetian or Geiseltalium).

The mostly laminated sediments of the Messel Formation have the consistency of „chocolate“, can be cut and split with knives and are informally called ”oil shale”. However, it is not a true oil shale since it does not contain mineral oil but kerogen, a solid bituminous early stage of mineral oil. Furthermore, it is no true shale, because the sediments were probably never covered by more than 200 m of rock and therefore no measurable temperature increase took place, a metamorphic step necessary for the genesis of true shale. Correctly, the sediments should be called kerogenous siltstones (MATTHESS 1966). The term ”oil shale” originates from the times of mining in the pit, it is still used today and will be adopted in this study. Fresh ”oil shale” from an excavation site consists of approx. 40% water, 35% clay minerals and 25% organic material (e.g. MATTHESS 1966, RULLKÖTTER et al. 1988). The organic part is kerogen, a bituminous substance of higher hydrocarbonates (MATTHESS 1966). These mainly originate from algae, especially from cell walls of the green alga *Tetraedron minimum* (GOTH 1990). For the genesis of kerogen, animal biomass was insignificant.

1.2.2 Biostratonomy of Messel fossils

The extraordinary preservation of the fossils is due to a special biostratonomy and conditions on the lake bottom. According to GOTH (1990), Lake Messel was at least 50 meters deep and meromictic, that is a deeper water body free of oxygen (monimolimnion), separated by a chemocline from the upper water body (mixolimnion) where oxygen was present. The latter was presumably full of life, with an autochthonous food web of different trophic levels (RICHTER & BASZIO 2001). Because of the warm and humid climate, the algae could greatly multiply and due to the seasonal day length changes, bloomed periodically. By decomposition of this and other organic material, all dissolved oxygen in the water was consumed in the monimolimnion (GOTH 1990). Due to these anaerobic conditions on the lake bottom, carcasses of animals and remains of plants could not completely decay and were not disarticulated by scavengers. Virtually no current was present at the bottom at the lake, also favouring the articulated preservation. The fossils are almost always articulated, as the specimens studied here. Anaerobic bacteria were responsible for the famous soft tissue preservation in outlining mammal fur on the sediment (WUTTKE 1983). Epidermal scales (probably original keratin remains) are present in some reptiles and the preservation of gut contents allows insights into the nutrition of the vertebrates.

Many representatives of the Eocene ecosystem around Lake Messel are preserved, such as algae, insects, fish, higher plants, amphibians, reptiles and mammals. Nevertheless, taphonomic biases were present which are often underestimated. Lightly built adult insects (e.g. Ephemeroptera, Diptera, Lepidoptera) are almost completely missing

Fig. 1: (Following page) Geological sketch showing the position of the Messel Pit and its surroundings (modified from MATTHESS 1966 in SCHAAL 1992).

Fig. 2: (Following page) Map of the Messel Pit superimposed on a grid (from SCHAAL & MÖLLER 1991). The arrows indicate the grid squares in which the Senckenberg specimens SMF ME 475a+b (F11) and SMF ME 1249a+b (D9) were found.

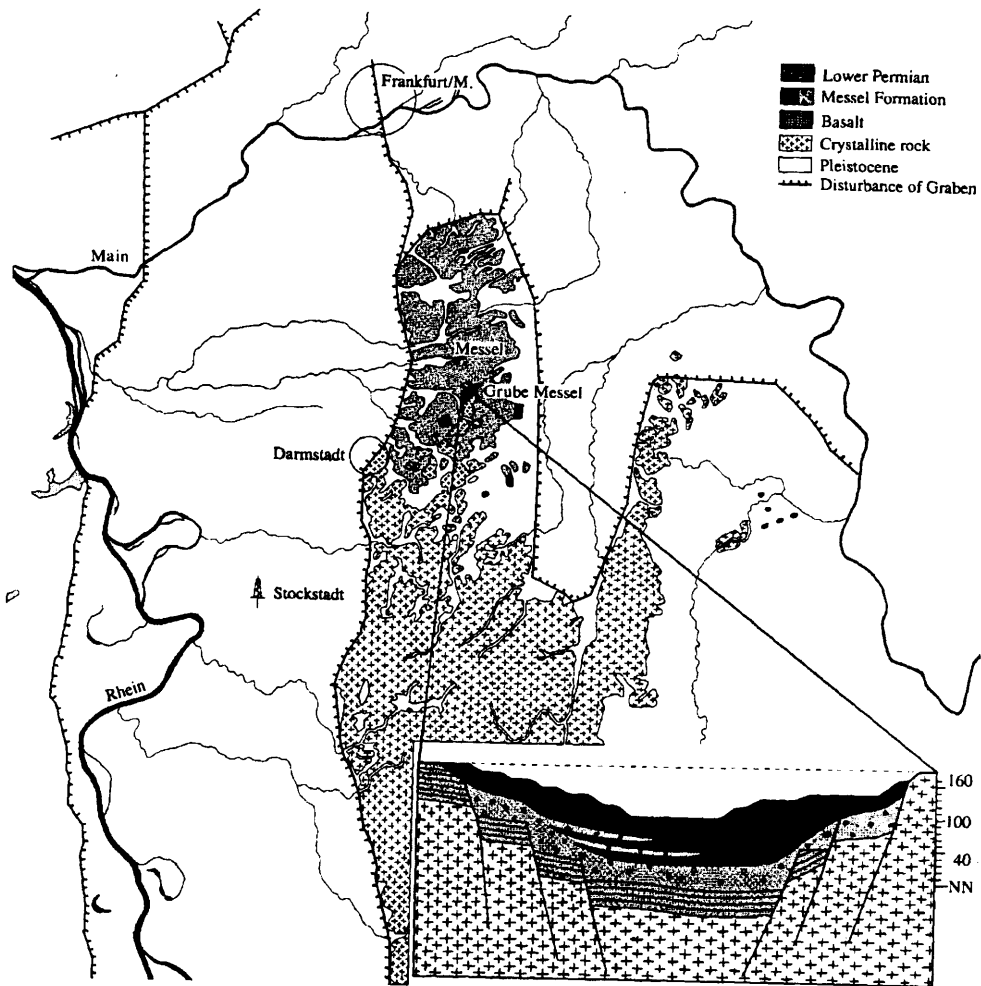


Fig. 1

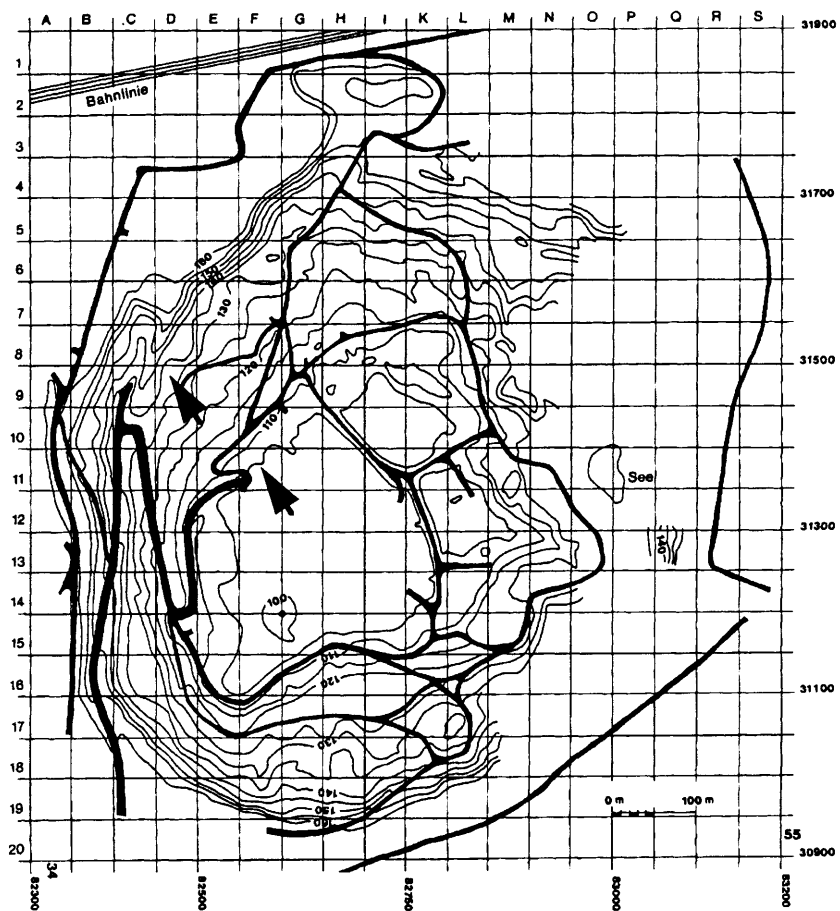


Fig. 2

(LUTZ 1987, 1991), they had two barriers to encompass, the water surface and the chemocline, before becoming embedded in the anaerobic sediments (RICHTER & BASZIO pers. comm.). Flying vertebrates (birds and bats) are strongly over-represented, which led to the theory of toxic gases above the water surface. These could have originated from decay processes at the lake bottom or from volcanic activities. Huge trees around the lake would have prevented the gas layer from being blown away by wind (FRANZEN et al. 1982, FRANZEN & KÖSTER 1994).

1.2.3 Eocene Lake Messel and its surroundings

During the Eocene, central Europe was situated 1300 km further South at about 38° Northern Latitude, nowadays corresponding to a position in the Southern Mediterranean (SMITH et al. 1982). Probably, also an eastward shift of several 100 km took place. In the Eocene, the world climate was much warmer and more humid than today. The poles were not iced and thus the sea level was much higher than today. As a consequence, a wet and warm paratropical climate must be assumed for Lake Messel, which is also supported by the plant remains present in Messel (ENGELHARDT 1922). In contrast to today's tropical ecosystems, Eocene Lake Messel went through distinct seasons, characterised by different day lengths throughout the year with an annual mean temperatures over 20°C and a high precipitation (SCHAARSCHMIDT 1992, WILDE 1989). Together with the formation of the Rhine Graben and the virtual absence of the Alps (which represented an archipel in the Tethys), Messel was situated rather close to the Tethys seashore at the border of the Upper Rhine Graben (GOTH 1990).

Unfortunately, the shoreline of Lake Messel is not preserved. There are three models for the reconstruction of Lake Messel morphology today. One model presented by HUMMEL (1925, 1927) and RIETSCHEL (1994) is based on the crater lake theory and therefore reconstructs Lake Messel to be not significantly larger than the extent of today's oil shale deposits of 700 x 1000 meters. Consequently, there must have been steep borders, no limnic inflows and the autochthonous fauna must have been poor in species and numbers of individuals. Another model shapes Lake Messel as a huge lake of which only the deepest part is preserved (SCHAAL 1992) and the marginal areas have been largely eroded. Finally, FRANZEN et al. (1982) see Lake Messel as a part of a limnic landscape with broad streams or rivulets connecting a number of lakes. In this model, all oil shale deposits around Messel would be contemporaneous and part of one large ecosystem. In all cases, the distant surroundings of the lake are described to be poor in relief and the lake itself was estimated to have a depth of 50 to 300 meters (IRION 1977). GOTH (1990) claims a depth of at least 50 meters, for the formation of a chemocline.

The botanical analysis states a plant succession that is typical for a broad marginal shallow water area, favouring the two latter models. As far as the flora is concerned, ENGELHARDT (1922) suggested connections with Southeast Asia and the presence of a "very warm climate" with "tropical-subtropical character". The shallow water was populated by water-lilies (ENGELHARDT 1922, SCHAARSCHMIDT 1992), which are currently under revision (WILDE pers. comm.). Around the lake were swampy areas with plants like sedges, aroids and ferns as well as reed-like plants (SCHAARSCHMIDT 1992). This belt was followed by a dense shrub with screw-pines and palms. Within the forest, plants of the walnut (Juglandaceae), tea (Theaceae), laurel (Lauraceae) and pea (Leguminosae) families and at a greater distance trees of the beech family (Fagaceae)

were present. The crowns of the trees were partly covered by lianas (Fig. 3, SCHAARSCHMID 1992).

This ecological setting was the home to a diverse fauna consisting of insects, amphibians, reptiles, birds and mammals that lived in the close surroundings of Lake Messel. Presumably little or no transport was necessary to bring these organisms into the favourable fossilising conditions of Lake Messel. In a strict sense, only algae, aquatic arthropods, fish, amphibians and some of the crocodiles were autochthonous members of the Lake Messel ecosystem. It is not the purpose of this study to further investigate this aquatic community, but to add to the knowledge of terrestrial biodiversity by describing a new Lacertilian (lizard) and investigating its palaeoecology.



Fig. 3: Schematic reconstruction of the vegetation in the vicinity of Lake Messel. Bushes and herbs are excluded from the diagram (from SCHAARSCHMIDT 1992).

1.2.4 History of the Messel Pit Fossil Site

In the middle of the last century, the "Messel brown coal" (oil shale) was discovered and privately mined. In 1884, the GEWERKSCHAFT MESSEL mining company was founded, but the Messel oil shale has bad burning properties when used as fuel for private purposes. However, it was possible to smoulder the sediment, that is to distil it dryly at very high temperatures. In the process, the kerogenous parts in the oil shale turned into mineral oil and paraffin. Around 1900, the first smoulder oven was erected, and in less than ten years there were 32 of them on the rim of the Messel Pit. The revenues from mining were never high and it was an expensive way to produce mineral oil. In the recession after World War I, the company was bought by the IG-FARBEN Industrial combine in 1924 and the equipment was modernised. In World War II Messel was an important fuel supplier, but after attacks the smoulder ovens overheated and deformed. From 1945 to 1953 Messel industry was rebuilt under American lead, as a part of the Marshall Plan. It was later given into German management as the PARAFFIN- UND MINERALÖLWERK MESSEL GMBH. In 1959 the YTONG company bought the Pit. Of special interest were the immense slag remains from the smoulder ovens as raw material for bricks. Oil shale was still mined as energy resource for YTONG until 1971. After the mining activities, a pit of 25 million cubic meters was left, an „ideal“ waste disposal site in the imagination of some people. New preparation techniques, especially the transfer method onto artificial resin plates made Messel widely known as an important fossil site. A fight of almost 20 years began between disposal site supporters and fossil site conservers. Eventually, in 1987 a court decided against the waste disposal site and in 1991 Hassia bought the pit in order to preserve it (SCHAAL 1992, SCHAAL & SCHNEIDER

1995). Since then, the Research Institute Senckenberg is in charge of the Pit and in December 1995 Messel was declared a World Heritage Site by the UNESCO because of the fantastic preservation of Messel fossils.

1.2.5 Previous work on Messel Lacertilia

For Tertiary Squamata (Sauria/Lacertilia, Serpentes, Amphisbaenia), the Messel Pit is one of the most important fossil sites (KELLER & SCHAAL 1992a). Lizards and amphisbaenians are much rarer than snakes. There are iguanian, scincomorphan and anguimorphan lizards in Messel. Several species were first described from the Eocene Geiseltal near Halle (East Germany) and were proved to be present in the Messel Pit Fossil Site as well: *Geiseltaliellus longicaudus* from the Geiseltal was described by KUHN (1944). ROSSMANN (1992, 2000) proved this species also to be present in Messel. It belongs to the "Iguanidae" and shows a close relationship to the basiliscine subfamily. However, ROSSMANN (1992, 2000) erected the new subfamily Messelosaurinae for the genus *Geiseltaliellus* and related forms from the Eocene of France, Belgium and North America. *Eolacerta robusta* was described by NÖTH (1940) for the Geiseltal as a member of the Lacertidae. MÜLLER, J. (1998, 2001) found this species to be present in the Messel Pit as well, one of the biggest Lacertilia from this locality. MÜLLER, J. suggests a relationship rather to the Scincoidea than to the Lacertidae. RIEPPEL (1980a) described an incompletely preserved Lacertilian from Messel and tentatively referred it to the genus *Eolacerta*. But according to RIEPPEL (1980a) "a particular affinity to the family Lacertidae cannot be supported". MÜLLER, J. (1998, 2001) assigned this specimen to *Eolacerta robusta*, as well. Representatives of the Anguidae in Messel are *Xestops* sp. (Glyptosaurinae) and *Ophisauriscus quadrupes* (Anguinae). *Xestops* genus has a characteristic armour of osteoderms, covering the body and large parts of the skull (KELLER & SCHAAL 1992a). *Ophisauriscus quadrupes* has been described for the Geiseltal by KUHN (1940) and proved to be present in Messel as well (SULLIVAN, KELLER & HABERSETZER 1999). A Varanoid from Messel, "*Saniwa*" *feisti*, was described by STRITZKE (1983) as a representative of the family Varanidae. Whereas KELLER & SCHAAL (1992a) attributed this species to the extinct family Necrosauridae (Varanoidea). Furthermore, KELLER & SCHAAL (1992a) gave three necrosaurid forms a preliminary designation as three genera and species, which are not described to date. The specimens which will be described in the present work were mentioned in KELLER & SCHAAL (1992a) as "finds of uncertain taxonomic position" and the authors state that "a definite classification among fossil or recent known forms has not been possible up to now". They observed a certain similarity of the orientation of the sculpture on the parietal bone to the Xenosauridae, a group of North American anguimorph Lacertilians. These lizards from the Messel Pit Fossil Site are not yet known from other comparable fossil sites (KELLER & SCHAAL 1992a).

2 Taxonomic and phylogenetic position of the new taxon

2.1 *Lacertilian relationships and paleontology*

2.1.1 Main concepts in lizard taxonomy – Historical overview

The taxonomy of the Lacertilia (lizards) has been revised several times and is still a point of discussion. Among others COPE (1864, 1892), CAMP (1923), MCDOWELL & BOGERT (1954) and ROMER (1956, Reprint edition 1997) are important early works for the present systematics of the Lacertilia. Many diagnostic characters, including osteological details, were examined for the first time among lizards by COPE (1864, 1892). CAMP (1923) gave an extensive historical review of saurian classification. He proposed two main groups, the Ascalabota (= Gekkota, Iguanidae, Agamidae + Chamaeleontidae) and the Autarchoglossa (= Scincomorpha + Anguimorpha). The Scincomorpha consisted of Xantusiidae, Scincoidea and Lacertoidea with the possible inclusion of Amphisbaenidae. The Anguimorpha comprised the Platynota (= Varanoidea, Mosasauroidae), the Anguioidea and Zonuridae.

MCDOWELL & BOGERT (1954) investigated the infraorder Anguimorpha. They mainly used CAMP's (1923) classification but transferred the Pygopodidae from Anguimorpha to Gekkota and followed COPE (1871) by including the Gerrhosauridae and Zonusauridae within the Cordylidae. ROMER (1956) erected four infraorders of the Lacertilia by considering osteological characters: the Iguania, the Nyctisauria (= Gekkota), Leptoglossa (= Scincomorpha) and Diploglossa (= Anguimorpha + Amphisbaenia). RIEPPEL (1980a) studied the phylogeny of Anguimorpha, investigating the head musculature, skull and atlas-axis complex of the different families and he included a cladistical analysis.

Because of the paraphyly of the taxon „Iguanidae“, FROST & ETHERIDGE (1989) proposed the recognition of eight families. Nevertheless, the term „Iguanidae“ is still used by some authors as a uniting term for non acrodont Iguanians (= Iguania without Agamidae and Chamaeleonidae) which are well aware of the paraphyly of „Iguanidae“ (e.g. RAGE & AUGÉ 1993, AUGÉ 1993, BORSUK- BIALYNICKA & ALIFANOV 1991). The term „Iguanidae“ is retained here as well, and used accordingly (also for reasons of simplicity) to characterise this group. It will be marked in inverted commas.

An important and more recent basal work for lacertilian/saurian taxonomy is "Sauria terrestria. Handbuch der Paläoherpetologie" by ESTES (1983) which gives a definition of each family of the Lacertilia and presents the known fossil species of each family. This handbook comprises all terrestrial Sauria (Eolacertilia + Lacertilia) and Amphisbaenia. Aquatic taxa were excluded. In his work he regarded the Lacertilia as a suborder of the order Sauria. The orders Sauria, Serpentes (snakes) and Amphisbaenia represented the Squamata. He followed ROMER (1956) in recognising four infraorders within the Lacertilia: Iguania, Gekkota, Scincomorpha and Anguimorpha. But there are differences to ROMER'S systematics below the infraorder level: ESTES did not include the Amphisbaenia into Anguimorpha, placed the Ardeosauridae within Gekkota and incorporated the Anniellidae as a subfamily into Anguidae. Within the Scincomorpha, there are three superfamilies: the Lacertoidea (Teiidae, Gymnophthalmidae + Lacertidae), Scincoidea (Scincidae + Dibamidae) and Cordyloidea (Paramacellodidae,

Xantusiidae + Cordylidae). As in ROMER (1956), two superfamilies are recognised within the Anguimorpha: Anguioidea (Anguidae, Xenosauridae and Dorsetisauridae) and Varanoidea (Varanidae, Helodermatidae and Necrosauridae). ESTES (1983) included the Dorsetisauridae within the Anguioidea and the Necrosauridae within the Varanoidea.

Cladistical works using numerical taxonomy dealing with higher-level squamate phylogeny followed. The one by ESTES et al. (1988) reviewed mainly osteological characters used in studies up to that time (Fig. 4). The authors did not use the term Lacertilia any more, but created a new taxon, the Scleroglossa, which incorporated the Gekkota and Autarchoglossa (= Scincomorpha + Anguimorpha). The Serpentes, Amphisbaenia and Dibamidae were included as Scleroglossa incertae sedis. The Squamata included Iguania and Scleroglossa. Within the Scincomorpha, the superfamily Cordyloidea was removed and the Cordylidae were assigned to the superfamily Scincoidea. The Xantusiidae were placed within the Lacertoidea. Another two taxa were erected: Lacertiformes (Lacertidae, Teiidae and Gymnophthalmidae) and Teiioidea (Teiidae + Gymnophthalmidae). BORSUK-BIALYNICKA (1983) studied the early phylogeny of Anguimorpha considering craniological characters. Other investigations on higher-level squamate phylogeny are done by PRESCH (1988), who dealt with relationships within the Scincomorpha. LEE (1997) investigated varanoid lizards and their affinity to snakes. Later cladistical works using numerical taxonomy by EVANS & CHURE (1998) and LEE (1998) based on the paper of ESTES et al. (1988). These three papers are the basis of the numerical taxonomy undertaken in the present study.

The present study uses the systematics of ESTES et al. (1988), but the term "Lacertilia" is still used as proposed in ESTES (1983).

The taxonomy of fossil lacertilians is chiefly based on isolated, more or less three-dimensionally preserved skull elements like frontoparietal complexes and mandibles. In contrast, fossils from the Messel locality allow an investigation of completely articulated specimens. This is a rare chance in the fossil record. In spite of this extraordinary preservation, there are also disadvantages which complicate the investigations. The fossils are embedded in a plate of artificial resin, so only one side of the specimen is visible. Furthermore the fossils are considerably flattened so that important structures cannot be studied from all views. Also, important structures can be covered by osteological elements. This is a problem especially with skull components, which bear important taxonomical features.

Fig. 4 (following page): Cladogram of squamate relationships after ESTES et al. (1988).

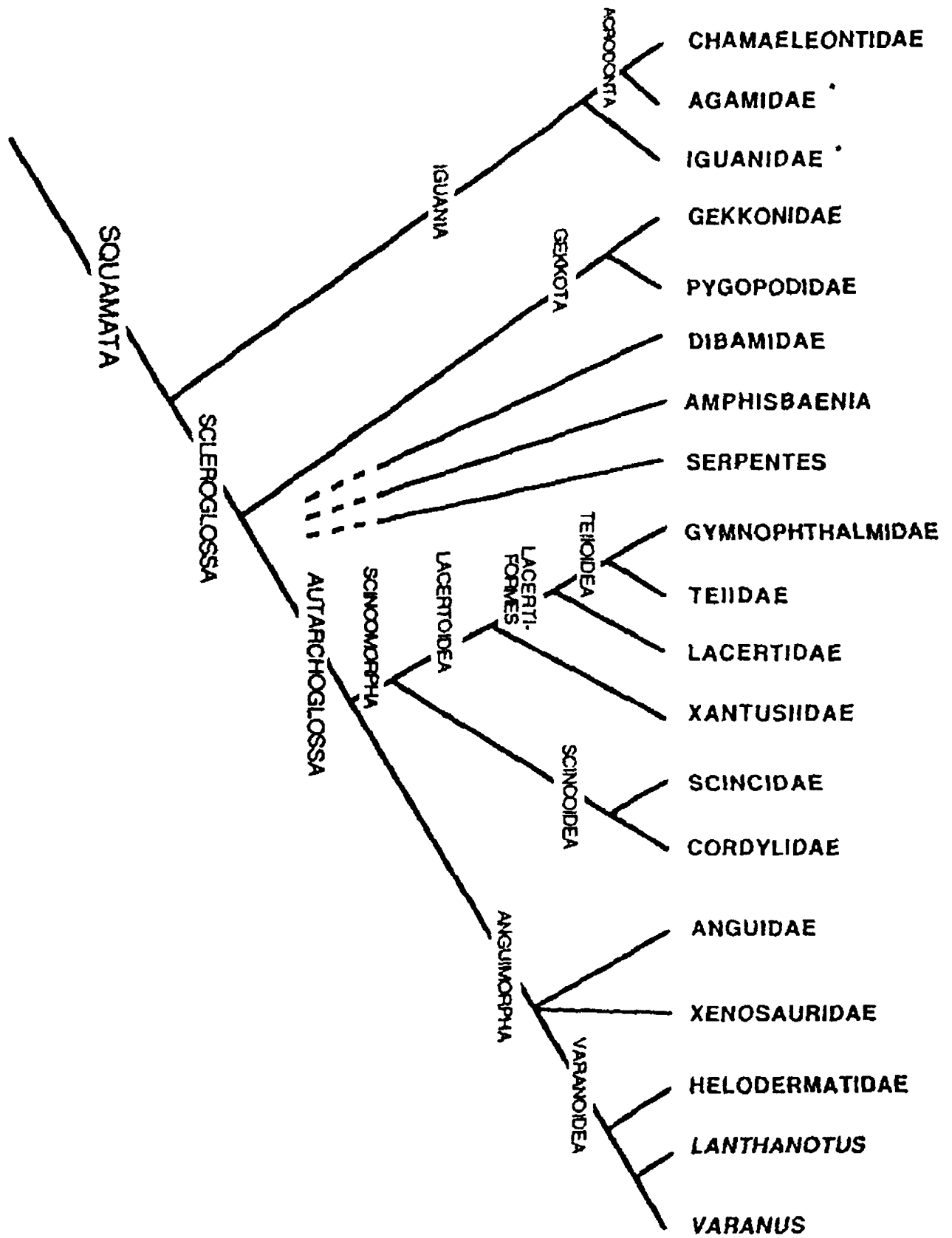


Fig. 4

2.1.2 Stratigraphic distribution of lizards

Fig. 5 shows the stratigraphic distribution of the Lacertilia. From the Upper Cretaceous up to now the following families persist. **Iguania**: „Iguanidae“, Agamidae (ESTES 1983, BORSUK-BIALYNICKA & ALIFANOV 1991, ALIFANOV 1993, GAO & FOX 1996); **Gekkota**: Gekkonidae (BORSUK-BIALYNICKA 1990, GAO & FOX 1996); **Scincomorpha**: Lacertiformes, Teiidae, Scincidae, ?Cordyliformes and Xantusiidae (ESTES 1969, 1983; BORSUK-BIALYNICKA 1988; GAO & FOX 1996); **Anguimorpha**: Xenosauridae, Anguidae, Helodermatidae and Varanidae (GILMORE 1928; ESTES 1964, 1983; GAO & FOX 1996; GAO & NORELL 1998). Since the Palaeocene the Chamaeleonidae and Lacertidae are recorded (ESTES 1983). The extinct families Bavarisauridae, Ardeosauridae (Gekkota), and Dorsetisauridae (Anguimorpha, Anguioidea) are only known from the Upper Jurassic (ESTES 1983). Paramacellodidae (Scincomorpha, Scincoidea) ranged from the Middle Jurassic (WALDMANN & EVANS, 1994) to the Middle Cretaceous (ALIFANOV 1993). Necrosauridae (Anguimorpha, Varanoidea) are present from the Upper Cretaceous to the Upper Eocene or Lower Oligocene (ESTES 1964, 1983; BORSUK-BIALYNICKA 1984b). The monospecific family Arretosauridae (Iguania), is only reported from the Upper Eocene (ESTES 1983).

2.1.3 Cladistics and numerical taxonomy

In order to investigate the phylogenetic relationships and the higher-level taxonomy of the new taxon, an approach using “numerical taxonomy” will be carried out. At the same time this method is tested and evaluated by varying the number of characters and of terminal taxa. Basically, “numerical taxonomy” is closely related to cladistics, but differs in some important features. Both methods should therefore not be synonymized (BORSUK-BIALYNICKA, pers. comm.). “Classical Cladistics” is a method of logical treatment of phylogenetic problems (or affinity problems) on the basis of characters precisely chosen for each level being studied. The outgroup analysis is basic in this method and at every single node the character (plesiomorph or apomorph) is critically evaluated. But with the increasing number of characters, a numerical evaluation using computers becomes necessary and can be combined with this “classical method”. On the other hand, “numerical taxonomy” leaves the evaluation of once chosen characters to the computer without repeatedly checking their significance for every node including the outgroup analysis (BORSUK-BIALYNICKA pers. comm.).

Nevertheless, in this study numerical taxonomy was used, because of the high number of characters and taxa. Character states of the new taxon are added to matrices of different authors. By varying the character matrices, this method is experimentally used, evaluating the different effects of the changes made in the matrix.

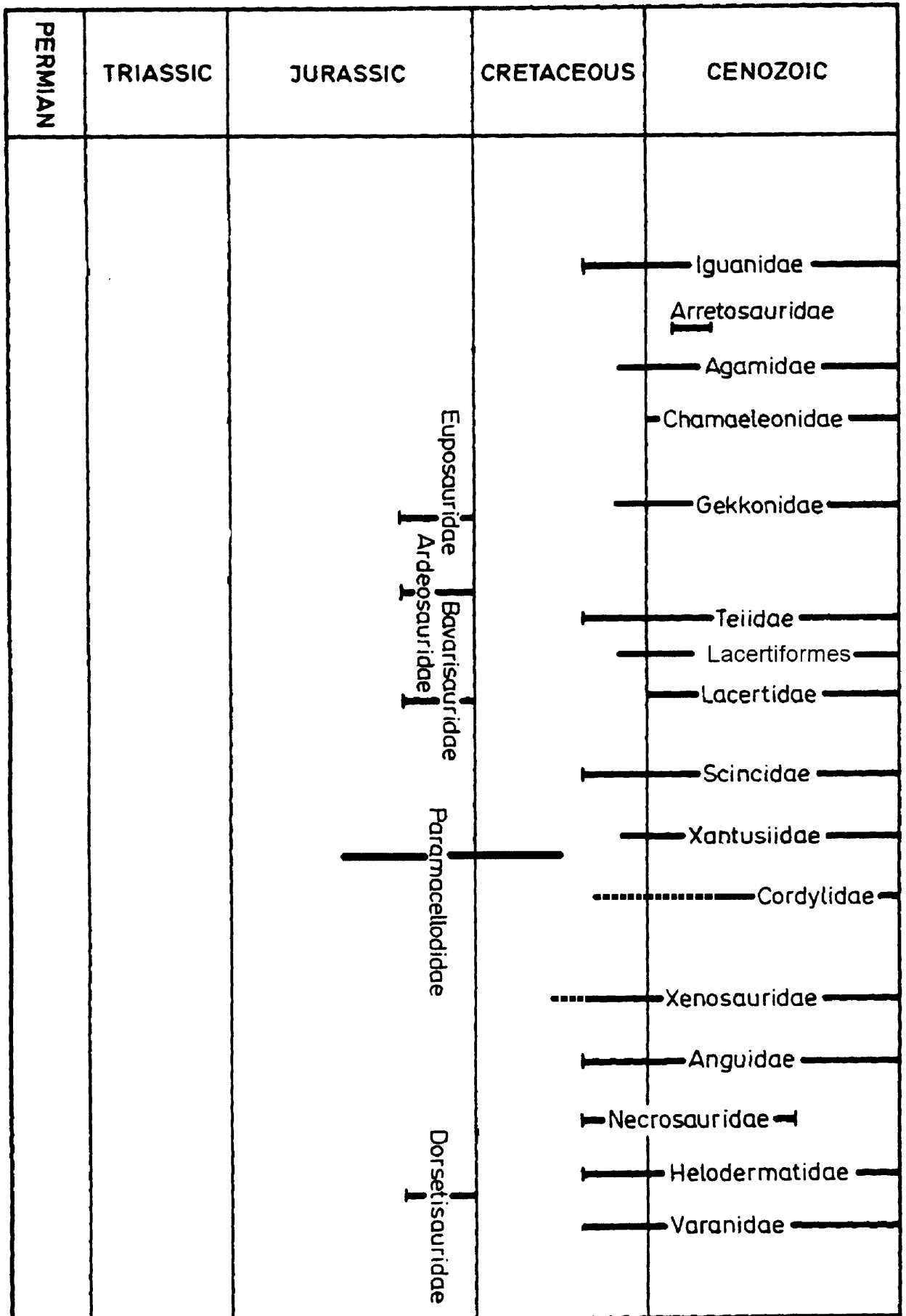


Fig. 5

Cladistics using numerical taxonomy is a method trying to reconstruct phylogenetic relationships. The cladistic program used here is "Phylogenetic Analysis Using Parsimony" (PAUP 3.1, SWOFFORD 1993). A matrix of character states for different taxa is required. The different character states are coded according to numbers representing the plesiomorph ("primitive" condition coded as 0) or apomorph state (derived conditions coded as 1,2 or 3 etc.). The trees are rooted by an outgroup taxon which must be defined, so that the importance of derived characters can be evaluated. The outgroup should be monophyletic and closely related to the ingroup taxa. This choice makes it more likely that the plesiomorphic character states are homologies rather than convergencies. The choice of the outgroup has a strong impact on the result. Also, an all plesiomorphic (all character states = 0) hypothetical ancestor can be chosen for the analysis. According to BORSUK-BIALYNICKA (pers. comm.) the philosophy behind the outgroup concept is that what is common outside a given ingroup is probably ancient (symplesiomorphy), i.e. inherited instead of "produced" by the ancestor of the ingroup (synapomorphy).

The software computes the most parsimonious tree, that is the shortest distance between all taxa. The distance is measured in steps, where each step represents one character state change from plesiomorph to apomorph state. In some cases, character reversals must be assumed, that is a change from the apomorph back to the plesiomorph condition. The result is one (or more) hypothesis in form of trees or cladograms, of the same (minimal) tree length. In many cases, more than one parsimonious tree is found. A consensus tree can then be calculated from the original trees. As all trees are equally parsimonious and therefore equally likely to represent the „true“ phylogenetic relationships, only the strict consensus tree is shown in this study, combining the whole information from the input trees. Therefore no 50% majority trees were calculated.

Consistency index (ci) and retention index (ri) are measures for the stability of the trees are found and given for any tree. The consistency index (KLUGE & FARRIS 1969) for a single character is defined as $c = m/s$. m represents the minimum amount of change that the character may show on any tree. s is the length (number of steps) required by the character on the tree being evaluated (FARRIS 1989, SWOFFORD & BEGLE 1993). Consequently c lies between 0 and 1. KLUGE & FARRIS (1969) state that c "is 1 if there is no convergence on the tree, and tends to 0 as the amount of convergence on the tree increases." But SWOFFORD & BEGLE (1993) say that "unfortunately, the lower bound on c is not 0 but is a function of the distribution of character-states in the data matrix." He gives an example where c can be no lower than 0.5. Therefore, FARRIS (1989) proposed two new indices to scale the consistency index between 0 and 1: The retention index is defined as $r = (g-s)/(g-m)$. g is the greatest amount of change that the character may require on any tree evaluated (FARRIS 1989; SWOFFORD & BEGLE 1993). It can lie between 0 and 1. There are also other indices measuring the stability of the trees, which can be calculated for every tree. The present study only uses the conventional indices consistency- and retention index, because only these can be compared to the ones obtained in previous works by ESTES et al. (1988), EVANS & CHURE (1998) and LEE (1998).

HENNIG (1966, 1969) defined the methodology of cladistics and used a cladistic approach to formulate hypotheses for the higher taxonomy and phylogeny of insects. Only shared derived characters are taken as evidence for close phylogenetic relationship. In his very strict rules, characters can only assume two states, that is either plesiomorph

or apomorph. Only in later versions, especially of the PAUP software package, multistate characters are allowed, that means that a character can have more than two character states, for example: the enclosure of Meckel's canal can be an open groove (state 0), enclosed by the dentary with a remaining suture (state 1) or the dentary tube is closed and fused (state 2). Different options can be chosen as to how the software deals with multistate characters. If they are ordered, character state 3 can only be achieved from character state 1 (plesiomorph condition), if character state 2 has been developed first. In contrast, unordered character handling allows evolution of character state 3 also directly from character state 1. This variability in character input is no longer congruent with HENNIG's idea of "pure cladistics". However, it is very useful when working with higher level taxa, because different representatives of some families might show a variety of character states.

Usually, a character matrix is established for the taxa in question, a numerical analysis is performed and the results discussed. In the present work a set of numerical analyses is made in order to take into account that different matrices, outgroups and taxon choices have an influence on the result. Therefore, data matrices from four authors (ESTES et al. 1988, EVANS & CHURE 1998 LEE 1998 and CALDWELL 1999) are used and then modified in order to test the results of previous analyses.

2.1.4 Previous cladistical work using numerical taxonomy

ESTES et al. (1988) did the first major cladistic study using numerical taxonomy of higher-level squamate phylogeny. Many later cladistical analyses are based on this paper. For their cladistical analysis, the authors used the PHYSYS package written by J.S. FARRIS as well as the PAUP software by D. SWOFFORD. At that time, options for treating multistate characters as unordered were not available, so they treated their characters as ordered. Other searching options and the software version are not given in the publication. An all-plesiomorphic ancestor was used for the computer analysis. The ESTES et al. (1988) matrix consists of 19 taxa and 148 characters.

EVANS & CHURE (1998) combined characters from ESTES et al. (1988) and GAUTHIER et al. (1988). They investigated the phylogenetic position of *Paramacellodus*, which is placed as a sister taxon of Scincoidea. A matrix of 212 characters was coded for 22 recent and fossil squamate ingroup taxa using the heuristic search option of PAUP 3.1 (SWOFFORD 1993) for their analyses. Rhynchocephalia was used as outgroup taxon. The multistate characters states were treated as unordered. These authors compiled mainly osteological and soft tissue characters from muscles, tongue and ear.

LEE (1998) compiled characters of ESTES et al. (1988), PRESCH (1988), CLARK & HERNANDEZ (1994), WU et al. (1996), EVANS & BARBADILLO (1997), LEE (1997), HALLERMANN (1998) and REYNOSO (1998) and a number of new characters. This set has 22 taxa and 230 characters, which are exclusively osteological. One reason for that was, that his study "attempts to investigate the impact of important new fossil taxa on phylogenetic relationships and character evolution, and these taxa can only be coded for osteological characters." Multistate taxa were interpreted as uncertainty and most of the character types were treated as unordered, some as ordered, depending if they form clear morphoclines or not. To root the tree LEE (1998) used a hypothetical ancestral taxon which possesses the character state of three successive outgroups to squamates: Sphenodontida, *Marmoretta* and Kuehnosauridae. LEE's analysis were performed by

using PAUP 3.1.1 (SWOFFORD 1993). As search options he used the "branch-and-bound" and the "heuristic search".

CALDWELL (1999) used 95 characters of which 89 were derived from the matrix of ESTES et al. (1988). As LEE (1998) did, CALDWELL (1999) used only osteological characters, including six new ones. He modified the state codings of more than half of the 89 characters. The remaining 41 characters by ESTES et al. (1988) either were not scored or subsumed in the character descriptions. The excluded characters were judged as redundant. CALDWELL analyses 26 extant and fossil taxa focusing on the relationships of snakes and mosasauroids.

As for the investigation on higher level taxonomy of Squamates all authors mainly used families as taxa. EVANS & CHURE (1998), LEE (1998) and CALDWELL (1999) included also fossil taxa in their analysis.

2.2 Material and methods

2.2.1 Material

Seven specimens of the new genus and species (including a cast) are available for the present work. Three specimens, including the designated holotype (SMF ME 3516, SMF ME 475a+b, SMF ME 1249a+b) are property of the Forschungsinstitut and Naturmuseum Senckenberg.

WDC-C-MG 122/123 belongs to the Wyoming Dinosaur Centre in Thermopolis and is part of the collection of Dr. POHL. The specimens SMNK-PAL 3813 and SMNK-Me 930a are property of the Staatliches Museum für Naturkunde Karlsruhe.

A cast of another specimen, exhibited in the Fossilien- und Heimatmuseum Messel, most probably also belongs to the new species described here. Unfortunately, it was impossible to trace the original specimen.

The specimen SMF ME 475a+b was found in Messel grid square F11 (Fig. 2), 0.5-1.5 m above Leithorizon alpha on September, 25th 1978, specimen SMF ME 1249a+b was found in Messel grid coordinates D9, 1.0-3.0 m above Leithorizon alpha on October, 1st 1982. SMNK-PAL 3813 was found in the early 80's on the fifth excavation level.

Extant material was used for comparative taxonomical and actuopaleontological studies (Tab. 1).

Species	Collection number
<i>Anolis equestris</i>	SMF 33231
<i>Basiliscus basiliscus</i>	SMF 67364
<i>Cordylus giganteus</i>	SMF 69842 SMF 69852
<i>Corucia zebrata</i>	SMF 81047 SMF 81048 SMF 81049
<i>Cyclura cornuta</i>	SMF 33229
<i>Dracaena guianensis</i>	uncatalogued
<i>Enyalioides ashaughnessyi</i>	SMF 67590
<i>Gekko gekko</i>	SMF 62320
<i>Gerrhonotus sp.</i>	SMF 69845 SMF 69846
<i>Iguana iguana</i>	SMF 33228
<i>Lacerta agilis</i>	SMF 44
<i>Ophisaurus apodus</i>	HLMD RA 1140 HLMD RA 1141
<i>Sceloporus magister</i>	SMF 58551
<i>Tiliqua nigrolutea</i>	SMF 33248
<i>Tiliqua scincoides</i>	SMF 33247
<i>Trachydosaurus rugosus</i>	SMF 33249/59034
<i>Tribolonotus gracilis</i>	SMF 80901
<i>Varanus bengalensis</i>	SMF 60428
<i>Varanus rudicollis</i>	SMF 67586
<i>Varanus salvadorii</i>	SMF 58064
<i>Varanus salvator</i>	SMF 33130 SMF 76293
<i>Varanus prasinus</i>	SMF 69649 LMA/Verteb.00/004 LMA/Verteb.99/030
<i>Zonosaurus laticaudatus</i>	uncatalogued

Tab. 1: Extant material used for comparative taxonomical and actuopaleontological studies.

2.2.2 Preparation

In the field, sediment packs are split with knives and vertebrate remains usually can be recognised by bone material on the sediment face. Stratigraphic and geographic position is then recorded. The find has to be kept wet at all times from the find up to final preparation. Evaporation of the high water contents in the sediment would cause cracks and thus destroy the specimen. The fossil is taken in total to the field research station, where its completeness is checked using radiographs. If parts are missing, the search goes on in adjacent sediment layers. The sediment is carefully removed from one side of the fossil with scalpels and needles. KÜHNE (1961) first recommended the “transfer

method” for the Messel fossils, a method which was used before for palaeobotany. A rectangular frame of clay or wood is modelled around the specimen and epoxy resin is poured into it. Formerly glass fibres were added into the resin. After drying, the remaining sediment layers are prepared from the back side. As a result of this transfer method, the fossil is embedded in artificial resin and can be kept dry and is ready for scientific analysis or display in the museum (ACKERMANN et al. 1992).

2.2.3 Documentation

Overviews and details of the specimens were scanned by the author as high resolution digital images. Specimen SMF ME 3516 was scanned with the assistance of Mrs. Beate Wesselkamp, FIS. The following technical set-up was used, largely corresponding with the computer devices described in HABERSETZER & SCHAAL (1994, see there for further details). A KONTRON colour scanner (Type Progres 3012, Chip size: 9 x 6 mm) is mounted on a heavy working stand (to avoid vibration) and connected via a special interface board with a computer (Intel 80486 processor with 128 MB RAM). The stand has a total height of 2.35 m, the maximum working distance from the desk plate is 1.40 m. The computer software used for operating the scanner and digitising the specimens is WINCAM 2.0. Objects can be scanned in different resolutions and saved as bitmaps before being further processed for printing or image analysis. All specimens were scanned in the highest possible resolution which is the oversize format (3072 x 2048 pixel). For overview scans, a 20 mm Nikon lens was used, while details were scanned with a 35 mm KONTRON lens.

The overview and detail sketches of the specimens have been made by the author, as well as the other figures including the radiographs, if not otherwise stated.

In the frontoparietal region the specimens are covered by osteoderms. To identify the orientation of the underlying skull elements it was necessary to x-ray the specimens. The radiographs were made by a FAXITRON 805 (Hewlett Packard) device. Instead of a double-layer x-ray-film, a single-layer repro-film (CQL4 by DUPONT and TYPOPHOT TP-CA by TYPON graphic) was used. Compared to the double-layer x-ray-films, these repro-films brought equally good results as far as the resolution is concerned and could easily be developed in a developing machine (EASYCOMPACT 40 by DUPONT). The specimen SMF ME 1249a+b was x-rayed for five minutes (epoxy resin plate without glass fibres), WDC-C-MG 122/123 for 7:50 minutes (epoxy resin plate with glass fibres) with a tube voltage of 50 kV in a distance of 46 cm from the x-ray source (focus) on the second shelf in the exposure chamber. The tube current was in all cases around 2 mA. The film was put into a lightsafe paperbag, because the resolution is higher than using an x-ray cassette. For the two larger specimens SMF ME 475a+b and SMF ME 3516 the x-ray chamber was too small, so the "lower drawer" has been used (with a film-focus-distance of 94 cm). Accordingly, the x-ray exposure time had to be raised significantly (40 minutes, Tab. 2). To visualise the sutures of the skull components the x-ray beam has to go vertically through the suture. Therefore the specimens were tilted in different angles (+/-10 degrees, +/-20 degrees) in order to allow the x-ray beam to hit the suture perpendicularly.

Specimen	Tube voltage [kV]	Tube current [mA]	Exposure time [min:sec]	Position in exposure chamber	Film-focus-distance [cm]
SMF ME 3516	50	c. 2	40:00	lower drawer	94
SMF-ME 475a	50	c. 2	40:00	lower drawer	94
WDC-C-MG 122/123	50	c. 2	7:50	second shelf	46
SMNK-PAL 3813	50	c. 2	6:00	second shelf	46
SMF-ME 1249a/b	50	c. 2	5:00	second shelf	46
SMNK-Me 930a	50	c. 2	2:25	second shelf	46

Tab. 2: X-ray setting of the Faxitron 805 device for the radiographs taken in this study.

2.2.4 Cladistical methods using numerical taxonomy

In a first step, the cladograms presented by authors dealing with squamate cladistics using numerical taxonomy (ESTES et al. 1988, EVANS & CHURE 1998 and LEE 1998) were tried to be reproduced and possible contradictions are discussed. In a next step, the character states of the new taxon are included in the different matrices without judging these cladograms a priori. In order to test the information yielded in osteological characters, PAUP analyses are performed with osteological characters only. The matrices will be reduced in a next step on characters, that are only visible in the new taxon to test the significance of these characters. If the results from the matrices place the new taxon congruently in one specific infraorder, the matrix will be reduced to this infraorder. All characters in the matrix will be retained. In all of the analyses, the outgroups chosen by the respective authors of the matrices are used here, as well.

At this point it should be stressed that PAUP is used here as an experimental tool for the formulation of phylogenetic hypotheses. The results are critically discussed and compared to those gained from comparative morphology.

The matrices of ESTES et al. (1988), EVANS & CHURE (1998), LEE (1998) and CALDWELL (1999) were used. The runs were carried out with the software PAUP 3.1.. Because of their relatively high number of taxa, all authors (search option of ESTES et al. 1988 unknown) mainly used the heuristic search. This option was used in the present study as well, as an exhaustive search is not practicable beyond 11 taxa (SWOFFORD & BEGLE 1993). The maximum number of trees to be saved was set to the highest possible value (32767). Two search strategies were applied:

1. Stepwise addition - **simple** addition sequence.

Stepwise addition implies that taxa are connected, "one at a time, to a developing tree until all taxa have been placed. Three taxa are chosen for the initial tree". After each round only that tree with the shortest length is saved for the next round. This is repeated until all taxa have been joined. The addition sequence decides which three taxa will be joined initially. The simple addition sequence connects the taxa in a simple algorithm: "First, the distance between each taxon and a reference taxon is calculated [...] the reference taxon and the two taxa closest to it form the initial three-taxon tree, and the remaining taxa are added in the order given by their rank in the array of advancement indices" (SWOFFORD & BEGLE 1993).

2. Stepwise addition: **random** addition sequence with number of replicates = 100. Same as above, but for a random addition sequence a pseudorandom number generator is used to obtain a permutation of the taxa to be used as the addition sequence.

Branch-swapping was applied to both search options with the setting: tree bisection-reconnection (TBR) and save all minimal trees (MULPARS). "Branch swapping" is a heuristic method performing sets of predefined rearrangements. The most effective algorithm is the tree bisection-reconnection (TBR), where "the tree is bisected along a branch, yielding two disjoint subtrees. The subtrees are then reconnected by joining a pair of branches, one from each subtree. All possible bisections and pairwise reconnections are evaluated" (SWOFFORD & BEGLE 1993).

Since the second search strategy is more thorough and was used also by LEE (1998) and CALDWELL (1999), this was chosen as search option for the present study.

In ESTES et al. (1988) multistate characters were treated as ordered, because there was no "unordered" option in their software version. But they suggested to treat multistate characters as unordered in future studies. Accordingly the characters of their matrix were treated here as unordered. Following ESTES et al. (1988), Serpentes, Dibamidae and Amphisbaenia were excluded in this study. They think it "possible that the limblessness and correlated characters swamp the analysis, linking distantly related forms [...]" (ESTES et al. 1988: 138). The question in the present study is the phylogenetic position of the new taxon within the Lacertilia, so these groups were not considered. Although ESTES et al. (1988) give data for *Sphenodon* in the matrix, they chose an all-plesiomorphic ancestor as outgroup for the computer runs.

As done in EVANS & CHURE (1998), characters of their matrix were treated as unordered and also the heuristic search option was used with Rhynchocephalia as outgroup taxon.

Using the matrix of LEE (1998) the multistate characters were treated as ordered or unordered following his specifications. Three outgroup taxa (Sphenodontidae, *Marmoretta* and Kuehnosauridae) were used to infer the "primitive" condition as coded in the ancestor.

As in the matrix of CALDWELL (1999), multistate characters were unordered. *Sphenodon* (Rhynchocephalia) was used as outgroup. As recommended by CALDWELL (pers. comm.), all taxa were retained when analysing the phylogenetic relationships of the new genus and species.

In the tree descriptions, there is a difference between "+" and "and". By convention, (Taxon A + Taxon B) means the higher clade comprising both Taxon A and B. This notation avoids creating new names for every clade that is found in a cladistical analysis. Doing so would almost double the names for taxa. The second option using "and" between two taxa does not imply a phylogenetic relationship, but is rather an enumeration of taxa.

2.2.5 Terminology

The terminology of skull and mandible elements is adopted from OELRICH (1956), ROGERS (1986, Fig. 6) and RAUSCHER (1992, Fig. 7). In figures and tables the Latin spelling for the elements (e.g. Praemaxillare) was used, but for readability within the text mainly the English spelling as in ESTES (1983) was preferred (e.g. Premaxilla), except for technical terms from RAUSCHER (1992). The plural form of the Latin noun “Processus” is identical with the singular form in spelling, although the “u” is prolonged in pronunciation. Therefore, in the following text the plural form will be marked by an underlined “u”.

Fig. 6 (following page): Terminology of skull and mandible elements. A: Dorsal skull of *Varanus*. B: Lateral skull and mandible. C: Ventral skull. D: Mandible (modified from ROGERS 1986).

Fig. 7 (following pages): Detailed terminology of skull and mandible elements distinguishable in the new taxon (from RAUSCHER 1992). A-C: Praemaxillare of *Lacerta agilis*. A: Dorsal. B: Ventral. C: Lateral, dexter. D+E: Right Maxillare of *Lacerta viridis*. D: Externally. E: Internally. F+G: Right Dentale of *Lacerta viridis*. F: externally. G: internally. H+I: Left Coronoid of *Lacerta agilis*. H: Externally. I: Internally. J+K: Left Jugale of *Podacris muralis*. J: Externally. K: internally. L+M: Left Pterygoid of *Ophisaurus apodus*. L: dorsal. M: ventral. N+O: Right Quadratum of *Ophisops elegans*. N: Rostral. O: Caudal. P+Q: Basioccipitale of *Lacerta vivipara*. P: Dorsal. Q: Ventral. ab – Area basisphenoidea; ac – Area coronoidea; al – Area lacrimalis; ame – Area maxillaris exterior; ami – Area maxillaris interior; ap – Area palatina; apa – Area postfrontalis anterior; app – Area postfrontalis posterior; at – Area transversa; cbd – Cornu basisphenoideus dext.; cbs – Cornu basisphenoideus sin.; cc (Pterygoid) – Pars anterior cristae columellaris; cc (Quadratum) – Condylus cephalicus; ccp – Pars posterior cristae columellaris; cd – Crista dentalis; cf – contactline between Lamina horizontalis and splenialis; ci – Carina inferior; cm (Jugale) – Crista medialis; cm (Quadratum) – Condylus mandibularis; com – Condylus occipitalis medialis; cp (Quadratum) – Crista pterygoidea; cp (Coronoid) – Crista praearticularis; ct – Crista tympani; ctd – Crista transversa dorsalis; ctv – Crista transversa ventralis; cv – Crista ventralis; cz – Carina zygomatica; d – Dentes pterygoidei; ec – Epiphysis columnaria; en – Excavatio nasalis; f – Foramina pro rami nervorum alveolarium superiorum/inferiorum; fa – Facies anterior; fb – Facies buccalis; fc (pterygoid) – Fossa columellae; fc (Coronoid) – Facies coronoidea; fd – Facies dentalis; fdo – Facies dorsalis; fi; Facies interna; fl – Facies lingualis; fp – Facies posterior; fsp – Facies sphenoidea; ft (Pterygoid) – Facies temporalis; ft (Quadratum) – Fossa tympanica; ftr – Facies transversa; fv – Facies ventralis; fze – Foramen zygomaticum exterior; fzi – Foramen zygomaticum interior; ic (Pterygoid) – Incisura cristae columellaris; ic (Dentale) – Incisura coronoidea; in – Incisura nasalis; ip – Incisura pterygoidea; is – Incisura postfrontalo-squamosalis; iso – Incisura suborbitalis; lh – Lamina horizontalis; lp – Lobus praearticularis; ma – Margo anterior; med – Margo exoccipitalis dext.; mes – Margo exoccipitalis sin.; mb – Margo basisphenoideus; md – Margo dorsalis; mf – Margo fenestra exonaria; mo – Margo orbitalis; mom – Margo occipitalis medialis; mp – Margo posterior; msu – Margo supraangularis; mv – Margo ventralis; o – Orificium canalis nervi alveolaris superioris/ inferioris; pa – Processus angularis; pb – Processus basisphenoideus; pc (Quadratum) – pc (Dentale) – Processus coronoideus; Pars columnaria; pdi – Processus dentalis inferior; pds – Processus dentalis superior; pm (Praemaxillare, Jugale) – Processus maxillaris; pm (Coronoid) – Processus massetericus; pn – Processus nasalis; pp (Pterygoid) – Processus palatinus; pp (Maxillare) – Processus praemaxillaris; pprf – Processus praearticularis; pq – Processus quadratus; ps (Dentale) – Processus supraangularis; ps (Coronoid) – Processus splenialis; pt (Jugale) – Processus temporalis; pt (Quadratum) – Pars tympanica; ptr – Processus transversus; pz – Processus zygomaticus; sd – Sulcus dentalis; sis – Sinus supraangularis; sld – Sinus lateralis dext.; sls – Sinus lateralis sin.; smb – Sulcus metabasisphenoideus; sp – Sulcus pterygoideus; spb – Sulcus probasisphenoideus; suc – Sulcus coronoideus; sy – Symphysis mandibularis; tt – Tuberculum contracornoideum.

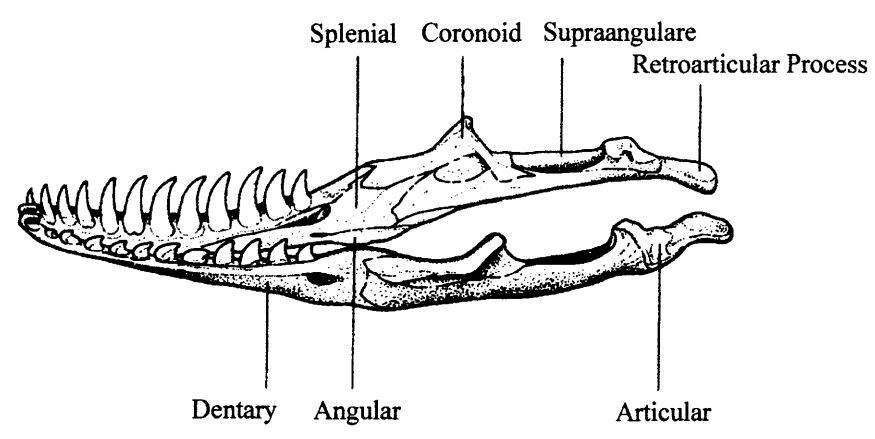
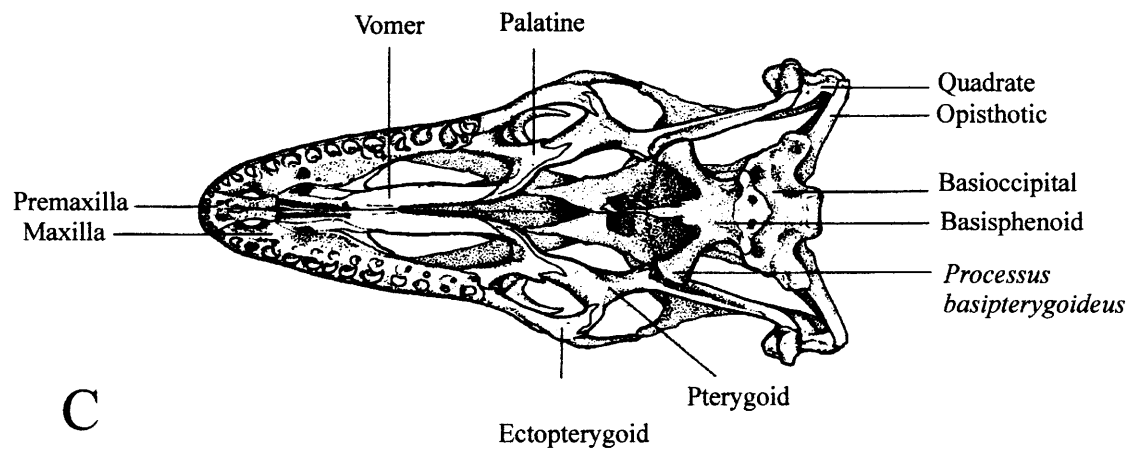
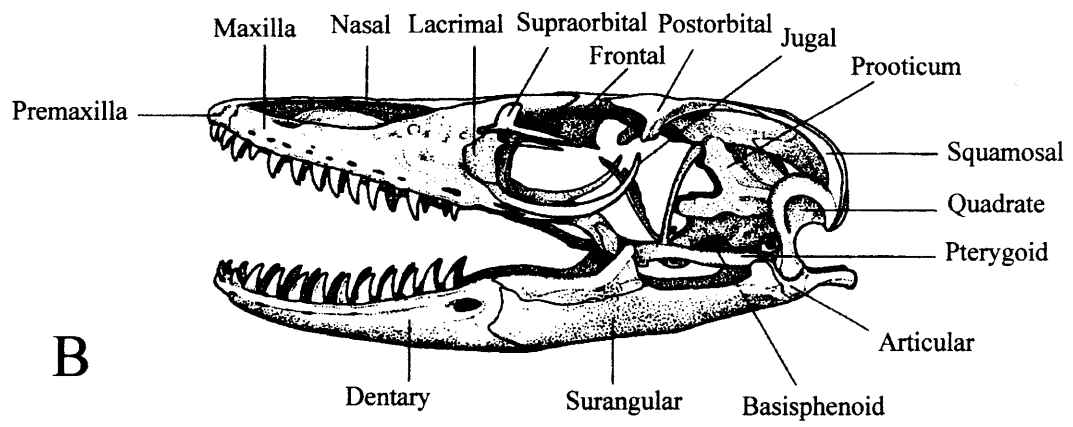
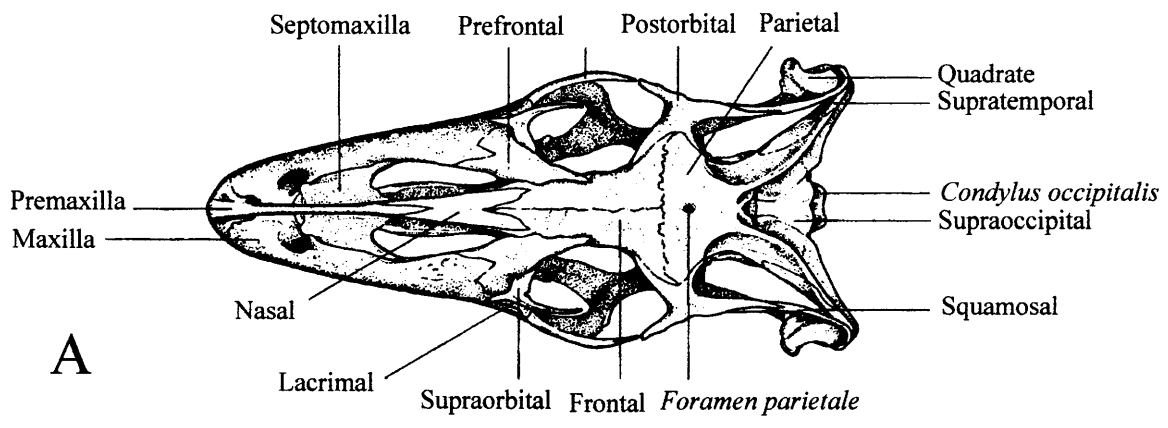


Fig. 6

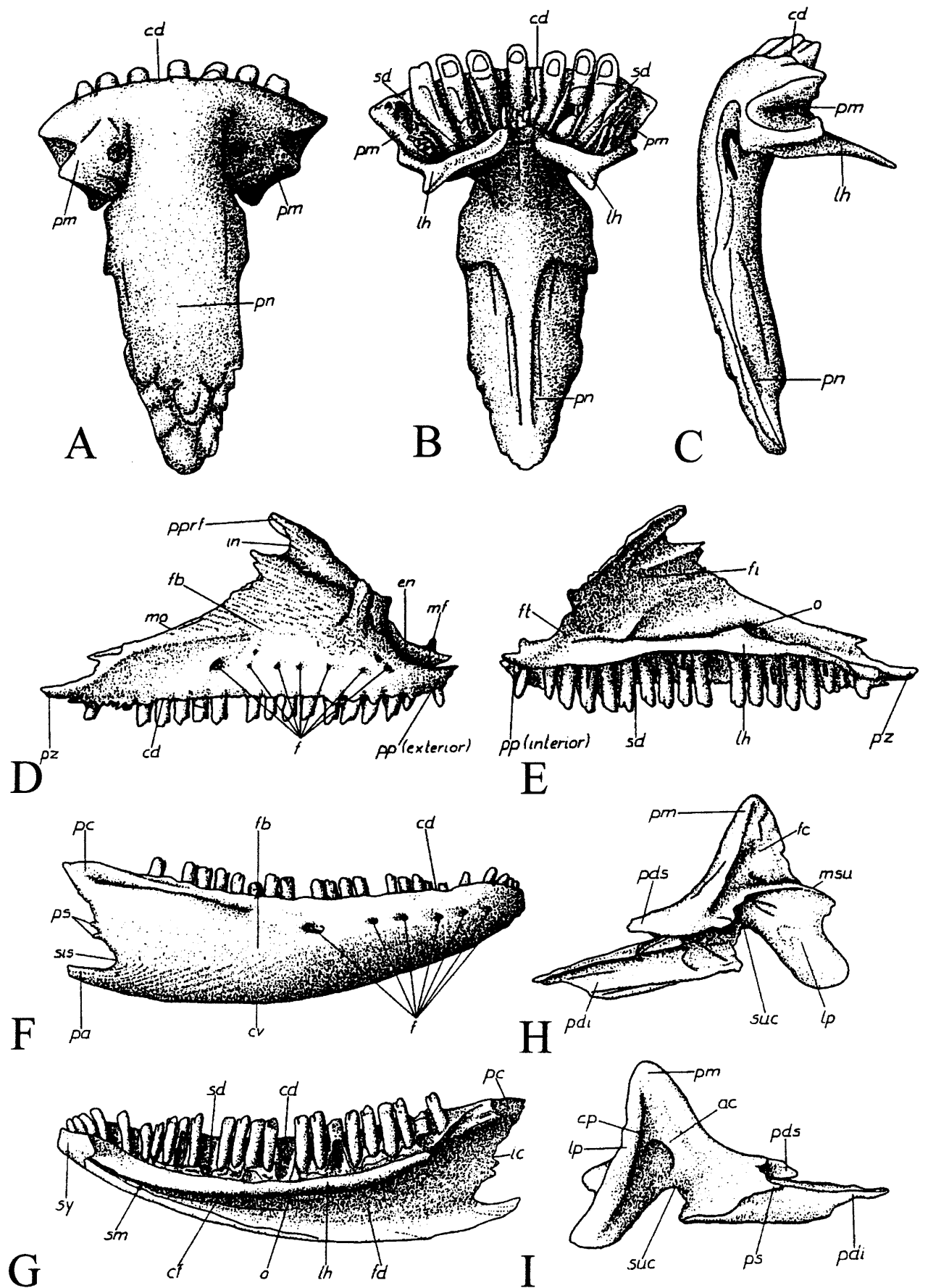
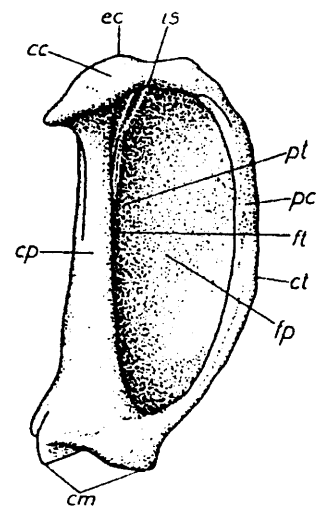
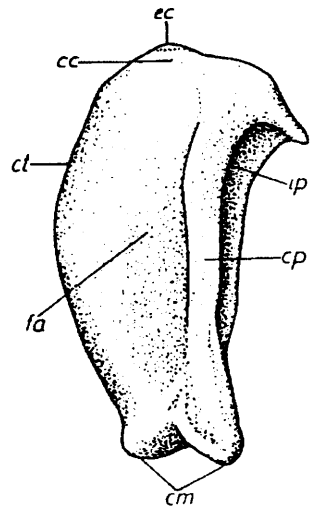
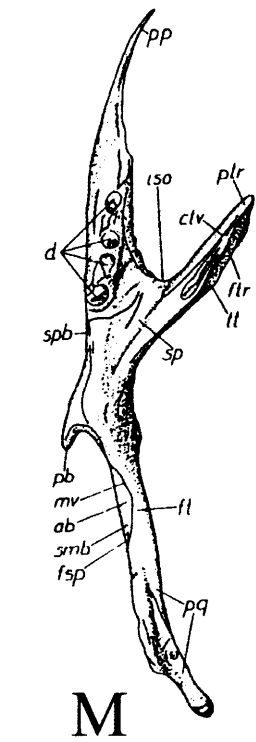
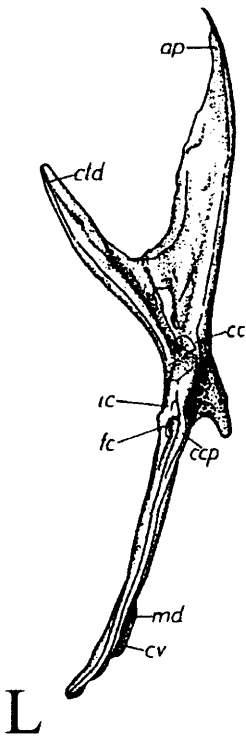
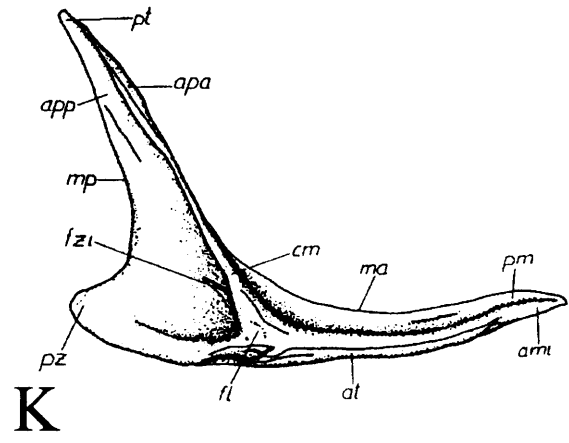
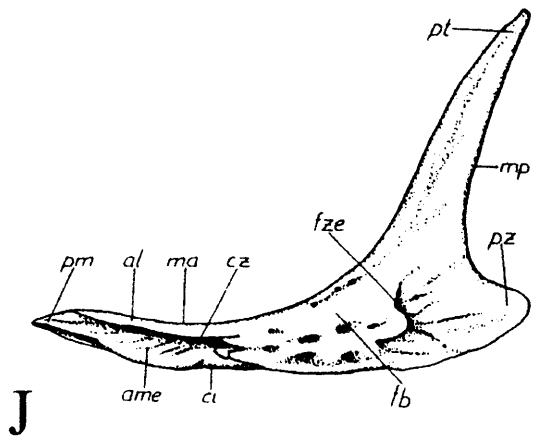


Fig. 7

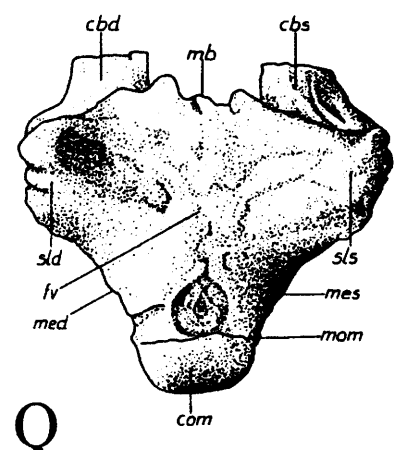
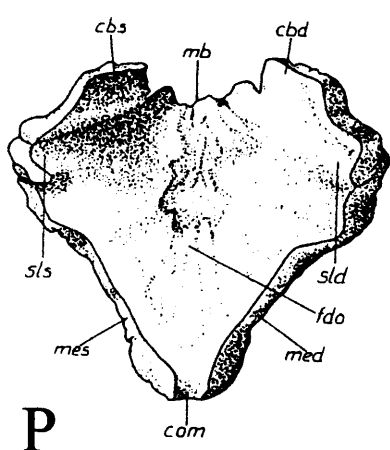


L

M

N

O



P

Q

Fig. 7

2.2.6 Abbreviations

E.r.: *Eolacerta robusta*

FIS: Forschungsinstitut Senckenberg (Senckenberg Research Institute)

G.l.: *Geiseltaliellus longicaudus*

LMA: Löbbecke Museum und Aquazoo, Düsseldorf

n.t.: new taxon

SEM: Scanning Electron Microscope

SMF ME : Senckenberg Museum Frankfurt Messel Collection Number

SMNK: Staatliches Museum für Naturkunde Karlsruhe

WDC-C-MG: Wyoming Dinosaur Centre - Collection - Messel Germany

2.3 Results

2.3.1 Systematic Paleontology

Superorder: Squamata MERREM 1820
Scleroglossa ESTES et al. 1988
Infraorder: Scincomorpha CAMP 1923
Superfamily: Scincoidea OPPEL 1811
Family: incertae sedis

Genus: nov. gen. (see remark below)

Diagnosis: As for type and only known species

Type species: gen. et spec. nov. (see remark below)

Remark: In order to prevent priority conflicts according to the „International Code of Zoological Nomenclature (1999)“ the new genus and species will be named in an official publication, which is to come after the disputation.

Synonymy: none

Material: Five articulated specimens, one isolated head with postcranial fragments, one cast. Designated holotype: SMF ME 3516; Designated paratypes: SMF ME 475a+b, WDC-C-MG 122/123, SMNK-PAL 3813; Additional material: SMF ME 1249 a+b, SMNK-Me 930a and a cast exhibited in the Fossilien- und Heimatmuseum Messel, of which the original specimen was not retraceable.

Stratigraphic and geographic occurrence: Messel Pit Fossil Site, Middle Eocene, Lutetium/Geiseltalium/MP11, near Darmstadt, Germany.

2.3.1.1 Diagnosis

An Eocene Scincoid, distinguished from all other species by the combination of scincoid, lacertid and unique character states:

- **Skull roof** heavily sculptured with unique pattern: Polygonal osteoderms on anterior skull region vermiculately sculptured; on posterior skull region spiny osteodermal crust with small spines standing more or less perpendicularly on skull surface, radially arranged on the parietal; Two or three rows of small spiny osteoderms projecting from rear end of skull forming a jagged crest (as in *Cordylus giganteus*) but with much smaller and more numerous spiny osteoderms.
- Lacertid arrangement of the four **supraorbitalia**, but with characteristic sculpture pattern.
- **Osteoderm** posterior to supraorbitalia with characteristic radial sculpture.
- **Osteoderms** on midline of nasofrontal area separated by a suture-like incision.
- Uniquely shaped **jugal**: more or less triangular with posterior process of jugal extending about half way back below the lower temporal fenestra, showing a gradual descending slope from the Processus temporalis to the Processus zygomaticus. Anterior process of jugal extends to the anterior most margin of the orbit.
- Fused **premaxilla** with five homodont, conical teeth, bearing apical lateral cutting edges.
- Processus zygomaticus of the **maxilla** extending to posterior margin of the orbit (as in *Tiliqua nigrolutea*, *Tiliqua scincoides*, *Trachydosaurus rugosus*, Scincidae).
- **Maxillary teeth** closely spaced and of scincoid type. Teeth in labial view: unstriated simple cones, tip more or less blunt, slightly pointed towards lingual side; teeth in lingual view: basal cross-section more or less rounded to oval, upper third of tooth lingually compressed so that the upper part of the tooth appears scythe-like in cross-section. Tip with longitudinal striations and anterior and posterior cutting edges.
- **Dentary teeth** closely spaced, showing same morphology as maxillary teeth (see above); Tip bears three to seven longitudinal striations; Teeth can be slightly recurved.
- **Dentary** makes up about 2/3 of the whole mandible extending back to the posterior margin of the orbit, showing a well developed Sinus supraangularis.
- Fused **articular/prearticular** with ridge along its lingual margin; retroarticular process, with small tubercle or flange on posteriomedial margin (as in Scincidae and Cordylidae).
- **Coronoid** with prominent, steep dorsal process and relatively small rounded ventral process.
- **Supra-angular**: short and compact, extends anteriorly well beyond the coronoid, with ridge on labial side (similar to *Tiliqua scincoides*).
- **Quadrate** straight and slender with a straight Crista tympani; Crista pterygoidea and Crista tympani with almost parallel orientation; Facies anterior with weakly developed ridge, more or less parallel to the Crista tympani disappearing in the lower part of the Facies anterior (as in *Tiliqua scincoides*, *Tiliqua nigrolutea*, *Trachydosaurus rugosus*, and *Cordylus giganteus*).
- **Clavicle** is a simple rod with distal end slightly broadened and curved anteriorly.
- Symphysial process of **pubis** anteriorly or even anteriodorsally directed.
- Neural spines of the **dorsal vertebrae** tall, straight and axe-shaped over whole length of the trunk.

- **Tail** almost 3.5 times as long as the head-trunk length with exceptionally high vertebrae number (at least 95).

2.3.1.2 Description

All specimens, except SMNK-Me 930a, are more or less completely articulated and well preserved, but partly heavily compressed and crushed. They are embedded in lateral or dorsolateral view. The smallest specimen (SMF ME 1249a+b) has a head-trunk length of about 13 cm, its skull is 5 cm in length. SMNK-Me 930a and the cast are about the same size. A larger one (WDC-C-MG 122/123) has a head-trunk-length of about 16 cm with a skull length of 5.6 cm. The three largest specimens (SMF ME 475a, SMF ME 3516 and SMNK-PAL 3813) are about equal in size with a head-trunk-length of 20-21 cm and head length of 6.4 to 7.5 cm. In Tab. 3 the dimensions and proportions of the skeletal elements of all specimens are given. The proportions of the skull and limbs to the head/trunk length is almost similar in all specimens.

2.3.1.2.1 Specimen SMF ME 3516, designated holotype

This large specimen (Fig. 8, Fig. 9) is embedded on a single plate. It is the most complete one, with limbs as well as the tail, which is extremely long and its end curled up ventrally. The trunk is visible in its right lateral, the head in its dorsolateral aspect. The head/trunk length is 20.3 cm of which the head measures 7.5 cm.

Skull

Dermal roof shield

Premaxilla. – The fused premaxilla shows its dorsolateral side, probably bearing rather a long Processus nasalis, which is broken and incomplete. It has slightly shifted ventrally and consequently is not any more articulated with the maxillaria. Only two premaxillary teeth are visible. It is not possible to count them on the radiography since they cannot be distinguished from the underlying dentary teeth of the left ramus of the mandible.

Maxilla. – The right maxilla is visible from its external (labial) side. The Processus praefrontalis is concealed by osteoderms, whereas the straight vertical margin of the Processus praemaxillaris is distinctly visible. The Facies buccalis is furrowed anteriorly and compressed. The relatively pointed Processus zygomaticus reaches back to the posterior margin of the orbit. About 22 maxillary tooth positions are present, 16 teeth are preserved. The lateral cutting edges of the labially smooth maxillary teeth are visible. Some teeth are slightly recurved. The anterior part of the left maxilla is preserved and shows the Facies interna. The Lamina horizontalis and the teeth are concealed. However, on the radiography about 18 teeth can be recognised (Fig. 8D).

Tab. 3: Dimensions and proportions of skeletal elements as well as tooth and vertebrae counts of the new genus and species in the seven specimens. Due to the preservation of the skeletal elements, the measurements are not exact and can vary in a range of several millimetres. Pm = Processus maxillaris, Pp = Processus praemaxillaris, Pz = Processus zygomaticus, Pr = Processus retroarticularis. All measurements in millimetres.

Length of [mm]	SMF ME 3516	SMF ME 475a	WDC-C-MG 122/123	SMNK -PAL 3813	SMF ME 1249a/b	SMNK-Me 930a	Cast
Skull	75	70	56	64	50	>45 (incomplete)	c. 40
Head/trunk	203	220	160	204	130	?	c. 134
Maxillare (Pp to Pz)	35	40	30	c. 34	26	?	?
Jugale (Pm to Pz)	>21	25	>19	27 (incomplete)	18	?	?
Mandible (ant. tip to P)	>55	63	48	?	43	?	c. 38
Dentale (labial)	>37	38	30	?	28	?	c. 25
Tail	710	280 (incomplete)	38 (incomplete)	?	?	?	>35 (incomplete)
Humerus	44	?	33	c. 35	>27 (incomplete)	?	c. 20
Radius/Ulna	37	?	22	c. 33	?	?	c. 18
Femur	43	?	31	>27 (incomplete)	25	?	c. 24
Tibia/Fibula	27.5	?	20	>25 (incomplete)	17	?	c. 15
4th digit of manus	40	?	30	c. 37	?	?	c. 18
4th digit of pes	60	?	37	?	25	?	c. 28
Count tooth position of Premaxilla	5?	?	5	?	?	?	?
Maxillare	22	27	>19	>12 (incomplete)	20	?	>12 (incomplete)
Dentale	23?	27	23	>23 (incomplete)	>20	?	>12 (incomplete)
Presacral vert. number	>21	>24	>26	28	26	?	?
Caudal vert. number	>95	>32 (incomplete)	?	?	?	?	?
Proportions of skull to head/trunk length	0.37	0.32	0.35	0.31	0.38	?	0.3
Head/trunk to Forelimb length	1.67	?	1.88	1.94	?	?	2.39
Head/trunk to hindlimb length	1.56	?	1.82	?	1.94	?	2

Tab. 3

Nasalia. – The nasalia are partly covered by osteoderms and the right maxilla. How far they reach back or if they are paired or fused is not visible. No outline could be seen on the radiography.

Frontalia, praefrontalia, postfrontalia/postorbitalia and parietal are covered by well preserved and heavily sculptured osteoderms. These show a characteristic pattern: The anterior skull region (prefrontal, frontal) is covered by vermiculately sculptured polygonal or rounded osteoscutes. Four supraorbitalia are present, two large scales are separated by a straight suture. A small supraorbital anterior and posterior to the large scales bordered by a marginal row of small slender scales are covering each orbit dorsally. Posterior to the supraorbitalia lies a rather large osteoderm on each side of the skull. It bears a spiny scutellation more or less perpendicularly and radially arranged towards the centre. The posterior skull (postorbital/postfrontal, parietal) bears a spiny osteodermal crust with the small spines more or less perpendicularly arranged to the skull surface and oriented towards the centre of the parietal. Three rows of perpendicularly oriented osteoscutes are projecting from the rear end of the skull, showing a jagged crest. On the midline of the nasofrontal area several osteoderms are separated by a distinct "fissure". The right orbita is concealed by the supraorbitalia. On the radiography the shape of the elements cannot be recognised.

Jugal. – Only the right jugal can be seen. It is slightly disarticulated from the maxilla, so that the furrowed Area maxillaris exterior is visible, showing a foramen. The Processus temporalis is covered by osteoderms. The well rounded prominent Processus zygomaticus can be observed. The anteriormost part of the Processus maxillaris and of the Area maxillaris exterior is deformed and shifted onto the right supraorbitalia.

Lacrimalia and Supratemporalia cannot be identified.

Squamosal. – Only the posterior part of the right squamosal is visible, the anterior part is concealed by osteoderms. It has slightly shifted posteriorly and is not any more articulated with the quadrate.

Palatal complex

Quadrate. – The right quadrate, visible in lateral view, is still articulated with the articular. The Crista tympani terminates in a small tubercle just above the Condylus mandibularis. The Condylus cephalicus has shifted anteriorly. In its resting position, the quadrate obviously was not directed vertically, but obliquely with the Condylus cephalicus directed posteriorly. The quadrate is slightly deformed and therefore not any more straight but a little curved posteriorly. Other palatal elements cannot be determined since they are covered by elements of the dermal roof.

Fig. 8: Gen. et spec. nov., designated holotype SMF ME 3516. **A:** Overview showing the long, ventrally curled up tail. **B:** Head and trunk. Intestinal contents are preserved in dark area of the lower thoracal region. **C:** Head with the well preserved and characteristic osteodermal cover. **D:** Radiography overview, optimised for the head region.

Fig. 9: Line drawing of the designated holotype SMF ME 3516 with identified skeletal elements.



Fig. 8A



Fig. 8B



Fig. 8C

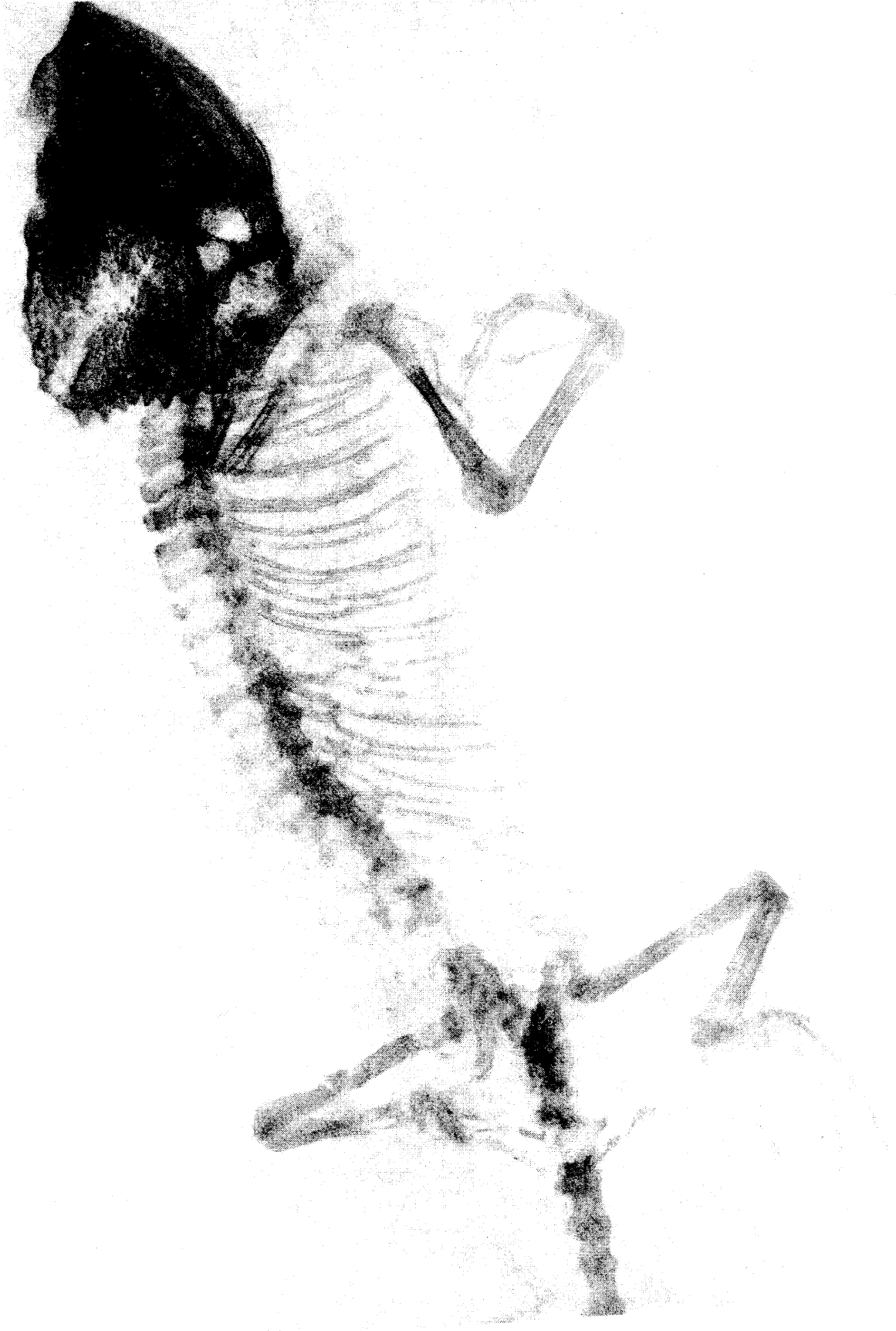


Fig. 8D

Braincase

For the largest part, the braincase is concealed as well, but posterior to the quadrate and below the squamosal lies an element which, most probably, represents a part of the right *exoccipital*. Other elements of the braincase are not identifiable.

Mandible

The right ramus of the mandible is visible in labial view, whereas the left ramus only shows the lingual view of its *Symphysis mandibularis*.

Dentary. – The elongated dentary represents about 2/3s of the mandible, extending back to the posterior margin of the orbit. Parallel to the *Crista dentalis* about nine foramina can be seen on the *Facies buccalis*. The posterior part of the *Facies buccalis* is compressed, probably along the *Sulcus meckeli*. The quite distinct *Sinus supraangularis* of the dentary can be observed. The dentary teeth are only visible on the radiography since they are covered by the maxillary teeth (Fig. 8D). About 23 dentary teeth can be determined. Since there are a lot of cracks in the ventral region of the dentary a *Processus angularis* was not identifiable.

Coronoid. – Since the skull is still almost completely articulated, the right coronoid is covered by the maxilla and the jugal, therefore only the relatively small ventral process is visible. On the radiography the outline of the prominent and steep *Processus massetericus* can be observed (Fig. 8D).

Supra-angular. – The dorsal part of the short compact supra-angular is partly covered by the *Processus zygomaticus* of the jugal. The supra-angular ridge is distinct. Only towards the dentary the suture is identifiable. No supra-angular foramina are visible.

Angular. – Since the mandible is deformed and bears a lot of cracks in that part, the angular could not be distinguished.

Articular/Prearticular. – These elements are considerably deformed and compressed, but the articular is still articulated with the quadrate.

Postcranial skeleton

Axial skeleton

As in the other specimens the *vertebrae* are embedded laterally and the high, axe-shaped neural processes are visible. There are at least 22 completely articulated presacral and 95 caudal vertebrae. On the posterior part of the tail (starting from about the 45. vertebra) several vertebrae show the right limb of the probably V-shaped haemal arch. If the „limbs“ are still attached is uncertain, since the vertebrae are embedded laterally. It seems that four of the posterior trunk vertebrae show an exceptionally long dorso-caudally directed transverse process, which is peculiar. The simple, elongate *dorsal ribs* are still more or less articulated. Several are broken. No rib segments could be identified. The blunt tips are flattened. As in the other specimens, it seems as if the last two or three posterior presacral vertebrae lack ribs, to those the term "lumbar

vertebrae” may be applied (HOFFSTETTER & GASC 1969). Remnants of the sternum and probably of meso- and/or xiphisternal ribs are present.

Pectoral girdle

Together with the coronoid the right slender scapula, with a broadened dorsal and ventral margin, still forms the glenoid fossa. The anteriorly curved rodlike clavicle lies along the anterior margin of the scapula. Its ventral tip as well as the anterior part of the coronoid is concealed by bone fragments, therefore no emarginations can be identified. The dorsal part of the scapular blade and the clavicle is flattened and partly crushed. Neither elements of the left part of the pectoral girdle nor the interclavicle are visible.

Pelvic girdle

The pelvic girdle is still articulated with the limbs. The elongated, slender ilia are visible and directed posteriodorsally. The dorsal margin is slightly curved and seems to taper towards its caudal process. Except for the ilium, the elements of the left half of the pelvic girdle are concealed by the sacrum. Below the right ilium lies the considerably deformed ischium. Its anterior process is pointed and directed anterodorsally. Only part of the acetabulum is visible. A pubis seems not to be preserved.

Pectoral appendages

The right pectoral limb is almost completely articulated, but it is not any more connected with the glenoid cavity of the pectoral girdle. The humerus lies almost parallel to the vertebral column. It has a relatively long and slender shape with broadened articulating surfaces. It is secondarily flattened except for a part in the middle. The olecranon of the ulna is visible. The sigmoid notch still articulates with the trochlear condyle of the humerus. Both epipodials are still in contact with the carpalia, which are difficult to distinguish. The proximal carpalia, radiale and ulnare are very indistinct, the distal carpalia 2, 3 and 4 can be recognised. The metacarpalia of digit ?II, III and IV are still in connection with the distal carpals. The metacarpal of digit ?V is concealed. Digit I could not be identified. The manus shows the typical phalangeal formula (2?),3,4,5,3. The Phalanges are relatively long, digit IV has about the length of the ulna. The digits are still bearing their deeply curved unguis phalanges. Between digit III and IV a few epidermal scales can be recognised. Covered by the anterior dorsal ribs lies the left limb. On the radiography, the humerus as well as radius and ulna become visible (Fig. 8D). The scapula conceals the ventral part of the humerus. The epipodials seem to be still attached to the humerus, their ventral part is not preserved. Except for a few phalanges of three digits which are situated below the right humerus, part of the carpalia as well as most of the left manus are concealed by the humerus of the right limb.

Pelvic appendages

Both posterior limbs are more or less complete, the right femur is slightly dislocated from the acetabulum of the pelvic girdle. Pro- and epipodials are flattened. The left limb is considerably compressed. The femur has about the length of the humerus and seems to be somewhat curved, moderately expanded proximally and distally. The distally situated medial and lateral condyles are not distinctly visible. The epipodials are slightly dislocated but still somewhat attached to the propodials. The slender fibula of the left limb lies on the stouter tibia, their distal articular surfaces are indistinct. Along the right tibia lies the fibula, both are still attached to the tarsalia. Between the femur and

the epipodials, sesamoid bones as a Patella tibialis and a parafibula seem to be present. The tarsals of the left limb are deformed and indistinguishable, whereas a few tarsal elements could be identified in the right limb. Whether the proximal tarsals astragalus and calcaneum are distinct or fused cannot clearly be decided. Two distal tarsals can be identified, most probably representing the 3rd and larger 4th tarsal. The right pes is completely preserved and articulated. The 5th metatarsal is stouter and shorter than the metatarsals I-IV. Digit III partly conceals digit II. As expected the phalangeal formula is 2,3,4,5,4. All five ungual phalanges are present, but incomplete in digit I and V. The left foot is incomplete and partly covered by the vertebral column. The three remaining metatarsals are much deformed. Digit ?II and III below the vertebral column show their ungual phalanges.

2.3.1.2.2 Specimen SMF ME 475a+b, designated paratype

SMF ME 475a (Fig. 10, Fig. 11) is a specimen embedded in lateral view, no limbs are preserved (except part of left humerus and femur) and the incomplete tail has a length of about 28 cm. This specimen is declared as a designated paratype because e.g. the jugal, teeth and mandible are very well preserved, showing important diagnostic features. With a head-trunk length of 22 cm (head: 7 cm) it is largest of the specimens investigated here. SMF ME 475b shows only a part of the anterior trunk region with a remnant of the right humerus.

Skull

Dermal roof shield

Premaxilla. – The premaxilla shows its left lateral view with two visible conical teeth, one of which is broken. Because of its lateral orientation the Processus nasalis is concealed.

Maxilla. – The left maxilla is visible in external view. The Processus zygomaticus extends to the posterior margin of the orbit, the anterior region of the Facies buccalis is pitted and more or less furrowed; About seven or more foramina are oriented parallel to the Crista dentalis. The maxilla bears around 27 pleurodont closely spaced tooth positions, 23 teeth are preserved. In labial view the teeth are simple cones, not striated with a smooth surface and a more or less blunt tip (Fig. 53A, p.117), which is slightly pointed to the lingual side, each tooth bears an anterior and posterior cutting edge. Maxillary teeth are not visible in lingual view.

Nasalia are not visible.

Frontalia, praefrontalia, postfrontalia/postorbitalia, parietal. – Because of the lateral position of the head these elements are not visible. As can be seen on a photograph made before transferring the specimen onto artificial resin, praefrontalia, frontalia, postorbitalia/postfrontalia and parietal table are covered by heavily sculptured osteoderms. A bowed element on the rear end of the skull is possibly the Processus exoccipitalis sinister of the parietal.

Jugal. – Only the left jugal is visible. It is a more or less triangular element with a posterior process (Processus zygomaticus) which extends about half way back below the lower temporal fenestra. The Margo posterior shows a gradual descending slope from the strongly built Processus temporalis to the Processus zygomaticus. The Facies buccalis is more or less pitted or sculptured with ten or more recognisable foramina. The anterior process of the jugal (Processus maxillaris) extends to the anterior most margin of the orbit, as well as the slender Carina zygomatica.

Lacrimals cannot be determined.

Squamosal. – The visible left squamosal is partly covered by osteoderms and somewhat twisted dorsally. It has a more or less slightly bowed elongated shape and is broadened posteriorly with a fine carina extending from the anterior to the posterior end, which is bearing a foramen.

Supratemporal. – An element below the squamosal probably represents a part of the left supratemporal which is also twisted dorsally.

Palatal complex

Quadrates. – The well preserved left quadrate slightly shifted rostrally and is twisted showing its caudal view. It is a straight, slender bone with a straight running Crista tympani. Crista pterygoidea and Crista tympani are almost oriented parallel to one another. It is not any more articulating but still in contact with the articular condyle and the squamosal. Part of the Condylus mandibularis has broken off. The right quadrate shows almost its rostral view, only the Crista pterygoidea is visible. The Facies anterior has a slightly developed ridge, which disappears in the lower part of the Facies anterior, it is arranged more or less parallel to the Crista tympani. The Condylus mandibularis is still attached to but not any more articulated with the articular condyle.

Pterygoid. – Below the left mandible lies the squashed right pterygoid in lateral view. It has a long and slender Processus palatinus. The Processus transversus broke off and the Processus quadratus could not be identified. The pterygoid has about 11 pointed, conical, partly broken teeth. On two teeth fine striations are recognisable.

Palatine. – Situated below the pterygoid a crushed fragment probably represents the right palatine. Between the Processus palatinus and the Processus transversus of the pterygoid lies a fragment with three pointed conical teeth, which might be palatinal teeth. They are bigger than those of the pterygoid.

The **Epipterygoid** has a rodlike structure broken into two fragments.

Fig. 10: Gen. et spec. nov. A-C: Specimen SMF ME 475a. A: Overview showing the long but incomplete tail. B: Head and trunk. C: Head showing the prominent posterior process of the jugal and the well preserved mandible. D: Counterplate SMF ME 475b, showing part of the thorax. E: Radiography overview of SMF ME 475a, optimised for the head region.

Fig. 11: Line drawing of SMF ME 475a with identified skeletal elements.



Fig. 10A



Fig. 10B

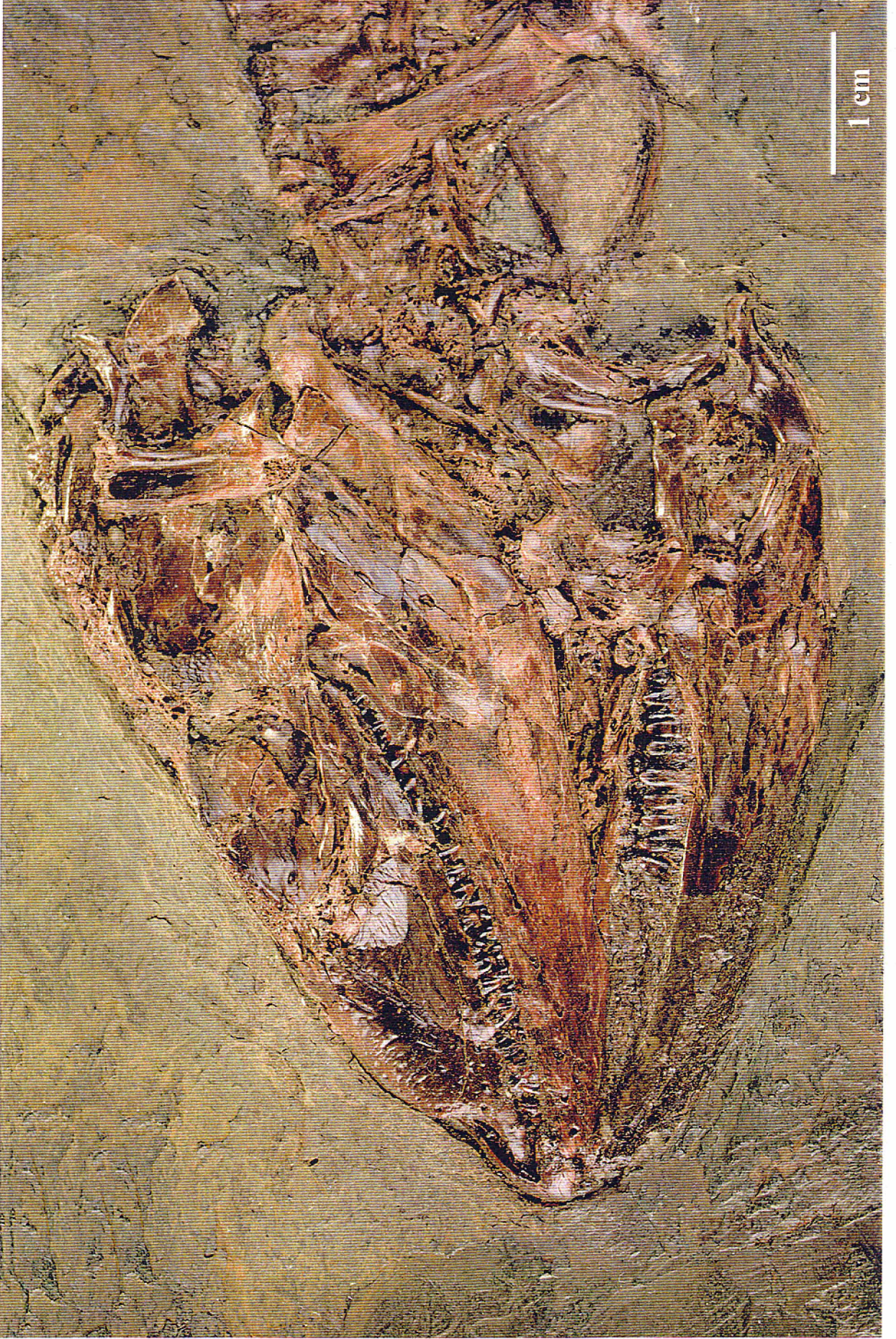


Fig. 10C



Fig. 10D

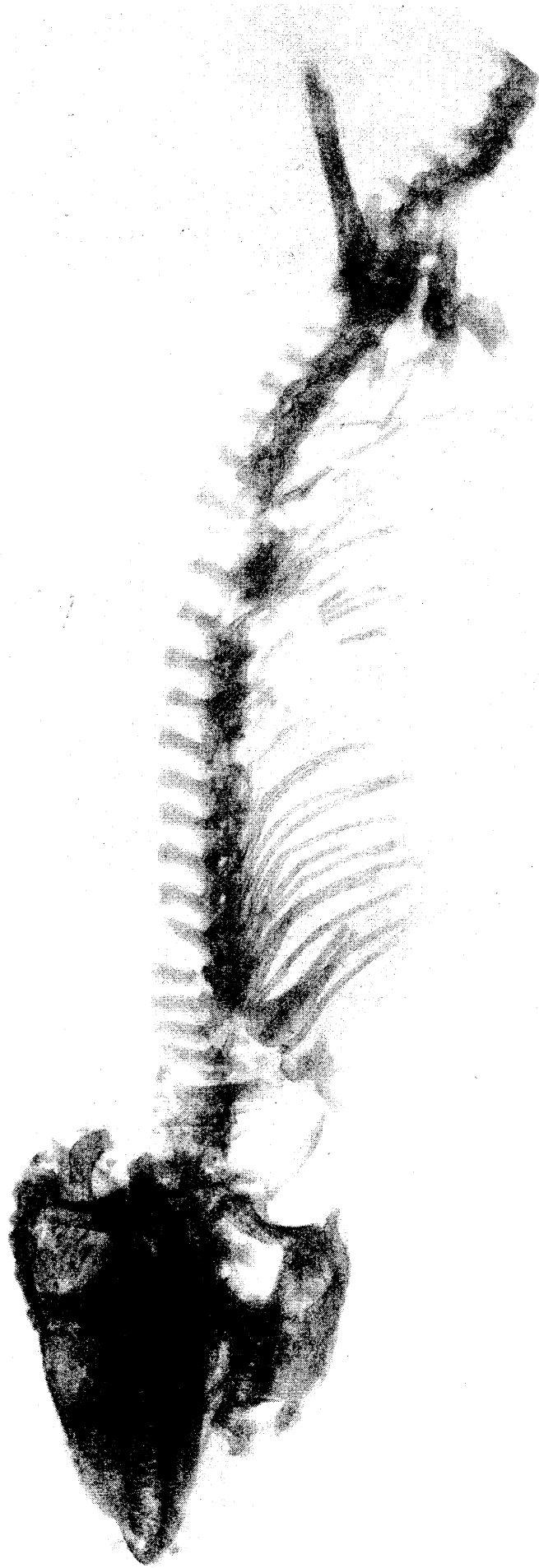
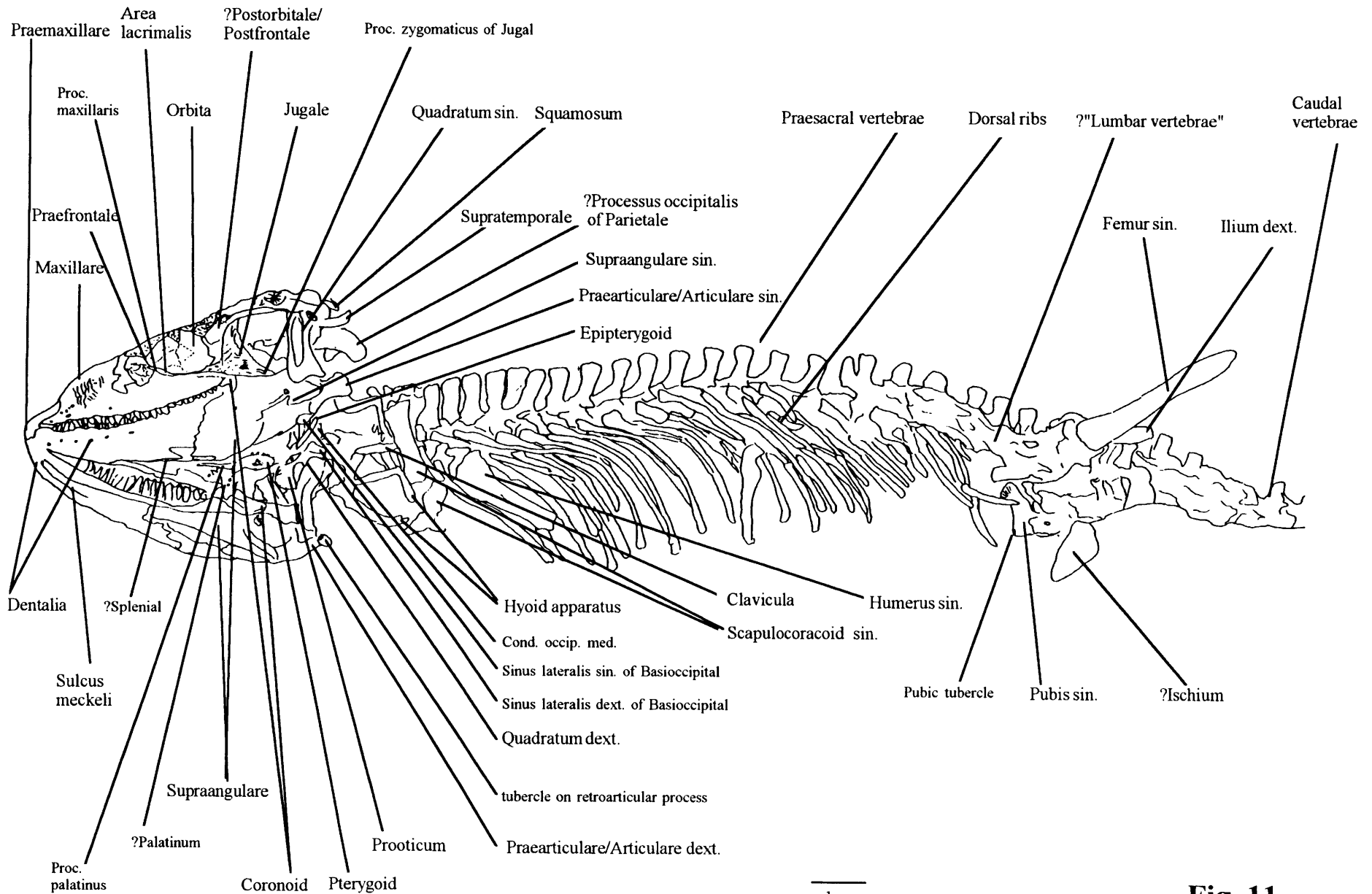


Fig. 10E



1 cm

Fig. 11

Vomer and Ectopterygoid are not identifiable, they are probably covered by the left ramus of the mandible.

Braincase/Neurocranium

Only few elements of the neurocranium can be determined. Below the epipterygoid lies most probably a part of the prootic, which shows a small denticle on its surface. Situated under the posterior part of the left ramus of the mandible, the basioccipital can be seen in ventral view. It has a prominent left and right Sinus lateralis pointing ventrally. On the Facies ventralis is a small tubercle.

Mandible

The left ramus of the mandible is visible in labial view and almost completely preserved, the right ramus is visible from its lingual side.

Dentary. – The dentary makes up about 2/3 of the whole mandible and extends back to the posterior margin of the orbit. On the Facies buccalis of the left dentary nine foramina are visible, more or less parallel to the Crista dentalis. The closely spaced dentary teeth are covered for their greatest length by the maxillary teeth. On the radiography 25 teeth could be determined, about 27 tooth positions are present (Fig. 10E). Like the maxillary teeth they are conical, smooth on the labial side with a more or less blunt tip. Some teeth show wear facets (Fig. 53A+B, p.117). The right dentary lacks its anterior part which is only present as a cast. The lingual view of the dentary teeth differs from their labial view: In their basal cross-section they appear more or less rounded to oval, the upper third of the crown is strongly compressed lingually so that the upper part of the tooth appears scythe-like in cross-section. The tip shows three to seven longitudinal parallel striations. Ten teeth are preserved. Eight more teeth can be counted from casts on the plate.

Supra-angular. – The supra-angular is a short, compact element with a fine ridge on the labial side directed dorso-caudally to rostro-ventrally to about the middle of the supra-angular, most probably following the suture between supra-angular and articular. Slightly above the ridge lies the posterior supra-angular foramen. There are three pits or holes on the anterior surface of the supra-angular, one of which most probably represents the anterior supra-angular foramen.

Articular/Prearticular. – Both elements are most probably fused, as it is the case among squamates (ESTES 1983). These elements show a ridge on its lingual side along their margin. The relatively short and blunt retroarticular process is slightly broadened posteriorly and somewhat bowed ventrally. On its posteromedial margin there is a small tubercle or flange. The Meckel's groove opens medially for the entire length of the mandible.

Coronoid. – The coronoid of the right ramus of the mandible is visible. The prominent dorsal process (Processus massetericus) is broken and lies parallel to the mandible, it is partly covered by an unidentifiable fragment (probably palatine or pterygoid). A fine ridge can be seen on the internal side of the coronoid, which probably represents the Crista praearticularis. The left coronoid is still articulated, the ventral process is rather small relative to the dorsal process, which is only visible on the radiography (Fig. 10E).

Hyoid apparatus

Below the cervical vertebrae two thin, rodlike structures represent parts of the hyoid apparatus, most probably the first or second ceratobranchials.

Postcranial skeleton

Axial skeleton

The axial skeleton is almost completely articulated. The dorsal vertebrae show their left lateral sides and bear prominently high, axe-shaped neural spines. At least 24 presacrals are present. The cervical vertebrae are crushed, thus their number cannot be determined. 30 to 32 caudal vertebrae are preserved, but completely flattened and no distinct features are visible, only within the first eight caudal vertebrae, transversal processes and neural spines are vaguely apparent. The dorsal ribs are still more or less articulated with the vertebrae. The last three or four presacral vertebrae seem to lack ribs, hence the term "lumbar vertebrae" (sensu HOFFSTETTER & GASC 1969) may be applied to those. The sternum cannot be determined. Some amorph bony substance in the anterior trunk region may be identified as remnants of the sternal ribs.

Pectoral girdle

Below the long slender left scapula lies part of the coracoid, showing the glenoid cavity for the humerus. The broken clavicle shifted away from the scapular blade. No interclavicle can be determined.

Pelvic girdle

The pelvic girdle is fragmentarily preserved and crushed. The anteriorly or antero-dorsally directed pubis shows an opening, the obturator foramen. On the margin of the symphyseal process of the pubis the ventrally directed pubic tubercle is situated. Ilium and ischium cannot be clearly determined. The right ilium is partly covered by the left femur.

Pectoral and pelvic appendages

Considerate parts of the limbs are missing. Only the left humerus and femur are incompletely preserved. An element next to the pubis either represents the ischium or the proximal part of the right femur.

2.3.1.2.3 Specimen WDC-C-MG 122/123, designated paratype

WDC-C-MG 122/123 (Fig. 12, Fig. 13, Fig. 14) consists of plate and counterplate. WDC-C-MG 122 shows the right side of the specimen with the skull in ventrolateral view, WDC-C-MG 123 the left side with the skull in dorsolateral view. Therefore it represents the only specimen where these two aspects can be studied in one individual in this quality. The limbs are present but incomplete and for the largest part the tail is lacking. The head-trunk-length of this specimen is 16 cm of which the head-length measures about 5.6 cm.

Skull

Dermal roof shield

Nearly all skull elements are still articulated.

Premaxilla. – WDC-C-MG 123: The preservation of the premaxilla is similar to that of the designated holotype, but the number of the teeth is better reconstructable. The slightly dislocated fused premaxilla in anterodorsal view bears five tooth positions. Four more or less blunt and conical teeth with lateral cutting edges are still in place (Fig. 52, p.116). The transition from the Processus maxillaris to the Processus nasalis appears as a gently rounded slope. The Processus nasalis itself is relatively slender, but as it is broken and crushed on its posterodorsal part, the length cannot be determined.

Maxilla. – WDC-C-MG 123: The left maxilla is visible from its external, the right maxilla partly from its internal side. The Facies buccalis is relatively smooth. A number of foramina are arranged parallel to the Crista dentalis along a crack. The Facies buccalis is irregularly pitted and furrowed. Although the maxillae are not any more articulated with the premaxilla, the Processus praemaxillaris of the left maxilla is still attached to the Processus maxillaris of the premaxilla. The relatively pointed Processus zygomaticus reaches back to the posterior margin of the orbita. The Margo orbitalis meets the Crista dentalis in an acute angle. The Processus praefrontalis is covered by the prefrontal and the supraorbitalia. The Margo fenestra exonaria, above the Processus praemaxillaris, is gently curved. The internal view of the right maxilla shows only the anterior part of the prominent Lamina horizontalis because the posterior area is covered by the nasalia and the right prefrontal. The Facies triangularis, a small triangular depression dorsal to the Lamina horizontalis can be distinguished. The left maxilla shows about 19 tooth positions, 17 teeth are preserved. The morphology of the teeth is as described for the specimen SMF ME 475a, the cutting edges on the tip are more distinct (Fig. 52, Fig. 53C, p.116, 117). But in this specimen the maxillary teeth are sometimes slightly recurved. The lingual view of the maxillary teeth is not visible. On WDC-C-MG 122 the right maxilla shows its labial view. For the largest part, the Facies buccalis as well as the Processus praefrontalis are not preserved. Parallel to the Crista dentalis five foramina are visible. At least 18 tooth positions are present with 16 preserved teeth.

Nasalia. – WDC-C-MG 123: The nasalia are paired. The naso-frontal suture cannot be distinguished since this area is covered by osteoderms.

Fig. 12: Gen. et spec. nov. A-C: Specimen WDC-C-MG 123. D-F: Counterplate of the same specimen WDC-C-MG 122. A: Overview. Intestinal contents are preserved in the dark areas near the anterior and posterior trunk region. B: Head in dorsolateral view, showing the prominent posterior process of the jugal and the characteristic supraorbitalia. C: Radiography, optimised for the head region. D: Overview. Abundant intestinal contents are preserved in the anterior thoracal region. E: Head in ventrolateral view with the well preserved mandible. F: Radiography, optimised for the head region .

Fig. 13: Line drawing of WDC-C-MG 122 with identified skeletal elements.

Fig. 14: Line drawing of WDC-C-MG 123 with identified skeletal elements.



Fig. 12A



Fig. 12B

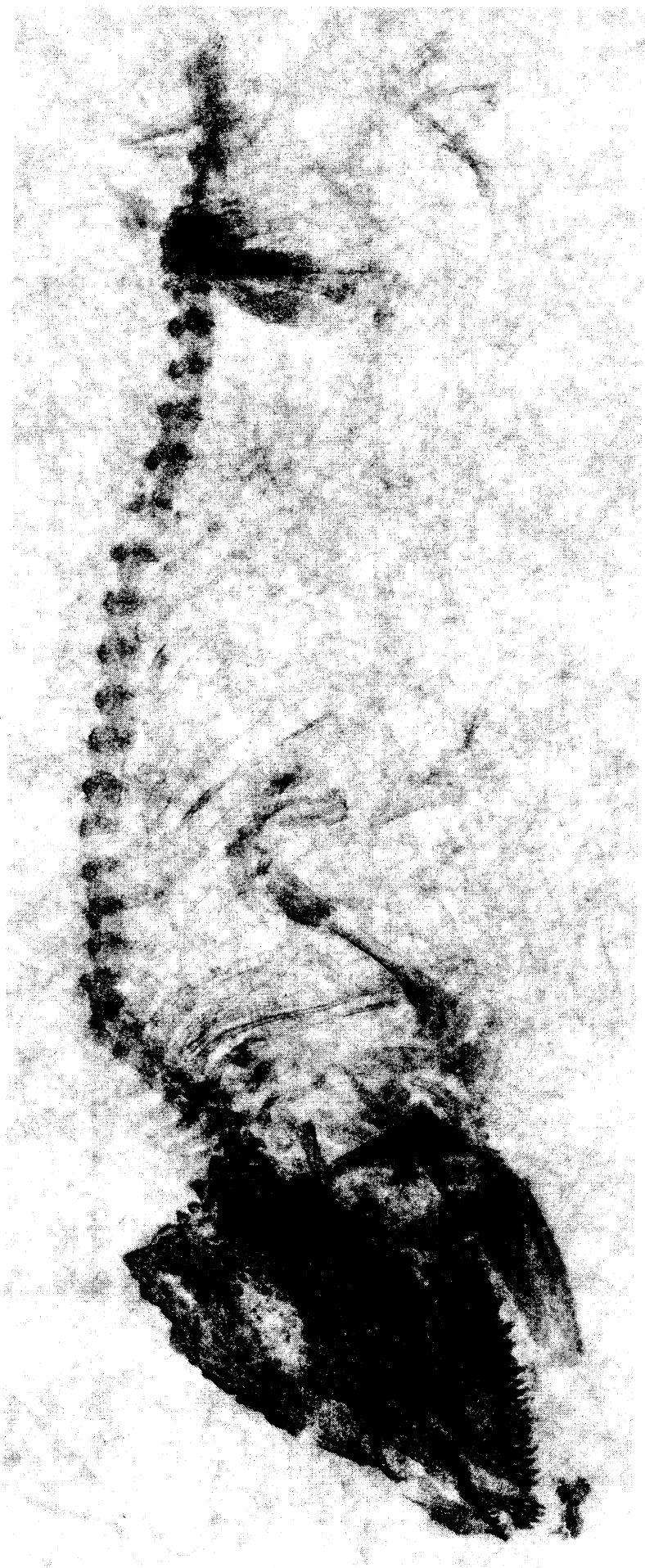


Fig. 12C



Fig. 12D



Fig. 12E



Fig. 12F

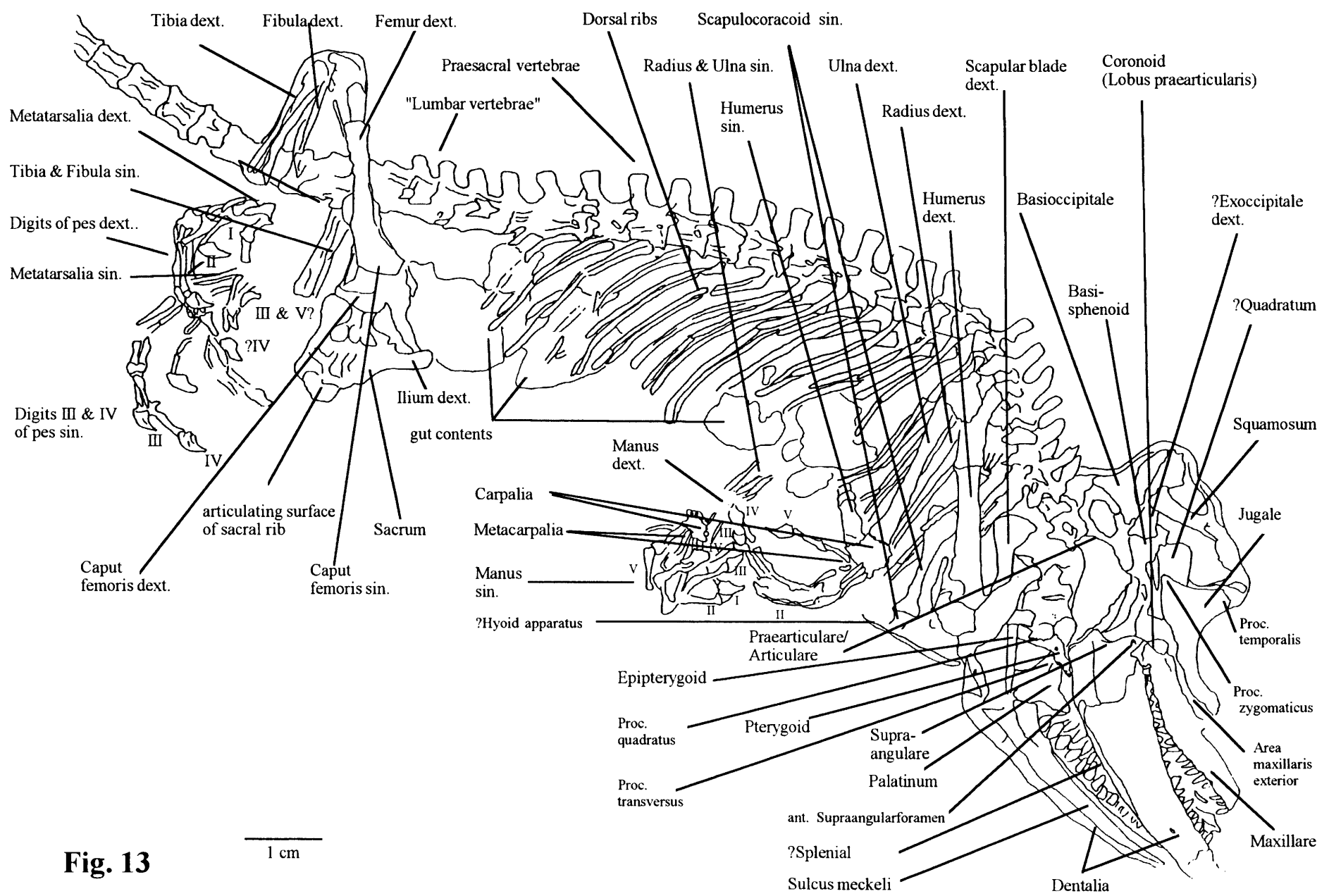


Fig. 13

1 cm

Praefrontalia. – The praefrontalia are covered by osteoderms for most of their dorsal extension. The right prefrontal is partly disarticulated. Even on the radiography their outline cannot be determined.

Frontalia, postorbitalia/postfrontalia, parietal. – These elements are covered by skull osteoscutes. Their characteristic pattern is very well visible. The arrangement of the supraorbitalia are more distinct than in the designated holotype (Fig. 52, p.116). In this specimen only two rows of perpendicularly oriented osteoscutes are projecting from the rear end of the skull. The indistinct shape of the frontal on the radiography shows a slight constriction between the orbitae (Fig. 12C). Neither the fronto-parietal or the naso-frontal suture can be recognised. On the radiography a suture on the midline of the frontal is visible, which would suggest paired frontalia. This suture can be seen most distinctly when the specimen is tilted for +20 degrees relative to the x-ray beam. But in this area also the osteoderms are separated by a fine “fissure”. However, the suture visible on the radiography is much more distinct and straight than the osteodermal “fissure”, which makes paired frontalia highly probable. The radiography shows that the Processus exoccipitali of the parietal are concave and seem to be rather short, the posterior part of the parietal table is probably constricted. Neither the frontoparietal suture nor a Foramen parietale can be distinguished. It is not possible to say by which elements the supratemporal fenestrae are closed (if closed at all), because at the largest part, the sutures and outlines of the skull elements are not visible on the radiographs even when tilted at different angles.

Jugal. – The left jugal shows its external view. The morphology of the jugal is identical to the one described in SMF ME 475a. The tip of the posterior process is covered by the left ramus of the mandible. The dorsal part of the strongly built Processus temporalis is covered by osteoderms. Between the Processus maxillaris and Processus temporalis lies the gently curved Margo anterior. There are six Foramina on the Facies buccalis which is only slightly sculptured. The Carina zygomatica shows a smooth margin with a long slender and smooth Area lacrimalis. Due to the slight disarticulation from the left maxilla, the Area maxillaris exterior is visible below with a pitted and furrowed surface. The Carina inferior is still covered by the left maxilla (Fig. 52, p.116). WDC-C-MG 122: The right jugal shows its external view as well. The tip of the Processus temporalis is not visible. The prominent posterior process (Processus zygomaticus) is slightly more pointed than in SMF ME 475a. The Foramen zygomaticum exterior can be distinguished. Four additional foramina are visible on the Facies buccalis. Almost the complete Area maxillaris exterior is visible, it broadens towards the Processus maxillaris and the Carina inferior has a smooth and gently curved outline.

Lacrimalia as well as **Supratemporalia** cannot be clearly distinguished.

Squamosal. – WDC-C-MG 123: Above the left quadrate slightly shifted ventrally lies the left squamosal in dorsal view. Its rostral part is covered by osteoderms. Its morphology is as described in SMF ME 475a. WDC-C-MG 122: The rostral part of the right squamosal is concealed as well. The foramen and the carina is visible on its dorsal side.

Palatal complex

Quadrates. – WDC-C-MG 123: The more or less laterally oriented left quadrate, which is still in articulation with the articular, shows its distinct and straight Crista tympani. The Facies posterior is concealed. WDC-C-MG 122: The right quadrate is considerably crushed and lies below the right jugal. Most probably it is visible in anterior view. The Condylus mandibularis can be distinctly recognised whereas the Condylus cephalicus and the Facies anterior is incompletely preserved. The vomera are concealed by the mandible.

Pterygoid. – WDC-C-MG 122: Only the left pterygoid is preserved. On the Processus palatinus four blunt-conical teeth can be recognised arranged in one line, the rostral part of the process is hidden under the right ramus of the mandible. The Processus transversus with its crushed tip emerges from the Processus palatinus. Between both lies the Incisura suborbitalis. The distal part of the strongly developed Processus quadratus has broken off. The right pterygoid most probably lies below the right ramus of the mandible.

Palatine. – Below the left pterygoid and still attached to it, the left palatine is visible. It is deformed and its orientation cannot be determined.

Ectopterygoid. – WDC-C-MG 123: Out of the left lower temporal fenestra a process emerges, which most probably represents the Processus pterygoideus major of the left Ectopterygoid. WDC-C-MG 122: The right Ectopterygoid most probably lies below the right ramus of the mandible.

Epipterygoid. – The thin rodlike right epipterygoid lies partly above the left ramus of the mandible (WDC-C-MG 122), whereas the fragmentary left Epipterygoid is covered by the left Ectopterygoid (WDC-C-MG 123).

Braincase/Neurocranium

Exoccipitalia, supraoccipital, basioccipital. – WDC-C-MG 123: In the posterior area of the skull there are some strongly crushed and deformed bone fragments which could be parts of the exoccipitalia or the supraoccipital. WDC-C-MG 122: In the area of the parietal table exists an elongated, ventrally bowed, and distally broadened bony element which most probably represents the right exoccipital. Below lies presumably the basioccipital with the Condylus occipitalis medialis. On the border between basioccipital and basisphenoid, which is also partly visible, quite a prominent tubercle exists. Both Cornua basisphenoidei cannot be determined.

Mandible

The mandible is completely articulated.

Dentary. – WDC-C-MG 123: On this plate the labially oriented left dentary lacks its rostral part, (except for the anteriormost tip) as well as the Crista dentalis, but the whole shape of the dentary is preserved as a cast. As described in the designated holotype, the dentary is an elongated bone, which represents about 2/3s of the mandible with a well developed Sinus supraangularis. The posterior part of the dentary is compressed parallel

to the Crista ventralis. The Facies buccalis is relatively smooth except for showing some fine ridges parallel to the Crista ventralis. Dentary teeth are lacking, except for four teeth at the anteriormost part of the dentary. The more or less pointed Processus coronoideus reaches back to the posterior margin of the orbit. Because of the compression parallel to the Crista ventralis, the suture between dentary and angular respectively supra-angular cannot be retraced in this area, even after radiography examination.

WDC-C-MG 122: The left dentary shows its lingual view, lacking the rostral part. The Lamina horizontalis (= subdental shelf) is well developed. In contrast to the designated holotype one can observe the medially open Sulcus meckeli. The Facies dentalis is slightly depressed in its posterior part. Eight pleurodont teeth are preserved, another six are present only as a cast. Together with those present on WDC-C-MG 123, at least 19 tooth positions are present, 12 are preserved. The teeth have the same morphology as described in SMF ME 475a. As the maxillary teeth, the dentary teeth are slightly recurved. The right dentary is visible from its labial side. It is almost completely preserved except for its anterior tip. On the slightly depressed Facies buccalis about four foramina parallel to the Crista dentalis can be observed. The Sinus supraangularis can be recognised as well. 21 dentary teeth are preserved (as can be seen on the radiography, Fig. 12F), the estimated number of tooth positions are 23/24. As the maxillary teeth, they are blunt-conical with lateral cutting edges having a smooth surface on their labial side. One tooth is bearing a wear facet.

Coronoid. – WDC-C-MG 123: The left coronoid is visible from its external view. The Processus massetericus as well as the Processus dentalis superior are covered by the left jugal. The small ventral process overlaps the supra-angular.

WDC-C-MG 122: The coronoid of the right ramus of the mandible shows part of its external view as well. The Processus zygomaticus of the maxilla covers partly the steep dorsal process (Processus massetericus), which is well rounded and quite large, as described for the designated holotype.

Supra-angular. – WDC-C-MG 123: The suture between the dentary and the supra-angular is visible for the largest part, whereas a clear suture to the articular cannot be determined. The supra-angular is, as described in the designated holotype, a short compact element compared to the dentary and extends anteriorly well beyond the coronoid. The rostro-ventrally to dorso-caudally directed ridge is not as distinctly visible as in the designated holotype, because in this area the supra-angular is compressed by sediment compaction. The posterior supra-angular foramen is below the ridge, differing from SMF ME 475a, where the foramen lies just above the ridge. Ventral to the coronoid lies the anterior supra-angular foramen.

WDC-C-MG 122: Towards the dentary, the suture can be distinguished for the largest part, along the Sinus supraangularis, whereas again no clear suture to the articular can be determined. The ridge between supra-angular and articular is distinctly developed. Both supra-angular foramina are visible.

Neither angular nor splenial can clearly be distinguished in their outline, because in this area there are several fine cracks, which can easily be mistaken for sutures. These can be distinguished, only for very short distances.

Prearticular/Articular. – WDC-C-MG 123: The prearticular/articular of the left ramus of the mandible is still articulated with the left quadrate. It is quite compressed and deformed as is the retroarticular process. Sutures cannot be determined. WDC-C-

MG 122: The articular of the right ramus is not any more articulated with the quadrate. The retroarticular process has a curved margin with its tip slightly bowed ventrally.

Splenia1. – WDC-C-MG 122: On the ventral margin of the right ramus of the mandible there appears to be a splenial which reaches far anteriorly, below the dentary.

Hyoid apparatus

On WDC-C-MG 122 below the left scapulocoracoid, there is a thin rodlike element which probably represents a part of the hyoid apparatus.

Postcranial skeleton

Axial skeleton

Except for the missing tail the axial skeleton is almost completely articulated. The head is still attached to the axial skeleton. No intercentra can be determined. All vertebrae are preserved in lateral view. The neural spines of the dorsal vertebrae are tall, straight and axe-shaped over the whole length of the trunk. At least 26 presacral vertebrae are present. The cervical vertebrae are partly deformed, some are disarticulated and lie below the right ramus of the mandible. The atlas-axis-complex as well as the number of the cervical vertebrae cannot be determined. The holocephal ribs are not any more articulated with the vertebrae but still are approximately in their original position. For each dorsal vertebra a pair of ribs can be attributed except for the last four or five presacral vertebrae, which might represent the "lumbar region". The compressed and deformed sacral vertebrae are dislocated and lie below the sacral region (WDC-C-MG 122). The articulating surface of the transversal process is visible. Eight compressed caudal vertebrae are preserved. No processes can be observed. A sternum could not be identified.

Pectoral girdle

WDC-C-MG 123: The left scapulocoracoid is partly preserved, the scapular blade is long, slender and slightly broadened dorsally. A suprascapula is not preserved. The glenoid cavity (Fossa glenoidales) for the Caput humeri can be observed. There seems to be no scapular-coracoid emargination. As to the presence of an anterior or posterior coracoid emargination no assertion can be made, because the ventral part of the coracoid is concealed. Along the anterior margin of the scapular blade lies the rodlike, anteriorly curved simple clavicle. An interclavicle cannot be identified. Anterior to the left scapula a part of the right scapular blade is visible. WDC-C-MG 122: Only the dorsal part of the right scapular blade can be identified. Next to the right humerus lie parts of the left scapulocoracoid, showing its internal side. The suture between scapula and coracoid is not fused.

Pelvic girdle

No elements of the pelvic girdle could be identified on WDC-C-MG 123, they are covered by the posterior limbs. On WDC-C-MG 122 at least the rather deformed ?right ilium is visible, which is still connected with the dislocated sacrum, showing its articulating surface of the transversal process.

Pectoral appendages

WDC-C-MG 123: The left limb is preserved in almost complete articulation. The relatively slender left humerus is still more or less articulated with the Fossa glenoidalis of the scapulocoracoid. The proximal and distal articulating surfaces are compressed, whereas the shaft is preserved three-dimensionally. Radius and ulna are still articulated with the humerus. As they are deformed and partly overlapping one another, it cannot be determined which element represents the radius and which one the ulna. The carpalia are preserved but indistinctly recognisable and cannot be distinguished from one another. All five metacarpalia and the ungual phalanx of digit IV are visible.

WDC-C-MG 122: The right front limb is completely articulated as well but considerably flattened. It lies on the dorsal ribs of the anterior trunk region. The Caput humeri of the right humerus is missing, the distal one is compressed. On this plate, part of the left humerus can be seen as well, it lies below the right manus. The ulna partly covers the radius. The olecranon cannot be recognised since the proximal articulating surface is heavily deformed. Parts of the carpalia and the remaining four digits of the left manus are preserved on this plate. Some of the phalanges are still covered by epidermal keratinous scales. The carpalia are preserved but single elements cannot be distinguished. Five metacarpals of the right limb are identifiable. The second through fifth digit is visible, the first one is missing. The fourth digit and part of the carpalia are covered by epidermal scales. The phalangeal formula for the manus is as in many Lacertilians: 2,3,4,5,3(?), retaining the early reptilian condition (ROMER 1956).

Pelvic appendages

Both hindlimbs are considerably flattened, except for the shaft of the right femur.

WDC-C-MG 123: The left hindlimb is disarticulated for the largest part. The femur has shifted ventrally for its entire length but is still connected with the epipodials. (The Caput femoris is situated on WDC-C-MG 122). Parallel to the femur lies the tibia, the fibula is partly covered by the femur. Above the sacrum the position of the right hindlimb is indicated, as part of the right femur, tibia and fibula. Anteriorly to the right femur and below the sacrum the femur continues.

WDC-C-MG 122: The right limb with parts of the pelvic girdle and the sacrum is dislocated from the axial skeleton and has shifted ventrally for about half the length of the femur. The femur is still articulated with tibia and fibula. The Caput femoris of the left femur is situated below the right femur. Only the fibula is still attached to the tarsals, single elements cannot be distinguished. On this plate, the tibia of the left foot is visible as well, situated anteriorly to the right foot. Tarsalia could not be identified in either foot. The left foot is incomplete. Digit II and the proximal phalanges of digit III and IV are situated on WDC-C-MG 123. Above, the digits of the right pes are indicated by an impression. These are situated on plate WDC-C-MG 122, as well as the metatarsals and the remaining phalanges of digit III and IV of the left foot. Digit I and V could not be identified. The digits of both feet lie close together. The right foot is complete, digit I, II and IV are visible, digit III and V cannot be distinguished from one another. Three of their ungual phalanges (III-V) are situated on WDC-C-MG 123. The phalangeal formula for the pes is 2,3,4,5,4(?).

2.3.1.2.4 Specimen SMNK-PAL 3813, designated paratype

This specimen consists of a single plate (Fig. 15, Fig. 16). It is well preserved but lacks its tail and a considerable part of the hindlimbs. Most of the diagnostic features (jugal, osteoderms, teeth) and the clavicle are very well accessible. Like the specimens WDC-C-MG 122/123 and the designated holotype the trunk is laterally embedded, the head dorsolaterally, showing its left side. The head-trunk length of this specimen is 20.4 cm of which the head-length measures about 6.4 cm.

Skull

Most of the skull elements are still articulated.

Dermal roof shield

Premaxilla. – The well articulated but slightly crushed premaxilla is seen in dorsal view. The Processus nasalis appears to be rather long and slender. The Processus maxillari are visible, but the premaxillary teeth are concealed by the resin plate.

Maxilla. – The left maxilla is visible from its external side. The largest part of the right maxilla is covered by the dorsal part of the skull, but on the radiography 12 maxillary teeth are visible (Fig. 15D). The slightly furrowed Facies buccalis of the left maxilla is compressed, showing several cracks. The Processus praemaxillaris is still in contact with the Processus maxillaris of the Premaxilla. The Processus zygomaticus is broken off and shifted ventrally. It reaches back to the posterior margin of the orbita. The prefrontal covers the Processus praefrontalis. Twelve conical maxillary teeth are still attached to the crushed and partly disarticulated Crista dentalis of the left maxilla. The morphology of the teeth is as described for SMF-ME 475a.

Nasalia. – The posterior part of the paired nasalia is covered by osteoderms. Therefore the naso-frontal suture cannot be identified.

Praefrontalia. – The left prefrontal below the frontal osteoderms is disarticulated and deformed, it covers the Processus praefrontalis of the left maxilla.

Frontalia, postfrontalia/postorbitalia and parietal are covered by the well preserved and strongly sculptured osteoderms. Their characteristic pattern perfectly corresponds to that described in the designated holotype and WDC-C-MG 122/123. The left supraorbitalia have shifted into the orbit and are not any more attached to the remaining osteoderms, whereas the right supraorbitalia still are. Posterior to those lie the osteoderms with the radially arranged spiny scutellation. Two rows of small spiny osteoderms are projecting from the rear end of the skull. A small hole is situated near the presumed fronto-parietal suture. It probably represents the Foramen parietale.

Fig. 15: Gen. et spec. nov. A: Overview of the specimen SMNK-PAL 3813. The hindlimbs are incomplete. Intestinal contents are preserved in the dark area near the "lumbar" region. B: Head, showing the typical osteodermal pattern. C: Left and right manus, the carpalia and several phalanges are covered by epidermal scales. D: Radiography overview, optimised for the head region.

Fig. 16: Line drawing of SMNK-PAL 3813 with identified skeletal elements.



Fig. 15A



Fig. 15B



1 cm

Fig. 15C

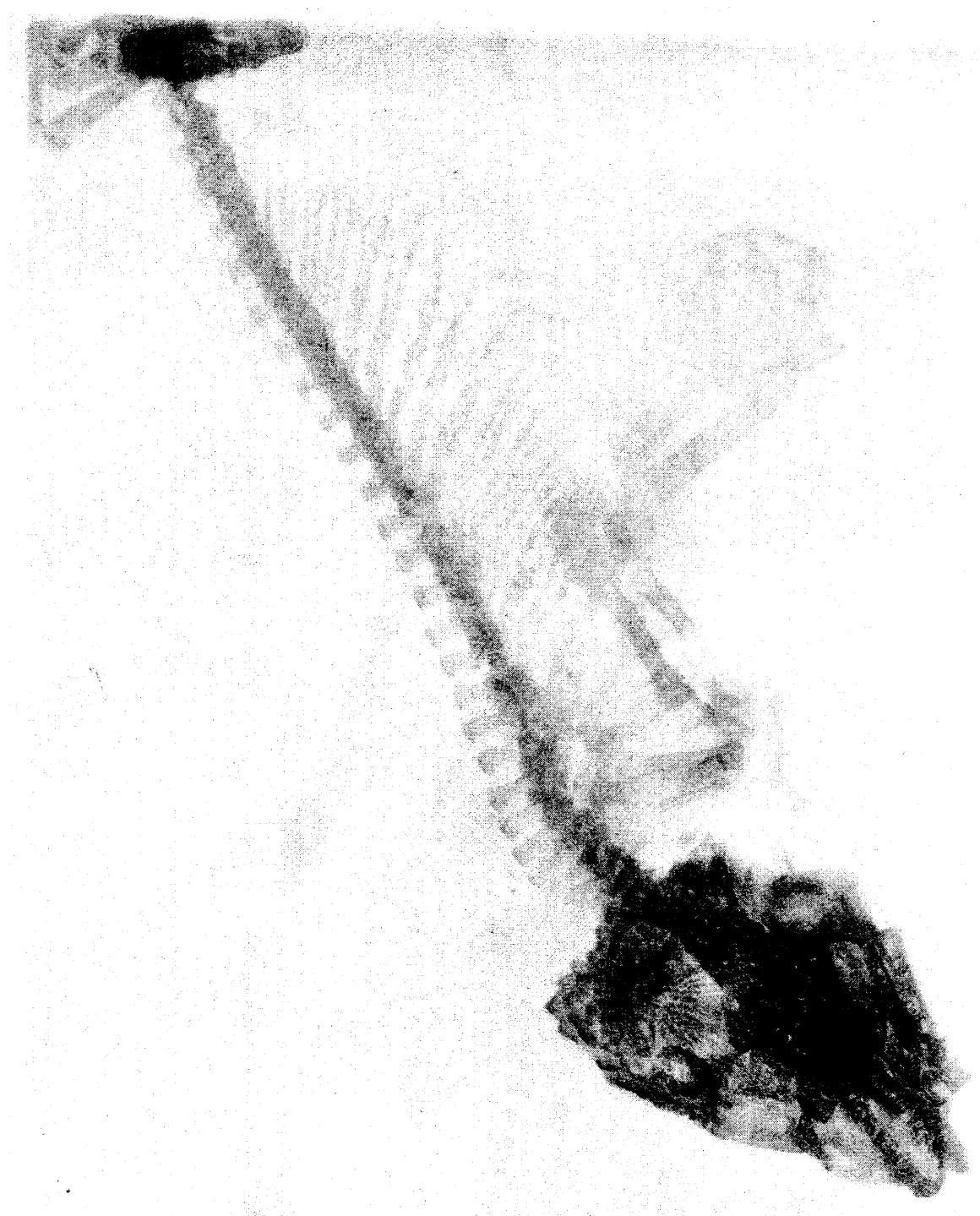


Fig. 15D

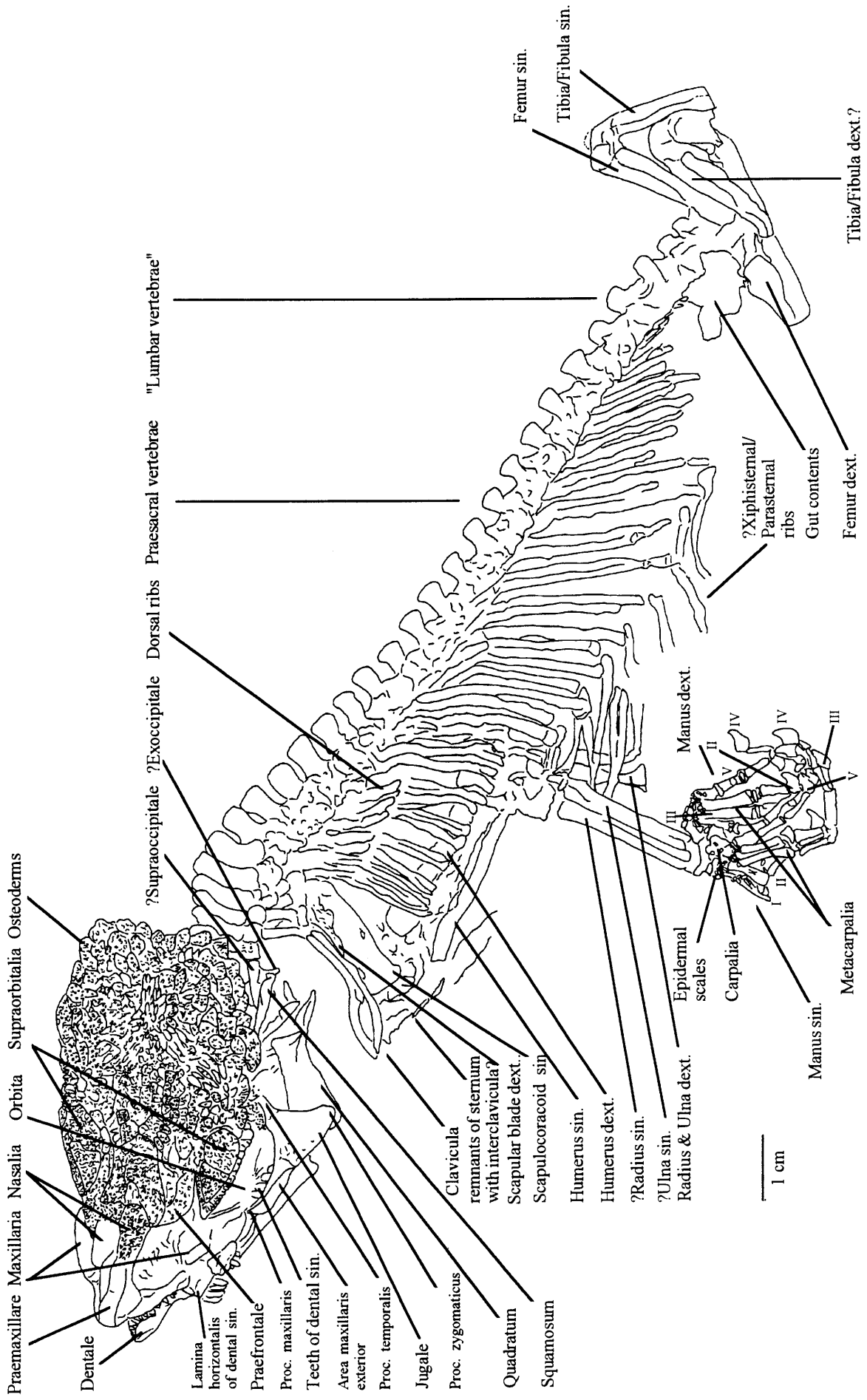


Fig. 16

Jugal. – On the furrowed *Facies buccalis* of the left jugal at least six foramina are present including the *Foramen zygomaticum exterior*. The ventrally shifted *Processus zygomaticus* of the maxilla reveals the rather smooth *Area maxillaris exterior* of the jugal. A crack separates the long and slender *Area lacrimalis* and the *Area maxillaris exterior* from the *Facies buccalis*. The prominent and well rounded *Processus zygomaticus* can be seen. The *Processus temporalis* is not any more articulated with the squamosal or the parietal. The *Processus maxillaris* has broken off and lies just below the supraorbitalia.

Lacrimalia and *Supratemporalia* cannot be identified.

Squamosal. – Below the questionable supraoccipital lies the ventrally shifted left squamosal in dorsolateral view. It is not any more articulated with the quadrate, anteriorly it is still attached to the postorbital/postfrontal. The posterior end is broadened. Along the slender squamosal, the carina is more or less distinct.

Palatal complex

Quadrate. – The disarticulated left, somehow flattened quadrate is visible in anterior view showing the *Facies anterior*. The quadrate has shifted anteriorly below the jugal. The *Condylus mandibularis* is more or less concealed by the prominent *Processus zygomaticus* of the jugal, but distinctly visible on the radiography (Fig. 15D). The more or less distinct *Crista pterygoidea* terminates in the *Condylus cephalicus*.

Other palatal elements cannot be determined.

Braincase/Neurocranium

Exoccipitalia/Supraoccipital. – Elements just above the squamosal most probably represent parts of the heavily deformed braincase: the supraoccipital and the left exoccipital. Other elements of the braincase are not identifiable.

Mandible

A huge part of the mandible is covered by elements of the dermal roof shield.

Dentary. – Below the *Crista dentalis* of the left maxilla, a part of the dislocated and twisted *Crista dentalis* of the left dentary is visible from the internal side. It shows the *Lamina horizontalis* and four lingually slightly recurved teeth with the parallel striations on the tooth crown. Four additional teeth of the left dentary are present just above the *Margo anterior* of the jugal. The rest of the left dentary is covered by the left maxilla and jugal. On the radiography altogether 13 dentary teeth can be recognised (Fig. 15D). The anterior tip of the right dentary, showing four conical teeth, can be seen just below the left maxilla. Further 19 dentary teeth can be identified on the radiography. Postdentary elements cannot be identified.

Hyoid apparatus

A hyoid apparatus could not be identified.

Postcranial skeleton

Axial skeleton

Except for the missing tail the axial skeleton is completely articulated. The presacral vertebrae with their high, axe-shaped neural processes are embedded laterally, as in the other specimens. 28 presacral vertebrae are present. The atlas-axis-complex as well as the number of the cervical vertebrae cannot be determined. The last three or four presacral vertebrae do not bear any ribs and thus can be termed “lumbar vertebrae”. Below that region intestinal contents are preserved. Vertebrae and ribs are considerably flattened and deformed, but the dorsal ribs are still more or less articulated to the vertebrae. The sacral vertebrae are covered by the tibia and fibula of the right limb. Below the pectoral girdle, remnants of the sternum are probably present as fragments. Attached to the posterior dorsal ribs, several xiphisternal or parasternal ribs could be identified.

Pectoral girdle

The two long and slender scapular blades are lying one upon the other, the left one covering its right counterpart. A suprascapula is not preserved. The coracoidea below the scapular blades are considerably deformed, but both humeri are still attached to the glenoid cavity (Fossa glenoidales). Along the anterior margin of the scapular blades the rodlike, anteriorly curved simple clavicles are present. Below the Scapulocoracoidea, within the remnants of the sternum, some rodlike fragments might represent the interclavicle.

Pelvic girdle

The pelvic girdle is concealed by the femur, tibia and fibula of the left limb. No structures could be determined on the radiography either.

Pectoral appendages

Both limbs are preserved in almost complete articulation, but all elements of both limbs are considerably compressed. Their position is more or less parallel to each other. In the radiography this becomes even more obvious (Fig. 15D). As mentioned above, both humeri are still attached to the glenoid cavity of the coracoidea. The right humerus is covered by dorsal ribs and lies above the left humerus. Both proximal articulating surfaces are distinctly preserved, whereas their distal articulations with the radius and the olecranon of the ulna cannot clearly be distinguished. Radius and ulna of the left limb are better preserved than those of the right limb. The proximal carpalia ulnare and radiale as well as the centrale are still more or less distinctly preserved. The distal carpalia are only indistinctly recognisable. The metacarpalia as well as the phalanges are almost completely articulated. All digits (I-V) can be recognised, as well as the strong recurved ungual phalanges, showing the expected phalangeal formula 2,3,4,5,3. Closely beside the left manus lies the right manus, also in a good state of preservation. The carpalia and several phalanges are covered by epidermal scales (Fig. 15C). The digits II-V are visible.

Pelvic appendages

Both hindlimbs are incompletely preserved and considerably compressed. The left hindlimb lies above the pelvic girdle. The proximal articulating surface of the femur is probably still attached to the acetabulum of the pelvic girdle. Below lies the deformed right femur. Both femora are still articulated with tibia and fibula. Due to their

preservation it cannot be determined which element represents the tibia and which the fibula. Tibia and fibula of the right limb lie across the vertebral column. The feet are not preserved, although some remains of the right tarsalia might be present.

2.3.1.2.5 Specimen SMF ME 1249a+b, additional material

SMF ME 1249a+b (Fig. 17, Fig. 18, Fig. 19) is the smallest specimen investigated here and is considerably compressed. The head-trunk length is 13 cm of which the head measures 5 cm. It is preserved on two plates (plate and counterplate) as WDC-C-MG 122/123, showing the left (SMF ME 1249a) and right (SMF ME 1249b) side of the specimen. The pectoral appendages are incomplete and only the base of the tail is preserved, with seven caudal vertebrae. In the middle of the trunk the vertebrae are disarticulated. Therefore, the posterior part of the body was rotated for 180 degrees. Consequently, SMF ME 1249a shows the vertebrae in right lateral view and SMF ME 1249b the left lateral view.

Skull

Dermal roof shield

Premaxilla. – SMF ME 1249a: Only a fragment of the Processus nasalis of the premaxilla is visible. SMF ME 1249 b: The premaxilla is anterolaterally embedded. Only one tooth can be identified. The number of the tooth positions cannot be determined. The tip of the Processus nasalis has broken off. The Processus maxillaris is still connected with the maxilla.

Maxilla. – SMF ME 1249a: The left maxilla shows its external view. The Facies buccalis is slightly furrowed. About nine foramina can be recognised, as in SMF ME 475a at least six are arranged parallel to the Crista dentalis. The Processus praefrontalis is covered by osteoderms. The upper part of the straight and smooth Margo orbitalis is concealed by the presumed prefrontal. The rounded Processus zygomaticus reaches back to the posterior margin of the orbit. About 20 tooth positions are present, 15 maxillary teeth are preserved. This is less than in the designated holotype and SMF ME 475a, which even has about 27 tooth positions with 23 preserved teeth. The morphology of the labial view is as described in the designated holotype. In this specimen also the lingual view of a few maxillary teeth can be observed through the backside of the plate: Like the lingual view of the dentary teeth, described in SMF ME 475a, they have a slightly compressed tip with about six parallel striations. SMF ME 1249b: The right maxilla is quite compressed and deformed. The external Facies buccalis is pressed in, the Processus praefrontalis is covered by the prefrontal. Processus praemaxillaris and Processus zygomaticus are well preserved. 13 maxillary teeth are still present.

Fig. 17: Gen. et spec. nov.: SMF ME 1249 a+b, the specimen is disarticulated in the mid trunk region. A-C: Specimen SMF ME 1249a. D-F: Counterplate SMF ME 1249b. A: Overview. B: Head in left dorsolateral view. C: Radiography overview, optimised for the head region. D: Overview. E: Head in right lateral view. F: Radiography overview, optimised for the head region.

Fig. 18: Line drawing of SMF ME 1249a with identified skeletal elements.

Fig. 19: Line drawing of SMF ME 1249b with identified skeletal elements.



Fig. 17A



Fig. 17B



Fig. 17C



Fig. 17D



Fig. 17E



Fig. 17F

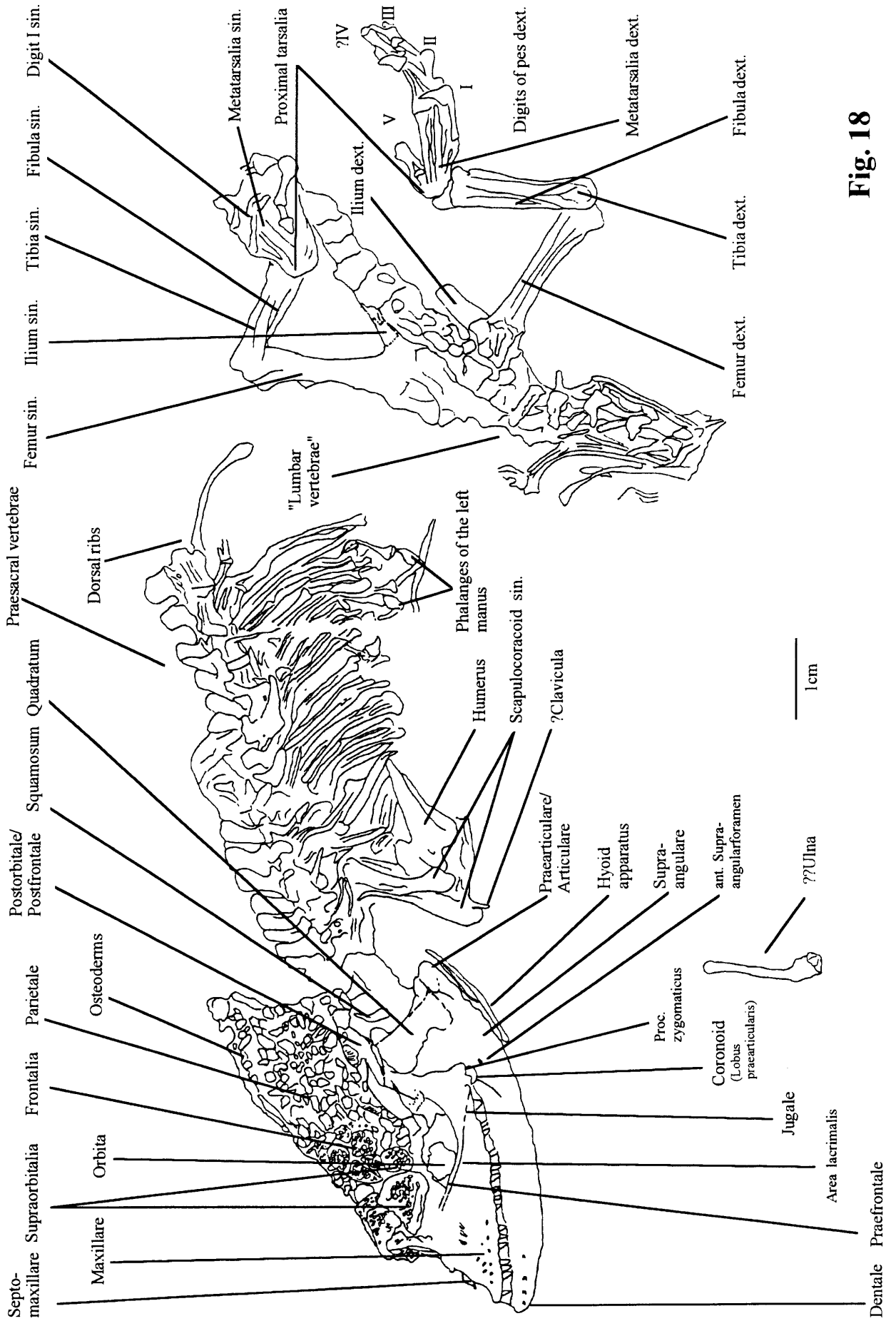


Fig. 18

Septomaxilla. – SMF ME 1249a+b: The more or less hookshaped, probably deformed septomaxilla projects from behind the maxilla.

Nasalia. – SMF ME 1249a+b: No nasalia can be determined, they are probably covered by the maxillaria or by osteoderms.

Frontalia and *parietal*. – SMF ME 1249a: As in the other specimens, these elements are covered by osteoderms. On the radiography of the skull, a suture is visible which most probably represents the suture between the frontalia (Fig. 17C). The orientation of the skull elements cannot be determined, because other sutures are not visible. It cannot be decided if the upper supratemporal fenestrae are open or closed. No Foramen parietale could be identified. On SMF ME 1249a the pattern of osteoderms corresponds with the one described for the other specimens.

Prefrontal. – SMF ME 1249a: The left prefrontal has crushed into the anterior margin of the orbit and therefore is considerably deformed. The dorsal part is covered by osteoderms.

SMF ME 1249b: The right prefrontal, anterior to the orbit, is compressed and deformed as well, its outline cannot be reconstructed.

Postfrontal/postorbital. – SMF ME 1249b: Posterior to the orbita a relatively large, more or less triangular shaped element probably represents the right postorbital. In lateral view it reaches down almost to the ventral margin of the orbit. It is sculptured and dorsally covered by osteoderms. Whether the postfrontal is lacking or fused with the postorbital, cannot be decided. SMF ME 1249a: Above the quadrate a small section of the left postfrontal/postorbital is visible.

Jugal. – SMF ME 1249a: The jugal has the typical triangular shape, but part of the posterior process (Processus zygomaticus) and the Margo posterior are broken off. The external Facies buccalis is pressed in. Osteoderms cover the Processus temporalis. The Area maxillaris exterior of the jugal is still articulated with the left maxilla. The Margo anterior is smoothly curved. The Margo anterior and posterior show several fine obliquely and horizontally oriented striations. SMF ME 1249b: The right jugal, also externally oriented, is much deformed. It rotated slightly, so that the jugal is not any more articulated with the maxilla and the posterior process is concealed by the right maxilla and dentary. Therefore, the Area maxillaris exterior becomes visible and shows three foramina parallel to the Carina zygomatica. The Processus temporalis is separated by a crack. The outline of the Margo posterior is indistinct and the tip of the Processus maxillaris has broken off. The Facies buccalis is slightly pitted and furrowed.

Because of the preservation of the specimen neither *Lacrimalia* nor *Supratemporalia* could be identified.

Fig. 20: Line drawing of SMF ME 1249 a+b, showing the areas of the preserved epidermal scales which are present on both feet and on or between the disarticulated phalanges of the left manus, spread over the dorsal ribs. A: Specimen SMF ME 1249a. B: Counterplate SMF ME 1249b.

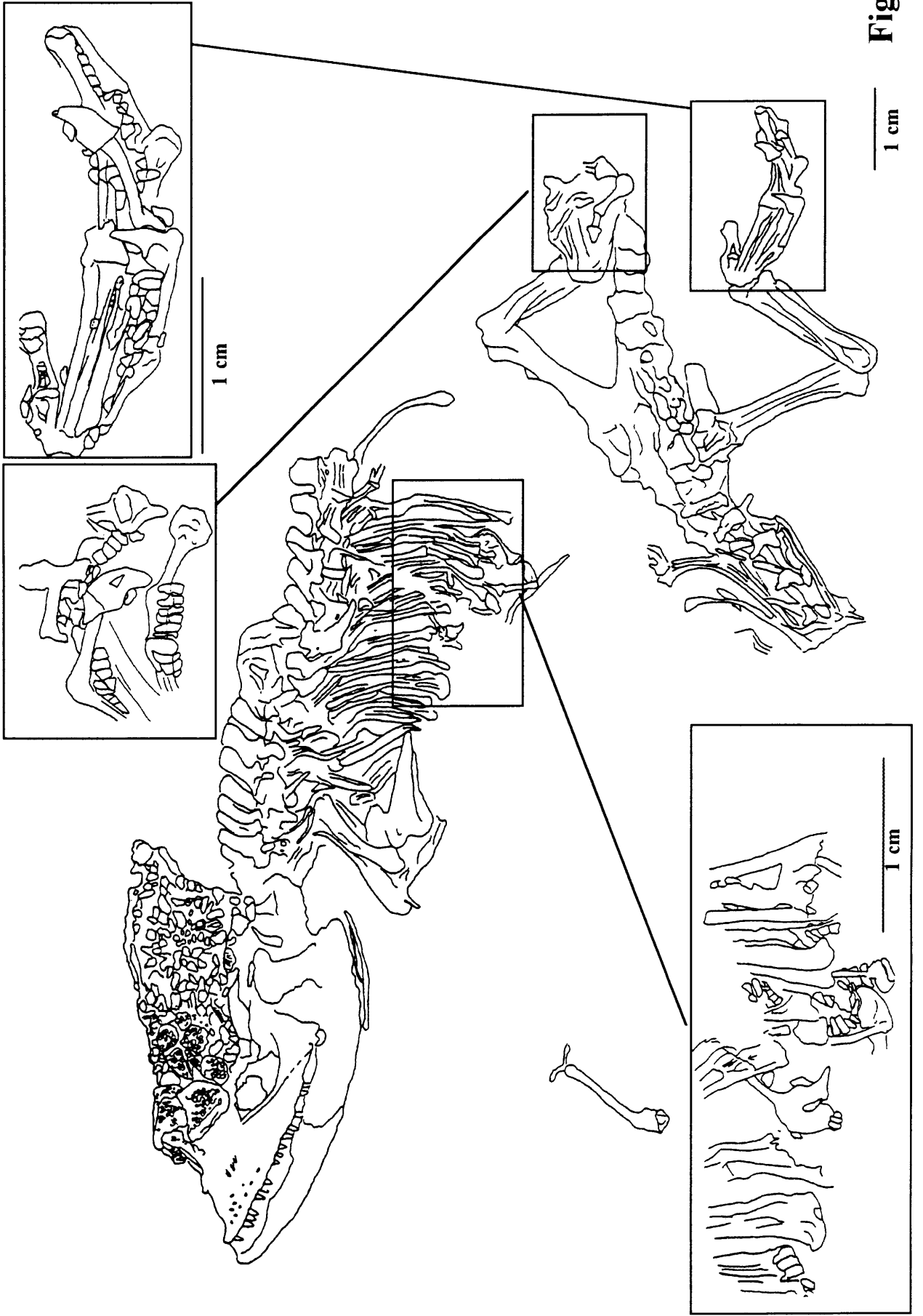
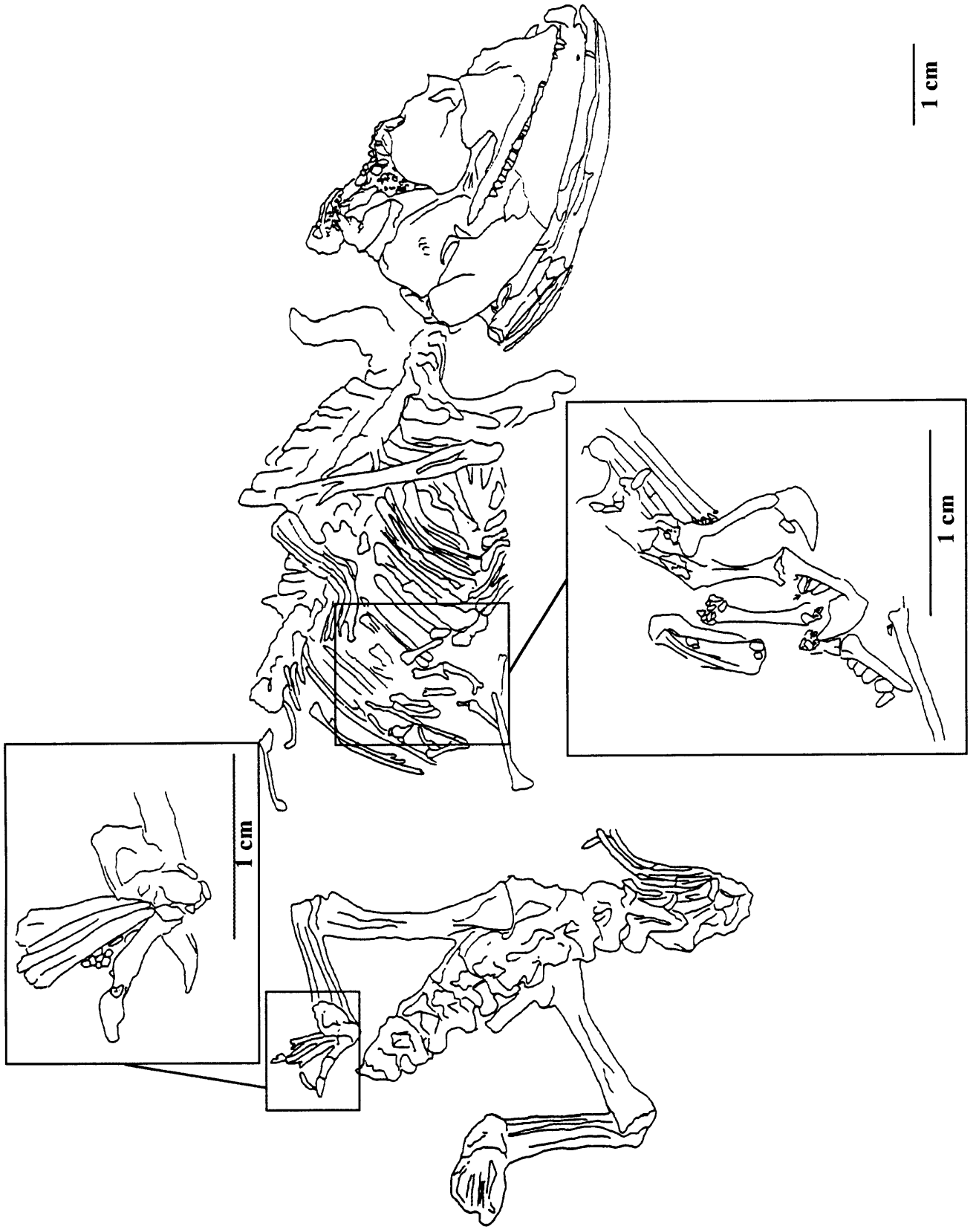


Fig. 20A



1 cm

Fig. 20 B

Squamosal. – SMF ME 1249a: The left squamosal lies posterior to the postfrontal/postorbital. It has rotated so that its posterior end, showing the foramen, points ventrally. It has a slightly bowed, rodlike outline. SMF ME 1249b: The right squamosal could not be identified.

Palatal complex

Quadrate. – The Condylus cephalicus of the left quadrate (SMF ME 1249a, caudal view) is inclined anteriorly and not any more articulated with the squamosal, whereas the Condylus mandibularis is still articulated with the articular. Most of the quadrate is deformed and the features are indistinct, but the Facies posterior and the Crista pterygoidea can still be recognised. The Crista tympani is not preserved. The right quadrate (SMF ME 1249b) is incomplete and much deformed. The remaining palatal elements are concealed by the dermal roof and cannot be identified on the radiographs either.

Braincase

SMF ME 1249a: The Braincase cannot be described because it is completely covered by osteoderms. SMF ME 1249b: In the area of the lower temporal fenestra some deformed fragments can be recognised, which probably originate from the prootic.

Hyoid apparatus

Below the mandible lie rodlike parts of the hyoid apparatus. As in the other specimens, these probably represent the first or second ceratobranchials.

Mandible

The mandible is still articulated and visible from their external sides. On SMF ME 1249b part of the left ramus of the mandible presents also its lingual side.

Dentary. – SMF ME 1249a: On the Facies buccalis of the external side of the left dentary about six foramina are visible parallel to the Crista dentalis. The dentary bears at least 20 tooth positions with 15 preserved teeth, as can be seen through the backside of the plate. The suture towards the postdentary elements is, as in the other specimens, indistinct. A Sinus supraangularis is quite well developed. The Processus coronoideus is covered by the coronoid. As described for the other specimens, the long dentary takes about 2/3 of the whole mandible. SMF ME 1249b: The Facies buccalis of the right dentary is compressed and bears several cracks. Three foramina can be recognised. 16 dentary teeth are preserved, about 21 tooth positions are present. The suture to the postdentary elements can be distinguished quite well, better than in the other specimens. The Processus angularis is relatively short and rounded. The lingual side of the left dentary with its medially open Sulcus meckeli can be observed. Through the backside of SMF ME 1249a, a part of the well developed subdental shelf (Lamina horizontalis) of the left dentary is visible. The morphology of the dentary teeth are as described for SMF ME 475a.

Coronoid. – SMF ME 1249a: The external side of the left coronoid is covered by the left jugal, only the lower part of the ventral process can be observed. On the radiography the well rounded dorsal process (Processus massetericus) of the coronoid is visible as a prominent steep element (Fig. 17C). The ventral process is relatively small, compared to the dorsal process.

SMF ME 1249b: The right coronoid is partly covered by the jugal as well. Through the backside of the plate and on the radiography (Fig. 17F), the internal side of the steep dorsal process (Processus massetericus) with the Crista praearticularis is well visible. The Processus dentalis inferior has broken off.

Supra-angular. – The supra-angular is quite a short, compact element, compared to the dentary and extends anteriorly well beyond the coronoid.

SMF ME 1249a: Both supra-angularia are quite deformed and compressed. The sutures are indistinct or even invisible, except the one bordering the dentary. Below the coronoid lies the supra-angular foramen, which is comparatively large. On the right supra-angular (SMF ME 1249b), part of the dorso-caudally to rostro-ventrally directed ridge can be seen. The posterior supra-angular foramen is situated below that ridge.

Angular. – Because the mandible is compressed and bears many fine cracks, the angular cannot be identified.

Articular/Prearticular. – The left articular/prearticular (SMF ME 1249a) is still articulated with the quadrate (external view). On SMF ME 1249b it can be observed in its internal view. The tip of the retroarticular process has broken off. On the posteromedial spelling margin of the retroarticular process a small tubercle is situated. Below, parallel to the lower margin of the mandible follows a distinct carina. The right articular is still articulated with the much deformed and incomplete quadrate as well. The Corda tympani foramen is situated mesially on the articulating surface of the left articular.

Splénial. – SMF ME 1249b: The splénial is visible on the ventral margin of the right ramus of the mandible, reaching far anteriorly, below the dentary, as in WDC-C-MG 122.

Postcranial skeleton

Axial skeleton

The **vertebrae** are laterally embedded, SMF ME 1249a shows the distinctly high, axe-shaped neural processes. The atlas-axis-complex is not identifiable. At least six cervical, about 26 presacral and about seven caudal vertebrae are present. All vertebrae are articulated except in the middle of the trunk where the vertebrae (21 and 22) are disarticulated. On SMF ME 1249a the posterior half of the body has rotated for 180 degrees showing its right side, whereas the anterior half of the body shows its left side. Accordingly, it is complementary on SMF ME 1249b. The last trunk vertebrae as well as the sacral and caudal vertebrae become shorter (from about 6 mm to 3 mm). They either really reduced their length or are „pushed“ into one another. As expected, the vertebrae are procoelous, which can be seen at the disarticulated vertebrae. The **dorsal ribs** are compressed and deformed but still more or less at their original position. A **sternum** cannot be identified, it is probably crushed and concealed by the anterior limbs and ribs. But in the anterior trunk region, still articulated with the dorsal ribs, about four pairs of poorly preserved sternal ribs are present (SMF ME 1249b). There is no evidence for a **meso-xiphisternum** or **parasternum**. As in the other specimens described above, the last dorsal vertebrae seem to lack ribs, which indicates a lumbar region.

Pectoral girdle

The whole pectoral girdle is strongly deformed and the elements are difficult to identify. SMF ME 1249a: The left scapulocoracoid has an oblong, deformed scapular blade. The glenoid cavity for the humerus is still visible. Along the anterior margin of the scapula lies the clavicle. Two small rodlike fragments below the Fossa glenoidales probably represent parts of the interclavicle. On SMF ME 1249b the right scapular blade is visible, which is as well in a quite deformed condition. Fragments below, probably represent part of the right coracoid.

Pelvic girdle

SMF ME 1249a: Since the posterior part of the body has rotated for 180 degrees, also the pelvic girdle has turned upside down. In its proximal part the right ilium is covered by the femur. The relatively long caudal process of the ilium is directed obliquely in a posterodorsal direction. Its dorsal margin is curved and ends in an abrupt straight edge (see SMF ME 1249b). The remaining parts of the pelvic girdle are strongly compressed and are not identifiable as single elements.

SMF ME 249b: On this plate, the left ilium and the impression of the right one are identifiable. Anteriorly to the left femur and proximally covered by it, lies the pubis. A Foramen n. obturatorii is not recognisable. Further elements of the pelvic girdle cannot be identified.

Pectoral appendages

SMF ME 249a: The left humerus, most probably showing its dorsal side, lies parallel to the vertebral column. The distal part of the humerus, as well as radius and ulna are lacking. The disarticulated digits of the left manus are spread over the dorsal ribs. Some phalanges are partly covered by epidermal scales (Fig. 20A). Carpalia and metacarpalia are lost or indistinguishable from rib fragments.

SMF ME 1249b: The right humerus is long and slender in shape, while the proximal and distal articular surfaces are missing. The humerus points posteriorly and covers obliquely the vertebral column. Only a small flattened section of radius and ulna are preserved, they form an angle of about 45 degrees with the humerus and point ventrally. The small preserved section of radius and ulna are compressed, strongly bent with cracks along their longitudinal axis and situated closely together, so that it is impossible to tell them apart. Both articular surfaces are lacking. Carpalia and metacarpalia are not identifiable. The digits of the right limb are also disarticulated and spread over the dorsal ribs. In some parts, only casts of the digits are visible and one cannot reconstruct whether they belong the left or right carpus. In close vicinity to two of the digits there are several epidermal scutes (Fig. 20B).

Pelvic appendages

Both pelvic appendages are more or less articulated but considerably flattened with several longitudinal cracks. Both limbs are angled. The femora have a length of about 2.5 cm and are thus a little shorter than the humerus (longer than 2.7 cm). The femur is sticklike in shape and slightly broadened proximally and distally. The Caput femoris has an elongated oval shape. Plate SMF ME 1249a shows the femora in dorsal view, while they can be seen in ventral view in plate SMF ME 1249b. On this plate the two condyles forming the articulating surface for the tibia are visible on the distal end of the right femur. Between both, there is a slight emargination ("popliteal space", ROMER

1956). A small process emerges below the Caput femoris that probably is the Trochanter internus. The right fibula covers the tibia.

SMF ME 1249a: The proximal articulating surface of the right fibula is covered by the tibia. The two areas for articulation with the femur are not well separated and show a convex outline. On this plate, tibia and fibula are visible in posterior view, on the counterplate the anterior part is visible. Both feet are still more or less articulated.

Astragalus and calcaneum seem to be fused, but as the tarsals are considerably deformed one cannot be sure. The distal tarsals cannot be distinguished. All metatarsalia are preserved. Metatarsus I of the left limb and metatarsalia I-V of the right limb are on plate SMF ME 1249a, whereas metatarsal II-V of the left limb and fragments of the metatarsalia II-IV are situated on counterplate SMF ME 1249b. The digits of both feet are preserved on SMF ME 1249a. The digits of the right pes are more or less complete, some phalanges, especially of digit V, are missing. Several digits of the left pes are disarticulated or incomplete and cannot be identified concerning their position, except for digit I. Several epidermal scutes are preserved on both feet (Fig. 20A+B).

2.3.1.2.6 Specimen SMNK-Me 930a, additional material

This specimen consists of the head and a few mainly unidentifiable disarticulated remains of the postcranium (Fig. 21, Fig. 22). It is thinkable that it represents an undigested food remain.

Skull

Dermal roof shield

No elements of the dermal roof shield can be recognised. When studying the radiography, the constricted frontal is visible (Fig. 21B). Only the osteoderms that cover largest part of the dermal roof shield are visible, showing the typical pattern. Only the supraorbitalia of the left skull side are recognisable. A cast probably of the jugal or the dislocated quadrate is projecting from the right side of the skull.

No other elements of the **palatal complex** or the **braincase** are preserved.

Postcranial skeleton

A fragment of about five presacral vertebrae is situated above the skull. Across lies a dorsal rib and probably a part of the scapular blade. Below the skull some unidentifiable, heavily deformed and compressed other postcranial elements are present. Most of it represents only a cast.

2.3.1.2.7 Cast from the Fossilien- und Heimatmuseum Messel, additional material

The original of this cast could not be retraced. Although it is more or less articulated, the preservation cannot be compared to any of the other specimens (Fig. 23, Fig. 24).

According to its tooth morphology, limb proportion and size, the cast almost certainly represents a specimen of the new genus and species, although other typical diagnostic features are not visible.

The head-trunk-length of this specimen is 13.4 cm of which the head-length measures about 4 cm, it is only slightly larger than the smallest specimen SMF ME 1249a+b.

Skull

The skull shows its ventral side.

Dermal roof shield

Premaxilla. – The considerably flattened and deformed Processus nasalis and Processus maxillari of the premaxilla can be seen from their dorsal side. The premaxillary teeth are concealed by these elements.

Maxilla. – A small part of the left maxilla is preserved showing a section of the Crista dentalis with about nine maxillary teeth, while about 12 tooth positions can be identified.

Other elements of the dermal roof shield are not visible. An element, possibly representing an osteoderm, is situated next to the maxilla.

Palatal complex

Quadrata. – The left quadrate is still somehow attached to the articular. Due to its fragmentary and deformed state, the orientation cannot be determined.

Pterygoid. – The long and slender Processus quadratus of the right and left pterygoid is recognisable. Four Dentes pterygoidei can be determined on the poorly preserved right Processus palatinus.

Elements of the **Braincase** cannot be distinguished.

Mandible

Dentary. – Below the right maxilla lies the right dentary in labial view with 12 preserved dentary teeth. The Facies buccalis is incompletely preserved. The lingual view of the left dentary shows the typical medially open Sulcus meckeli. Eight conical dentary teeth are visible, some of them are slightly recurved. No striations on the tooth crown are preserved on the cast.

The postdental elements cannot be distinguished from one another. Only the lingual side of the Prearticular/Articular of the right ramus of the mandible and the retroarticular process of the left ramus can be recognised.

Fig. 21: Gen. et spec. nov. A: SMNK-Me 930a. Only the osteodermal cover of the head and a few mainly unidentifiable disarticulated remains of the postcranium are preserved. B: radiography.

Fig. 22: Line drawing of SMNK-Me 930a with identified skeletal elements.

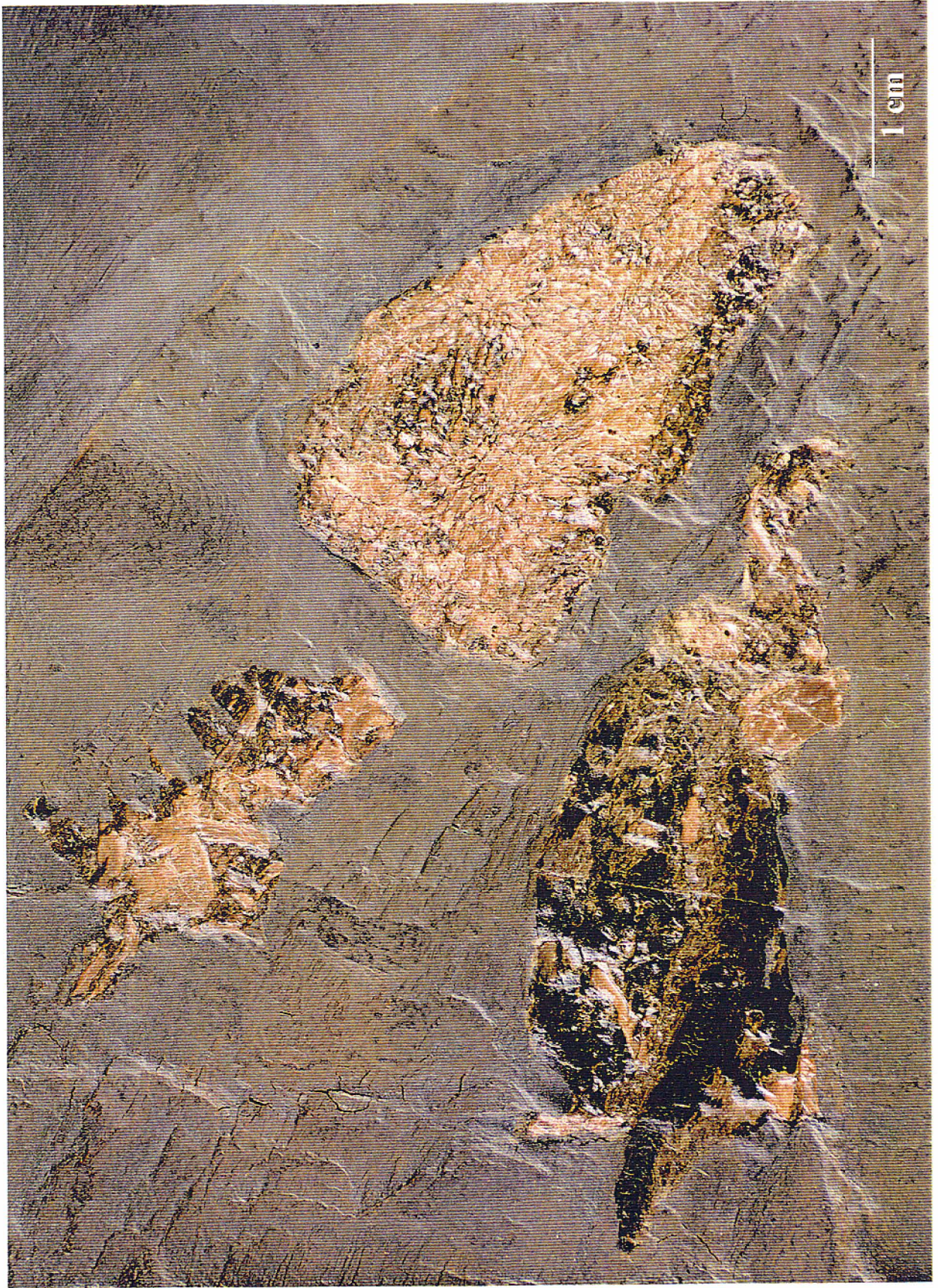


Fig. 21A



Fig. 21B

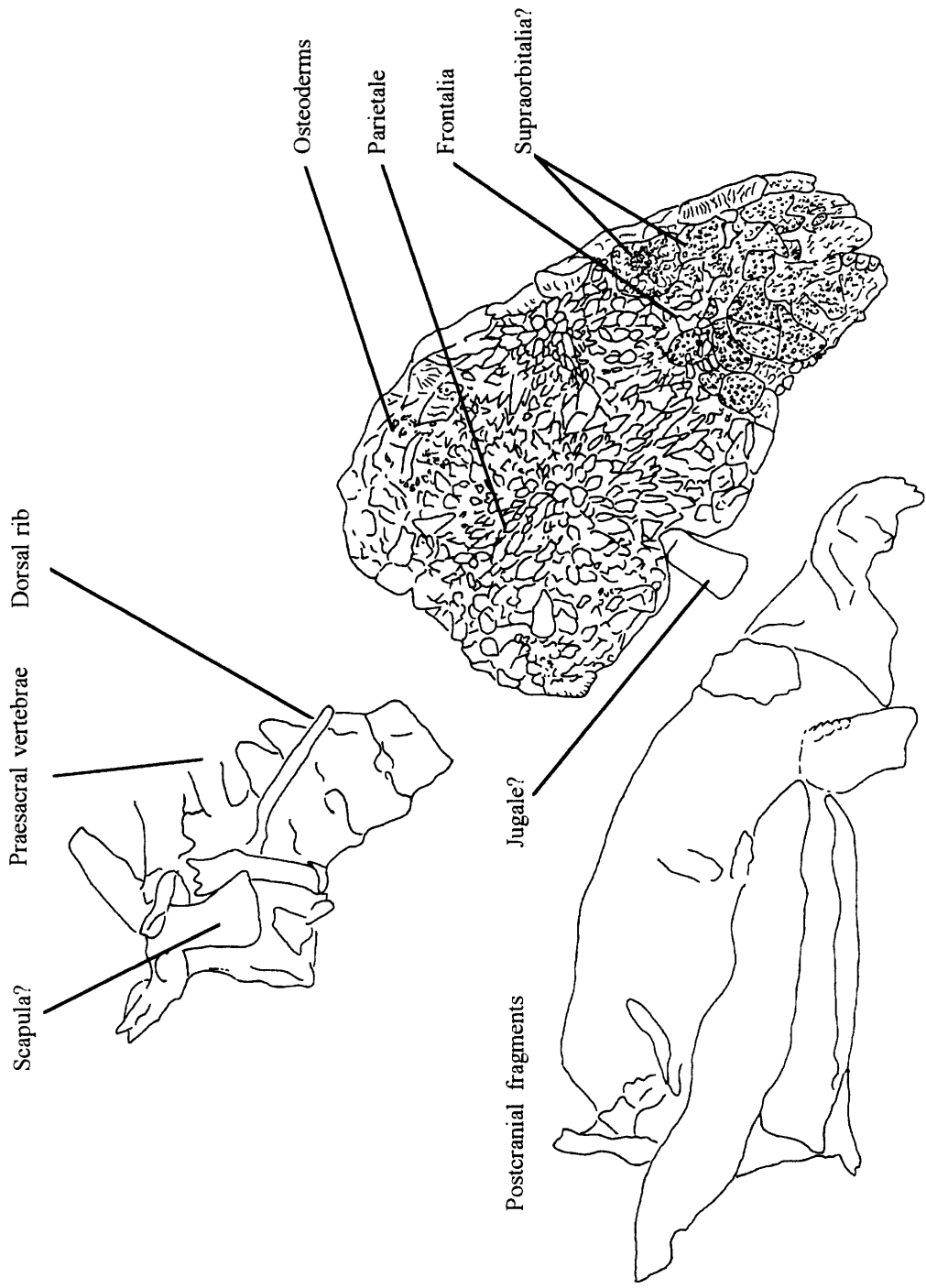


Fig. 22

Postcranial skeleton

Axial skeleton

The axial skeleton is almost completely articulated, most of the tail is missing. Due to the much compressed preservation, no presacral vertebral count can be made. Only one axe-shaped neural spine is visible next to the left humerus. The dorsal ribs are still articulated with the vertebrae. As in the other specimens, the last presacral vertebrae lack dorsal ribs. Below this “lumbar” region the presence of intestinal contents is indicated. Only a few, poorly preserved caudal vertebrae are present, the number of which cannot be determined.

No elements of the **pectoral** or **pelvic girdle** can be distinguished.

Pectoral appendages

This specimen has somehow twisted, it shows the ventral aspect of the head, but the trunk in a lateral position, as in the other specimens. Both limbs are disarticulated from the pectoral girdle. The left limb lies below the thorax, with the proximal part of the humerus covering some dorsal ribs. The right limb is mainly situated above the thorax, with the proximal part of the humerus and the manus on the vertebral column. Radius and ulna of both limbs are not distinguishable from one another due to their deformed state. The single elements of the carpalia and metacarpalia of the left manus are not identifiable, but the digits ?I, III and IV can be identified.

The heavily compressed and deformed right manus lies on the thorax, no elements can be distinguished.

Pelvic appendages

Both articulated limbs seem to be still attached to the pelvic girdle. The right limb most probably lies above, the left limb below the ventrally oriented caudal vertebrae. Due to the considerable deformation of the limbs it cannot be determined which element represents the tibia and which the fibula. Tarsalia and the long metatarsalia are indistinctly preserved. Digit I, III and IV in both feet can be determined with some certainty.

Fig. 23 (following pages): ?Gen. et spec. nov. A: Overview of the cast shown in the Fossilien- und Heimatmuseum Messel. B: Head in ventral view.

Fig. 24: Line drawing of the cast from the Fossilien- und Heimatmuseum Messel with identified skeletal elements.

Tab. 4: A table of identifiable skull elements in the different specimens described here. 3= Element present and well preserved; 2= Element deformed, crushed or incomplete; 1= Element present, but partly or completely covered; 0= Element not preserved or unidentifiable; (X)= visible on radiography.

Tab. 5: A table of identifiable postcranial elements in the different specimens described here. Legend as in Table 4.

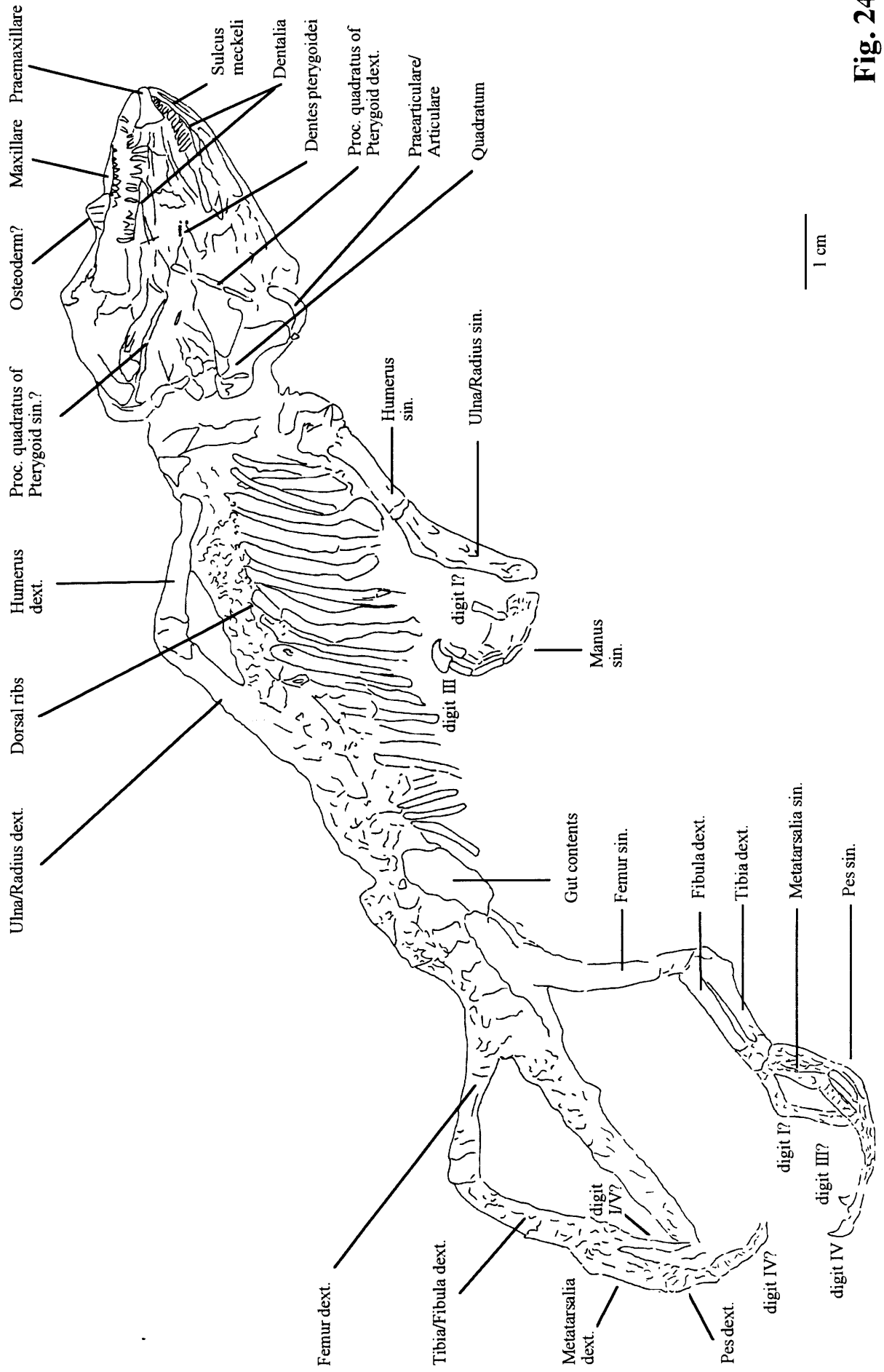
Fig. 25 : General reconstruction of the skull and mandible of the new genus and species. The dotted lines indicate reconstructed elements which are not visible in the specimens. A-C: Skull. A: Ventral view. B: Dorsal view. C: Lateral view. D+E: Mandible. D: Labial view. E: Lingual view.



Fig. 23A



Fig. 23B



1 cm

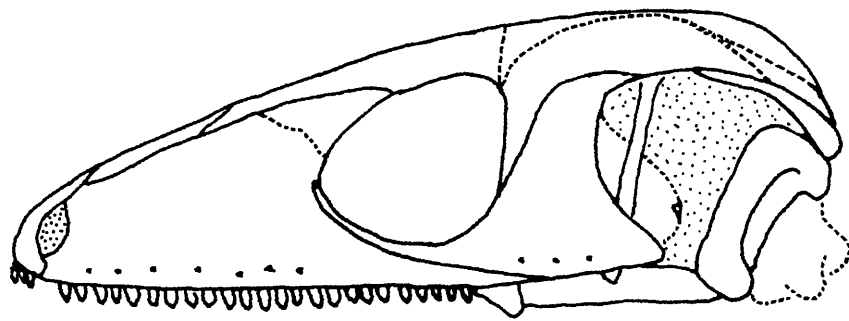
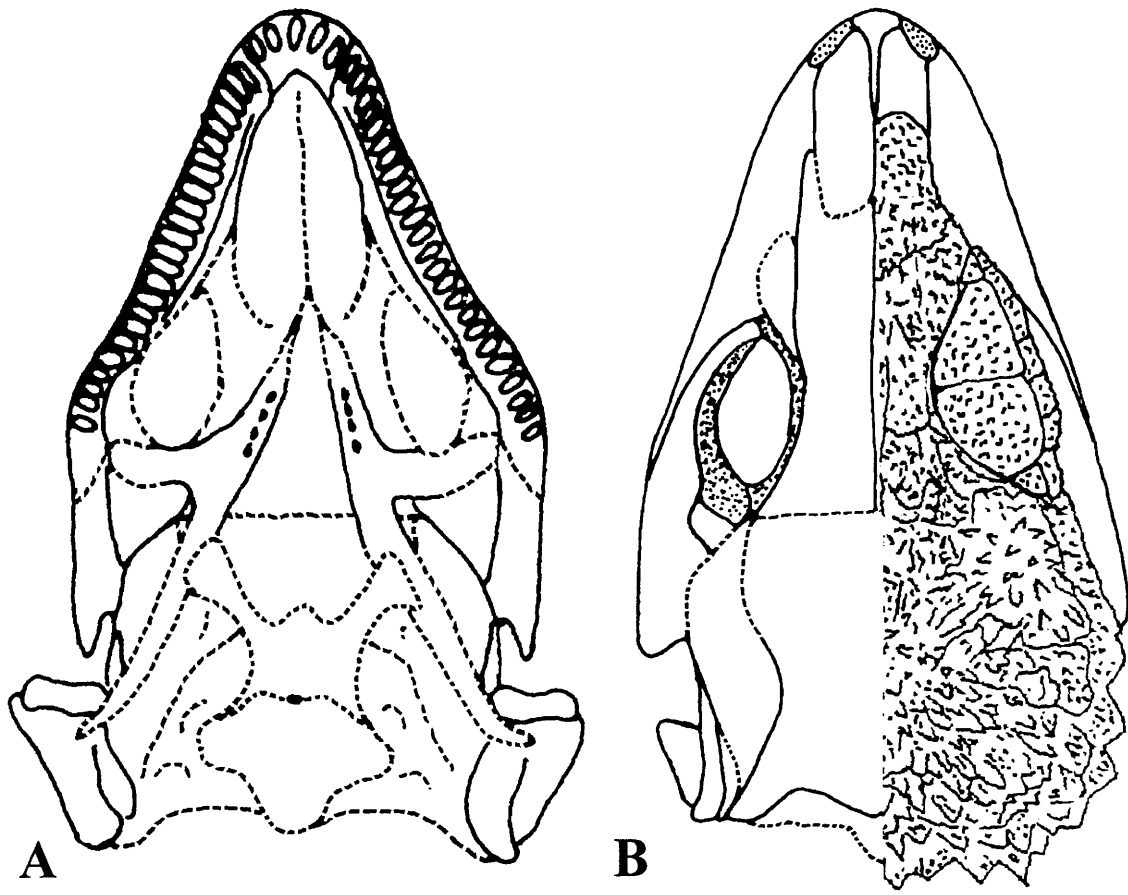
Fig. 24

Element	SMF ME 3516	SMF ME 475a	WDC-C-MG 122/123	SMNK -PAL 3813	SMF ME 1249a/b	SMNK-Me 930a	Cast
Skull osteoderms	3	1	3	3	3	2	0
Praemaxillare	3	1	3	1	1	0	2
Maxillare	3	3	3	1/2	3	0	2
Nasalia	1	0	1	1	0	0	0
Frontalia	1	1	1	1	1	1	0
Parietale	1	1	1	1	1	1	0
Praefrontalia	1	1	1	1	1	1	0
Postfrontalia	1	1	1	1	1	1	0
Jugale	3	3	3	3	2	???	0
Lacrimalia	0	0	0	0	0	0	0
Supratemporalia	0	1	0	0	0	0	0
Squamosum	1	3	1	1	3	0	0
Quadratum	1	3	1/2	2	2	???	2
Pterygoid	0	2	2	0	0	0	0
Epipterygoid	0	2	1	0	0	0	0
Palatinum	0	2	0	0	0	0	0
Prooticum	0	2	0	0	??	0	0
Supraoccipitale	0	0	??	2	0	0	0
Basioccipitale	0	2	2	0	0	0	0
Exoccipitalia	1	0	2	2	0	0	2
Dentale	3	3	3	1	3	0	2
Coronoid	3 (X)	2	1	0	3 (X)	0	0
Supraangulare	1	3	3	0	0	0	0
Angulare	0	0	0	0	0	0	0
Articulare/Praearticulare	2	3	2	0	3	0	2
Hyoid apparatus	0	2	2	0	2	0	0

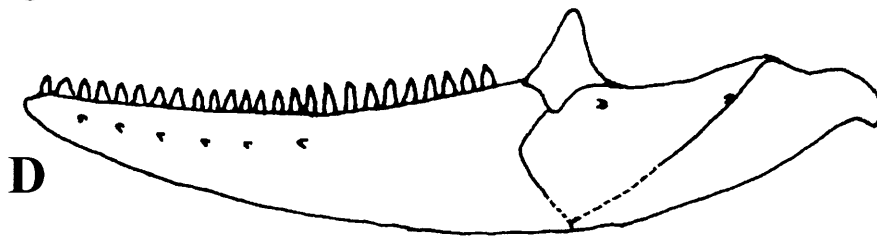
Tab. 4

Element	SMF ME 3516	SMF ME 475a	WDC-C-MG 122/123	SMNK -PAL 3813	SMF ME 1249a/b	SMNK-Me 930a	Cast
Praesacral vertebrae	3	3	3	3	2	2	2
Caudal vertebrae	3	2	0	0	0	0	2
Dorsal ribs	3	3	3	3	2	0	2
Sternum	2	0	0	2	2	0	0
Meso/Xiphisternal ribs	2	0	0	3	0	0	0
Scapulocoracoid	3	3	3	2	2	0	0
Clavicula	3	2	3	3	2	0	0
Interclavícula	0	0	0	?2	?2	0	0
Ilium	3	0	2	0	2	0	0
Ischium	2	0	0	0	0	0	0
Pubis	0	3	0	0	1	0	0
Humerus	3	2	3	1	2	0	2
Ulna	3	0	2	3/1	2	0	2
Radius	3	0	2	3/1	2	0	2
Manus	3	0	3	3	0	0	2
Femur	3	2	2	2	2	0	2
Tibia	3	0	1	2	2	0	2
Fibula	3	0	1	2	2	0	2
Pes	3	0	2	0	2	0	2

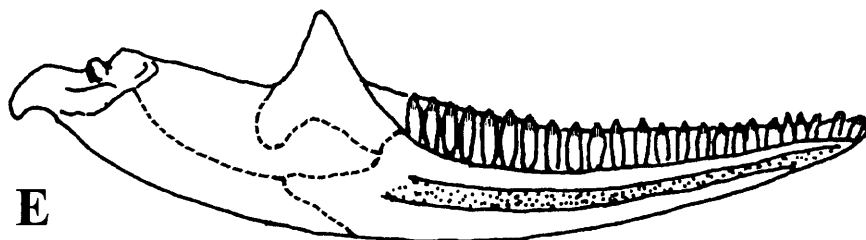
Tab. 5



C



D



E

5 mm

Fig. 25

2.3.2 Intraspecific variation

The four specimens described above belong to a single species. Although there are differences between the specimens, I consider these as intraspecific variation: The differences in size between the individuals (Tab. 3, p.26) can be a question of age or sexual dimorphism. The proportions of the head and limblength to the head/trunk-length being quite similar in all specimens (Tab. 3), also suggests the attribution to a single species.

The Facies buccalis of the maxilla and jugal of SMF ME 475a is stronger furrowed than in all other specimens. This is most probably due to the advanced age of this largest specimen.

The maxillary teeth number varies from about 20 in the two smaller individuals (WDC-C-MG 122/123 and SMF ME 1249a+b) to approximately 22 to 27 in the two larger specimens SMF ME 3516 and 475a. The dentary teeth number varies in the same range as the maxillary teeth number: The two smaller individuals have at least 20 to 23 dentary teeth, whereas the larger individual SMF ME 475a has about 27 dentary teeth. The dentary teeth in the designated holotype are difficult to determine on the radiography, but there seem to be at least 23. Such a variability in tooth counts is not unusual, e.g. within different sizes of the species of *Iguana iguana*, the maxillary as well as the dentary teeth number can vary from 16 to 30 (EDMUND 1969).

Although the presacral vertebrae number is difficult to determine, because most of the cervical vertebrae are covered by osteoderms or are damaged, there seems to be variation in the presacral vertebrae number from at least 22 to about 28 (in the smaller specimen WDC-C-MG 122/123). This difference also occurs in extant species. ARNOLD (1998) reports that in some Lacertidae the presacral vertebral number varies between the sexes.

2.3.3 Results of numerical taxonomy

2.3.3.1 Complete matrices

In order to test the reproduceability of the matrices by the authors in question, the unaltered original matrices were analysed with the two search options used here. In a second step, the character states of *The new genus and species* were added to this matrices and the results compared.

2.3.3.1.1 ESTES et al. (1988)

2.3.3.1.1.1 Matrix excluding the new genus and species

ESTES et al. (1988) presented cladograms including and omitting Serpentes, Dibamidae and Amphisbaenia. With the PAUP software of an unknown version the authors obtained a single tree including these groups with a length of 406 steps and a consistency index of 0.42. When Serpentes, Dibamidae and Amphisbaenia were deleted, the tree length was significantly shorter (323 steps) and the consistency index was

higher (0.51). All of these trees were not reproducible in this study with neither of the two search options (simple and random addition with TBR), even when characters were treated as ordered. Unfortunately, the authors have not published the exact search options they used. The two search options used in the present analysis produced two identical trees, no matter if characters are treated as ordered or unordered. Because the original tree depicted in ESTES et al. (1988: Fig. 5c) is not reproducible in this study, the tree that was generated here (Fig. 26) is referred to as reference tree.

Fig. 26 shows the tree reconstructed in the present study with the matrix from ESTES et al. (1988). Although Serpentes, Dibamidae and Amphisbaenia were deleted from the matrix, the two search options produced identical cladograms which are more similar to the PAUP cladogram in ESTES et al. (1988: 138) including these groups. The only difference apart from the absence of the three taxa is the position of Gekkota, being a sistergroup of Scincomorpha (present study) rather than being collectively placed with Serpentes, Dibamidae and Amphisbaenia to Anguimorpha as in ESTES et al. (1988).

The differences of the cladograms obtained here to the one depicted in ESTES et al. (1988: Fig. 5c) without Serpentes, Dibamidae and Amphisbaenia is significantly larger: The Gekkota were placed as a sistergroup to Scincomorpha alone and not to (Scincomorpha + Anguimorpha). Additionally, the Scincoidea were placed as a sistergroup to Lacertoidea rather than to Anguimorpha. Anguidae and Xenosauridae are presented as sistergroups.

ESTES et al. (1988) presented two cladograms which were obtained from a PHYSYS analysis. The first one included Serpentes, Dibamidae and Amphisbaenia, the other one is a consensus tree with these groups deleted. The PAUP-tree obtained here (without Serpentes, Dibamidae and Amphisbaenia) shows much more congruences to the PHYSYS tree (ESTES et al. 1988: Fig. 5a), than to the PAUP trees. The first PHYSYS tree also shows Scincoidea as a sistergroup to the Lacertoidea, Gekkota as a sistergroup to all Scincomorpha and Anguidae and Xenosauridae are presented as sistergroups. In the consensus tree the Gekkota, Xenosauridae and Anguidae are not resolved.

When comparing the tree lengths, those trees which were generated in the present study, were much shorter and had a higher consistency index than those presented by ESTES et al. (1988), with ordered or unordered characters. With both search options used here, identical tree lengths and consistency indices were obtained here. When including the taxa snakes, dibamids and amphisbaenians the tree length was 333 steps and the consistency index 0.50. With these groups deleted a tree length of 274 steps and a consistency index of 0.59 resulted. This might explain the differences between the trees from literature and the ones generated in the present study. ESTES et al. (1988) used an older PAUP version or hardware which obviously was not able to find shorter cladograms. Even when no branch swapping was applied, 89 trees were generated with tree length between 362 and 340 steps, all shorter than that of ESTES et al. (1988).

Tab. 6: Tree length, indices and number of trees obtained when using different matrices. *n.t.* = new taxon, ci = consistency index, ri = retention index. All results obtained with second search strategy.

Matrix	Multistate	Tree length without n. t.	Tree length including n. t.	ci without n. t.	ci including n. t.	ri without n. t.	ri including n. t.	# trees without n. t.	# trees including n. t.
ESTES et al. (1988)									
Complete matrix	unordered	264	270	0.60	0.59	0.67	0.67	1	1
Only osteolog. characters	unordered	219	225	0.61	0.60	0.67	0.66	3	6
Char. only visible in n. t.	unordered	82	87	0.65	0.61	0.74	0.72	2	4
Only Scincomorpha	unordered	95	103	0.87	0.85	0.68	0.64	3	11
EVANS & CHURE (1998)									
Complete matrix	unordered	435	443	0.55	0.54	0.54	0.53	15	6
Only osteolog. characters	unordered	353	361	0.52	0.51	0.53	0.53	7	20
Char. only visible in n. t.	unordered	109	117	0.50	0.47	0.59	0.58	510	66
Only Scincomorpha	unordered	104	113	0.81	0.79	0.64	0.62	2	1
LEE (1998)									
Complete osteolog. matrix	ord./unord.	646	655	0.79	0.79	0.67	0.67	2	1
Char. only visible in n. t.	ord./unord.	250	260	0.80	0.78	0.70	0.68	9	15
Only Scincomorpha	ord./unord.	275	286	0.93	0.91	0.64	0.60	3	1
CALDWELL (1999)									
Complete osteolog. matrix	unordered	464	468	0.68	0.67	0.60	0.61	21	27

Tab. 6

2.3.3.1.1.2 *Matrix including the new genus and species*

When the character states of the new genus and species are included with either ordered or unordered characters, the trees remain unchanged and the new taxon is placed throughout as a sistergroup to the Lacertidae (Fig. 27). Both are placed as sistergroup to Teiioidea (Teiidae + Gymnophthalmidae). As a consequence, the trees increased in length by six steps and the consistency index decreased slightly: Tree length = 280, ci = 0.58 (Tab. 6).

2.3.3.1.2 EVANS & CHURE (1998)

2.3.3.1.2.1 *Matrix excluding the new genus and species*

The investigation carried out by EVANS & CHURE (1998) yielded five trees with a length of 435 steps, a consistency index of 0.55 and a retention index of 0.54. Interesting features of all five trees are: *Paramacellodus* is placed as sistergroup to Scincoidea. Lacertidae and Xantusiidae are linked with Scincoidea instead of Teiioidea. Serpentes, Amphisbaenia and Dibamidae cluster with either Gekkota or Anguimorpha. The authors present a strict consensus tree calculated from these five trees.

Using the first search strategy (simple addition sequence with TBR) it is possible to reproduce also five trees with the same tree lengths and indices as in EVANS & CHURE (1998). The strict consensus tree (Fig. 28) is identical to the one shown in Fig. 4 of EVANS & CHURE (1998).

The second search option (random addition with TBR) produces 15 instead of five trees. The strict consensus tree (Fig. 29) differs significantly from the one published by EVANS & CHURE (1998): Gekkota, Anguidae, Xenosauridae, (Amphisbaenia + Dibamidae), Varanoidea and Serpentes are unresolved on a higher level together with *Ardeosaurus*, *Bavarisaurus*, *Eichstättisaurus* and Iguania, the latter being already unresolved in the author's cladogram. Scincoidea and Xantusiidae are unresolved and placed on the same level as (Teiioidea + *Meyasaurus*). Both search strategies produced the same tree length, consistency and retention indices (Tab. 6) as were obtained in EVANS & CHURE (1998).

Fig. 26 (following page): Tree generated from complete matrix of ESTES et al. (1988), without character states of the new genus and species. All cladograms shown here are calculated with the 2. search strategy, except when mentioned otherwise.

Fig. 27 (following page): Tree generated from complete matrix of ESTES et al. (1988), including character states of the new taxon.

Fig. 28 (following page): Strict consensus tree from five trees. Complete matrix of EVANS & CHURE (1998) without character states of the new taxon, with 1. search strategy.

Fig. 29 (following page): Strict consensus tree from 15 trees. Complete matrix of EVANS & CHURE (1998) without character states of the new taxon, with 2. search strategy.

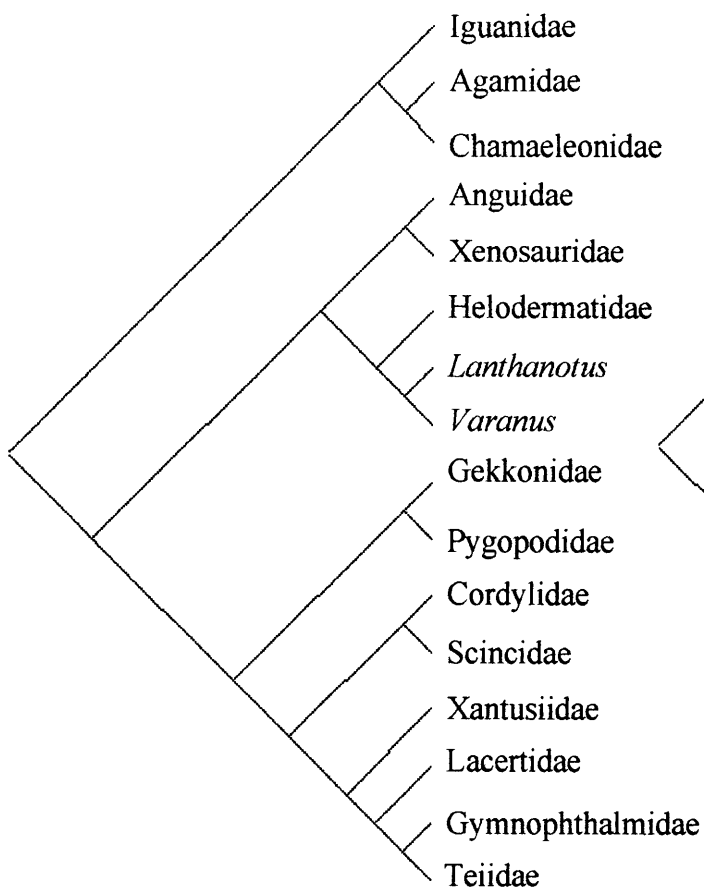


Fig. 26

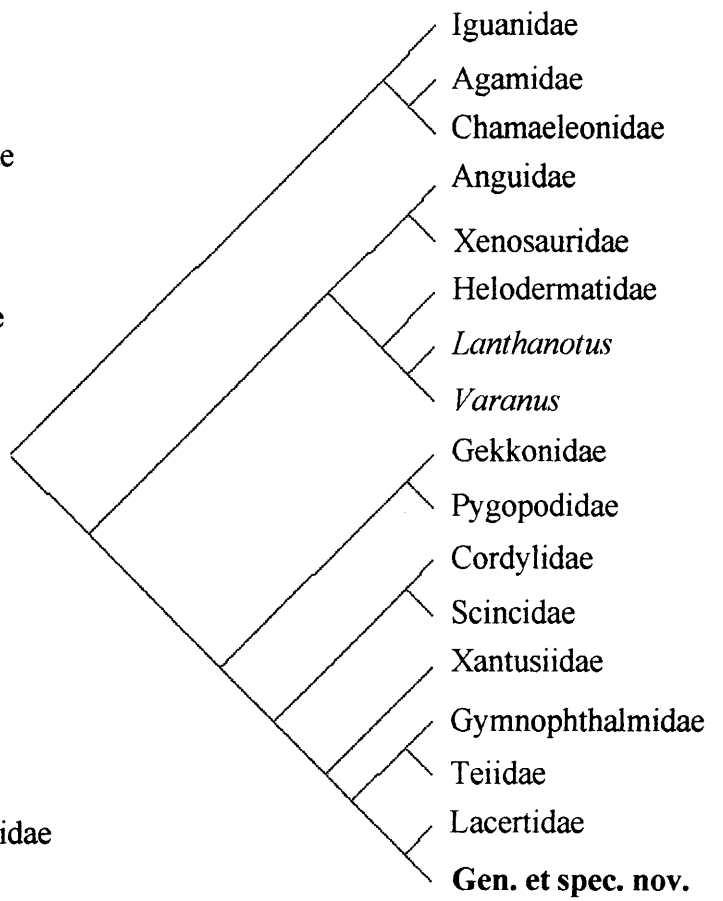


Fig. 27

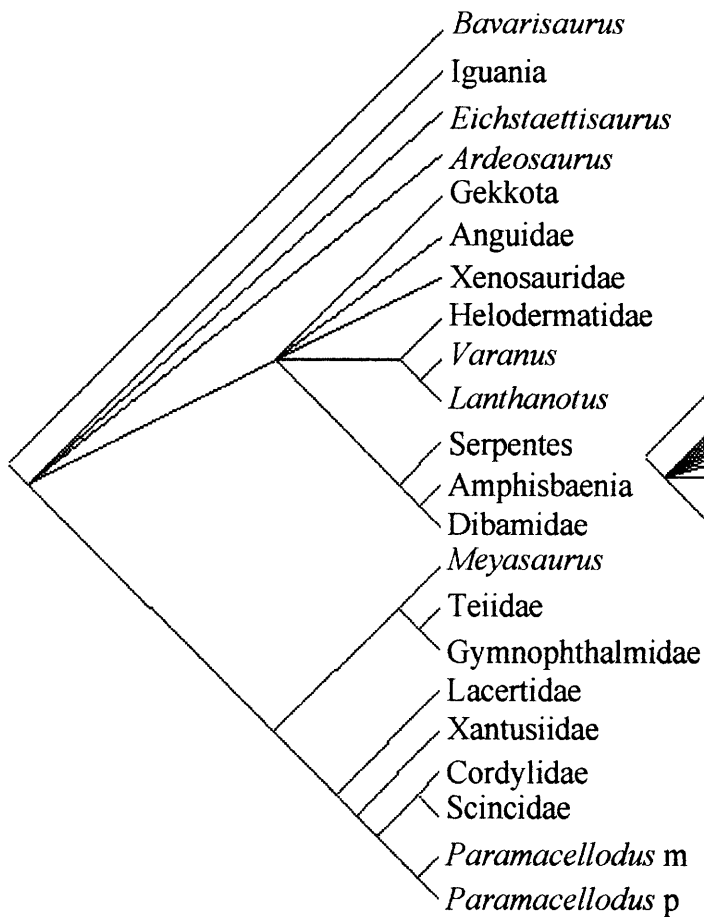


Fig. 28

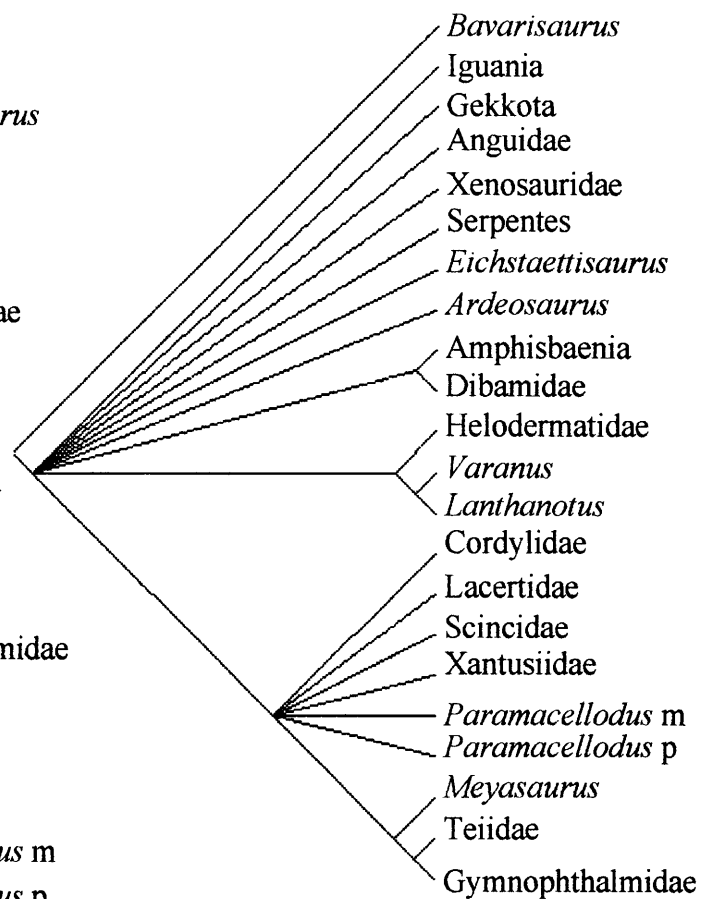


Fig. 29

2.3.3.1.2.2 *Matrix including the new genus and species*

The results from the first search option do not change when adding the character states of the new genus and species to the matrix. It is placed throughout as a sistergroup to Lacertidae. Both Lacertidae and the new taxon are collectively placed as a sistergroup to Xantusiidae, Scincoidea and *Paramacellodus*, as can be seen in the strict consensus tree (Fig. 30). The length and indices of the trees change slightly when adding the character states of the new species: The tree length is eight steps longer (443 steps), the consistency and retention indices diminish slightly ($ci = 0.54$, $ri = 0.53$) (Tab. 6).

When using the second search strategy, only six trees were generated compared to 15 without the new taxon. The first five trees generated under these conditions are identical with the ones from the first search option. The strict consensus tree (Fig. 31) resembles the consensus tree without the new taxon out of 15 trees. The difference is that Scincoidea, Lacertidae and Xantusiidae are now resolved. The new genus and species was again placed as sistergroup to the Lacertidae. Both taxa are collectively placed as a sistergroup to (Xantusiidae + Scincoidea). The indices and the tree length remain the same as in the first search option.

2.3.3.1.3 LEE (1998)

2.3.3.1.3.1 *Matrix excluding the new genus and species*

Only the data matrix that produced the cladogram in LEE's Fig. 4 is used for the present analysis. The other data matrices are designed to resolve the position of early snakes and Mosasauroida, which are irrelevant for the phylogenetic position of the new genus and species.

With both search options the two trees, respectively the strict consensus tree of LEE (1998) could be reproduced (Fig. 32). But the tree lengths are considerably longer, than in the one of LEE (646 instead of 336 steps), the consistency index is higher (0.79 instead of 0.57) and the retention index is identical (Tab. 6).

2.3.3.1.3.2 *Matrix including the new genus and species*

When adding the character states of the new genus and species, only one tree was generated (Fig. 33), identical – except for the new taxon – with one of the two equally parsimonious trees by LEE (1998). The new species was placed at the base of Scincoidea and Anguimorpha using either search options. The tree is nine steps longer (655) than the one excluding the new taxon, and the indices slightly decrease (ci , ri Tab. 6). As already mentioned, only the strict consensus tree is described and depicted here which originates from the data matrix of LEE (1998), without early snakes and Mosasauroida. However, a run was performed including these groups. The results concerning the position of the new genus and species are identical with the ones described above, showing the new taxon placed at the base of Scincoidea and Anguimorpha. The enlargement of the matrix in terms of taxa had no effect on this position. Both search options yielded the same results. Obviously, the first search option (simple addition sequence + TBR) is sufficient to reproduce the cladograms of LEE (1998) and EVANS & CHURE (1998).

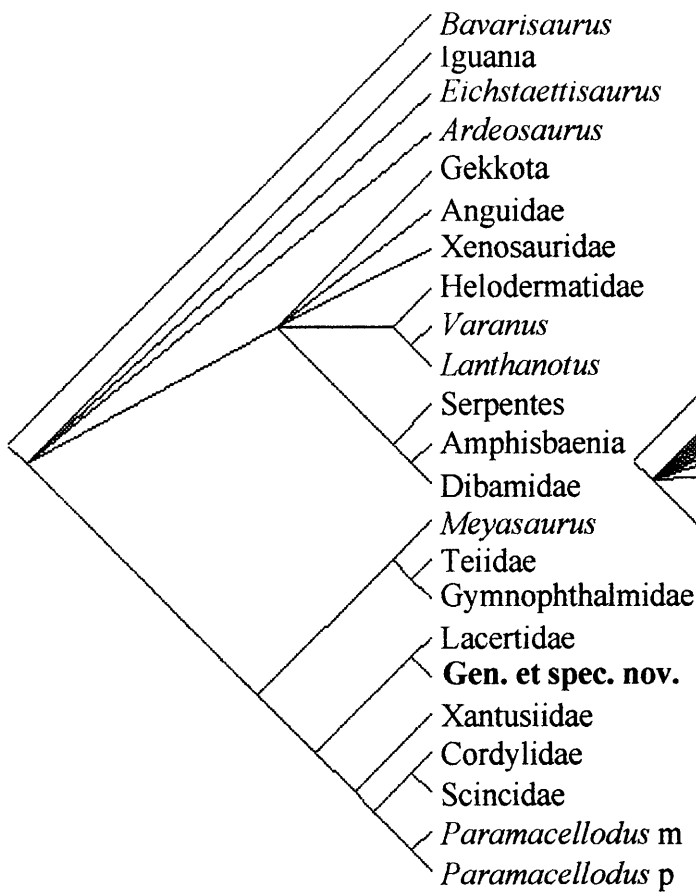


Fig. 30

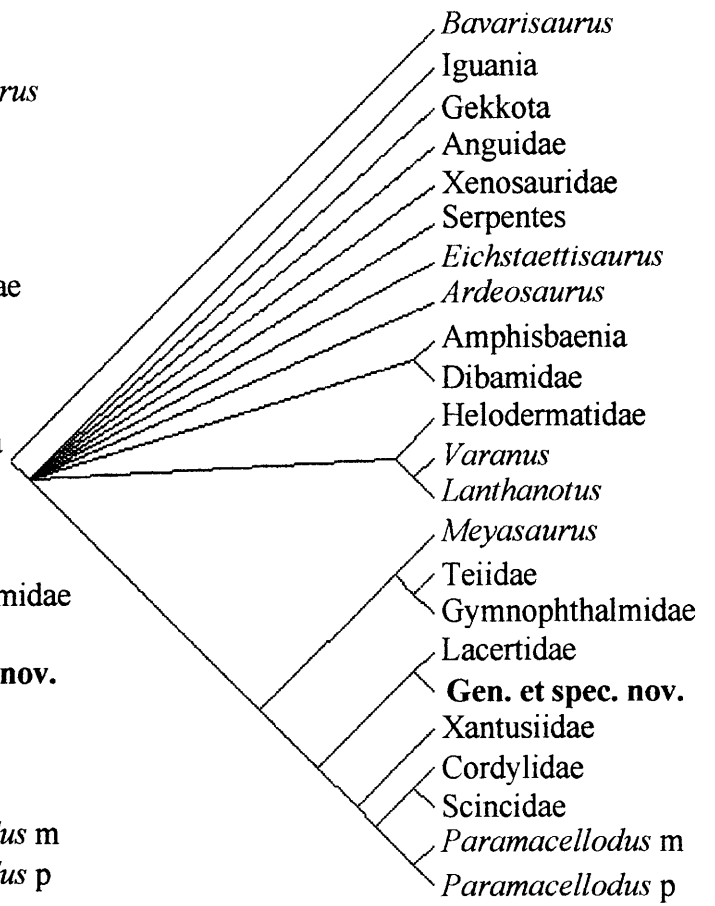


Fig. 31

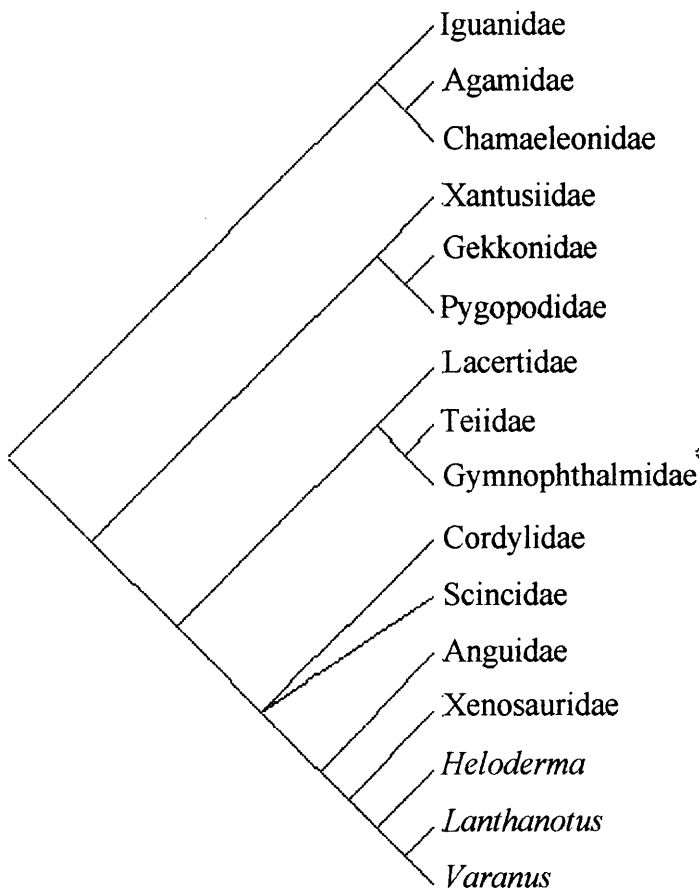


Fig. 32

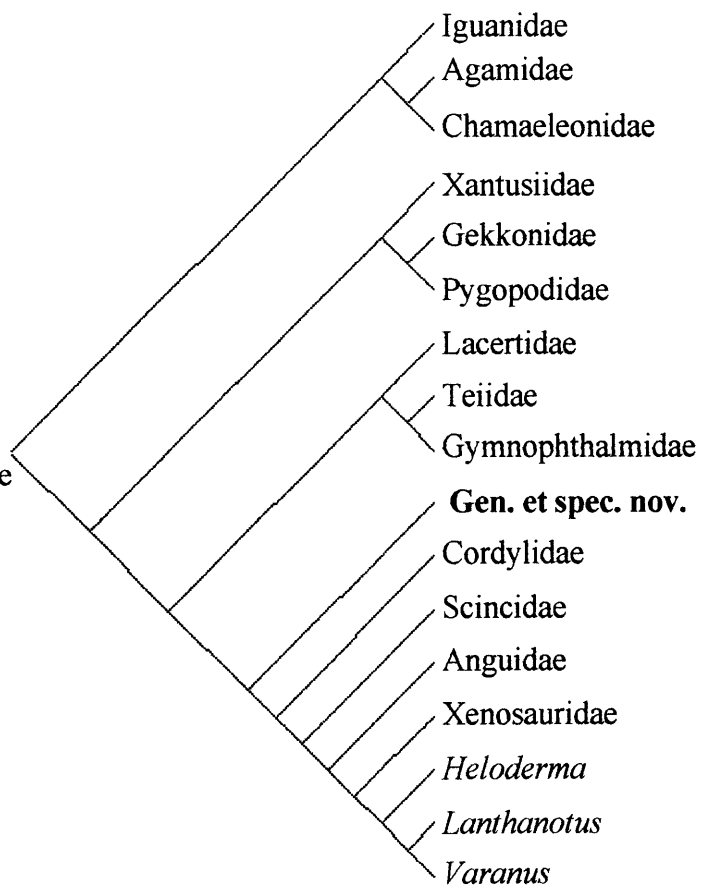


Fig. 33

Fig. 30 (previous page): Strict consensus tree from five trees. Complete matrix of EVANS & CHURE (1998) including character states of the new taxon, with 1. search strategy.

Fig. 31 (previous page): Strict consensus tree from six trees. Complete matrix of EVANS & CHURE (1998) including character states of the new taxon, with 2. search strategy.

Fig. 32 (previous page): Strict consensus tree of two trees generated from complete matrix of LEE (1998) without character states of the new taxon.

Fig. 33 (previous page): Tree generated from complete matrix of LEE (1998) including character states of the new taxon.

2.3.3.1.4 CALDWELL (1999)

2.3.3.1.4.1 Matrix excluding the new genus and species

21 shortest cladograms were generated, three more than in CALDWELL (1999), although the same heuristic search options were used. Except for the position of Xantusiidae, Cordylidae and Scincidae the strict consensus tree is identical with that of CALDWELL (1999). The tree length, as well as the consistency and retention indices are the same (tree length: 464 steps, $ci = 0.68$; $ri = 0.60$).

2.3.3.1.4.2 Matrix including the new genus and species

27 shortest cladograms were generated. The trees have a length of 468 steps with a consistency index of 0.67 and a retention index of 0.61. The position of the new taxon in the strict consensus tree is completely unresolved. Therefore further analysis with reduced matrices are not performed.

2.3.3.2 Matrices limited to osteological characters

As only osteological characters are available from the fossil record, their value is now tested for the construction of phylogenetic hypotheses – using numerical taxonomy – by deletion of all soft tissue characters from the matrices used in this study.

Fig. 34 (following page): Strict consensus tree generated from the complete matrix of CALDWELL (1999) without character states of the new taxon.

Fig. 35 (following page): Strict consensus tree generated from the complete matrix of CALDWELL (1999) including character states of the new taxon.

Fig. 36 (following page): Strict consensus tree from three trees. Matrix of ESTES et al. (1988) limited to osteological characters, without character states of the new taxon.

Fig. 37 (following page): Strict consensus tree from six trees. Matrix of ESTES et al. (1988) limited to osteological characters, including character states of the new taxon.

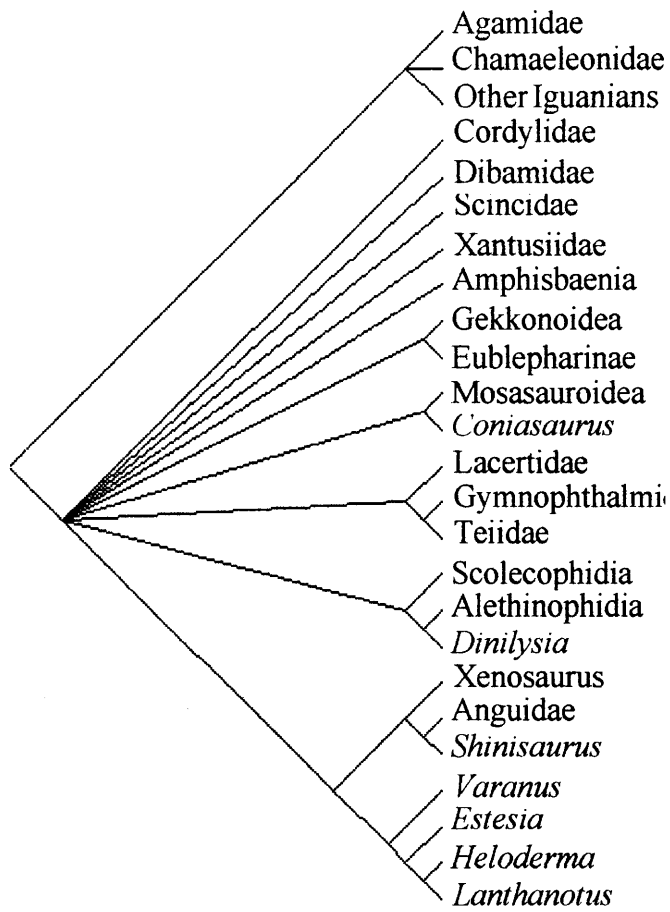


Fig. 34

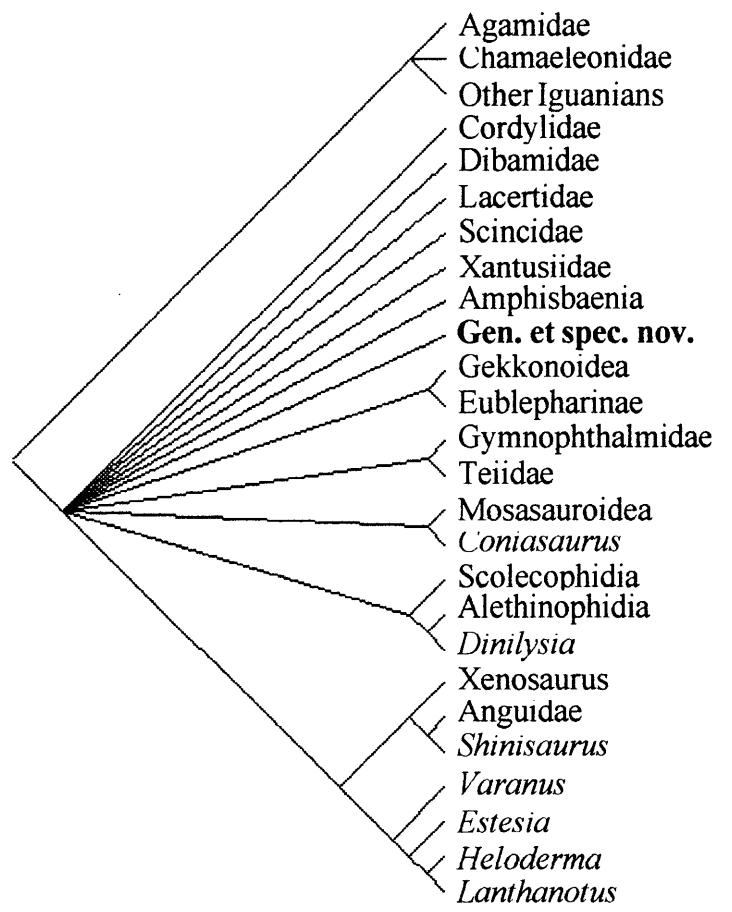


Fig. 35

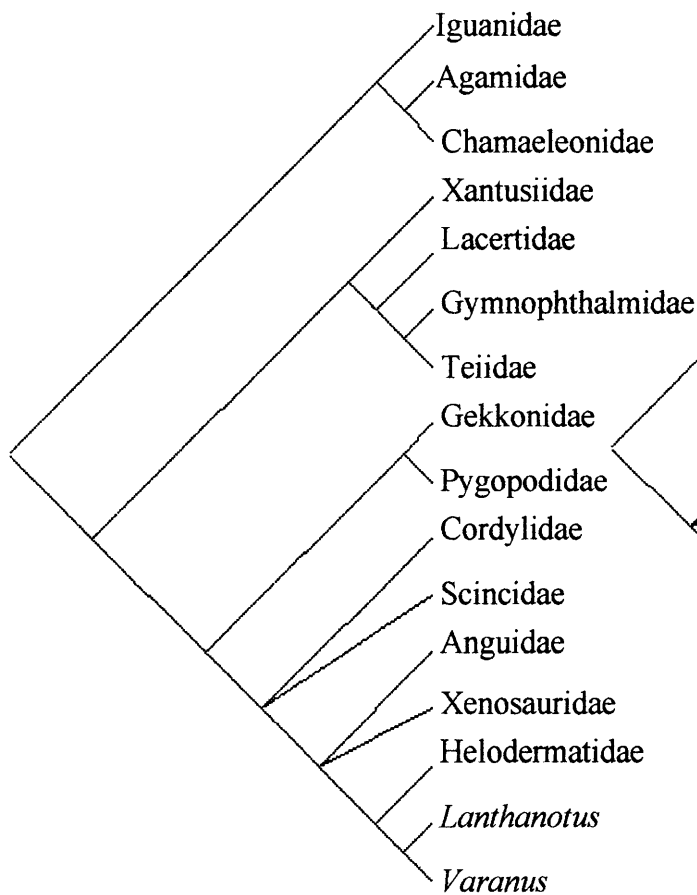


Fig. 36

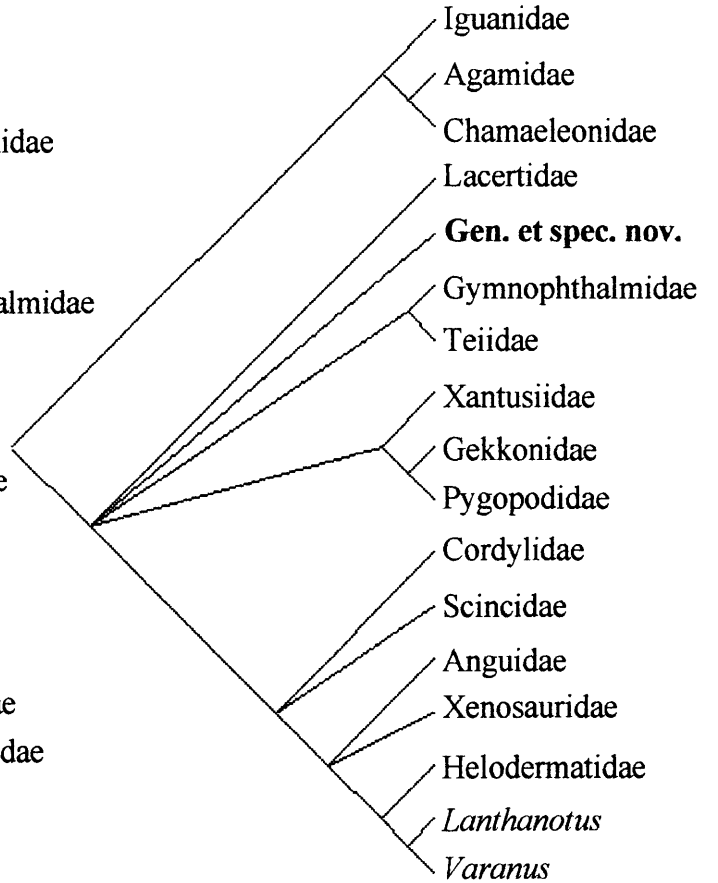


Fig. 37

2.3.3.2.1 Reduced matrix of ESTES et al. (1988)

2.3.3.2.1.1 Matrix excluding the new genus and species

When using only osteological characters, three trees are produced (in contrast to one tree if using all characters). The strict consensus of the three trees shows Scincoidea and Anguioidea as taxa with unresolved affinities (Fig. 36). The difference to the reference tree (with all characters included) is that the Scincoidea are no longer the sistergroup of Lacertoidea but of Anguimorpha. The Lacertoidea are sistergroup to the Gekkota, Scincoidea and Anguimorpha. The Gekkota are sistergroup to Scincoidea and Anguimorpha rather than to Scincoidea and Lacertoidea. This tree is quite similar to the PAUP-tree shown by ESTES et al. (1988: Fig. 5c), except for the position of the Gekkota and the unresolved Scincoidea and Anguioidea. The tree in ESTES et al. (1988) presents the Gekkota as a sistergroup to Scincomorpha and Anguimorpha. There are also congruences with the tree generated with the complete matrix of LEE (1998), as the position of Scincoidea, being the sistergroup of Anguimorpha. Also the Lacertoidea (Lacertidae, Xantusiidae, Teiidae, Gymophthalmidae) give up their derived position for a more basal one (sistergroup of Gekkota + Scincoidea + Anguimorpha).

2.3.3.2.1.2 Matrix including the new genus and species

When adding the matrix of the new genus and species to the osteological character matrix of ESTES et al. (1988), six trees are generated. They are six steps longer (225) than the tree excluding the new taxon. The consistency index slightly decreases (from 0.61 to 0.60). A strict consensus tree (Fig. 37) again shows the Scincoidea and Anguioidea as unresolved. The new genus and species together with Lacertoidea and Gekkota is unresolved, as well. It is placed either as sistergroup to Lacertidae or Scincoidea and Anguimorpha (Fig. 38), the same position when using the purely osteological matrix by LEE (1998). Furthermore, the tree is congruent with the one depicted in LEE (1998) except for the position of Lacertiformes and (Xantusiidae + Gekkota), which are placed as sistergroups here, rather than (Xantusiidae + Gekkota) as sistergroup to (Lacertiformes + Scincoidea + Anguimorpha).

Fig. 38 (following page): Matrix of ESTES et al. (1988) limited to osteological characters, including character states of the new taxon. One of six equally parsimonious trees showing the new taxon as sistergroup to Scincoidea + Anguimorpha.

Fig. 39 (following page): Strict consensus tree from seven trees. Matrix of EVANS & CHURE (1998) limited to osteological characters, without character states of the new taxon.

Fig. 40 (following page): Strict consensus tree from 20 trees. Matrix of EVANS & CHURE (1998) limited to osteological characters, including character states of the new taxon.

Fig. 41 (following page): Matrix of EVANS & CHURE (1998) limited to osteological characters, including character states of the new taxon. One of 20 equally parsimonious trees showing the new taxon as sistergroup to (Scincoidea + Anguimorpha + Gekkota + Serpentes + Amphisbaenia + Dibamidae).

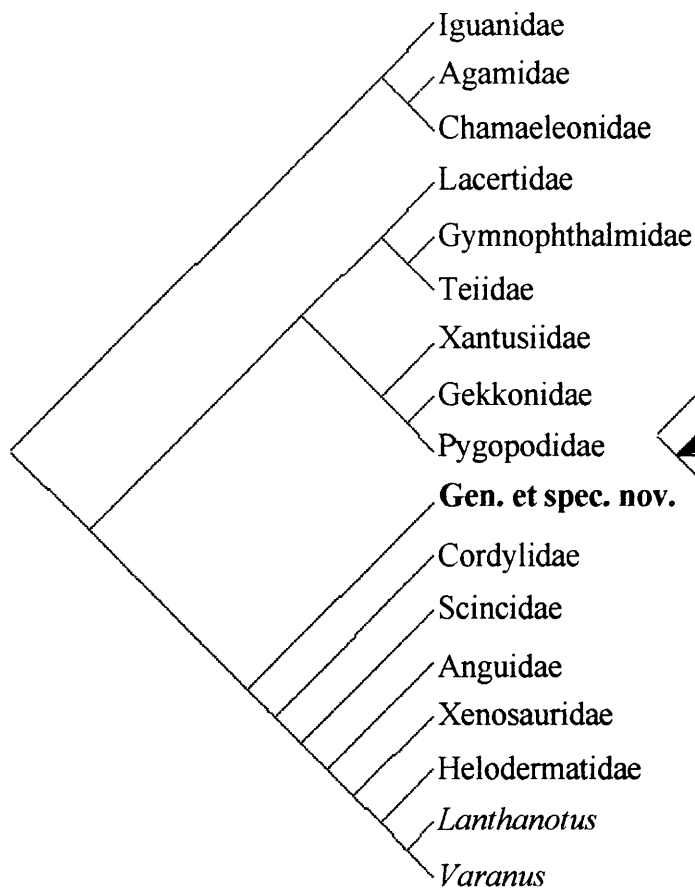


Fig. 38

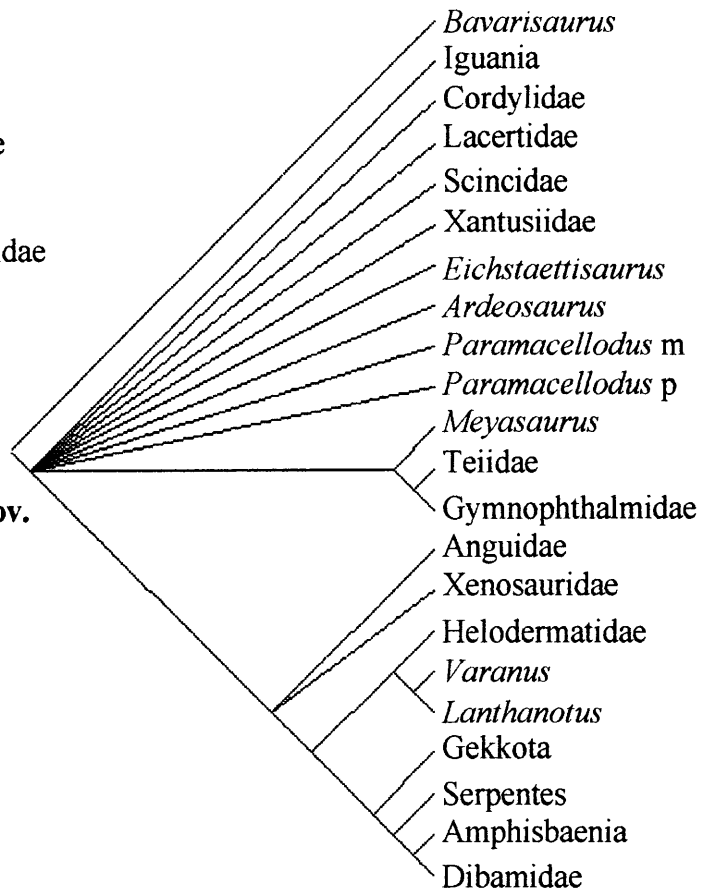


Fig. 39

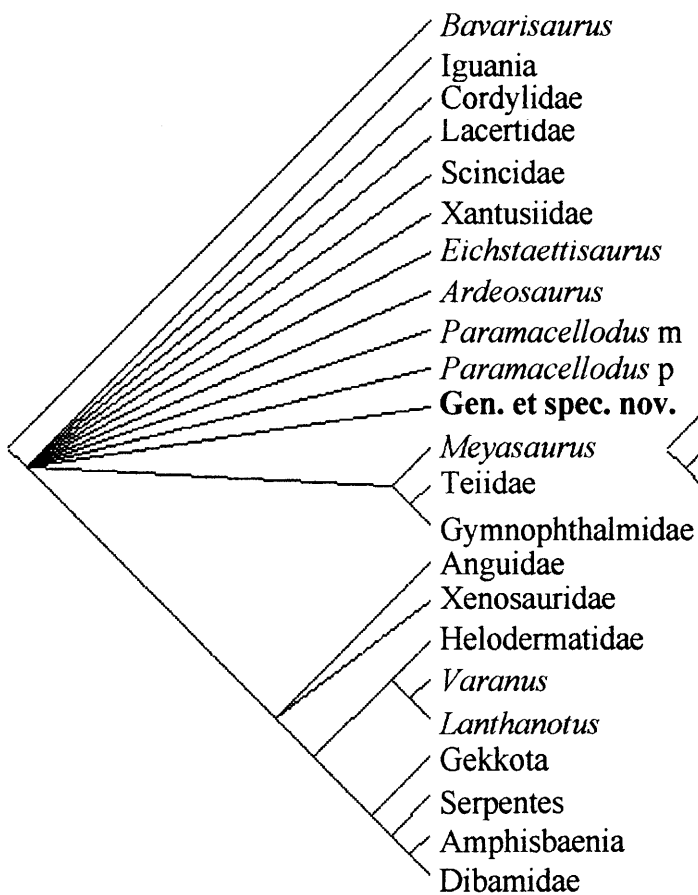


Fig. 40

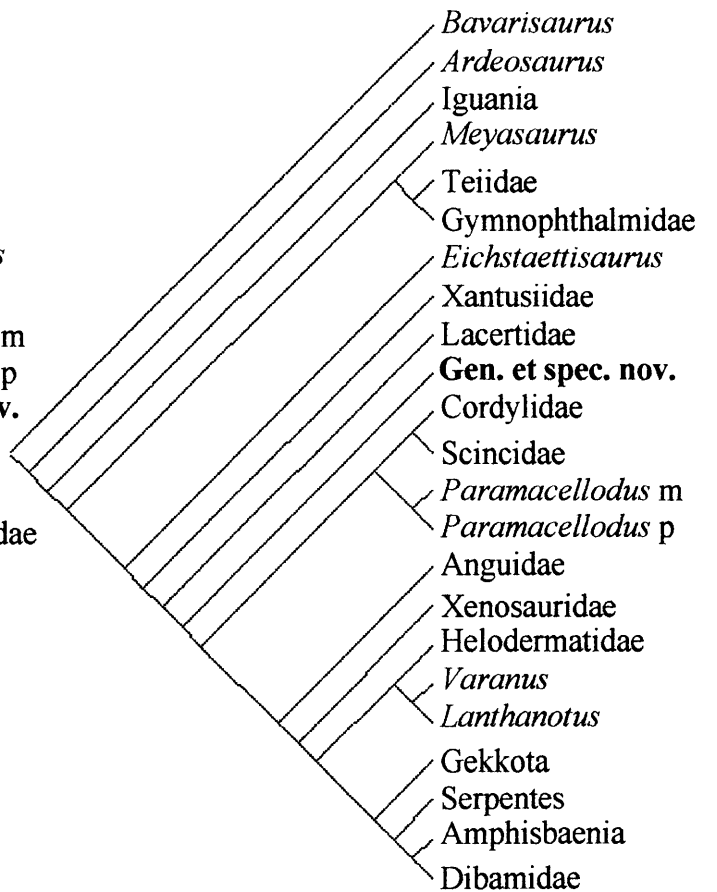


Fig. 41

2.3.3.2.2 Reduced matrix of EVANS & CHURE (1998)

2.3.3.2.2.1 Matrix excluding the new genus and species

Seven trees were generated, with the matrix reduced to osteological characters. The strict consensus tree (Fig. 39) shows Iguania and Scincomorpha as unresolved taxa. Within the Anguimorpha, the Anguioidea are unresolved. Only Varanoidea and (Snakes + Amphisbaenia + Dibamidae) are shown as monophyletic as it is the case in the original cladogram published by EVANS & CHURE (1998).

2.3.3.2.2.2 Matrix including the new genus and species

When adding the characters of the new genus and species, 20 trees were found. These trees are eight steps longer (361) than the ones without the new taxon. The strict consensus tree (Fig. 40) does not differ from the one where the new genus and species is excluded. It is, as expected, unresolved, because the whole Scincomorpha clade is unresolved. Two different positions of the new taxon are proposed: Either sistergroup to (Scincoidea + Anguimorpha + Gekkota + Serpentes + Amphisbaenia + Dibamidae, Fig. 41) or to Lacertidae.

2.3.3.2.3 LEE (1998)

As LEE (1998) used osteological characters only, the results have already been shown in the chapter on unaltered matrices.

2.3.3.3 Matrix limited to characters visible in the new genus and species

2.3.3.3.1 Reduced matrix of ESTES et al. (1988)

2.3.3.3.1.1 Matrix excluding the new genus and species

Only two trees are produced with this limited matrix. The trees are 82 steps long. The relationship of Anguinae and Xenosauridae is unresolved. The strict consensus tree (Fig. 42) is similar to the one which was generated, when the matrix of ESTES et al. (1988) was reduced to osteological characters. The difference is that here the Scincoidea are sistergroups and the lacertoid clade is divided in two clades: (Gymnophthalmidae + Teiidae) and (Lacertidae + Xantusiidae).

Fig. 42 (following page): Strict consensus tree from two trees. Matrix of ESTES et al. (1988) reduced to characters only visible in the new taxon, without its character states.

Fig. 43 (following page): Strict consensus tree from four trees. Matrix of ESTES et al. (1988) reduced to characters only visible in the new taxon, including its character states.

Fig. 44 (following page): Strict consensus tree from 66 trees. Matrix of EVANS & CHURE (1998) reduced to characters only visible in the new taxon, including its character states.

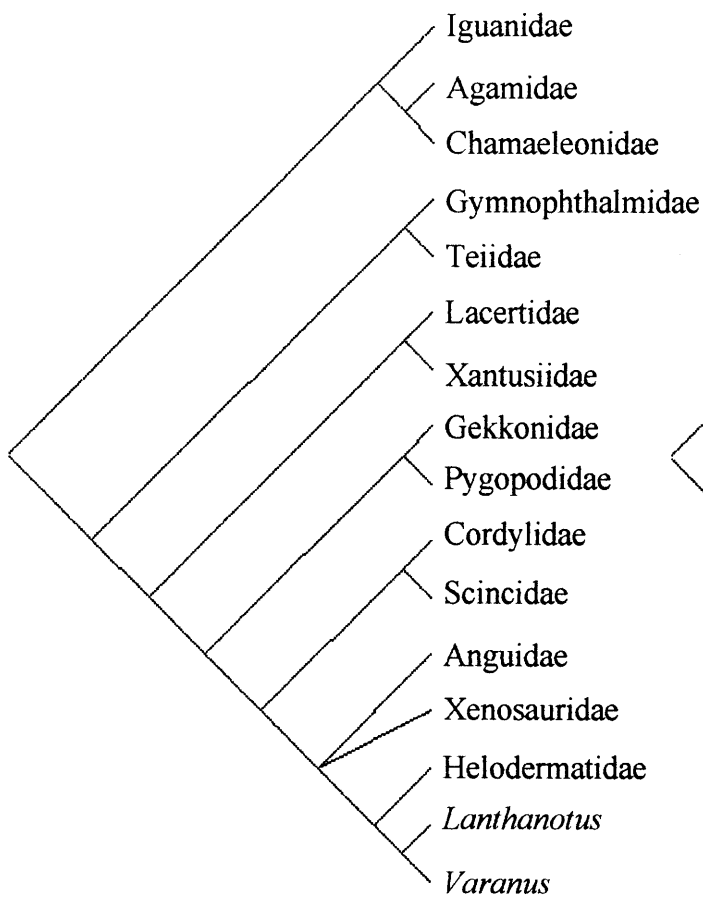


Fig. 42

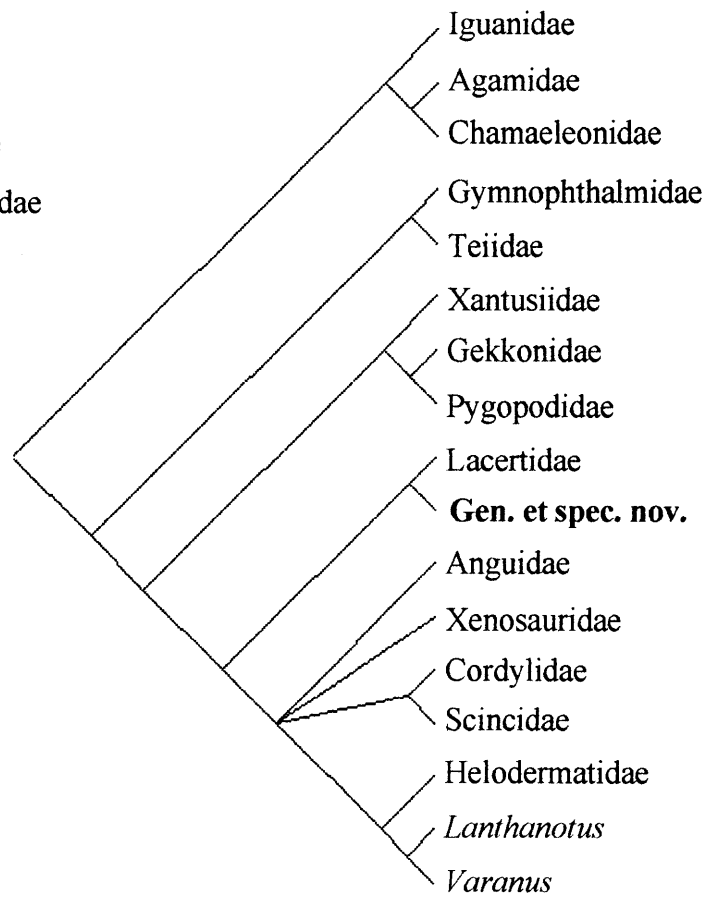


Fig. 43

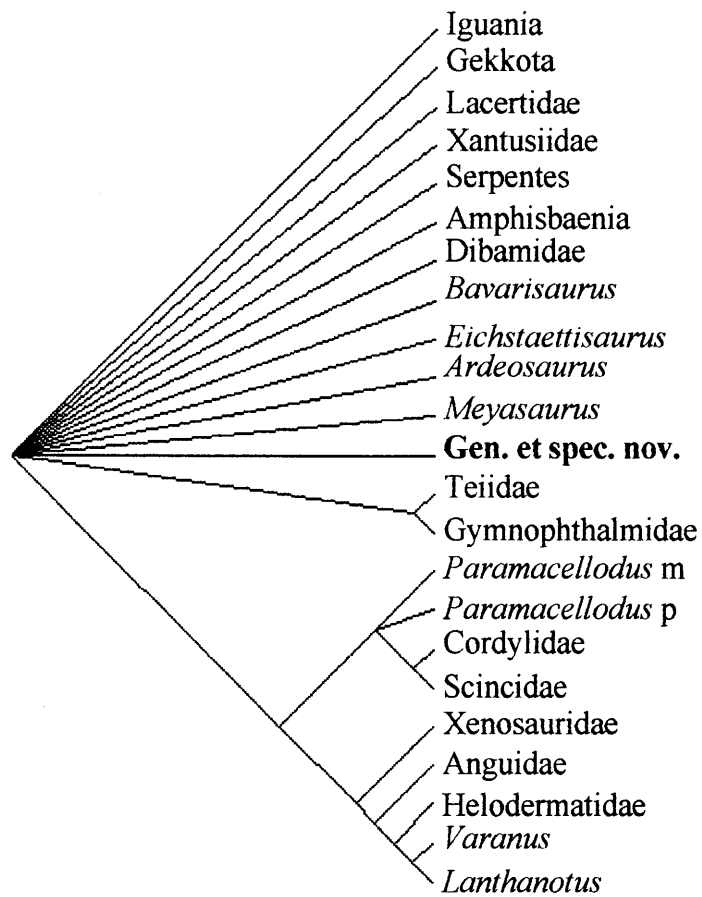


Fig. 44

2.3.3.3.1.2 Matrix including the new genus and species

When adding the character states of the new genus and species, four trees are generated, which are five steps longer (87) than without the new taxon. It is consistently placed as sistergroup of the Lacertidae, both taxa being the sistergroup of (Scincoidea + Anguimorpha). In the strict consensus tree (Fig. 43), Anguioidea as well as Scincoidea are unresolved and Xantusiidae are the sistergroup of the Gekkota.

2.3.3.3.2 Reduced matrix of EVANS & CHURE (1998)

2.3.3.3.2.1 Matrix excluding the new genus and species

As many as 510 trees were generated with a length of 109 steps. In the strict consensus tree, only the Scincoidea with the Paramacellodidae and Anguimorpha are resolved. Congruently with EVANS & CHURE (1998), Scincoidea and Varanoidea are monophyletic. (It was not possible to print the strict consensus tree from 510 trees).

2.3.3.3.2.2 Matrix including the new genus and species

When adding the new genus and species the tree number is reduced to 66 trees, which require eight more steps (117). But the strict consensus tree (Fig. 44) is the same when excluding the new taxon: Together with the Iguania, Gekkota, Lacertoidea, Serpentes, Amphisbaenia and Dibamidae, the new taxon is unresolved. Scincoidea and Anguimorpha are the only resolved clades. The new species is placed in three different positions: As sistergroup of Lacertidae, of (Scincoidea + Anguimorpha + *Meyasaurus* (Lacertilia inc. sed.)) and at the base of all Lacertilia, except Ardeosauridae and Bavarisauridae being more ancestral.

2.3.3.3.3 Reduced matrix of LEE (1998)

2.3.3.3.3.1 Matrix excluding the new genus and species

Nine trees are generated with this matrix. In the strict consensus tree (Fig. 45), only the Anguimorpha and Scincoidea are resolved, while Lacertoidea + Gekkota form one and Iguania two separated unresolved clades (Chamaeleonidae and „Iguanidae“ + Agamidae). (Scincoidea + Anguioidea) and Varanoidea remain one monophyletic clade with a sistergroup relationship (Fig. 45).

Fig. 45 (following page): Strict consensus tree from nine trees. Matrix of LEE (1998) reduced to characters only visible in the new taxon, without character states of the new taxon.

Fig. 46 (following page): Strict consensus tree from 15 trees. Matrix of LEE (1998) reduced to characters only visible in the new taxon, including character states of the new taxon.

Fig. 47A+B (following page): Matrix reduced to scincomorph taxa, without character states of the new taxon. Both trees are congruent in all three matrices studied here.

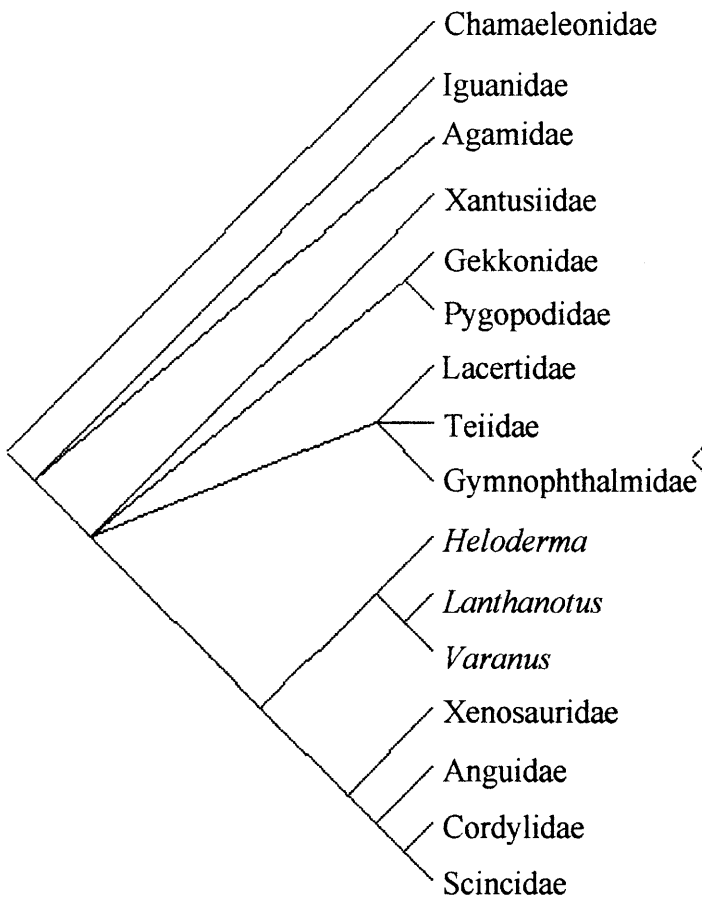


Fig. 45

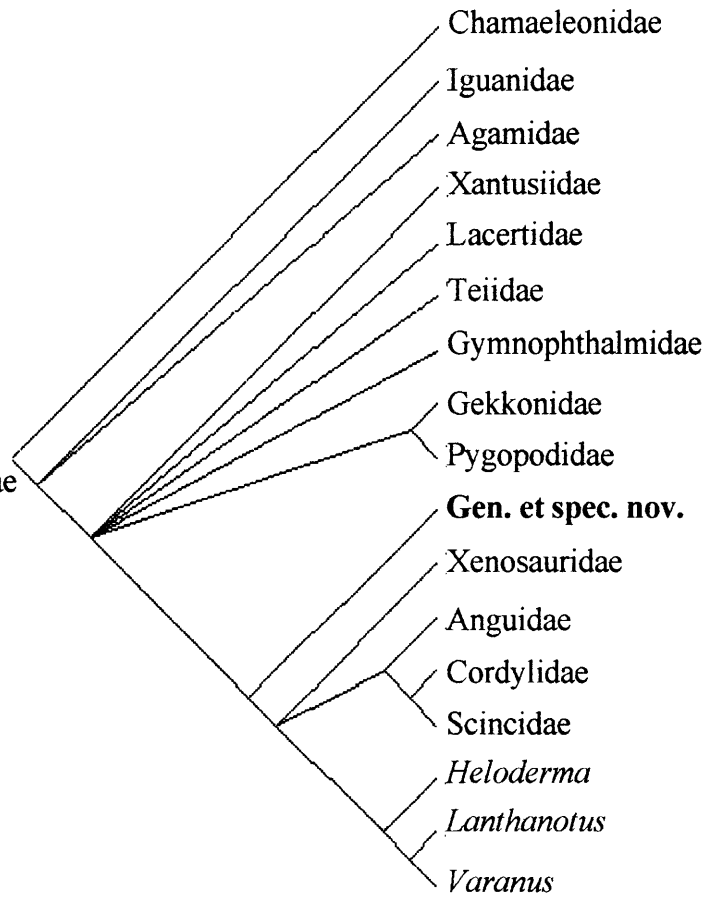
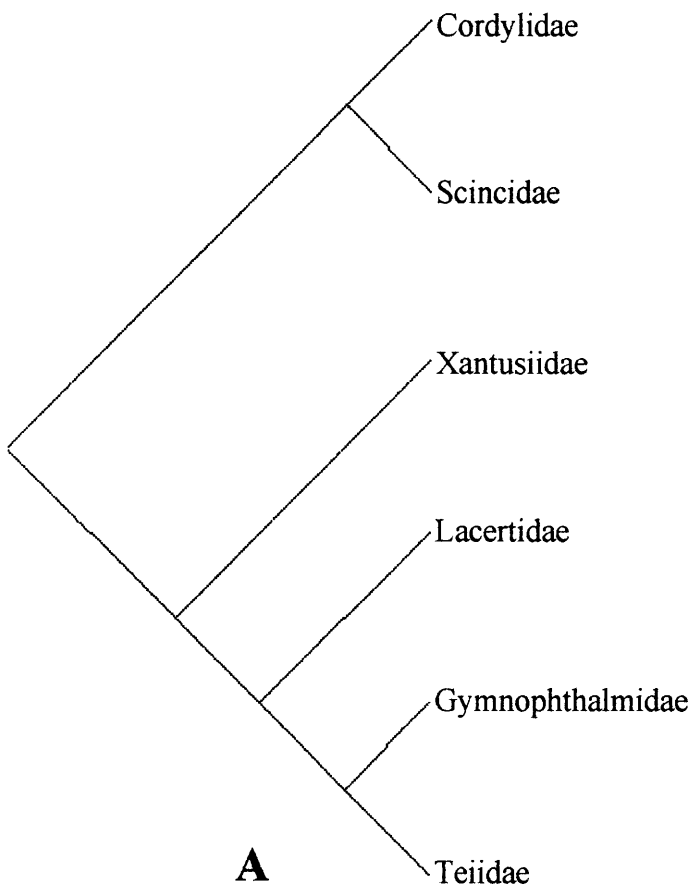
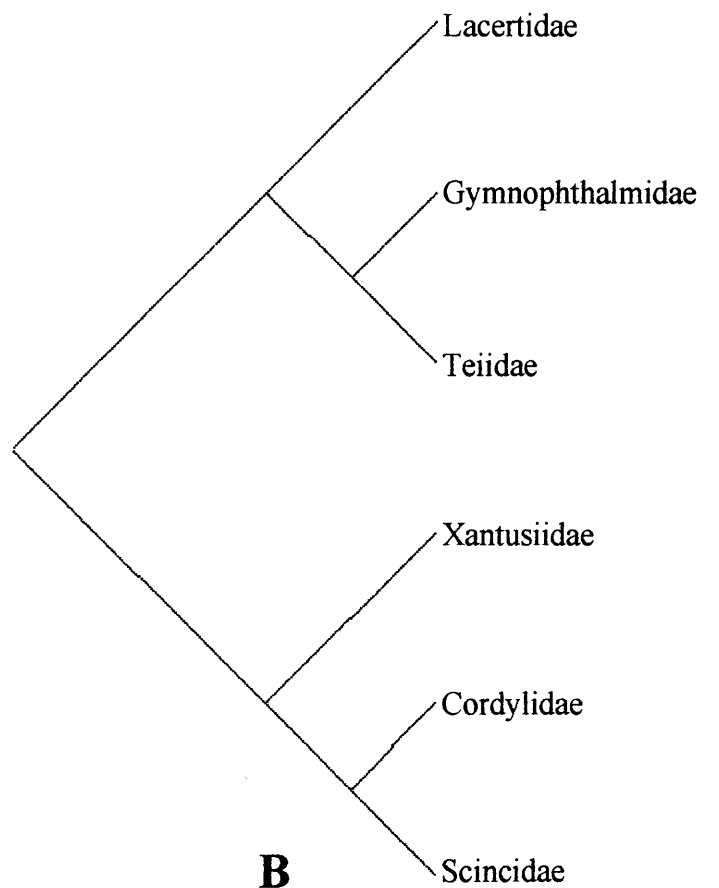


Fig. 46



A



B

Fig. 47

2.3.3.3.2 Matrix including the genus and species

15 trees are generated. In the strict consensus tree (Fig. 46) the main clades remain unchanged. Within the (Gekkota + Lacertoidea)-clade the Lacertiformes (Lacertidae, Teiidae and Gymnophthalmidae) do not form a separate clade any more and Xenosauridae, Anguidae and Scincoidea are unresolved but still form a separate clade. The new species is placed as sistergroup to (Scincoidea + Anguimorpha).

2.3.3.4 Taxa limited to Scincomorpha

As the previous analyses have never shown other affinities of the new genus and species than within the infraorder Scincomorpha, the three matrices used in this part of the study are here restricted to this taxon. All characters in the matrix were retained. „Iguanidae“ respectively Iguania were taken as an outgroup, because they belong to the Lacertilia, but are considered as the most primitive taxon within this group.

2.3.3.4.1 Reduced matrix of ESTES et al. (1988)

2.3.3.4.1.1 Matrix without characters of the new genus and species

Three trees are produced. In the first tree, the Scincoidea are the sistergroup of the Lacertoidea, the second tree shows Lacertidae as sistergroup to Teiioidea and (Xantusiidae + Scincoidea) and the third tree presents Lacertiformes as sistergroup to (Xantusiidae + Scincoidea). The first tree (Fig. 47A) corresponds to the scincomorph clade of the trees presented by ESTES et al. (1988: Fig. 5a & 6).

2.3.3.4.1.2 Matrix including characters of the new genus and species

When including the character states of the new genus and species into the matrix, 11 trees are generated. The strict consensus tree (Fig. 48) shows one unresolved clade including the new taxon, Lacertidae, Xantusiidae, Teiioidea (Gymnophthalmidae + Teiidae) and Scincoidea. The new taxon has been placed as sistergroup to every taxon involved here. The tree length increased by eight steps (from 95 to 103 steps). The consistency and retention index decreased slightly when adding the new species (Tab. 6).

Fig. 48 (following page): Strict consensus tree from 11 trees. Matrix of ESTES et al. (1988) reduced to scincomorph taxa, including character states of the new taxon.

Fig. 49 (following page): Tree generated from matrix of EVANS & CHURE (1998) reduced to scincomorph taxa, including character states of the new taxon.

Fig. 50 (following page): Tree generated from matrix of LEE (1998) reduced to scincomorph taxa, including character states of the new taxon.

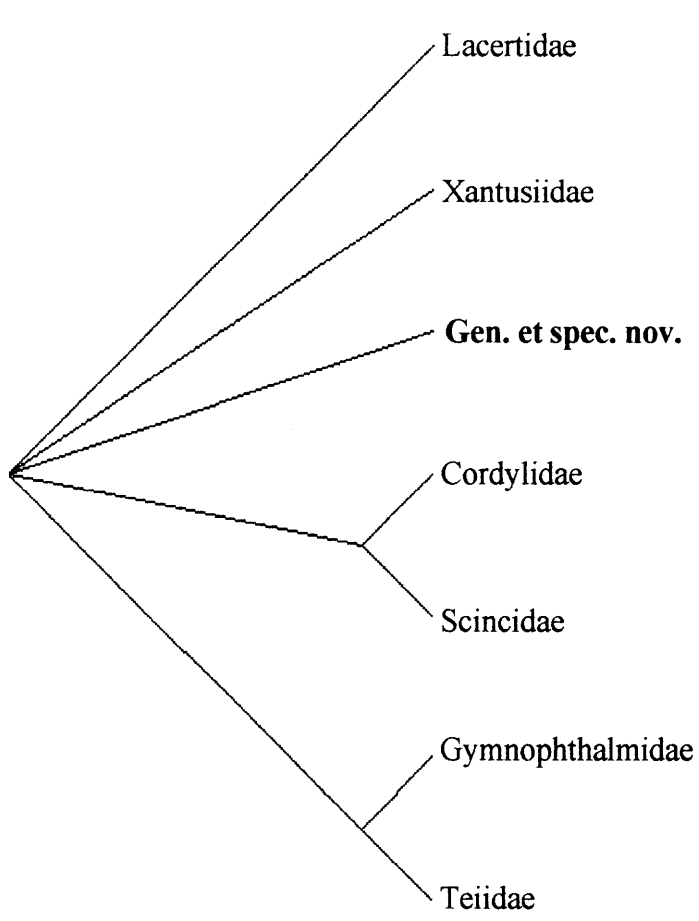


Fig. 48

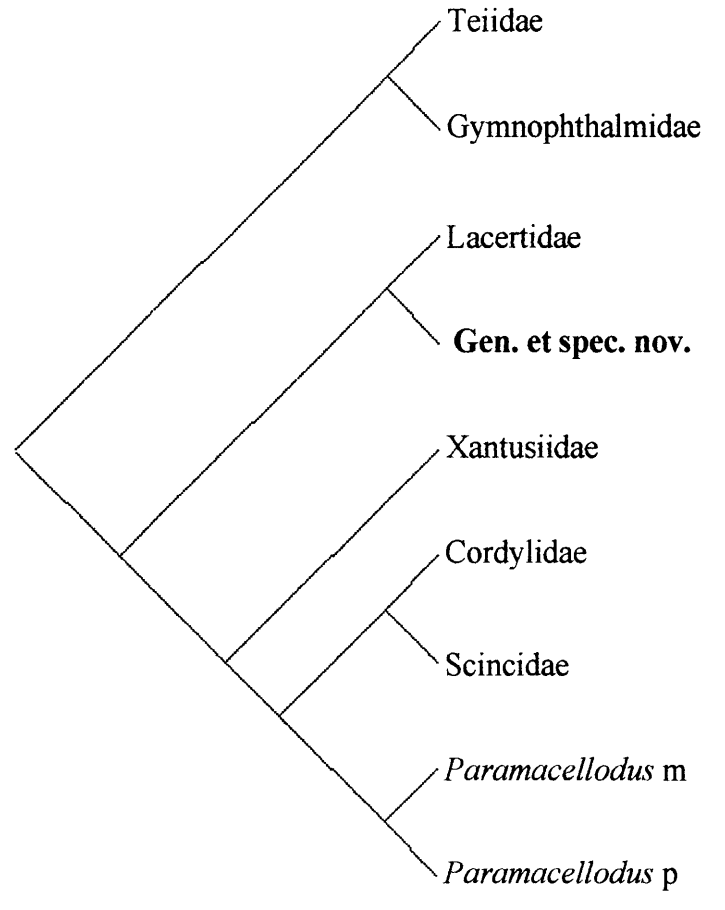


Fig. 49

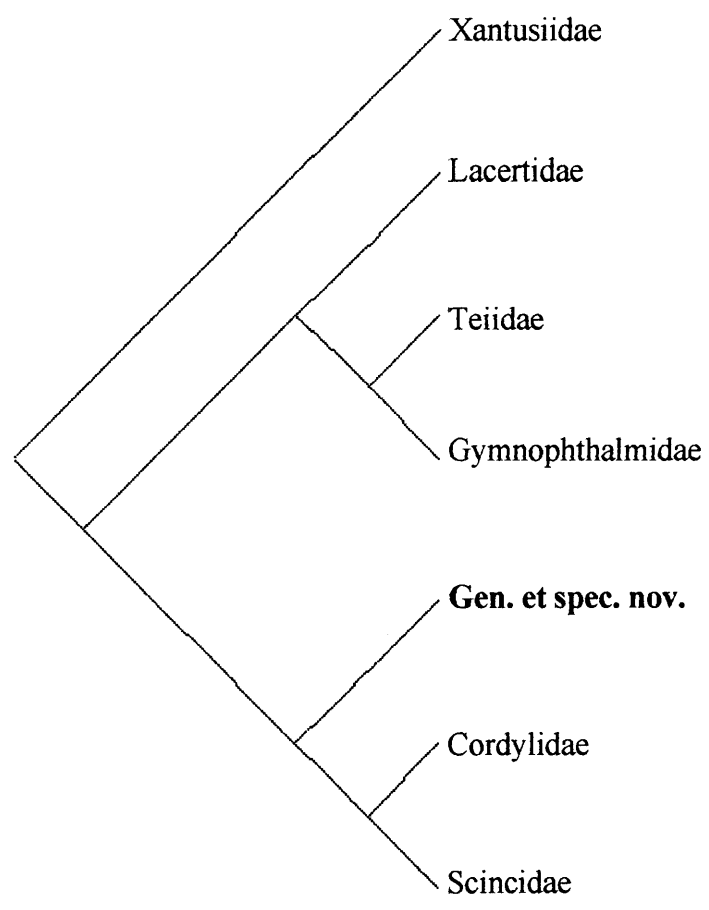


Fig. 50

2.3.3.4.2 Reduced matrix of EVANS & CHURE (1998)

2.3.3.4.2.1 Matrix excluding the new genus and species

Two trees are generated. The first tree shows Scincoidea including *Paramacellodus* as sistergroup to Lacertoidea. In the second tree, the Xantusiidae change their position and become sistergroup to Scincoidea including *Paramacellodus* rather than to the Lacertiformes as in the first tree. Both trees (Fig. 47) are congruent with tree 1 and 3 of the reduced matrix of ESTES et al. (1988).

2.3.3.4.2.2 Matrix including character states of the new genus and species

When adding the character states of the new taxon only one tree resulted (Fig. 49), similar to the second tree without the new taxon and placing it as a sistergroup to the Lacertidae. The tree length was increased by nine steps (113) and the consistency index diminished from 0.81 to 0.79 (Tab. 6).

2.3.3.4.3 Reduced matrix from LEE (1998)

2.3.3.4.3.1 Matrix without character states of the new genus and species

Three trees are generated. Two trees are congruent with those of the reduced matrix of EVANS & CHURE (without *Paramacellodus*, see 3.4.2.1) as well as tree 1 and 3 of the reduced matrix of ESTES et al. (1988). Thus the two trees in Fig. 47 are congruent in all reduced matrices studied here. The first tree complies with the favoured scincomorph relationship presented by ESTES et al. (1988: Figs. 5a & 6).

2.3.3.4.3.2 Matrix including character states of the new genus and species

Only one tree is produced (Fig. 50). The new genus and species is placed as the sistergroup of Scincoidea. Both taxa together with the Lacertiformes are placed as sistergroup to Xantusiidae. Except for the position of Xantusiidae this phylogenetic relationship of the scincomorph taxa is congruent with the one postulated by ESTES et al. (1988: Figs. 5a and 6).

Indices of trees

In Tab. 6 all consistency and retention indices, as well as the tree lengths and numbers of produced cladograms are given. When adding the new taxon to the matrix the trees necessarily become longer and the indices increase slightly. Except for the matrices reduced to Scincomorph taxa, the consistency index shows a range from 0.47 to 0.80. It increases considerably in the cladograms reduced to Scincomorph taxa (up to 0.93). The retention index varies from 0.53 to 0.74.

2.4 Discussion

2.4.1 Taxonomic position of the new genus and species based on comparative morphology

After the investigations made here, it is impossible to attribute the new genus and species to any known recent or fossil Lacertilian family with certainty. The specimens show characters of different families and even infraorders. The following remarkable characters could have developed secondarily within the new taxon and could probably justify the establishment of a new family. For reasons of conservativeness, a monospecific family is not created in the present study. One should wait for the discovery of other taxa with similar character combinations before undertaking this step and more comparative material should be available. Another difficulty is, that diagnostic characters cannot be determined because of taphonomic effects. Although the fossils are almost completely articulated, important characters are covered by bone (e.g. osteoderms covering the skull), structures are flattened and therefore cannot be analysed in three dimensions.

2.4.1.1 Key characters of the new genus and species

Jugal

There is one remarkable primitive character state which I consider very important for higher level taxonomy. It was mentioned by GAUTHIER et al. (1988) and taken up by EVANS & CHURE (1998): The posterior process of the jugal extending about half way back below the lower temporal fenestra. This character state is present in the new taxon and – after GAUTHIER et al. (1988) – elsewhere exhibited in some primitive Lepidosauromorph groups (Younginiformes and Rhynchocephalia) and other diapsid Reptiles (Areoscelidia, Archosauromorpha). But in these groups the posterior process generally contacts the quadratojugal closing the lower temporal fenestra (GAUTHIER et al. 1988). This is not the case in the new genus and species which (as every squamate) lacks the quadratojugal. As a synapomorphy for squamates, GAUTHIER et al. (1988) report the posterior process of the jugal to be much reduced or absent. EVANS & CHURE (1998) coded (in their data matrix) no posterior process and a rounded angled margin of the jugal in all lacertilian families they studied. GAUTHIER et al. (1988) suppose that the posterior process of the jugal was lost separately in Kuehnosauridae and Squamata, rather than in their common ancestor. But it seems that there is no posterior process within Iguania and Gekkota, but some families within the infraorders Scincomorpha and Anguimorpha possess a more or less weakly developed posterior process (pers. obs., Fig. 51). The status as a synapomorphy for Squamata is thus questionable. Lacertidae can have a posterior process (ARNOLD 1989), although it is rather small. Teiidae can have a posterior process as well, as in *Polyglyphanodon sternbergi* (ESTES 1983: Fig. 15). In a more reduced state this feature appears among Scincoidea: Within the Scincidae, for example *Tiliqua nigrolutea* has a very small posterior process. Cordyliformes: A tiny process is featured in *Zonosaurus madagascariensis* and *Pseudocordylus capensis*, a larger one in *Cordylus tropidosternum* (LANG 1991: Fig. 21b, 24, 39, pers. obs.). It occurs within Xantusiidae as well, as depicted in SAVAGE (1963) in the species *Lepidophyma flavimaculatum*. Within Anguimorpha, the Anguinae (especially Gerrhonotinae and Diploglossinae) and the Xenosauridae have a small posterior process of the jugal. Generally speaking, this character is more common within Scincomorpha: Cordyliformes, Scincidae (much reduced in *Tiliqua nigrolutea*),

Xantusiidae, Lacertidae and Teiidae, whereas the last three families mentioned have the most distinct posterior process of all, especially *Polyglyphanodon sternbergi* (Teiidae, pers. obs.). But this species has a rather thin elongated process unlike the new taxon where the posterior margin of the jugal slopes down gradually into the posterior process. So it is possible that this feature was lost quite early by Iguania and Gekkota whereas it was still present in the common ancestor of Anguimorpha and Scincomorpha. Probably it has been reduced independently within both infraorders in a different degree. The Scincomorpha retained a posterior process which seems not to be as reduced as in other squamates and it was prominent within the new genus and species (Fig. 52).

Skull sculpturing

The dorsal aspect of the skull is heavily sculptured like in many Anguimorpha and Scincomorpha, but with a characteristic pattern of osteoscutes and showing a jagged crest on the rear end of the skull similar to *Cordylus giganteus*, but with more numerous and much smaller spiny osteoderms. The supraorbitalia are arranged as in Lacertidae, but also showing the characteristic sculpture pattern (see type diagnosis and Fig. 52) not present in Lacertidae.

Quadrate

Another remarkable plesiomorph character is present in the new taxon. Since the quadrate has a straight Crista tympani in caudal view, which is parallel oriented to the Crista pterygoidea one can most probably conclude the body of the quadrate to be straight in lateral view. According to GAUTHIER et al. (1988) the normal derived condition for squamates is an anteriorly bowed quadrate for support of the middle ear cavity. But GAUTHIER mentions also that in some squamates a straight quadrate has been developed secondarily (e.g. chamaeleons). According to EVANS & CHURE (1998) both states are present in Iguania and Gekkota. *Varanus salvator* obviously also possesses a straight quadrate as well (pers. obs.). However, as there is no connection of the new species to these groups, this character probably was either retained or developed secondarily and independently in a few groups within the squamates.

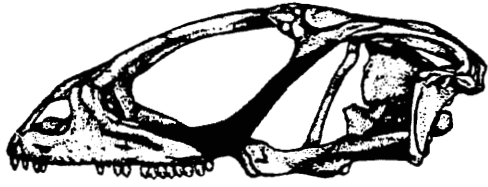
Marginal tooth morphology

The marginal teeth have a scincoid morphology, the tip being lingually concave and striated (e.g. as in *Tiliqua scincoides*). The lateral cutting edges are similar to those in *Cordylus giganteus* and the family Paramacellodidae. But the anterior and posterior cutting edges are not as distinctly set apart by an Angulus mesialis and distalis as RICHTER (1994) shows it to be present in the Paramacellodidae. The new genus and species bears no cuspis lingualis as the latter family does (Fig. 53).

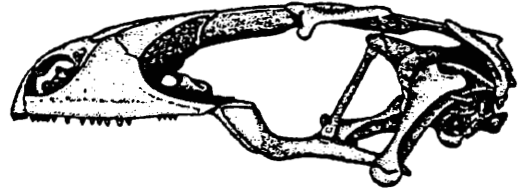
Fig. 51 (following page): Jugalia in several families of the Lacertilia and in the new taxon showing the different morphology of the posterior process (drawings from RIEPPEL 1980a&b, 1984; ESTES et al. 1988; LANG 1991).

Fig. 52: Premaxilla, maxilla, jugal and supraorbitalia of WDC-C-MG 123.

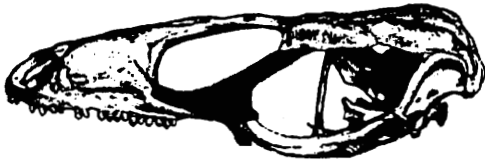
Fig. 53: Marginal tooth morphology of the new genus and species. A -B: SMF ME 475a. C: WDC-C-MG 123. A: Maxillary and dentary teeth in labial view, arrow indicates wear facet. B: Dentary teeth in lingual view, showing parallel striations on the tooth tip, arrows indicate replacement teeth. C: Premaxillary and maxillary teeth in labial view, showing the lateral cutting edges on the tooth tip (arrows).



Morunasaurus annularis, Iguanidae



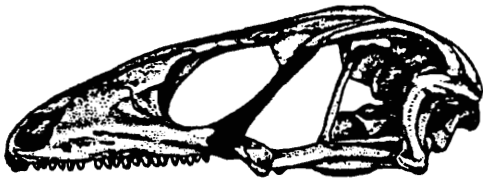
Hemitheconyx caudicinctus, Gekkonidae



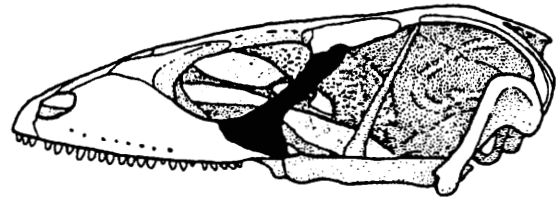
Lacerta lepida, Lacertidae



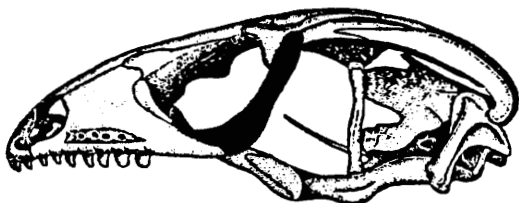
Tupinambis nigropunctatus, Teiidae



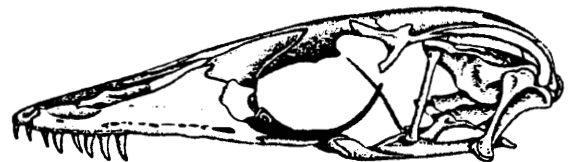
Eumeces obsoletus, Scincidae



Cordylus tropidosternum, Cordylidae



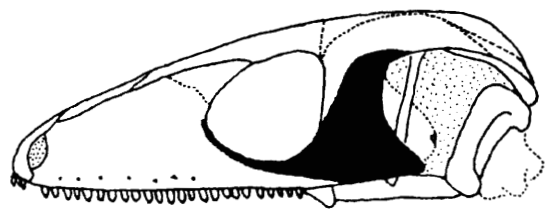
Ophisaurus apodus, Anguidae



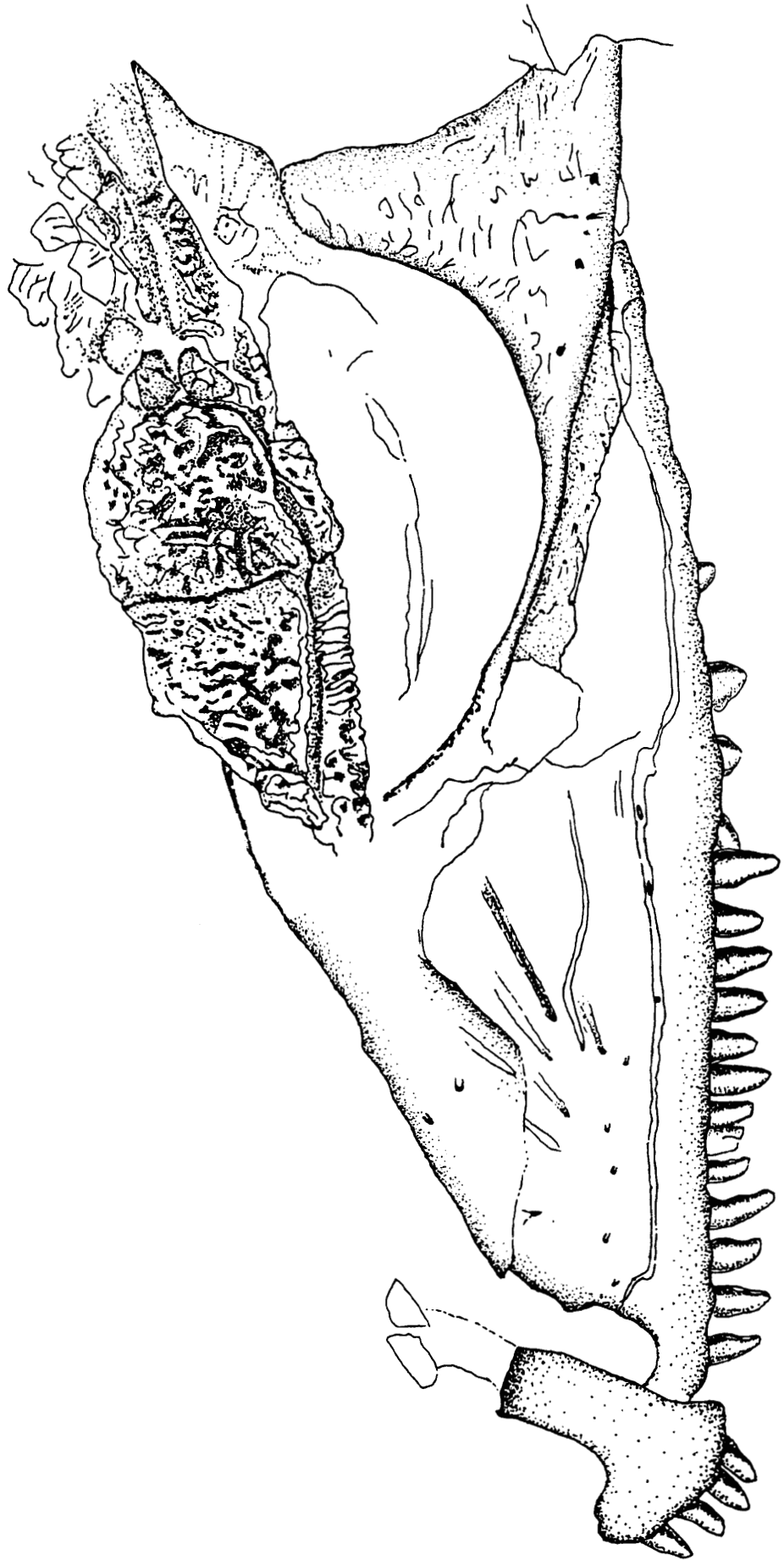
Varanus salvator, Varanidae



Diploglossus lessonae, Anguidae



Gen. et spec. nov.



5 mm

Fig. 52

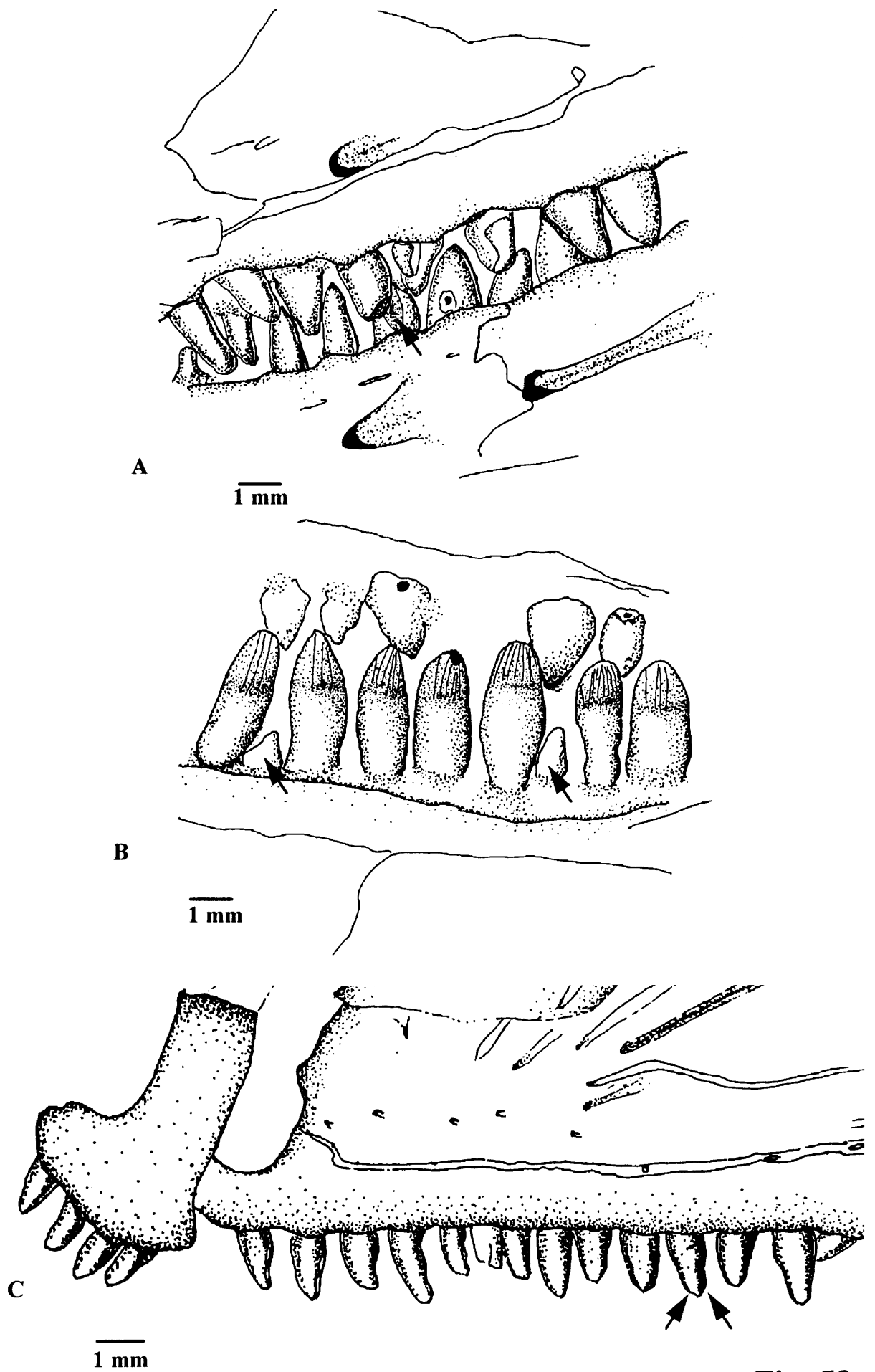


Fig. 53

Mandible

On the posteriomedial margin of the retroarticular process a small tubercle is present (Fig. 25E), a character which according to ESTES et al. (1988) only occurs in Scincoidea (Cordyliformes and Scincidae, for further discussion see below).

The skull and mandible of the new genus and species are reconstructed in Fig. 25. Those elements which could not be identified are indicated with dotted lines.

2.4.1.2 Taxonomic relationship of the new genus and species to higher taxa

In this chapter, congruences and inconsistencies of the characters of the new genus and species with those of higher lacertilian taxa are discussed. For didactic reasons, the systematic order is not followed, but the taxa are discussed according to their varying taxonomical distance to the new taxon.

Iguania and Gekkota

It is quite clear that the new genus and species neither belongs to the Iguania nor to the Gekkota. The Iguania tend to have a rather high short skull with widely opened temporal fenestrae, fused frontals and uniformly possess a dorsal process of the squamosal (ESTES 1983). This is clearly not the case in the new taxon. According to ESTES et al. (1988) some synapomorphies of the Gekkota are: Absence of postorbital or supratemporal arch, jugal is reduced or lost, fused frontals, pterygoid teeth lost, retroarticular process offset medially with lateral notch. None of these synapomorphies can be applied to the new species. But they do share characters with families of the infraorders Scincomorpha and Anguimorpha. This is not unusual, since Anguimorpha and Scincomorpha are commonly regarded as closely related groups (BORSUK-BIALYNICKA 1984b).

Anguimorpha

When compared to the infraorder Anguimorpha, the new genus and species shows a number of congruent characters as the possession of supraorbitalia (or palpebral ossifications: osteoderms covering the orbit dorsally) and cephalic osteoderms. Unfortunately, these characters are equivocal, as there are convergencies in Lacertidae and Scincoidea (Scincomorpha) for both characters (ESTES et al. 1988). The type of tooth replacement, which would be a helpful character, cannot be ascertained, even not with standard x-ray techniques. Out of the four available specimens, only two show the lingual aspect of the dentary. Both specimens bear only one or two visible replacement teeth between two functional teeth (Fig. 53), but it cannot be determined in which way the replacement takes place. Resorption pits are not visible. The following Anguimorph characters are not shared by the new taxon: Meckel's groove opens ventrally, dorsal body osteoderms, more than 26 presacral vertebrae (ESTES et al. 1988). The last character is difficult to determine, because nearly all cervical vertebrae are crushed or covered by skull elements. The different specimens of the new genus and species have presacral vertebrae counts from about 22-26 (or more). All other osteological characters concerning Anguimorpha, mentioned in ESTES (1983) and ESTES et al. (1988) cannot be determined. Those characters corresponding with the Anguimorpha also occur within Scincomorpha and there are several characters preventing an attribution to Anguimorpha. Therefore, there is no clear evidence for the new species belonging to this infraorder. To investigate the relationships of the new taxon to Anguimorpha more

closely, a further comparison with lower taxa of this infraorder is undertaken in the following paragraphs.

Varanoidea

It is quite clear that the new genus and species is not a representative of the Varanoidea, because the following 13 characters clearly contradict an attribution to this group: Skull usually long and slender (except Helodermatidae); Bony external nares greatly expanded posteriorly; Frontal coming close or incorporated into opening; Long slender process of premaxillary partially separating nares; Nasals usually slender and fused; Adductor musculature attached on dorsal surface of parietal (except in Helodermatidae and some Necrosaur, BORSUK-BIALYNICKA pers. comm.); Maxilla short, not extending far back under orbit; Intramandibular jaw joint usually well developed; Teeth with striated bases; Bases with infolded dentine; Teeth recurved, trenchant, widely spaced; Premaxillary teeth much smaller than maxillary teeth; Less than 13 maxillary teeth (ESTES 1983, ESTES et al. 1988).

Anguidae

All Anguidae have osteoscutes enclosing body and tail except for a lateral fold and some areas on limbs and neck (ESTES 1983). But they can be reduced as in the arboreal *Abronia taeniata* (GAUTHIER 1982). The new species also lacks body osteoderms. As functional morphology seems to influence the absence of body osteoderms, the taxonomic value of this character state is questionable. An attribution to a subfamily of the Anguidae can be excluded because of the following divergent characters from the four subfamilies: Both Anguininae and Anniellinae have reduced or absent limbs (ROMER 1956), the Anguininae have a toothless palate, pointed, fanglike teeth (ROMER 1956), the Anniellinae are small in size, their tooth number is reduced and they have a short tail (ESTES 1983). They reduced the temporal arch and the jugal and lost their squamosal. Palatal teeth are absent, and they have an elongate body with 71-74 presacral vertebrae (ROMER 1956). The Glyptosaurinae can have head osteoderms with a vermiculate and tuberculate sculpture (GAUTHIER 1982) but their size, shape and arrangement is very different from those of the new genus and species. Additionally, Glyptosaurinae possess obtuse cheek teeth with crowns bearing a horizontal cutting edge. Striations occur both lingually and labially on the teeth (ESTES 1983), which is not the case in the new taxon, where they are only present on the lingual side. The Diploglossinae have an increased number of presacral vertebrae (31-40, may be as high as 72-74 in *Ophiodes*), a toothless palate (ESTES 1983) and caudal vertebrae with two pairs of converging transverse processes (ESTES et al. 1988). Thus, there are three characters in which they differ from the new genus and species. Some members of this subfamily resemble the new taxon in having blunt-conical, closely spaced teeth (ESTES 1983), but in contrast to it, the striation on the tooth crown in Diploglossinae is not fine but rather coarse (ESTES 1983). The Gerrhonotinae have fused, hourglass-shaped frontals with a small interorbital distance and lost the dentition of the palatine (ESTES 1983), which is not the case in the new species.

Xenosauridae

The sculptured osteodermal crust on the skull of the new genus and species shows a very distant resemblance to the Xenosauridae, as was already noted by KELLER & SCHAAL (1992a). As *Exostinus lancensis* (GILMORE 1928, ESTES 1964), it possesses parietals with a heavy pustular sculpture of fused osteoderms oriented towards the centre of the bone. Xenosauridae possess a widened and sculptured jugal or a dilated

and sculptured postorbital branch of the jugal (ESTES 1983), which is in some respect comparable to the new taxon. Yet, there are a number of characters incompatible with Xenosauridae like a broad quadrate, no palatal teeth and a short tail (ROMER 1956). Furthermore the supraorbitalia of Xenosauridae are represented only as one small element at the anterior margin of the orbit, as in *Shinisaurus*, whereas those in the new species are lacertid-like. According to GAUTHIER (1982), all Xenosaurinae tend to develop faint anterior tooth cusps near the posterior end of the maxillary and dentary tooth rows. This is not the case in the new genus and species, where tooth morphology is very consistent throughout the tooth row. Furthermore, the new taxon does not seem to possess fused, hourglass-shaped frontals (as postulated for Xenosaurinae according to ESTES 1983, ESTES et al. 1988). The Shinisaurinae are represented only by one species *Shinisaurus crocodilurus*. An attribution to the subfamily Shinisaurinae can be excluded because of their overall appearance: The skull is shortsnouted and its dorsal surface is strongly arched in profile, furthermore the temporal musculature originates on the dorsal surface of the parietal table, which is not the case in the new taxon. The teeth are homodont and unicuspid as in the new species, but the crowns are unstriated (GAUTHIER 1982).

Scincomorpha

The new genus and species can be assigned to this infraorder for the following reasons: Within Scincomorpha, there are representatives in all families showing a tendency to close the supratemporal fenestra either with the postorbital or the postfrontal (ESTES 1983). This fenestra is to be seen in context with the Adductor mandibulae muscle complex. The plesiomorph condition in Lacertilia is, that the origin of this musculature extends onto the dorsal surface of the parietal (ESTES et al. 1988). Consequently, the supratemporal fenestra is open and the muscle can expand in this area. Ventral attachment of the Adductor mandibulae complex to the parietal is a derived condition and appears to be a scincomorph character (reversals in Teiidae and sometimes in Gymnophthalmidae). It is also a separate synapomorphy of Gekkota and a convergently acquired condition in some Iguania (ESTES et al. 1988). BORSUK-BIALYNICKA (1988) suggests that the closure of the supratemporal fenestra is of some advantage for the ventral type of mandibular muscle attachment. She regards the closure of this fenestra as primitive for Scincomorpha and probably synapomorphic for this infraorder. The advantage of a closed supratemporal fenestra might be an expansion of the muscle attachment area, although space for muscle enlargement during contraction is lost. As in Scincidae, Lacertidae, Xantusiidae and Cordyliformes, the supratemporal fenestrae of the new taxon are completely covered by osteoderms (Fig. 9, Fig. 14, Fig. 18) and it cannot be decided whether or which skull bones participate in their closing, even after examination with standard x-ray methods (see description). However, on the radiography of WDC-C-MG 123 it seems that the parietal is constricted to a certain degree and bears rather short, curved *Processus exoccipitali*. Since the squamosal is quite slender, the main contribution to the closure (or near closure) presumably is made by the postorbital or the postfrontal, or by fusion of both elements. This would sustain an attribution to the Scincomorpha which show a tendency to close the supratemporal fenestra either with postorbital or postfrontal (or both) with some additions by the squamosal and the parietal (ESTES 1983). According to ROMER (1956), "the function of the fenestra [as muscle expansion area] is destroyed when covered by osteoderms and further closure by underlying bones might reasonably follow". It can therefore be assumed that the supratemporal fenestra is closed in the new genus and species by skull

elements. The fenestra being closed, no matter if by osteoderms or skull elements, there must have been a ventral attachment of the adductor muscles. This condition, together with the assumed contribution of the skull elements to the closure of the supratemporal fenestra strongly sustains an attribution to the Scincomorpha.

BORSUK-BIALYNICKA (1988) tentatively regards the character "anteroventral border of the orbit formed by maxilla" as a synapomorphy of Scincomorpha. But this condition is absent in Cordyliformes, Lacertidae and Teiidae, where the anteroventral border of the orbit is formed by the jugal (BORSUK-BIALYNICKA 1988, ESTES et al. 1988). The same condition is present in the new genus and species (Fig. 52). Therefore, this character does not falsify the assignment of the new taxon to Scincomorpha.

As can be assumed from the radiographs (Fig. 8D, Fig. 12C, Fig. 21B), the new taxon has a parietal which reaches quite far back posteriorly, covering the braincase dorsally. According to ESTES et al. (1988) this is a character which only occurs within Chamaeleonidae (Iguania), Cordyliformes, Lacertidae, Xantusiidae (Scincomorpha) and Xenosauridae (Anguimorpha). As discussed above, an attribution to the Iguania and Anguimorpha can be excluded and this character also points to an attribution within Scincomorpha.

Supraorbitalia occur within Anguioidea, Varanoidea, Scincoidea and Lacertidae. Yet, their morphology differs considerably in these taxa: Xenosauridae and Varanidae have a single, small element restricted to the anterior margin of the orbit. In *Ophisaurus apodus* (Anguidae) the supraorbitalia do not differ morphologically from the other cephalic osteoderms. There are three large mesial ones bordered laterally by a row of smaller ones. Within Scincoidea there usually are four large osteoderms of approximately same size of which the central ones are separated by a curved suture. These are bordered by a row of small slender scales covering the orbit dorsally. The two central osteoderms are larger than the anterior and posterior one. More or less the same condition is found in Lacertidae, but the two central osteoderms are considerably larger than the others and the separating suture is straight. So it seems Scincomorpha can also be distinguished from Anguimorpha in number and morphology of supraorbitalia. The ones in the new genus and species largely matches the condition in Lacertidae, but the sculpture is very different (Fig. 25, Fig. 52). However, for other reasons, close relations to this family will be excluded (see below).

In most families of the infraorder Scincomorpha, body osteoscutes are present (ESTES 1983). Yet Lacertidae (ESTES et al. 1988) and some Cordylidae lack body osteoscutes (LANG 1991), but still retain cephalic osteoderms. The same is the case in the new taxon in a very characteristic manner. But the specific morphology of the cephalic osteoderms is not found in any extant representative of either Lacertidae or Cordyliformes (pers. obs.). Still, the fact that only cephalic osteoderms are present is a further argument for an attribution of the new genus and species to this infraorder, although, there obviously is an influence of functional morphology on the absence or presence of body osteoderms, which will be discussed in chapter 3.

The presence of an open or closed Meckelian Groove in the mandible seems not to be a good character for higher level taxonomy, but the way how it opens is important. Only Gekkota show a consistently closed Meckelian Groove. Iguania either have a closed or opened groove, as do Scincomorpha. In Anguimorpha the Meckelian Groove is always

open (ESTES et al. 1988). There is a difference as to how the groove opens: If a representative of the Scincomorpha has an open Meckelian Groove, it always opens medially for its entire length (ESTES et al. 1988, EVANS & CHURE 1998). In contrast, Meckel's groove always opens ventrally in all Anguimorpha (ESTES et al. 1988). The new genus and species has a medially opened Meckelian Groove (Fig. 10C, Fig. 11, Fig. 12D, Fig. 13, Fig. 25), corresponding to the condition in Scincomorpha. Because of other crucial characters discussed above, an attribution to Iguania, which can also display a medially open Meckelian Groove (ESTES et al. 1988), is not longer considered.

The character "lateral process of coronoid overlapped anteriorly by dentary so that lateral exposure of process is limited to a narrow wedge between dentary and surangular" was introduced by ESTES et al. (1988). According to the authors, this character is a synapomorphy of Scincomorpha, which is reversed within Lacertoidea and in some Scincidae. BORSUK-BIALYNICKA (1988) gives a comprehensive overview of the phylogenetic significance and distribution of the character "coronoid/dentary contact" in Squamata. The overlapping dentary in the new taxon represents an incipient state and can be regarded as plesiomorphic for Scincomorpha BORSUK-BIALYNICKA (1988 and pers. comm.). The new genus and species corresponds to the synapomorphic condition, again sharing an important character with Scincomorpha. As the character is variable within Lacertoidea and Scincidae, it will be discussed again in the respective taxa.

Another character which can be used for an attribution to either infraorder Scincomorpha or Anguimorpha is the development of the subdental shelf. When analysing the matrices of ESTES et al. (1988) and EVANS & CHURE (1998) it is striking that in Scincomorpha, the subdental shelf is well developed (exceptions in Gymnophthalmidae), whereas Anguimorpha show a rather weak structure or even lack it (BORSUK-BIALYNICKA 1985). This character is useful for a distinction of both infraorders. Because the new taxon shows a strongly developed shelf (Fig. 10C, Fig. 11, Fig. 12D, Fig. 13, Fig. 25), the taxonomic attribution to Scincomorpha is strongly supported.

The number of presacral vertebrae can give a hint for the distinction of Scincomorpha from Anguimorpha, if articulated specimens are available. There is a wide range within Scincomorpha with developed limbs, 23 to almost 40, but a certain stabilisation at 26 is noticeable in Scincidae, Cordyliformes, Lacertidae and Teiidae. Within Anguimorpha the lowest number in one genus (*Shinisaurus*, Xenosauridae) is 26, but they mostly have 29 or more presacral vertebrae (HOFFSTETTER & GASC 1969). In the new genus and species about 24-26 presacral vertebrae are present and an attribution to Scincomorpha is further supported by this character.

According to ESTES et al. (1988), an anteriorly directed and elongate symphyseal process with an anteroventral pubic tubercle is a derived character state and represents an independent acquisition in Scincomorpha (reversal in Teiids) and Anguidae. It occurs in all of the following families of the Scincomorpha: Cordyliformes, Scincidae, Lacertidae, Gymnophthalmidae and Xantusiidae. The rather short pubis of the new taxon seems to be directed anteriorly or anterodorsally and bears a ventral pubic tubercle. This orientation of the pubis is congruent with the one in this group, but the short pubis length does not match the condition of the named families. However, this character is here evaluated as rather supporting than contradicting an attribution to

Scincomorpha. Although, according to BORSUK-BIALYNICKA (pers. comm.) the condition present in the new taxon might be a plesiomorph character.

Although many characters are poorly known in the new genus and species, this species shows several affinities to the Scincomorpha which allow an attribution to this infraorder. In a next step, the lower level taxonomy within the Scincomorpha is analysed in order to make an attribution on a more detailed level.

Lacertoidea

ESTES et al. (1988) mention only four osteological synapomorphies for the superfamily Lacertoidea. Among these are structures on the dorsal surface of the retroarticular process, presence of a prearticular crest, parietal tab morphology and "the posterior border of the retroarticular process is not twisted obliquely". Unfortunately, only the latter of these characters can be determined in the new genus and species and will be discussed here. This character is very well suited to distinguish Lacertoidea from all other Scincomorpha and Anguimorpha. All Lacertoidea show a straight retroarticular process, whereas all remaining Scincomorpha and Anguimorpha show some degree of oblique twisting in this element. In the new taxon, the retroarticular process is not twisted, corresponding to the condition in Lacertoidea (sensu ESTES et al. 1988) and further underlining its relation to the Scincomorpha, if not even to Lacertoidea. However, because of a single character visible in the new species, an attribution to the superfamily Lacertoidea cannot be made. For this reason, all families of the Scincomorpha are discussed in terms of diagnostic characters.

Lacertidae

The following characters by ROMER 1956, ESTES 1983 and ESTES et al. (1988) strongly suggest a classification within the Lacertidae: Osteoscutes limited to the skull, short supratemporal processes and palpebral ossifications (= supraorbitalia). At the same time, all of these characters occur convergently in other groups as well (Lacertidae, Xantusiidae, Scincidae, Cordyliformes, Xenosauridae, Varanidae). Therefore, they are not exclusively present in this family. The new taxon shares all of these characters, but because of their wide distribution an attribution to other families cannot be excluded.

According to ROMER (1956), a typical character for Lacertidae are bi- or tricuspid teeth, which are at least present in posterior tooth positions (MÜLLER, J. 1998). Although in mammalian taxonomy tooth morphology is of great importance, it does not play such a role in Lacertilian systematics. But I consider tooth morphology as an important character not only for the functional morphology. The new genus and species clearly has a tooth morphology differing from the lacertid type in having unicuspid teeth throughout the tooth row.

In Lacertidae, the coronoid lateral process is not overlapped by the dentary anteriorly, but overlaps the dentary labially (ESTES 1983). ROMER (1956) even describes the coronoid as being broadly exposed externally in this family. As already mentioned above, the synapomorphic scincomorph character state of the "lateral process of coronoid overlapped anteriorly by the dentary" (ESTES et al. 1988) is reversed in Lacertoidea (and some Scincidae). But it is present in the new species, which strongly contradicts a relation to Lacertidae.

There are a number of characters which – if seen on the level of presence or absence – are congruent with those of Lacertidae. Yet, the special way in which they are formed, prohibit a clear attribution. Two of these characters are supraorbitalia and the cephalic osteoderms. The supraorbitalia of the new genus and species consist of two large and two small supraorbital scales bordered by a row of small slender scales (see description). In number and arrangement they therefore are consistent with the pattern found in Lacertidae, a condition which BORSUK-BIALYNICKA et al. (1999) consider to be synapomorphic for this family. But the elements of the new taxon bear a characteristic ornamentation, which is not found in Lacertidae. This family mostly bears supraorbitalia with a more or less smooth surface. The same is true for other cranial osteoderms. As mentioned above, there is quite a number of groups which have cephalic osteoderms also covering the supratemporal fenestra, but the new genus and species has a unique characteristic arrangement pattern and ornamentation of osteoderms (see description). Furthermore, the osteoderms seem to be limited to the dorsal aspect of the skull and there is no evidence for laterally free osteoderms as in Lacertidae. Since the preservation of the specimens is very good, one can assume that at least traces of lateral osteoderms would be preserved. Furthermore, on the posterior aspect of the skull, there are no distinct osteoderms (except for one osteoderm on each side posterior to the supraorbitalia), but rather an osteodermal crust.

An attribution of the new species to the family Lacertidae is very questionable, those characters which positively sustain such a relation, are also present in other groups. Furthermore, a number of diagnostic characters are not shared by the new taxon and therefore inhibit an attribution to this family.

Teiidae

An attribution to the Teiidae can be excluded because of the following eight synapomorphies which are missing in the new genus and species: The tendency to develop molariform or multicuspid teeth, a generally heterodont dentition with a diastem between premaxilla and maxilla, the absence of free osteoscutes on head or body, an open temporal fenestra and rarely present supraorbitalia are listed in ESTES (1983). ESTES et al. (1988) add two synapomorphies being the fusion of frontals and the jaw adductor musculature attaching onto the dorsal surface of the parietal. Finally ROMER (1956) finds that pterygoid teeth occur rarely in this family, but when present, they are feebly developed.

The contact or close contact of jugal and squamosal is a character which has been independently reversed several times in Autarchoglossa (Scincomorpha and Anguimorpha), but is considered as a synapomorphy of this group (ESTES et al. 1988). Nevertheless, contact or close contact of these skull elements hints to a selection of taxa: Iguania, some Scincomorpha (Scincidae and Teiidae), Anguimorpha (Xenosauridae) and some Gekkota (Ardeosauridae). In contrast, jugal and squamosal are well separated in some families of the Scincomorpha (Cordyliformes, Gymnophthalmidae, Lacertidae, Xantusiidae) as well as in some Anguimorpha (Anguidae and Varanus). This character would allow a restriction to a number of families in question. Unfortunately, it is not visible in the new genus and species, since the Processus zygomaticus of the jugal and the rostral part of the squamosal is covered by osteoderms.

Gymnophthalmidae

It is obvious that the new genus and species is no member of this family, since all members of this family are small lizards with reduced temporal arches, usually have no pterygoid teeth, often show a closed and fused Meckel's groove (a suture is no more visible), lack osteoderms and have fused frontals (ESTES 1983). Additionally, the anteroventral border of the orbit is formed by the maxilla and not by the jugal (BORSUK-BIALYNICKA 1988) as in the new taxon.

Xantusiidae

There are a few characters of the Xantusiidae which are congruent with the new genus and species like the short supratemporal processes and conical cheek teeth (ESTES 1983). Skull osteoderms are present only in one or two species (SAVAGE 1963). The following characters contradict an attribution to this family: Xantusiidae have lost their pterygoid teeth, the maxillae extend just beyond the anterior edge of the orbits (rather weak character states), the Meckelian Groove is closed and fused, the coronoid process of the dentary extends dorsally onto the anterolateral surface of the coronoid (ESTES et al. 1988) and they lack supraorbitalia (LANG 1991).

Scincoidea

There is one synapomorphy within Scincoidea which only occurs in Cordyliformes (Cordylidae + Gerrhosauridae) and Scincidae: "presence of a small tubercle or flange on the posteriomedial margin of the retroarticular process" (ESTES et al. 1988). According to the author, this character is absent in any other squamate or non-squamate lepidosauromorph in which it can be determined. This definitive synapomorphy or rather autapomorphy of Scincoidea is present in the new genus and species and therefore strongly supports an affinity to this superfamily. Furthermore, the retroarticular process seems to be slightly inflected medially and broadened posteriorly which is also the case in Scincoidea. This character further supports the relation of the new taxon to the Scincoidea.

Two additional characters of Scincoidea are shared by the new genus and species: Supraorbitalia and cephalic osteoderms are present, but these characters are convergently developed in Lacertidae and Anguimorpha, as well (ESTES et al. 1988). The special sculpturing of the supraorbitalia and the cephalic osteoderms seem to be an autapomorphy of the new taxon.

The following three characters of the new genus and species are incongruous with Scincoidea: In contrast to the Scincoidea the new taxon does not have an obliquely twisted retroarticular process. However, a twisted retroarticular process is the derived condition and there is no reason to exclude the taxon from the Scincoidea for bearing a plesiomorph character. Two of the synapomorphies listed by ESTES et al. (1988) for Scincoidea are "body osteoderms always present both dorsally and ventrally" and "lateral coronoid process of dentary extends dorsally onto the anterolateral surface of the coronoid". But according to LANG (1991), two genera within Cordylidae (*Platysaurus* and *Chamaesaura*) reduce their body osteoderms and *Chamaesaura* does not match the second synapomorphy. Within some Scincidae this synapomorphy is reversed to its plesiomorph state as well (ESTES et al. 1988). Presence or absence of body osteoderms must be seen in a context of functional morphology and ecology (Cordylidae which lack body osteoderms are crevice ecomorphs). Thus, the two synapomorphies established by ESTES et al. (1988) are not shared by all Cordylidae and do not falsify the assignment of

the new genus and species to the Scincoidea. Two possible explanations for the preservation of a plesiomorph character can be given: The presence of a stem group taxon representing an early branch of the same evolutionary line. A second reason might be the presence of a regressive character which is not expressed in the phenotype but is still present in the genotype and may sometimes appear in primitive members of this group (BORSUK-BIALYNICKA pers. comm.). To encounter the above argumentation using negative evidence, additional and more informative characters will be discussed in the respective family sections of the Scincoidea.

Although the tooth morphology is doubtlessly influenced by adaptations to food resources, there are also features which seem to be of taxonomic importance as well and have been described for the single families in ESTES (1983) and RICHTER (1994). There are consistent features which occur in all members of the superfamily Scincoidea and – with this special morphology – cannot be found in an other lacertilian family: A typical feature in the tooth tip of the Scincoidea is an anterior and posterior cutting edge, which were described as *Crista mesialis* and *Crista distalis* by RICHTER (1994) for Paramacellodidae (an extinct Jurassic/Cretaceous family, see below). This also occurs in Cordyliformes and according to EDMUND (1969) “some Scincidae have laterally compressed tooth tips or crowns to form cutting edges”. The tooth crowns can be striated (both labially and lingually or only lingually) and concave lingually. This has been described as a synapomorphy of the Scincidae by ESTES (1983) but can be observed also in Paramacellodidae and within Cordyliformes. The teeth often have a more or less blunt conical outline. Although there are exceptions like the multicuspid herbivorous *Angolosaurus*, this tooth morphology, which is also present in the new genus and species, is considered here as a characteristic feature in the Scincoidea.

Scincidae

Compared to the blunt conical teeth of the Scincidae, the new taxon has teeth which are slightly more pointed than in this family. The anterior and posterior cutting edges are more distinct in the new genus and species than in Scincidae. As mentioned above, it has striated and lingually concave tooth tips as the Scincidae (ESTES 1983). But this family also has labially striated tooth crowns.

The following characters of Scincidae are also shared by the new taxon: Frontals and nasals paired and scapular fenestrae usually absent (ESTES 1983). But paired frontals and nasals are plesiomorph characters and the absent scapular fenestrae can appear in other families, too (BORSUK-BIALYNICKA pers. comm.). Unfortunately, other important derived characters of this family, such as “supratemporal fenestra roofed principally by postfrontal” or the “bony secondary palate”, are not determinable in the new taxon.

According to ESTES (1983), a key character of Scincidae is “jugal contribution to lower border of orbit small or none”. Yet, in the new genus and species the jugal extends to the anteriormost border of the orbit. This condition contradicts an attribution to Scincidae.

Characters of the four subfamilies of this family are now discussed in context with the characters seen in the new taxon. The most primitive subfamily *Scincinae* shares some characters with it. These are usually paired frontals, a complete supratemporal arch, limbs usually present and some species bear pterygoid teeth. But these are all plesiomorph characters shared by many other groups and therefore are inconclusive. The

retroarticular process is rather short in the new species, corresponding to the condition found in *Tiliqua nigrolutea* and *Trachydosaurus rugosus*.

The new genus and species does definitely not belong to the subfamilies *Feylininae* or *Acantinae*, which are limbless forms. The first subfamily lacks postorbitalia and jugalia, the second subfamily has no supratemporal arch and reduced prefrontals and squamosals (ESTES 1983). The *Lygosominae* can be excluded as well, because they have a single frontal bone, paired premaxillaries, 6-15 premaxillary teeth and there is a trend of digit and limb reduction in the group as well (ESTES 1983).

Cordyliformes (Cordylidae and Gerrhosauridae)

Since COPE (1871) these two taxa have caused constant discussion about their taxonomic position and proposed affinities, of which LANG (1991) gives an historical review. The question was whether these two taxa should be recognised as different families or subfamilies within the Cordylidae. According to LANG (1991), the recognition of these taxa as subfamilies or families is subjective. He confirms the monophyly of both taxa and revives the "Cordyliformes" (FITZINGER 1826) to include both Cordylidae and Gerrhosauridae".

In Gerrhosauridae, the anterolateral border of the orbit is formed by the jugal (LANG 1991), the frontals are paired (LANG 1991, ESTES 1983, ROMER 1956) and the pterygoid bears teeth. Unfortunately, only the first character is derived, the following two are plesiomorph and all of them occur in many different families of the Lacertilia. The value of these characters for a family diagnosis is therefore rather low, although the new genus and species exhibits all of these.

Another character which is not useful for a family diagnosis because of large variation spans is the vertebral count. According to LANG (1991) the Gerrhosauridae have presacral vertebrae numbers from 27 up to 38 (modal number 28), whereas the Cordylidae have 23 to 37 with a modal number of 26. So the vertebrae number would only be of some value if it is below 27. Since the vertebrae number of the new taxon is not exactly determinable (it is around 26), one cannot really use this character for an attribution. Additionally, the special phalangeal formula of Gerrhosauridae (2-3-4-4-3) does not correspond with the one present in the new species, which shows the ancestral formula (2-3-4-5-3) present in Cordylidae and typical for the Lacertilia. There is a persistence of this primitive phalangeal number generally present in reptiles (ROMER 1956). A good synapomorphy for the family (convergent only in Xantusiidae) is the entire closure of the supratemporal fenestra by postfrontal and squamosal (LANG 1991). Because of reasons already described, this character cannot be evaluated in the new taxon.

As well the supraorbitalia of the Cordylidae differ from those of the new genus and species. *Cordylus giganteus* has four osteoderms, bordered by a row of small slender scales covering the orbit dorsally as in the new species, but the anterior and posterior osteoderm is larger. Also the suture of the two central osteoderms is slightly curved rather than straight as in the new taxon. So its palpebral ossifications are much more similar to those of the Lacertidae, as described above.

According to ESTES (1983) and ESTES et al. (1988), Cordyliformes have paired frontals and no scapular fenestrae. These plesiomorph characters occurring in many families are

also present in the new taxon. A better character is the tooth morphology of Cordylidae. Members of the family can have blunt, striated teeth with lateral cutting edges. As said above, this tooth morphology seems restricted to Scincoidea. The teeth of *Cordylus giganteus* somewhat resemble those of the new genus and species: They are conical with an anterior and posterior cutting edge, the tips are slightly recurved. However, they clearly differ in not having a rounded base nor do they bear any visible striations on the lingual side of the tooth crown.

Cordylidae (sensu LANG 1991) are the only group in which osteoderms can be restricted to the dorsal aspect of the head (as in *Chamaesaura* and *Platysaurus*, LANG 1991). In Lacertidae, osteoderms are commonly present on the lateral head portions, as well. The osteoscutes of the new genus and species are limited to the dorsal aspect of the head as in *Chamaesaura* and *Platysaurus*, whereas in *Cordylus giganteus* the head is completely covered with osteoscutes. The osteoscutate pattern of the new taxon differs quite strongly from the one found in Cordyliformes: There are no borders of osteoscutes on the parietal, even on the standard radiographs. This supports the hypothesis that there rather is an ornamented osteodermal crust instead of clearly bordered osteoderms covered with a spiny scutellation.

Remarkable is the resemblance of the new genus and species with *Cordylus giganteus* in possessing a row of spiny osteoderms overlapping the posterior margin of the parietal, showing a jagged crest projecting from the rear of the head. The difference is that the osteoscutes are much smaller and more numerous in the new genus and species than in *Cordylus giganteus*. Within Scincomorpha and Anguimorpha these occipital spines are found among recent taxa only in *Cordylus giganteus* and *Cordylus warreni* (LANG 1991:147). But they seem to be also present in the cordylid *C. cataphractus* and the scincid *Tribolonotus gracilis*. However, they seem to be restricted to the Scincoidea, which would further support the attribution of the new taxon to this superfamily (Fig. 54).

All Gerrhosauridae as well as most of the Cordylidae have osteoderms covering the entire body but they can be reduced as in *Platysaurus* or *Chamaesaura*. Similar to the condition in *Cordylus giganteus* the Condylus cephalicus of the quadrate of the new genus and species obviously was not oriented vertically but ascending posteriorly in its resting position. This character most probably has no taxonomic value but rather tells more about the mobility of the mandible.

As already discussed above, the direction of the retroarticular process of the new genus and species is incongruous with Cordyliformes (not or only very slightly directed medially or twisted obliquely).

Fig. 54: Skull of A: *Cordylus giganteus* (Cordyliformes, SMF 69852) and B: *Tribolonotus gracilis* (Scincidae, SMF 80901) showing the osteodermal cover with the occipital spines.

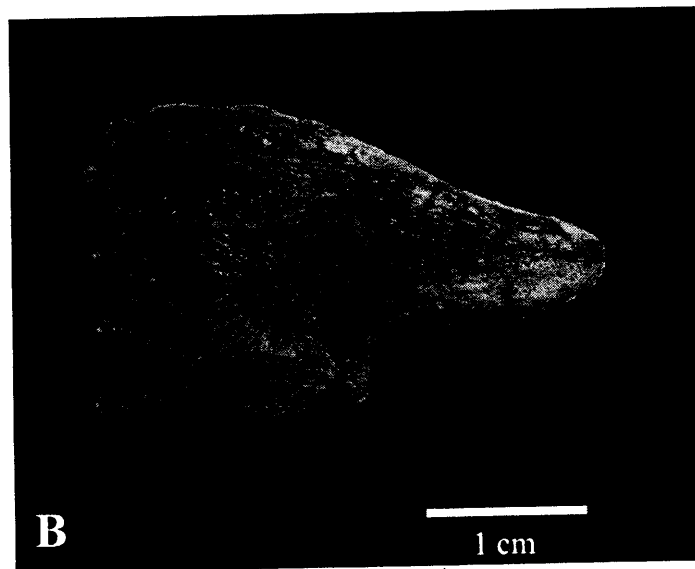
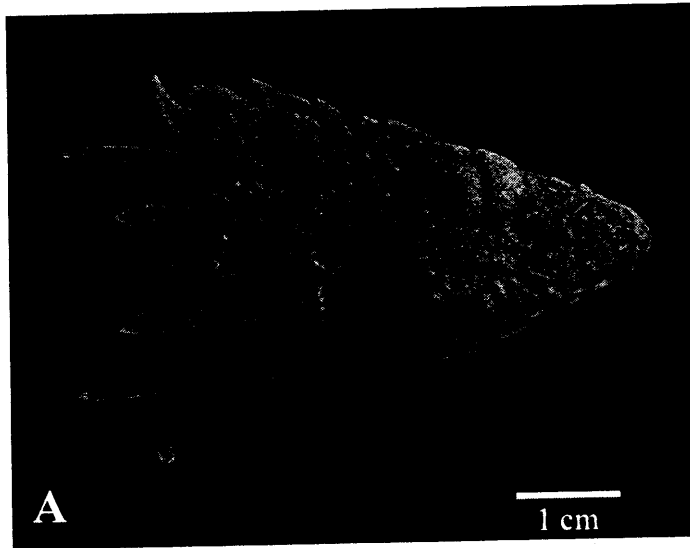


Fig. 54

In Cordyliformes, the clavicles can be simple curved rods (as in *Chamaesaura* and *Platysaurus*, LANG 1991). This only occurs elsewhere within Iguania and *Varanus* (ESTES et al. 1988) and therefore makes the character valuable for an attribution of the new species, which has a corresponding clavicle morphology. Iguania and Anguimorpha largely being excluded as possible relatives, a relationship to Cordyliformes is supported by this character.

Although the new genus and species shares many characters with Cordylidae and Gerrhosauridae, there are still differences in some characters, which contradict an attribution to these Cordyliformes: Only some Cordyliformes seem to have a feebly developed posterior process of the jugal, whereas this process is a distinct character in the new species. Furthermore, the sculpture of the osteodermal crust on the skull, as well as the supraorbitalia differ considerably from those present in Cordyliformes. The posterior skull osteoscutes are smaller and more numerous in the new taxon. As well in Cordyliformes, the maxilla never seems to reach back to the posterior margin of the orbit. Additionally, there are differences in the orientation of the retroarticular process.

Paramacellodidae

The Paramacellodidae is a group of fossil lizards found from the Middle Jurassic (WALDMAN & EVANS 1994) to the Middle Cretaceous (ALIFANOV 1993). ESTES (1983) erected this family and placed it within the superfamily Cordyloidea. According to him the Paramacellodidae possibly will prove to be a synonym of the Cordyliformes. The superfamily Cordyloidea was replaced by the Scincoidea (ESTES et al. 1988). RICHTER (1994) and EVANS & CHURE (1998) confirm the position of the Paramacellodidae within the Scincoidea. This family shows tooth characters which strongly resemble those of the new genus and species: The teeth are blunt-conical, slightly recurved and finely striated on their concave lingual faces (ESTES 1983) with two cutting edges on the tooth tip with almost parallel striations, as in *Paramacellodus* (shown in RICHTER 1994, Fig. 55). As discussed above, this is not a synapomorphy of this family. But some features typical for a paramacellodid teeth, as a Cuspis lingualis and dominating anterior and posterior striae (Fig. 55), are not present in the new genus and species. Furthermore, it has no premaxilla with nine tooth positions and an open upper temporal fenestra as in *Paramacellodus* (EVANS & CHURE 1998). Members of this family both lack and bear body osteoderms and can either have normal and reduced limbs (ESTES 1983).

Another Scincoid in Messel

The new genus and species is the second scincoid found in Messel. Interestingly enough, the Messel Pit Fossil Site yields another lizard of uncertain taxonomic position. On the basis of new material, MÜLLER, J. (1998, 2001) redescribed *Eolacerta robusta* NÖTH 1940 and suggested an attribution rather to the Scincoidea than to the Lacertidae, to which this species has been assigned before. Because of several plesiomorph characters and incongruities, a definite taxonomic attribution was not possible (MÜLLER, J. 1998, 2001). But there are clear differences between the new taxon and *Eolacerta robusta*: The latter does not bear the characteristic osteodermal pattern on its dorsal aspect of the skull. The supratemporal fenestrae are open. Only a small posterior process on the jugal is present, by far not as prominent as in the new genus and species. The Processus maxillaris of the jugal does not reach the anterior most edge of the orbita. The teeth are similar but can sometimes be bicuspid. The clavicle is more or less loopshaped rather than simply curved as in the new taxon. Its tail is much longer than that of

Eolacerta robusta. Altogether this taxon is larger than the new species (the head/trunk length is about 30 cm) and much more robustly built.

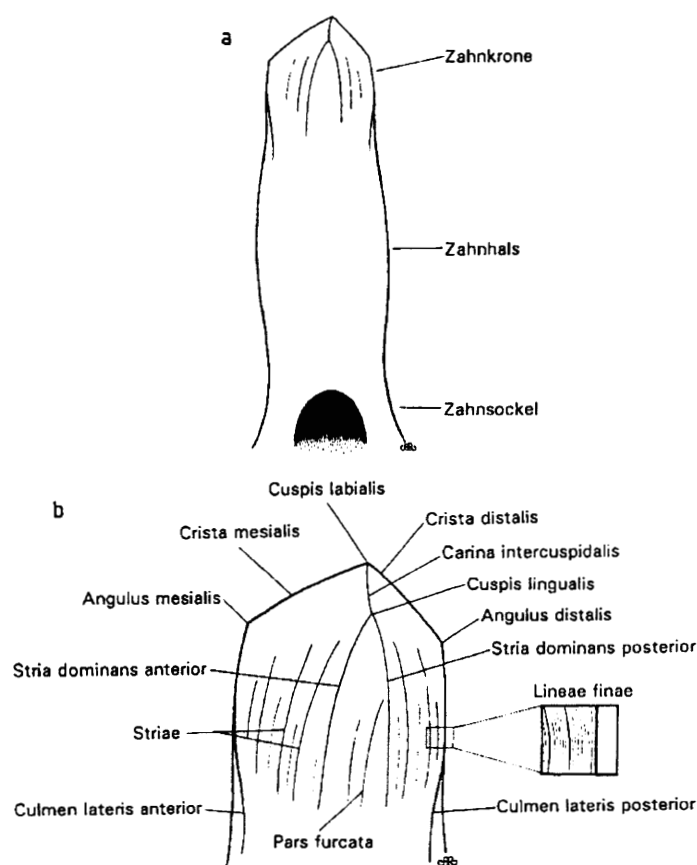


Fig. 55: Terminology of a paramacellodid tooth (lingual view). a: total view; b: fine structure of the crown (RICHTER 1994).

2.4.1.3 Conclusions

The new taxon is placed within the Scincoidea mainly because of its characteristic tooth morphology, the shape of the medial margin of the retroarticular process and its special head osteoscutes with occipital spines. There is rather a stronger affinity towards the Cordyliformes (especially to the Cordylidae) than to the Scincidae or Paramacellodidae. Still, an attribution is difficult, but the persisting differences to Scincoidea could partly be due to a phylogenetic change: An example is the posterior process of the jugal, which could have been reduced from the Eocene up to now. Therefore, the new genus and species is placed as a family incertae sedis within the Scincoidea. There are remarkable primitive characters in the new taxon, such as the posterior process and the straight quadrate. It combines plesiomorph and apomorph scincoid characters in a mosaic manner. It most likely represents a fossil descendant of a stem group taxon of (Cordyliformes + Scincidae), but the exact phylogenetic position of the new taxon regarding Scincidae, Cordyliformes and Paramacellodidae remains unresolved (Fig. 56).

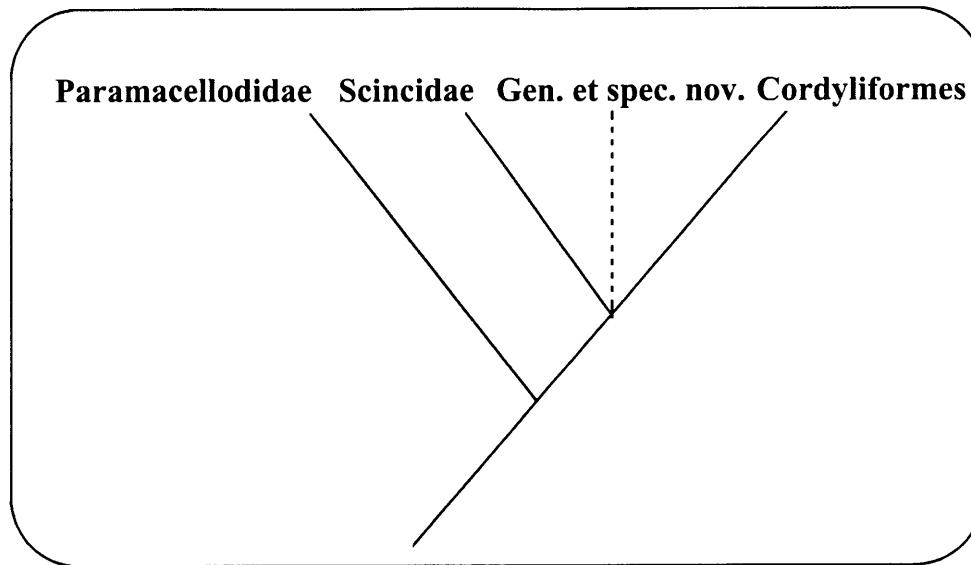


Fig. 56: This cladogram shows the most favoured, but unresolved relationship of the new genus and species within Scincoidea.

2.4.2 Phylogenetic reconstruction using numerical methods

2.4.2.1 General comments on numerical taxonomy

It must be stressed, that numerical taxonomy is only one method among others to formulate phylogenetic hypotheses. Although it is a mathematical method and reproducible, the subjectivism of the author plays the same important role as in other phylogenetic methods, such as comparative morphology. There are several factors which can considerably influence the resulting cladogram biased by the subjectivism of the author: The choice of taxa and characters, character state coding (which character states are present in the respective taxon), choice of outgroup, the used software, which search option is applied, if multistate characters are treated as ordered or unordered, interpretation of the character states as reversals, convergences or shared derived characters.

For the attribution of fossil taxa, where usually only a small part of the characters is codeable, it is necessary, to have a broad recent data basis available. Only this way the cladogram becomes stable and reproducible, also when new taxa are added. In this respect, the matrices of all authors were very useful, because the trees did not change considerably when the new taxon was added.

There are a number of problems with character coding, of which special examples are named here:

- Often the presence or absence of a character has to be coded, i.e. the presence or absence of supraorbitalia. But the special morphology and the number of the elements in question is not further asked for, even if it differs considerably in the different families of the Lacertilia.
- A specific problem with fossil taxa, which may still possess very primitive characters, is that these characters are not any more considered in a matrix and therefore are not taken into account. This was the case here, since the character

coding of the posterior process of the jugal, was only present in the matrix of EVANS & CHURE (1998).

- A general problem in taxonomy is the influence of the functional morphology on the characters. I believe there are a lot of characters which are at least somewhat influenced by functional morphology. In most cases, it is impossible to differentiate between taxonomical and functional factors. Still, there are characters where the influence of both factors are quite clear, for example the closure of the supratemporal fenestra: The fenestra being closed has functional reasons (jaw adductor musculature), but which elements are responsible for that closure and to what extent, is a taxonomical character. A character state which is used in the matrices of ESTES et al. (1988), EVANS & CHURE (1998) and LEE (1998), is the presence or absence of body osteoderms. Especially their absence I consider highly influenced by ecological factors. Although of course – due to the adaptive character of evolution – evolutionary novelties that are recognised as synapomorphies, have most often a functional value (BORSUK-BIALYNICKA pers. comm.). It cannot be denied that certain characters which were developed under a strong functional influence are good taxonomic characters, if parallelisms and convergencies can be excluded.
- The decision whether a character state is primitive or derived is difficult to make and often controversial. Whether multistate characters are believed to form a morphocline or not is a subjective decision. Another difficulty in the analysis of fossil taxa is the reduced information on characters. For example, the new genus and species shows only about one third of the osteological characters which are analysed in the matrices. This is the reason to test the quality of the characters which could be found in the new taxon.
- PAUP means Phylogenetic Analysis Using Parsimony. "Parsimony methods search for minimum-length trees. Trees that minimise the amount of evolutionary change needed to explain the available data [...]." But one has to keep in mind that the shortest tree not necessarily is showing the true phylogenetic relationships.
- The characters in this study were not weighed, so each character has the same influence on the resulting tree. Although, I would consider some characters more important for taxonomy than others, but again the selection of those characters is subjective. For example, I consider the tubercle on the posteromedial margin of the retroarticular process and the posterior process of the jugal much more important than the presence and absence of body osteoderms or a fused premaxilla. Additionally, it is always possible that character complexes, which are not recognised as such, are coded as independent characters. Therefore, this character complex is weighed unintentionally. However, not weighing the characters still seems to be the most neutral approach.
- The treatment of character states as reversals is controversial, too. The occurrence of atavisms is possible, but highly improbable. It seems more likely that newly evolved characters "reverse" (in the sense of atavisms), than widely shared characters (synapomorphies).

Nevertheless, when being aware of the problems of the numerical taxonomy, it is an interesting method and I use it as a further, rather experimental tool for the systematical

attribution and for the phylogenetic position of the new genus and species. The interpretation of cladograms has to be very careful and the results of the comparative morphology should be taken into account as well.

2.4.2.2 Complete matrices

ESTES et al. (1988), EVANS & CHURE (1998), LEE (1998) and CALDWELL (1999) differ in their views of phylogenetic relationships within Squamata (Fig. 4, Fig. 28, Fig. 32). There are some consistent features in all three papers: The sistergroup relation of Teiidae and Gymnophthalmidae. Iguania, Gekkota and Varanoidea (except Mosasauroida in CALDWELL 1999) form separate, monophyletic clades. ESTES et al. (1988) and EVANS & CHURE (1998) have some further congruences in their cladograms. They both present trees where Scincomorpha and Anguimorpha are separated in two clades and Scincidae and Cordylidae (Cordyliformes) are sistergroups. Lacertidae are the sistergroup to Gymnophthalmidae and Teiidae (Teiioidea) in the cladograms by LEE (1998) and ESTES et al. (1988). Both authors place Anguioidea into the same clade as Varanoidea.

LEE (1998) presents an unusual cladogram (Fig. 32), which separates the Scincoidea from the Lacertoidea. The consecutive taxa Scincidae and Cordylidae are now placed at the base of Anguimorpha. According to LEE (1998) "The uniting of scincids and cordylids with anguimorphs contradicts all recent cladistic analyses of squamates", although he used all informative characters in ESTES et al. (1988), PRESCH (1988), WU et al. (1996) and EVANS & BARBADILLO (1997). The author also points out that already COPE (1900), FÜRBINGER (1900) and CAMP (1923) "[...] grouped cordylid cordylids with basal anguimorphs".

ESTES et al. (1988) present the Scincoids in two different positions: At the base of the Lacertoidea (Lacertidae, Xantusiidae, Teiidae + Gymnophthalmidae) and – similar to LEE (1998) – at the base of Anguimorpha, but as sistergroups. This result was obtained when snakes, Amphisbaenians and Dibamids were deleted. So, the deleting of these taxa obviously changes the position of other taxa. ESTES et al. (1988) also obtained slightly different cladograms when using different software programs. Thus, the choice of the taxa and of the software makes quite a difference in the result. This is the reason for which different approaches with reduced matrices are taken in the present study. Since there is and will still be discussion of the phylogeny of squamates, it is difficult to decide which cladogram is the most probable for a reference.

In the first approach using complete matrices, the new genus and species cannot be placed in an unequivocal position within Lacertilia. It is placed at two equally probable positions: If its characters are added to the matrices by ESTES et al. (1988) and EVANS & CHURE (1998), the new taxon appears as a sistergroup to Lacertidae (Fig. 27, Fig. 31). This congruent result is not surprising, since the matrices of EVANS & CHURE (1998) are mainly based on the characters introduced by ESTES et al. (1988). A sistergroup relationship of the new taxon to Lacertidae can be excluded: As mentioned above, there are characters (e.g. tooth morphology) which do not match those of the new genus and species and are not considered in the character matrix. Surprisingly, five of the seven apomorphies of Lacertidae and the new species listed by PAUP 3.1 (with the matrix of ESTES et al. (1988)), are not visible in the new taxon. The two remaining characters (palpebral ossifications and cephalic osteoderms) are also present in Scincoidea and

other families. In the matrix of EVANS & CHURE (1998) the same can be observed, six out of seven listed apomorphies are also not visible in the new genus and species. Therefore it cannot be retraced why PAUP placed it as sistergroup to Lacertidae.

An interesting tree (Fig. 33) was obtained when using the matrix by LEE (1998). The new taxon is placed at the base of Scincoidea + Anguimorpha (= Diploglossa COPE 1864) and these are collectively placed as a sistergroup to the Lacertiformes (Lacertidae, Teiidae and Gymnophthalmidae) clade. This result hints towards the taxonomic position of the new genus and species obtained in the comparative morphology. Seven out of twelve apomorphies combining the new species with Scincoidea and Anguimorpha are visible in the new taxon. One character is considered by LEE (1998) to be highly derived (separable cranial osteoderms present over entire skull table, character state 2). Since the strict consensus tree with the unresolved Scincoidea becomes resolved when adding the new taxon, it seems to have a stabilizing effect on LEE's cladogram.

2.4.2.3 Matrices reduced to osteological characters

To further clarify the position of the new genus and species in the system of Lacertilia, the matrices were reduced to osteological characters. A phylogenetic hypothesis is only of value for the positioning of fossil taxa, if the tree does not collapse when its characters are reduced to osteological ones. For the first time, a congruent position of the new taxon is calculated from the three different matrices: Although its position was unresolved when reducing the matrices of ESTES et al. (1988) and EVANS & CHURE (1998) to osteological characters, one consistent hypothesis shows a sistergroup relationship of the new species with (Scincoidea + Anguimorpha, Fig. 38, Fig. 41). The reduced matrix by ESTES et al. (1988) produces a strict consensus tree (Fig. 36) which resembles much more the one of LEE (1998), in which exclusively osteological characters are used. This is a highly interesting result. ESTES et al. (1988) at that time could not use the unordered option for character states, while LEE (1998) chooses several characters as ordered, others as unordered. The osteological characters of ESTES et al. (1988) were left unordered in this study. Therefore, apparently divergent cladograms in literature can become much more similar, when limited to osteological characters. Reducing the matrix of ESTES et al. (1988), the Lacertoidea are no longer a crown group within Scincomorpha. Instead, the whole clade takes a basal position within Lacertilia, even more basal than Gekkota. When including the new genus and species, the position of the clade does not change but becomes unresolved because of the unequivocal position of the new species. This change in the position of the Lacertidae is highly significant for the new taxon, as it is always placed as a sistergroup to this family in the analyses. This basal change is only due to the restriction to osteological characters. Thus, it can be assumed that only soft tissue characters define this family as derived. But the paleontologist can base his analyses on osteological characters only, and only these can be taken into account when attempting a phylogenetic classification of organisms. Apart from the indisputable value of soft tissue morphology (e.g. epidermal scale and tongue morphology), osteological characters remain the only practicable information source for fossil Lacertilia (even in Messel) and the reconstruction of phylogenetic hypotheses which include fossil taxa.

Using the reduced matrix of EVANS & CHURE (1998) the new genus and species is either placed as sistergroup to Lacertidae or to (Scincoidea + Anguimorpha + Gekkota +

Serpentes + Amphisbaenia + Dibamidae, Fig. 41). As for the last three taxa, they are not considered here, since they are no Lacertilia and their phylogenetic relationship will not be discussed here. As the Gekkota are regarded as a relatively ancestral group, this position does not really make sense. However, it is remarkable that one probable position of the new taxon is sistergroup to Scincoidea and Anguimorpha.

2.4.2.4 *Matrices reduced to characters visible in the new genus and species*

If the matrix by EVANS & CHURE (1998) is reduced to characters which are identifiable in the new genus and species, the original tree is not longer reproducible and as much as 510 trees are generated. The addition of the new taxon character states to this strongly reduced matrix considerably reduces the number of trees obtained from 510 to 66 (Fig. 44). Therefore, the new taxon has a certain stabilising effect, although still the resulting tree does not reflect a debatable phylogeny of Lacertilia. Still all taxa including the new taxon are one unresolved clade, except for Scincoidea and Anguimorpha. One possible position of the new genus and species is again at the base of (Scincoidea + Anguimorpha). Yet, equally parsimonious positions are sistergroup to Lacertidae or at the base of all Lacertilia, except Ardeosauridae and Bavarisauridae, those being more ancestral. It has been discussed above why a sistergroup relationship to Lacertidae is not acceptable. Also the position of the new taxon being at the base of all Lacertilia, obviously is impossible and therefore not further discussed. Besides, as the strict consensus tree shows, the number of unresolved clades of taxa is too high to formulate a phylogenetic hypothesis. This result clearly shows that the data basis was too strongly reduced and not enough information is available to resolve the position of the taxa.

This is not the case in the matrix by LEE (1998) when making the same selection of characters without adding the character states of the new genus and species (Fig. 45): It is remarkable that (Scincoidea + Anguioidea) and Varanoidea still form a monophyletic clade in the cladograms reduced to character states visible in the new taxon, and forming a sistergroup relationship. Although Iguania and (Gekkota + Lacertoidea) are unresolved, they form separate clades and the relationships of the higher level taxa are similar to the ones showed when the matrix was unaltered. Still, no statement can be made on members within Iguania or (Gekkota + Lacertoidea), since these are unresolved. This shows that enough characters are present in the new taxon for a classification within Scincoidea and Varanoidea. When actually adding the new taxon, its position remains unchanged compared to the complete matrix, it is placed again at the base of Scincoidea and Anguimorpha (Fig. 46). So a close relationship of the new genus and species to this superfamily is a consistent feature when using the matrix of LEE (1998).

As described in the results, the strict consensus tree of ESTES et al. (1988, Fig. 42) does not differ considerably from the one, when the matrix was reduced to osteological characters: Still the Lacertoidea are in a basal position and the Scincoidea are the sistergroup of Anguimorpha, which is similar to the original tree by LEE (1998). So, there are enough characters present in the reduced matrix to form a phylogenetic hypothesis. The addition of the character states of the new genus and species do not considerably change the tree (Fig. 43). Only Gekkota and Lacertidae change their position and the new species becomes sistergroup to the latter family. This is very surprising in the light of the strong limitation of available information. Even more interesting is the fact, that by addition of the new taxon characters, the Xantusiidae

become a sistergroup of Gekkota and the Lacertidae are in the sisterclade to (Scincoidea + Anguimorpha). In these two instances, the tree is even more similar to the original one by LEE (1998).

The reduction of the matrices by the different authors to the characters that are visible in the new species shows that only in one case (EVANS & CHURE 1998) not enough information was present for the establishment of phylogenetic hypotheses. Therefore the argument, that not enough characters are available in the new genus and species to make a cladistic analysis using numerical taxonomy, does not hold true in the light of the investigations made here.

2.4.2.5 Matrices reduced to Scincomorpha

Based on previous investigations comprising all taxa, it can be excluded that the new genus and species belongs to any high-level taxon but to the Scincomorpha, which has also been shown in the investigations using comparative morphology.

If the data matrices are reduced to the taxa of Scincomorpha (without new taxon), three trees are generated with the matrix by ESTES et al. (1988) and LEE (1998), and two trees with the matrices by EVANS & CHURE (1998), respectively. Consistent features in nearly all cladograms is the monophyly of Scincoidea and Lacertiformes. The position of Xantusiidae seems not to be certain, since the taxon changes its position. It is particularly interesting that the two cladograms in Fig. 47 are produced by all of these taxon-reduced matrices. This relationship within Scincomorpha is favoured by ESTES et al. (1988). Such a congruent result was not obtainable in earlier analyses made in this study with the matrices published by different authors.

If the characters of the new genus and species are added to the taxon-reduced matrix by ESTES et al. (1988), its position is not resolved (Fig. 48). But again one of the proposed positions was as sistergroup to Scincoidea. The matrix by EVANS & CHURE (1998) produces only one tree. As expected, the new taxon is placed as sistergroup to the Lacertidae (Fig. 49). Both form the sistergroup to (Scincoidea + Xantusiidae). As a consequence Lacertidae is no longer the sistergroup of Teiioidea. An attribution to Lacertidae cannot be excluded after a detailed analysis using numerical cladistic methods, but can be denied by the results from the comparative morphology.

When adding the new genus and species to the reduced matrix of LEE (1998) only one of three trees remains, presenting the taxon again as sistergroup to Scincoidea. That means that it somehow stabilises the cladogram and produces a single resolved tree (Fig. 50). The same phylogenetic relationship within Scincomorpha (except for the position of Xantusiidae) is favoured by ESTES et al. (1988). The result of the present analysis further corroborates the scincoid affinity of the new taxon, supporting the results obtained by comparative morphology.

Measures for tree stability

The consistency and retention indices of the cladograms are rather low (Tab. 6). But the those of the complete matrices without the new taxon are the same as given in the papers of EVANS & CHURE (1998), CALDWELL (1999) and LEE (except ci) or even higher as in ESTES et al. (1988). The significance of these indices is not discussed by any of the authors. Probably a high value (approaching 1) is not obtainable with a matrix

containing so many characters and taxa, and thus the possibilities of convergences are very high. The consistency indices are higher (around 0.8), when the matrix is reduced to scincomorph taxa. This means quite a high consistency in the respective trees. But since the matrix is reduced, the trees necessarily become shorter and the possibilities of convergences are reduced, as well. Therefore, it is difficult to compare the values of the different matrices. Since the lower bound of *ci* is not zero but a function of the distribution of character states in the data matrix (SWOFFORD & BEGLE 1993), an assessment of the values is difficult to make. When looking at the retention indices, they stay around 0.6. So, the stability obviously is not higher in the reduced matrix. The retention index values in the present study seem to neither strengthen nor contradict the respective trees.

2.4.3 Synthesis of the results obtained by comparative morphology and numerical taxonomy

The phylogeny of the Lacertilia is still subject of current discussions and these phylogenetic problems will most probably not be solved in the near future. Most workers present a new cladogram in their respective papers, representing their understanding of lacertilian phylogeny. Unfortunately, a synthesis of all these cladograms is rarely made in the course of a major revision and it is uncertain whether such a synthesis is possible at all. The new genus and species cannot really contribute to clarify lacertilian phylogeny, although it represents a descendant of a basal representative of Scincomorpha. It does not unify this infraorder or parts of it as a monophyletic taxon. Numerical taxonomy is a tool to formulate phylogenetic hypotheses based on complex character analyses. This is the reason why it was used here as an experimental tool, as already mentioned above. A critical review of the cladograms, which only represent phylogenetic hypotheses is necessary and there has to be a feed-back from the results of undertaken morphological studies. Which of the cladograms presented in literature comes closest to the true phylogeny of Lacertilia cannot be decided here. However, the taxonomic position of the new species sustains the tree presented by LEE (1998). It is the only one which combines the Scincoidea with Anguimorpha as monophyletic Diploglossa.

An unequivocal phylogenetic position of the new taxon cannot be obtained with the numerical taxonomy approach using unaltered matrices. As mentioned above, the new taxon is either placed as sistergroup of Lacertidae or of (Scincoidea + Anguimorpha). Although there are certain affinities to the Lacertidae (e.g. arrangement of the palpebral ossifications), a close relationship to this family can be excluded (see above). But as both Scincoidea and Lacertoidea are closely related groups, it is not surprising that certain traits of Lacertidae are also present in the new genus and species. Although this taxon never was placed as a strict sistergroup to the Scincoidea alone, their close relationship is a consistent feature of the cladograms which were produced using the matrix of LEE (1998) and reducing the matrix of ESTES et al. (1988) and EVANS & CHURE (1998) to osteological characters. In the latter cases other positions occur as well. LEE (pers. comm.) considers the alternative position of the new genus and species not very surprising, since the resolution of the tree with respect to scincomorphs is not very certain. Although there are only a few good areas of resolution – such as monophyly of Iguania, Scleroglossa, Lacertiformes, Scincoidea, and Anguimorpha – the relationships *between* these clades are at best poorly resolved (LEE pers. comm.). As already mentioned, an osteological character matrix is more appropriate for fossil taxa, as only

these characters are available. Therefore I consider the matrices of LEE (1998) and CALDWELL (1999) the most useful ones when dealing with fossil taxa, since they only use osteological characters. Furthermore it is remarkable that the new taxon obviously stabilises unresolved trees, when using the complete and reduced scincomorph matrix of LEE (1998). So, the numerical analysis somehow supports the results of the comparative morphology. Based on the present investigations, the new taxon represents a descendant of the common ancestor of (Scincoidea + Anguimorpha) as shown in Fig. 33. As the numerical taxonomy method is very problematic, the classical morphologic analysis is to be treated with a much larger impact on the results concerning the taxonomic position of the new genus and species. The morphologic analysis in the present study places it into close relationship of the Scincoidea. To what extent there are affinities to other high level taxa (such as Anguimorpha or other Scincomorpha) cannot be decided on this basis. As stated above, it most probably represents a fossil descendant of a stem group taxon of (Cordyliformes + Scincidae) but the exact position remains unresolved (Fig. 56).

3 Microhabitat Reconstruction of the new genus and species

3.1 Introduction

3.1.1 Palaeoecological Reconstructions

Mode of life reconstruction is an interesting field in paleontology, as the fossil is put into an ecological context and sometimes information on its behaviour can be gained. The aim of any palaeobiological reconstruction is the definition of an “ecological niche” for the fossil in question. But it is difficult to define ecological niches for extant animals, because the interactions with abiotic and biotic factors are so complicated that sometimes years of observation in the original habitat are necessary to gain a data basis on which ecological statements can be made. Thus it is much more difficult to attempt such a classification for fossil organisms, therefore the term “paleo-econiche” is preferred here. One way to approach this problem is to define a limited number of parameters for the ecological niche (Fig. 57). These parameters can then be identified on different levels of confidence, according to the available data. PIANKA (1986) states that an animals morphology reflects its ecology. Unfortunately, in most cases, the remains of the animals are so sparse that such an ecological reconstruction is hardly possible. While most squamates are known from tooth bearing elements only (which have the highest potential for preservation), the specimens from the Messel Pit mostly are preserved in complete articulation. Therefore, postcranial information is available and body measurements can be taken on the basis of which a careful paleo-econiche definition is possible. According to the principles of actuopaleontology, investigations of extant skeletons are necessary to obtain an extant frame in which the fossil taxon in question can be placed. Because of the excellent preservation of the new genus and species, measurements and qualitative investigation of the postcranium (esp. the limbs and tail) can be made, which can give hints to its mode of life.

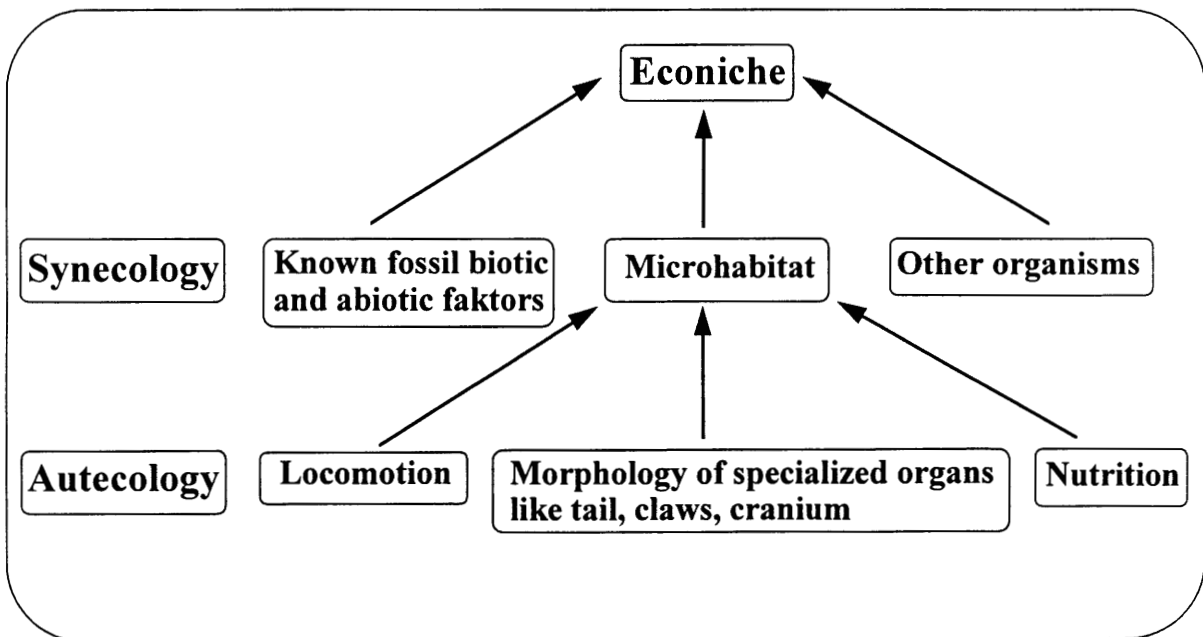


Fig. 57: The reconstruction of a paleo-econiche is based only on indirect evidence and can never be as complex as its extant equivalent. It is only possible to formulate hypotheses on the paleo-econiche based on data collected from the autecology and synecology of the fossil in question. Autecological data can be gained from the locomotor apparatus, specialised organs and nutritional remains in order to reconstruct the microhabitat. On the next level, sedimentary and paleontological data from the fossil locality form the basis for the reconstruction of the paleo-econiche.

3.1.2 Functional Morphology of the Postcranium

3.1.2.1 Limb span proportions

ARNOLD (1998) investigated the structural niche, limb morphology and locomotion of lacertid lizards and thus compiled a valuable data basis for palaeoecological reconstructions, although the purpose of his paper purely was the investigation of extant species. As a result, he found different correlations for ground dwellers and climbers among lacertids in certain indices which are derived from postcranial body measurements. ARNOLD (1998) measures the limbs of Lacertidae by “[...] the total span of a pair of limbs when fully outstretched, from tip of the longest digit on one side to that on the other”. In his Fig. 3 he shows the distribution of selected species of Lacertidae in terms of hindlimb span/snout-vent-length in relation to the ratio of foreleg/hindleg spans. The hindlimbs are always longer than the forelimbs. According to ARNOLD (1998) “[...] the kind of structural habitats species occupy correlates quite clearly with limb proportions”: Ground dwelling species of open habitats that scarcely climb have very long hind legs and short front legs. In contrast, ground dwelling forms living in dense vegetation and climbing forms have shorter, more or less subequal, limbs.

Although the new genus and species does not belong to the Lacertidae, ARNOLD’s (1998) results shall form the basis for the definition of the parameter “locomotion and microhabitat” of the new taxon. For comparison, the ratios of two other Messel lizards are also included here: *Geiseltaliellus longicaudus*, for which a facultatively bipedal locomotion is assumed (ROSSMANN 1992, 2000), and *Eolacerta robusta*, a generalised Lacertilian according to MÜLLER, J. (1998, 2001).

GARLAND & LOSOS (1994) pointed out that it is most important to understand the functional effect of a certain (e.g. a longer leg) measurement and then to correlate the data with the mode of life of the animals in question. ARNOLD (1998) gives such a functional interpretation of differences in limb proportions: Ground dwelling forms in open habitats get most of their forward thrust when running on their hindlimbs. The thrust is enhanced by greater hindlimb length relative to the forelimbs. At the same time, open habitats allow the effective use of long legs and high speeds are necessary to evade predators in situations where cover is sparse. In contrast, ground dwelling forms in dense vegetation do not need high speeds and the concealment from predators is easier.

While ARNOLD (1998) investigated the ecology of the family Lacertidae, PIANKA (1986) worked on the ecology of desert lizards from different families. In such desert microhabitats, where only restricted spaces are available, lizards benefit from short limbs since long legs actually impede efficient locomotion and that shorter legs are advantageous for species that exploit closed-in microhabitats. He found out that among Australian skinks (*Ctenotus*) and geckos those species who “spend a lot of time in the open away from cover tend to have longer hind legs, relative to their snout-vent length, than those that stay closer to safe retreats.” According to ARNOLD (1998), similar fore- and hindlimb proportions occur in climbers and their relatively longer forelimbs (in comparison to their hindlimbs) contribute effectively to upward locomotion. The absolute limb length is shorter in climbers than in ground dwellers, although their ratio is almost equal. ARNOLD explains the absolute limb shortness with the low gearing which is likely to be beneficial when moving upwards against the force of gravity. As a consequence, with shorter legs the mobility would be better. This morphological

correlation is also present in other lizard taxa: Already LUNDELIUS (1957) and COLLETTE (1961) stated that in the genera of *Sceloporus* and *Anolis* terrestrial species also tend to have longer hind legs than arboreal species.

3.1.2.2 *Femur and tibia*

ARNOLD (1998) also studied the proportions of the hindlimbs in Lacertidae by using the index tibia length/femur length. He found that this ratio is lowest in climbing lacertids, whereas ground dwelling forms show rather high values and gives a functional interpretation for these results, as far as terrestrial Lacertidae are concerned: An increased tibial length relative to the femur enhances the forward thrust when running on hindlimbs in ground dwelling forms of open habitats. However, no advantage of a relatively shorter tibia is given in ARNOLD (1998) and a hypothesis on this case will be presented in the present work. LUNDELIUS (1957) already pointed out that an elongation of the distal segment in both limbs, but especially in the hindlimb, relative to the proximal segments, is commonly seen in fast running terrestrial lizards. For mammals the same index is called crural index (tibia/femur x 100, HOWELL 1965).

3.1.2.3 *Manus and pes*

ARNOLD (1998: Tabs. 2 and 3) presents characteristic structures of the manus and pes in ground dwelling and climbing Lacertidae. There are differences in length and shape of the digits and phalanges. Both HILDEBRAND (1988) and ARNOLD (1998) point out the importance of the characteristic terminal phalanx morphology of each digit and the claw that covers it. Both are short, deep and strongly recurved in climbing forms, which is important for clinging and hooking on the substrate. The tips of the much curved claws can interlock with small cracks or crevices. On large stems, claws are even more secure than grasping digits (HILDEBRAND 1988). Whereas in ground dwelling forms the terminal phalanges and claws are relatively long, shallow and curve gently downwards (ARNOLD 1998).

3.1.2.4 *Tail morphology*

The designated holotype (SMF ME 3516) yields important information concerning mode of life and locomotion of the new genus and species: As already mentioned in the description, this specimen has a very long preserved tail with its distal portion curled up ventrally. It is 3.5 times as long as the head-trunk-length. Consequently, some previous work on tail length and prehensility in Lacertilia is compiled below. Additionally, a quantitative actuopaleontological approach will be taken in comparing the length distribution of caudal vertebrae in prehensile and non- prehensile tails. The following extant monitor lizards were analysed: *Varanus salvator*, *Varanus rudicollis* and *Varanus bengalensis* do not have prehensile tails. *Varanus bengalensis* is mainly ground dwelling, even may become bipedal at faster speeds, but can also climb fairly well (SPRACKLAND 1992, BENNETT 1996). It has a laterally compressed and keeled tail (EIDENMÜLLER 1997). *Varanus salvator* has a generalised mode of life, being a burrower, climber and swimmer (SPRACKLAND 1992), *Varanus rudicollis* is mainly arboreal (SPRACKLAND 1992, EIDENMÜLLER 1997) but also searches for prey on the ground (BENNETT 1996) and possesses a laterally compressed and weakly keeled tail (EIDENMÜLLER 1997). *Varanus prasinus* and *Varanus salvadorii* are both arboreal species, *Varanus prasinus* has a long prehensile tail. *Varanus salvadorii* is a very large

monitor lizard, using its long tail as a counterbalance and for whipping (SPRACKLAND 1992, EIDENMÜLLER 1997), but also as a prehensile organ (BENNETT 1996, MÜLLER, T. pers comm).

3.1.2.4.1 Tail length

The tail often is extremely long in matrix climbers and may help to spread weight in these, so long tails contribute to the maintenance of balance in a three-dimensional habitat (ROMER 1956, HILDEBRAND 1988, PIANKA 1986, ARNOLD 1998). Data for **relative tail lengths** in Lacertidae are provided by ARNOLD (1998): He found that very long tails are frequent in climbing Lacertidae (*Takydromus*, *Gastropholis*, *Psammotromus algirus*) which have relative tail lengths over three times as long as the snout-vent length. A long tail helps to keep balance among stems and twigs and spreads weight in flimsy vegetation (ARNOLD 1997, 1998). In the same work, ARNOLD (1997) records that in the two main clades of *Takydromus* there are independent shifts to increased climbing in vegetation and this is associated with greater tail length. Also PIANKA (1986: 67) states that many climbing species have evolved extraordinarily long tails that serve as effective counterbalances. In contrast COLLETTE (1961) found that within five species of *Anolis* a short relative tail length has been correlated with arboreality. Additionally, even the tail lengths of prehensile tails can vary considerably (see below). Therefore, no relative tail length measurements of extant species are taken in the present study and compared to the fossil ones.

3.1.2.4.2 Prehensile tails

BAUER (1998) and ZIPPEL & GLOR (1999) state that **tail prehensility** was developed convergently in several families of the Lacertilia and only a small percentage of individuals in each group possesses the character. In Chamaeleonidae a prehensile tail is typical for the family as a whole. In the genus *Polychrus* (“Iguanidae”) the tail can be 2 or 3 times the snout-vent length. Prehensile tails are also present in the Gekkonidae. There are members of the scincids with short (*Corucia zebrata*) and long (*Sphenomorphus flaviceps*) prehensile tails. Within Anguinae members of the arboreal alligator lizards *Abronia* have prehensile tails, which can be slightly longer than the snout-vent length as in *Abronia taeniata* (OBST et al. 1988). Long prehensile tails are present in the emerald monitors *Varanus beccarii* (pers. obs.) and *Varanus prasinus* (TRUTNAU 1986).

3.1.3 Aims of the present study

The data published by ARNOLD (1998) and PIANKA (1986) on limb measurements will here be used as a basis to interpret the locomotion of the new genus and species. The morphology of specialised organs like the tail, manus and pes is additionally used to reconstruct its microhabitat.

3.2 Material and Methods

ARNOLD (1998) measured limb spans in extant Lacertidae, i.e. from the tip of the left longest digit to the tip of the right longest digit when the legs are fully outstretched. In order to include taxa other than Lacertidae, measurements of specialised representatives from different Lacertilian families („Iguanidae“, Chamaeleonidae, Agamidae, Gekkonidae, Scincidae, Teiidae, Varanidae) were included in the present study: PIANKA

(1986) gives a number of anatomical data and statistic evaluations for different families of extant desert lizards. For the present study those lizards were selected, which are specialised either for a ground dwelling or an arboreal habitat. PIANKA did not measure fore- and hindlimb spans as did ARNOLD (1998), but measures forearm- and hindleg-length. To be comparable to the ratios of ARNOLD (1998), PIANKA'S measurements were doubled. As a consequence these measurements are definitely underestimated in comparison to ARNOLD'S data set, because the width of the respective girdles are not included in the values. Instead of adding some kind of (e.g. percentile) correction values, these doubled values are plotted into the diagram of ARNOLD'S data and the differences will be discussed on the basis of shifted polygons.

Additional comparative data of fossil and extant species included in this study were either collected from the specimens (gen. et spec. nov., *Varanus prasinus*, *Corucia zebrata*) or taken from literature: for *Geiseltaliellus longicaudus* from ROSSMANN (1992, 2000) and for *Eolacerta robusta* from MÜLLER, J. (1998). All measurements from the new genus and species were taken by using callipers: The right fore- and hindlimbs of the specimens SMF ME 3516 and WDC-C-MG 122/123 are quite completely preserved and the single elements were well measurable. The limbs are measured from the tip of the longest digit (digit IV) to the Caput humeri (Caput femoris, respectively). These measurements of a single extremity are doubled. Accordingly, measurements of the right femur and tibia of the same specimens were also taken. In the fossil specimens, the snout-vent length is determined by measuring the length from the premaxilla to the pectoral girdle. The values for a comparison of the fossil specimens with data published by ARNOLD (1998) and PIANKA (1986) were obtained by adding the length of appendicular elements without respect to girdle width, because the latter is hardly reconstructable. Thus, these osteological data are of a similar nature as the ones by PIANKA, being also underestimated in comparison to ARNOLD'S data set. The measurements of the forelimbs with (ARNOLD) and without girdles (PIANKA) are here defined as anterior appendage length and abbreviated as AAL. The measurements of the hindlimbs with (ARNOLD) and without girdles (PIANKA) are accordingly defined as posterior appendage length and abbreviated PAL.

In order to evaluate the crural indices of the Messel Lacertilia, the data set published by ARNOLD (1998) is used in an actuopaleontological context and extended by data from PIANKA (1986). Value ranges for climbing and ground dwelling extant lizards are compared to those of the Messel specimens.

Caudal vertebrae length were measured by using callipers in the extant species *Varanus prasinus* and *Varanus salvadorii* and compared to the measurements taken from the designated holotype, the only specimen with a complete tail.

To further investigate the morphology of the terminal phalanges, the manus and pes of some extant lizards were x-rayed: The ground dwelling lizards *Lacerta agilis* and *Sceloporus magister* and the arboreal lizards *Corucia zebrata* and *Varanus prasinus*. The tube voltage was 50 kV with an exposure time of 1 to 1:15 minutes.

3.3 Results

3.3.1 Limb span proportions

Fig. 58 corresponds to the bivariate plot in ARNOLD (1998: Fig. 3) with the addition of selected highly specialised species from PIANKA (1986). The values obtained for the different specimens of the new genus and species, *Geiseltaliellus longicaudus* and *Eolacerta robusta* from the Messel Pit as well as the extant specimens of *Varanus prasinus* and *Corucia zebrata* were included. A summary of the morphometric data is given in Tab. 7.

The data sets including ARNOLD (1998) and PIANKA (1986) match quite well, although slightly different measurements were used. Obviously, the girdle width measurement which is neglected in the data set of PIANKA (1986) has no significant effect in the formation of the ratios and causes no dramatic shifts of the value ranges. Consequently, the hints which can be gained for the mode of life of the animals in question are hardly biased in any direction.

In the diagram (Fig. 58), ARNOLD's regular climbers form a cluster which is completely situated within the polygon of arboreal lizards from PIANKA. The congruence of both author's data is not as high in the group of terrestrial lizards: While the polygon of terrestrial desert lizards (PIANKA) is well separated from the two arboreal polygons, the ground dwelling Lacertidae of ARNOLD's investigation partly fall into the value range of the PIANKA's climbing forms. These species are *Nucras boulangerii*, *Mesalina 'A'*, *Psammodromus hispanicus*, *Eremias persica*. Although the data on ground dwellers gathered by ARNOLD on the family Lacertidae show a trend towards higher values in comparison to PIANKA's data from different families, there are large congruences of the two groups of terrestrial lizards.

The clusters of ground dwelling forms show that the hindlimbs of these forms are relatively longer than the forelimbs and are also longer in comparison to the respective snout-vent-length. In contrast, climbing forms have relatively shorter hindlimbs and the forelimbs increase in length becoming more or less subequal in comparison to the hindlimbs. As can be seen, the new taxon clearly falls into the range of value of arboreal forms as far as the ratio PAL/AAL is concerned. In the ratio PAL/SVL it is placed slightly outside the polygon of arboreal forms, which is caused by relatively long hindlimbs in comparison to the snout-vent-length. Apart from the extant *Chamaeleo dilepis*, which has slightly longer fore- than hindlegs, the new taxon has the highest PAL/AAL values of 0.93 (SMF ME 3516) and 0.97 (WDC-CM-G 122/123) in the sample, as fore- and hindlimbs are almost equal in their length.

Fig. 58: Limb proportions of different Lacertilia including the new genus and species. Based on ARNOLD (1998: Fig. 3) with additional data from other extant lizard families (data from PIANKA 1986) and three fossil lizards from Messel. *Varanus prasinus* and *Corucia zebrata* were measured for the present study. As stated in ARNOLD (1998) for Lacertidae, the kind of structural habitats species occupy largely correlate with limb proportions. According to this diagram, the new taxon clusters close to the arboreal species. AAL = Anterior Appendage Length; PAL = Posterior Appendage Length; SVL = Snout-Vent Length; *G. l.* = *Geiseltaliellus longicaudus*, data taken from ROSSMANN (1992, 2000); *E. r.* = *Eolacerta robusta*, data from MÜLLER, J. (1998).

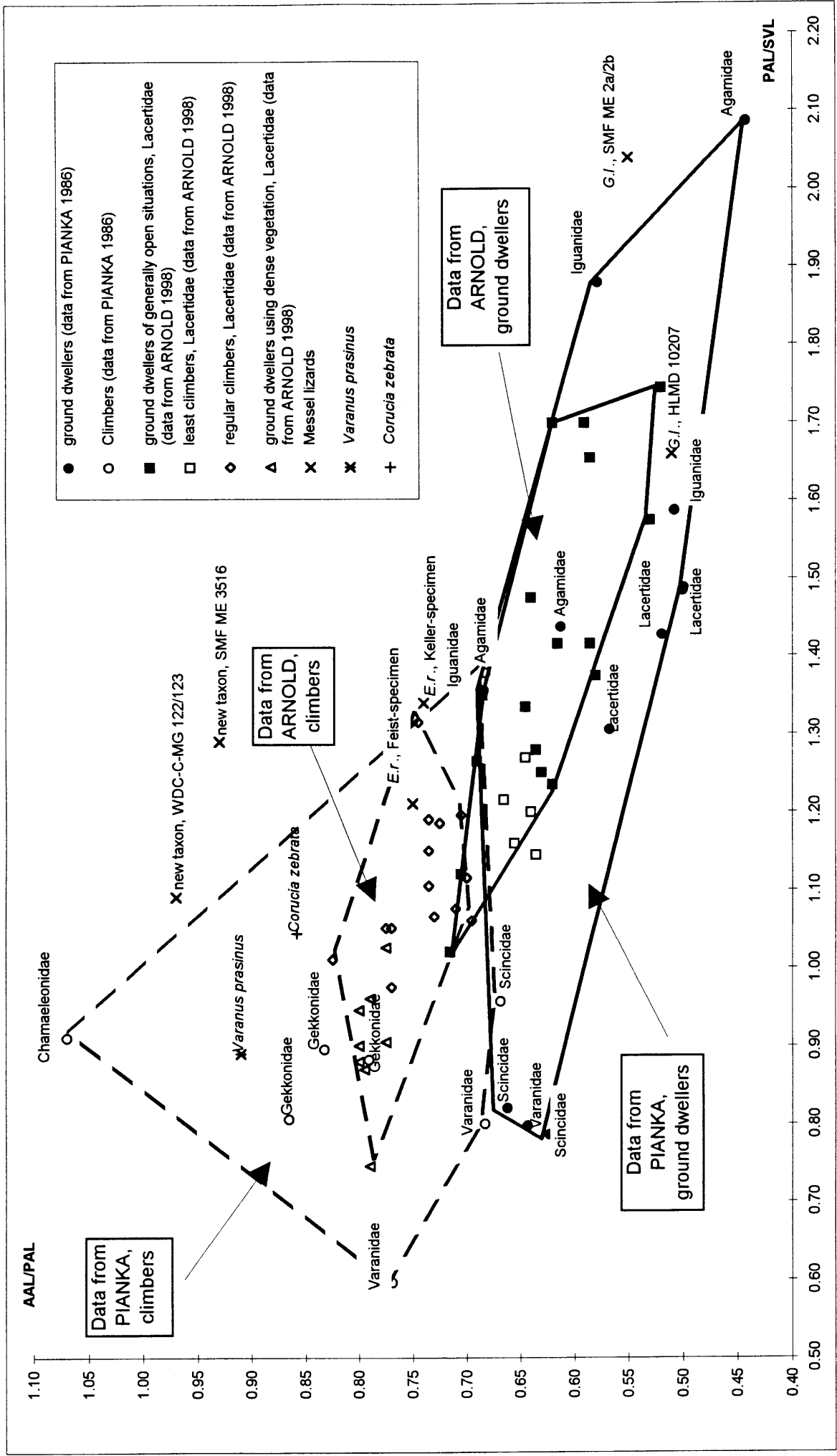


Fig. 58

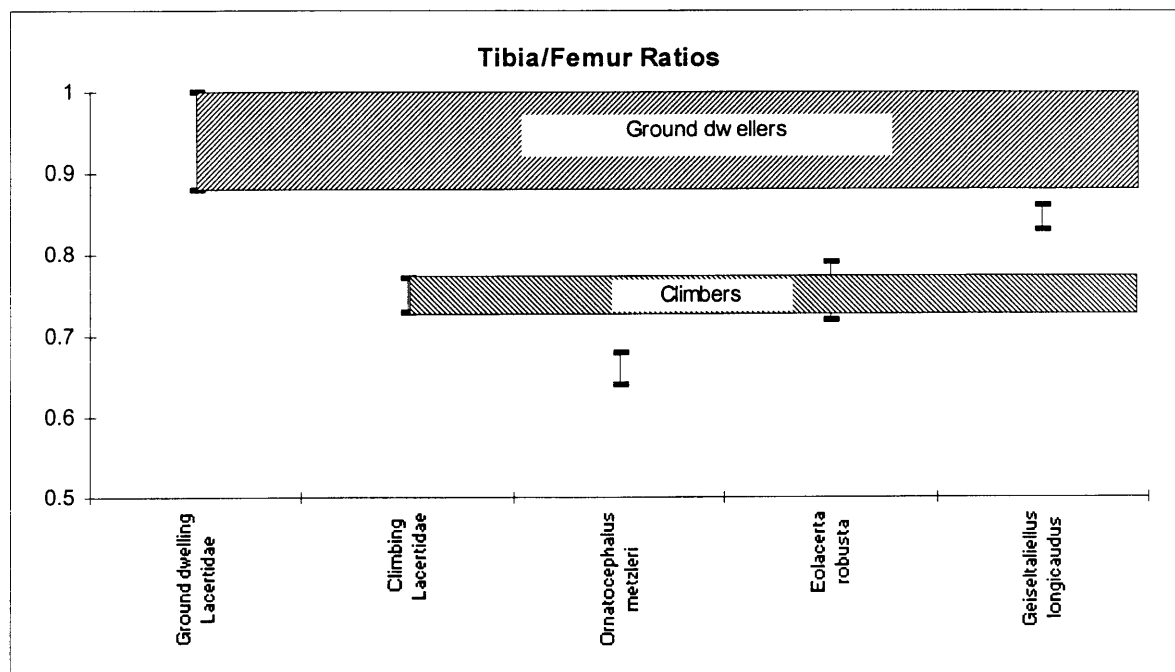
Species	PAL/SV	AAL/PAL	Species	PAL/SV	AAL/PAL
<i>Callisaurus draconoides</i> (IG)	1.88	0.58	<i>Lacerta pater</i> (LA)	1.11	0.74
<i>Crotaphytus wislizeni</i> (IG)	1.59	0.51	<i>Lacerta perspicillata</i> (LA)	1.07	0.73
<i>Sceloporus magister</i> (IG)	1.36	0.68	<i>Lacerta trilineata</i> (LA)	1.20	0.64
<i>Agama hispida</i> (AG)	1.38	0.68	<i>Lacerta viridis</i> (LA)	1.06	0.70
<i>Ctenophorus clayi</i> (AG)	1.44	0.61	<i>Lacerta vivipara</i> (LA)	0.90	0.80
<i>Ctenophorus fordi</i> (AG)	2.09	0.44	<i>Latastia longicaudata</i> (LA)	1.24	0.62
<i>Chamaeleo dilepis</i> (CH)	0.91	1.07	<i>Meroles anchietae</i> (LA)	1.70	0.62
<i>Diplodactylus ciliaris</i> (GE)	0.88	0.79	<i>Meroles ctenodactylus</i> (LA)	1.70	0.59
<i>Diplodactylus elderi</i> (GE)	0.81	0.87	<i>Meroles reticulatus</i> (LA)	1.66	0.59
<i>Pachydactylus rugosus</i> (GE)	0.90	0.83	<i>Mesalina 'A', SW Arabia</i> (LA)	1.12	0.71
<i>Ctenotus helenae</i> (SC)	0.79	0.62	<i>Mesalina balfouri</i> (LA)	1.28	0.64
<i>Ctenotus pantherinus</i> (SC)	0.82	0.66	<i>Mesalina ercolini</i> (LA)	0.96	0.79
<i>Ctenotus piankai</i> (SC)	0.96	0.67	<i>Nucras boulengeri</i> (LA)	1.02	0.72
<i>Eremias lugubris</i> (LA)	1.49	0.50	<i>Nucras lalandei</i> (LA)	0.75	0.79
<i>Eremias lugubris</i> (LA)	1.49	0.50	<i>Ophisops e.schlueteri</i> (LA)	1.42	0.62
<i>Ichnotropis squamulosa</i> (LA)	1.31	0.57	<i>Pedioplanis lineocellata</i> (LA)	1.48	0.64
<i>Meroles suborbitalis</i> (LA)	1.43	0.52	<i>Philochortus intermedius</i> (LA)	1.25	0.63
<i>Cnemidophorus tigris</i> (TE)	1.49	0.50	<i>Podacris hispanica</i> (LA)	1.12	0.70
<i>Varanus eremius</i> (VA)	0.80	0.64	<i>Podacris muralis</i> (LA)	1.08	0.71
<i>Varanus gilleni</i> (VA)	0.60	0.77	<i>Podacris peloponnesiaca</i> (LA)	1.15	0.64
<i>Varanus tristis</i> (VA)	0.80	0.68	<i>Podacris s. campestris</i> (LA)	1.16	0.66
<i>Acanthodactylus schimdti</i> (LA)	1.38	0.58	<i>Poromera fordi</i> (LA)	1.32	0.75
<i>Acanthodactylus scutellatus</i> (LA)	1.42	0.59	<i>Psammodromus algirus</i> (LA)	1.27	0.65
<i>Adolfus alleni</i> (LA)	0.91	0.78	<i>Psammodromus hispanicus</i> (LA)	1.27	0.69
<i>Algyroides nigropunctatus</i> (LA)	1.19	0.73	<i>Pseuderemias mucronata</i> (LA)	1.75	0.52
<i>Eremias persica</i> (LA)	1.35	0.69	<i>Takydromus amurensis</i> (LA)	1.03	0.78
<i>Gastropholis echinata</i> (LA)	1.05	0.77	<i>Takydromus septentrionalis</i> (LA)	1.05	0.78
<i>Gastropholis vittata</i> (LA)	0.98	0.77	<i>Tropidosaura montana</i> (LA)	0.88	0.80
<i>Heliobolus lugubris</i> (LA)	1.58	0.53	Gen. et spec. nov. (WDC-C-MG 122/123)	1.09	0.97
<i>Holaspis guentheri</i> (LA)	1.01	0.83	Gen. et spec. nov. (SMF_ME 3516)	1.29	0.93
<i>Ichnotropis capensis</i> (LA)	1.34	0.65	<i>G. l.</i> (HLMD 10207)	1.66	0.51
<i>Lacerta agilis bosnica</i> (LA)	0.95	0.80	<i>G. l.</i> (SMF-ME 2a/2b)	2.04	0.55
<i>Lacerta andreanskyi</i> (LA)	0.87	0.80	<i>E. r.</i> (Feist-specimen)	1.21	0.75
<i>Lacerta bedriagae</i> (LA)	1.20	0.71	<i>E. r.</i> (Keller-specimen)	1.34	0.74
<i>Lacerta jayakari</i> (LA)	1.19	0.74	<i>Corucia zebrata</i> (SC)	1.04	0.86
<i>Lacerta laevis</i> (LA)	1.22	0.67	<i>Varanus prasinus</i> (VA)	0.89	0.91
<i>Lacerta oxycephala</i> (LA)	1.15	0.74			

Tab. 7: Limb proportions of lizards from various families with different modes of life. 1. section: Data from PIANKA (1986); 2. and 3. section: Data from ARNOLD (1998); 4. section: Data from the new taxon, *Geiseltaliellus longicaudus* (*G. l.*, data taken from ROSSMANN 1992, 2000), *Eolacerta robusta* (*E. r.*, data taken from MÜLLER, J. 1998), *Varanus prasinus* and *Corucia zebrata* (own measurements). AAL = Anterior appendage length; PAL = Posterior appendage length; SVL = Snout-Vent length; IG = "Iguanidae"; AG = Agamidae; CH = Chamaeleonidae; GE = Gekkonidae; SC = Scincidae; LA = Lacertidae; TE = Teiidae; VA = Varanidae.

As expected, the fossil *Geiseltaliellus longicaudus* with its long hindlegs falls into the ground dwelling cluster, whereas the generalised *Eolacerta robusta* falls into the arboreal cluster near the least climbers and takes an intermediate position between the new genus and species and *Geiseltaliellus longicaudus*. It is striking that the fossil specimens consistently show higher values in PAL/SVL than the extant representatives of the sample in their respective microhabitat. These values are not influenced by body size. The larger varanids (*Varanus gilleni*, *Varanus eremius* and *Varanus tristis*) even have much lower PAL/SVL values than e.g. the rather small Agamid *Ctenophorus fordi* which shows the highest value of 2.09.

3.3.2 Proportion of femur and tibia

As mentioned in the introduction, the crural index (= ratio of tibia length/femur length) is low in climbing lacertids and high in entirely ground dwelling forms (ARNOLD 1998). This is caused by a comparatively longer tibia in ground dwellers. Fig. 59 shows that the arboreal and terrestrial value ranges of this ratio are well separated from one another. The same index is particularly low in the two measured specimens of the new genus and species, even lower than in extant Lacertidae. The values of *Eolacerta robusta* (MÜLLER, J. 1998), presumably a generalised basal scincoid, and *Geiseltaliellus longicaudus* (ROSSMANN 1992, 2000) which was described as a cursorial and facultatively bipedal Basiliscine („Iguanidae“), show an interesting distribution in comparison to extant Lacertidae and especially relative to the other fossil taxa: One specimen of *Eolacerta robusta* produces a value which is situated slightly below the range of extant climbing Lacertidae, while the other specimen of the same species ranges between climbers and ground dwellers among this extant family. The values of the two specimens of *Geiseltaliellus longicaudus* are situated between the ground dwelling and climbing value ranges formed by the extant representatives of the family Lacertidae, showing more affinities to the range of ground dwellers.



<i>Specimen</i>	<i>Femur length [mm]</i>	<i>Tibia length [mm]</i>	<i>Ratio T/F</i>
<i>Geiseltaliellus longicaudus</i>			
HLMD 10207	22	19	0.86
SMF ME 2a+b	23	19	0.83
<i>Eolacerta robusta</i>			
Feist specimen	57	45	0.79
Keller specimen	58	42	0.72
Gen. et spec. nov.			
SMF ME 3516	30.5	19.5	0.64
WDC-C-MG 122/123	43	27.5	0.64

Fig. 59 (previous page): Ranges of femur and tibia proportions in extant ground dwelling and climbing Lacertidae (data from ARNOLD 1998), in the new taxon, *Geiseltaliellus longicaudus* (data from ROSSMANN 1992, 2000) and *Eolacerta robusta* (data from MÜLLER, J. 1998). According to ARNOLD (1998) the values are low in climbing lacertids and high in entirely ground dwelling forms. Within the Messel lizards the ground dwelling, cursorial *Geiseltaliellus longicaudus* shows the highest ratio, whereas the new taxon shows the lowest value. The generalised *Eolacerta robusta* takes an intermediate position. The generally lower values of these lizards are probably caused by their different taxonomic identity. These results also indicate a climbing mode of life and arboreality for the new taxon, while the generalised ecology of *Eolacerta robusta* and the cursorial adaptation of *Geiseltaliellus longicaudus* is supported. Below, table showing the ratios of Tibia/Femur in the different specimens.

3.3.3 Length of tail vertebrae

Fig. 60 shows the logarithmic value of caudal vertebrae lengths in the new genus and species, *Varanus prasinus*, *V. salvadorii*, *V. salvator*, *V. rudicollis* and *V. bengalensis* depending on the respective vertebral position. The logarithms were calculated in order to make the measurements comparable. Logarithmic values are commonly used for comparing measurements from animals with large size differences (e.g. HOFFSTETTER & GAYRARD 1964 and GASC 1974). An alternative method is the definition of indices, but it is difficult to define an adequate size index for squamate vertebrae (SCHAAL et al. submitted). Additionally, statistical noise is reduced with the logarithmic method while it can be enhanced using indices (JOHNSON 1955). The graph of the new species shows more variation than the others, because the measuring of vertebrae is more difficult due to the problem of identifying vertebral lengths in the fossil material. Nevertheless a clear trend is recognisable: The comparative measurements show that the graph of the new taxon has the same characteristics as the one of *Varanus prasinus* (arboreal, prehensile tail) in exhibiting a strong size decrease in the distal tail portion. In contrast, the graphs of all other specimens – the non-prehensile tailed *Varanus salvator*, *Varanus rudicollis* *Varanus bengalensis*, as well as the one of *Varanus salvadorii* – fade out gently in their distal portions, showing only a slight decrease in size.

Fig. 60 (following page): Length of tail vertebrae (logarithmic plot) in the extant species *Varanus prasinus*, *V. salvadorii* (both with prehensile tails), *V. salvator*, *V. bengalensis* and *V. rudicollis* (all without prehensile tails) in comparison to the new taxon. In their distal tail portions, the vertebrae of *V. prasinus* and the new taxon show a stronger decrease in length than those of all other specimens including *V. salvadorii*. Black: Prehensile tails; Light grey: Non-prehensile tails; Dark Grey: New taxon.

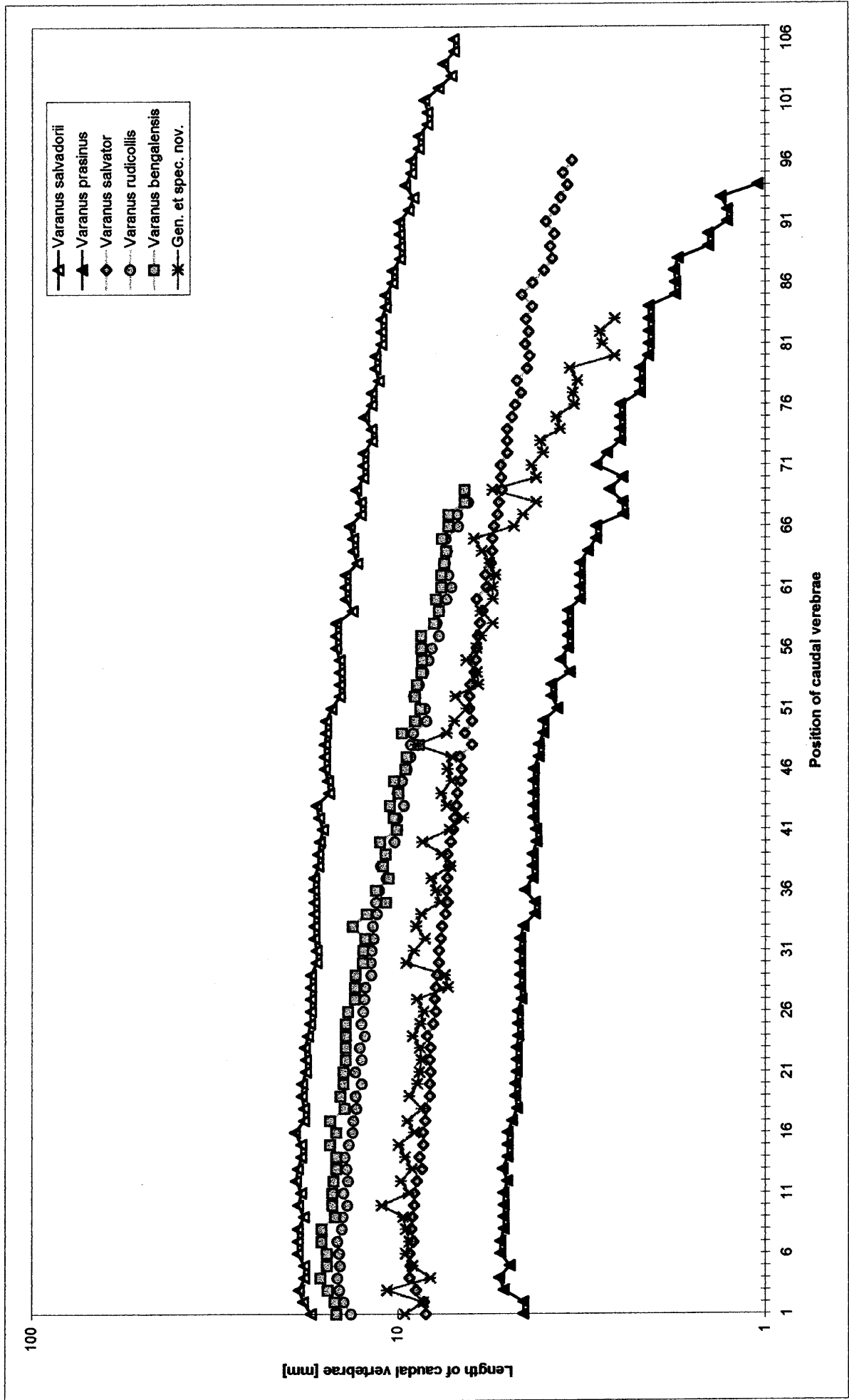


Fig. 60

3.3.4 Structure of manus and pes

ARNOLD (1998: Tabs. 2 and 3) lists characteristics of manus and pes in ground dwelling and climbing Lacertidae. Most of these characters are not determinable in the new genus and species, such as the cross section of and the articulation within digits or their flexibility. However, the following characteristics are typical for climbing Lacertidae and are also present in the new taxon:

- Digit 4 is longest in the manus and the long size of digit 5 in the pes (it is short and often miniaturised in ground dwelling lacertids)
- the shape of the phalanges being slender.

On the other hand, there also is a character of the pes in the new species which is congruent with ground dwelling forms, such as the digit and metatarsal 4 markedly longer than digit and metatarsal 3. Analysing the given characters in a functional context, it most probably is advantageous to possess long digits as a climbing form. This allows a more effective grip rather than a short or miniaturised 5th digit as it is found in ground dwellers. The new taxon has rather large feet which is advantageous for gripping, reaching and pulling (HILDEBRAND 1988).

Comparing the terminal phalanges of manus and pes of the new genus and species to Lacertidae with different locomotory types (Fig. 61), it becomes clear those of the new species show the characteristic “climbing type” with a deeply recurved shape (Fig. 61D+G) as described in ARNOLD (1998). In contrast, ground dwelling lizards have gently curved, long and shallow phalanges. This becomes also obvious when comparing the terminal phalanges of other ground dwelling and climbing lizards: The ground dwelling lizards *Lacerta agilis* (Lacertidae) and *Sceloporus magister* (“Iguanidae”) have somewhat straight, shallow terminal phalanges, whereas the arboreal and scansorial lizards *Corucia zebrata* and *Varanus prasinus* have strongly recurved and robust phalanges (Fig. 62). Similar differences in claw morphology can be found in tree-climbing mammals and birds. These animals tend to have sharp claws that are abruptly recurved at the tip in contrast to their close terrestrial relatives with more blunt, gently curved claws (POCOCK 1922; PETERKA 1937, BOCK & MILLER 1959, CARTMILL 1985).

Fig. 61: Manus (A-D) and pes (E-G) in different locomotory types of Lacertidae (from ARNOLD 1998) compared to the new genus and species (brought approximately to same size). A and E: *Acanthodactylus erythrurus*, ground dwelling; B and F: *Lacerta oxycephala*, rock climbing; C: *Holaspis guentheri*, climbing in vegetation matrix; D and G: New taxon.

Fig. 62: Radiographs of manus and pes from ground dwelling and climbing lizards. A+B: *Lacerta agilis* (ground dwelling). C+D: *Sceloporus magister* (ground dwelling). E+F: *Corucia zebrata* (climbing). G+H: *Varanus prasinus* (climbing). A,C,G and E: Manus. B, D, F and H: Pes. A-D: Gently curved, shallow terminal phalanges of ground dwelling lizards. E-H: Deeply recurved terminal phalanges of climbing lizards with large bases.

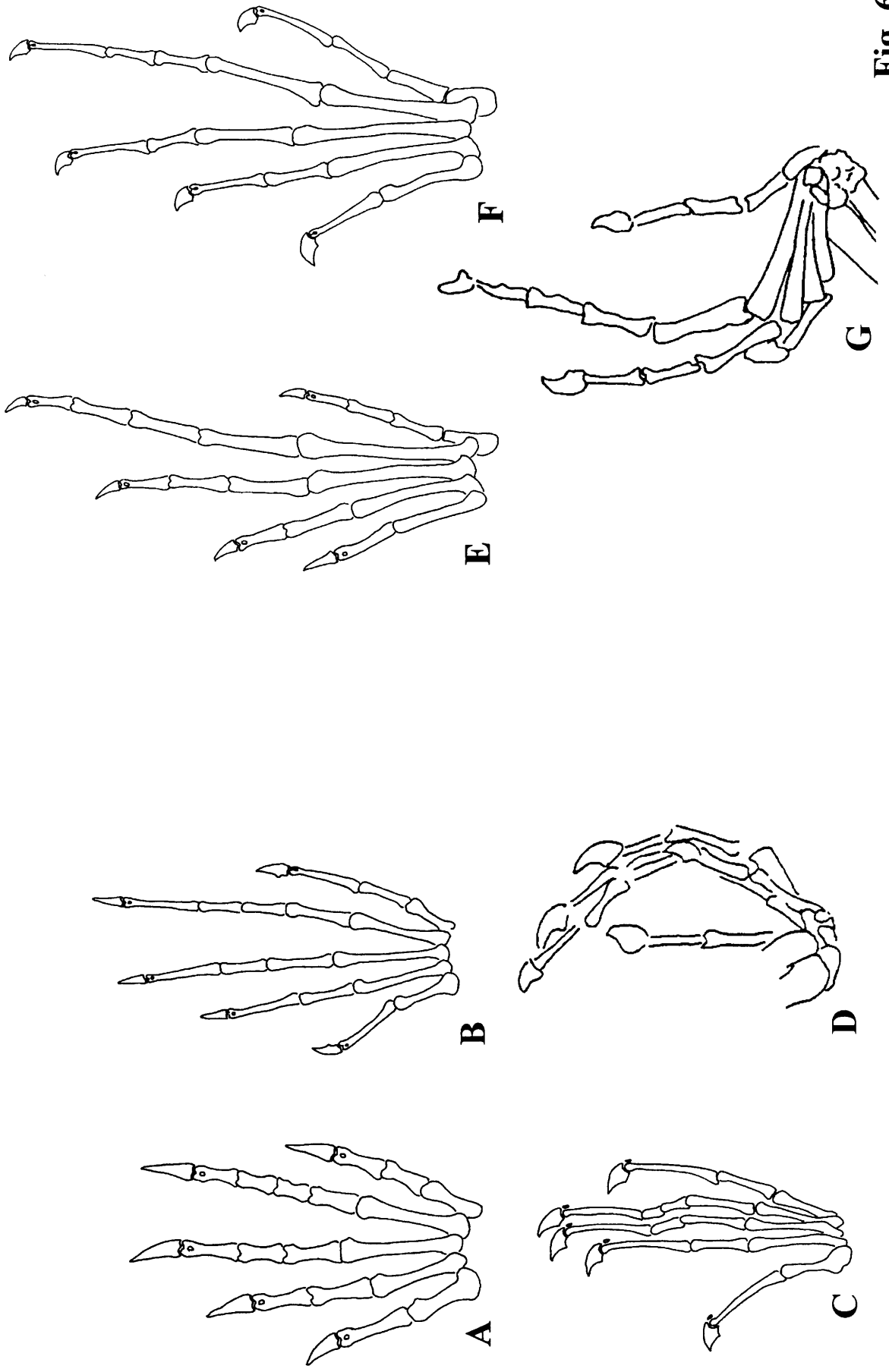


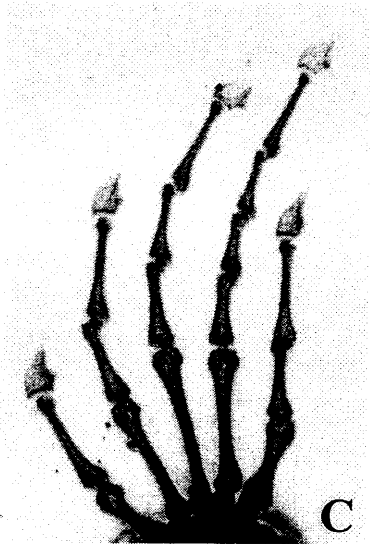
Fig. 61



A



B



C



D



E



F



G



H

Fig. 62

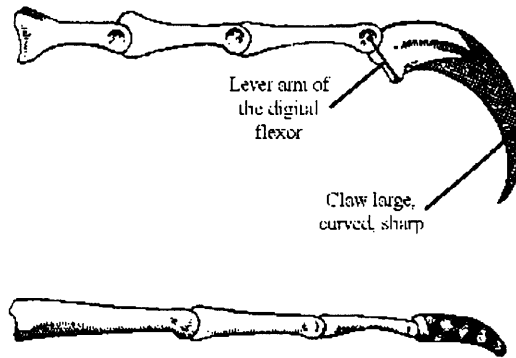


Fig. 63: Claw of a climbing (above) and nonclimbing (below) bird (from HILDEBRAND 1988).

HILDEBRAND (1988) shows that the basis of the terminal phalanx acts as a lever arm for the digital flexor. In looking at a claw of a climbing and non-climbing bird this correlation becomes apparent (Fig. 63). A similar comparison made with extant lizards x-rayed in the course of this study also supports this observation. The new taxon also shows a large base, compared to the terrestrial lizards.

Furthermore, the phalanges of the new genus and species are rather slender. Being compressed and somewhat flattened, they appear even more robust and thicker than they probably were in the living animal. Although ARNOLD (1998) studied these variations in manus and pes mainly within Lacertidae, the same author points out that there are parallel developments in other families such as the Teiidae and Agamidae.

3.4 Discussion

3.4.1 Microhabitat reconstruction for the new genus and species

Different actuopaleontological approaches of qualitative and quantitative nature have been taken here to attempt a microhabitat reconstruction for the new genus and species. These approaches strongly suggest an arboreal mode of life for the new fossil taxon described here. The morphometric evidence is taken from the fore- and hindlimb proportions and the ratios between femur and tibia. Qualitative analyses of the tail, manus, pes and claws also hint towards a paleo-econiche in the trees surrounding Eocene Lake Messel.

3.4.1.1 Function of the tail

The tail length yields ambiguous evidence for the mode of life. A long tail is not only advantageous for balance in climbers but also in cursorial ground dwelling forms when running on hindlimbs. Consequently, from the study of literature it can be concluded that long tails are not necessarily correlated with climbing, whereas prehensile tails are. Therefore, hints of prehensility must be found for an arboreal mode of life reconstruction in fossil lacertilians. Prehensile tails in extant arboreal lizards can either

be short as in Chamaeleonidae and the Solomon tree skink *Corucia zebrata* or long as in the Emerald monitors *Varanus beccarii* (pers. obs.) and *Varanus prasinus* (TRUTNAU 1986) as well as in the scincid *Sphenomorphus flaviceps* (OBST et al. 1988).

The ventrally curled up distal portion of the tail in SMF ME 3516 clearly hints towards tail prehensility in the living animal. Other fossils from the Messel locality with presumed prehensile tails show the same mode of preservation, like the opossum *Peradectes* sp. (KOENIGSWALD & STORCH 1992), whereas the cursorial lizard *Geiseltaliellus longicaudus* and the mammal *Leptictidium nasutum* (KOENIGSWALD, STORCH & RICHTER 1992) with straight balancing tails show also a straight embedded tail without any curvature. It has long been known that the Messel fossils were embedded in a relaxed position, mostly reflecting some sort of embryonic posture. It can consequently be assumed that the distal tail curvature which is seen on the epoxy resin plate was also typical for the tail in a relaxing position. In prehensile tails the flexor tendons of the „hook“ are short enough to passively prevent the „hook“ from opening up (HILDEBRAND 1988).

The characteristic, abrupt length decrease of the distal caudal vertebrae in the prehensile tail of *Varanus prasinus* and the new genus and species in comparison to the non-prehensile tailed *Varanus salvator*, *V. rudicollis* and *V. bengalensis* also hints towards the presence of a prehensile tail in the new taxon. One would expect that a gripping organ shows a strong size reduction of vertebrae distally, because short elements are more flexible and mobile, so it can grip on smaller branches. It therefore is here concluded that the new taxon most probably had a prehensile tail comparable to the one of *Varanus prasinus*. However, *Varanus salvadorii* who can also use its tail as a prehensile organ, does not show such an abrupt size reduction. The reason could be that *Varanus salvadorii* has not such a specialised prehensile tail as does *Varanus prasinus*, e.g. there are no specialised scales on the ventral side of the tail as in *Varanus prasinus* (KLEMMER pers. comm.). Furthermore *Varanus salvadorii* also uses its tail for whipping. Its tail seems to be a more generalised organ. Of course, such a hypothesis should be tested on a broader data base.

The presence of the V-shaped haemal arches in the new taxon (starting from about the 45th tail vertebra) is not crucial for the reconstruction of a prehensile tail, as haemal arches with the same morphology are also present in non-prehensile tailed lizards, as in the prickly tail iguanid *Hoplocercus* sp. or the agamid bearded dragon *Amphibolurus* (pers. obs.).

Basically two types of prehensile tails can be distinguished in extant Lacertilia and the question arises which type the new genus and species possessed. The first type is the one present in Chamaeleons, where the tail is capable of bending primarily in the dorsoventral plane because of the arrangement of the zygapophyses (ALI 1948, ZIPPEL & GLOR 1999). It is only the distalmost portion of the tail that is coiled around the grasped object, the rest of the tail remaining straight and rigid. The second type is represented by *Corucia zebrata*, which uses its entire tail in gripping branches or perches, the distalmost tip contributing no more than the rest. In contrast to the first type, it is not restricted to bending in a single plane and can even encompass branches helically (ZIPPEL & GLOR 1999). As in all specimens of the new taxon, no soft tissues are preserved and the morphology of the zygapophyses cannot be determined. Therefore, the muscle system controlling the tail cannot be reconstructed. But according to its

ventrally coiled distal portion of the tail it can be better compared to the chamaeleon tail, where bending is restricted to the dorso-ventral plane. The presence of a long prehensile tail does not mean that this organ is exclusively used for gripping. By curling the distal end of it, a certain amount of mass is concentrated at the distal end of the body. As a consequence, a movement of this mass – together with the length of the tail – can be used to counterbalance the body weight in the tree-dimensional matrix. This movement with a concentrated mass appears to be more effective than a movement with an uncurled, long tail. The latter would result in a whipping effect of the distal portion, being more or less uncontrollable with a certain tail length. By curling up the distal tail portion, it is thus functionally shortened. At the same time of course, the tail was certainly also used for gripping. However, gripping with a long tail has to be distinguished from gripping with a short tail as in *Corucia zebrata*. In this latter case, the animal can hold its entire body weight with its strong, short tail (Fig. 64). The long tail of the new genus and species could secure support by grabbing branches, but it probably was too fragile to hold the entire body weight. The habitus of the tail is best comparable to the extant arboreal Emerald monitors *Varanus prasinus* and *Varanus beccarii*, who have long prehensile tails (2x snout-vent length). Its distal part is also curled up ventrally in resting position (pers. obs., Fig. 64C).

Summing up the qualitative and quantitative evidence, we can assume that the new genus and species most probably possessed a prehensile tail which characteristically is long, strong, sensitive and curled at the end. It is most probable that the tail served both purposes, balance and gripping. The long tail could secure support by grabbing branches, but probably was too fragile to hold its entire body weight.

3.4.1.2 *Limb proportions and habitat*

The intersection of the climbing polygon of PIANKA (1986) with the ground dwelling polygon of ARNOLD (1998) shows that the mode of life is often not restricted to a certain habitat (Fig. 58). Although species might live in a special econiche, they might also be able to maintain their position in another habitat. But a different trend of climbing and ground dwelling lizards is recognisable. And it makes sense for a climbing lizard to have rather short subequal limbs instead of large impeding hindlimbs. When a relatively large arboreal animal, like the new genus and species, is walking along a horizontal branch it is advantageous to have relatively short limbs to keep “the body’s centre of mass close to the support” to prevent “to topple to one side or the other” (CARTMILL 1985). Furthermore this species is rather large and according to GARLAND & LOSOS (1994) larger species use less open habitats and have relatively shorter legs.

ARNOLD (1998) points out that the most characteristic value for the determination of the microhabitat is the proportion of forelimb/hindlimb length. In this value, the new genus and species clearly clusters with arboreal forms and this result is congruent with other qualitative and quantitative features of the new taxon which all strongly hint towards arboreality.

Fig. 64 (following page): A-C: Prehensile tailed lizards. A: The skink *Corucia zebrata* can hold the entire body weight with its strong, short tail (from HONEGGER 1975 in STARCK 1979). B: The Emerald monitor *Varanus beccarii* with its very long prehensile tail (KIRSCHNER et al. 1996). C: The aguid *Abronia oaxacae* (from CAMPBELL & FROST 1993).

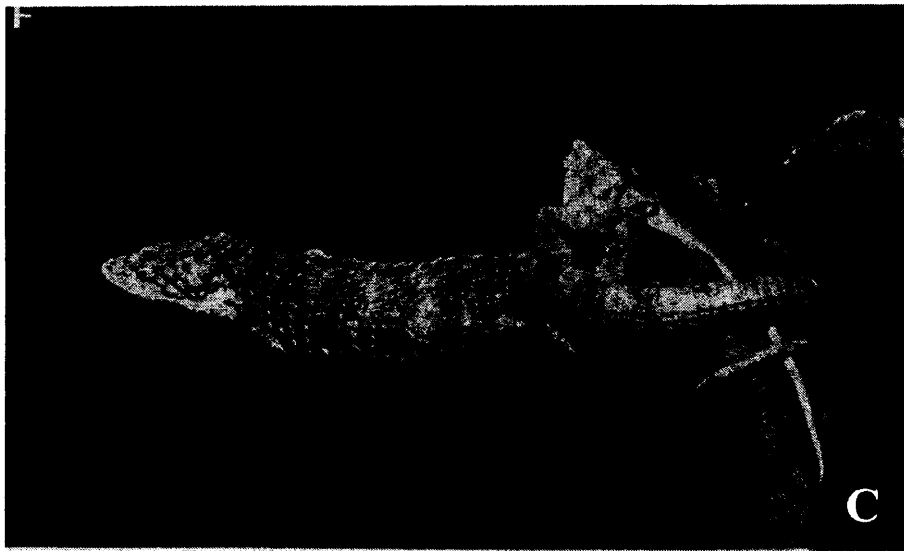
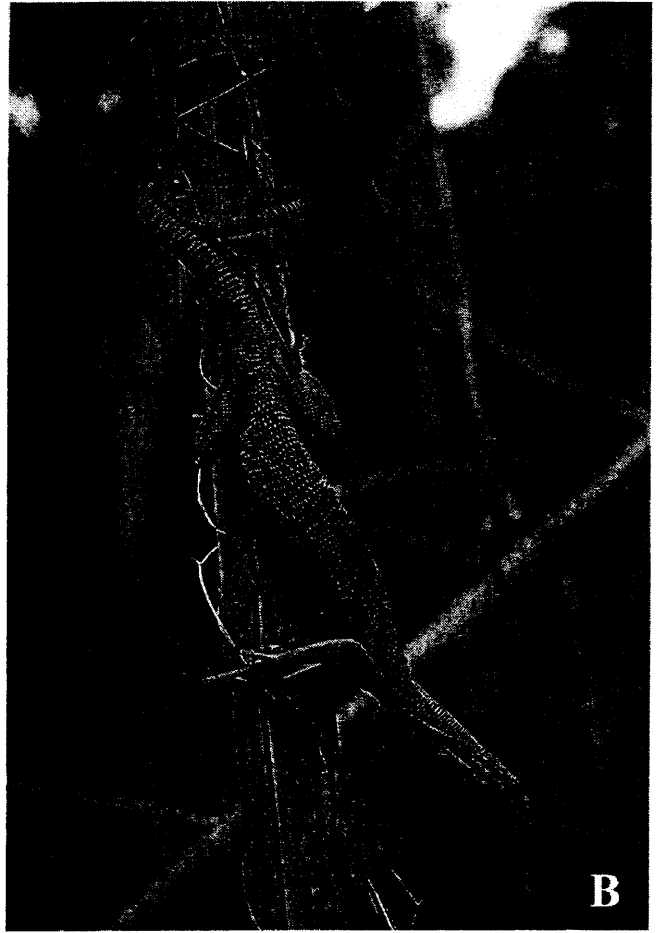


Fig. 64

Relatively similar front- and hindlimb length can also have completely different reasons than arboreality. In desert habitats, e.g. it is crucial for the animal in question to get the body far off the ground in order to avoid extreme heating. This can cause equal fore- and hindlimb lengths, as well (ARNOLD 1984, GREER 1989). But such a habitat can safely be excluded for the Eocene Messel environment, so that arboreality of the new genus and species represents the by far most probable ecological interpretation.

3.4.1.3 Advantages of a relatively short tibia

The high ratios of tibia/femur are an adaptation of the ground dwelling forms according to ARNOLD (1998). As a consequence, for climbing forms it is obviously advantageous that the tibia is considerably shorter. The following functional discussion is an attempt to interpret this result: The shortening of the distal element (tibia) could increase the mobility of the range of the manus in order to find a new grip in dense vegetation below the body. The length of the proximal element (femur) can easily be compensated by different degrees of inclination in the knee joint. In contrast, a long distal element would initially define a rather large radius in which the manus can find a grip. In contrast, long distal elements are characteristic for fast ground runners of all kinds, the best example being horses.

All of the values calculated from the three fossil specimens are lower than the value ranges of extant Lacertidae. This could be caused by the different taxonomic identity of the fossils, as none of them is a representative of the family Lacertidae, which is the basis for the comparative extant value ranges. In any case, these results indicate a climbing mode of life and arboreality for the new genus and species, while the generalised ecology of *Eolacerta robusta* and the cursorial adaptation of *Geiseltaliellus longicaudus* is supported.

3.4.1.4 Tall neural spines

The neural spines of the dorsal vertebrae are tall, straight and axe-shaped over the whole length of the trunk, comparable to the morphology in the highly arboreal *Chamaeleo* (HOFFSTETTER & GASC 1969: Fig. 40). Tall neural spines are important for a strong epaxial trunk musculature (especially for m. transversospinalis and m. longissimus dorsi). This could generally be advantageous in arboreal species for trunk stabilisation. A large, heavy head as in the new genus and species requires tall neural spines in the cervical vertebrae for a broad muscle insertion area. In mammals tall neural spines are present where they form insertion areas for muscles and tendons in species with large heads (STARCK 1979). It can safely be assumed that – as in mammals – the large head of the new species is held by such a muscle-tendon system. To my knowledge, no detailed investigations were undertaken concerning the functional morphology of neural spines in Lacertilia. Starting such an investigation would imply a huge analysis of extant representatives and therefore is beyond the scope of the present study. STARCK (1979) further describes the correlation between neural spine orientations in mammals: If the neural spine has an inclined orientation, a lateral movement is facilitated, while a straight orientation improves a dorsoventral movement. This functional context is not transferred to the neural spine morphology of the new taxon, because muscles and their insertion areas cannot be homologized between mammals and Lacertilia without a thorough analysis.

3.4.1.5 *Moving in a three-dimensional habitat*

There have to be adaptations to move in a discontinuous three-dimensional habitat with no flat or level surfaces to stand on. Consequently, friction must be increased.

According to CARTMILL (1985) there are two ways to generate a vertical force against the gravitational force:

- by interlocking the surface of the animal with that of its support
- by developing bonds between the animal and its support that are too strong to break by the animals weight.

Obviously, the new genus and species developed both mechanisms. The first mechanism is exemplified by using its recurved claws to climb and cling to the surface by interlocking with it. With the help of its prehensile tail, an additional bond between itself and its support was generated. It is also essential to keep balance in such a habitat. The long tail might have been important as a counterbalance to the large head or vice versa.

In this context, the question arises whether the new taxon was able to climb downwards with its head first, as do most arboreal vertebrates. One advantage of this ability is that dangers in the path can easily be spotted. CARTMILL (1985) describes a problem connected with head first downward climbing: The claws tend to point the wrong way and cannot be dug in at the proper angle. In order to solve this problem, the hindlimb is twisted in a way that the foot can be applied to the support with the digits pointing laterally caudad. For lizards with a more or less primitive tetrapod locomotor posture, this orientation presents no great problem (CARTMILL 1985). Also the long prehensile tail is most important when climbing downwards, as a support behind when crossing from one branch to the next which may break or prove unreachable.

As stated in the description, the new genus and species has completely lost its body osteoderms with exception of the dorsal aspect of the head. LANG (1991) proposes that presence or absence of body osteoderms does not reflect phylogeny but rather ecomorphological adaptations. He further states "that cordylids which lack dorsal and ventral body osteoderms are rather flattened crevice ecomorphs." This is not considered for new fossil taxon, since – as stated above – it was most probably arboreal. GAUTHIER (1982) mentions the gerrhonotine long-limbed and prehensile-tailed arboreal anguid *Abronia taeniata*: "Its skull is overlain by a moderately thick and deeply sculptured osteodermal crust; however its body osteoderms are much reduced owing to the need for increased mobility in a three-dimensional habitat". Therefore it is highly probable that the arboreal mode of life is the reason for the lacking body osteoderms in the new taxon. This reduction could well reflect an adaptation to an arboreal mode of life which contributes to a higher mobility in a three-dimensional habitat.

Different actuopaleontological approaches of qualitative and quantitative nature have been taken here to attempt a microhabitat reconstruction for the new taxon. These approaches strongly suggest an arboreal mode of life for the new taxon described here. The morphometric evidence is taken from the fore- and hindlimb proportions and the ratios between femur and tibia. The prehensile tail, equally long limbs, strongly recurved terminal phalanges and lacking osteoderms hint towards a paleo-ecniche in the trees surrounding Eocene Lake Messel.

4 Nutrition

4.1 Introduction

The aim of this chapter is to gain information for reconstructing the diet of the new genus and species. The extraordinary preservation conditions of Messel vertebrates allow the analysis of food remains, found here in three specimens. Additionally, the tooth morphology and the possibilities of cranial kinesis are compared to these results. The body weight is estimated based on literature data and own measurements in the scincid *Corucia zebrata*.

4.1.1 Nutritional remains from Messel vertebrates

A number of tetrapod fossils from the Messel Pit Fossil Site show intestinal remains. Predominantly mammals were subject to stomach content analyses and preserved food remains led to the identification of a presumably preferred diet by these animals: The primitive insectivores *Macrocranium tupaiodon*, *Pholidocercus hassiacus*, *Leptictidium nasutum* and *Buxolestes piscator* (MAIER, RICHTER & STORCH 1986, RICHTER 1987, KOENIGSWALD, STORCH & RICHTER 1992a, STORCH & RICHTER 1994), the bats *Palaeochiropteryx tupaiodon*, *Hassianycteris magna* and *Archaeonycteris trigonodon* (RICHTER & STORCH 1980, RICHTER 1987, HABERSETZER, RICHTER & STORCH 1992, RICHTER 1993, HABERSETZER, RICHTER & STORCH 1994), small primitive horses *Propalaeotherium parvulum* and *Propalaeotherium hassiacum* (RICHTER 1987, FRANZEN 1992b), even-toed ungulates *Messelobunodon schaeferi* and *Massilabune martini* (SCHAARSCHIDT in TOBIEN 1980, RICHTER 1981, RICHTER 1987, FRANZEN & RICHTER 1992), the large rodent *Ailuravus macrurus* (RICHTER 1987, KOENIGSWALD, STORCH & RICHTER 1992b), the ant-eater *Eurotamandua joresi* (RICHTER 1987, STORCH & RICHTER 1992a) and the pangolin *Eomanis waldi* (RICHTER 1987, STORCH & RICHTER 1992b). An anuran was found with a vertebrate prey as stomach content (KELLER & WUTTKE 1997). Intestinal contents of reptiles were hardly studied to date, but are subject to current research (BASZIO, RICHTER & WEBER in prep.).

RICHTER (1988) points out that information gained from stomach contents must be interpreted very carefully, as a number of taphonomic biases influence type and abundance of preserved structures: Some kinds of nutritional remains have a better preservation potential than others. Plant fragments are best preserved, because lignin, suberine and cutine are contained in the cell walls making them much more resistant than animal tissues. For this reason, RICHTER (1988) stresses that an omnivorous vertebrate fossil most probably will be classified as a plant-eater, based on the poor preservation potential of zoological tissues in contrast to the mentioned resistant substances in plant tissues.

Another problem is the identification of diagnostic structures in a stomach content. Although plant tissues may be preserved in an astonishing quality (i.e. plant cuticula and parenchymatic cell casts, RICHTER 1988: Pl. 1, Fig. 2 and Pl. 2, Fig. 10), it is difficult to make a taxonomic attribution of these fragments. Only in rare cases, stigmata or epidermal cell patterns are diagnostic for a certain plant group. The same is true for insect cuticulae from stomach contents. Their ultrastructure often is preserved in surprising detail, but only small and compacted cuticular fragments are available due to chewing and compaction by sediment (RICHTER 1988: Pl. 1, Fig. 7). Unfortunately (but

for obvious reasons), insect taxonomy is based on “macro-characters” such as wing venation, which hardly can be expected in stomach contents. Therefore, extensive extant investigations must be undertaken in order to identify ultrastructural insect cuticula characters that hold for a taxonomic group, as done in RICHTER & BASZIO (2001). The taxonomic identification level of prey in question consequently is rather low. The variation of ultrastructural cuticula patterns is very large depending on the body region, but certain basic patterns often can be attributed to families of insects (RICHTER & BASZIO pers. comm.). Although an identification on family level might appear unsatisfactory, the hints for the reconstruction of an paleo-econiche often are sufficient.

4.1.2 Teeth and diet

Tooth morphology is of taxonomical importance. The conical, monocuspid teeth with lingual striations of the new genus and species are of scincoid morphology. But the tooth shape is also related to the nutrition. The basic tooth form of the earliest true reptiles is conical or cylindroconical, a correlation with their carnivorous or piscivorous mode of life (EDMUND 1969).

A large amount of variation can be recorded in a number of different families of extant Lacertilia.

A relation between tooth morphology and diet is clearly present in the „Iguanidae“ (Iguania). This herbivorous family has laterally compressed and blade-like, multicuspid crowns. The multicuspid teeth of those species which take greater amounts of plant material, begin more anteriorly in the tooth row. With increasing herbivory the degree of the lateral compression of the teeth increases. (HOTTON 1955; MONTANUCCI 1968, THROCKMORTON 1976).

Within the family Gerrhosauridae (Scincomorpha), the herbivore species *Angolosaurus scoogi* also possesses polycuspid teeth (LANG 1991). Most representatives of this family have conical teeth. Members of the gerrhosaurid genus *Gerrhosaurus* accept a wide variety of food, including arthropods, fruits and berries, snails, even other reptiles and juvenile mammals. *Tetradactylus* and *Tracheloptychus* (Gerrhosauridae) live on arthropods (BARNARD 1996). Most members of the Scincoidea have conical teeth which are more or less blunt, often with lateral cutting edges. The highly specialised scincid *Corucia zebrata* (strictly arboreal, nocturnal and wholly vegetarian, PARKER 1983) has laterally compressed, more or less triangular multicuspid teeth (pers. obs.). However, a strict correlation between multicuspid teeth and herbivory is not necessarily found in other lizard – esp. scincid – families. For example, the predominantly herbivorous representatives of the family Scincidae *Tiliqua scincoides*, *Tiliqua nigrolutea* and *Trachydosaurus rugosus* (COGGER & ZWEIFEL 1992; TRUTNAU 1986; BECH & KADEN 1990) have conical and monocuspid teeth, with lateral cutting edges (pers. obs.). Other scincids, such as *Chalcides ocellatus* and *Eumeces schneiderii*, are more or less omnivorous (SCHNEIDER 1981, DAREWSKI 1981). The usual food of *Cordylus giganteus* (Cordylidae) consists of arthropods, occasionally vegetation, and small mammals or birds are taken as well.

BORSUK-BIALYNICKA (1983) states that Anguimorphan predators changed their dentition from the closely to the loosely spaced type. Another example of the high variability of tooth morphology within Lacertilia are the teeth of the only poisonous lizards *Heloderma suspectum* and *Heloderma horridum* (Varanoidea) with special grooves for the venom and sharp-edged flanges (EDMUND 1969).

Recently NYDAM et al. (2000) described the dental specialisations of the Late Cretaceous Teiid lizard *Peneteius aquilonius*, which has “mammal-like” molariform teeth. The *upper* and *lower* molariform teeth are distinctly different in shape. Whereas in other Teiidae or „Iguanidae“ with heterodont dentition the different tooth shapes are between *anterior* and *posterior* teeth. The oral food processing of *Peneteius aquilonius* was probably as efficient as in an insectivorous mammal.

4.1.3 Lacertilian cranial kinesis

Cranial kinesis (intracranial mobility) can occur - more or less distinctly - in all tetrapod classes except in mammals. Basically two types of kinesis are recognised: The possible displacement between the dermatocranium and the underlying neurocranium (between supraoccipital and parietal bones) is called **metakinesis**. **Mesokinesis** describes the relative motion between adjacent components of the dermatocranium, in lizards a transverse hinge at the frontoparietal suture. Skulls with meta- and mesokinetic joints are known as **amphikinetic** (VERSLUYS 1912, FRAZZETTA 1962, RIEPPEL 1978a, BRAMBLE & WAKE 1985). The mesokinetic condition seems to be a derived feature within the Lacertilia and is absent in the earliest known lizards (CARROLL 1977, BRAMBLE & WAKE 1985). FRAZZETTA (1962) was the first who offered a detailed biomechanical analysis of cranial kinesis in lizards. This has become the most cited and debated model for the mechanism of skull movement. He recognised five functional units: parietal, muzzle (snout), epipterygoid, the basal and the quadrate unit. The basal unit forms the palatal complex and consists of pterygoid, ectopterygoid, jugal and posterior region of palatine. The muzzle unit is elevated as the mouth opens. This involves forward rotation of the quadrate, protraction of the basal unit to which the quadrate is pinned (pterygoquadrate joint), and upward rotation of the muzzle about the mesokinetic (frontoparietal) hinge. As the jaws close, all intracranial motions are reversed (FRAZZETTA 1983, Fig. 65). This model is supported by several studies. In carnivorous lizards raising and lowering of the muzzle relative to the parietal unit has been reported during feeding (FRAZZETTA 1962, 1983; BOLTT & EWER 1964; RIEPPEL 1978b; BRAMBLE & WAKE 1985). But other studies indicate that in several species of lizards quadrate mobility is independent of mesokinesis (THROCKMORTON & CLARKE 1981, SMITH 1982). In general, however, the quadrate does swing forward as the mouth opens and backward as it closes (BRAMBLE & WAKE 1985). According to FRAZZETTA (1962: 315) an amphikinetic skull is advantageous to seize and maintain prey because upper and lower jaw seize the prey at about the same instant. Mesokinesis allows to manipulate food by moving relative to the lower jaw (FRAZZETTA 1983, BRAMBLE & WAKE 1985, HILDEBRAND 1988).

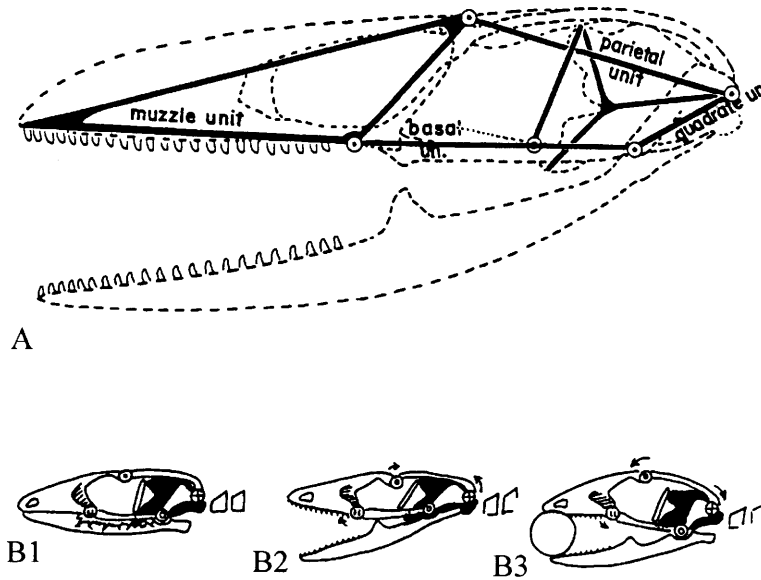


Fig. 65: Skull kinesis. Lateral view of a *Gerrhonotus* skull. A: Diagram showing the functional units in the skull. B1: Skull at rest. B2: Skull protraction. The snout is elevated at the mesokinetic hinge as the mouth opens. B3: Skull retraction. All intracranial motions are reversed (from FRAZZETTA 1983).

Streptostyly is said to be associated with cranial kinesis. The mandible can be moved relative to the upper jaw. Since the loss of the quadratojugal in modern lizards, the quadrate is free and can move anteroposteriorly and – to a lesser extent – mediolaterally with respect to the braincase. Still, the function of streptostyly is not quite clear (BRAMBLE & WAKE 1985). The quadrate rather reduces than increase the gape while swinging anteriorly as the mouth opens (THROCKMORTON 1976; RIEPEL 1978b; SMITH 1978, 1980, 1982; THROCKMORTON & CLARKE 1981; BRAMBLE & WAKE 1985). There is no evidence for transport of food through the mouth. Streptostyly probably permits to spread the jaw joints laterally, “thereby enlarging the transverse diameter of the oropharyngeal passage for large food items”. This is more definitely established in snakes. The anteroposterior displacement of the quadrate can alter the length, angle of insertion, and moment arms of the mandibular adductor muscles in the group (BRAMBLE & WAKE 1985).

An amphikinetic skull is typical for modern lizards, so generally meso- and metakinetic joints are present (FRAZZETTA 1962). The degrees tend to vary with diet, in the carnivorous *Varanus* kinesis is highly developed, but limited to streptostyly in the herbivore *Uromastix*. It is absent in the adult *Iguana* (THROCKMORTON 1976), and insectivorous chamaeleons are secondarily akinetic, probably because of adaptations in context with the specialised tongue. FRAZZETTA (1962) already suggested that herbivorous lizards might be expected to have skull systems with limited kinetic movement. But although THROCKMORTON (1976) did not observe any cranial kinesis during the feeding of the two herbivorous *Uromastix aegyptius* (Agamidae) and *Iguana iguana* („Iguanidae“), he also states that the meta- and mesokinetic joints remain mobile in all „Iguanidae“ and Agamidae. A herbivorous diet not necessarily requires a qualitative change in cranial kinesis. THROCKMORTON (1976) suggests that only the degree of movement at the kinetic joints may be greater in insectivorous lizards than in *Iguana* and *Uromastix*. KING (1996) states that to a herbivore, more powerful jaw

muscles could be useful to break down its food thoroughly. DALRYMPLE (1979) speculates that kinesis might be disadvantageous in a skull which is acted upon by powerful jaw muscles. He also points out that the importance of kinesis may be less related to diet than to lizard growth patterns or developmental pathways. Summing up, the lack of cranial kinesis can carefully be interpreted as a hint towards herbivory, if additional evidence is present.

4.2 Material and Methods

The preservation of the Messel fossils is almost unique in sometimes allowing the analysis of the last meal. In order to further test these results, tooth morphology and cranial kinesis are taken into account. The gut content analysis is based on three specimens (SMF ME 3516, WDC-C-MG 122/123, SMNK-PAL 3813), which exhibit preserved remains of intestinal contents. The specimen WDC-C-MG 122/123 shows abundant intestinal contents in the pectoral region and in the abdominal part, which is preserved on plate and counterplate. The intestinal contents of the other specimens are situated towards the abdominal region (Fig. 8B, Fig. 12A&C, Fig. 15A).

Food remains can have different appearances in Messel, according to their origin. Plant remains fossilise as a dark, massive coaly substance, insect cuticulae appear as dark shiny stains, whereas bones are heavily crushed and sometimes digested to an amorphous yellowish mass (BASZIO pers. comm.). Usually, intestinal food remains are situated in the rib cage and can be found farther anteriorly than expected. They can also still be “in situ”, in the anterior part of the lumbar region or shifted posteriorly. In rare cases, they drifted outside the body outline due to taphonomic processes (i.e. the opening of the abdomen, BASZIO pers. comm.). Still, it is impossible to differentiate between stomach and gut contents, because a reconstruction of these soft tissue part is impossible in the Messel fossils (RICHTER 1988).

A small sample is taken from the intestinal contents and prepared for scanning electron microscopy. Due to the consistency of the material, several freshly broken surfaces can be created under a microscope (Leica Wild M3Z) with low magnifications (i.e. 25x, 40x). After sputtering the sample with Gold-Palladium for three minutes at 10 kV, the sample is investigated in the Scanning Electron Microscope (CAMSCAN 24). Digital photography was employed using a frame grabber with the ORION 4.2 software in a resolution of 2048 x 1365 pixel. All these processing steps were done by the author.

The tooth morphology and the cranial morphology of the new genus and species have already been described in the taxonomical part. The specimens showing the best labial and lingual view of the teeth are SMF ME 475a and WDC-C-MG 122/123, while the best information on cranial morphology can be derived from SMF ME 3516, SMNK-PAL 3813 and WDC-C-MG 122/123.

Three specimens of the scincid species *Corucia zebrata* were weighed on a scale and the snout-vent length from the tip of the snout to the cloaca was measured. Unfortunately, only alcohol material was available. Consequently, the weight is overestimated. In order to correct this value, a factor of 0.86 was applied to the measured weight. This factor was experimentally found by POUGH (1973) in weighing freshly killed animals and repeating the procedure with the same material after 12 months in alcohol.

4.3 Results

4.3.1 Intestinal contents

Specimen WDC-C-MG 122/123 shows the largest amount of intestinal contents. Both the anterior and posterior contents mainly consist of plant remains, as does the fossilised food of all other specimens. The gut contents consist of a dark, massive coaly substance, typical for plant remains. Also some scattered arthropod cuticulae are found in the intestinal contents of WDC-C-Mg 122/123 and SMNK-PAL 3813.

4.3.1.1 Plant remains

A large part of the plant material consists of **peridermal (cork) tissue** (pers. obs., confirmed by WILDE pers. comm.). This is to be found in all of the three studied specimens with intestinal contents. The flattened, layered and highly ordered rows of cell walls are clearly recognisable (Fig. 66). The regular arrangement of cells originates from synchronous cell divisions of the “Phellogene” in the cork-cambium. The latter is divided in the inner Phellogen, which is rich in chloroplasts and in the outer cork tissue (Phellem, SITTE et al. 1998). This is an external tissue built of dead cells, the cell walls are covered with an impermeable suberine layer. Suberine is a substance consisting of highly polymerised esters and unsaturated fatty acids. This suberine layer is additionally permeated by wax (SITTE et al. 1998, RAVEN et al. 1988). Fig. 66C-G show the abundant and well developed pit-canals (for intercellular transport) in the form of small peglike protuberances (pers. obs.) which are typical for peridermal tissue (WILDE pers. comm.).

Plant cuticula is preserved in all of the three specimens (Fig. 67), although it is relatively rare. In SMNK-PAL 3813 there is only one fragment, which can be identified as such a cuticular remain (Fig. 67S). But no stomata are recognisable in all of the cuticular fragments. The absence of these hints towards a cuticula originating from the peridermal tissue, in contrast to a leaf cuticula. Fig. 67F+R show layers of peridermal tissue situated below the cuticula. According to WILDE only three structures are potential stomata (Fig. 67T-V), although only the one figured in Fig. 67T can safely be identified as a stoma.

Common structures in the plant material are **fragments of twigs or stalks** (Fig. 68), they are preserved in the specimens WDC-C-MG 122/123 und SMNK-PAL 3813. The cells are elongated (prosenchymatic) and remains of conducting elements, wood respectively phloematic fibres can safely be identified (WILDE pers. comm., Fig. 68Q-T). Probably the circular cell walls thickenings of the conducting elements were preserved in this case. Fig. 68B, C, E and G picture prosenchymatic cells. Fig. 68E shows the preserved cell wall, cell lumen and its cast.

The specimens WDC-C-MG 122/123 and SMNK-PAL 3813 additionally seem to contain **sclerenchymatic tissue** (Fig. 69), the largest amount of which is preserved in the first specimen. Large amounts of this tissue would hint towards seeds or fruits (WILDE pers. comm.). Sclerenchymatic tissue also contains numerous and well developed pit-canals. These are here preserved as small pegs as well, because the interior of the cell is casted. According to WILDE (pers. comm.) this is a typical preservation of plant cells in Messel. The mechanisms leading to this result remain enigmatic. As a rule, sclerenchymatic tissue appears to be less ordered than cork tissue. Both cell types are

more or less isodiametric. Sclerenchymatic cells often show lignified secondary cell walls and act as important stabilising elements. The thick secondary cell walls contain many characteristic, simple pit-canals (RAVEN et al. 1988). In SMF-ME 3516 only isolated cells with pit-canals are identifiable (Fig. 69V+W). Fig. 69W shows the cross section of a cell with the incorporated pit-canals. With the preservation found in the investigated specimens, it is difficult to distinguish sclerenchymatic tissue from peridermal tissue. According to WILDE (pers. comm.) it seems more likely that this tissue partly represents cork, resp. peridermal tissue, as well.

The structures depicted in Fig. 70 represent fragments of a **seed or fruit husk**. A complex wall composed of sclerenchymatic cells is visible. The layer consisting of fibres arranged in a zigzag pattern (Fig. 70E+F) most probably has a stabilising function (WILDE pers. comm.). The tissue in cross section shows prosenchymatic cells with a large number of pit-canals (Fig. 70G). The upper face bears pores (Fig. 70A+B). This characteristic tissue was only found in WDC-C-MG 122/123.

Additionally there are some plant remains which can be characterised by cells showing a distinct “bubbly” or “foamy” inner structure (Fig. 71). They probably represent dead cells which were filled with **organic secretions** in the living plant. Unfortunately, the nature of these secretions cannot further be characterised, but it could have been resin, ethereal oils or tannic acids. This foamy structure is a preservational mode which is probably caused by processes of chemical separation which are not completely understood to date. Such cells occur generally in parenchyme or peridermal tissue and it is very likely that the tannic acids were produced in these cells (WILDE pers. comm.). These structures were also preserved in the prosenchymatic cells of the conducting elements (Fig. 68A+B). These structures were found in the specimens WDC-C-MG 122/123 and SMNK-PAL 3813.

In the specimen WDC-C-MG 122/123 one type of **pollen** was found, bearing a characteristic “spiny” sculpture and possessing at least two apertures (Fig. 72). According to WILDE (pers. comm.) these pollen belong to the **Juglandaceae** (walnut family), which represented a main part of the Eocene forest surrounding Lake Messel. In two cases, four pollen were found in a single plant remain. This possibly hints to catkins of Juglandaceae, which have already lost most of their pollen. The pollen have characteristic, bulge-like folds (Fig. 72B-D, J+M) and bear three pores (SCHAARSCHMIDT 1992). As all of the pollen are still situated in plant tissue, all three pores are not visible. In Fig. 72F two pores are recognisable, while Fig. 72C, M+N shows one of the pores.

Following pages:

Fig. 66: Peridermal (cork) tissue found in the intestinal contents of WDC-C-MG 122/123, SMF ME 3516 and SMNK-PAL 3813. The flattened, layered and highly ordered cell rows are clearly recognisable. A-I: From WDC-C-MG 122/123. J-Q: From SMF ME 3516. R-X: From SMNK-PAL 3813. C-G: Abundant and well developed pit-canals in form of small peglike protuberances, typical for peridermal tissue. D: Enlargement of C. P: Enlargement of O. V: Enlargement of U. SEM.

Fig. 67: Plant cuticula and a few isolated stomata found in the intestinal contents of WDC-C-MG 122/123, SMF ME 3516 and SMNK-PAL 3813. The absence of stomata hints towards a cuticula originating from peridermal tissue, in contrast to a leaf cuticula. A-L: From WDC-C-MG 122/123 with the most abundant cuticula remains. M-R: From SMF ME 3516. S: From SMNK-PAL 3813. This is the only identifiable fragment of cuticula in this specimen. T-V: Potential isolated stomata found in the intestinal contents of WDC-C-MG 122/123. D: Enlargement of C. F+R: Layers of peridermal tissue are situated below the cuticula. SEM.

Fig. 68: Fragments of twigs or stalks found in the intestinal contents of the specimens WDC-C-MG 122/123 and SMNK-PAL 3813. The cells are elongated and remains of conducting elements (wood resp. phloematic fibres) can be found. A-O: From WDC-C-MG 122/123. P-X: From SMNK-PAL 3813. B,C,E+G: Elongated (prosenchymatic) cells. R: Enlargement of Q. Q-X: Wood resp. phloematic fibres. SEM.

Fig. 69: Sclerenchymatic tissue, containing numerous and well developed pit-canals found in the intestinal contents of the specimens WDC-C-MG 122/123, SMNK-PAL 3813 and SMF ME 3516. The cell types are more or less isodiametric. A-H: WDC-C-MG 122/123. I-U: SMNK-PAL 3813. V+W: From SMF ME 3516, only isolated cells with pit-canals are preserved. B: Enlargement of A. J: Enlargement of I. L+M: Enlargement of framed areas in K showing cell lumina with distinct pit-canals. P, R+T: Enlargements of framed areas showing cells with peg-like preserved pit-canals. W: Cross section of a cell with casts of pit-canals. SEM.

Fig. 70: Fragments of a seed or fruit husk from found in the intestinal contents of WDC-C-MG 122/123. B: Enlargement of A, face with pores. D: Enlargement of C, a complex wall of sclerenchymatic tissue is visible. E+F: Fibres are arranged in a zigzag pattern, most probably for stabilisation. G: Tissue in cross section, prosenchymatic cells with a large number of pit-canals are present. SEM.

Fig. 71: Cells with a distinct “bubbly” or “foamy” inner structure, probably representing organic secretions such as ethereal oils or tannic acids. This structure is probably caused by processes of chemical separation which are not yet completely understood. A-H: from WDC-C-MG 122/123. I-O: from SMNK-PAL 3813. Arrows and enlargements show probably peridermal cells filled with this characteristic structure. SEM.

Fig. 72: Pollen belonging to the Juglandaceae (walnut family) found in the intestinal contents of WDC-C-MG 122/123. They have a characteristic “spiny” sculpture, bulge-like folds and at least two apertures. A+I: Fragments of probable catkins. B-E: Enlargements of A. J-M: Enlargements of I. H: Enlargement of framed area in G. B-D, J+N: Pollen showing the characteristic bulge-like folds. F: Pollen with two recognisable pores. C, M+N: Pollen with one visible pore. SEM.

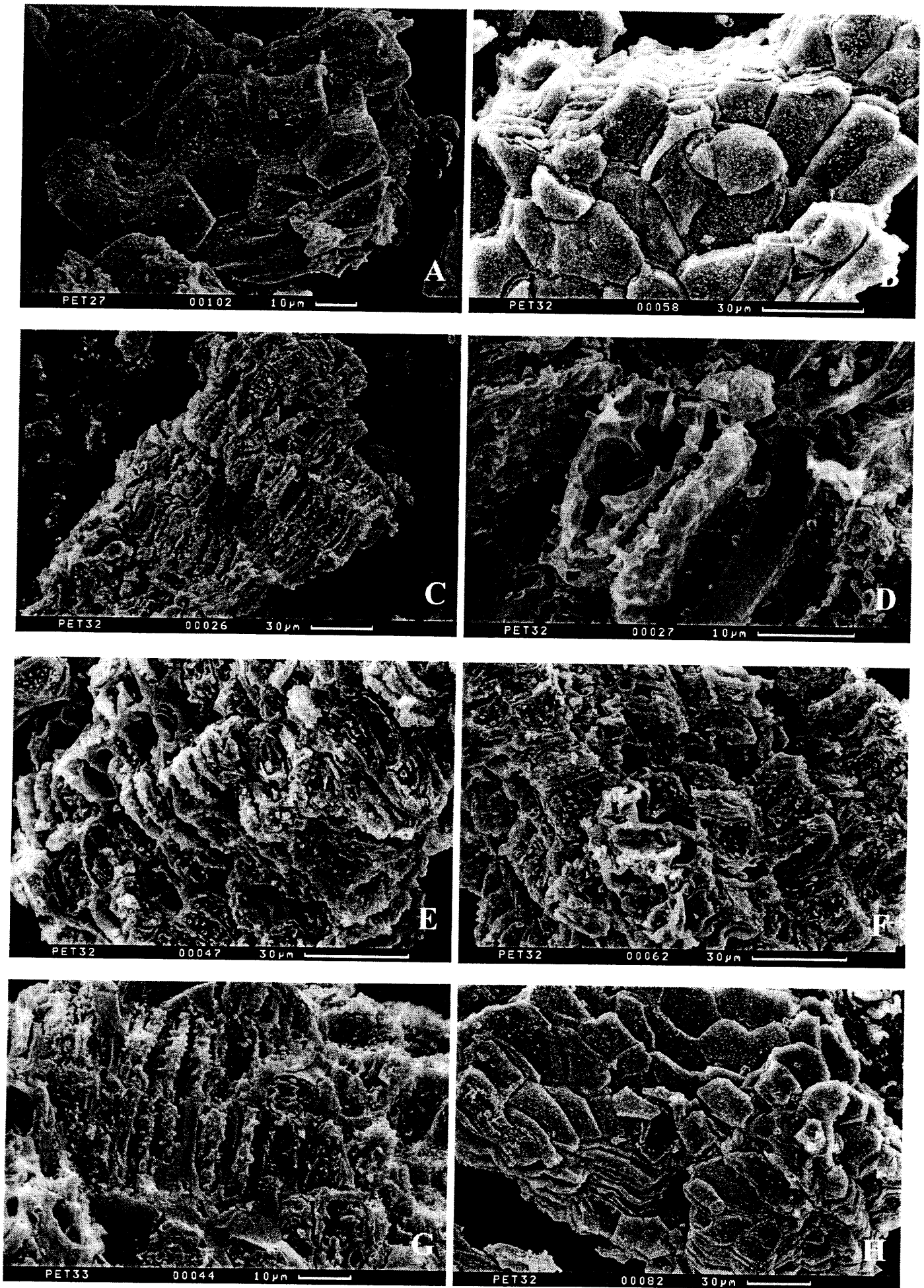


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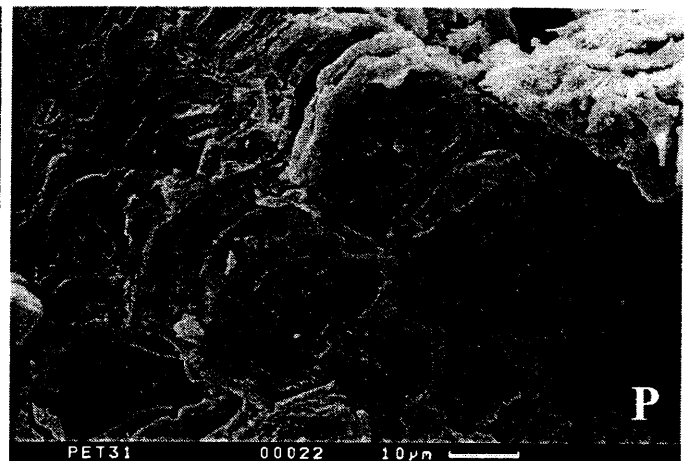
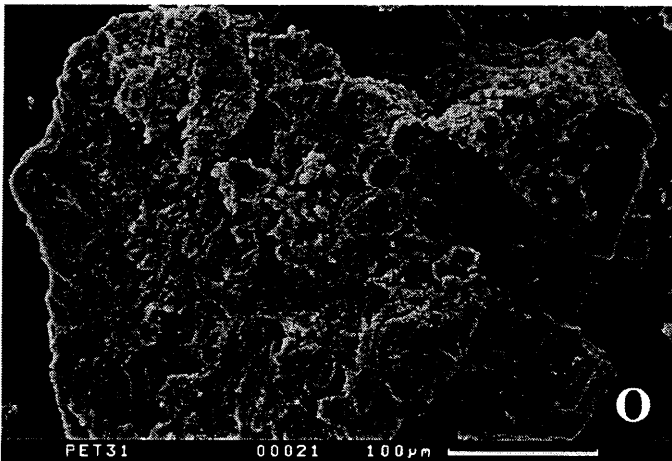
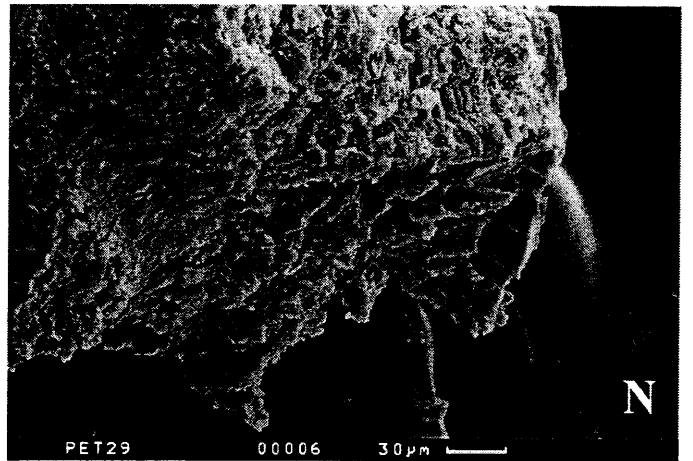
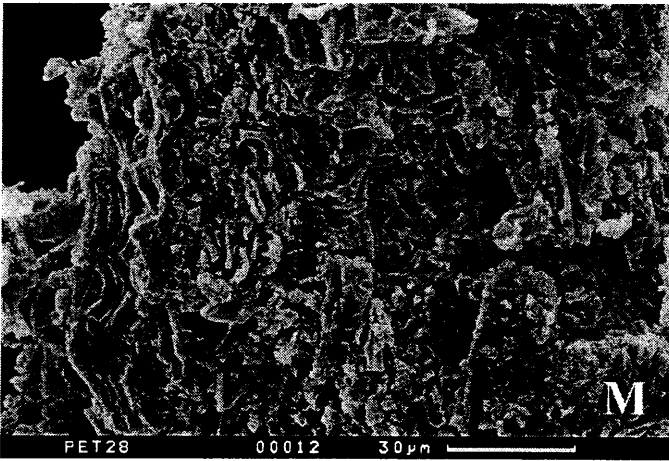
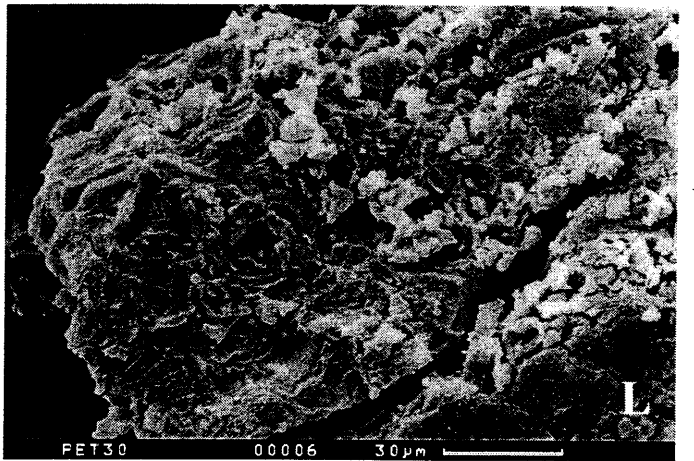
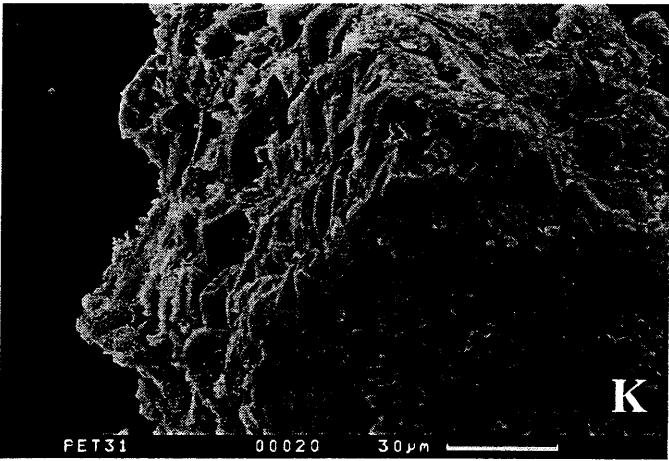
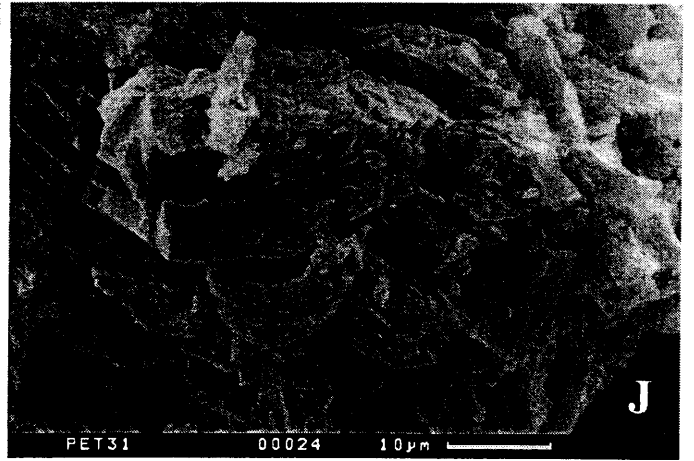
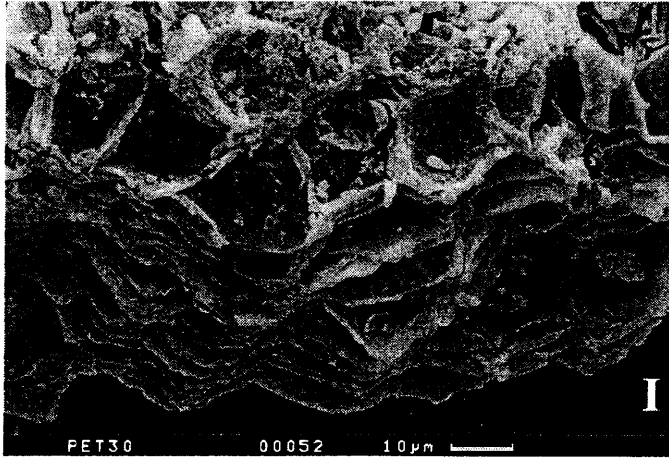


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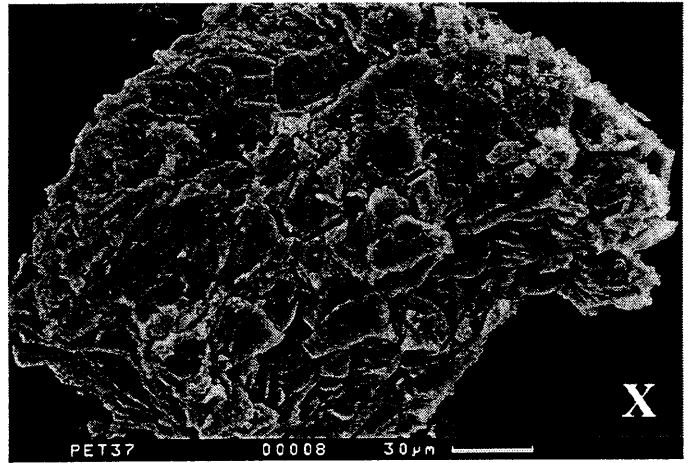
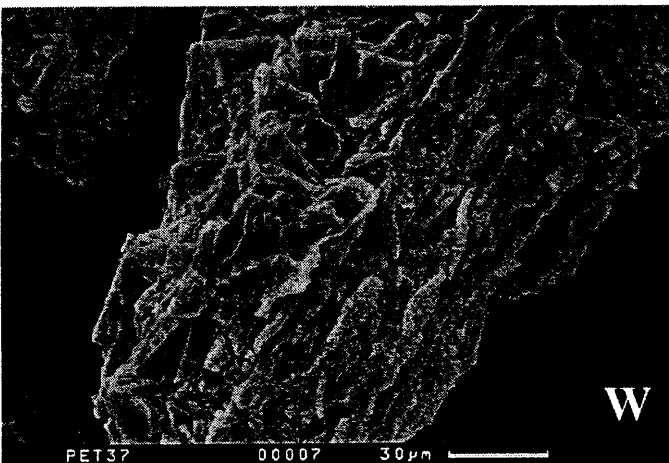
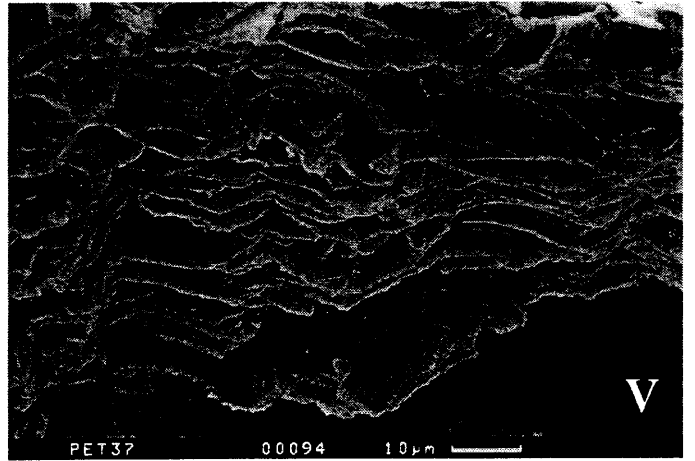
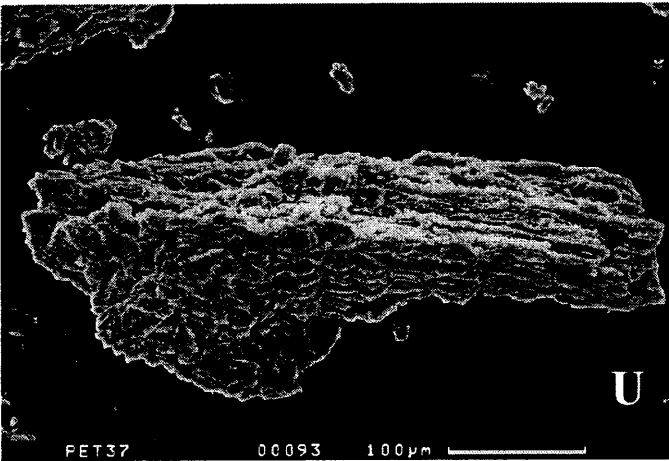
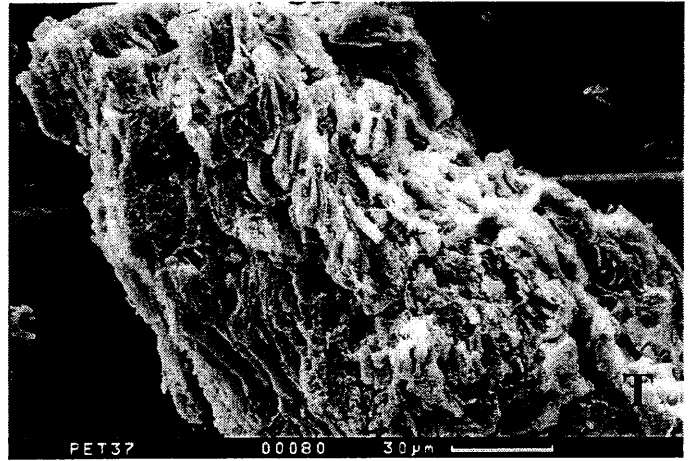
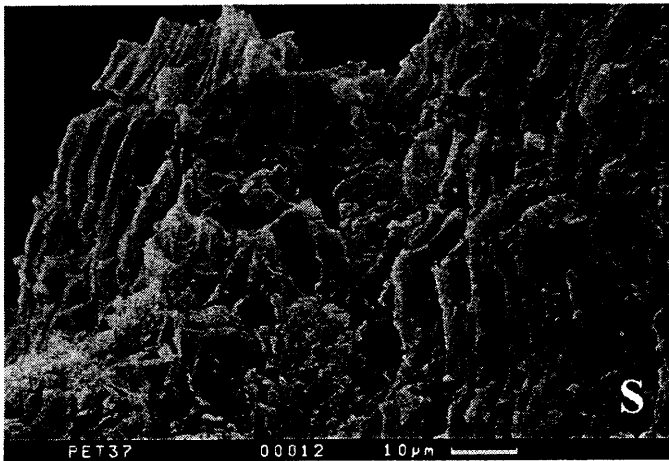
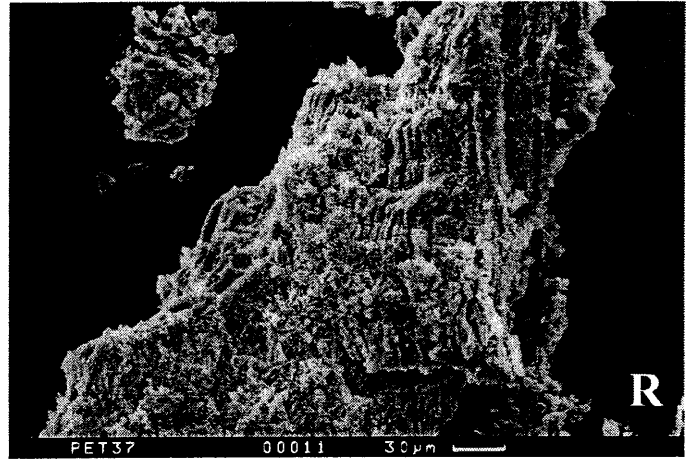
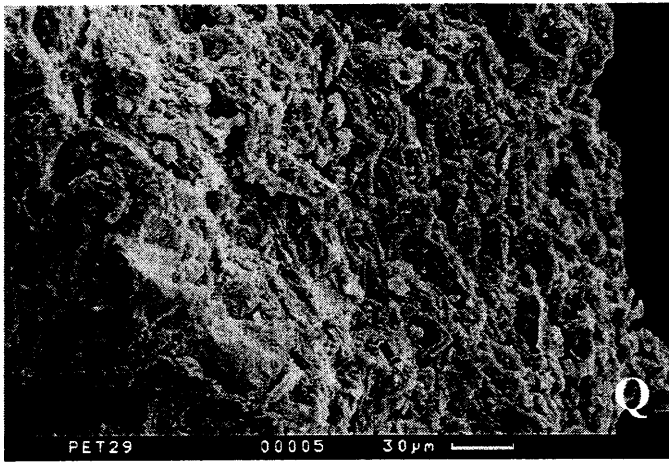


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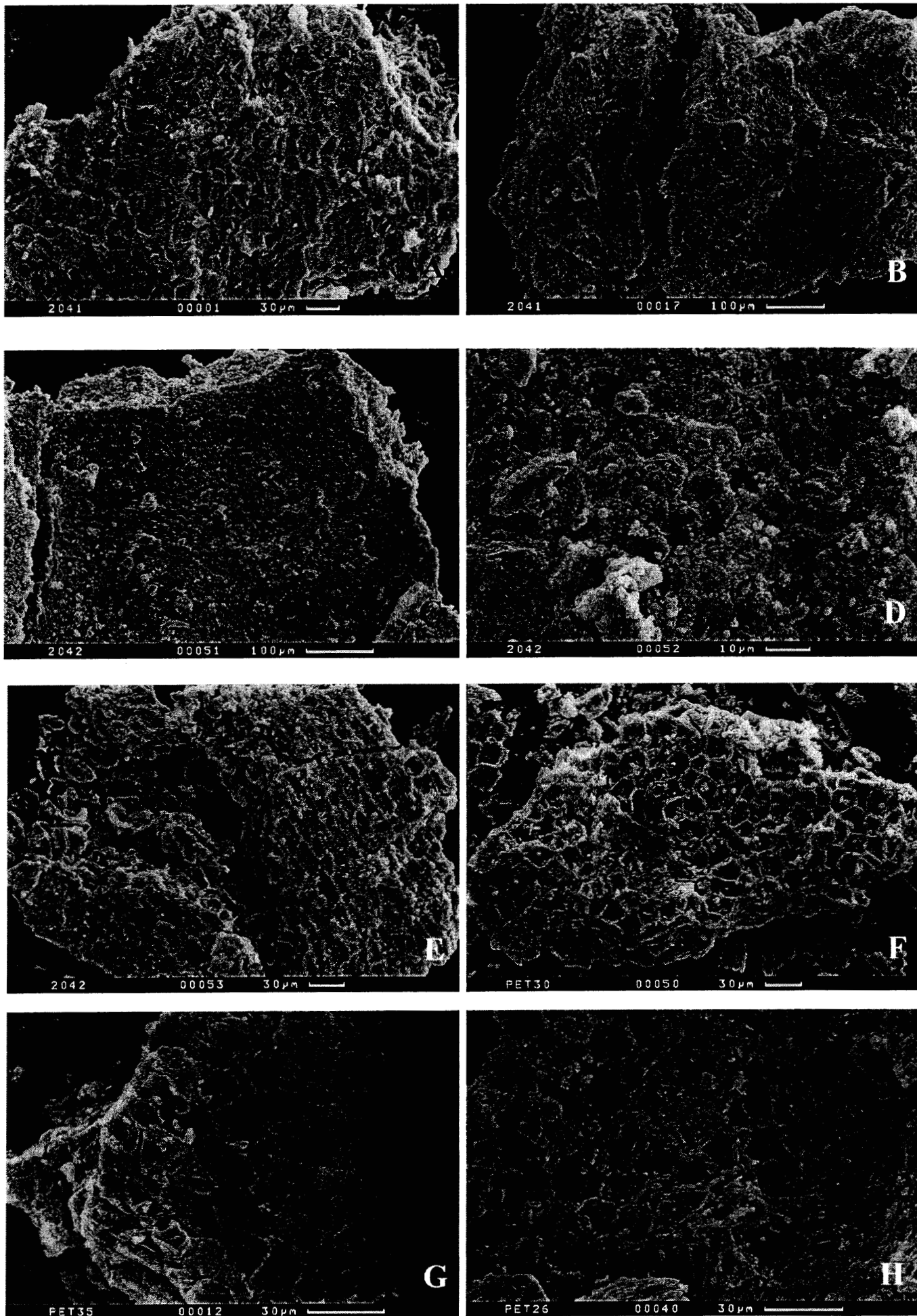


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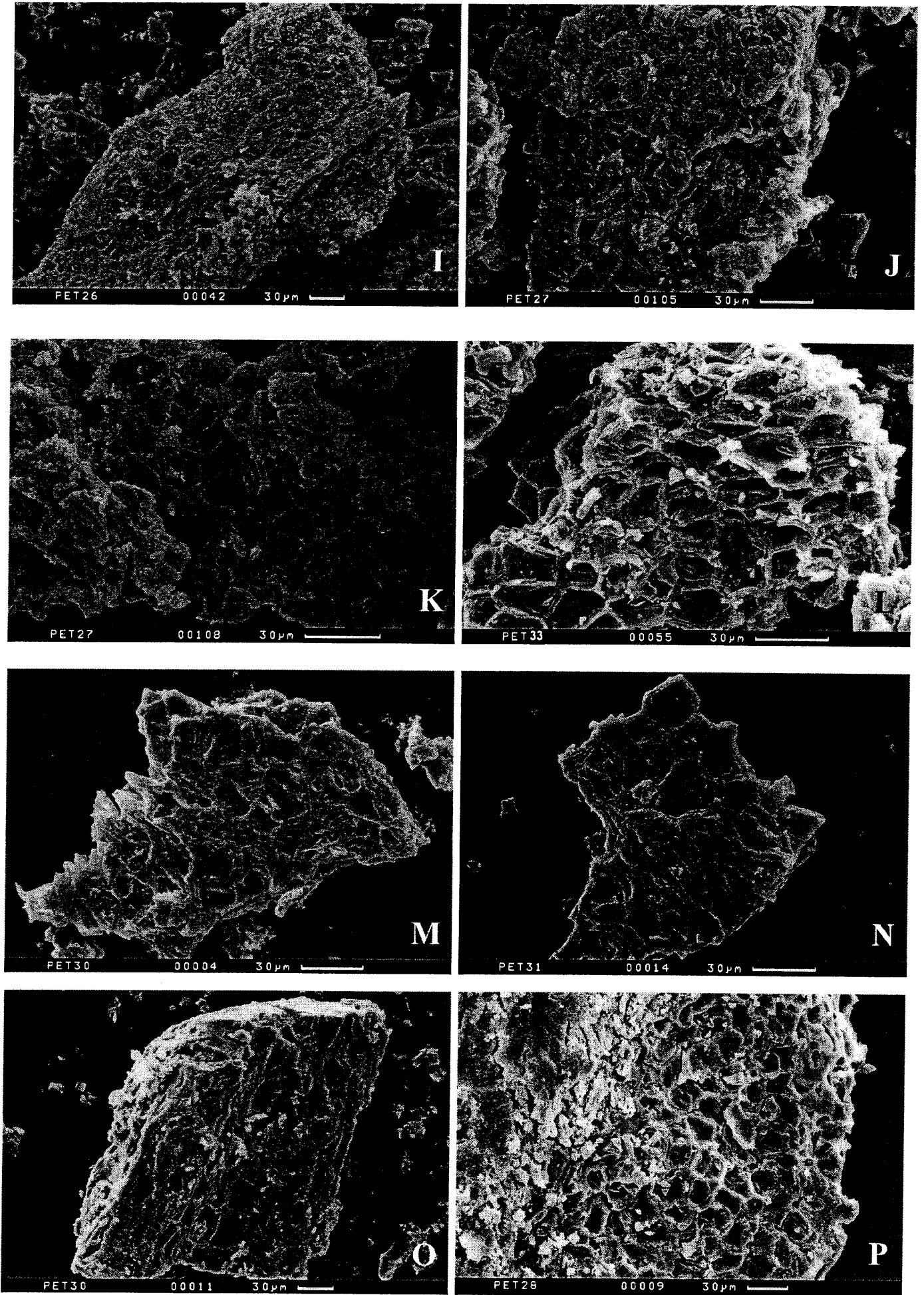


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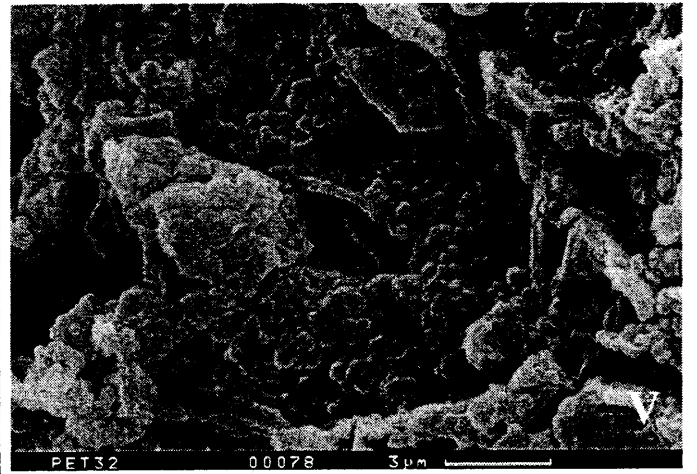
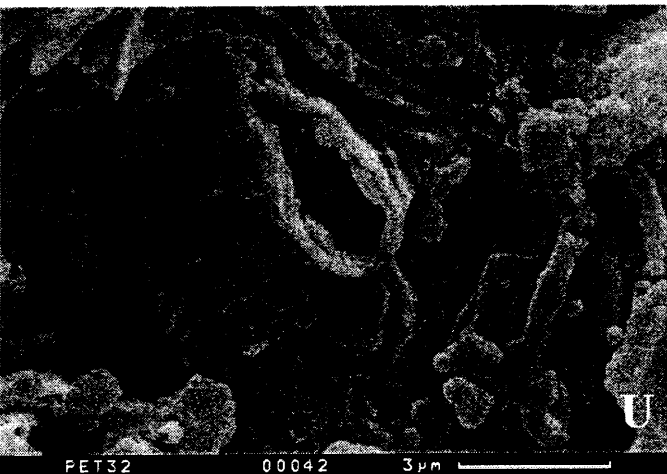
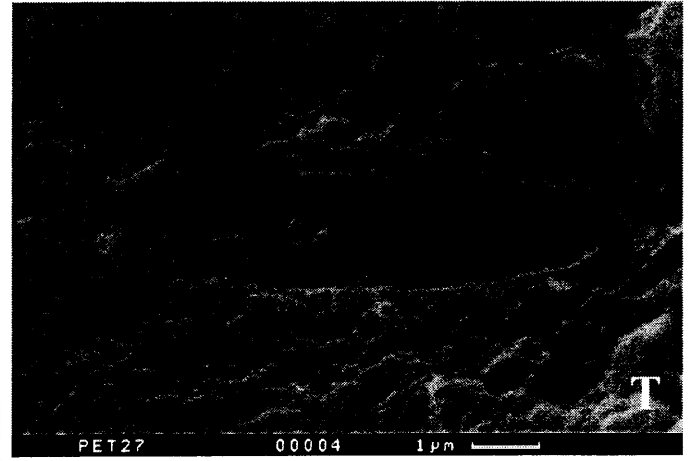
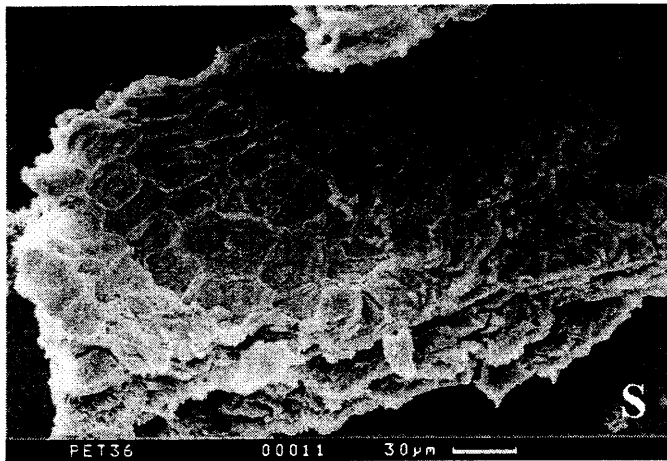
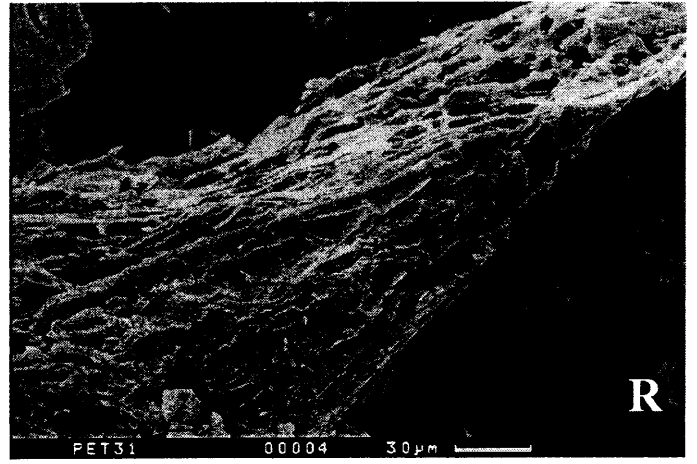
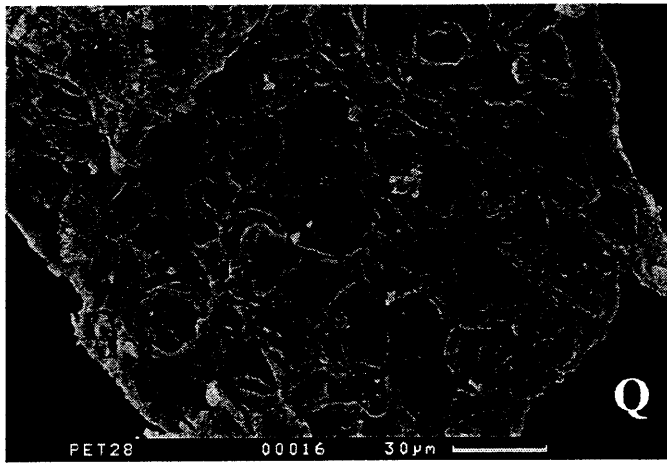


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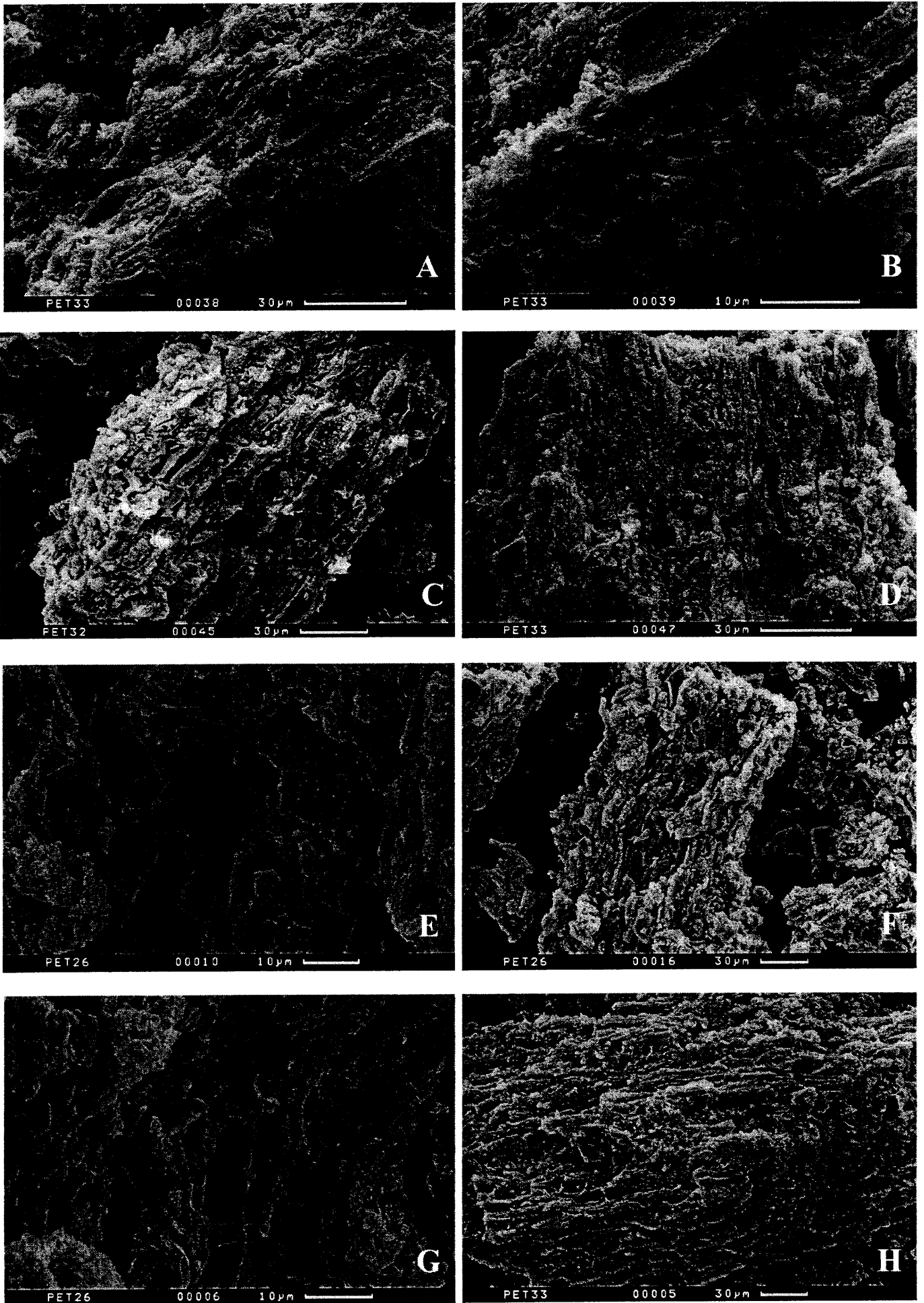


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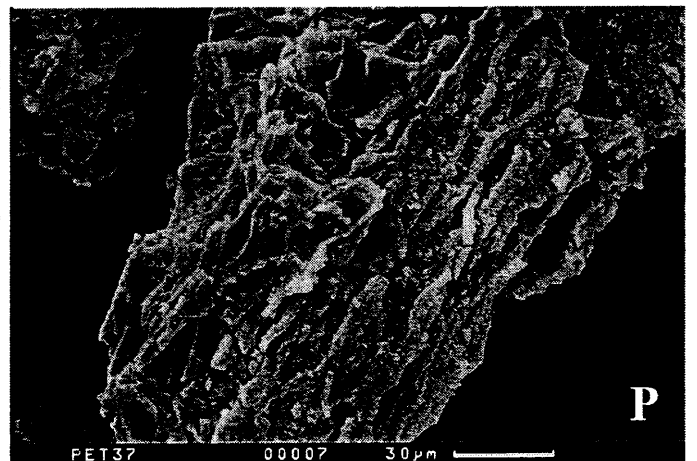
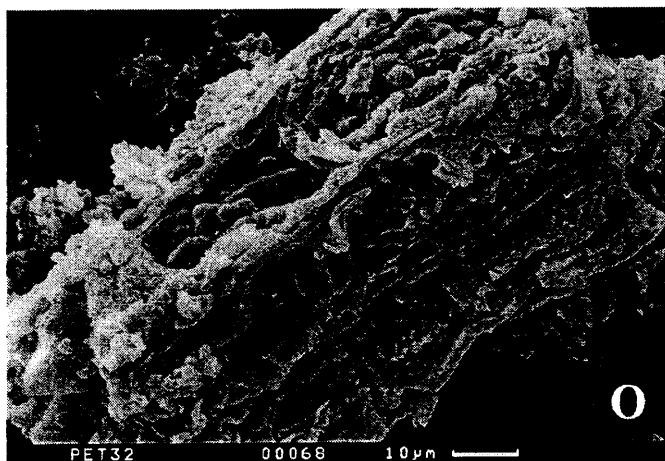
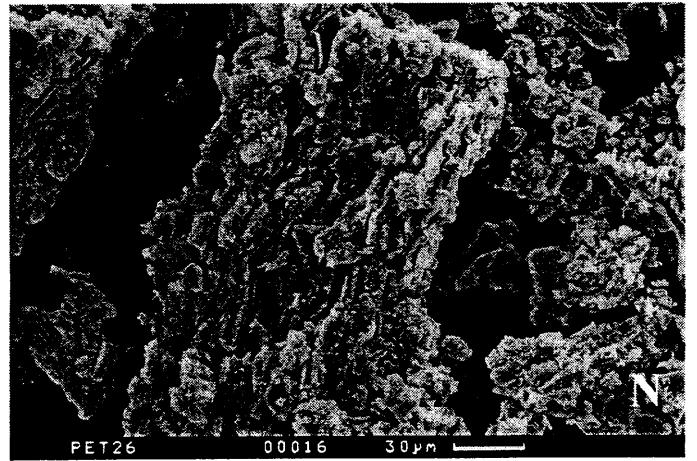
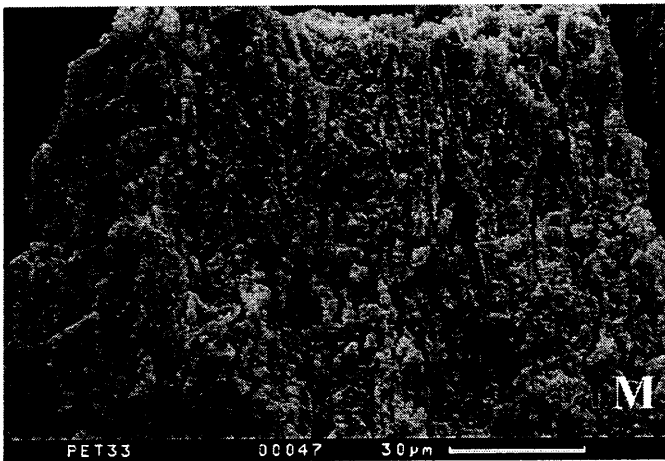
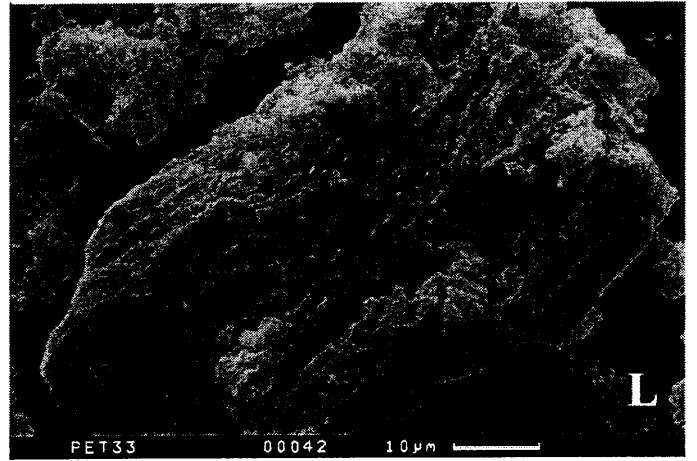
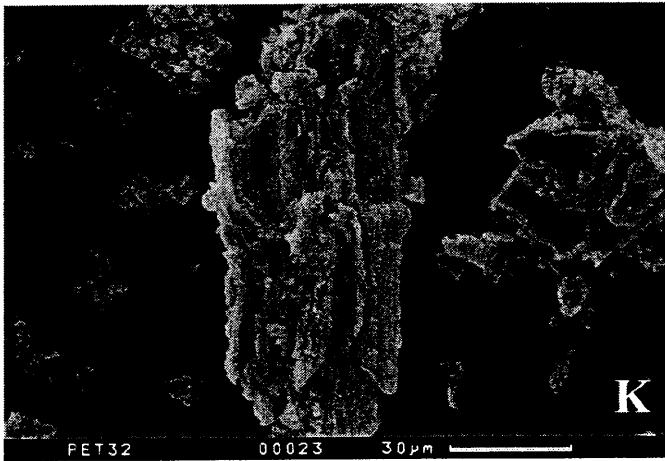
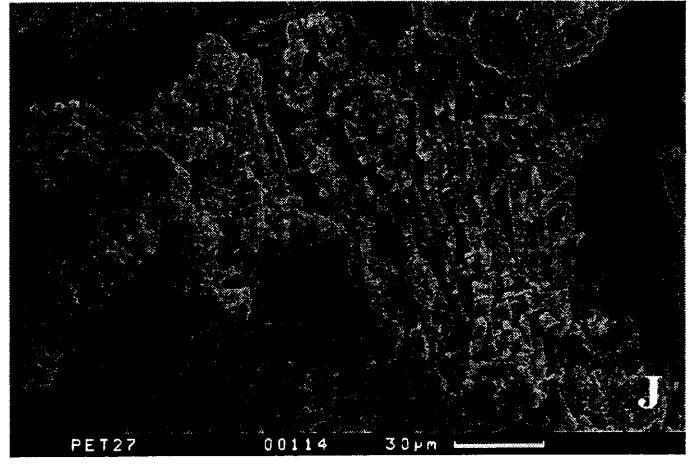
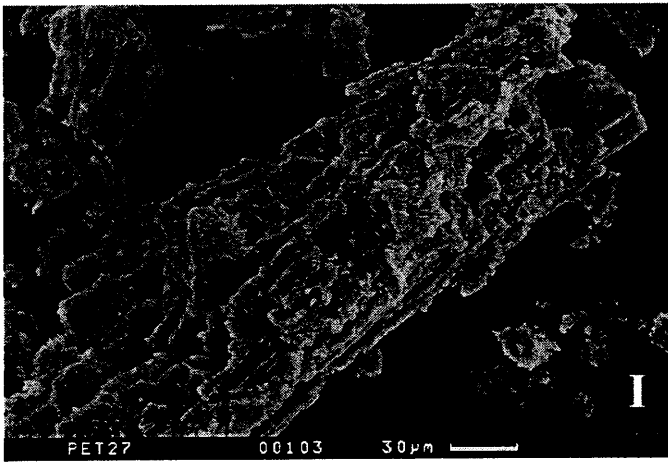


Fig. 68

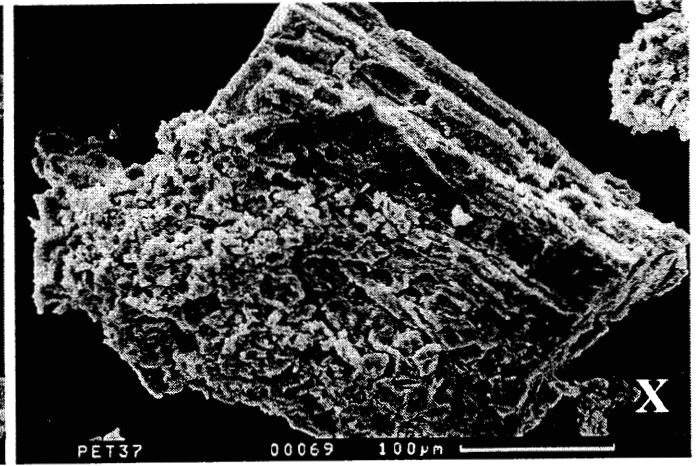
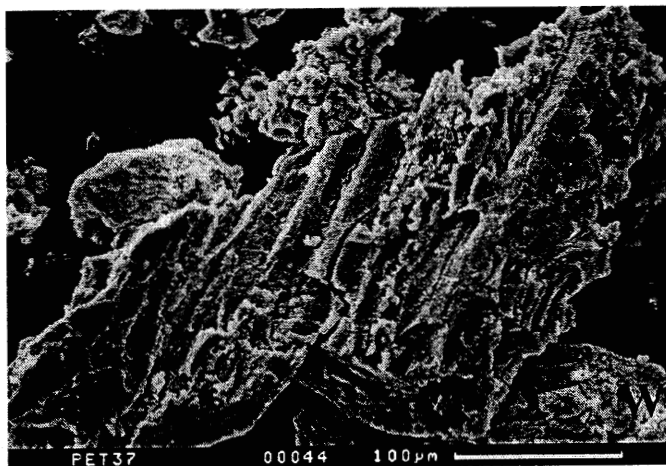
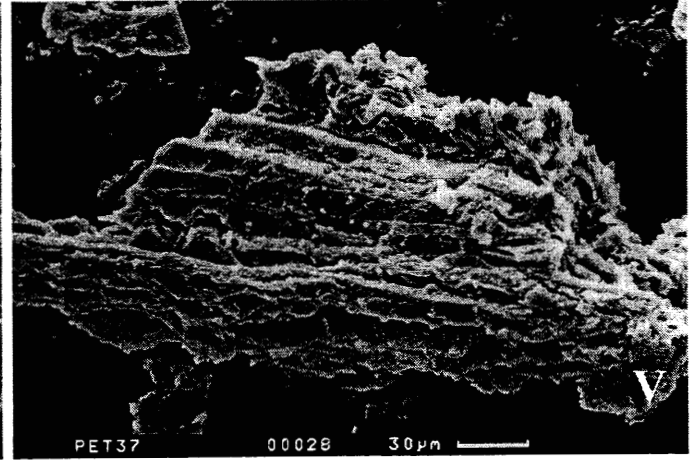
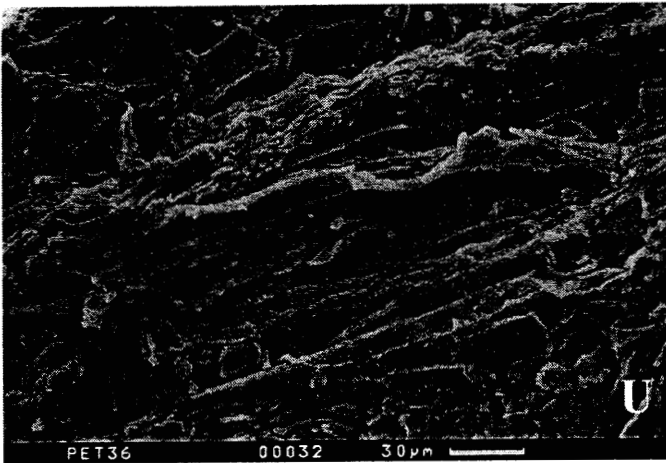
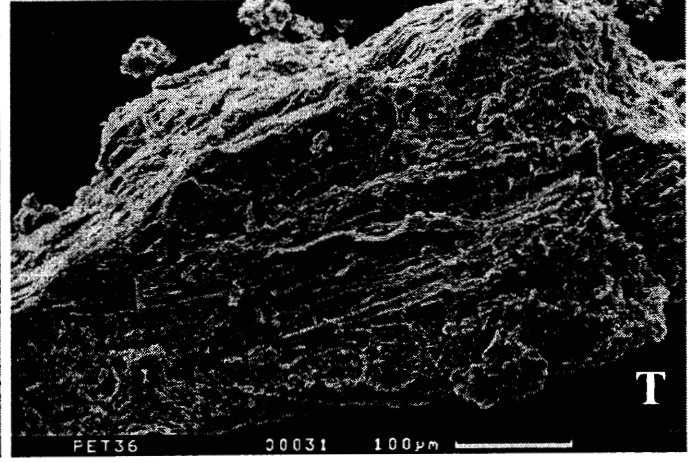
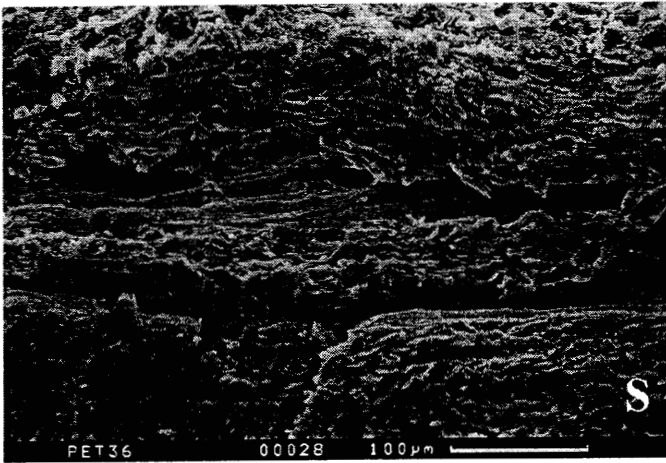
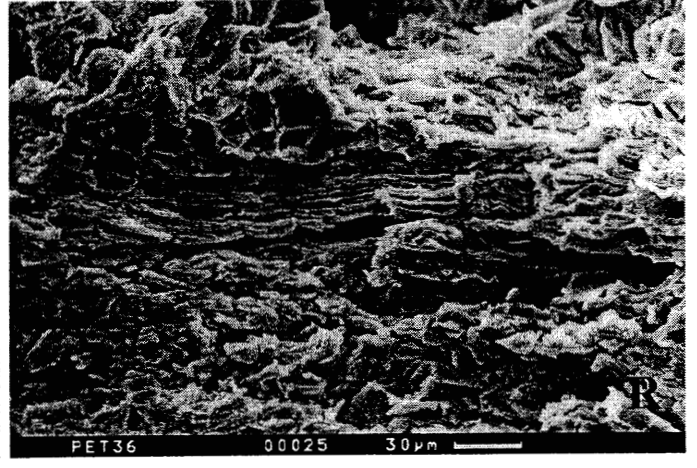
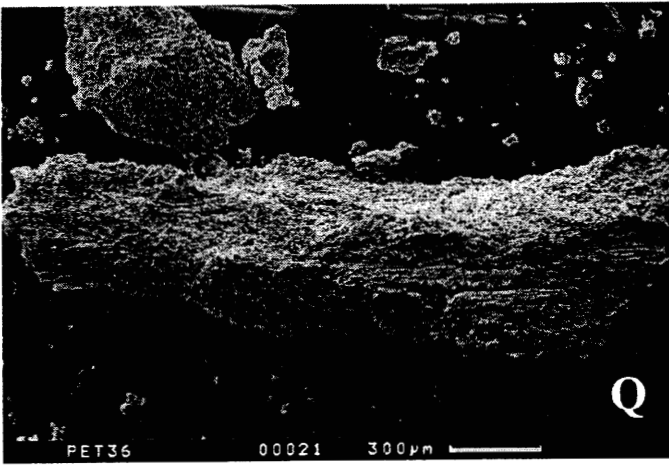


Fig. 68

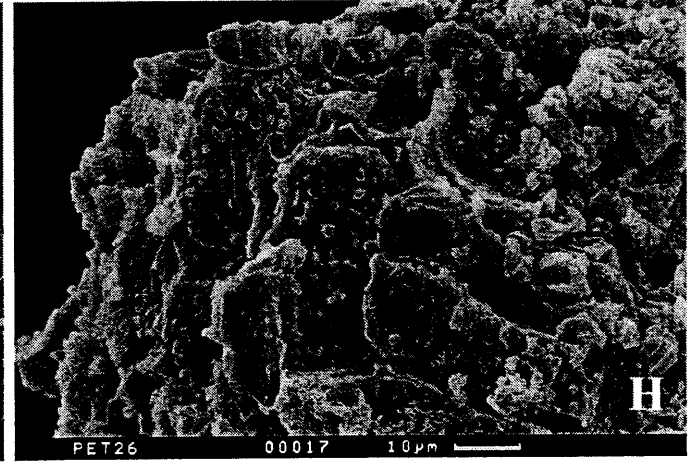
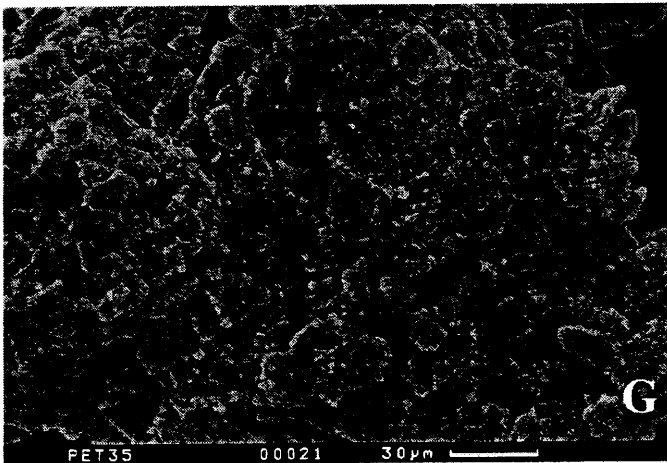
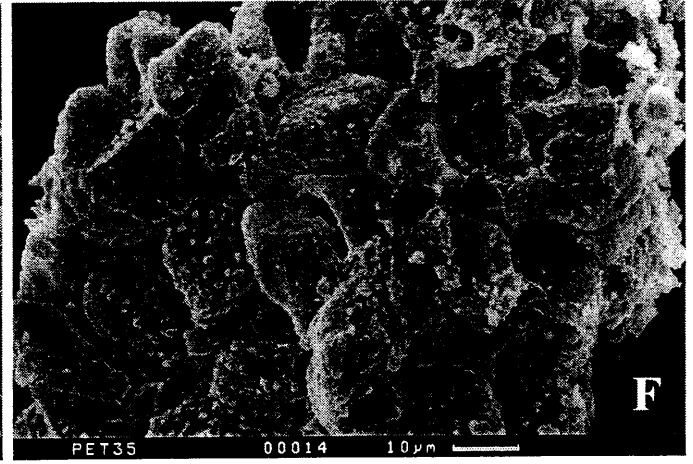
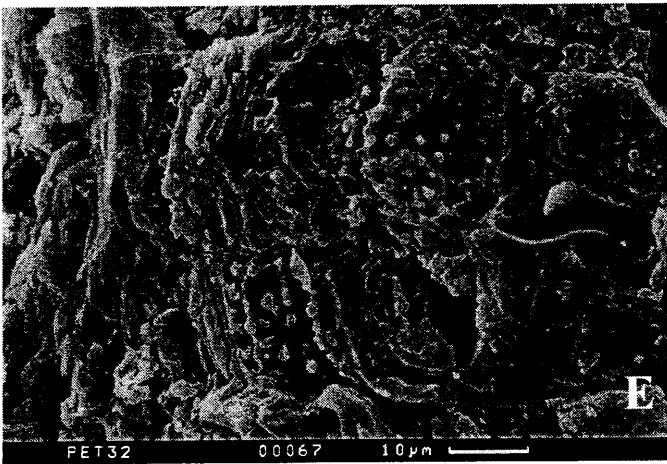
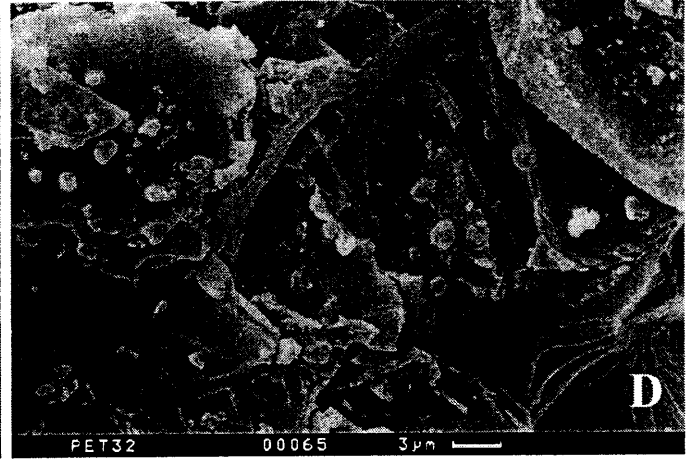
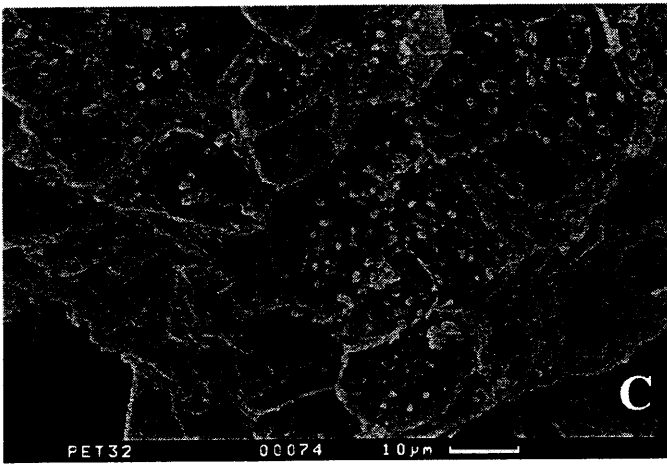
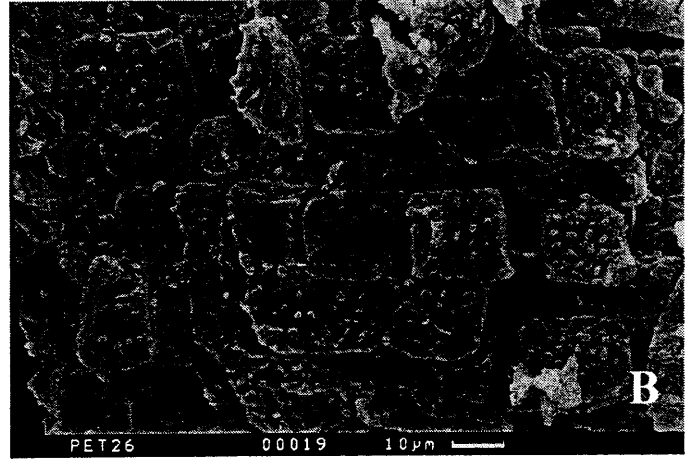
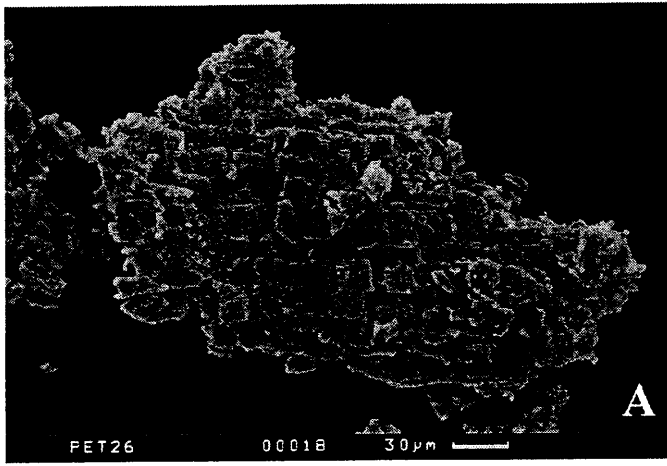


Fig. 69

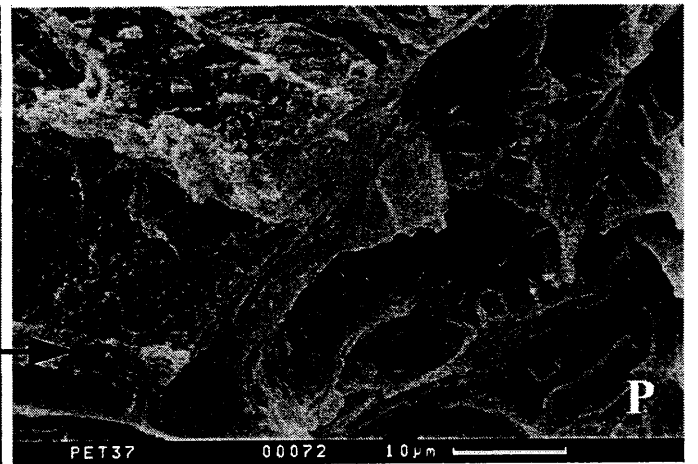
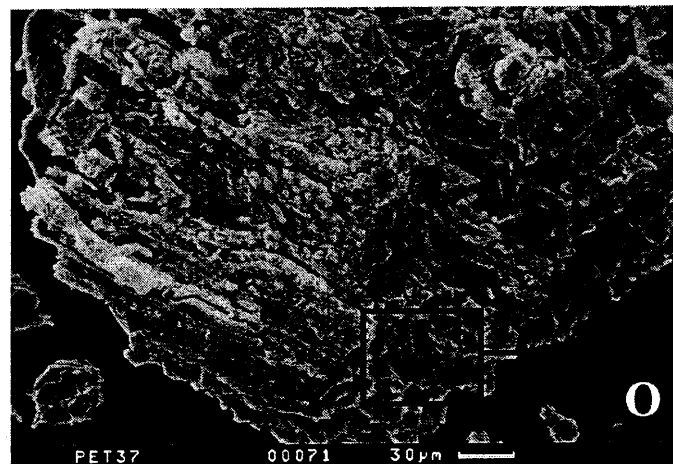
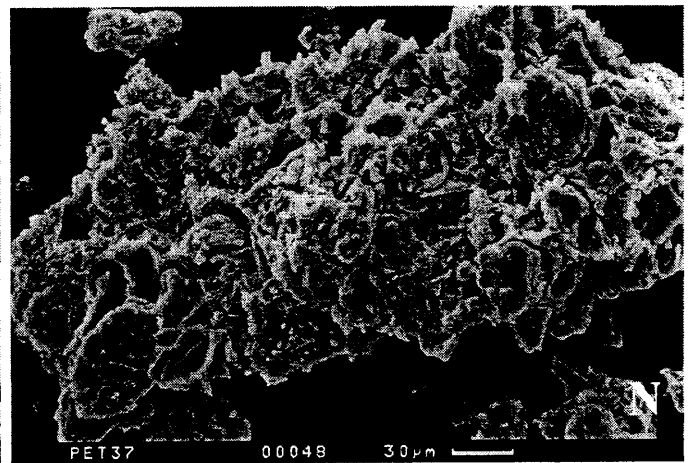
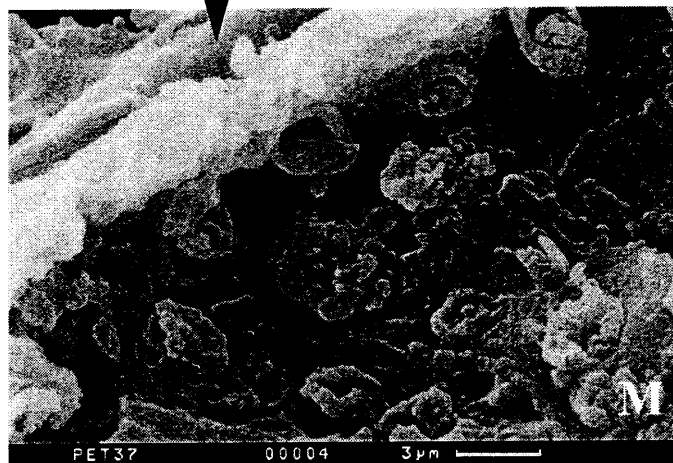
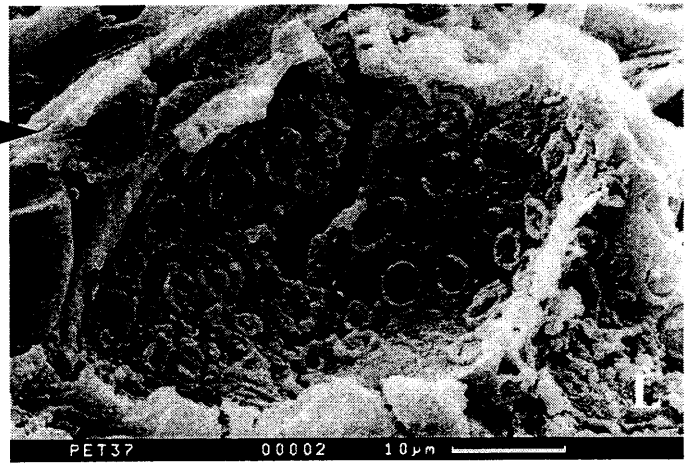
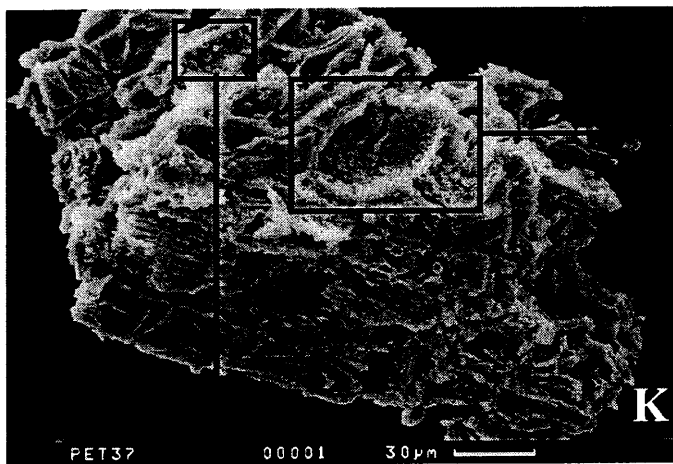
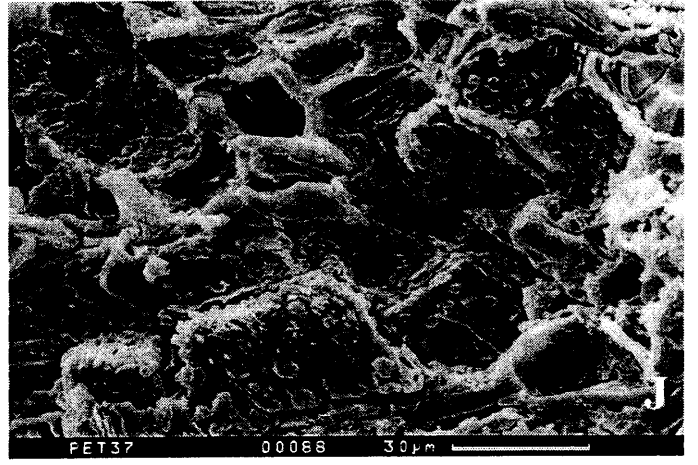
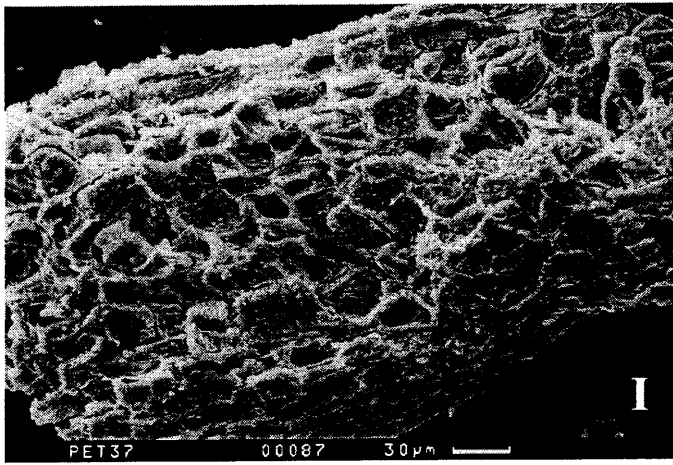


Fig. 69

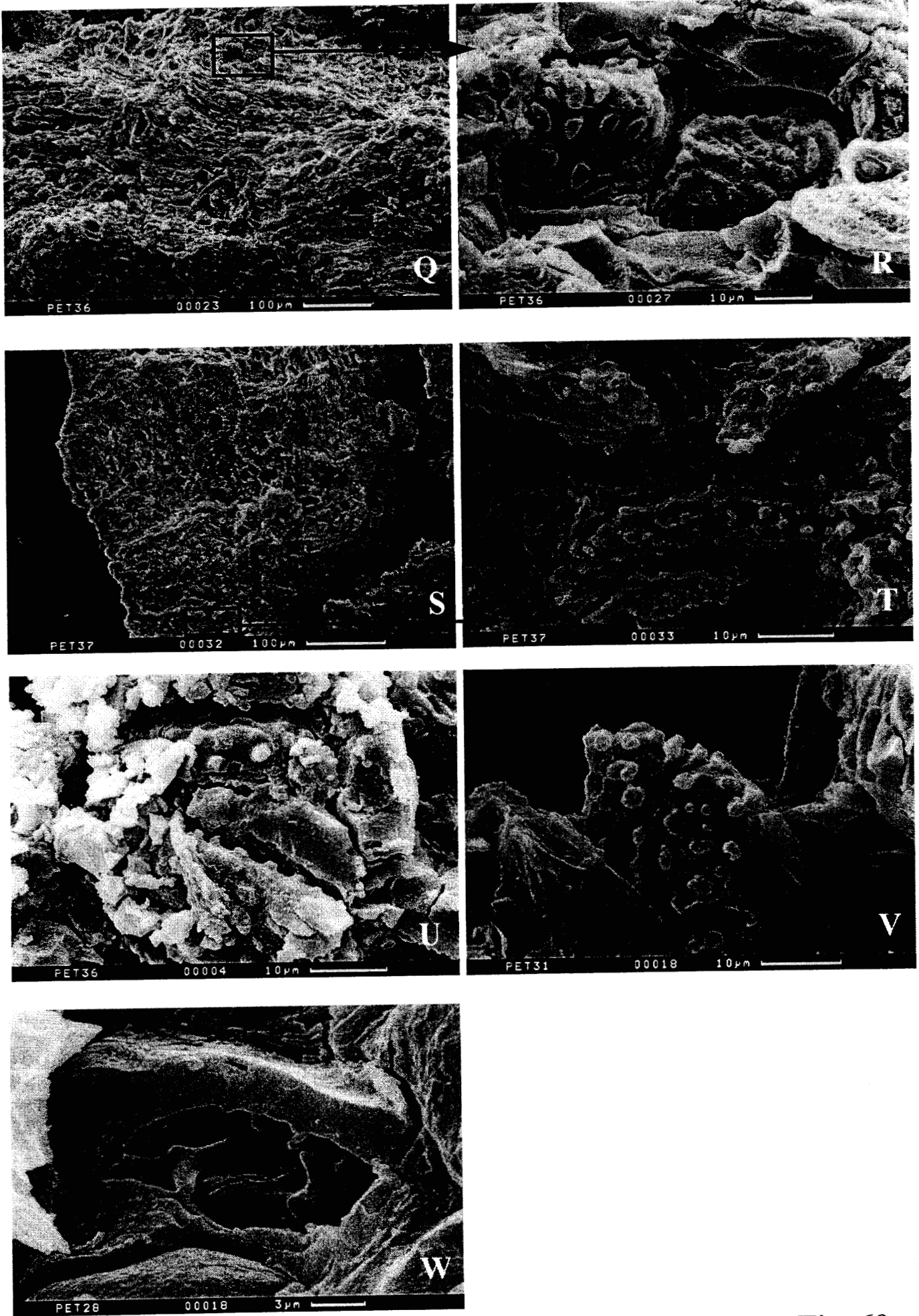


Fig. 69

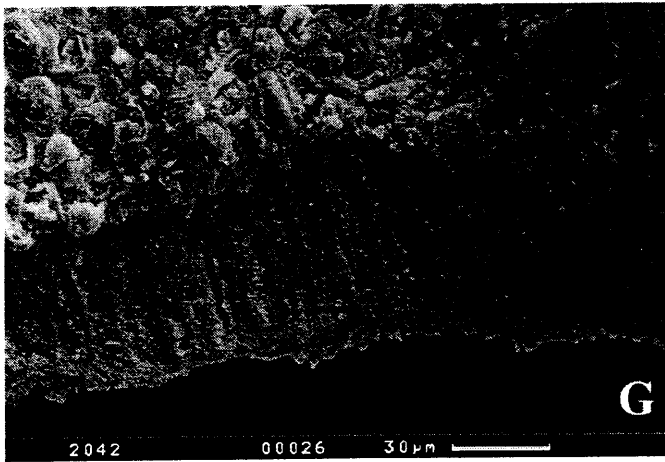
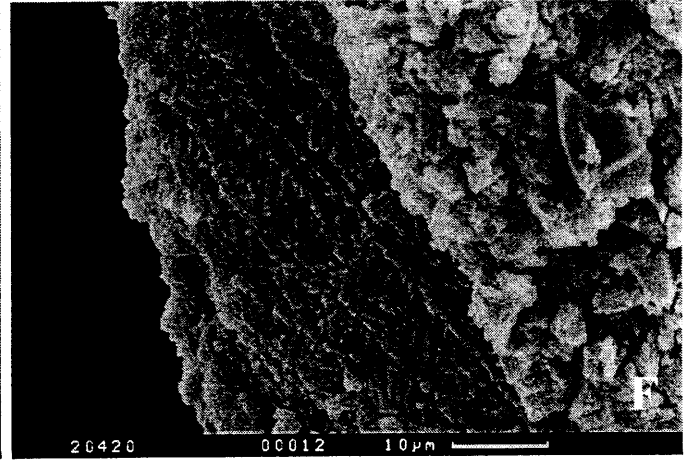
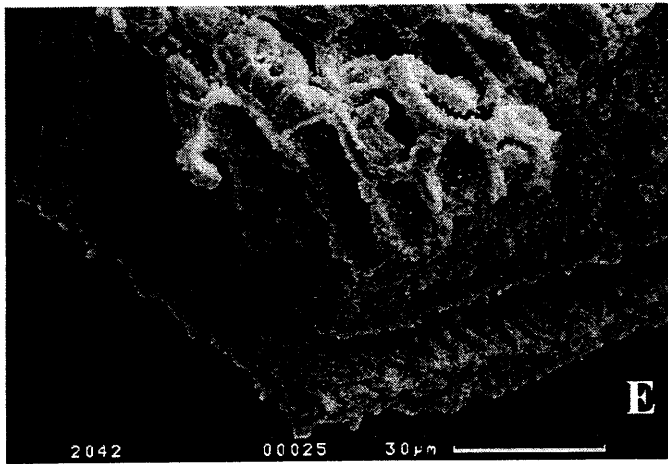
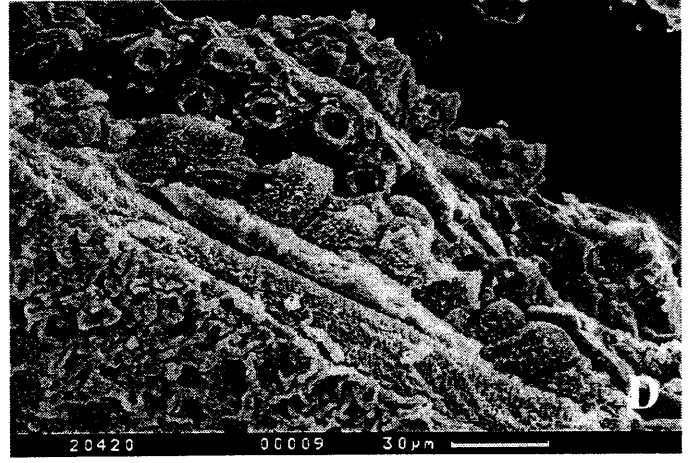
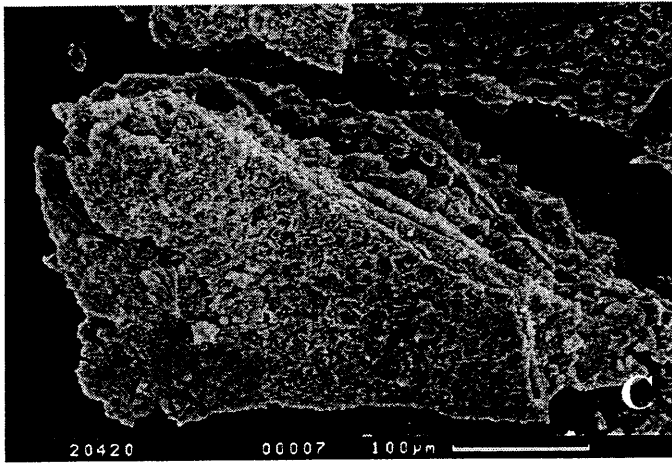
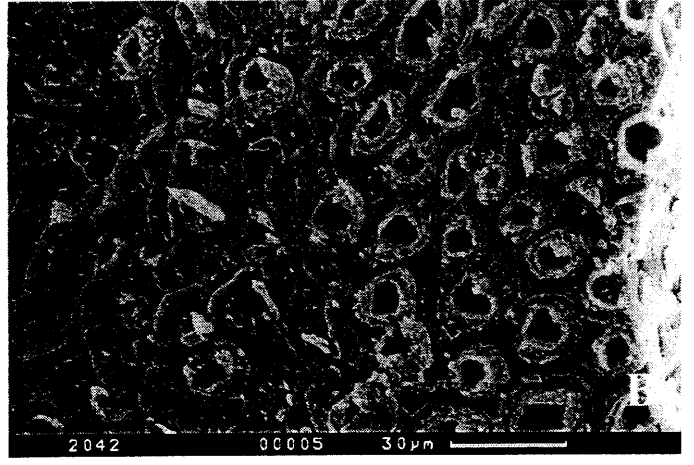
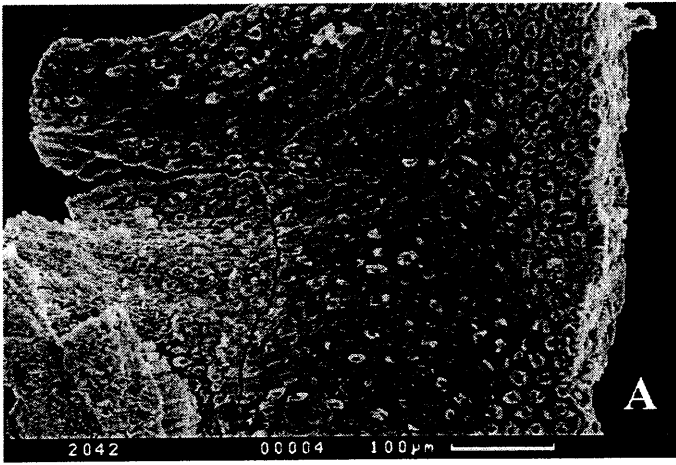


Fig. 70

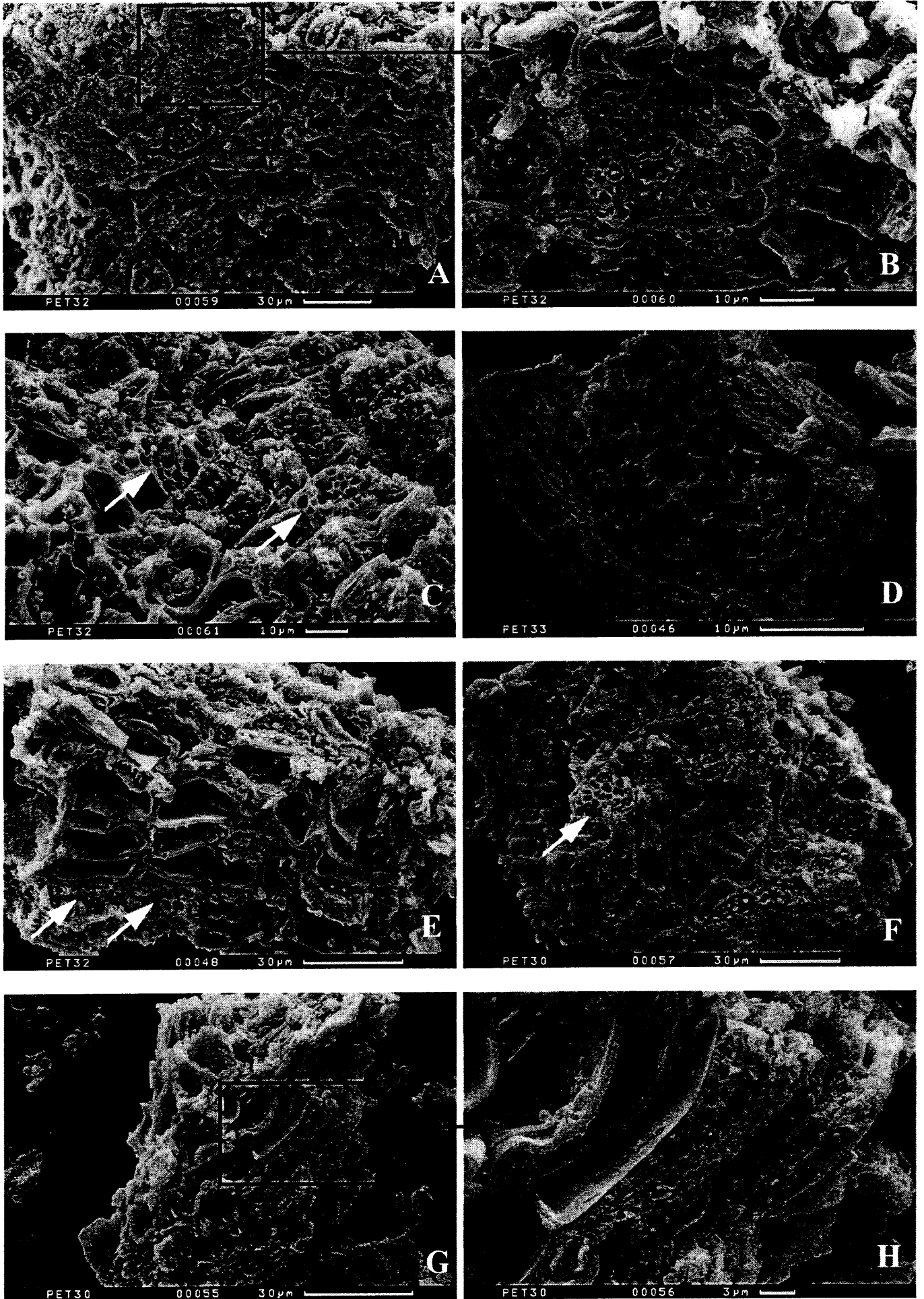


Fig. 71

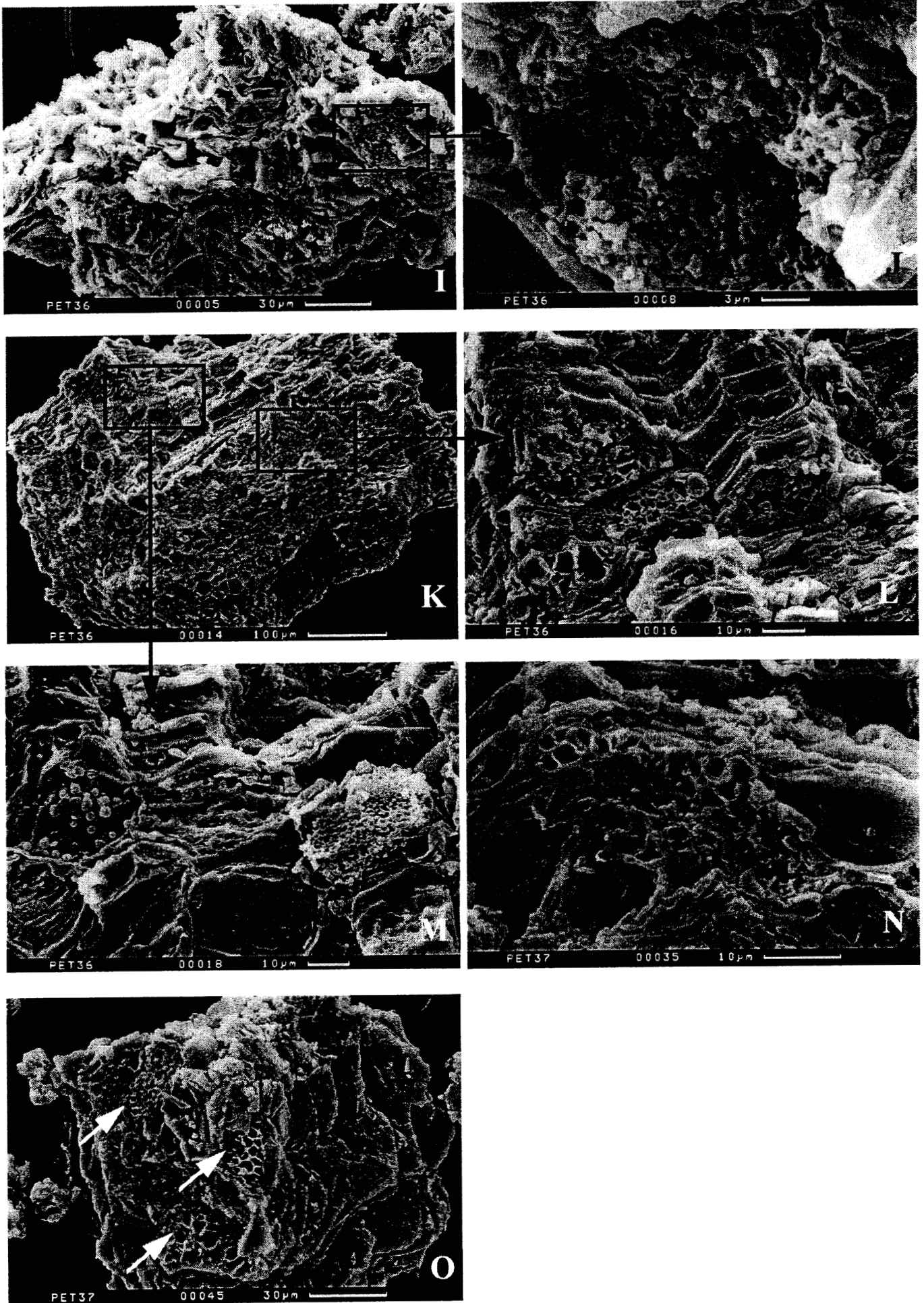


Fig. 71

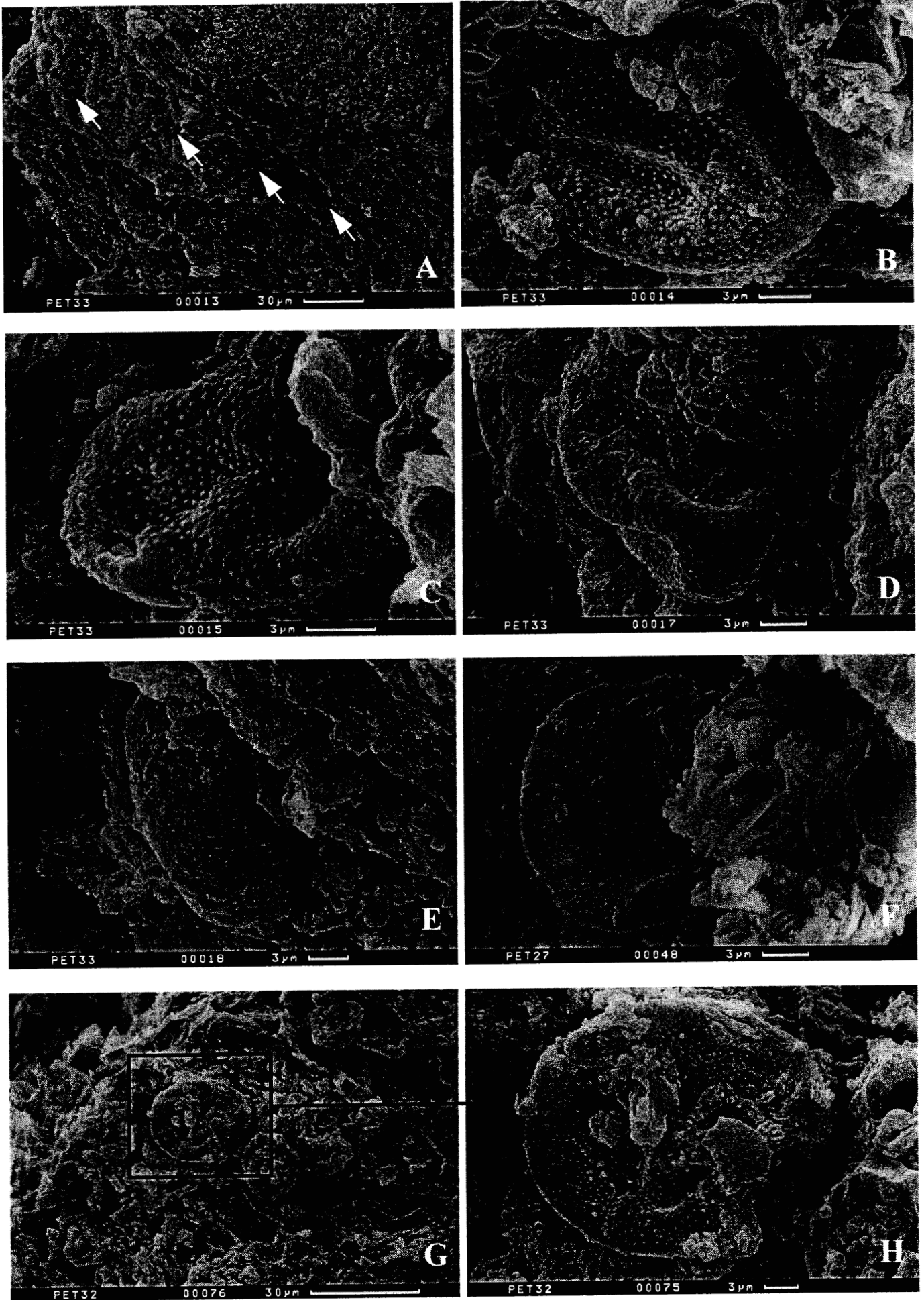


Fig. 72

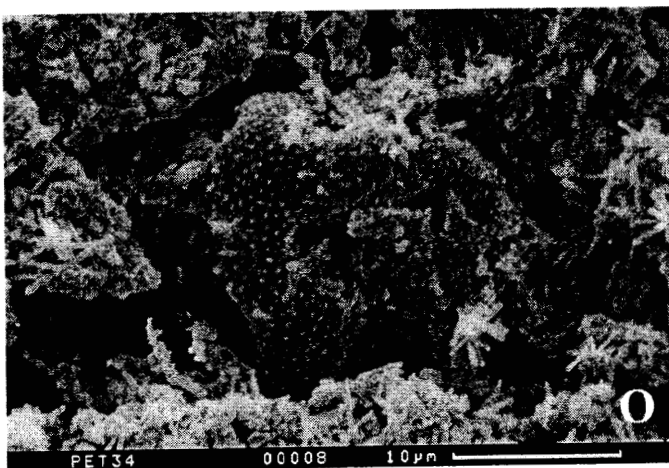
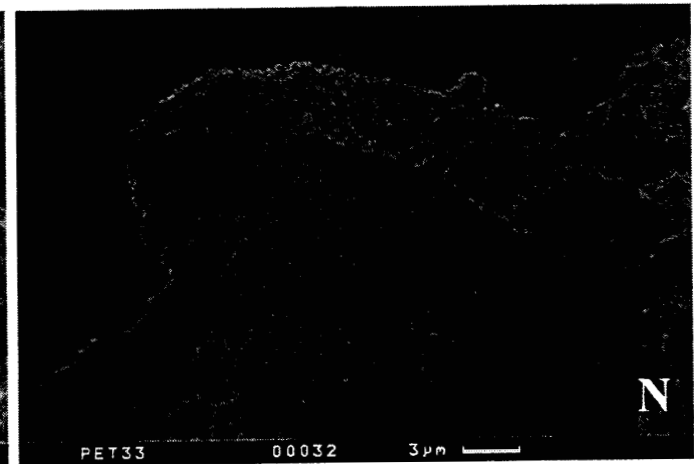
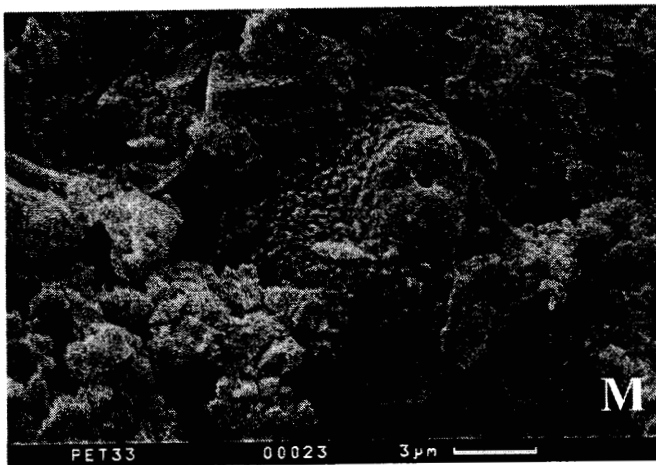
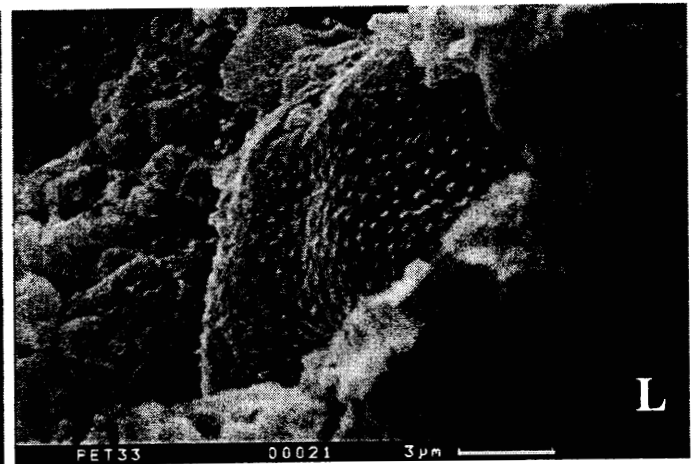
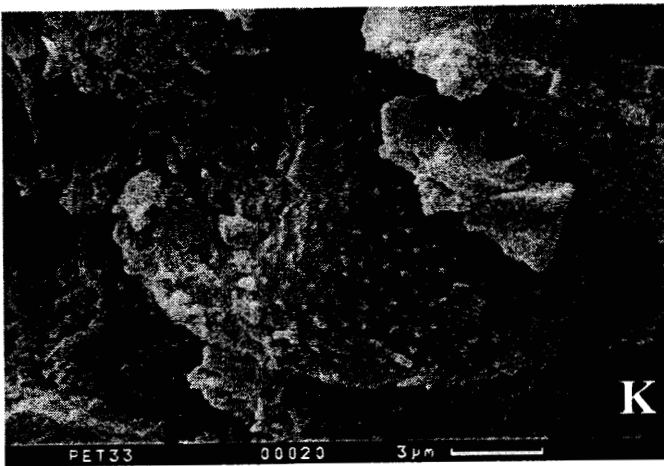
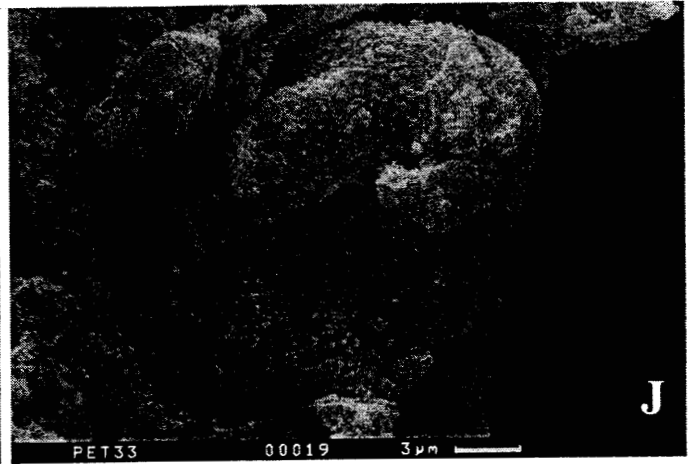
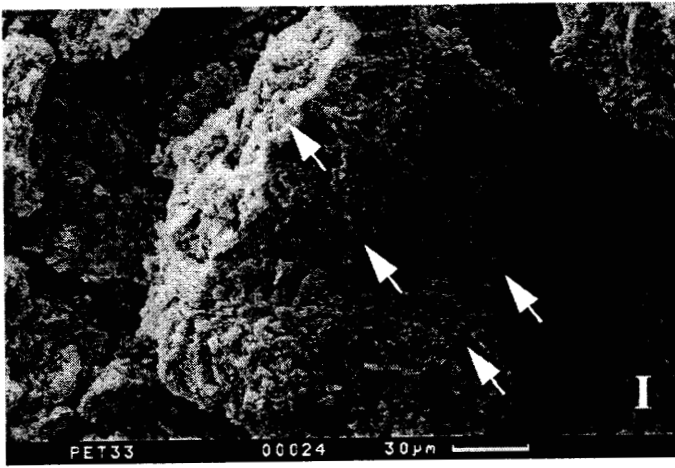


Fig. 72

4.3.1.2 Remains of arthropod exoskeletons

WDC-C-MG 122/123 and SMNK-PAL 3813 show a number of arthropod cuticula fragments (Fig. 73, Fig. 74), whereas in SMF ME 3516 no safe cuticular fragments could be identified. It is very difficult to identify arthropod prey from such small cuticular fragments. It cannot totally be excluded these fragments belong to Arachnida, but an attribution to insects is much more probable. Scales and leg armature of extant Lepidoptera and Trichoptera have been analysed in the SEM in order to develop a basis for prey identification in Messel insectivores (BASZIO & RICHTER in press, BASZIO & RICHTER in prep.). Unfortunately, most of the remains collected from the new genus and species do not belong to these two insect groups. But it is almost safe to assume that the partially thick layers of cuticula found here (Fig. 73E+F) belong to Coleoptera. A closer identification is almost impossible without further hints because of the immense diversity in this group (BASZIO, pers. comm.).

In WDC-C-MG 122/123 insect cuticula with a characteristic honeycomb- or weblike sculpture prevails, sometimes pores are present (Fig. 73). This pattern can be characterised by its more or less irregular elements in a “rooflike” arrangement. The single elements have a smooth surface and vary from 6-10 μm in length. This cuticula type can bear more or less evenly spaced, linearly arranged depressions (Fig. 73G-I). These small pores (approx. 7 μm) held true insect hair or scales. The cuticula layer is very thick (Fig. 73E+F), hinting towards coleopteran origin (BASZIO pers. comm.). The layers seem to be stacked, which could either represent a taphonomic effect or the presence of wing or elytra cuticula. A safe identification of these organs can only be made, if the curvature from the dorsal to the ventral part or the organ is visible (BASZIO, pers. comm.). Unfortunately, this is not the case in the fragments discussed above.

In the same specimen of the new genus and species, a different type of depressions is present on a cuticula fragment with the same pattern as described above (Fig. 73R+S): These depressions are more or less circular, with a diameter of approx. 28 μm . They have a small pore that is situated slightly outside of the centre of the depression. This hints towards a cuticula of scale-bearing coleopterans, such as can be found in the extant genus *Anthrenus* (BASZIO pers. comm.). It has to be stressed, that no attribution to *Anthrenus* sp. is intended at this point, as not enough structures are preserved and especially the characteristic scales are absent.

Some cuticular fragments in WDC-C-MG 122/123 show a hexagonal and pentagonal structures with an element size of approx. 5 μm (Fig. 73P+Q). An identification or characterisation of this cuticula cannot be given at the present time.

The insect cuticula in SMNK-PAL 3813 represents a different type. Its surface is smooth and structureless, but bears distinct pores with a vaulted margin on one side and a size of approx. 1.5 μm (Fig. 74E-O). The pores are densely spaced with a distance of approx. 5 μm from each other.

A peculiar pattern is present on a different cuticula fragment (Fig. 74A-D). Circular depressions with a diameter of approx. 5 μm are densely spaced. A sculpture is not present. Therefore, this cuticular type is different from the one described from WDC-C-MG 122/123. It is thinkable that it originates from a different part of the body or has a different function (sensory field?). Interestingly, the oilshale cast of this structure is also present (Fig. 74C+D). Although this cuticula cast is in direct vicinity to the former

described cuticula type, they do not necessarily belong to the same insect. Experience from insectivorous mammals shows that most different (identifiable) cuticulae from various lepidopteran families can be closely stacked one over the other (BASZIO, pers. comm.).

Other cuticular fragments from the same specimen show a thorn- or hairlike sculpture (Fig. 74P-T). It is safe to classify them as insect thorns in contrast to true insect hairs which always insert into pores. All of these thorns are broken off, or strongly compressed distally. They have a proximal width of 2 to 3 μm . No cuticular sculpture is identifiable, but the cuticula seems covered by some substance, perhaps wax. The distance between the thorns is approx. 7 μm . The very same fragment shows cross sections of wing venations (Fig. 74T-V) and therefore represents wing cuticula. The venation diameter is approx. 2 μm . The wing surface itself shows neither a sculpture nor the presence of pores for the reception of scales or true insect hair (apart from the described thorns). This excludes the scale-bearing insect orders Lepidoptera, Trichoptera and Diptera (Culicidae), but a closer identification cannot be given at this point. In one case, pores can be seen in the vicinity of a wing venation (Fig. 74T), a position, where true insect hair can be found in all extant insect orders. The thickness of the cuticula is approx. 2 μm . Lepidopteran wing cuticula is significantly thinner (partially less than 1 μm) whereas Coleopteran cuticula (ca. 5-8 μm) is thicker (BASZIO pers. comm.).

All of the cuticular fragments described above most probably originate from a variety of insects, a closer identification is not possible at the present time.

A different sculpture pattern on an insect cuticula consists of characteristic longitudinal ridges (Fig. 73T+U). This fragment originates from a Lepidopteran scale. It can be identified by the spacing of its longitudinal ridges (approx. 1 μm) and by the hardly visible, perpendicularly orientated, much smaller ridges which almost contact one another. Traces of the internal scale structure cannot be found as this scale is not as well preserved as in mammalian insectivores of Messel. This scale type corresponds to the one commonly found in the intestinal contents of the Messel bat *Palaeochiropteryx tupaiodon* (BASZIO & RICHTER in prep.). The question of whether this scale belongs to a moth or a dayflying butterfly cannot be answered at the present time. Fig. 73V+W shows an unidentifiable insect cuticular fragment with a longitudinal ultrastructure.

Following pages:

Fig. 73: Fragments of insect cuticula with a characteristic honeycomb sculpture in a “rooftile” arrangement found in the intestinal contents of WDC-C-MG 122/123. A-O: Characteristic rooftile arrangement. P+Q: Hexa- and pentagonal structures. S: Enlargement of R, honeycomb sculptured cuticula with circular depressions, comparable to the one of the extant scale bearing coleopteran *Anthrenus*. U+V: Fragment of a Lepidopteran scale with longitudinal ridges. W+X: Unidentifiable insect cuticula with longitudinal ridges. E+F: Thick cuticula, hinting towards coleopteran origin. B: Enlargement of A. D: Enlargement of C. H: Enlargement of G. SEM.

Fig. 74: Insect cuticula found in the intestinal contents of SMNK-PAL 3813. A-D: Cuticular fragment with densely spaced circular depressions, possibly representing some kind of a sensory field. C+D: Cast of the structure described in A+B. E-O: Cuticula with a smooth and structureless surface, bearing distinct pores. P-S: Cuticula with thorns. T-V: Wing cuticula with wing venations. SEM.

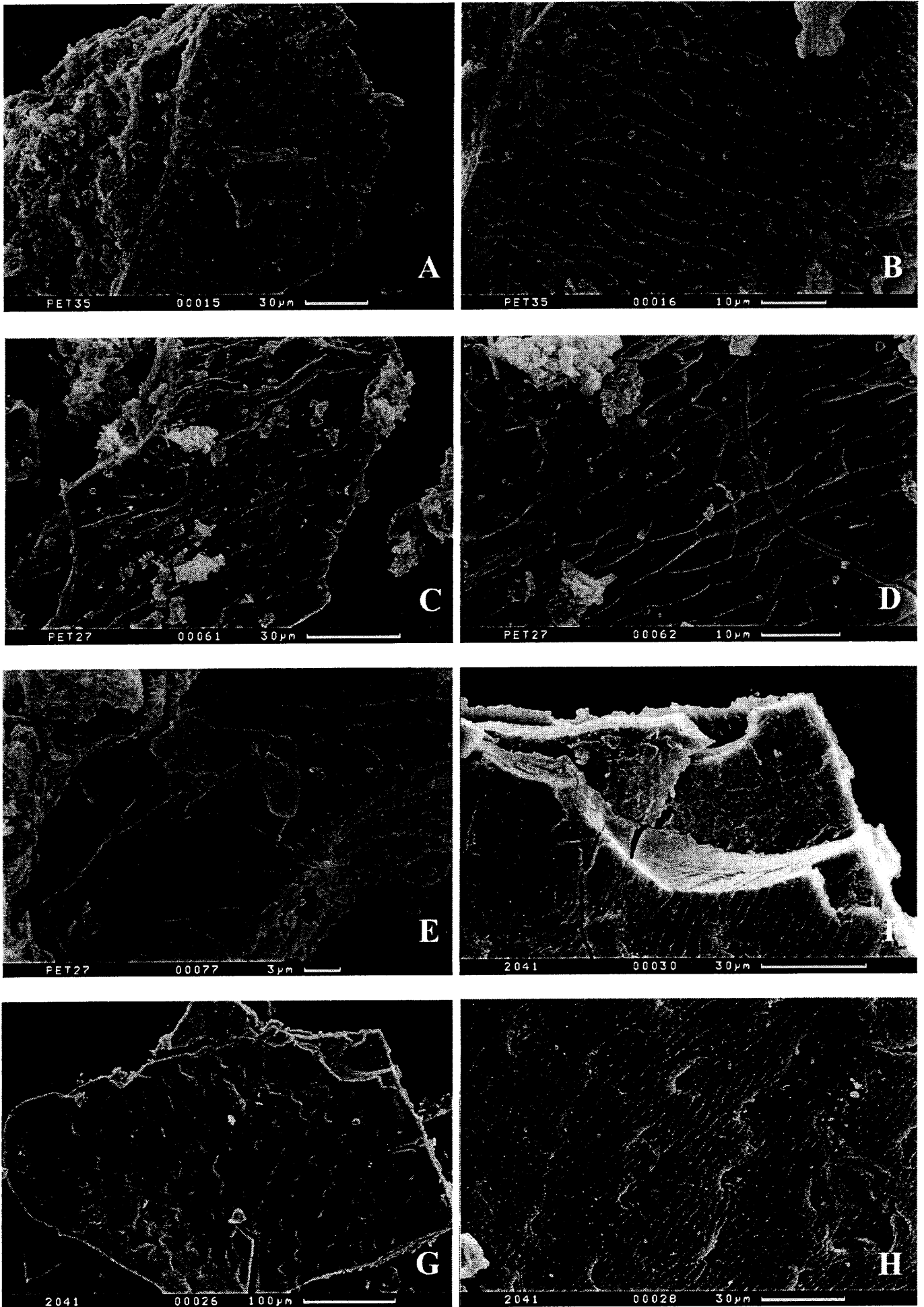


Fig. 73

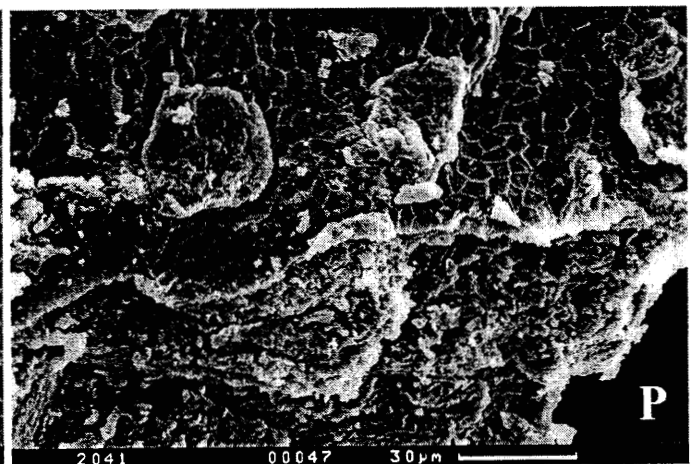
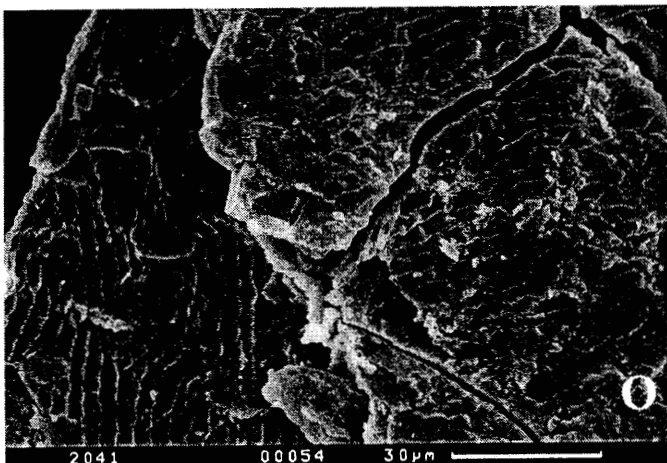
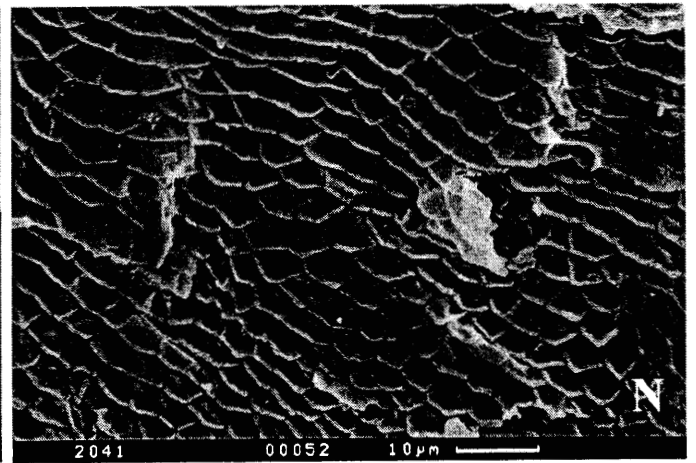
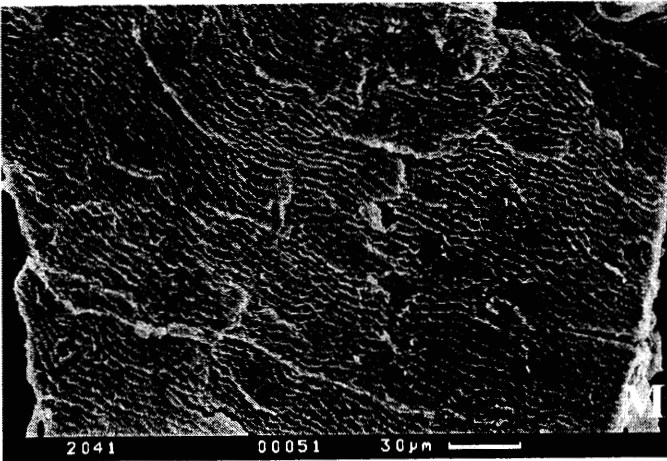
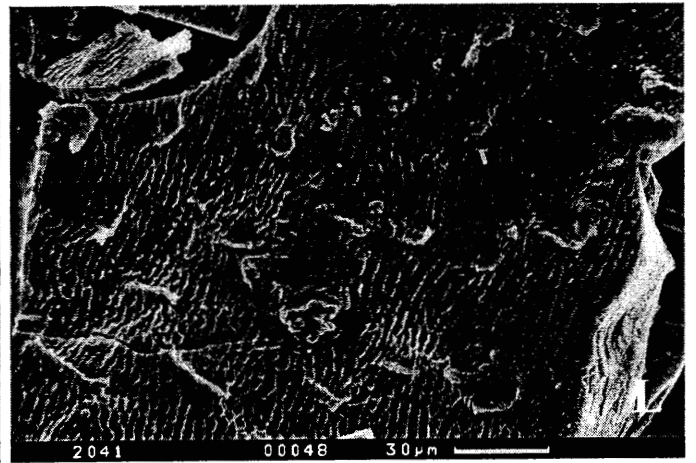
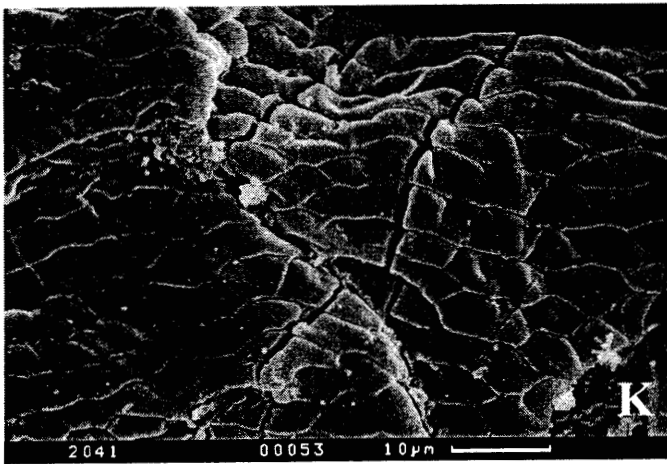
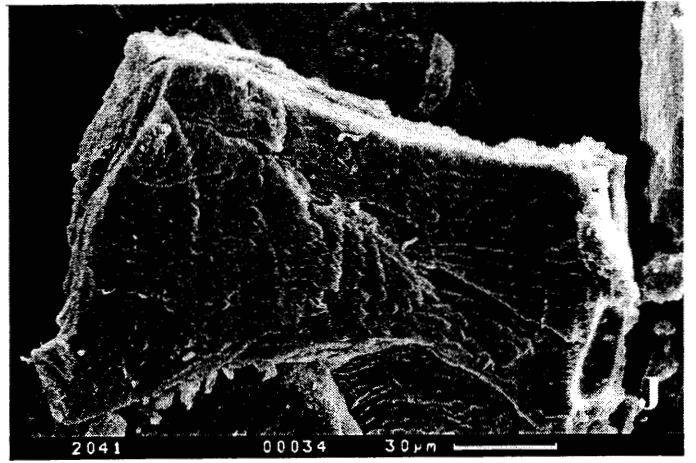
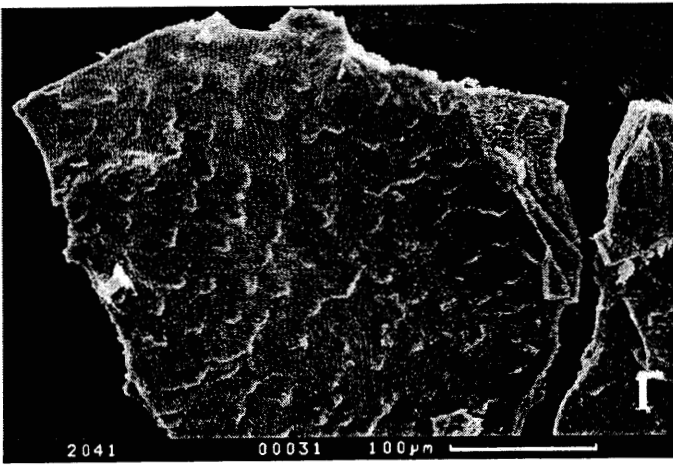


Fig. 73

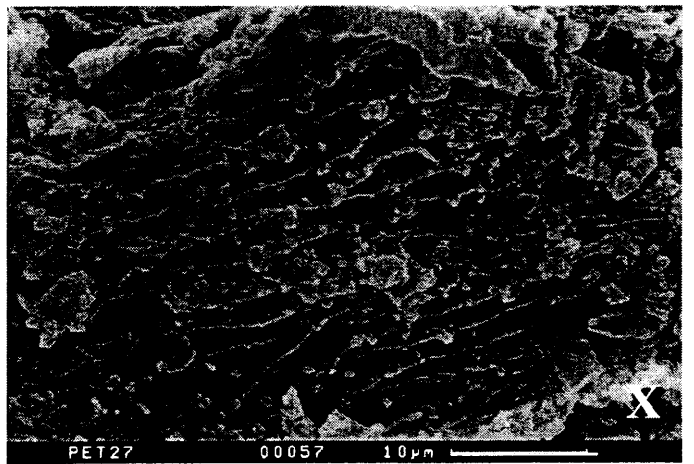
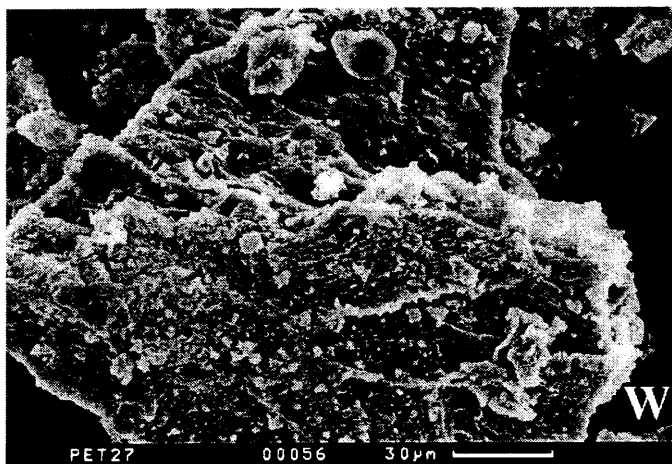
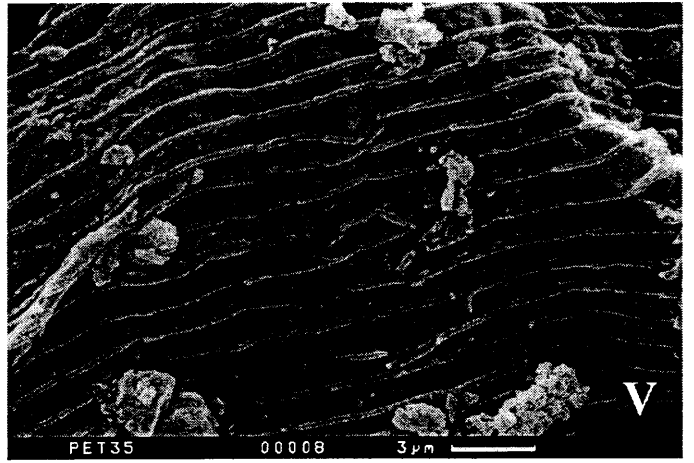
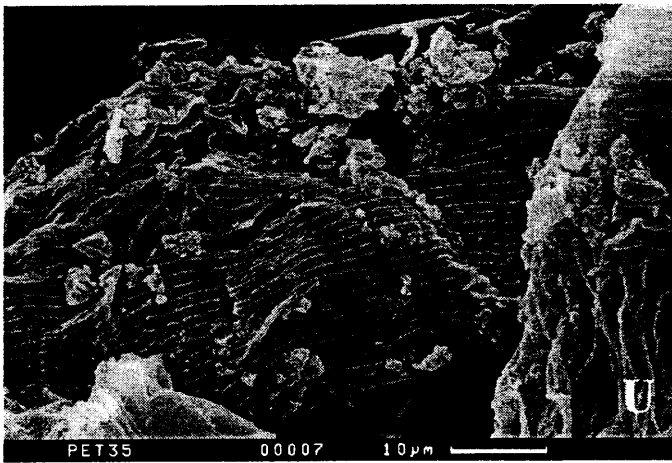
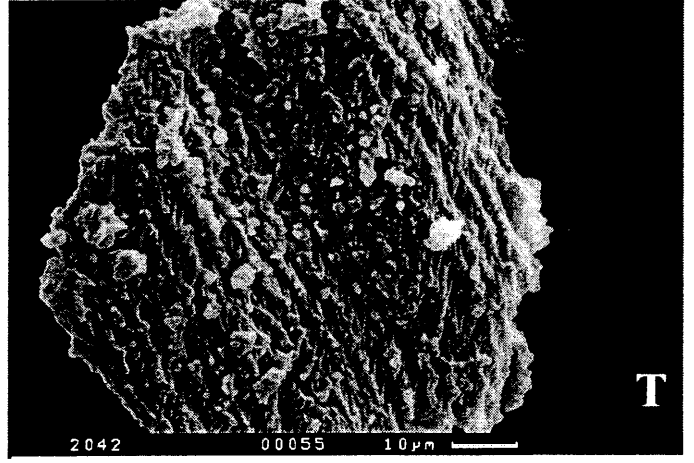
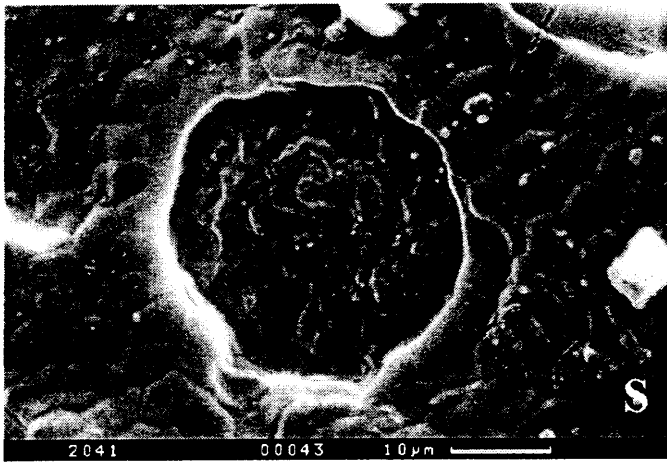
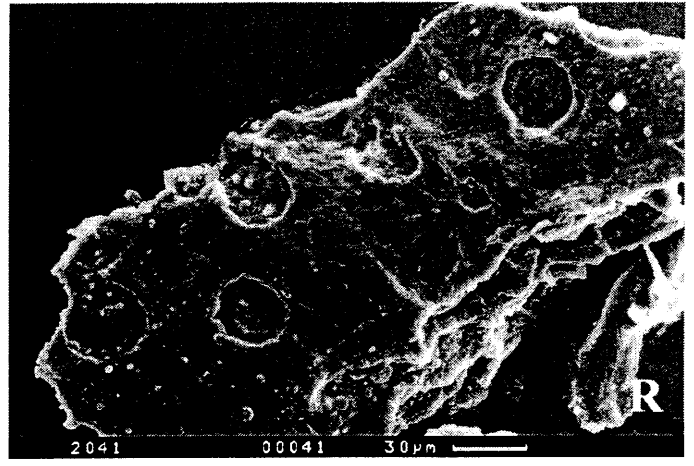
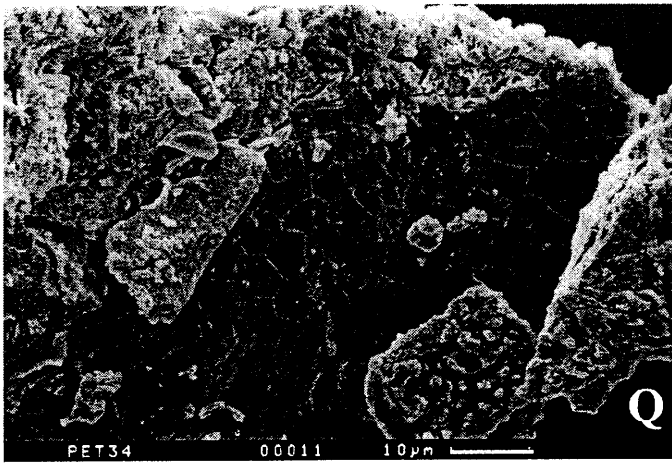


Fig. 73

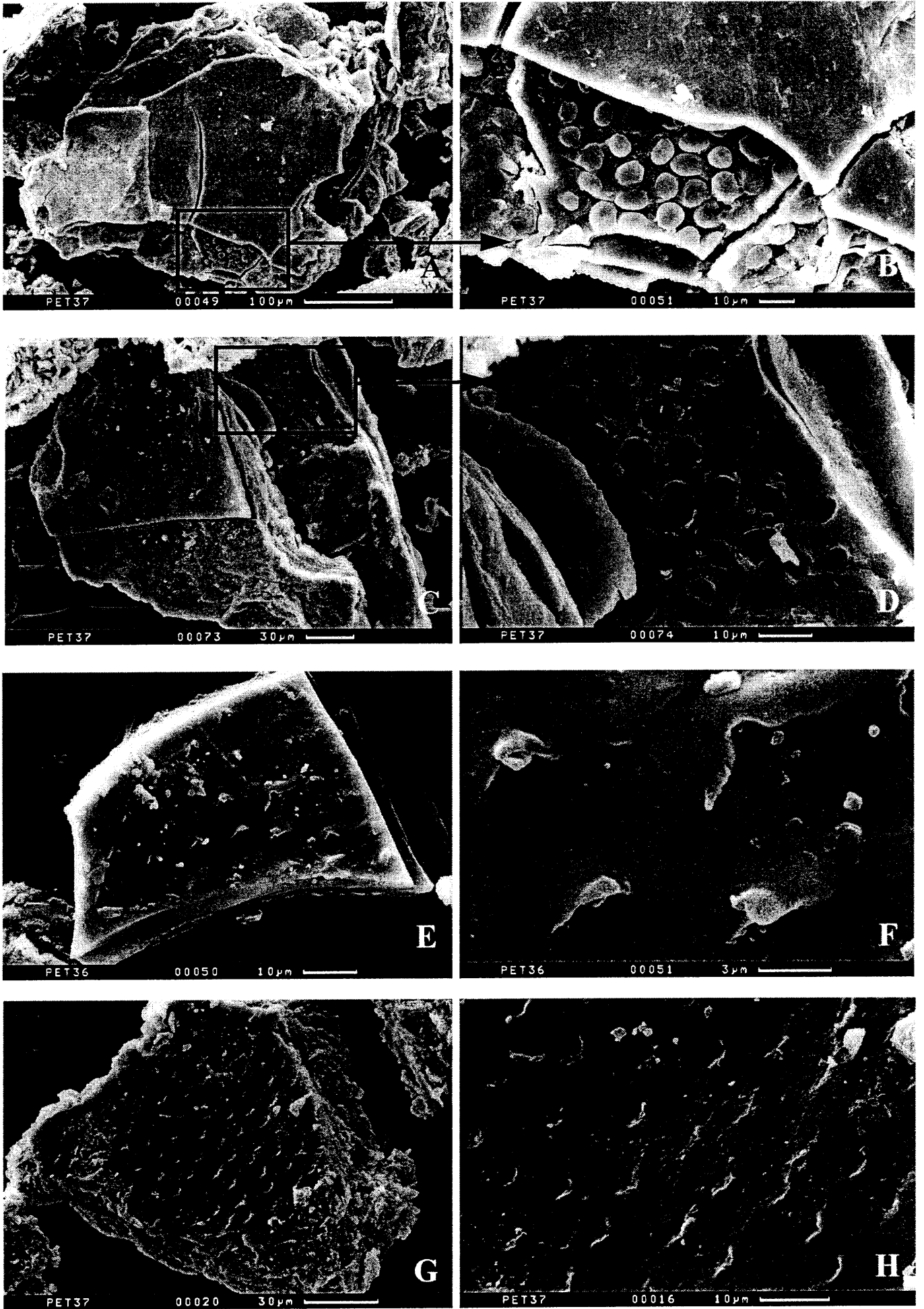


Fig. 74

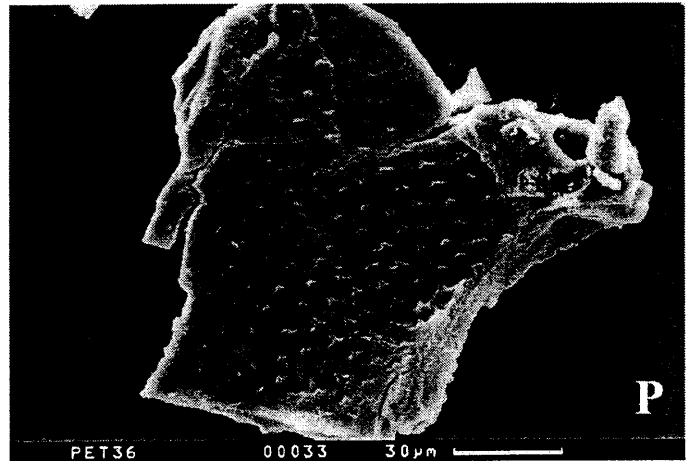
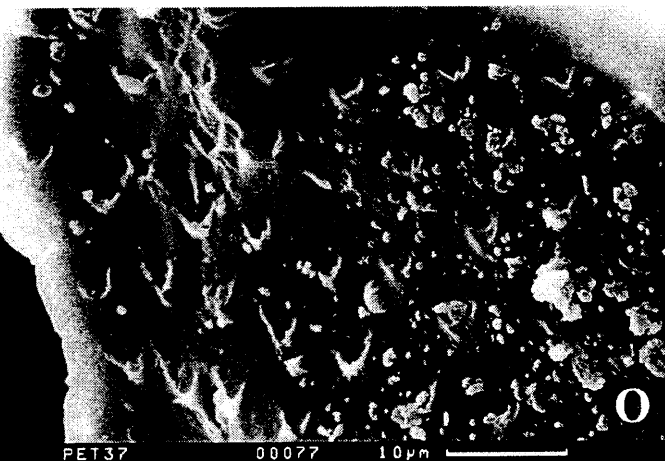
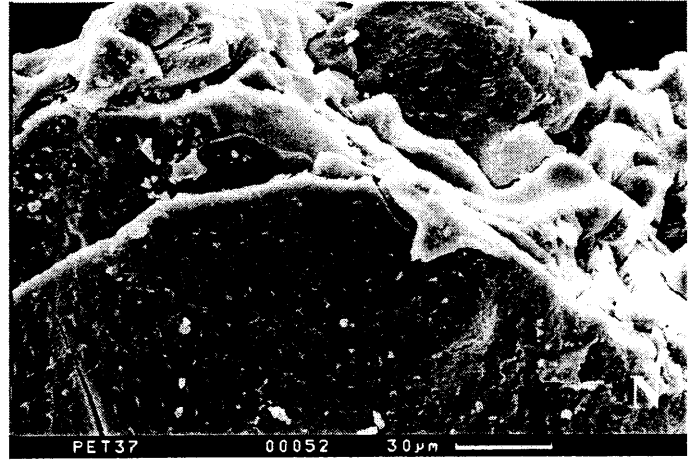
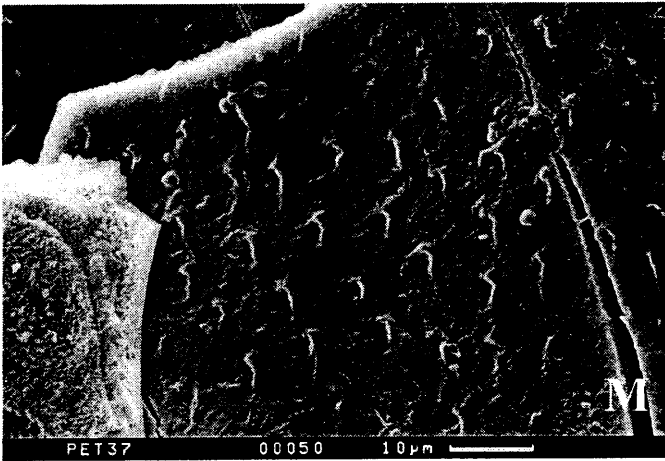
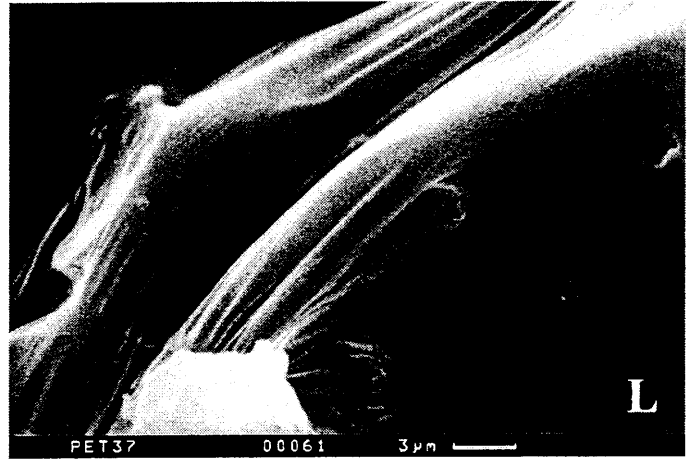
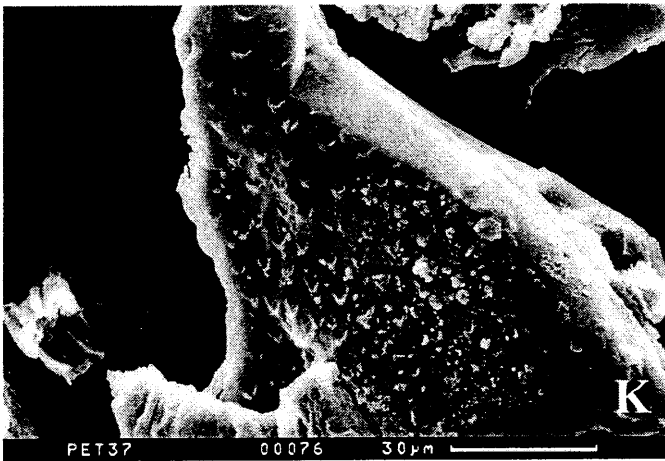
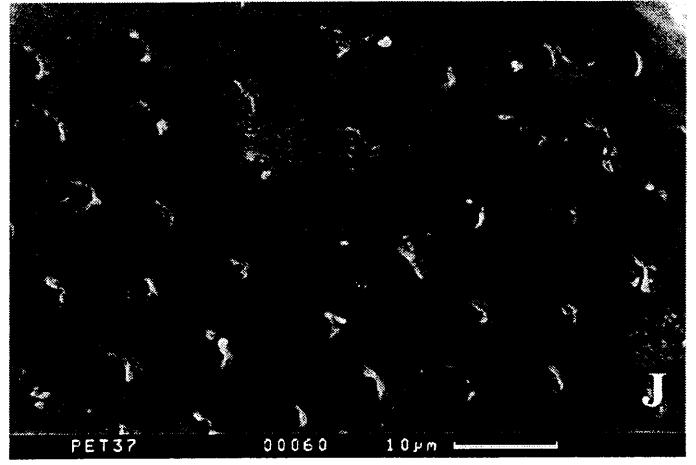
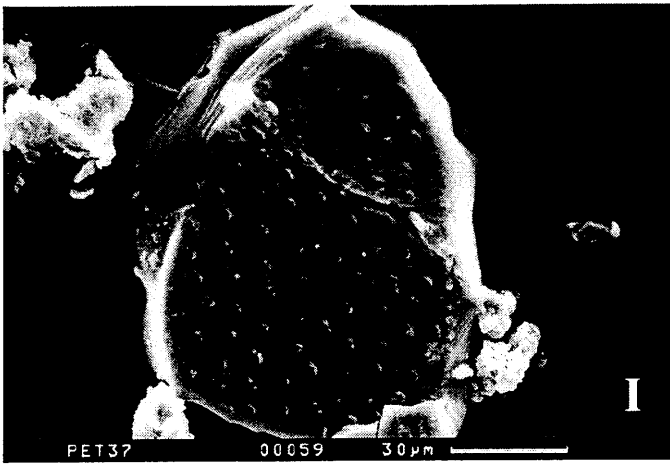


Fig. 74

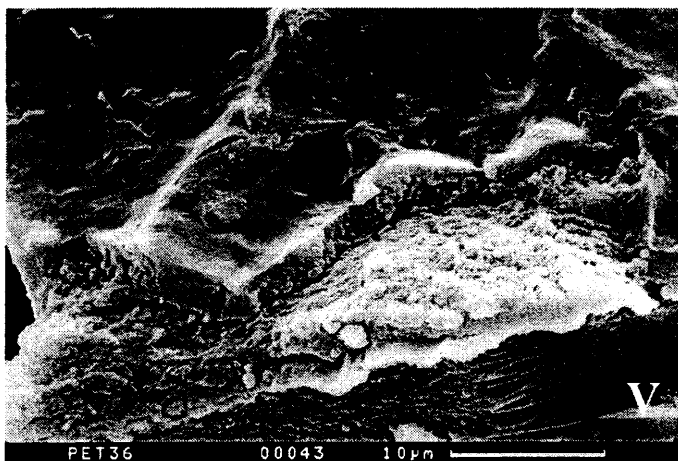
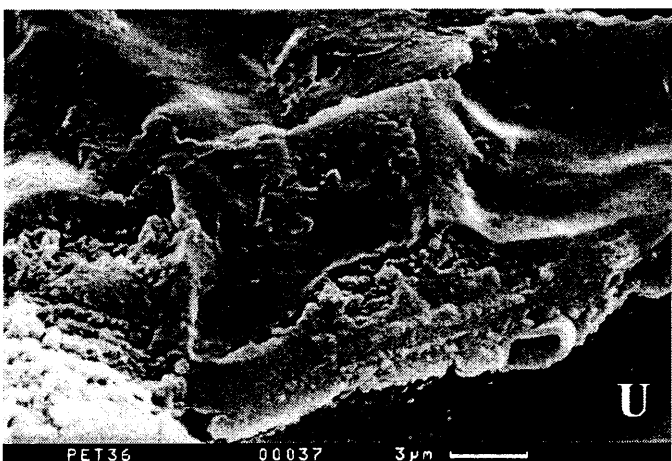
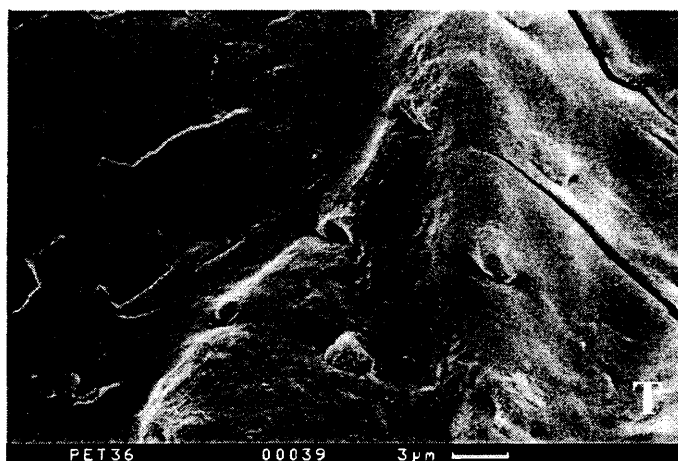
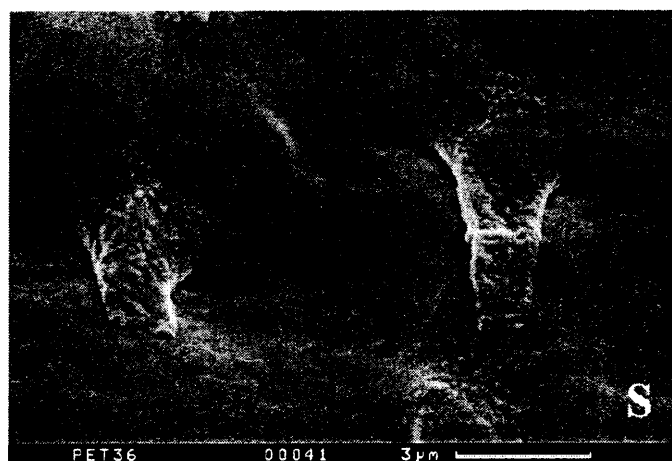
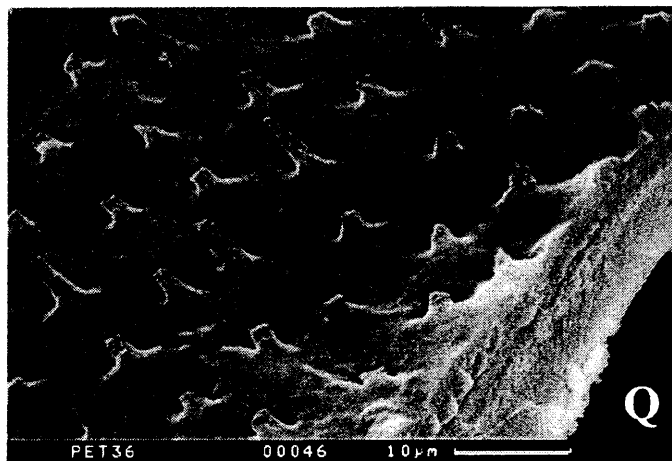


Fig. 74

4.3.2 Estimated weight of the new genus and species

An important information for the reconstruction of the ecological paleo-econiche in fossil species is the body weight. Therefore, it is attempted here to estimate this parameter for the new species based on literature and own measurements. POUGH (1973) investigated the relationship between body weight and snout vent length in lizards. In his analysis he included „Iguanidae“, Agamidae, Chamaeleonidae, Cordylidae, Gerrhosauridae, Scincidae, Lacertidae, Teiidae, Anguidae and Varanidae. He did not include any legless species and measured only those who appeared in good health and were neither fat nor thin. Unfortunately, he does not give a table where weight and length measurements are listed for the different representatives. Additionally, the data basis in the weight range from 200 g to 900 g is rather poor, represented only by five specimens. All of these weigh approximately 300 g and have a rather large size range from 16 to 28 cm. The graph is fitted by eye, which might explain the large differences in estimated weight with very small changes in snout-vent length. Unfortunately, the data are poorest in the length measurement range of the new taxon. Following POUGH (1973), the weight of the larger representatives (SMF ME 475a+b and 3516, SMNK 3813) ranges around 400 g, while the smaller specimens (SMF ME 1249a/b, WDC-C-MG-122/123) are estimated to approximately 60 to 100 g.

In order to verify these estimates, snout-vent length measurements and weights were taken from an extant lizard species with a snout-vent length comparable to the new genus and species: *Corucia zebrata*, an arboreal scincid (Scincoidea) which also has a relatively large head. One juvenile and two older specimens were available. These lizards can reach a snout-vent lengths over 30 cm (PARKER 1983). The snout-vent lengths of the two older ones were about one cm larger than the largest specimen of the new species, the juvenile about one cm shorter than the smallest specimen. (Tab. 8). As only alcohol material was available, a correction factor of 0.86 was applied to the measured weight in order to take the preservation liquid into account (POUGH 1973). Based on the measurements taken from *Corucia zebrata*, the weight estimate for the new taxon is roughly 260 -300 g for the smaller specimens and around 600 g for the larger ones (Tab. 8). The limbs and tail were relatively longer than in *Corucia zebrata*, so it was probably a little heavier.

In spite of the large divergence between both estimates, it seems safe to assume that larger specimens of the new species weighed (probably much) more than 400 g. SOKOL (1967) and POUGH (1973) point out that heavier lizards (above 300 g) tend to a herbivorous nutrition because it is energetically inefficient for a large animal to hunt. It has to utilise plant material that is readily available and requires only little energy (POUGH 1973).

Taxon	Snout-vent-length [mm]	Weight [g] after POUGH (1973)	Measured weight [g] (alcohol material)	Calculated weight [g] with correction factor
<i>Corucia zebrata</i> SMF 81047	228	400	700	602
<i>Corucia zebrata</i> SMF 81048	230	400	690	593
<i>Corucia zebrata</i> SMF 81049	120	50	300	258
new taxon SMF-ME 475a	220	400	-	estimated 600
new taxon SMF-ME 3516	203	350	-	estimated 600
new taxon SMNK-PAL 3813	200	350	-	estimated below 600
new taxon WDC-C-MG 122/123	160	100	-	estimated 300
new taxon SMF-ME 1249a/b	130	60	-	estimated 260

Tab. 8: Snout-vent-lengths and weights of three specimens of *Corucia zebrata* and the new taxon reconstructed after the diagram in POUGH (1973). The extant alcohol specimens were measured and weighed, showing large differences from the estimation figures based on literature, even when the preservation liquid is taken into account, for which POUGH (1973) suggests a correction factor of 0.86.

4.3.3 Tooth morphology in the new genus and species

A detailed description of the teeth (conical, monocuspid teeth with lingual striations and lateral cutting edges) has already been given in the taxonomic part of the present work. The significance of their morphology will be discussed below.

4.3.4 Cranial kinesis in the new genus and species

As the head osteoderms cover the dorsal aspect of the skull including the frontalia and even part of the nasalia, a kinesis between frontal and parietal (mesokinesis) obviously was prohibited. Whether any metakinesis was possible in the new taxon is a matter of speculation as none of the crucial elements is accessible. Apart from this, the knowledge of kinesis of extant Lacertilia is often gained from cinematographic investigations. In the new species the cranial kinesis might be limited to streptostyly. A lack of cranial kinesis is also reported for the Scincidae *Corucia zebrata*, *Tiliqua scincoides* and *Trachydosaurus rugosus* (HERREL et al. 1998; DE VREE & GANS 1987, 1989). All of these species are mainly herbivorous, but insects and invertebrates (snails) can also be part of their diet (COGGER & ZWEIFEL 1992, TRUTNAU 1986, BECH & KADEN 1990).

HILDEBRAND (1988: 622) states that carnivorous lizards (employing inertial feeding, gulping their food) tend to have light heads, making it easier to accelerate. In contrast plant eating, lingual feeding lizards have rather large heads, another argument that the new species with its large heavy head is mainly herbivorous.

4.4 Discussion

4.4.1 Tentative diet reconstruction for the new genus and species

The gut contents of all three specimens mainly consist of plant material, which would suggest the new genus and species as primarily herbivorous. The presence of some insect cuticulae in two specimens indicate either unintentionally swallowed insects or an additional food resource. The body weight estimate also classifies it as a predominant plant-eater (according to the classification method in POUGH 1973). The covering of the frontoparietal suture by osteoderms obviously prohibited mesokinesis, which would be important for seizing prey. So, the large, rather akinetic skull makes agile predation rather improbable. All three independent lines of evidence hint towards a primarily vegetational diet, of course with the option of catching insects at certain times.

Peridermal tissues and remains of twigs or stalks represent the main part of the plant remains from the intestinal contents. In all three specimens peridermal (resp. cork) tissue was identifiable, two of them had remains of twigs or stalks. Although the number of available individuals is low, the fact that the same structures were identified in two or all three specimens suggests that an actual food resource is identified instead of accidentally swallowed plant remains. But no leaf cuticula was found. Obviously, this arboreal lizard fed predominantly on young twigs; a very unexpected and unusual ecological “niche”. The question arises, whether tasty ethereal oils or resins led to the feeding of those plant elements. Additional food obviously consisted of fruits, seeds and insects. The identified pollen in one of the specimens (WDC-C-MG 122/123) is not valuable as a hint to a food resource, as pollen occur everywhere and are often found in the Messel sediments. Additionally, Juglandaceae were quite common in Messel (WILDE, pers. comm.). Still, it is quite striking, that two catkins with few remaining pollen in situ could be identified in the stomach contents. This makes it rather improbable that these were eaten unintentionally.

As indicated above, there are taphonomic biases which influence type and abundance of preserved structures and plant material is more resistant than animal tissue (RICHTER 1988). But although additional food sources cannot be wholly excluded, the abundance of plant material, respectively twig remains, is obvious and most peculiar in the sense that no extant lizard is specialised on that kind of food. However, WILSON & LEE (1974) state that “the majority of herbivorous lizards probably depend largely upon leaves and small stems”, where fruit and flowers are not available – an assumption that most probably does not hold for the Eocene Messel biotope.

It appears that the conical teeth are of the “omnivore type”. The generalised tooth shape of the new genus and species is capable of coping with all kinds of food. Although it seems to be quite a specialised herbivore, the teeth do not show special adaptations for this food. But most of the mainly herbivorous or omnivorous members of the Scincoidea have no specialised tooth shape. So in the new taxon the conical tooth shape with its lateral cutting edges was probably sufficient to chop off small twigs. To my knowledge, there is no information on the function of lateral cutting edges in literature. Furthermore, twigs are not the only food resource for this lizard, insects and fruits/seeds probably also were part of its nutrition. But some physiological adaptations were probably needed to digest the food efficiently (see below). It is conceivable that in this very specialised lizard group, the herbivore mode of life could have led to a morphological adaptation of

the teeth in the course of evolution. Still, it is advantageous to retain a generalised tooth morphology in order to have the option to exploit different food resources. In any case, more research needs to be done on tooth morphology correlation to diet.

4.4.2 Herbivory in lizards

According to SOKOL (1967) “there are very few, if any purely herbivorous lizards. Most of the so-called herbivores take some animal matter. There is a complete cline from primarily herbivorous to primarily carnivorous forms [...]”. The infraorders Iguania and Scincomorpha seem to have the greatest number of omnivores and herbivores (SOKOL 1967). Even though according to SZARSKI (1962) lacertilian herbivores do not utilise their food efficiently, the ready availability and sheer volume may compensate for inefficient utilisation. As SZARSKI (1962) and POUGH (1973) state, it is remarkable that only a few modern reptiles are known to be predominantly herbivorous, although plant food is more abundant and much easier available than animal food. As has been shown, the new genus and species is most probably a representative of an arboreal and herbivorous scincoid in the Eocene. Today, only a few extant herbivorous species belong to the families „Iguanidae“, Agamidae, Scincidae, and Teiidae (SZARSKI 1962). The same author finds it “astonishing that no radiation ever took place among plant eating lizards”. In my eyes, there is no reason why such a radiation should not have taken place under certain circumstances, although fossil evidence for such a radiation is difficult to find. It is thinkable that the insectivorous “niche” was taken by competing mammals. As a consequence, lizards as the new taxon could have been forced into the herbivorous niche because they are less agile than mammalian representatives.

Herbivorous lizards have to develop some strategies to avoid predators: they live on islands which lack predators (like the two iguanids *Amblyrhynchus cristatus* (when on land) and *Conolophus subcristatus* on the Galapagos islands and *Corucia zebrata* on the Solomon Islands), the agamid *Uromastix* possesses a spiny tail as a defence against predators or they seek refuge in trees. Most herbivorous lizards are larger than their carnivorous relatives and consequently are sought by fewer kinds of predators (SZARSKI 1962). Potential predators around the Messel lake could have been Carnivora (SPRINGHORN 1980, 1982), Creodonta (an extinct carnivorous order of mammals, SPRINGHORN 1982, MORLO & HABERSETZER 1999), several terrestrial crocodiles (KELLER & SCHAAL 1992b, ROSSMANN 1999) and most probably snakes (BASZIO, pers. comm.). In Eocene times, the pressure by mammalian predators was by far not as high as in modern ecosystems. This is due to the fact that modern Carnivora were not as highly evolved and radiated. As a highly arboreal and quite large Scincomorph, the new genus and species was rather safe from arboreal creodonts and snakes and probably was therefore able to feed on branches and twigs with low danger of being caught by these predatory groups. Today this very niche is filled more effectively by herbivorous mammals whose capability of quick flight probably has coevolved with arboreal predators of all kinds. In comparison insectivorous lizards have to be quicker and more agile from the start in order to catch their prey. Consequently, they have a metabolism high enough to escape mammalian predators.

4.4.3 Jaw mechanics

The plesiomorph condition in lizards is the reduction of the lower temporal arch, which is an advantageous evolution for the expansion of the jaw musculature. According to RIEPEL & GRONOWSKI (1981) “the loss of the lower temporal arcades obviously removes constraints upon the architecture and size of the jaw musculature and may have

been an important factor in the emergence of the squamate reptiles.” However, this loss causes a potential instability of the skull where the quadrate is no longer stabilised (RIEPEL & GRONOWSKI 1981, HERREL et al. 1998). In many lizard species, firm ligamentous connections (jugomandibular and quadratojugal ligaments) are found in a similar position where the lower temporal arch was situated. HERREL et al. (1998) propose – as CLEUREN et al. (1995) suggested for crocodylians – that these temporal ligaments have a stabilising function for the quadrate during feeding. LAKIER (1926) even homologized the quadratojugal ligament with the reduced quadratojugal bone. The results of IORDANSKY (1996) and HERREL et al. (1998) give hints that there is a link between ligament insertion and degree of skull modification: **Jugomandibular ligaments** appear to be confined to robust skulls in which only the lower temporal arcade is reduced (plesiomorph construction), whereas **quadratojugal ligaments** seem to be allied to skulls with further skeletal modifications (loss of upper temporal and/or postorbital arches, mobile construction). The same authors further postulate that the jugomandibular ligament emerged “in forms built for strenuous biting which are further characterised by robust, largely akinetic skulls.” The shift of the ligament insertion from the quadrate to the lower jaw “can help to protect the joint against the consequently higher joint forces [...]”. As the new genus and species has a robust, largely akinetic skull, it probably possessed such a **jugomandibular ligament** as well and was thus capable of strenuous biting. But due to its large posterior process of the jugal, the ligament must have been shorter than in extant lizards (Fig. 75). As a consequence the jaw musculature could not expand as much but the quadrate was better stabilised. This condition seems to represent a transitional stage in the evolutionary reduction of the lower temporal arch.

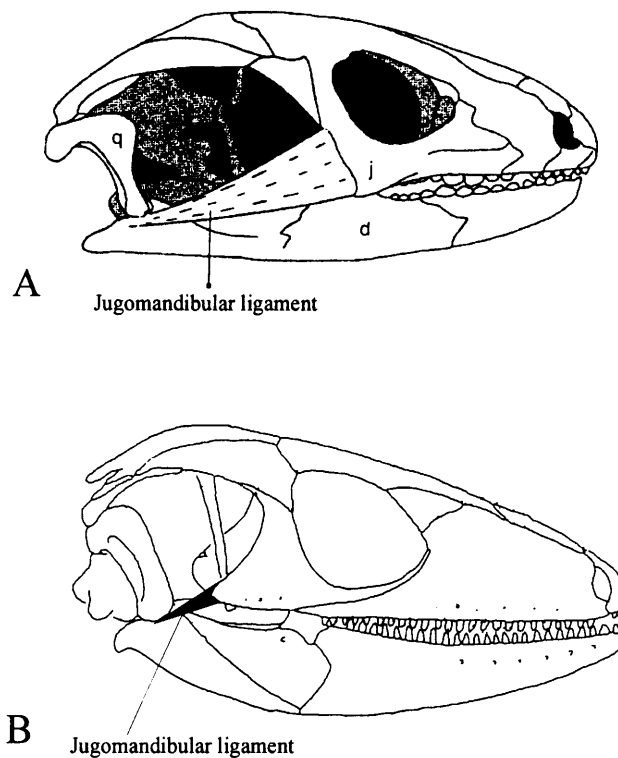


Fig. 75: Temporal ligaments. A: The Jugomandibular ligament in the skink *Tiliqua scincoides* (from HERREL et al. 1998). B: The jugomandibular ligament reconstruction of the new taxon.

The tooth row in the new species is extremely elongated. It reaches back as far as the posterior margin of the orbit. This arrangement is not found in any extant lacertilian, as far as I know. But there seems to be a trend of a tooth row prolongation in herbivorous representatives, as in *Iguana iguana* and *Cyclura cornuta*, where the tooth row reaches back half of the orbital length. In contrast, the carnivorous *Varanus salvator*, *Lanthanotus borneensis* and *Heloderma suspectum* have tooth rows that reach only the anterior margin of the orbit. As far as I know, a functional cause for this relation is not yet understood. One reason could probably be more strenuous biting for processing tough plant tissue in contrast to comparatively mellow fleshy food: The largest bite force occurs proximal to the hinge. So it is advantageous that the tooth row extends into this area. But further investigations have to be undertaken to verify this observation.

The high coronoid process present in the new genus and species probably serves as a structure to enhance bite force, which is also useful for the processing of high fibre food. LUNDELIUS 1957 states that a jaw with a longer posterior segment cannot exert as great a force, but produces a faster jaw closure. KING (1996: 10) describes different biomechanical principles that were developed in reptiles to increase bite force by elongating the moment arm. The latter is a line drawn from the jaw hinge at right angles to the vector of the jaw muscle. The bite force is increased when the muscle inserts anteriorly on the mandible, when the jaw hinge is elevated or depressed or when the muscle inserts on the coronoid process (Fig. 76). The exceptionally high coronoid process in the new taxon would cause a long moment arm, increasing the bite force.

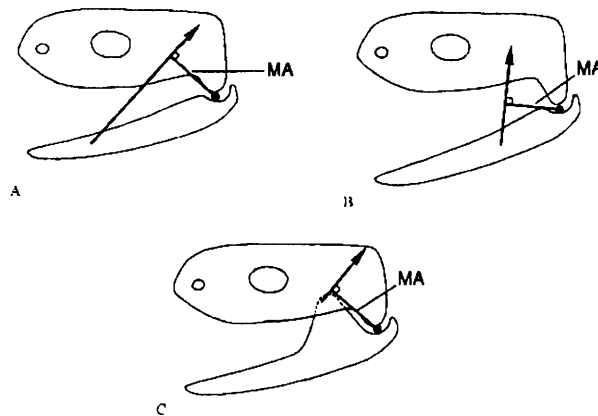


Fig. 76: Diagram illustrating the effect on the moment arm of various skull modifications. A: When the muscle inserts anteriorly on the mandible; B: When the jaw hinge is elevated or depressed; C: When the muscle inserts on the coronoid process (from KING 1996).

4.4.4 Digestive abilities

Based on the diet reconstruction, the question arises how the new genus and species was able to digest considerable quantities of cellulose. SZARSKI (1962) notes that plant food is digested with more difficulty than animal food. He points out, that in contrast to mammalian and avian herbivores, reptiles do not possess such highly efficient grinding devices and do not make use of symbiotic bacteria, fungi, and protozoa. „It is therefore

probable that herbivorous reptiles use only a small part of the calories potentially available in their food. In consequence, they may have a low metabolic rate and their females produce fewer eggs than females of related carnivorous forms. As a result, plant-consuming lizards would be more susceptible to predation, and here lies the factor which may always have hampered their radiation” (SZARSKI 1962). Since lizards do not have sophisticated masticatory adaptations, the food remains are well preserved. This corresponds well with the observed intestinal contents of the new taxon.

However, already POUGH (1973) considers the absence of symbiotic micro-organisms in the guts of all herbivorous reptiles as incorrect in some cases and gives several examples from lizards. According to NAGY (1977) there are herbivorous lizards such as the iguanid *Sauromalus obesus* (Chuckwalla) which can develop cellulase activity with a digestion and assimilation appearing to be similar to that of a non-ruminant mammalian herbivore. As *Sauromalus obesus*, these have small simple acidic stomachs but with enlarged intestines with a caecum. This cellulase activity indicates a symbiotic intestinal flora. Furthermore iguanine lizards can have a modified gastrointestinal tract with complicated valvular partitions in the colon (IVERSON 1980). The same author suggests that the colic partitioning present in several herbivorous species of the „Iguanidae“, in *Corucia* (Scincidae) and *Uromastix* (Agamidae) is related to the evolution of herbivory in these lizards. This modification of the colon is proposed to be advantageous to increase the internal absorptive surface area with only little increase in volume, to retain food longer so that it can be thoroughly digested and providing stable microhabitats for micro-organisms (IVERSON 1980, KING 1996). So if the new genus and species primarily fed on such hard digestible plant matter as twigs, it can be assumed that it had to have such a modified gastrointestinal tract in order to digest its food more or less efficiently.

Of course, there is no evidence for the presence of a specialisation towards herbivory in the digestive tract of the new genus and species. Only in a single case a compartment for the digestion of plant remains was identified in *Hallensia* (Perissodactyla) from Messel (FRANZEN 1990). A similar identification of intestinal tracts cannot be expected in other specimens. In any case, it must be assumed that the new taxon was adapted to digest large quantities of plant material. This seems not impossible, since at least in some cases, the same physiological level was already present in the Eocene as it is today. As an example, it has been shown by HABERSETZER et al. (1992, 1994), that a Messel bat species (*Palaeochiropteryx tupaiodon*) was capable of active ultrasonic insect hunting, as do modern bats, based on the analysis of the cochlea and intestinal contents.

As a mainly herbivorous lizard, the new genus and species probably had a fleshy tongue, because this would be important to secure leaves, stems, and flowers “attached to the main body of the plant which tends to pull the leaf back out of the lizard’s mouth [...]” Herbivorous lizards cannot swallow the plants as a whole as insectivorous lizards do with their prey, so they have to crop their food first. The food is not chewed, so whole chunks of plant material enter the gut where reduction takes place (THROCKMORTON 1976). In the new species the tongue was probably not used for lingual prehension, that means a protrusion of the tongue beyond the mandible. This is common only in all living members of the Iguania and not found in the Scleroglossa (Gekkota, Scincomorpha + Anguimorpha). These groups solely ingest by jaw prehension, a condition which apomorphically characterises this group (WEISHAMPEL 1995).

This study shows the importance of detailed qualitative and quantitative investigations in extant Lacertilia. It is only on this basis, that sufficiently reliable statements can be made on the palaeobiology of fossil lizards. In some cases, it is even difficult to define the microhabitat, syn- and autecology of extant species, because of lacking field observations. Only if data are available for a large number of extant species, a comparable approach can be taken for the fossil ecosystem of Messel.

4.5 “Synecology” of Messel Lacertilians and arboreal vertebrates

Several Lacertilians from Messel have been described. Interestingly, everyone of them represents a different ecomorph: *Eolacerta robusta* is supposed to be a generalised lizard that mostly dwelled on the bottom of the Messel woods, perhaps sometimes showing tendencies to climb with its strong claws. Its diet probably was as unspecialised as the microhabitat. The living animal may have had the habitus of the extant lacertid *Timon lepidus*, but significantly larger, as it is one of the largest Lacertilians ever found in Messel (MÜLLER, J. 1998, 2001). *Geiseltaliellus longicaudus* possibly was a facultative bipedal runner, thus being a cursorial, highly active member of the Messel Herpetofauna. Because of its long tail and morphology of the claws, it was also able to climb fairly well. The long tail could have served as well as a balance when running on the hindlimbs or when climbing in the branches. It probably fed on fruits and small animals (ROSSMANN 1992, 2000). Typically ground dwelling and burrowing is the mode of life of the anguid lizard *Ophisauriscus quadrupes* with its strong osteodermal armour. The strong and pointed teeth were probably useful for eating insects and snails. This lizard “could have lived in areas densely covered with medium high vegetation or perhaps even in more open habitats.” (KELLER & SCHAAL 1992a, SULLIVAN et al. 1999). The Necrosauridae (Varanoidea) of Messel were predators, with their carnivore dentition, they could overpower small prey animals, including vertebrates. The body was slim, with powerful limbs and a long tail. They could reach a length of 60 cm (KELLER & SCHAAL 1992a).

The following interpretations are highly speculative and solely based on potential interactions of the respective animals. As far as trophic relations to other vertebrates are concerned, there is hardly any evidence in form of e.g. intestinal contents. Based on the results of the present study, the new genus and species fills the paleo-econiche of an arboreal Lacertilian in the Messel ecosystem. It therefore competed not as much with the other members of the Herpetofauna, but probably more with the already strongly specialised arboreal mammals such as *Heterohyus nanus*. This rather small arboreal insectivore (head and body length 12.5 cm, tail 18 cm) had prolonged digits in order to drive insect larvae out of tree barks (KOENIGSWALD et al. 1992a, KOENIGSWALD 1998a). The food resources are divided between the new taxon and *Heterohyus* insofar, as the new taxon probably ate mainly plant material and insect imagines instead of larvae. A competition between the new species and the arboreal snakes of Messel which belong to the *Palaeopython/Paleryx*-Group (BASZIO, pers. comm.) cannot be suspected: These snakes most likely fed predominantly on larger prey such as birds and arboreal mammals. It is thinkable that the fossil lizard could have been even a potential prey to these snakes. *Peradectes* sp. is a small opossum with a long prehensile tail. Therefore a climbing habit among thin branches is assumed. The head and body length is about 9 cm, the tail 16.5 cm (KOENIGSWALD & STORCH 1992). The largest of the Messel rodents is *Ailuravus macrurus*. The head and body had a length of 40 cm, the tail reached 60 cm

in length. According to its morphology an arboreal mode of life is assumed and it probably moved through the tree canopy with large leaps. The habitus is similar to a giant squirrel. *Ailuravus macrurus* was a specialised leaf-eater (KOENIGSWALD et al. 1992b, MARTIN 1998). The primitive mammal (order Proteutheria) *Kopidodon macrognathus* also was a large (head-body length: 55 cm, tail 60 cm) tree dwelling fruit-eater (KOENIGSWALD 1992, 1998b). There also have been primates in Messel, as the prosimian *Europolemur koenigswaldi* could easily climb through trees with its grasping hands (FRANZEN & KOENIGSWALD 1992, FRANZEN 1998). So there was quite a number of arboreal mammals, probably competing in some way or other with the new genus and species. Fig. 77 shows a life reconstruction of the new taxon as an arboreal, prehensile tailed lizard with a large head and curved claws. Juglandacean leaves are indicated, as these plants represent one of its presumed habitats.

Fig. 77: Life reconstruction of the new genus and species as an arboreal, prehensile-tailed lizard on a Juglandacean tree. Remarkable is the large sculptured head and the climbing adaptations such as the extraordinary long prehensile tail and the strongly recurved claws (Drawing by W. WEBER).



Fig. 77

5 Stratigraphic and geographic distribution of the Scincoidea

5.1 Scincidae

Early Scincidae are already known from the Upper Cretaceous of North America (Western Canada, *Penemabuya*, *Orthrioscincus* and *Aocnodromeus*, GAO & FOX 1996). *Contogenys sloani* from the Upper Cretaceous/Lower Palaeocene from Montana (ESTES 1969, 1983) are considered by GAO & FOX (1996) to be more closely related to the Xantusiidae than to the Scincidae. *Sauriscus cooki* (ESTES 1964) is a doubtful skink, but can most probably be referred to the Scincoidea (ESTES 1983). Doubtful remains of the family have even been reported from the Lower Cretaceous of Spain (RICHTER 1994). North America and Europe (France, Spain) was populated by Scincidae from the Lower Miocene to the Upper Pliocene (TAYLOR 1941; HOLMAN 1975, 1976, 1977a, 1981; ESTES 1983; BARBADILLO 1989; BAILON 1991). The Upper Eocene genus *Paracontogenys* was originally assigned to the Scincidae (SCHATZINGER 1975, ESTES 1983), but according to GAO & FOX (1996) this is questionable and it may be attributed to the Xantusiidae. Early Palaeocene material from Colorado (SULLIVAN & LUCAS 1996) and Upper Oligocene material from Nebraska and North Dakota (SULLIVAN & HOLMAN 1996) was tentatively referred to the Scincidae. In the upper Miocene, Scincidae are also present in Australia (ESTES 1980, 1983). Problematic attributions to the Scincidae are jaw fragments from the Lower Miocene of the Czech Republic (Dolnice, ROCEK 1984) and from the middle Miocene of France (Sansan, AUGÉ & RAGE 2000). There are Scincidae in the Plio-/Pleistocene of Spain (BARBADILLO 1989, BAILON 1991). During the Pleistocene the Scincidae are still present in North America, they are recorded from Puerto Rico, Kazakhstan and from the Balearic Islands (BOULENGER in BATE 1919; BRATTSTROM 1953a/b; AUFFENBERG 1956; DAREVSKI & TSCHUMAKOV 1962; HOLMAN 1968, 1972, 1977b; ALCOVER et al. 1980; PREGILL 1981; MEYLAN 1982; ESTES 1983). Nowadays the Scincidae are one of the most successful modern lizard families, with a cosmopolitan distribution. Scincidae is the richest family of Scincomorpha in terms of species and individual numbers, their distribution centres in Southeast Asia, Australia and Africa (OBST et al. 1988, KABISCH 1990).

The origin of the Scincidae is difficult to determine. There are different theories about the paleobiogeography of this group. Because of its morphology the subfamily Scincinae seems to be the most primitive group and independently gives rise to the other three subfamilies Feylininae, Acontinae and Lygosominae. The present extensive distribution of the Scincinae in Africa, Madagascar and the islands of the Western Indian Ocean appears to indicate their origin in this region (GREER 1970). ESTES (1983b) proposes an Asian origin of the Scincidae in the Jurassic, probably not arriving in Africa and North America (over the Bering connection) before the Late Cretaceous. According to this author, the family dispersed through Laurasia and into Australia, South America and Africa.

5.2 Cordyliformes

There are only rare fossil records of the Cordyliformes: A doubtful record already exists in the Upper Cretaceous of Western Canada (GAO & FOX 1996). Fossil Cordyliformes from the Tertiary are known from the Lower Miocene of Kenya (VAN COUVERING 1979, ESTES 1983), the Lower Eocene of Belgium (Dormaal, HECHT & HOFFSTETTER 1962, GODINOT et al. 1978, RAGE 1978, ESTES 1983, AUGÉ 1990) and the Upper Eocene/Lower Oligocene of France (Phosphorites du Quercy, St.-Néboule,

HOFFSTETTER 1942, 1955, 1962; ESTES 1983; AUGÉ 1987). In the late Eocene of England the Cordyliformes were also reported (MILNER 1986, RAGE & AUGÉ 1993). The Late Oligocene specimen of “*Lacerta*” *rottensis* from Germany (Rott near Bonn) was assigned to the Cordyliformes with some doubt by BÖHME & LANG (1991). The extant population of the Cordyliformes became limited to Africa – mainly south of the equator – including Madagascar (KABISCH 1990). According to ESTES (1983b) this group appears to have evolved on the North America–Greenland–Great Britain–Iberian Peninsula plate starting in the Late Jurassic. A restriction of the Cordyliformes probably resulted through the separation by Cretaceous epicontinental seas.

5.3 *Paramacellodidae*

The Paramacellodidae are the oldest known Scincoidea ranging from the Middle Jurassic (Bathonian) of Scotland (Skye) with the genus *Paramacellodus* (WALDMAN & EVANS 1994, EVANS & CHURE 1998a) to the Lower Cretaceous (Barremian, *Paramacellodus*, *Becklesius*) of Spain (RICHTER 1994) or probably even to the Aptian/Albian of Mongolia (ALIFANOV 1993). During the Upper Jurassic this family was present in Portugal (Oxfordian, Kimmeridgian) with *Becklesius* (SEIFFERT 1973, ESTES 1983, EVANS & CHURE 1998a), North America (Kimmeridgian, Utah and Wyoming) with *Paramacellodus* (PROTHERO & ESTES 1980, ESTES 1983a, EVANS & CHURE 1998 a&b), Tanzania (Tendaguru, ZILS et al. 1995, EVANS & CHURE 1998a, BROSCINSKI 1999), China (*Mimobecklesisaurus*, ?Kimmeridgian, LI 1985, EVANS & CHURE 1998a) and Kazakhstan (*Sharovisaurus*, Kimmeridgian, HECHT & HECHT 1984). ESTES (1983) referred *Pseudosaurillus*, *Saurillus* und *Saurillodon* from the Upper Jurassic of England and Portugal tentatively to the Paramacellodidae. EVANS & CHURE (1998a) doubt this attribution since these genera are poorly preserved or the morphology is quite unlike typical Paramacellodidae. In the Lower Cretaceous the Paramacellodidae occur with *Paramacellodus* and *Becklesius* in the Purbeck Limestone Formation of England (Berriasian), in Spain (Barremian, RICHTER 1994) and Morocco (?Berriasian-?Aptian, RICHTER 1994, BROSCINSKI & SIGOGNEAU-RUSSELL 1996). This family thus had a temporal range of at least 60 Million years and a global distribution (EVANS & CHURE 1998a). ESTES 1983 stated that this family may prove to be fossil Cordyliformes, but the present material is too incomplete to verify that. According to BROSCINSKI & SIGOGNEAU-RUSSELL (1996) the finding of *Paramacellodus marocensis* in the Lower Cretaceous of Morocco is of great importance, as it represents the first unambiguous appearance of the family Paramacellodidae on the African continent, adding to the known Laurasian expansion. *Paramacellodus* was found even South of the equator in Tanzania, which is up to now the oldest known Paramacellodid on this continent. This proves that the distribution of Paramacellodidae was not restricted to the Northern hemisphere (BROSCINSKI 1999). Above that, their existence on the African continent gives another hint towards a link with the Cordyliformes (BROSCINSKI & SIGOGNEAU-RUSSELL 1996, BROSCINSKI 1999). The centre of distribution of the Paramacellodidae remains unclear. Migrations are conceivable either from the northern hemisphere to Africa or vice versa (BROSCINSKI 1999).

5.4 Gen. et. spec. nov.

The paleobiogeography of the Scincoidea remains unclear. Yet, if the Scincoidea prove to be monophyletic, what I believe they are, their presumed Laurasian origin had to evolve during the Lower Jurassic at the latest. The origin and exact relationship of the new taxon to the Scincidae, Cordyliformes and Paramacellodidae cannot be resolved at

the present time (Fig. 56, p.132). However, it may represent an interesting link between Cordyliformes and Paramacellodidae, especially if the Paramacellodidae will prove to be a synonym to the Cordyliformes, as ESTES (1983a) suggested. The presence of the new species in the Lower Middle Eocene of Messel does neither support nor contradict the current opinions of Scincoid Paleobiogeography. A problem in reconstructing paleobiogeography and phylogeny is that the fossil material often is fragmentary and an attribution to a certain family is not always unequivocal. According to MÜLLER, J. (1998) several of the Cretaceous and Tertiary Scincoidea may represent stem group taxa, making an unequivocal attribution much more difficult.

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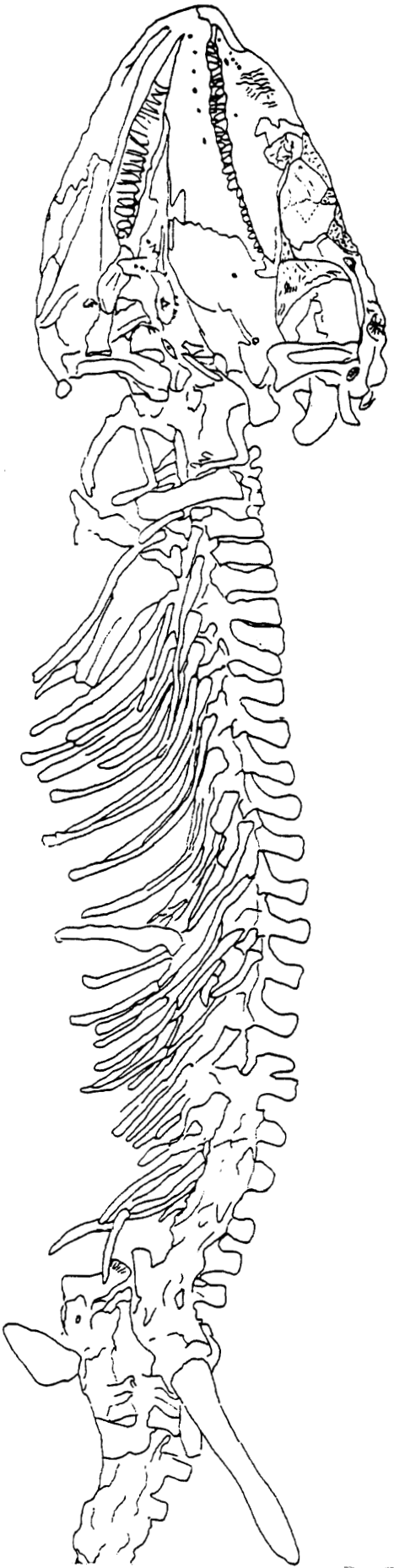
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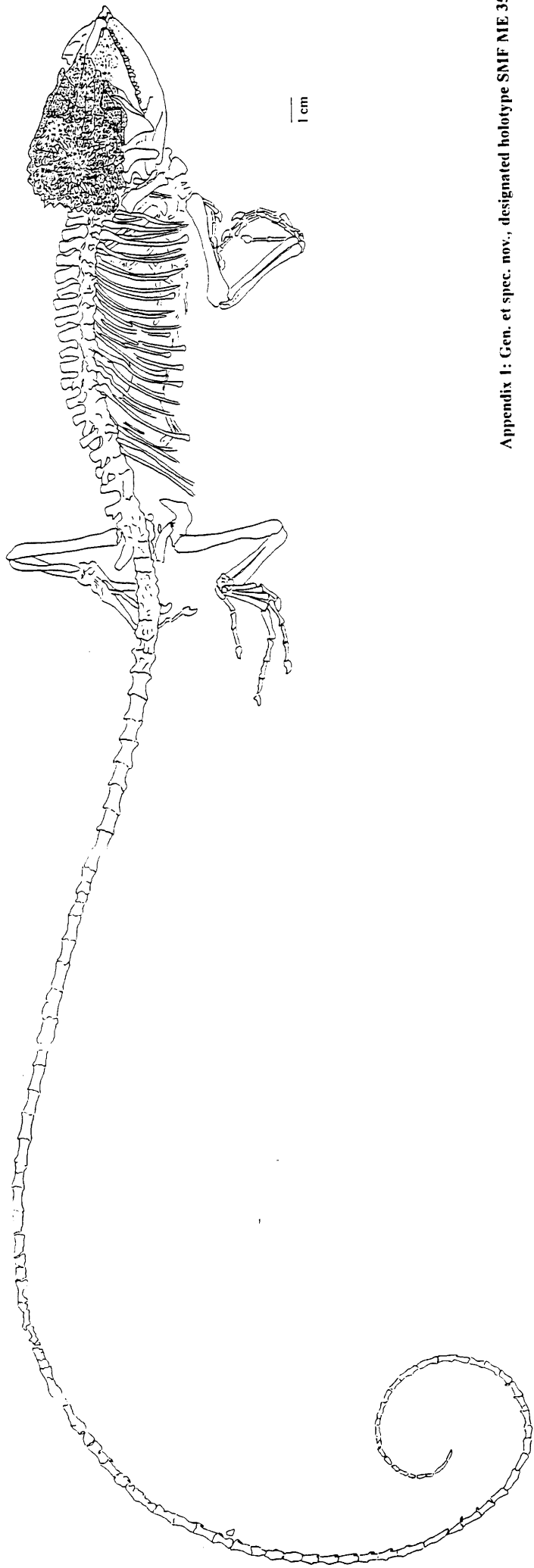
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**9 Appendix 1-7: Line drawings of the specimens of
the new genus and species**

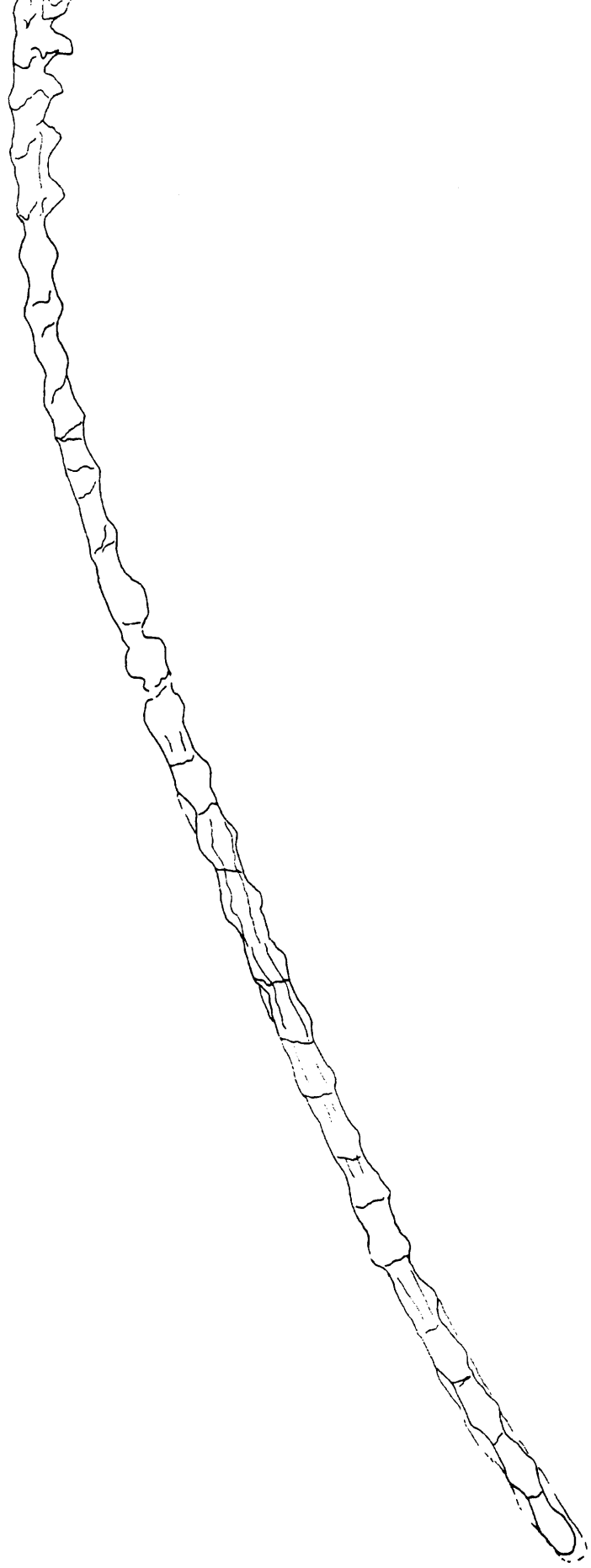


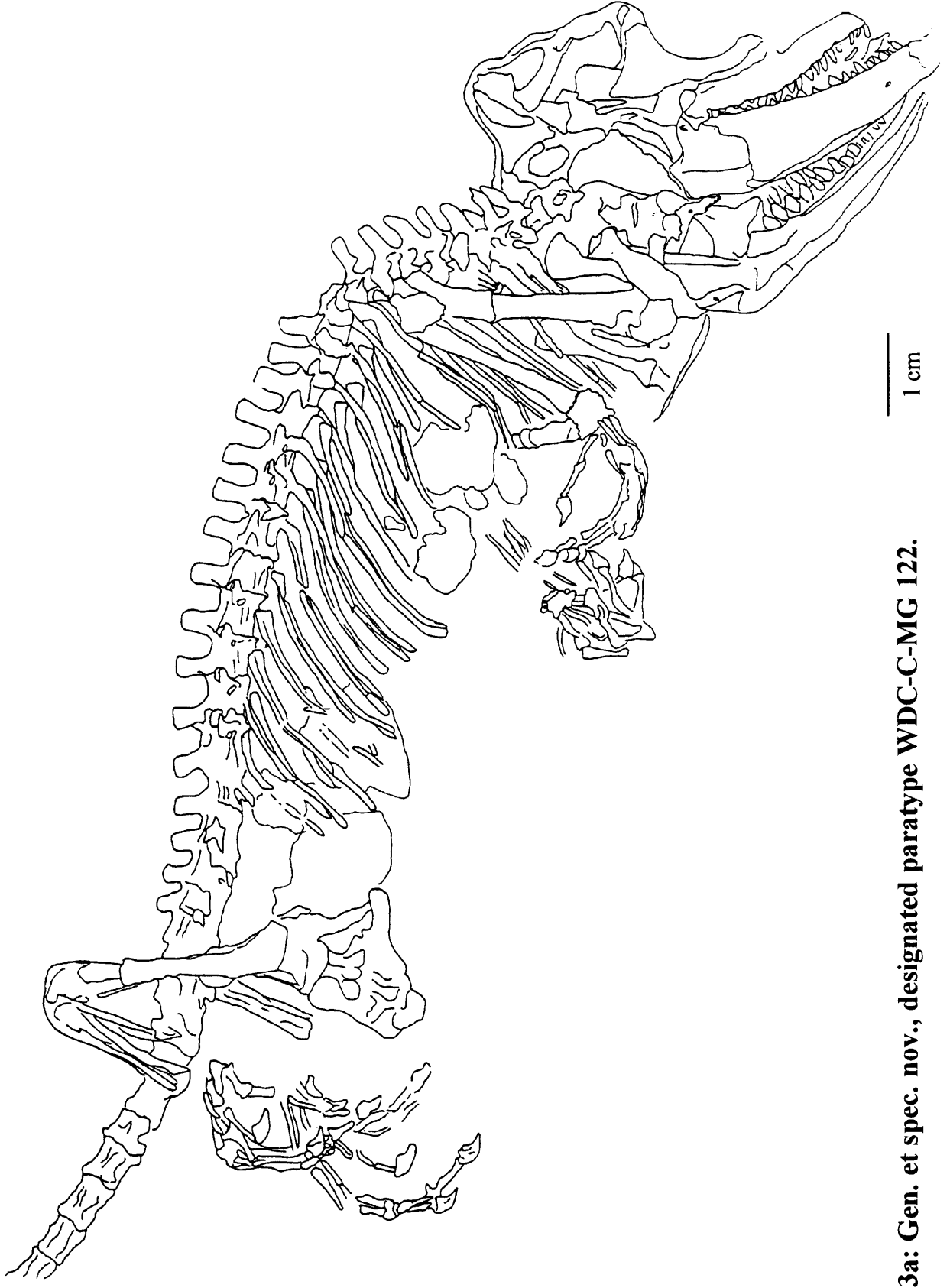
1 cm

Appendix 2: Gen. et spec. nov., designated paratype SMF ME 475;

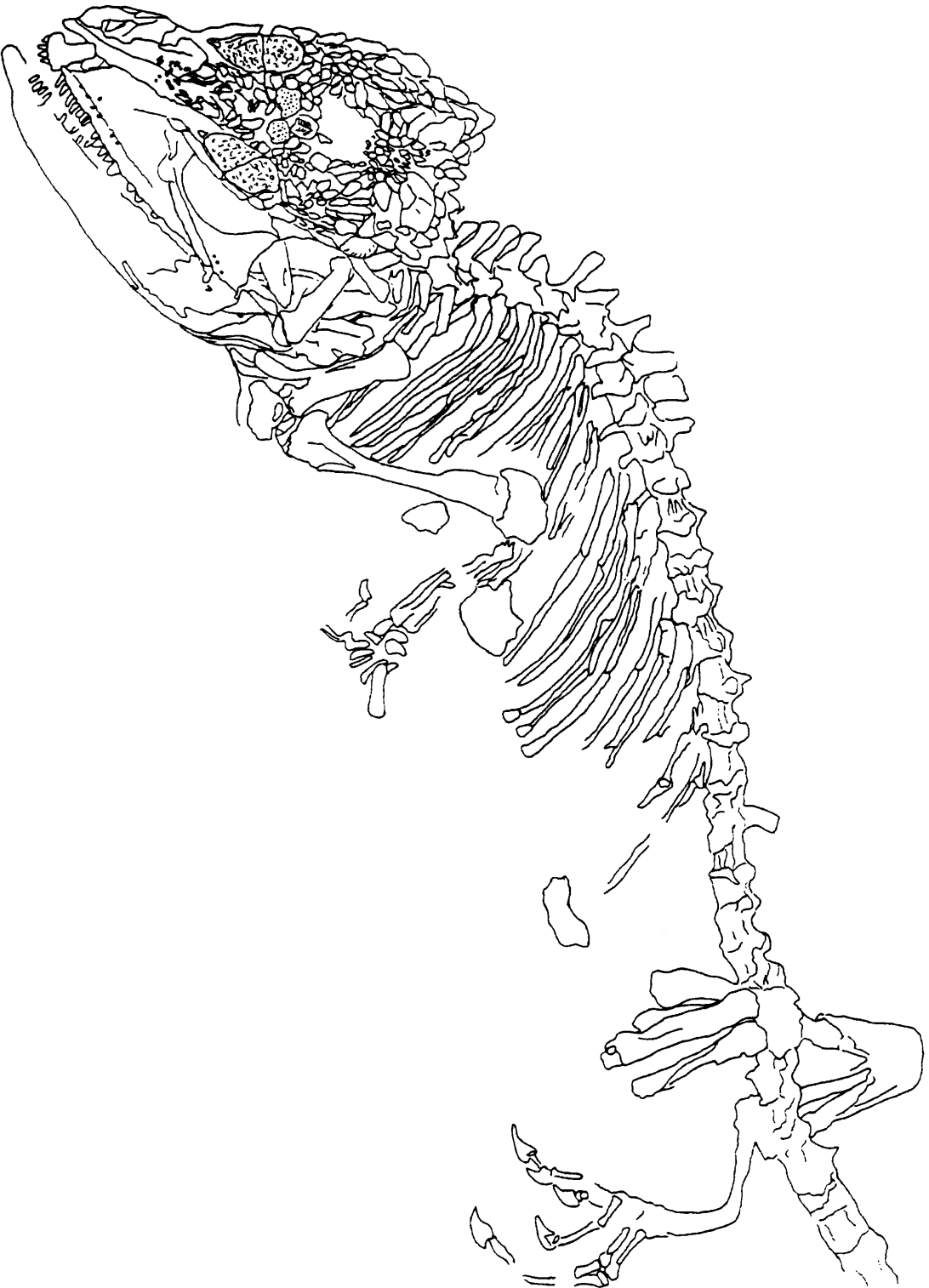


Appendix 1: Gen. et spec. nov., designated holotype SMF ME 3516.



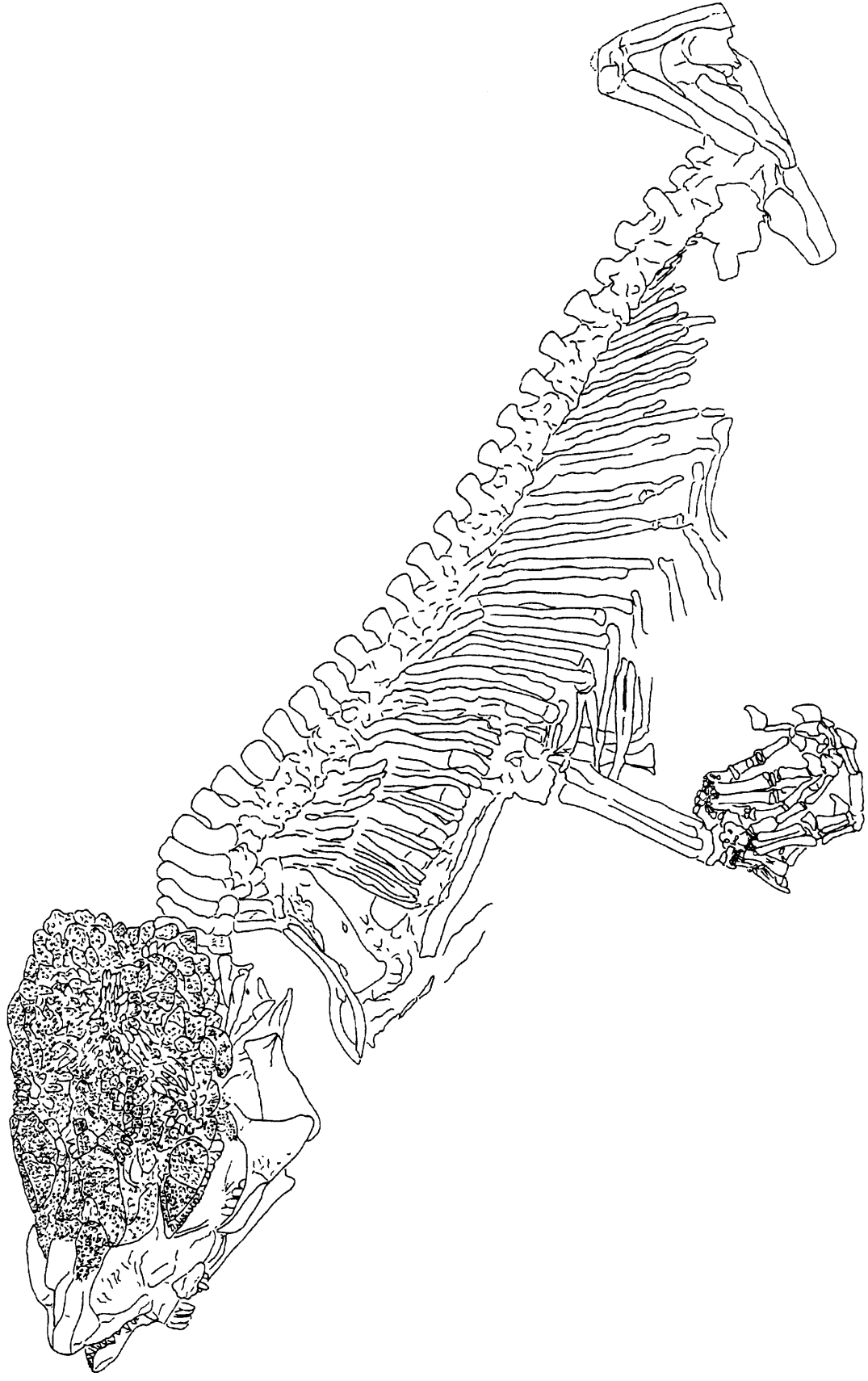


Appendix 3a: Gen. et spec. nov., designated paratype WDC-C-MG 122.



1 cm

Appendix 3b: Gen. et spec. nov., designated paratype WDC-C-MG 123.



Appendix 4: Gen. et spec. nov., designated paratype SMNK-PAL 3813.



Appendix 5a: Gen. et spec. nov., SMF ME 1249a, additional material.



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1 cm

Appendix 5b: Gen. et spec. nov., SMF ME 1249b, additional material.



1 cm

Appendix 6: Gen. et spec. nov., SMNK-Me 930a, additional material.



Appendix 7: ?Gen. et spec. nov., cast from the Fossilien- und Heimatmuseum Messel, additional material.