CONTRIBUIÇÃO PARA O CONHECIMENTO DA FAUNA DO KIMERIDGIANO DA MINA DE LIGNITO GUIMAROTA (LEIRIA, PORTUGAL)

III PARTE

V — UPPER JURASSIC LIZARDS FROM CENTRAL PORTUGAL

by

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VI — TEETH OF ORNITHISCHIAN DINOSAURS FROM THE UPPER JURASSIC OF PORTUGAL

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VII — CHELONIA FROM THE UPPER JURASSIC OF GUIMAROTA MINE (PORTUGAL)

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CONTENTS

PREFACE

«The evolutionary story of the Lacertilia is divided into two very unequal portions, a Triassic-
-Jurassic chapter very poorly known, and a fairly well-documented story beginning in the late Creta-
ceous and extending to the present; between the two there is an intermezzo formed by the appearance
of the mosasaurs and other aquatic lizards of the Cretaceous.»

(ALFRED SHERWOOD ROMER, 1968)

«As to how long the Kuehneosaurs (or the eolacertilians) persisted we can only conjecture.
The eolacertilians possible were caught up in the wave of reptilian extinction that marked the close
of the Triassic; if so, they must given rise to the later lizards before then. Conversely, they may have
continued into the early Jurassic, when they became the ancestors of some of the lizards that
appear as well-established forms in the late Jurassic.»

(EDWIN HARRIS COLBERT, 1970)

Within the actual knowledge of lacertilians and their evolution the occurrence
of Triassic and Jurassic lizards leads to a conclusive importance. In the Upper Trias-
sic the lacertilian morphogenesis was already completed and indeed to a highly specia-
lized degree which is documented by the appearance of gliding forms (see ROBINSON,
1962; COLBERT, 1970). On the other hand the hitherto known Jurassic references are
specimens of an insufficient evidence, excepting the numerous Lower Kimmeridgian
remains from the Portuguese coalmine, Guimarota (see KÜHNE, 1968). Such forms are
also found in the Upper Kimmeridgian sediments on shore about 70 km SW of the loca-
lity Guimarota. The Upper Jurassic lizards of Portugal presented here enlarge the
record of the lacertilian evolution.

W. G. KÜHNE has explored mesozoic tetrapods for more than 30 years and
hereby discovered the important localities of fossil vertebrates from the Rhaetian of
England and the Kimmeridgian of Portugal. In my studies of the Portuguese skeletal
remains Prof. KÜHNE encouraged me with critical advice. I am grateful to him and
his former staff, particularly to Prof. B. KREBS and Miss E. DRESCHER for the assis-
tance to my work carried out at the Institute of Paleontology, Free University Berlin.

The evidence of the rich vertebrate material from Portugal would not have been
revealed without Prof. S. HENKEL's mission in the field. For the photographs produced
with the scanning electron microscope, I am indebted to Prof. J. G. HELMCKE of the
Max-Planck-Institute of Micromorphology and his team in the Technical University
Berlin. I would especially like to thank Dr. PAMELA L. ROBINSON, London for the kind
gift of a comparison material *(Kuehneosaurus)* from an Upper Triassic fissure-filling
at Emborough, England. Finally I would like to express my thanks to Mr. P. BERNDT
and Miss M. GRADE for drawing most illustrations in the text.

Deserving thanks, the Deutsche Forschungsgemeinschaft has generously subsidized
the Guimarota researching project.

The present contribution is, in the main, a translation of my thesis on the
Upper Jurassic Lacertilia from the Guimarota mine, added to which are the lacertilian
remains of the Upper Kimmeridgian from Porto das Barcas and Porto Pinheiro.

A. Introduction

South of the Central Portuguese provincial town of Leiria lies the coalmine Guimarota. There lignite was mined, but utilized only for the lime-kiln in the vicinity of the mine and 10 years ago the output ceased. Recently, in 1972, Guimarota was reopened by Prof. HENKEL's enterprise with the expectation of discovering the complete skeletons of Jurassic mammals.

Until now, more than a thousand lacertilian fragments of the numerous vertebrate remains have been obtained from the layer FA_{11} of the geological section exposed in the pit (see HELMDACH, 1968). Of these, the smaller part was yielded by manual splitting of the coal, the main part by washing and dressing the pit heap (for the methods see HENKEL, 1966, KÜHNE, 1968).

The stratigraphic position of the Guimarota complex has been determined by the ostracods as Lower Kimmeridgian (see HELMDACH, 1971). There appear *Cetacella inermis* MARTIN, 1958, *Dicrorygma kimmeridgensis* KILENYI, 1969, *Poisia bicostata* and *P. clivosa* HELMDACH, 1968, *Theriosynoecum hemigymnon* HELMDACH, 1968 and *Th. wyomingense* (BRANSON, 1935), *Timiriasevia mackerrowi* BATE, 1965. Their vertical distribution is shown in Fig. 1.

Apart from the Guimarota, two additional localities with tetrapod remains had already been discovered in 1961 on the Mid-Portuguese coast. Methodical exploitations of the most promising beds were undertaken at Porto das Barcas (Monti) and Porto Pinheiro in 1962, 1967 and 1968. The tow places are not more than 3 km apart. The stratigraphic age of the layers was determined by the appearance of the ostracod *Cetacella armata* MARTIN, 1958 as Upper Kimmeridgian (see KRUSAT, 1969, HELMDACH, 1971). The lacertilian fragments from the two Upper Kimmeridgian localities can be included among distinct taxa of the Guimarota-Lacertilia.

The vertebrate faunae, which the Upper Jurassic sediments of Portugal yielded until now, will be morphologically described in separate taxonomic groups by several contributors of the Institute of Paleontology, Free University Berlin.

The subject of the study presented here is the lacertilian material obtained from the Guimarota pit and the coastal localities Porto das Barcas and Porto Pinheiro.

The term «lacertilian» is to be used for Lacertilia (= Sauria) *sensu lato,* i. e. the group Lacertilia comprising the pro- and eolacertiformes. In the systematic classification the lizards were first named «Sauria» «McCARTNEY, 1802, but now the term «Lacertilia» WAGLER, 1830 in the meaning after GÜNTHER, 1867 has been accepted. In the zoological system the lacertilians are placed as following:

Class — Reptilia
Subclass   Lepidosauria
Order₁   Araeoscelidia
Order₂   Eosuchia
Order₃   Squamata (Lecertilia *s. l.* and Ophidia)
Order₄   Rhynchocephalia.

The known abundance of lacertilian forms is distributed in the taxonomic categories mentioned below (following the system after ROMER, 1966):

Lacertilia (= Sauria) sensu lato

1. Infraorder. — *Prolacertiformes*
        Prolacertidae
        Thalattosauridae
        Tanystropheidae

2. Infraorder. — *Eolacertilia*

    Kuehneosauridae
    Cteniogenyidae SEIFFERT, 1970

3. Infraorder. — *Gekkota* (= Nyctisauria)

    Gekkonidae
    Pygopodidae

4. Infraorder. — *Iguania*

    ?Teilhardosauridae
    Agamidae
    Iguanidae
    Chamaeleonidae

5. Infraorder. — *Scincomorpha* (= Leptoglossa)

    ?Ardeosauridae
    Xantusiidae
    Scincidae
    Cordylidae (incl. Gerrhosauridae, Zonuridae)
    Lacertidae
    Teiidae
    ?Dibamidae

6. Infraorder. — *Anguimorpha* (= Diploglossa)

    Superfamily$_1$: Anguoidea

        Anguidae
        Anniellidae
        Xenosauridae (incl. Shinisauridae)

    Superfamily$_2$: Varanoidea (Platynota)

        Varanoidea (Platynota)
        Dorsetisauridae HOFFSTETTER, 1967
        Aigialosauridae
        Mosasauridae
        Dolichosauridae
        ?Necrosauridae
        Parasaniwidae
        Helodermatidae
        Varanidae
        Lanthanotidae
        Palaeophidae (Cholophidae)
        Simoliophidae

7. Infraorder. — *Amphisbaenia* (= Annulata)
    Amphisbaenidae.

idea of evolution results to account for the the paleontological documents, the following From the comparative morphology of origin and the phylogeny of lacertilians:

SCINCOMORPHA ANGUIMORPHA AMPHISBAENIA   Ophidia

GEKKOTA   IGUANIA   SCINCO – ANGUIMORPHA

EOLACERTILIA

Lacertilia s.l. – PROLACERTIFORMES   Rhynchocephalia

Eosuchia

Araeoscelidia

Captorhinomorpha

Prae – Microsauria
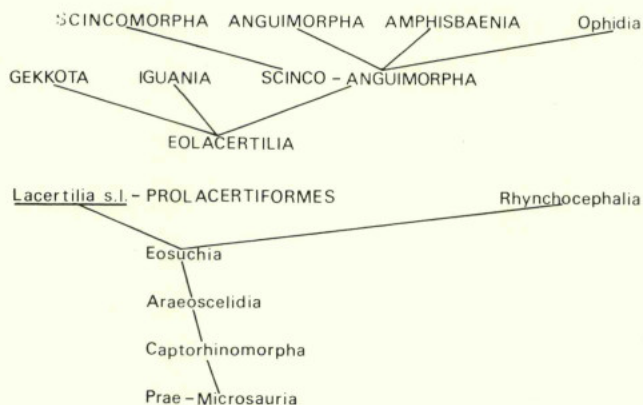
The standard profile section of the Guimarota mine and the more distant environs (Fig. 1):

The preceding Lusitanian section has been composed of corresponding statements (from HELMDACH, 1966, 1968, HÖLDER, 1964, MOUTERDE et al., 1971, LAPPARENT & ZBYSZEWSKI, 1957, RUGET-PERROT, 1961 and ZBYSZEWSKI, 1965).

As the underlying bed of the 2. Lusitanian lignite series, a rich shelly layer with *Isognomon* and *Trigonia* is supposed to mark the stratigraphic division of Upper Oxfordian and Lower Kimmeridgian. The marls with driftwood of Porto das Barcas and Porto Pinheiro are stratigraphycally ranged by the appearance of the ostracod *Cetacella armata* MARTIN, 1958 (see HELMDACH, 1971) and also by the evolutionary degree of the Mesozoic mammals compared with the findings of the Guimarota.

The special facies profile of the Guimarota is quoted from HELMDACH's thesis (1968). The specifications of the ostracods relate to their first appearance in the section. The vertical hachure signifies partly carboniferous layers. In the general map (after RUGET-PERROT, 1961) the vertical hachure marks the distribution of the Middle Portuguese Mesozoic surrounded with crystalline rocks and the Paleozoic.

The coalmine Guimarota is situated about 1,5 km SSE of the midtown, Leiria. The approach to the mine branches off from the main road Leiria-Cortes, opposite the branch to Vidigal (see HELMDACH, 1966). The geographical co-ordinates of the locality are after the Carta Militar de Portugal (sheet Leiria, No. 297) 142,75 NS (resp. 0°20')/307,5 EW or the degree of longitude 8°48'/of latitude 39°43'.

The Upper Jurassic vertebrate fauna of the Guimarota mine is composed in unequal amounts of representatives of the following systematic groups:

Osteichthyes	Holostei
	Teleostei (Otolithi)
Chondrichthyes	Selachii
Lissamphibia	Urodela
	Anura
Chelonia	Cryptodira
Lepidosauria	Eosuchia
	Lacertilia s. l.

Standard profile of the Guimarota mine
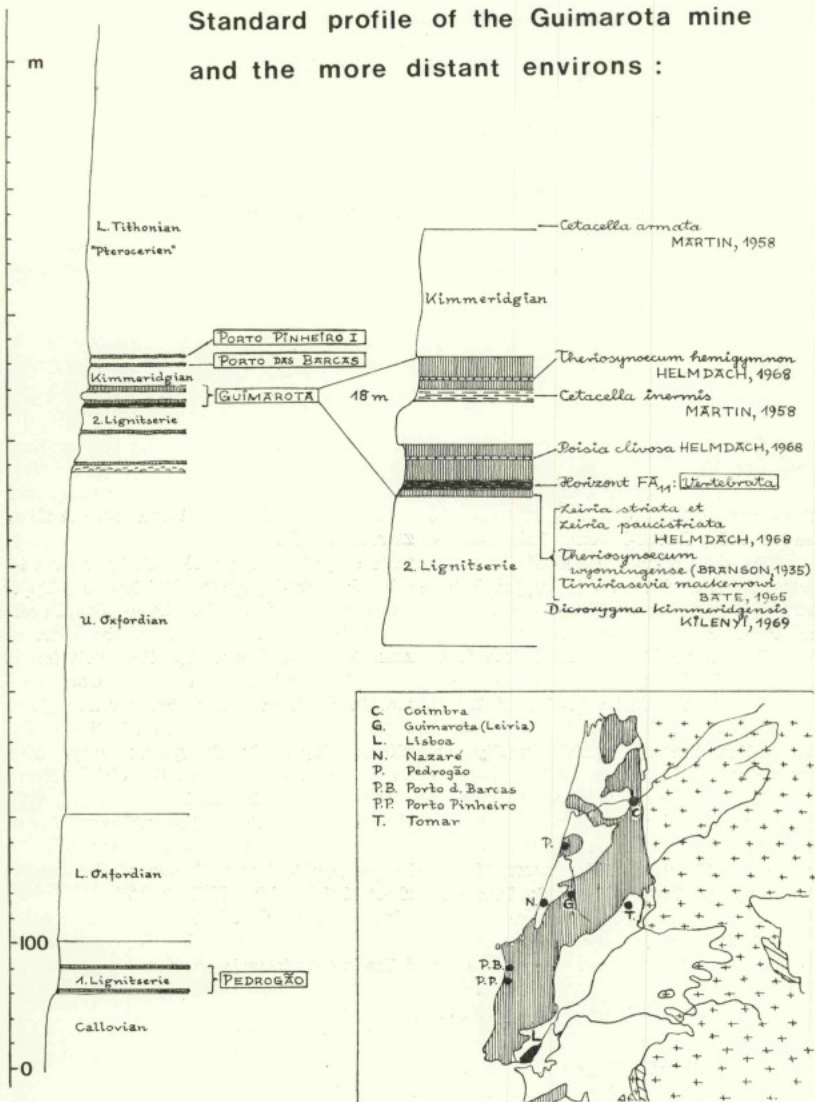# and the more distant environs :

Fig. 1 — Standard profile of the Guimarota mine and the more distant environs.

Archosauria . . . . Crocodilia
Pterosauria
Saurischia
Ornithischia

Mammalia . . . . Docodonta
Multituberculata
Pantotheria.

B. *Cteniogenys reedi* SEIFFERT, 1970

Kuehneosaurus ROBINSON, 1962 and *Kuehneosuchus* ROBINSON, 1967a, both from the Upper Keuper of England, and *Icarosaurus* COLBERT, 1966 from the Upper Triassic of North-America are ancestral lacertilian types being not unspecialized on all accounts. The vertebral column and the ribs of these forms are developed for gliding similarly
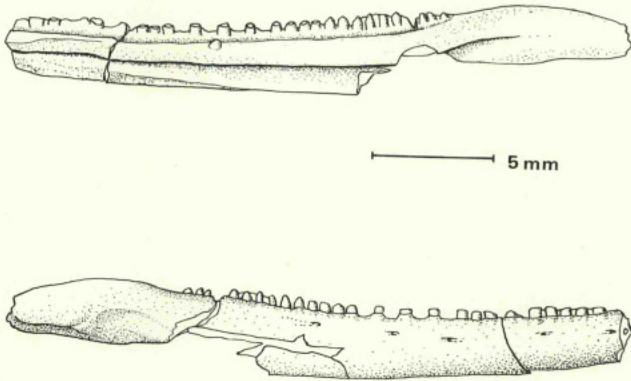

⊢————————⊣ 5 mm

Fig. 2 — Gui. 51, right dentary of *Cteniogenys reedi;* notice the replacement tooth on the lingual side and the attachment area for the angular on the posterior part of the external side (below).

those of the recent gliding lizard *Draco* (Agamidae). Our knowledge about the Mesozoic small reptiles is relatively scant by the fact that most of the known Jurassic and Cretaceous sediments are marine formations. In regard to the high degree of specialization of the Upper Triassic gliding lizards we can expect, that additional lacertilian findings will reveal the variety of the early specializations. This postulate of ROMER (1966) is verified with the presence of the Upper Jurassic Lacertilia from Portugal.

From the «mammal layer» of the Upper Jurassic Morrison-Formation in «Quarry No. 9» Como Bluff, Albany County, Wyoming ten specimens of a lacertilian incertae sedis have become known. At first in 1909 GILMORE has published a broken dentary (U. S. National Museum, Catalogue No. 6134), describing this one as holotype of *Cteniogenys antiquus* in 1928. The other nine remains, already found by W. H. REED in 1879, 1881, 1882 and preserved in the Yale Museum, were just identified as *Cteniogeys* by GILMORE (1928).

In the coalmine Guimarota the same genus, but an other species is recovered with a lot of fragmentary jaw-bones. The Guimarota species also appears in the fauna of the two Upper Kimmeridgian localities Porto das Barcas and Porto Pinheiro.

Family Cteniogenyidae SEIFFERT, 1970

Type genus: *Cteniogenys* GILMORE, 1828.

Diagnosis. — (see GILMORE, 1928, p. 162-164, pl. 20).
Very long and slender dentaries with more than 35 teeth disclosed as cylindric-conical with slightly compressed crowns, pleuro-thecodont and hollow. The convex external surface is grooved by foramina in a line running parallel to the dentary border (crista dentalis). The Meckelian groove is exposed at the lingual side of the dentary.
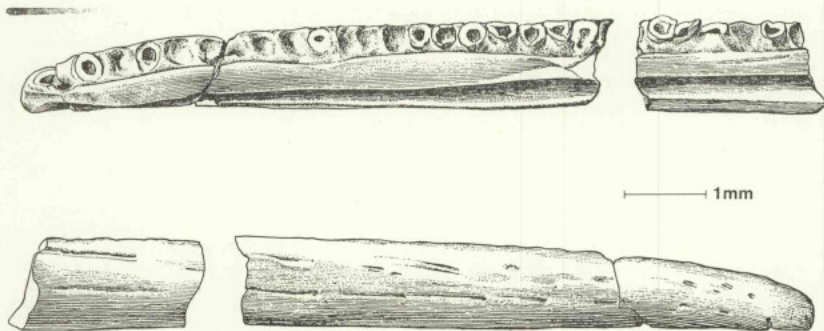

Fig. 3 — Gui. A. 33, *Cteniogenys reedi*, right dentary (holotype); above: lingual view showing the extended subdental ridge and the Meckelian groove; below: labial view, remarkable groovings and foramina.

Type species of the genus. — *Cteniogenys antiquus* GILMORE, 1928 (No. 6134 of the U. S. Nat. Mus., coll. MARSH-party besides a nominated paratype No. 1068 and eight further specimens in the Yale Museum, coll. REED). In 1909 the dentary fragment of the holotype was delivered with 25 teeth, but because of the fragility of the specimen 24 teeth were still preserved in 1928.
Derivatio nominis of the new species from Portugal. — *reedi:* after W. H. REED, whose collection of nine specimens from Wyoming has helped to clear up the form *Cteniogenys.*

Holotype. — A right dentary, Gui. A. 33.

Formation and locality. — In the Kimmeridgian of Portugal.

Diagnosis and description of the species. — Extended jaws with ca. 40 conical teeth and more, showing characteristic peated enamel (striae) on the lingual side of the superior part of the teeth. As those of *Kuehneosaurus* ROBINSON, 1962 from the Upper Keuper of Emborough Quarry, England (s. dentary P. L. R. 53 of ROBINSON's collection) there are mostly to be seen about seven striae, of which the both external ones converge subparallelly with the outline to lingual cutting edges on the cusp (Pl. 1, 3). This feature is certainly affected by function of the masticators and by the food. The

dentary has in common the presence of a very low parapet of bone along the labial side of the teeth, and to which the teeth adhere close to their bases on their labial sides. The mode of tooth implantation is non-thecodont, rather subpleurodont; the teeth are fastened by attachment bone around their bases. The tooth replacement occurs by resorption close to, but not at the hollowed base of the old tooth, and the new tooth arises lingually to the old one. The dentaries have an elongated subdental ridge and a slender, lingually running Meckelian groove, anteriorly forming a ventral fossa at the symphyseal area. The symphysis of *Cteniogenys* is slight and obviously car-
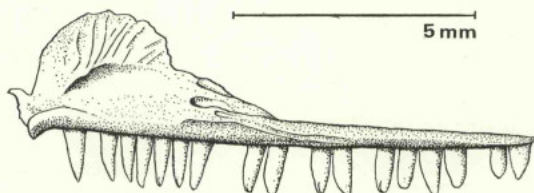

Fig. 4 — Gui. L. 234, right maxilla of *Cteniogenys reedi*, lingual view.

tilaginous-ligamentous. The Meckelian groove is extensively covered with the splenial indicated by the attachment area on the lingual surface of the subdental ridge. The posteriorly broad splenial thins in the middle of the dentary up to the symphysis. A separate canalis alveolaris inferior opens approximately under the 26th-30 th tooth (about under the fifteenth from behind). Ahead of this foramen the attachment area of the splenial distinctly continues on the anterior subdental ridge. Equally the attach-
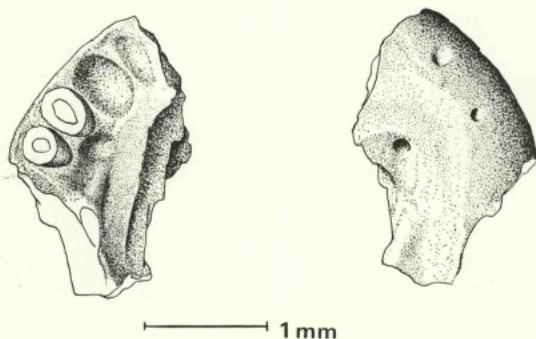
Fig. 5 — Gui. 345, right premaxilla of *Cteniogenys reedi*.

ment of the angular stretches to the anterior part of the dentary, running on the inferior border. The attachment areas are well to be seen on the specimens Gui. 51, Gui. A. 21, Gui. A. 26 like on *Kuehneosaurus* (cf. material of P. L. ROBINSON, London). From the appearance of the specimen Gui. 51 *Cteniogenys reedi* seems to lack a separate coronoid as *Kuehneosaurus*. «This element may have been present as a small bone» (COLBERT, 1970 about *Icarosaurus* and *Kuehneosaurus*). The posterior part of the jaw

cannot be diminished, because the insertion of the M. adductor mandibularis takes place in an areal dimension (cf. contrary to *Ophryoessa superciliosa*, a long-snouted iguanid).

The long stretched maxilla reveals a large and anterior advanced orbit. Thus the facial skull gives the impression of being relatively short. The maxillae rise dorsally only with the anterior part of the bone (s. Gui. 286, Gui. 332, Gui. L. 234).
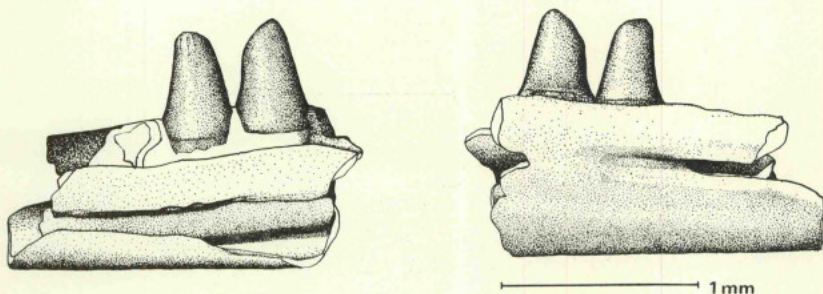
Fig. 6 — Fragment of a right dentary of *Cteniogenys reedi* (Porto Pinheiro I. L. 27), left: lingual view; right: labial view.

On their internal side there exist two foramina probably for the passage of nerve fibres of the N. V_2 with a parasympathetic portion of the N. VII (after HALLER v. HALLERSTEIN, 1934 there are very close connexions between the trigeminus and the facialis). As to be seen of the recent *Tupinambis* those rami (N. vidianus) of the N. pterygo-palatinus pass through an opening formed by the palatine as basal, the maxilla as lateral and the lacrimal as dorsal bordering; they unite the N. infraorbitalis (rr. maxillares alveolares,
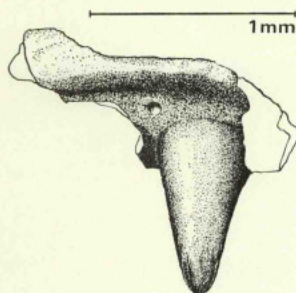
Fig. 7 — Maxillary tooth of *Cteniogenys reedi* (Porto das Barcas 1962).
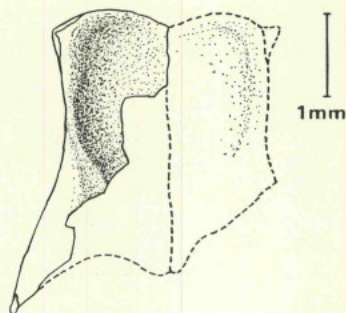
Fig. 8 — Gui. 82, parietal probably of *Cteniogenys reedi*.

rr. cutanei externi et rr. salivares) with rami communicantes aborales. For the nerval exit there are located foramina maxillo-facialia on the external side of the maxilla. As particularity the internal side of the right maxilla Gui. L. 234 anteriorly has a concavity and above it a fine lamellar longitudinal fanning caused by the affixture of the nasal. The nares of *Cteniogenys reedi* are apparently proceeded between the premaxillae to the mesial line (s. Gui. 345); the naris is obviously unpaired as that of *Kuehneosaurus*.

Paired parietal bones in the Guimarota material might add to *Cteniogenys reedi* (s. Gui. 82, Fig. 8) on account of the adequate presence of *Kuehneosaurus* and *Icarosaurus*.

Discussion. — There is an extensive conformity with the dentaries and maxillae of *Kuehneosaurus* ROBINSON, 1962 and *Icarosaurus* COLBERT, 1966 and those of *Cteniogenys reedi*. As distinguished from *Cteniogenys* the subdental ridge of *Kuehneosaurus* becomes more thin anteriorly and rather conssiderably on the posterior part of the dentary; apparently this causes the surangular to extend further in the forepart. On the nominated paratype *Cteniogenys antiquus* GILMORE, 1928 reveals a rule-shaped subdental ridge of a certain, constant height contrary to *Kuehneosaurus* and *Cteniogenys reedi*.

The Lusitanian *Cteniogenys reedi* corresponds essentially with the morphology of the jaws, to the Upper Triassic gliding lizards. The anatomy of the pleurothecodont teeth is identical as is the number (ca. 40 and more). The length of the jaws, the straight Meckelian groove in the dentary, the uniformity and the mode of tooth attachment, the slight symphysis and the skull bones in pairs refer to the eolacertilian nature of *Cteniogenys*. Dr. ROBINSON supposes the Upper Triassic gliding lizards to be a separate family (Kuehneosauridae) because of the special vertebral column and the long period of time in comparison with *Cteniogenys,* I therefore propose the new family Cteniogenyidae for unspecialized Eolacertilia.

C. *Macellodus* and *Saurillus*

1) Verification of the genera

After a discourse with Prof. S. HENKEL and Prof. B. KREBS from the Institute for Paleontology of the F. U. Berlin, HOFFSTETTER (1964) has published the existence of scincomorph remains from the Portuguese coalmine Guimarota and referred to a possible relationship with the Purbeck formsof South-England, which were first described by R. OWEN in 1854 and 1855.

HOFFSTETTER's revision (1967) of the lacertilian material from the lowest Middle-Purbeck (mammalian beds) of Swanage relies on the numerous material of the BECKLES-collection in the British Museum, London (170 saurian specimens). In LYDEKKER's «Catalogue of the Fossil Reptilia and Amphibia in the British Museum, Part I» (1888) the following remains of the BECKLES-collection (purchase 1876) are labelled as «Species *Macellodus brodiei* OWEN 1855»: No. 48230-2, 48233, 48368, 48370, 48385. The catalogue No. 48233-DD now bears the new label R. 8242. This is a left dentary fragment 12 mm in length with 25 teeth resp. alveoli at least. The named specimen is not mentioned in HOFFSTETTER' publication (1967), although regarded by LYDEKKER (1888) as a typical specimen of *Macellodus brodiei* OWEN 1854.

The first description of lacertilians from the Latest Jurassic of Swanage resulted from the remains of the BRODIE-collection. This material, described by OWEN, 1854 and 1855 had never been in the hands of LYDEKKER, as the BRODIE-collection was not purchased by the British Museum before 1895, after the complection of LYDEKKER's catalogue. Certainly BRODIE has repeatedly given minor donations to the British Museum since 1853 (s. ZEUNER, 1939), but no Purbeck lacertilians were found among them.

In reviewing probably all the Purbeck material of the British Museum HOFFSTETTER (1967) misses BRODIE's finds described by OWEN and takes them to be lost.

In addition to the reptiles there also exist mammalian jaws in BRODIE's gathering at Durdlestone, which were turned up again at the Sedgwick Museum in Cambridge (CLEMENS, 1963). That these fossils have arrived at Cambridge is of no surprise

considering SEDGWICK as BRODIE's instructor, who was certainly provided with donations. Apart from the three registered mammalian remains, the curator Dr. FORBES could not find any other material of the RRODIE-collection at the Sedgwick Museum.
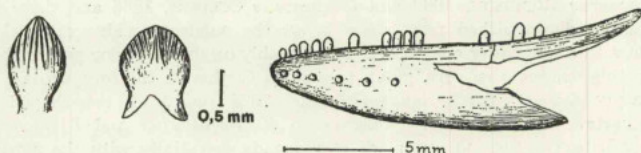
Fig. 9 — *Macellodus brodiei* OWEN, 1854, coll. BRODIE (after R. OWEN, 1854 p. 424, and 1861, pl. 8).
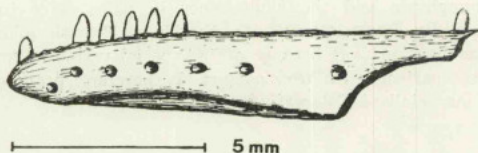
Fig. 10 — *Macellodus brodiei* incl. *Saurillus obtusus* after LYDEKKER [1888], Brit. Mus. R. 8242, coll. BECKLES («*Pseudosaurillus* or *Saurillus*» after a drawing by Dr. HENKEL and Dr. KREBS).
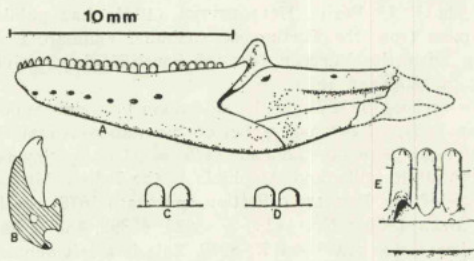
Fig. 11 — *Macellodus brodiei* after HOFFSTETTER, 1967 Brit. Mus. R. 8081, coll. BECKLES (after R. HOF-FSTETTER, 1967, p. 351).

Among the fossils of the BRODIE-collection at the Dorchester Museum there are no lacertilian remains, too. The British Museum only has three unimportant specimens, which had once been purchased with the BRODIE-assets.

By the genera *Macellodus* OWEN, 1854 and *Saurillus* OWEN, 1855 the authors OWEN, LYDEKKER and HOFFSTETTER mean disparates. With the lack of the types LYDEKKER thinks both genera identical and unites them with *Macellodus brodiei* OWEN, 1854. The missing type of *Macellodus brodiei* OWEN 1854, a ca. 25 mm long, with remarkable ventrally curved maxilla, is larger than the two paratypes, fragmentary dentaries (the well preserved one is ca. 17 mm long). After OWEN (1854, 1861) the three

specimens reveal a special dentition, apart from the size and shape of the jaw which differs from *Saurillus obtusus* OWEN, 1855 (type: a 10 mm long right dentary). The teeth of *Macellodus* are firmly attached in the alveoli, the crowns broad and laterally compressed, the cusps roughly rounded and slightly pointed, if unused. The name of the genus is explained by the spade-shaped teeth. The enamel has a special longitudinal striation. The base of the tooth is constricted facing the crown. OWEN has compared the teeth of *Macellodus* with those of *Hylaeosaurus* and *Echinodon* and distinctly illustrated the differences.

On account of the features of the type specimens from the BRODIE-collection (*Macellodus brodiei* OWEN, 1854) and the different jaws from the BECKLES-material, the union of the genera *Macellodus* and *Saurilus,* within the definition of LYDEKKER (1888), cannot be upheld. The specimen Brit. Mus. R. 8242 is due to compare with *Saurillus* OWEN, 1855 (p. 123) and *Pseudosaurillus becklesi* HOFFSTETTER, 1967.

To describ the neotype Brit. Mus R. 8182, coll. BECKLES as *Macellodus brodiei* OWEN, 1854 after HOFFSTETTER (1967) is not justifiable in my opinion ,as not corresponding with OWEN's description of *Macellodus*. Of the missing originals, the illustration of the 17 mm long dentary in OWEN, 1854 (p. 424) reveals a much longer superior suture with the surangular than the 14 mm long dentary of the neotype R. 8182, of which the inferior suture with the surangular and angular is obviously longer. As those sutures of bones are not plesiomorphously developed in the anatomic situations of the recent Lacertilia, the acute-angled kerf on the posterior part of the dentary has taxonomic signification. That is characteristic of Scincomorpha and for diagnostic use by the special development within this group.

After OWEN (1854, 1861) the teeth of *Macellodus* are obviously broad, stout, probably subpleurodont and bulging defined to the base of the tooth; with regard to the dimensions, HOFFSTETTER (1967) remarks «est suspecte (dents de 1 mm de diamètre!)». The longitudinal striations of the enamel diverge laterally, but converge in the middle to the cusp.

2) *Macellodus* cf. *brodiei* OWEN, 1854

From the Guimarota mine three isolated teeth (Gui. L. 138, Gui. L. 139, Gui. L. 158) conform with the given anatomy of the teeth of *Macellodus*. A few similar ones are also present from the locality of Porto Pinheiro.

Diagnosis. — Broad spatulate teeth with longitudinal enamel striation, diverging laterally and converging to the cusp admedially.

Description and discussion. — The breadth of the three teeth from the Guimarota material corresponds with that of *Macellodus* OWEN, 1854 (0,8-1,0 mm). The teeth are used and therefore shortened (ca. 1 mm height). The fine enamel striae exist on both sides of the teeth, but they are much more slighly developed on the more convex labial side. The teeth have a minor pulp cavity. They are broken at the base (s. the waist of the specimen Gui. L. 138). The postulated real mitral form (or spadeshaped, spatulate) of the teeth differs from the neotype of HOFFSTETTER (1967) (Pl. I, 1, 2).

Macellodus brodiei OWEN, 1854 is identical with *Macellodon Brodiei* OWEN, 1861; that may be seen as a lapse of OWEN. In my opinion the three specimens of *Macellodus* described by OWEN, 1854 belong to different forms; surely the large maxilla opposite to the minor dentary fragments. The systematic position of *Macellodus* OWEN, 1854 can only be speculated. As the dentaries are broken at the posterior part, the position of the indicative sutures is doubtful. The rootlike base and the enamel morphology

of the teeth refer rather to a relationship with *Lisboasaurus* SEIFFERT, 1970 from the Guimarota, being related to the anguimorph *Dorsetisaurus* HOFFSTETTER, 1967 from Swanage.

The above nomenclaturally deserted neotype (Brit. Mus. R. 8182, coll. BECKLES) for *Macellodus* after HOFFSTETTER appears to be related to the specimen Brit. Mus. R. 8082 (*Becklesisaurus scincoides* HOFFSTETTER, 1967). There is only a difference in the size of the jaws; *Becklesisaurus scincoides* (R. 8082) is about two third larger than R. 8182 and R. 8081. The slender torsion of the angular, observed by HOFFSTETTER (1967) on the external side of the jaw R. 8082, is not delivered on the fragment R. 8182.

I suggest the following specimens of the BECKLES-collection Brit. Mus. R. 8182, R. 8081, R. 8099, R. 8113, R. 8120, R. 8184, R. 8197, R. 8204 (ascribed to *Macellodus brodiei* by HOFFSTETER) relate to the genus *Becklesisaurus* HOFFSTETTER, 1967. The Kimmeridgian vertebrate remains of Portugal include numerous fragments of comparable jaws.

3) *Becklesisaurus hoffstetteri* SEIFEERT, 1970

The species of the genus. — *Becklesisaurus scincoides* HOFFSTETTER, 1967 (p. 360-362) from the Purbeck of Swanage.

The species *hoffstetteri* is named after Prof. ROBERT HOFFSTETTER (Paris), who has described corresponding forms from the BECKLES-collection in the British Museum and named the genus *Becklesisaurus*. This species appears both in the Kimmeridgian of Portugal and in the Lower Cretaceous of Spain.
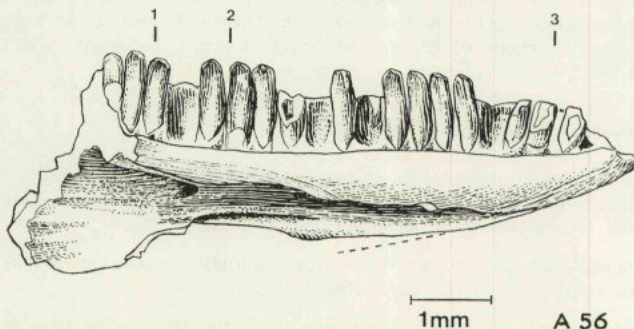
Fig. 12 — Gui. A. 56, *Becklesisaurus hoffstetteri,* left dentary (holotype), lingual view; between 1 and 2, the opening of the canalis alveolaris inferior can be seen, situated under the 17th tooth.

Diagnosis and discussion. — Dentaries with ca. 24 pleurodont, oblong teeth, of which the cusps lingually present a characteristic striation projecting as a cutting edge, and with an extending suture for an anterior elongated splenial.

The special morphology of the teeth of *Becklesisaurus hoffstetteri* has also been illustrated by HOFFSTETER (1967) for his «*Macellodus brodiei*» (R. 8182 and paratypes) and *Becklesisaurus scincoides* (R. 8082). Against the smooth convex labial side of the teeth, the lingual side presents a special enamed striation to the cusp. After the preliminary parallel run, two lingual edges converge to a prominent cusp; therefore

a smaller area between the edges is featured complying with the outline of the tooth, and the teeth achieve a chisellike aspect. in the anterior and mid part of the jaw the described cusp is not located on the middle of the tooth shaft, but eccentrically to rear, so that the edge of the superior tooth seems to be recurved. On the posterior teeth the cusp removes to the middle. The teeth have a cutting anterior, occlusial and posterior edge. The cusps are partly of light colour and transparent. The pulp cavity is
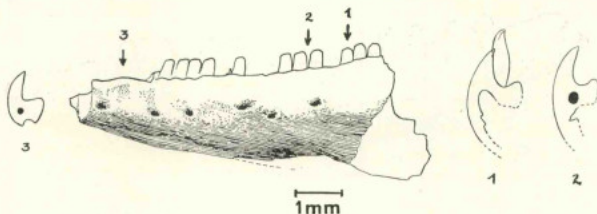
Fig. 13 — Gui. A. 56, labial view of the left dentary (holotype) of *Becklesisaurus hoffstetteri*. The cross-sections (1, 2, 3) show the development of the canalis alveolaris inferior.

relatively broad. Several teeth indicate an «iguanid» form of tooth replacement (after EDMUND, 1960, 1969) with a median basal fossa (s. the 17th tooth of the holotype Gui. A. 56). Basal foramina are in the middle of the tooth base. These features are to be found equally on «*Macellodus brodiei*» after HOFFSTETTER, 1967 and *Becklesisaurus scincoides* HOFFSTETTER, 1967. The dentary and the striation of the lingual tooth crowns are similar to the situation of the Upper Cretacious *Sauriscus cooki* ESTES, 1964 and
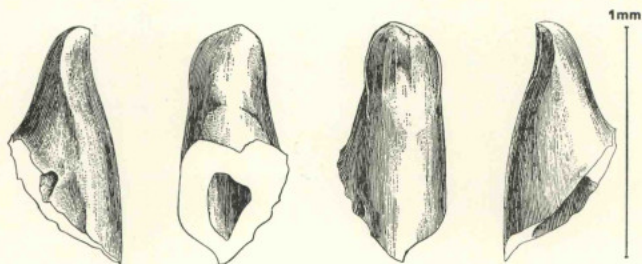
Fig. 14 — Gui. A. 56, tooth from the anterior part of the left dentary of *Becklesisaurus hoffstetteri* (holotype), from left to right: posterior, labial, lingual, anterior views.

of some species of the genus *Eumeces* (both genera are skinks). *Sauriscus* has in addition characteristic bifid teeth. The description of the dentary of *Sauriscus cooki* ESTES, 1964 conforms in a way with *Becklesisaurus hoffstetteri:*

«Posteriorly a deep notch for angula and surangular sets off a slender, pointed, dorsal coronoid process of the dentary, and a ventral angular process. There is the usual row of mental foramina. The Meckelian groove is quite restricted anteriorly, forming only a very shallow ventral groove. Posteriorly it enlarges and the internal mental canal opens under the nineteenth tooth. (— under the 18th tooth of 24 on

Becklesisaurus hoffstetteri Gui. A. 56 —) The type dentary bears twenty-seven teeth and in the other, somewhat smaller, specimens the number of teeth varies from twenty--three to twenty-five. The teeth are pleurodont, and project about one-fourth of their height above the parapet. The anteriorly broad subdental ridge thins out posteriorly and is separated from the teeth by a prominent subdental hollow. The teeth are closely spaced, subcylindric, slinghtly compressed at the crown, slightly inclined posteriorly»
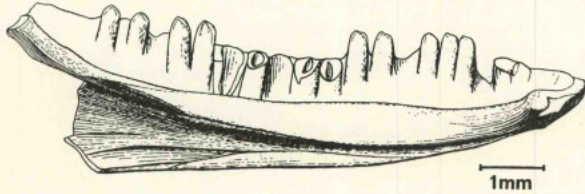
Fig. 15 — Gui. A. 45, *Becklesisaurus hoffstetteri;* in the row of teeth, the cusp is moving from behind to the middle of the tooth.

(p. 118); thereby the scincomorph character of *Becklesisaurus hoffstetteri* becomes distinct. At the base of the pleurodont attached teeth the lingual bony subdental ridge (regula subdentalis) forms a subdental hollow (sulcus subdentalis). This sulcus is typical of Scincomorpha (ESTES, 1964; HOFFSTETTER, 1967). The anterior broad subdental ridge thins out posteriorly making room for the splenial. The long attachment area for the splenial indicates an anterioly elongated splenial, which is not preserved
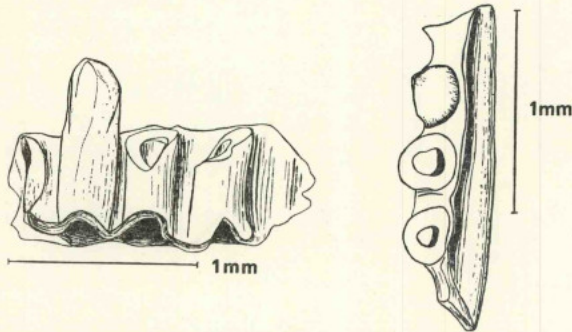
Fig. 16 — Gui. GE. 7, dentary fragment of *Becklesisaurus hoffstetteri* with a tooth, which has a distinct cutting edge and a lingual cusp.

on the Portuguese *Becklesisaurus*. The splenial closes the so-called Meckelian groove under the subdental ridge in large extention. This semicanalis or sulcus primordialis Meckeli includes in vivo the Meckelian cartilage and additionally in the posterior broadened part besides the vessels (A. and V. alveolaris inferior) the nerve alveolaris inf. (main branch of the N. mandibularis, V_3). The N. alveolaris inf. runs under the 18th tooth in a separate bony channel (canalis alveolaris inf.) and becomes parted from the supply of the teeth (plexus dentalis inf.) rami cutanei by ca. six foramina dento-facialia on the external side (labial) of the dentary (this allows

conclusions about the squamation and the salivary apparatus of the jaws, after OWEN, 1855, p. 123).

As represented by the Scincomorpha of the Guimarota and the recent *Chalcides chalcides,* also by *Saurillus* and *Pseudosaurillus* after HOFFSTETTER (1967, p. 356-360) the skinks and their related ancestors have developed a special attachment area for the muscle genioglossus on the ventral anterior part of the dentary. The M. genioglossus originates in the anterior lower margin of the dentary under the symphysis and reaches the ventral and lateral parts of the tongue. The muscle is used for the movement
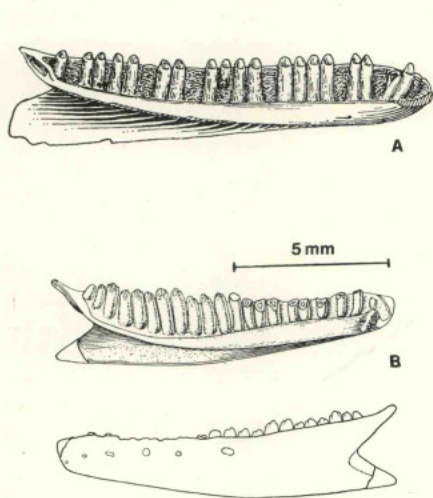
Fig. 17 — A: *Eumeces* cf. *fasciatus* (skink), Pleistocene of Florida, after W. AUFFENBERG, 1956, p. 165. B: *Sauriscus cooki* ESTES, 1964 (scincid), Lance-Formation, Upper Cretaceous, after R. ESTES, 1964, p. 118.
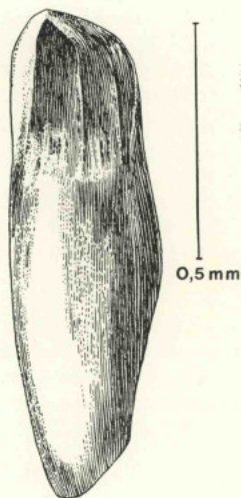
Fig. 18 — Gui. A. 56, tooth of *Becklesisaurus hoffstetteri* (lingual view) from the middle part of the left dentary (holotype), with pleurodont tooth attachment.

and protrusion of the tongue (s. BOBISON & TANNER, 1962; WETTSTEIN, 1931, 1932). *Becklesisaurus hoffstetteri* presents an extended, slender and notched attachment area for the genioglossus. The symphyseal region is relatively small, a feature also on the dentary Brit. Mus. R. 8099 (I class this specimen to the genus *Becklesisaurus* HOFF-STETTER, 1967). The development of the posterior part of the dentary of *Becklesisaurus hoffstetteri* is different to *Becklesisaurus scincoides* HOFFSTETTER, 1967 and «*Macellodus brodiei*» after HOFFSTETTER (1967). The superior process of the dentary to the coronoid, the processus coronoideus, rises dorsally on *Becklesisaurus hoffstetteri,* whereas on «*Macellodus brodiei*» after HOFFSTETTER (1967) and *Becklesisaurus scincoides* HOFF-STETTER, 1967 it is scarcely curved to the coronoid. «*Macellodus brodiei*» after HOFF-STETTER (1967) differs from *Becklesisaurus scincoides* HOFFSTETTER, 1967 apart from the size by the stronger development of the posterior ventral process of the dentary (processus angularis). Regarding the other conformity there are at the most presented two species of the genus *Becklesisaurus*. The coronoid of *Becklesisaurus hoffsteri* is

delivered only in fragmented bony remains on the processus coronoideus of the dentary Gui. A. 56; the anterior process of the coronoid has left behind a long attachment area on the lingual side of the dentary as on the related Purbeck forms from Swanage. As an ancestral feature of anguimorph habitus the sulcus primordialis Meckeli is very broad and large before the entry of the N. alveolaris inf. on the posterior internal side of the dentary. In the anterior part the sulcus runs diminishing to the ventral external side under the symphysis.

The maxillae of *Becklesisaurus hoffstetteri* are easily identified with the aid of the above described typical teeth. With the premaxillary teeth the number of the teeth in the upper jaw is multiplied contrary to that of the lower jaw. The left maxillae Gui. GE. 14 is associated with a fragment of the premaxilla, which has smaller teeth (s. also specimen P. P. I-L. 6). The following statement offers a rough survey of the allocation of the teeth in the upper and lower jaws of different lizards:

	premaxilla	maxilla	dentary
Tupinambis sp.	6	12/13	14/15
Lacerta lepida	7	21	26
Scincus scincus	2	19/20	20/21
Chalcides chalcides	3	14	16
Becklesisaurus hoffstetteri	4	21/22	23/24
Cordylus giganteus (*)	7	24	26
Varanus sp.	4	12	13
Iguana iguana	5	26	29
Pachydactylus bibroni (*)	9	32	32

(*) These statements are from EDMUND [1969].

labial   lingual

0,5 mm
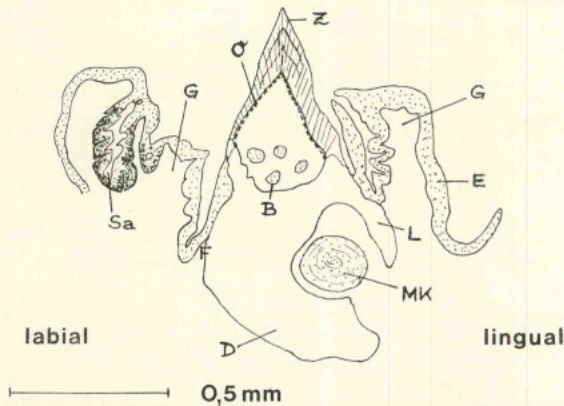
Fig. 19 — Cross-section of the dentary of a recent rhynchocephalian embryo, shortly to be hatched (modified after HARRISON, 1901 in WETTSTEIN, 1932, p. 172). B: Blood-vessels (A. and V. alveolaris inferior); D: Dentary; E: Epithelium of mucous membrane; F: Exit for cutaneous and salivary rami of the N. alveolaris inferior through Foramina dento-facialia; not cut in this section; G: Gingiva; L: Subdental ridge; MK: Meckelian cartilage in the Sulcus primordialis Meckeli; O: Odontoblast layer; Sa: Glands; Z: Tooth.

From the form of the maxilla (s. Gui. GE. 14, Gui. L. 31 and Gui. L. 34; similarly the right maxilla Brit. Mus. R. 8197 from Swanage) *Becklesisaurus* does not have a long snout, but rather a relatively short facial skull. The anterior part of the orbit is situated above the maxilla. A special curve of the posterior maxillary part indicates the onset of the jugal (s. Gui. L. 31, Gui. L. 56). The specimens Gui. 398 and P. P. I-L. 6 present the base of the naris. On the external side of the right maxilla Gui. L. 34 the dermal squamation has been traced. This bony ornamentation is also to be seen on the maxilla R. 8197 in the British Museum (published by HOFF-STETTER, 1960). Further more the external side of the maxilla presents numerous openings for the exit of the rami cutanei of the N. alveolaris superior (N. V_2).

The ornamental relief on the external side of the maxilla does not generally exist. The specimen Gui. L. 31 lacks it, whereas it is extraordinary well developed on the similarly formed maxilla Gui. L. 34. This attribute can be regarded as a sex- or race-feature.

The functional correlation of the characteristic teeth to the kind and form of the food, which certainly relates to be mobility of the tongue and the posteriorly risen coronoid (for the insertion of parts of the muscle adductor mandibulae), is not clear. Assuming a partial herbivorous alimentation it must be considered after OSTROM (1963):

«Since one of the principal saurian muscles (M. adductor posterior) that must be called into play in generating these mandibular grinding motions has its origin on the reptilian quadrate, effective grinding or mastication, other than a simple vertical chopping by repeated adduction, is precluded in the Squamata where the quadrate is free».

4) *Saurillus* cf. *obtusus* OWEN, 1855

From the same stratum of the ca. 115 m thick section in Durdlestone (Durlston, South-Swanage), where *Macellodus brodiei* OWEN, 1854 and mammalian remains had been found, a right scincomorph dentary of the BRODIE-collection was described as *Saurillus obtusus* by OWEN, 1855. After OWEN the stratum has the number K. 93 in AUSTEN's stratigraphical guide, described by different authors as 30-35 cm of thick limnetic marls (named «dirt bed, containing shells», «grey earthy, dirt bed», «marly freshwater shale with selenite, plant remains and vertebrates» or «mammalian beds» of the lowest Middle-Purbeck). The «dirt bed, containing shells» is not to be mistaken for a 10 cm stratum on the base of the Lower-Purbeck, which is known as «dirt bed, carbonaceous clay» (s. OWEN, 1871; SIMPSON, 1928).

The type specimen has «moderately long, conical, blunt-pointed teeth» (OWEN, 1855), which are neither broad nor flattened as of *Macellodus*. The external side of the 10 mm long dentary presents an acute-angled scincomorph, and a V-shaped configuration of the posterior end, where the surangular fits in. There are six foramina dento-facialia after OWEN (1855); the anterior openings are occasionally associated with a smaller one. The specimen R. 8130 from the BECKLES-collection of the British Museum corresponds in essential features with the type of OWEN, 1855 from the BRODIE-collection. Since the number of the teeth varies, the difference of 23 teeth on the dentary R. 8130 and at least 21 teeth of the holotype is insignificant, especially as the latter one is obviously a smaller individual. Because the holotype is not found today, the specimen Brit. Mus. R. 8130 should be considered as a type of an intimate relationship. For that HOFFSTETTER (1967) has created the new species *Saurillus robustidens* based on the supposed different number of the teeth on the specimen R. 8130 contrary to the lost original.

From the Guimarota material numerous remains can be attributed to the form *Saurillus obtusus* OWEN, 1855 (not HOFFSTETTER, 1967). But only one minor fragment
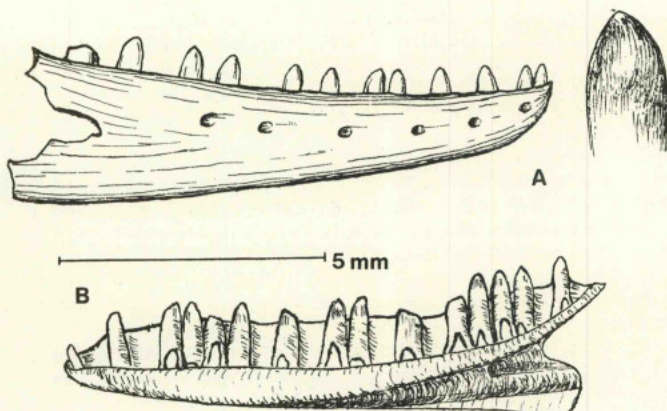
Fig. 20 — A: *Saurillus obtusus* OWEN, 1855, coll. BRODIE (after R. OWEN, 1855, p. 123). B: Brit. Mus. R. 8130, coll. BECKLES, *Saurillus robustidens* HOFFSTETTER, 1967; in contrast to OWEN's description of *S. obtusus* this right dentary does not bear Clunt teeth; lingually the teeth show a chisel-shaped cusp.
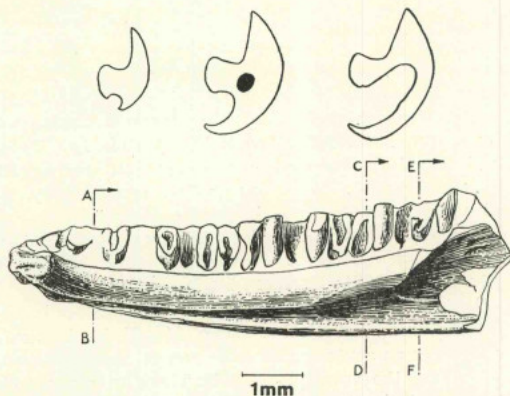
Fig. 21 — Gui. 5, right dentary of *Saurillus* cf. *obtusus* OWEN, 1855 (non HOFFSTETTER, 1967) from the Guimarota, lingual view; the cross-sections show the formation of the canalis alveolaris inferior.

with one tooth has come from the Upper Kimmeridgian of Porto Pinheiro (P. P. I-L. 4), which can be compared with *Saurillus obtusus* OWEN, 1855 (p. 123).

Diagnosis (s. OWEN, 1855) and discussion. — Dentaries with 22-23 conical, pleurodont teeth, the cusps of which are modestly curved lingualwards, and with a nearly straight and even thick subdental ridge, which dorsally develops an only a slightly indicated subdental hollow. A narrow Meckelian groove ventrally runs under the subdental ridge.

The specimen Gui. 5 equals the specimen Brit. Mus. R. 8130 from the relations of *Saurillus obtusus* OWEN, 1855 in many details. They differ by the configuration of the subdental ridge. The right dentary from the Guimarota is a little smaller than R. 8130. On both dentaries the N. alveolaris inf. enters approximately under the 18th
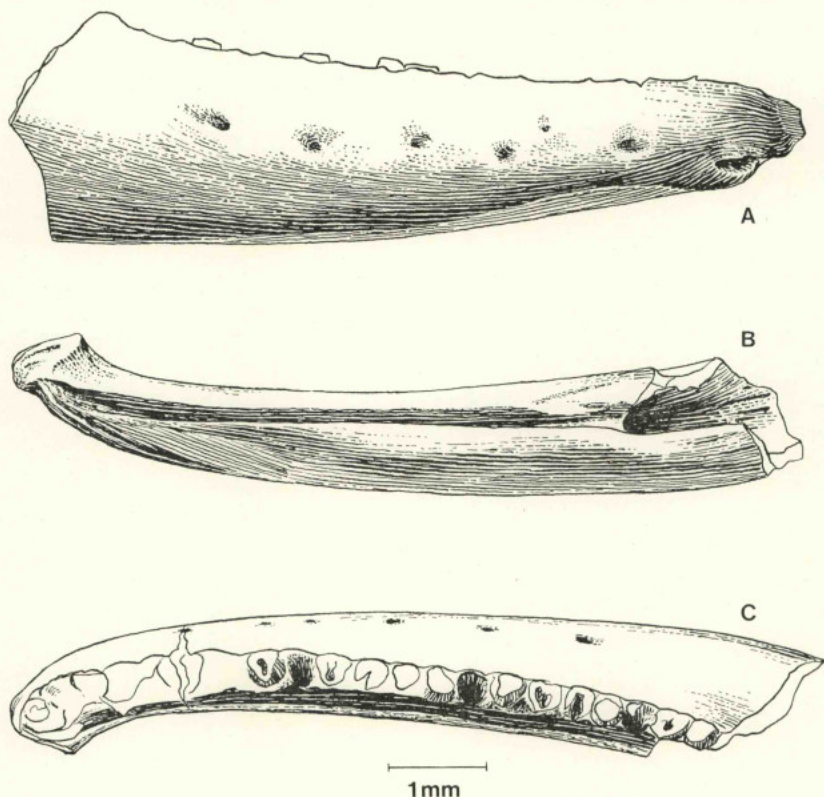
Fig. 22 — Gui. 5, *Saurillus* cf. *obtusus* OWEN, 1855, a right dentary from the Guimarota; A: labial view, in the anterior part the insertion of the M. genioglossus is ventrally marked; B: ventral view, straight run of the Meckelian groove; C: dorsal view, presence of a sulcus subdentalis.

tooth in the canalis alveolaris inf.; the heigh of the lower jaw measures 1,85 mm on the specimen Gui. 5 and 1,9 mm on R. 8130. The dentary of Gui. 5 might have born 22-23 teeth, the dentary R. 8130 presents 23 teeth. The partly preserved tooth fragments of Gui. 5 broken at the superior margin of the dental parapet. The teeth are closely placed, cylindric, conical; lingually the tooth cusp is chiselshaped, and on the tooth cross-section a narrow tubular pulp cavity can be seen. On the subdental ridge an attachment area for the splenial is to be seen under the 15th-20th tooth. This splenial mark is well preserved on several specimens of the Guimarota (Gui. 110, Gui. 255, Gui. 383). On the Guimarota specimens of *Saurillus* cf. *obtu-*

sus the posterior jaw bones are not present. The left dentary Gui. L. 29 indicates an acute-angled scinomorph limitation of the posterior end. The symphyseal region is developed as an approximately square swelling with a certain surface morphology, which has synchondrosially been connected with the pendant. The M. genioglossus has anteriorly left a muscle mark on the ventral external side of the dentary (on Gui. 5: 2,1 mm length and 0,3 mm breadth). As a primitive feature, a long and narrow Meckelian groove extends ventrally under the symphysis. The development of the subdental hollow is also ancestral. The Guimarota remains of *Saurillus* cf. *obtusus* present a variation of a distinguishable subdental hollow (Gui. 5, Gui. 419) to a distinct projected broad subdental ridge (Gui. 241, Gui. 322, Gui. 325). The thickness of the subdental ridge varies moderately, too. The subdental hollow is not yet developed on related ancestors, as may be seen on a comparable lacertilian dentary fragment from the Latest Bajocian (yielded by washing of the sapropelitic marls of the Causse du Larzac at Nant, Southern France). On the Middle Jurassic specimen the Meckelian groove also extends to the symphysis ventralwards.

The fragmentary maxillae Gui. 338 and Gui. 401 have the typical teeth of *Saurillus* (conical, blunt looking, externally convex and smooth, curved both lingual- and backwards, see also the dentary Gui. 223 and the fragment P. P. I-L. 4). The named maxillae are preserved with the anterior parts presenting a remarkable concavity for the naris (cf. the maxillae R. 8085, R. 8104 and R. 8118 from the BECKLES-collection of the British Museum).

The left dentary fragment Gui. 376 shows an abnormality anteriorly, where it is flexed off ventralwards without a spot of rupture. Since on the labial side a regeneration of the bone can be seen, a former violation of the lower jaw it may be supposed that it is due to.

From HOFFSTETTER's description (1967) in his *Paramacellodus oweni* the unity with *Saurillus robustidens* HOFFSTETTER, 1967 may be deduced. *Saurillus robustidens* R. 8130 is here reviewed as intimately related with *Saurillus obtusus* OWEN, 1855.

5) *Saurillus proraformis* SEIFFERT, 1970

Derivatio nominis. — *proraformis:* formed like the bow of a ship, referring to the appearance of the dentaries of the Kimmeridgian from the Guimarota.

Type species of the genus. — *Saurillus obtusus* OWEN, 1855 (non HOFFSTETTER, 1967) from the Purbeck of Swanage.

Diagnosis and discussion. — Relatively short, stout dentaries with 15-16 conical, pleurodont teeth, the cusps of which are a little curved back- and lingualwards; in addition the broad Meckelian groove totally runs on the lingual side of the dentary.

The pleurodont dentition presents closely placed, cylindric teeth with coniform cusps. The tooth crown is labially convex and lingually concave. The superior third surpasses the margin of the dental parapet; the pulp cavity is relatively broad. The entry of the canalis alveolaris inf. (for the N. alveolaris inf.) is located under the 11th-12th tooth. The canalis lies in the central dentary; therefore the foramina dentofacialia (mostly five) are approximately placed in the middle of the external side. The subdental ridge continually thins backwards; a distinct subdental gutter is developed. The relatively broad Meckelian grove extends on the internal side of the dentary, closed by the splenial (s. Gui. 49). By their height and breadth the dentaries appear to be compact. At the entry of the canalis alveolaris inf. the ca. 7 mm long dentary Gui. 7 has a height of 2,1 mm. The coronoid has three processes of the same length (s. Gui. 50), an anterior one to the dentary, a posterior one to the surangular and a dorsal
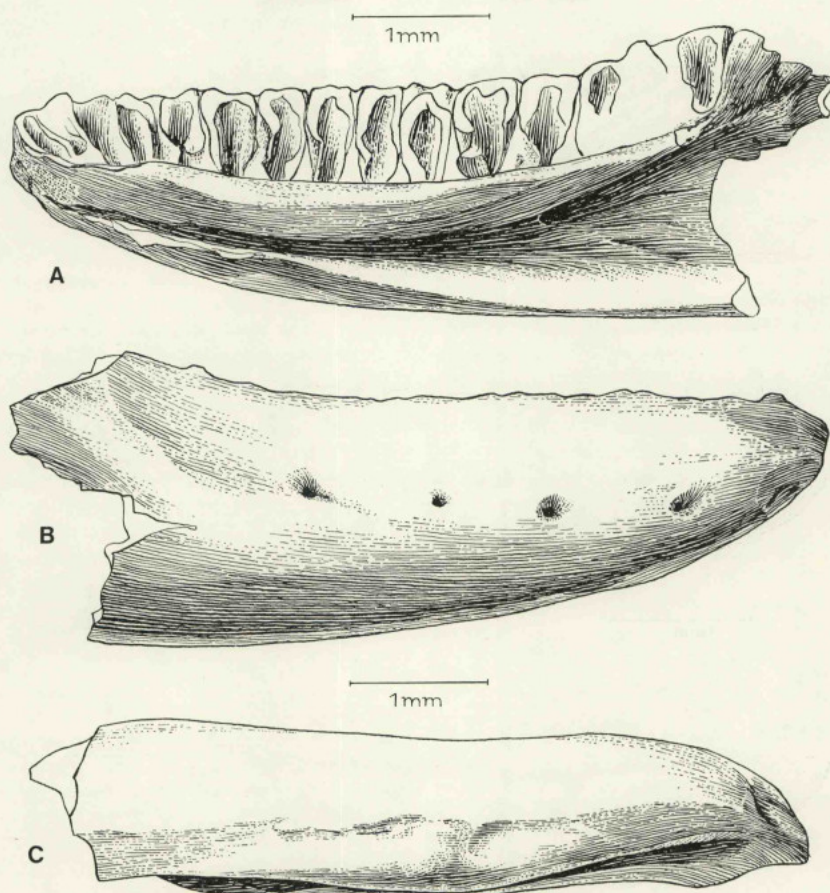
Fig. 23 — Gui. 7, *Saurillus proraformis*, right dentary (holotype); A: lingual view, posteriorly broad sulcus cartilaginis Meckeli; B: labial view, few foramina dento-facialia; C: ventral view, marks of muscle insertions.

one as processus massetericus for the insertion of the M. adductor mandibulae. The surangular is cuneiformly fitted in the acute-angled, scincomorph posterior part of the dentary. On the specimen Gui. 49 the suture is obliterated by coossification, indicating an adult individual. On the anterior external side of the surangular there is an opening, probably for the exit of a ramus of the nerve mandibularis (N. V$_3$). The angular mainly forms the ventral external side of the posterior part of the lower jaw (s. Gui. 49 and Gui. 50), whereas *Iguana* and *Varanus* show it located more on the ventral middle region of the jaw; on the latter one it is considerably reduced. The anterior end of the angular presents on the internal side of the jaw a foramen nervi mylohyoidei
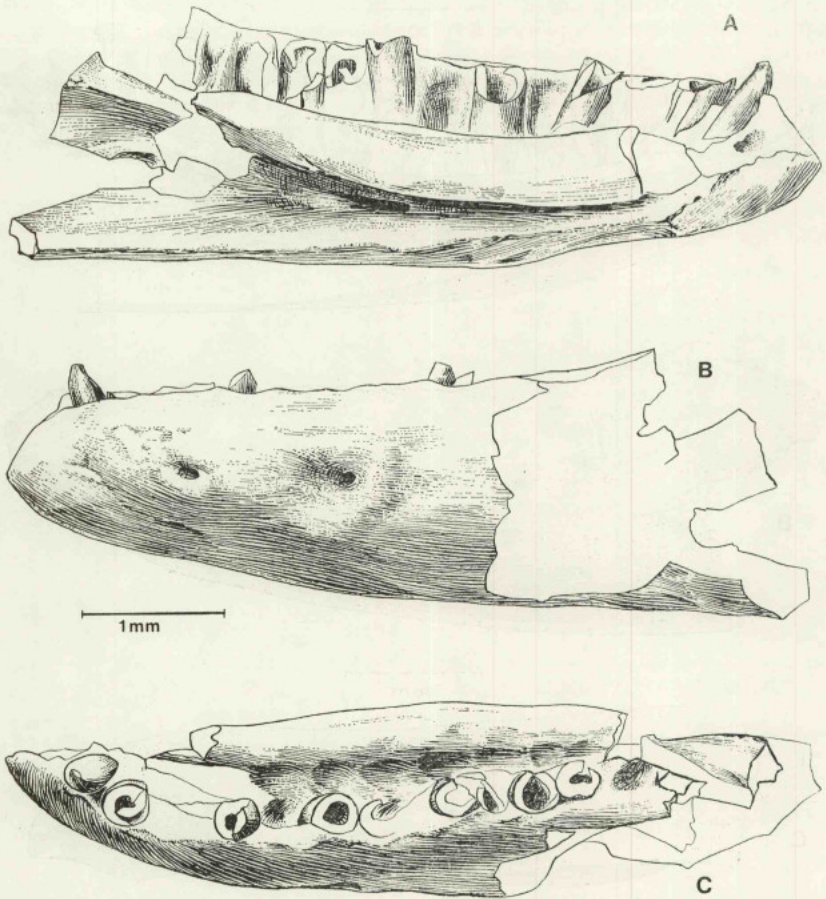
Fig. 24 — Gui. 10, left dentary of *Saurillus proraformis* from the Guimarota; A: lingual view, large Meckelian groove; B: labial view, few foramina dento-facialia; C: dorsal view, distinct sulcus subdentalis.

(a ramus of the N. V₃ for the motorial innervation of the M. mandibulohyoideus III after ROBISON & TANNER, 1962) under the suture to the splenial. This feature is obviously plesiomorphus (s. HOFFSTETTER, 1967), but the other described features are characteristic of the Scincomorpha.

A long, slender, oval fossa Meckeli exists on the internal side of the lower jaw (for the taking up of the N. mandibularis). The fossa Meckeli is formed by the surangular and gonial-articular. On the specimen Gui. 50 the gonial (= prearticular after WILLISTON, the seventh bone of the lower jaw) is apparently not yet tied to the

articular. That gonial is distinguished by a ventral rough area on the posterior internal side, which is caused by the insertion of a strong M. pterygomandibularis (s. WETTSTEIN, 1931; ROBISON & TANNER, 1962). Regarding the relatively large breadth and length of the muscle insertion a powerful masticatory and grinding movement is to be assumed for the consumotion of consistent food.

The processus retro-articularis is fragmentary presented on the specimens Gui. 49 and Gui. 50. It is only a little ventrally inclined and has a distinct fossa retro-articularis, ahead of which the fovea articularis is located for the articulation with the condyle mandibularis of the quadrate. In the interior of the fossa retro-articularis there are two separated little foramina, a third opening externally lies on the posterior internal side of the processus retro-articularis.

⊢——————⊣ 1mm

Fig. 25 — Gui. 49, *Saurillus proraformis,* fragment of a right lower jaw; the dentary is co-ossified with the surangular, which locks into the posteior end of the dentary, acute-angled; in the surangular the foramen antero-externum is present (exit of the SIEBENROCK's nerve after HOFFSTETTER, 1967).
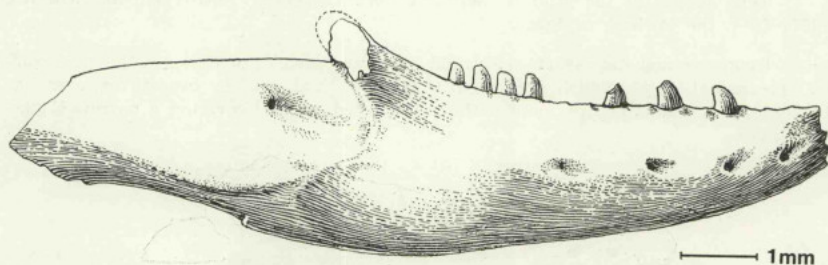
The maxillae of *Saurillus proraformis* are easily identified by their morphology and the low number of teeth (s. Gui. A. 75). A long attachment area for the jugal is present. From a large extending posterior concavity of the maxilla (s. Gui. 335, Gui. A. 75 and Gui. A. 87) an orbit located above the posterior part of the maxilla and a short snout can be concluded, also indicated by the compact dentaries.

Above the fossa Meckeli a nerve channel (for SIEBENROCK's nerve after HOFFSTETTER (1967), a ramus of N. V_3) runs in the surangular, with the exit on the anterior side. The foramen antero-externum supraangulare is found in the posterior extension of the cuneiform anterior part of the surangular. In this anatomical position it is only known of Scincidae and Gerrhosauridae; in addition *Xantusia riversiana* can be compared.

As distinguished from the gerrhosaurids the splenial of *Saurillus proraformis* has no process to the coronoid, which represses the anterior side of the processus dentalis on *Gerrhosaurus,* but the splenial leavelike fits in the Meckelian groove, so that the processus dentalis is attached with a large inferior margin as on scincids and lacertids. Whereas on *Gerrhosaurus* the processus supraangularis of the coronoid extends to the fossa Meckeli and the prearticular, it is not elongated on *Saurillus proraformis,* but approximately equal in length as the processus dentalis; that is the case with the Scincidae, too.

On the jaws of cordylids the processus retro-articularis is emphasized and ventrally inclined, on those of *Saurillus proraformis* it is scarcely so. A farther difference is the development of the splenial extending to the external side of the lower jaw of cordylids, but not of *Saurillus. Saurillus proraformis* differs from the Lacertoidea by the existence of a distinct subdental hollow and the absence of a long fourth coronoid

process to the external side of the dentary. The genus *Saurillus* represents an ancestral form of the Scincidae.

6) *Saurillus henkeli* SEIFFERT, 1970

This form is closely related with *Saurillus proraformis*, having differences in the proportions of the lower jaw. The dentary is rather straightly stretched and not shaped like a bow. Hitherto this species is only known from the Guimarota mine.

Derivatio nominis. — *henkeli:* after Prof. SIEGFRIED HENKEL (Berlin), who has carried out the recovery of the fossil vertebrates from the Guimarota.

Type species of the genus. — *Saurillus obtusus* OWEN, 1855 (non HOFFSTETTER, 1967) from the Purbeck of Swanage.

Diagnosis and discussion. — Straight extending, slender dentaries with ca. 15 conical, pleurodont teeth, which are slightly recurved and project two difths over the border of the dental parapet, and with an elongated splenial covering a narrow Meckelian groove.
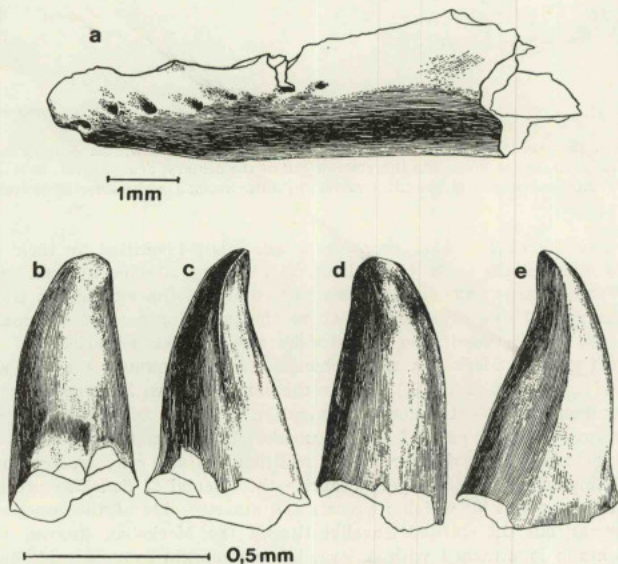
Fig. 26 — Gui. 6, *Saurillus henkeli*, left dentary (holotype); a: labial view, a row
of foramina dento-facialia; b-e: one tooth of the specimen, b: labial, c: posterior,
d: llingual, e: anterior view.

The lower jaw of *Saurillus henkeli* has a remarkable similarity with that of the recent *Chalcides chalcides*. The inferio margin of the slender dentary runs almost straight as that of the subterrestric living skink *Chalcides*, the skull of which is flattened for burrowing (s. HAAS, 1936). The straightly running subdental ridge considerably thins backwards; a distinct subdental hollow is developed. The posterior process

of the coronoid to the surangulalr presents a strong, medially directed crest (Gui. 28). The posterior part of the lower jaws is slim; internally there is a long furrowlike fossa Meckeli between the surangular and gonio-articular as on *Chalcides, Scelotes, Chamaesaura* and *Pseudocordylus;* but opposite to the cordylids the processus retro-articularis of *Saurillus henkeli* is not prominently inclined ventrally. On the ventral internal side of the gonio-articular the insertion area for the M. pterygomandibularis is less marked than that one of *Saurillus proraformis.*

The maxillae are of fragile structure (Gui. 292, Gui. L. 27, Gui. L. 173). The openings of the exit for the rami cutanei of the N. alveolaris superior (N. V_2) are located closely above the maxillary crest obviously confined to this straight row. This habitus is found on *Pseudosaurillus becklesi* HOFFSTETTER, 1967 and «*Saurillus obtusus*» after HOFFSTETTER (1967), non OWEN, 1855, also on the recent *Chalcides chalcides*. From the limitations of the maxillae and the dentaries a short facial skull can be assumed. The specimen Gui. 254 (a left premaxillary fragment) reveals pairs. The premaxilla bears four teeth, like *Chalcides*. The morphology of the skull with the straight and slender lower jaw suggests the presence of a burrowing skink.

The postcranial skeletal remains (Gui. L. 30) offer the expected morphological features in comparison with the skeletons of *Chalcides chalcides* and *Chalcides guentheri*. The limbs are on the point of being reduced as may be seen by the shortened femur. As for the support of the vertebral column, a zygosphene-zygantrum-articulation is developed for additional winding locomotion. Seven vertebrae with ribs, a femur a humerus, a tibia with fibula are collected on the piece Gui. L. 30. The colour and the consistence of the bony remains of *Saurillus henkeli* corresponds with that of the postcranial skeleton Gui. L. 30 (s. also the chapter about the forelimbs).

Annotation. — As «*Saurillus obtusus*» after HOFFSTETTER (1967), non OWEN, 1855 and *Pseudosaurillus becklesi* HOFFSTETTER, 1967 are only different in the size, they are to be considered for the present as being congenerically related. The jaw remains of these Swanage forms are distinguished by numerous slim, conical teeth (ca. 30 pleurodont teeth on the dentary).

D. *Lisboasaurus* SEIFFERT, 1970

1) *Lisboasaurus estesi* SEIFFERT, 1970

HOFFSTETTER (1967) describes an anguimorph lacertilian genus from the lowest Middle Purbeck of Swanage, *Dorsetisaurus purbeckensis,* which is characterized by lanceolate teeth:

«La couronne, revêtue d'un email très brillant, est comprimée, avec des bords tranchants convergeant en une pointe légèrement déjetée vers l'arrière. On observe une certaine hétérodontie: les dents antérieures sont plus élancées, les postérieures plus larges et moins aigues. Ces dents sont creuses, et, de ce fait, leur partie comprimée est souvent écrasée lors de la fossilisation.» (HOFFSTETTER, 1967).

Derivatio nominis. — *Lisboasaurus:* this lacertilian is named after the capital of Portugal, following the geographical derivatio of the name *Dorsetisaurus* HOFFSTETTER, 1967, to which the new genus is related. *estesi:* after the paleoherpetologist Prof. RICHARD ESTES (Boston), who has recognized first (on visiting Berlin in 1967) the relationship of the Guimarota genus with the English form *Dorsetisaurus*.

Lisboasaurus is represented by several bony remains and isolated teeth from the Kimmeridgian of Portugal.

Diagnosis of the genus. — *Lisboasaurus* has lanceolate teeth with a root-like teeth base («mosasauroid»), a lingual cusp and a special enamel gloss.

Diagnosis of the species. — The species is characterized by labio-lingually compressed, smooth teeth, the bulgy bases of which are lingually linked by a mediana groove, which continues on the inferior part of the tooth. The maxilla has a relatively long prefrontal process and a longer, broad jugal process; between them an anteriorally shifted notch exists for the attachment of the prefrontal. There are divisions for at least 15 teeth, the first of which has obviously been very enlarged.
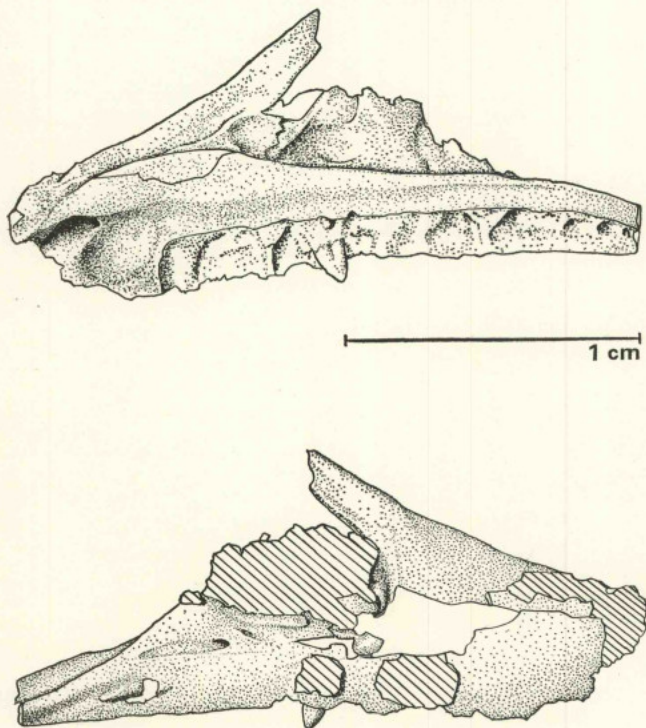
Fig. 27 — Gui. 37, *Lisboasaurus estesi,* right maxilla (holotype); above: lingual view, the preserved tooth shows a grooved, bulgy base with a pleurodont mode of attachment; below: labial view.

Discussion. — The extraordinary form of the dentition of *Lisboasaurus* manifests a similarity with that of the Lower Cretaceous Aigialosauridae and the Upper Cretaceous Mosasauridae. The aigialosaurid with the best known dentition is *Opetiosaurus bucchichi* KORNHUBER, 1901 from the Lower Cretaceous of Lesina, Dalmatia; KORNHUBER describes:

«Jede Zahnkrone ist nämlich von einem Sockel, d. i. von einem knöchernen Säulchen oder einer Stütze, von durchschnittlich 5 mm Höhe, getragen, dem sie, genau abgegrenzt und von einer zarten, wallartigen Erhöhung umgeben, aufsitzt. Der Sockel ist cylindrisch und endet, nach oben sich etwas verschmälernd, stumpf conisch mit der

kreisförmigen Ansatzstelle des Krönchens. Die Seite des Sockels ist schwach gestreift, in der Mitte mit einer deutlichen, rinnig vertieften Längsfurche versehen, die fast den vierten Theil von der Sockelbreite einnimmt. Die Zahnkronen haben durchschnittlich 2 mm Durchmesser an ihrer Basis und über 3 mm Höhe; sie sind mit ihrer kegelförmigen Spitze etwas nach hinten gekrümmt und von einem glänzenden, bräunlichen Schmelze überzogen, der keine Zähnelung, sondern nur eine schwache Streifung erkennen läßt... Die beschriebenen Sockel sind dem Kieferrande aufgewachsen und scheinen etwas in die Unterlage eigesenkt zu sein.»

The big aquatic mosasaurs with secondary subthecodontly fixed teeth (s. McDOWELL & BOGERT, 1954) are presumably derived from the aigialosaurids. There is a convergence to the mosasaurs in the jaw construction and the dentition by the toothed birds Hesperornithiformes from the Upper Cretaceous of North America (s. MARSH, 1880; KORNHUBER, 1901; GREGORY, 1951, 1952). By GREGORY (1952) the lower jaw of *Ichthyornis* MARSH, 1873 have been emended as jaw remains of a small mosasaur. The adaptation to the aquatic, piscivorous mode of life of the Mosasauridae and Hesperornithiformes has caused the similar opportune phenotypic features to evolve. For the aigialosaurids KORNHUBER (1901) accepts the tooth structure of mosasaurs described by CUVIER. Accordingly the base of the tooth is only hollow in the period of increase; it becomes completely solid. At first the teeth are joined by connective tissue, then coossify with the jaw by means of a bone-like substance resembling the cementum dentis. Contrary to the mammalian teeth the «mosasauroid» teeth have no roots of dentine covered with cement. To exclude mistakes the special base of «mosasauroid» teeth is better termed as a socle, not as a root.

From the Guimarota no emitted solid teeth of *Lisboasaurus estesi* with a resorbed base have been found. The mode of attachment on the jaw is pleurodont despite the special socle (Gui. 37). The tooth base of *Lisboasaurus estesi* has a longitudinal groove like *Opetiosaurus*. Therefore on the lingual side the teeth seem to be seated on double-socles. The alveoli present a distinct concavity as *Dorsetisaurus purbeckensis* HOFFSTETTER, 1967. The description of the dentition of *Dorsetisaurus* corresponds on the whole with that of *Lisboasaurus;* in lieu of the special development of an tooth socle with a median longitudinal groove, on *Dorsetisaurus* an enlarged tooth base is formed with a medial foramen, creating the impression of a furrowy base. Because of the relationship in the tooth structure and attachment *Dorsetisaurus* and *Lisboasaurus* presumably have derived from common ancestors. The maxilla of *Dorsetisaurus* differs from that of *Lisboasaurus estesi,* which instead of an anterior nasal concavity has a considerably straight dorsal bony margin like *Varanus* sp. and some amphisbaenids. With the heterodonty and the connection to the prefrontal the maxilla forms a relationship with the situations on the amphisbaenid *Rhimeura matcherii* BAUR, 1893, Oligocene.

The deformed skeletal remains Gui. L. 177 offer an unpaired diagenetically distorted fragmentary frontal, a broad fragmentary parietal, a broad quadrate, a strong pterygoid, and badly preserved fragments of the lower jaw, procoelous vertebrae and ribs. The strong procoelous vertebral centrum (s. Gui. L. 177) has a relatively big condyle, also laterally an oval articular facet for an unicipital rib. The habitus is distinctly anguimorph. In the posterior part of the vertebra a strong spina dorsalis rises oarblade-like dorsalwards (Gui. L. 33).

Annotation. — For *Dorsetisaurus* HOFFSTETTER (1967) has nominated the new anguimorph family Dorsetisauridae, which are classed to the Anguoidea; but he accentuates chiefly non-anguid pronounced features (p: 364 and 369). Because of the tooth construction and the maxillary shape *Lisboasaurus* can be added to the Varanoidea. A relationship with *Dorsetisaurus* can be found by the characteristic tooth morphology.

2) *Lisboasaurus mitracostatus* SEIFFERT, 1970

Derivatio nominis. — *mitra:* mitriform; *costatus:* groined; the name of the species refers to the mitral form of the teeth with a lingual enamel fluting.

Type species of the genus. — *Lisboasaurus estesi* from the Kimmeridgian of Portugal.

⊢————————⊣ 1 mm
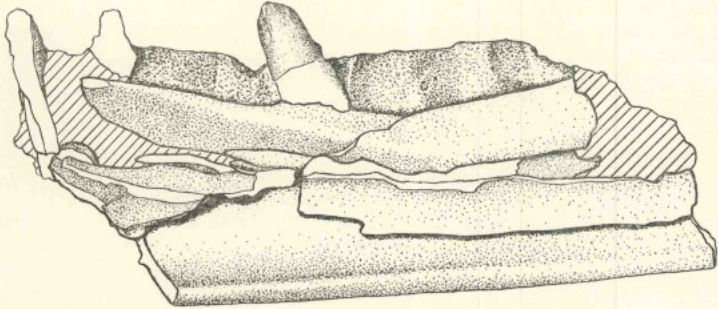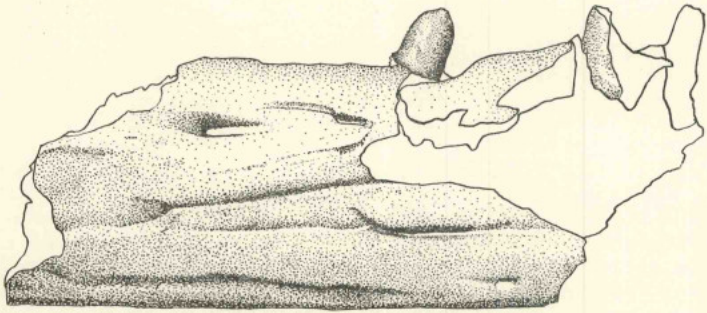
Fig. 28 — Gui. 34 — *Lisboasaurus mitracostatus,* fragment of a left dentary (holotype); above: lingual view; below: labial view.

Diagnosis. — The jaws have mitral pleurodont teeth with a socle and with a lingual cusp, which is fortified by a medial enamel rugosity and accompanied by some lateral flutes. The external side of the jaw presents numerous foramina and short, narrow channels.

Discussion. — The material of *Lisboasaurus mitracostatus* consists of some small jaw fragments and isolated teeth presenting a heterogeneity. The emitted solid teeth are without socle; therefore they are relatively short and mostly rather broad. The lingual cusp of these teeth is dorsally set off and often shifted backwards, so it is distinguishable to which side the jaw belongs. Partly the toothed jaw remains distinctly differ in tooth breadth and thickness of the enamel rugosity. From the different development of the teeth I had proposed two subspecies in 1970, but probably these forms (*L. mitracostatus mitracostatus* and *L. mitracostatus lacinianus*) are only on another place located ingredients of integral jaws. *Lisboasaurus mitracostatus* differs from *Lisboasaurus estesi* by the enamel rugosity. *Lisboasaurus estesi* has nearly smooth teeth and a distinct socle groove. The base of the teeth of *Lisboasaurus mitracostatus* seems to be affixed subthecodontly. The teeth of both species are labio-lingually compressed.

0,5 mm
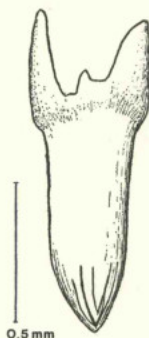
Fig. 29 — Gui. 24, tooth from a maxillary fragment of *Lisboasaurus mitracostatus*, lingual view. The teeth have a socle which has been put in the maxilla (resp. in the jaw). The tooth reveals a pleurodont attachment. The upper lingual tooth part is ribbed and shows a lingual cusp.

The jaw remainder Gui. 24 presents a little replacement tooth in one alveolus; EDMUND, 1969 on «mosasauroid» teeth:

«The replacement tooth develops distolingually to the crown of its predecessor on the surface of the bone near the alveolar margin. This area of bone and the base of the tooth become deeply resorbed, and the replacement migrates into a cavity in the base where it grows to a large size before the loss of the old crown.»

The old tooth above the replacement tooth is the largest one and distinctly offset for use in comparison with the other ones. Below the other delivered teeth there do not exist any more replacement teeth, therefore a wavelike replacement can be assumed.

The channelled structure on the external side of the jaw (s. Gui. A. 15) is probably to be referred to as the dermal squamation. Contrary to *Lisboasaurus mitracostatus* the external side of the jaw of *Dorsetisaurus purbeckensis* HOFFSTETTER, 1967 is not channelled; in the herpetology the features correlated with the squamation are significant in separating the species. A similar channelling on the labial side is to be seen on *Cteniogenys reedi*.

The following anguimorph features are to remark:

a) the solidity of grown out teeth with a filled base;
b) the lack of a subdental gutter and of an internal opening for the N. alveolaris inf., which runs in the sulcus primordialis separated of the Meckelian cartilage by a bony intramandibular septum [after Estes, 1964];
c) the lack of a bony roofed superior temporal opening;
d) the fusion of skull bones, an unpaired parietal, fused frontals and premaxillae;
e) the Meckelian groove is located ventral anteriorly and not covered by the splenial there.

Annotation. — The teeth of *Lisboasaurus mitracostatus* have a similar morphology (cf. P. P.-L. 26) as those of *Macellodus brodiei* Owen, 1854, which is different by spatulate teeth and special directed enamel striae.

E. *Introrsisaurus pollicidens* Seiffert, 1970

Derivatio nominis. — *introrsus:* turned inwards; *pollex, pollicis:* thumb; the name refers to the morphology of the teeth, which are inclined lingualwards like a thumb with the nail side.
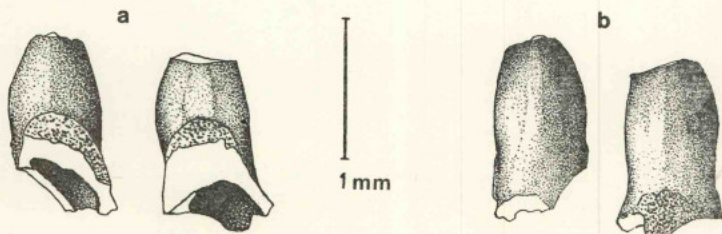
Fig. 30 — Gui. A. 73, teeth of *Introrsisaurus pollicidens;* a: labial view, base showing surface of contact for the pleurodont attachment at the dentary; b: lingual view, curved inwards (lingualwards) with a median elevation.

Diagnosis. — Pleurodont attached teeth with a crown little broadened, which is inclined lingualwards looking like a finger end. The labio-lingually compressed crown is labially convex, lingually the tooth presents a basi-occlusially running medial elevation. Thereby the tapered sides of the tooth are distinctly set off.

Discussion. — This form is only represented in the Guimarota material with the specimens Gui. 43, Gui. A. 73 and Gui. L. 232. The jaw fragment Gui. L. 232 is light brown, a foramen dento-faciale is preserved. Alveoli are obviously not present. The tooth of Gui. L. 232 is red-brown coloured, whereas the teeth of Gui. A. 73 are dusky because of more intense chemical reactions. On the lingual surface of the teeth a fine striation is visible. The teeth appear to be obliquely implanted and slightly recurved backwards. The evidence on *Introrsisaurus pollicidens* is limited by the incomplete delivery. The description of the teeth of *Coniosaurus crassidens* Owen, 1851 (id. Coniasaurus) from the Upper Cretaceous of Europe by Owen (1851) and Nopcsa (1908) corresponds to a certain degree with *Introrsisaurus pollicidens:*

«Die Zähne sind dem Kiefer pleurodont aufgesetzt und unterscheiden sich durch den Mangel eines Sockels von den Zähnen der Aigialosauriden oder Mosasauriden. Sie sind an ihrer Basis kontrahiert und genau so dem Kieferknochen aufgesetzt, wie man dies bei den hinteren stumpfen Zähnen von *Varanus niloticus* antrifft. Die poröse kanal durchzogene Knochensubstanz ist bei beiden Formen ebenfalls die gleiche... Die vorderen, stumpfkonischen, im Querschnitt runden Zähne zeigen in ihrer Mitte bloβ eine kleine Aufblähung und an ihrem Vorderteile einen markiert vorspringenden Flügel, der jedoch nicht bis an die Krone heranreicht und an den weiter hinten gelegenen Zähnen an Gröβe zunimmt.» (NOPCSA, 1908, p. 57-58).
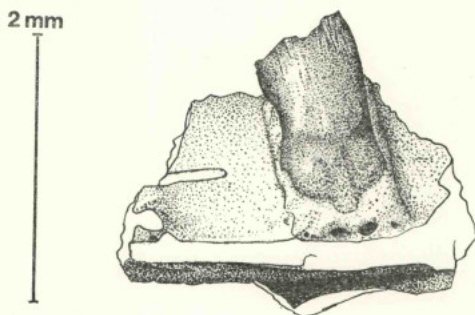
Fig. 31 — Gui. L. 232, *Introrsisaurus pollicidens,* recurved tooth with broken top, pleurodont attachment presumably fragment of a left dentary).

The systematic position of *Coniosaurus* is uncertain; the form is classed to the dolichosaurids or the aigialosaurids (by KUHN (1963) to the Iguania).

The described lacertilian material from the Kimmeridgian of Portugal is probably distributed on the following systematic categories:

Infraordo. — *Eolacertilia*
    Cteniogenyidae
        Cteniogenys reedi SEIFFERT, 1970

Infraordo. — *Scincomorpha*
    Scincidae
        Becklesisaurus hoffstetteri SEIFFERT, 1970
        Saurillus cf. obtusus OWEN, 1855
        Saurillus proraformis SEIFFERT, 1970
        Saurillus henkeli SEIFFERT, 1970

Infraordo. — *Anguimorpha*
    Dorsetisauridae
        Lisboasaurus estesi SEIFFERT, 1970
        Lisboasaurus mitracostatus SEIFFERT, 1970
    Dolichosauridae
        ?Introrsisaurus pollicidens SEIFFERT, 1970

Incertae sedis
        Macellodus cf. brodiei OWEN, 1854.

F. The bones of the skull

1) Os parietale

a) Specimens Gui. 82, Gui. L. 14: paired parietals with relatively long processus parietales. The pineal foramen is presumably situated between the frontals and the parietals. The fact that they are in pairs indicates that the specimens belong to the eolacertilian form of Guimarota.

b) Specimens Gui. 170, Gui. L. 22, Gui. L. 25, Gui. L. 42, Gui. L. 52, Gui. L. 53: relatively thick unpaired parietals, looking robust and sturdy. On the inferior side strong lateral ridges accentuate a large cavity of the cranium in the parietal. On the dorsal side a special relief is developed, known of Scincidae and Lacertidae. The osteodermally formed squares resemble that of *Lacerta lepida* and also of *Chalcides chalcides*. There exists a minute parietal foramen. The irregular lateral borders of the parietal indicate a secondary annexation of dermal bones, which close the supratemporal opening

5 mm
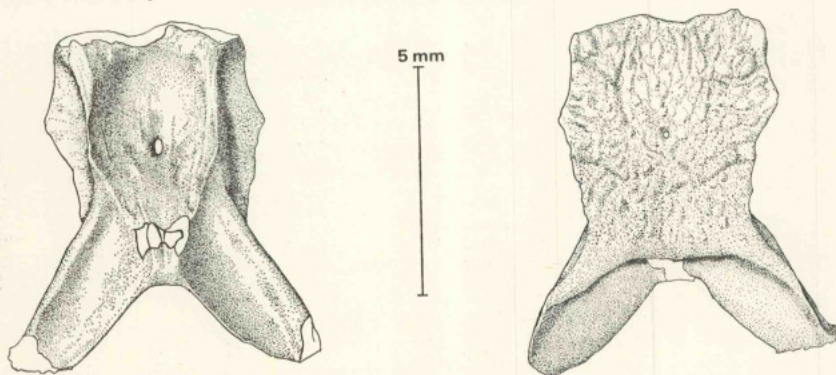
Fig. 32 — Gui. 170, scincomorph parietal with a small centric foramen; right: dorsal view, surface pattern produced by the scutes; left: ventral view.

(a scincomorph feature). On the posterior part of the processus parietales, there is a notch for the attachment of the squamosal; that refers to the hockey-stick shape of the squamosals. The internal side presents extended, slender impressions of the hemispheres. In the posterior part of each side a short ridge branches off medially from the internal lateral borders; this one connects with the processus anterior of the tectum synoticum (BARROWS & SMITH, 1947). Both ridges converge on a median swelling on the posterior end of the parietal; the latter is notched to connect with a dorsal supraoccipital process. Corresponding situations are found on Cordylidae (by McDOWELL & BOGERT, 1954) and Xantusiidae (by BARROWS & SMITH, 1947). On Lacertidae a homologous sagittal ridge is developed, which includes a foramen for the cartilaginous rest of the processus ascendens tecti synotici (s. HAAS, 1936). On some Scincidae only this foramen exists, but very distinctly.

c) Specimens Gui. 75, Gui. L. 28, Gui. L. 43, Gui. L. 141, Gui. GE. 12: unpaired parietals with straight lateral borders, which converge slightly behind. The dorsal surface is nearly smooth and only a very sparse pattern is suggested (Gui. GE. 12). A median parietal foramen is distinctly developed. On the posterior transversal margin of the parietal there is a median process, which is emphasized by two lateral dents;

5mm

Fig. 33 — Gui. GE. 12, parietal of a scincid with a nearly smooth dorsal surface; left: ventral view; right: dorsal view.

2mm

Fig. 34 — Gui. 171, right frontal element with a dorsal surface granularly patterned; left: dorsal view, in the anterior part a lateral area of contact for the the right prefrontal; right: lateral view, dorsal orbital border.
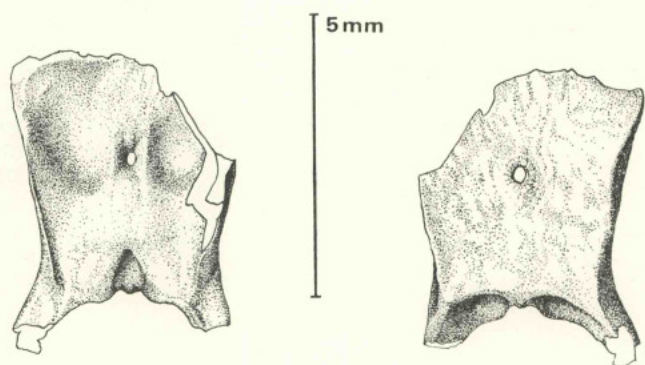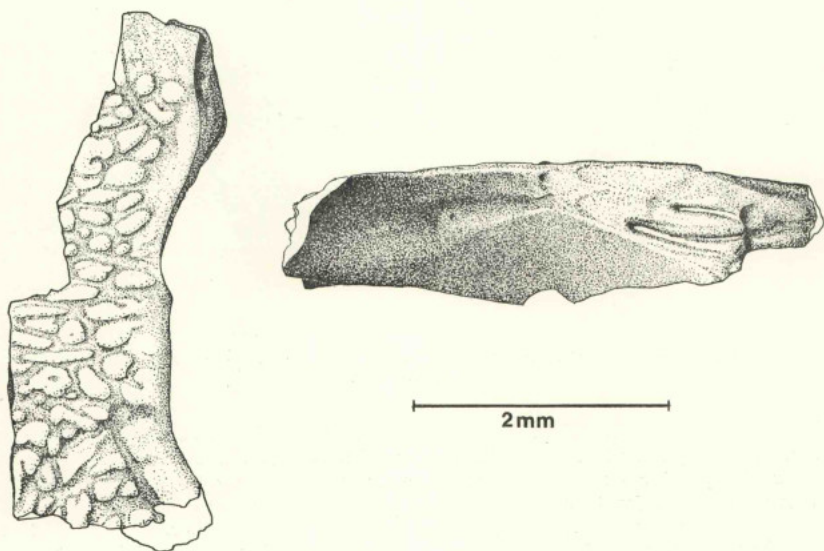
that is the connection point with the supraoccipital. On the internal side posteriorly, a fossa is to be seen, opening backards, which is partly filled with the cartilaginous rest of the processus ascendens tecti synotici (after HAAS, 1936), which becomes the supraoccipital posteriorly (s. Gui. L. 43, Gui. GE. 12). These features are found in the family Scincidae.

d) Specimens Gui. L. 23, Gui. L. 40, Gui. L. 41, Gui. GE. 9: unpaired, relatively broad parietals with a distinct relief, which does not reveal any clear arrangement of squares. A central parietal foramen is present. The ventral side is prominently formed. The connection with the supraoccipital is only weakly indicated.

e) Specimen Gui. L. 44: an unpaired parietal with a smooth surface and a straight ,high lateral border. On the ventral side posteriorly, a median sulcus exists for the attachment of a supraoccipital process. Ahead of this groove an opening directed backwards lies on a slight elevation.

2) Ossa frontalia

The numerous frontals of the Guimarota material are represented as paired elements. The specimen Gui. GE. 3 is the only fused os frontale; it is very long and offers lateral ridges for the dorsal bordering of the orbits; the dorsal surface is grained. The paired disposition can be seen distinctly. The half frontal Gui. L. 104 presumably belongs to a related form of Gui. GE. 3.
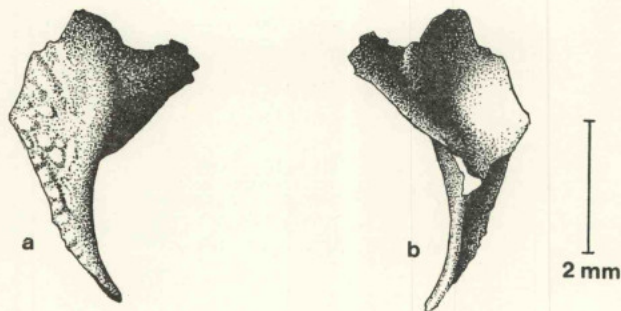
Fig. 35 — Gui. 157, right prefrontal; a: dorsal view, surface granularly patterned; b: ventral view.

Most of the frontalia fragments have a grained surface and ventrally a short, broad, lateral process in the anterior part (s. Gui. L. 36), which is medially directed (after HAAS, 1936: for enclosing the telencephalon). The posterior ends are concave in formation in order to connect with the anteriorly rounded parietal.

Some specimens are very long (Gui. GE. 30) and also reveal a long lateral ridge extending ventrally, which anteriorly turns to the descending process. Different frontalia fragments also present a long lateral ridge, but which forms medially a concave curve (Gui. 171, Gui. L. 111).

The specimens of Gui. L. 235 are made remarkable by a transversal groove (in front convex) on the dorsal posterior part of the frontal, like *Lacerta lepida*. From this groove the posterior frontal part broadens out to the the parietal. Apart from the Lacertidae these square formations also appear on Cordylidae (incl. Gerrhosauridae)

PLATE I

Fig. 1 — Gui. L. 139, *Macellodus* cf. *brodiei* OWEN, 1854 (cf. OWEN, 1861, pl. 8), lingual view of a tooth (stereo-scan-photo).
Fig. 2 — Gui. L. 138, *Macellodus* cf. *brodiei* OWEN, 1854, lingual view of an abrased tooth (stereo-scan-photo).
Fig. 3 — Gui. 380, lingual view of a tooth of *Cteniogenys reedi* (stereo-scan-photo).
Fig. 4 — Gui. 18, lingual view of a tooth of *Lisboasaurus mitracostatus* (stereo--scan-photo).
Fig. 5 — Gui. A. 41, tooth from the posterior part of a left dentary of *Becklesisaurus hoffstetteri*, lingual view (stereo-scan-photo).
Fig. 6 — Gui. A. 73, *Introrsisaurus pollicidens;* left: labial view of a tooth, with contact face of the base for the pleurodont attachment at the dentary; right: lingual view, tooth recurved inwards with a median elevation.

PLATES

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Two nova genera and seven novae species were already established in my thesis (1970) conscious of the dictum «entia non sunt multiplicanda praeter necessitatem» (WILLIAM of OCCAM, 1290-1349).

For the present the records are preserved under the named notations in the Guimarota-collection of the Institut für Paläontologie, Freie Universität Berlin. A later transfer into the collection of the Serviços Geológicos de Portugal, Lisboa, is intended; the type specimens of the other Guimarota faunas are scheduled for the same institution.

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The osteodermal squamation sometimes impresses its pattern to the skull bones and gives them a characteristic relief, as to be seen in some maxillae (Gui. L. 34), prefrontals (Gui. 157), frontals (Gui. L. 235) and parietals (Gui. 170) (Pl. II, 1).

K. Summary

By the management of Prof. Dr. S. HENKEL and Prof. Dr. W. G. KÜHNE, Institut für Paläontologie, Freie Universität Berlin, the little coal-mine Guimarota at Leiria (Central Portugal) yielded a rich vertebrate fauna consisting of Mammalia and abundant skeletal elements of fishes, amphibians and reptiles. The lacertilians are described with regard to the important indication of terrestrial synecologic life with the Upper Jurassic mammals. Certain findings from the localities Porto das Barcas and Porto Pinheiro have been recognised.

Skeletal elements	Anatomic number	Yielded number from Guimarota	Ratio — individuals
Jaw bones (excl. articular)	4	520	130
Articular	2	46	23
Quadrate	2	45	22,5
Squamosal	2	7	3,5
Pterygoid	2	53	26,5
Basi-occipital	1	2	2
Supra-occipital	1	1	1
Parietal	1	48	48
Frontal	2	160	80
Prefrontal	2	2	1
Nasal	2	2	1
Jugal	2	30	15
Presacral vertebrae ca.	26	232	9
Scapulo-coracoid	2	3	1,5
Clavicle	2	1	0,5
Sternal apparatus	1	1	1
Humerus	2	48	24
Radius	2	4	2
Ulna	2	7	3,5
Acetabulum	2	38	19
Femur	2	13	6,5
Tibia	2	5	2,5
Fibula	2	2	1

The ratio of the mandibles to the maxillae is 4,5 : 1.

The Lacertilia of the Guimarota are recorded by cranial and post-cranial bones often fragmented. Nine species are represented, partially very numerous specimens of certain types.

The lacertilian fauna of the Portuguese Kimmeridgian is composed of three systematic groups: Eolacertilia, Scincomorpha, Anguimorpha. The anguimorphian taxa are the rarest component. The plenty of eolacertimorphian dentaries from the Guimarota-coal refers to the phylogenetic connection with the Upper Triassic Kuehneosauridae. The family Cteniogenyidae is proposed for non-specialized Eolacertilia. The Scincomorpha demonstrate different types: there are species with modified teeth, with beginning reduction of the extremities and with the development of a vertebral zygosphene-zygantrum articulation.

of the reptiles are equally formed and the pieces have been yielded as isolated bones, it is impossible to prove that they belongto the lacertilians. Based on the proportions, the bone colour and the conic shape of the longer phalanges (typical for the lacertilians), the pieces Gui. L. 223 and Gui. L. 224 can be supposed to belong to the Guimarota lizards.

Already described by BROILI (1926) and KÜHNE (1956), the phalanges distales of the tetrapod lacertilians have a robust and thick proximal part, which is not so long in the lizards as in *Oligokyphus*. The terminal phalanges (Gui. 159, Gui. L. 227 and Gui. L. 228) can be compared with those of *Lacerta lepida, Varanus* sp. and even *Chalcides chalcides*. The dorsal articulary process for the insertion of the extensor of the terminal phalange, stretching proximalwards, and the robust ventral apophysis are correlated with the vigorous flexion of the claw (Gui. L. 159). This corresponds with the motion of strong treading (stalking after BROILI, 1926), which is deduced from the osteology of the proximal extremity. The trivial asymmetries of the terminal phalanges refer to the position in the different lateral links. The claw-bearing phalangesges distales are curved downwards and terminally tapered. On the plantar side between the saddle joint and the flexor apophysis, there is an opening (foramen nutricium). The lateral sides are distally flattened. The presented terminal phalanges probably belong to different taxa.

6) The bony tissue

The histological study of some hollow bones (Gui. L. 229, Gui. L. 215) from the Guimarota material reveals the presence of numerous cavities of the osteocytes in the bone. The lumen of the cells is relatively large, slitlike or oval, and shows dendritic processes. The osteocytes also appear in the peripheral region of the bone in the cortex. A HAVERS's system could not be stated. The same observations were made with the ulna of *Lacerta lepida* (juvenile individual) and the femur of *Chalcides chalcides*.

J. The dermal ossifications

The name Squamata for the Lacertilia and Ophidia (Serpentes) refers to their scaly skin. Above all a dermal ossification appears in the Scincomorpha and Anguimorpha, which even closes secondarily the superior temporal fenestra in the skull of many Scincomorpha (Xantusiidae, Lacertidae and Cordylidae, incl. Gerrhosauridae). Most of the Scincomorpha have composed osteoderms, in the Anguimorpha the dermal ossification produces simple bony scales (HOFFSTETTER, 1962).

In the Guimarota material numerous composed osteoderms have been found, which probably belong to the described scincomorph taxa. It is remarkable that no scale offers the distinct, smooth border for imbrication as described by HOFFSTETTER (1967) of the osteoscutes, which are assumed to belong to the scincomorph «Paramacellodus oweni». But these osteoscutes of Swanage are obviously simply formed and can rather be ascribed to the anguimorph *Dorsetisaurus*.

Several osteoderms of the Guimarota lacertilians reveal a surface which is rooflike angled, compared to it, the inner side is smooth and scarcely concave. These scales have certainly been components of the squamation at the lateral flanks of the animal, as the osteoderms of *Cordylus cordylus* are equally formed in this region. Some osteoderms seem to have a square shape (Gui. L. 37). The specimen Gui. L. 241 is the only osteoderm which indicates the imbrication of the osteoderms with the development of a special border.

The proximal part and the medial diaphysis of a tibia (Gui. L. 207) probably belong to the taxonomic relationship of Gui. L. 90. The two areas for the trochlea femoris are not distinguishable at the proximal end of the fragment Gui. L. 207. But this specimen shows a broad depression in the anterodorsal side, which has probably been referred to as the M. tibialis anticus (WETTSTEIN, 1931). Marginally near it, a bony crest is developed, which can be homologized with the cnemial crest (ROMER, 1956) of the ancestral reptiles. This marginal apophysis distinctly appears in the recent Scincomorpha. It can be referred to as the insertion of the M. extensor quadriceps femoris. The ventral enlargement has seved as the insertion of the M. pubo-ischiotibialis.

The proximal fragments of the fibula are rod-shaped and show a nearly circular articulary area, which laterally rises to a weak, proximal apex capitis fibulae, for the articulation with the femur. The contact area with the tibia is recognizable. The smaller element of the two proximal fragments differs by the presence of a ridge for the origin of the M. flexor primordialis communis (after WETTSTEIN, 1931) and by the colour of the bone. This piece belongs to the left side of the body, the second proximal fibular end to the right side.

The distal fibular ends (Gui. L. 216) are characteristically enlarged to the tarsal joint and have a triangular side. The broader articulary part is medially directed towards the tibia. A lateral malleolus posterior is lacking. The smaller piece belongs to a right fibula, the bigger one presumably to a left fibula, which has a marginal apophysis. This apophysis has probably developed for the insertion of the caput femorale of the M. triceps surae. The distal fibular end can easily be mistaken for the proximal end of the metatarsale II. The specimens Gui. 95, Gui. 176, Gui. L. 210 and Gui. L. 217 can be regarded as fragments of fibulae, which have broken ends.

4) Tarsus and metatarsus

It the present Guimarota material no tarsal element is represented. Because the tarsus (the astragalo-fibulare, the os cuboideum and an adjacent second, smaller os tarsale) can be coherently isolated by maceration in the lab, it has to be assumed, that in the natural disintegration post-mortem the terminal links of the tarsus are lost in a like manner.

The piece Gui. L. 191 probably is a left os metatarsale V. In the lacertilians the metatarsale V is proximally angled to the tarsus with a flat process, because the bone is fused in the course of development with a fibular os tarsale; it is the shortest metatarsal bone. On the proximal plantar side of the piece Gui. L. 191, the M. abductor digiti V (after SCHAEFFER, 1941) has formed a depression and a crest for the insertion. The apophysis, situated at the interior edge (processus hamatus after SCHAEFFER, 1941) for the insertion of the caput fibulare (femorale) of the M. triceps surae, is fragmentary. The opposed, dorsal side is weakly concavely curved and offers foramina nutricia and muscle marks of the extensors.

From the Guimarota, several isolated fragments of metacarpalia resp. metatarsalia are present (Gui. L. 222). The nearly symmetrical ends can be attributed to the corresponding bone of the digitus IV in the anterior or posterior extremity.

5) The phalanges

Because completely preserved lacertilian skeletons have so far not been found in the Guimarota, a form of the phalanges cannot be stated. There are present isolated pieces: relatively long phalanges proximales (Gui. L. 224), ph. mediales (Gui. L. 225) and short, robust ph. mediales distales (Gui. L. 226). Because the phalanges

the presumed strong dorsal retraction of the posterior extremity, are for the purpose of a form of motion, as described for the forelimb (cf. the chapter on the humerus).

The remains Gui. L. 30 show a swall rod-shaped femur, which indicates the presence of a lacertilian with the beginning of a reduction of the extremities.

The specimen Gui. 193 represents a relatively big left femur with a trochlea femoris, which resembles that of *Varanus* sp. and *Saniwa ensidens*. The fibular articulary part is fragmentary. This bone presumably belongs to a varanoid taxon. The right femur Gui. 16 and the left one Gui. L. 71 are relatively long bones with only a short trochanter internus. A linea aspera is not developed. Together with the specimen Gui. 193, they can be presumed to be related to the Varanoidea.

3) Tibia and fibula

The crus of the lacertilians consists of the robust anteroventral tibia and the long slender, posterodorsal fibula. Both bones stand together with their ends, they are proximally connected by articulation. The two medial diaphyses are separated by the so-called spatium interosseum.
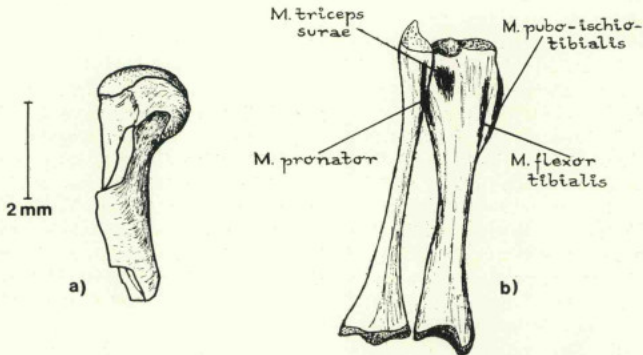

Fig. 61 — a) Gui. L. 199, proximal part of a fragmentary femur, the trochanter medius has been broken off; b) skeleton sketch of tibia and fibula of a tetrapod scincomorph lizard, flexor side.

The well preserved left tibia Gui. L. 90 (of 53 mm length) anteroventrally offers a proximal crest for the insertion of the M. pubo-ischiotibialis and distally of it, a second, medial apophysis for the insertion of the M. flexor tibialis (cf. SEIFFERT, 1970). On the opposite, fibular side of the tibia, a small articulation for the caput fibulae exists. Distally the depression in the bone indicate the origin and the pull effect of the M. triceps surae. The bipartition of the tibial articulary area for the trochlea femoris is suggested. The distal end is curved inwards; that supposes a saddle-shaped tarsal joint. The malleolus anterior has presumably been present; in this region, the distal end of the tibia has been broken. With the development of the apophyseal and articulary peculiarities, the tibia Gui. L. 90 is similar to that of *Lacerta lepida*.

The hollow bone Gui. L. 208 has fragmentary ends, but shows a distinct trunk-shaped, concave distal end. Probably this bone is the left tibia of a lizard; the fibular side of the tibia, fixed in palavit, is exposed.

more proximally than the femoro-tibial one (s. WETTSTEIN, 1931). The very small patella of the lizards has developed into the tendon of the M. quadriceps.

The right femur (Gui. L. 120) offers a well developed, but fragmentary trochanter internus and shows distally of it a linear tuberosity (linea aspera) of the bone. Further more a distinct fossa intertrochanterica posterior is developed. The condylus tibialis is latero-ventrally rendered prominent. The second specimen Gui. L. 209 corresponds with the habitus of the femur Gui. L. 120. At the going over of the trochanter internus to the distal femur shaft, there is a tubercle-like thickening, which can be correlated with the insertion of the adductors. The Mm. caudofemoralis and pubo-ischiotrochantericus function as the main adductor (after WETTSTEIN, 1931). The M. caudo-femoralis (= retractor dorsalis) of Sphenodon originates from the proximal ends of the haemapophyses of the first 8-9 caudal vertebrae. The muscle inserts with a thick terminal tendon distally of the trochanter internus. «Knapp vor diesem Ansatz sendet der Muskel einen schmalen Sehnenstrang distalwärts, der längs des Femurs verläuft und an der lateralen Seite des Epicondylus fibularis femoris inseriert» (WETTSTEIN, 1931). This muscle effects both an adduction and a rotation of the femur (dorsal retraction). As a profound, autochthonous pelvic muscle, the M. pubo-ischiotrochantericus (= M. obturator externus) runs from the ventral region of the pelvis to the trochanter internus, on which the muscle inserts on, proximally of the M. caudofemoralis. The M. obturator externus functions as a vigorous adductor (s. WETTSTEIN, 1931).

The M. caudo-iliofemoralis (M. piriformis after some authors) is the important auxiliary muscle of the M. caudofemoralis. The muscle originates completely from the ilium (as in the chameleon), or only partly and then additionally on the transverse processes of both sacral and the first caudal vertebrae. After the presentation of RIBBING (1938), the M. caudo-iliofemoralis of the Gekkonidae (Uromastix) seems to originate from some sacral and caudal vertebrae. In Sphenodon this muscle originates only from both sacral vertebrae. The insertion is as variable as the origin. The M. caudo--iliofemoralis mostly inserts on the femur together with the M. caudofemoralis, which can have grown together with it. That is the posterior facies femoris in Sphenodon, where the inserts muscle by a tendon distally next to the trochanter internus. Sometimes the muscle also grows together with the M. retractor ventralis, which secondarily originates dorsally of the M. caudofemoralis from some anterior caudal vertebrae and runs to the ligamentum ilio-ischiadicum. This is obviously correlated with the migration of the M. retractor ventralis dorsalwards in the course of development; in Heloderma a muscle originates from the ligamentum ilio-ischiadicum and unites with another muscle, originating from a caudal vertebra, to the so-called M. piriformis (RIBBING, 1938). Hence it follows that the distal tubercle-like thickening at the trochanter internus in the specimen Gui. L. 109 has been caused by one of the noticed addutors. The M. caudo-iliofemoralis can be assumed as such, which is situated between the two main adductors. Such a tubercle at the trochanter internus has only been proved in the Scincomorpha (Lacerta, Scincus, Chalcides).

The above described conditions are also found in four proximal femur fragments (Gui. L. 199). On these remains a further, distincter tubercle is present, which appears on the anterior facies of the femur between the caput femoris and the trochanter internus. Probably this spheric apophysis has to be referred to the insertion of the tendon of the M. caudofemoralis (retractor dorsalis). This is obviously the so-called trochanter anterior, observed in the Lacertidae and Agamidae by SIEBENROCK (1894, 1895). It also exists in Chalcides. Proximally of this tubercle, a foramen nutricium is present below the caput femoris. The four femora Gui. L. 199 seem to be very slender and laterally flattened in their proximal part. The piece Gui. L. 218 can be attributed to these forms. The morphological peculiarities of these femora, correlated with

NAUCK (1938) states that the spina iliaca of lacertilians is prominent by an ilium, which is distinctly curved caudally with the position of the acetabulum near the vertebral column, «was für die Übertragung der Gliedmaßenstöße auf den Rumpf und für die Ausbildung der Symphyse bedeutsam wird». WETTSTEIN (1931) also reflects upon these conditions (he gives the complementary angles) and deducts the mode of heavy motion of *Sphenodon*.

Because of the distinct spina iliaca and the recurved pars iliaca, the specimens Gui. L. 60 and Gui. L. 95 can be attributed to a tetrapod anguimorph taxon, the presence of which in the Guimarota is evident by other bony elements.

Most of the other pelvic bones offer the at first straight and then ca. 45° inclined ilia, directed dorsalwards; they probably belong to the scincomorph taxa (s. Gui. 169, Gui. L. 80, Gui. L. 85, Gui. L. 212). It is possible that some fragment (Gui. L. 144, Gui. L. 211) are to be referred to eolacertiform specimens.

The pelvic bones of the Lacertilia s. l. presumably develop from the plate elements in forms — as in the Triassic *Macrocnemus bassanii* NOPCSA, 1930 (s. PEYER, 1937), *Tanystropheus longobardicus* (BASSANI, 1886) and in the Claraziidae — to the strap-like decomposition in the recent tetrapod lacertilians and the reduction in the limbless Squamata. The aquatic *Askeptosaurus italicus* NOPCSA, 1925 (s. KUHN-SCHNYDER, 1952) from the Triassic has been specialized as «early» referring to this.

2) Femur

The caput femoris of the lacertilians is characteristically curved, corresponding with the oval forms of the acetabulum; the curvature is in vivo directed forward. The femur is connected by a capsule ligament with the pelvis in the socket of the joint (BRONN & HOFFMANN, 1890). A proximal crest-like bony process, which appears ventrally of the caput femoris, is a muscle apophysis, the trochanter internus (medius or tibialis). It is robustly developed and situated to the right of the more proximal caput; thereby the fossa trochanterica is reduced (ROMER, 1956). In some lizards on the postero--dorsal surface near the caput femoris, a tuber exists, which is correlated with the attachment of the M. iliofemoralis (the trochanter externus, posterior or fibularis). After SIEBENROCK (1895) and NAUCK (1938) two trochanters are present in the Agamidae and three in the Lacertidae. The two trochanters, always developed in the Lacertidae and Agamidae, are the trochanter internus and the small trochanter anterior. In contrast the trochanter anterior is lacking in the varanids, whereas a weakly developed trochanter posterior (fibularis) is present. In *Sphenodon* the fibular trochanter is lacking.

The longitudinal marks on the facies anterior femoris indicate the insertion of the M. pubo-ischiofemoralis internus; a ridge which appears sometimes (linea pectinea), which runs distally of the interior trochater, serves as the insertion of the M. adductor femoris (s. ROMER, 1956). In lepidosaurs a linea aspera as the distal continuation of the linea pectinea has not been observed until now; in the femur Gui. L. 120 it is present. In the lacertilians a fourth trochanter for the insertion of the caudofemoral musculature has not been proved. The femur of lizards with a rudimentally posterior extremity (as in *Chalcides tridactylus*), only offers certain tuberosities instead of the trochanters (BRONN & HOFFMANN, 1890).

The distal end of the femur has tw condyles, which are very differently developed. The condylus tibialis consists of two differing large articulary rolls; they are separated by an intracondylar furrow, which also extends to the distal bone shaft. Therewith two areas exist for the articulation with the tibia. The fibula articulates with a small facet on a so-called condylus fibularis, which is dorsocaudally situated on the posterior distal part of the femur. With this condition the femoro-fibular joint lies

dian, both ossa pubis form the symphysis pubica; on it, a straight tendon (ligamentum medianum pelvis) generally inserts, which originates from the symphysis of the two ossa ischii. The ligamentum can become cartilaginous or ossify as in *Varanus* sp. It borders the relatively broad foramen pubo-ischiadicum (= cordiforme) with the os pubis and os ischii. In many lizards the symphysis ischiadica is caudally elongated by the connective tissue, which can be ossified to the so-called os hypoischium or cloacae. In the gerrhosaurs the hypoischium is forked behind (s. BRONN & HOFFMAN, 1890; NAUCK, 1938).

The Guimarota material presents 22 right and 16 left pelvic fragments, of which the ilia are abundantly represented. The three elements are mostly fused. Some isolated fragments (Gui. L. 211) indicate a sutural connection.
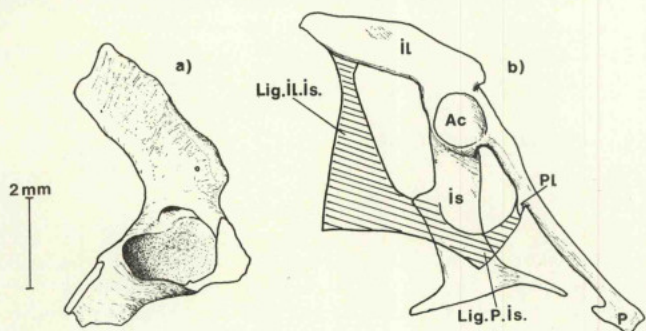

Fig. 60 — a) Gui. L. 211, pelvic fragment, right lateral view; b) pelvis of *Lacerta muralis*, right lateral view, Ac: Acetabulum; Il: Ilium; Is: Ischium; Lig. Il. Is.: Ligamentum ilio-ischiadicum; Lig. P. Is.: Ligamentum pubo-ischiadicum; P: Pubis; Pl. Processus lateralis pubis [after ROMER, 1942, p. 265].

The piece Gui. L. 60 is a left pelvis with broken ends. The pars pubica is broad and reveals a relatively large foramen obturatorium. A robust praepubic process, directed lateralwards, is present. The pars ischiadica seems also to have been broadened and caudally to have a tuber ischii. The ilium rises characteristically dorsalwards and is curved backwards.

The specimen Gui. L. 95 has a pars iliaca with a distinct spina iliaca anterior; whereas in the pelvis Gui. L. 60, this spina is only indicated by the anterior edge of the ilium. In most of the other ilia fragments the spina iliaca is scarcely distinct and can mostly be seen only on the external side (facies acetabuli) of the pars iliaca (Gui. L. 80, Gui. L. 85, Gui. L. 144, Gui. L. 211) as in the recent *Chalcides chalcides*.

The high rising shape of the ilium, which is weakly curved backwards, is also known of the pygopodids, but in these forms the pars pubica and pars ischiadica are reduced to the acetabulum (s. GASC, 1967). Because of the reduction of limbs in *Anguis fragilis,* the ventral pelvic parts are also reduced, whereas the shortened pars iliaca rises straight to the sacrum (s. HERTER, 1960). *Sphenodon punctatus* has a broad, weakly recurved ilium and a well developed ventral pelvic girdle adequate for a tetrapod form (s. WETTSTEIN, 1931).

In the agamids, varanids and tetrapod anguids, the distal pars iliaca shows an angle of 5-10° inclined to the body axis, whereas in the gekkonids the angle is 30°, in the Scincomorpha ca. 45° and in *Sphenodon* ca. 70°.

4) The carpus

The carpus of the non specialized lacertilians usually consists of nine small bones, in the proximal row: the radiale scaphoid), os centrale, ulnare (triquetrum), os pisi-forme — and in the distal row: the ossa carpalia I-V. A tenth bone sometimes appears rudimentally between the radiale and ulnare, the so-called os intermedium (in *Lacerta, Tupinambis, Ameiva, Teius, Tiliqua, Eumeces, Xantusia, Gerrhonotus, Zonurus, Varanus, Heloderma*), which is always present in the Rhynchocephalia.

By the distal intercalation of the os centrale between the radiale and ulnare, both bones are always separated (BRONN & HOFFMANN, 1890; GEGENBAUR, 1898). This modification of the centrale is characteristic of the lacertilians (ROMER, 1965). From the ossa carpi of the Guimarota Lacertilia, the os centrale (Gui. L. 122) is only repre-sented, which can be regarded as a right specimen in comparison with the carpus of *Lacerta lepida* and *Varanus* sp. The palmar side of the fossil centrale offers a foramen nutricium; this area proximally has a characteristic inclination, ending in an acute angle, because the scaphoid and triquetrum border on the centrale. Because the formation of the areas varies between the right and the left carpal bones, a taxonomic statement by the carpus is impossible.

5) The metacarpus

On a small coal piece (Gui. L. 215), a hollow bone is present, which has broken ends. It is associated with two very small, dispersed bones and fragmentary procoelous vertebrae. One of the cylindric small bones, well preserved, is axis-symmetrically formed and offers a distal articulation, which is broadened lateralwards; concluding from this feature, based on the symmetric shape, the bone can be regarded as an os metacar-pale IV. The lateral enlargements for the articulation with the proximal phalange IV are distinctly developed (phalangeal saddle link; SIEBENROCK, 1894). In contrast to the nearly symmetric os metatarsale IV of the tetrapod lacertilians, the metacarpal ele-ment (Gui. L. 215) is relatively short, and proximally a little broadened. In the lizards with a start in the reduction of limbs, the conditions of the metacarpus and metatarsus are nearly similar. If the piece Gui. L. 215 belongs to a specimen of *Saurillus henkeli*, the fact cannot be exclude that the described bone is a metatarsale IV.

I. Bones of the pelvic limb

The posterior extremities are connected by the pelvic girdle with the trunk. The pelvic girdle is dorsally closed by an attachment to the sacrum.

1) The pelvic girdle

In contrast to the shoulder girdle, the pelvic apparatus develops endochondrally and ossifies in the ontogenesis. Each side has three bones, which form a socket of a joint for the femur (acetabulum). If the bones (os pubis, ischii and ilium) are co--ossified, they are termed together as os coxae and differentiated in the pars pubica, ischiadica and iliaca. The pars pubica presents the anterior ventral part, the pars ischiadica the posterior ventral one. The ilium forms the dorsal part of the pelvic girdle.

In the lacertilians the N. obturatorius always runs through a special opening (foramen obturatorium or diazonale) in the os pubis, coming from the cavum pelvicum to adductors. Cranially of the foramen obturatorium there is a small process, the tuberculum pubis or the praepubis, which is laterally directed downwards. In the me-

distal part of the ulna has a rounded condyle for the articulation with the os trique-
trum (ulnare), the os lunatum (intermedium) and the os pisiforme. A processus sty-
loideus ulnae is not developed.

In the Guimarota material, the radius is represented by three isolated distal
ends; Gui. L. 171 concerns the distal fragments of two right radii, which show sty-
loid process situated on the right lateral side in dorsal aspect, when the distal end is
turned to the observer. The ventral side of these radii is flattened (as the ulnar
proximal end of the radius); this flatness of one side is present in both fragments
(Pl. IV, 4). The piece Gui. L. 229 probably is the distal end of a left radius.
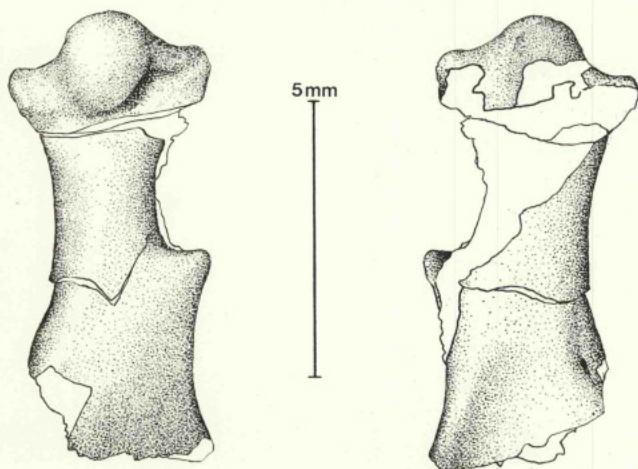
Fig. 59 — Gui. 98, fragment presumably of a right humerus, which is assumed
to belong to a tetrapod with fossorial and/or arboricolous mode of life;
left: posterior view; right: anterior view.

The ulna of the Guimarota lacertilians is represented by two right (Gui. L. 4)
and three left (Gui. L. 205) proximal parts of this bone. In contrast to the relatively
slender olecranon ulnae of *Varanus* sp., the bony olecranon of the fossil remains is
very robustly developed on the outside; the tip of the olecranon is obtusely rounded.
These conditions are also found in the ulna of *Lacerta lepida*. The cavitas radialis
ulnae, which is at right angle to the cavitas sigmoidea, is not chiefly marginally de-
veloped as in *Varanus* sp., but more towards the middle of the olecranon; at this point
the articulary area is bordered by an edge. The cavitas trochlearis is a little inclined
outwards. Below the olecranon, the ulna reveals a weak concavity on the outside, which
passes away into the subparallel bony edges. The form of the olecranon allows the taxo-
nomic statement of the found ulnae to be of non-varanoid lacertilians. This is also
valid for the distal ulna fragment Gui. L. 205. On the other hand the specimen Gui.
L. 221 resembles the distal end of the ulna in the varanids.

The anguid *Glyptosaurus sylvestris* MARSH, 1871 (s. GILMORE, 1928) has an equally distinct supinator crest; but in contrast to the mentioned Guimarota forms, the epicondylus ulnaris is only weakly developed with a modest broadening. The size of *Glyptosaurus* assumes the development of a crest for the extensor antebrachii radialis by function. Because in the bones of the extremities the functional differentiation is expressed, the features are not unconditional evidence of the systematic position.

Another humerus type (Gui. L. 86; Gui. L. 127 and Gui. L. 201) reveals a robust central portion, which broadens distally with a certain torsion. The proximal caput humeri is distinct, but not very broad. The tuberculum minus is weakly developed, but the deltopectoral, lateral bony crest is clearly marked. Because these fragmentary humeri are relatively small and scarcely differentiated, they could belong to lacertilians which tend to reduce their extremities (this type is represented by the scincomorph skeletal remains Gui. L. 30).

The specimens Gui. L. 81, Gui. L. 108 and Gui. L. 129 are fragments of relatively large and robust humeri. The piece Gui. L. 81 offers the dorsal presence of a long edge for the insertion of the pectoralis and deltoideus on the caput humeri; this would be typical of the Sauria. But the belonging to the Guimarota lacertilians can be presumed only, because the indicative foramen ectepicondyloideum cannot be clearly recognized (s. Gui. L. 129).

The four specimens Gui. L. 203 are in accordance with the habitus of the lacertilian humerus; the bony ends are distinctly broadened, but not rectangularly formed. A fossa supratrochlearis with an obvious foramen nutricium is present. This humerus type can be attributed to a scincomorph taxon. Probably the specimen Gui. L. 214 also belongs to this group.

The singular bone fragment Gui. 98 has been enigmatic so far, until it was compared with the humerus and femur of digging and arboricolous vertebrates, e. g. of Xenarthra *(Panochthus, Cyclopes, Myrmecophaga, Tamandua),* of Marsupialia *(Phascolarctos),* of Tubulidentata *(Orycteropus)* and of the badger. In these animals the anterior limb has a characteristic shape caused by the function of the shoulder musculature, especially by the M. deltoideus. The presented bone shows a remarkable process on the postero-lateral side as if it might be a right humerus. Probably this process has been developed by the insertion of the vigorous tendon of the fused deltoid musculature (pp. acromialis et scapularis), as it is known of fossorial and arboricole mammals.

3) Radius and ulna

The proximal articularly area of the saurian radius forms an oval concavity, which permits the condylus radialis (capittelum) humeri a certain rotation motility. The distal end of the radius is rather broader, flat and also oval. The characteristic processus styloideus radii reveals a crescent-shaped distal articulary area, which is adapted to articulate with the os scaphoideum (radiale); this articulation only allows a very restricted mobility.

As a special proximal formation the ulna has an elongated headed part, the olecranon. The articulary area of the olecranon articulates with the trochlear condyle of the humerus; it is termed as cavitas or incisura sigmoidea (= trochlearis). The M. triceps brachii inserts as extensor of the elbow-joint on the tip of the olecranon. In recent lizards the tendon sometimes includes a cartilaginous or bony piece, the so-called patella ulnaris (BRONN & HOFFMANN, 1890; ROMER, 1956). The main motion of the ulna to the radius is rotation inwards and outwards. Radius and ulna develop corresponding articalary areas on their proximal points of contact (incisura radialis ulnae). The

similarly and inserts as extensor of the carpus on the distal end of the ulna, on the os pisiforme and on the os metacarpale V. The muscle originates on the epicondylus radialis, which offers a distinct tuberosity (s. specimens Gui. L. 47). If a strong tramping movement of the body swinging is assumed as mode of locomotion, a strong M. flexor carpi ulnaris has to be postulated. That is conceivable for *Saniwa ensidens,* in consideration of the reconstruction of this lizard (s. GILMORE, 1928). If a broad epicondylus ulnaris is formed by function, the feature of the breadth cannot be used for taxonomic diagnosis.
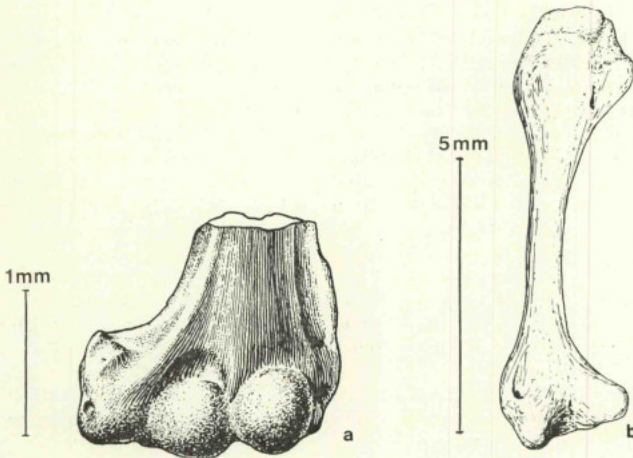
Fig. 58 — a: distal end of a left humerus (Gui. L. 145), ventral view; b: left humerus (Gui. L. 47), postero-dorsal view, with foramen ectepicondyloideum.

The distal parts of three humeri (Gui. L. 145) reveal a peculiarity. They offer a lateral, marginal crest on the epicondylus radialis; both condyles have a spheric shape, whereas the condylus radialis capitellum) is generally ellipsoidally formed in other lacertilians. A further feature of this humerus type is the prominent epicondylus ulnaris with nearly rectangular edges. The lateral distal crest of the humerus is used as the attachment for the M. extensor. antebrachii radialis and is regarded as an ancestral feature of the Lepidosauria (WETTSTEIN, 1931; ROMER, 1956). In the Eosuchia, Rhynchocephalia and Chelonia, this muscle of the forelimb is composed of three parts (M. supinator, Mm. extensor carpi radialis longus et brevis); but in the Lacertilia it is two-part or even only one-part (M. supinator + M. extensor carpi radialis caput longum et caput breve). By the contraction of this muscle, the distal anterior extremities are adduced and the carpus is extended (WETTSTEIN, 1931). The actualistic conceptions can be applied to the specimen Gui. L. 145, accordingly by the described morphological siutations of the epicondyles, an intense reciprocal action of abduction and adduction of the «forearm» can be assumed. Because after WETTSTEIN (1931) the M. supinator originates on the lateral area, the M. extensor carpi radialis on the distal area of the epicondylus radialis, the crista supinatoris of the present fragmentary humeri indicates a bipartition of the M. extensor antebrachii radialis, i. e. a prime feature. I attribute the specimens Gui. L. 145 to an eolacertiform taxon.

unimportant. In the literature by ROMER (1956) there is only found the figure of a lacertilian humerus with a fossa supratrochlearis and a foramen nutricium. In the humerus of *Varanus* sp., the fossa and the foramen are very weakly developed, but distinctly so in *Lacerta lepida.*

All the lacertilian humeri from the Guimarota mine have a foramen ectepicondyloideum and a distinct fossa supratrochlearis, the opening of which has presumably been used as the entry of a blood vessel, because there is no cavity for the passage of the N. medianus on the extensor side.

Bavarisaurus (or *Homoeosaurus*) *macrodactylus* should be reviewed as to whether the fossa supratrochlearis of the humerus reveals an opening for the canalis entepicondyloideus or not. For that purpose, the specimen is to be roentgenised or prepared after KÜHNE's method (1961) by corroding it with acetic acid; thereby the dorsal side of the humeri would be discolosed. Because the ommission of the foramen entepicondyloideum is described in the genus-diagnosis of the rhynchocephalian *Homoeosaurus,* it can not be used the comparison of homoeosaurids and lacertilians. We have to cognise that the fossa supratrochlearis is more or less distincty developed in the humerus of lepidosaurs (s. *Champsosaurus* and *Hescheleria* in PEYER, 1936; *Scincus* in EL-TOUBI, 1938; *Sauranodon* in HUENE, 1952) and that the canalis nervi mediani begins there in the Rhynchocephalia and in different other groups (s. above). In the therapsid *Oligokyphus* for instance, the foramen entepicondyloideum is not situated in the fossa supratrochlearis, but ulnarly adjacent (s. KÜHNE, 1956). Therefore we want to determine, that a foramen (entepicodyloideum) in the fossa supratrochlearis is an outlet for the N. medianus. Any other opening in this interepicondylar fossa, without a second corresponding foramen on the dorsal side of the humerus, is differently termed to prevent any mistakes.

In the lacertilian remains of Guimarota, the humeri with a specially formed distal part are abundant; their epicondylus ulnaris appears at a distinct angle to the humerus shaft, directed medialwards. In contrast to the remarkable medial broadening, the distal part of the humerus does not distinctly enlarge to the epicondylus radialis; but the epicondylus radialis is curved outwards to include the N. radialis. The N. radialis leaves the humerus on the flexor side, closely to the capitellum.

The specimen Gui. L. 47, fastened to palvit, offers the well preserved dorsal side, which has a fragmentary distal condylar part. Medially of the proximal articulary area, a well developed tuberculum minus is present for the insertion of the M. subcoracoscapularis after ROMER (1956). Below the tuberculum minus, there obviously is a foramen nutricium, which can also be observed on the same place in recent lizards. The head of the humerus has an extended, curved lateral edge for the insertion of the Mm. Pectoralis and deltoideus. The extensor of the anterior extremity has been fixed to the dorsal base of the proximal articulary enlargement. The tuberosity for the attachment of the carpal extensors is situated below the dorsal foramen nervi radialis on the epicondylus radialis; the flexors of the forelimb originate on the epicondylus ulnaris. The left humerus Gui. L. 47 represents the type which is the most numerous one in the Guimarota material (s. Gui. 181, Gui. L. 128, Gui. L. 146, Gui. L. 187). The quantity of the right and left isolated fragments is equal (14 : 14). Of the recent and fossil Varanoidea, only *Saniwa ensidens* LEIDY, 1870 has a comparable humerus with the distinctly angled detached epicondylus ulnaris. Because of the remarkable breadth of the epicondylus ulnaris, a broad insertion area for the flexors of the distal anterior extremities can be assumed. This supposition suggests itself in considering, that the M. flexor carpi ulnaris, wrich originates on the epicondylus ulnaris, is inserted on the medial side of the ulna and on the os pisiforme. This muscle abduces the «forearm» and simultaneously extends the «hand». The M. extensor carpi ulnaris functions

fimbriatus, Lacerta lepida and *Cordylus cordylus* (cf. HOFFSTETTER, 1964), the medial margin of the coracoid part shows a narrow fenestral incision. A scapulo-coracoid suture is not preserved.

2) Humerus

The lacertilians are different in the formation of the skeletal elements of the forelimb. The modifications of the skeletal parts increase in the distal direction (GEGENBAUER, 1898).

In the prime repetiles, the humerus has an oblique position to the ground and offers a torsion curvature, which brings the distal articulary areas of the humerus into a suitable position to articulate with the distal anterior extremities. As a result of the tendency to lift the body of the ground and to bring the extremities under the body to support it, the humerus becomes stretched and releases the torsion (NAUCK, 1938).

The saurian humerus is a long, unimportantly curved hollow bone, which has broadened ends. The proximal end offers two protuberances for the muscles, the tuberculum mediale (= ulnare or minus) and the larger tuberculum laterale (= radiale or maius). The lateral process is characteristically directed outwards and downwards. On the flexor side between the two processes, there is the so-called fossa intertubercularis or bicipitalis, the point of the insertion of the M. latissimus dorsi. The caput humeri is formed as a slender oblong proximal enlargement.

The condylus radialis (capitellum) and the broader condylus ulnaris (trochlea) are situated together on the broad distal end of the humerus; both radius and ulna articulate with them (BRONN & HOFFMANN, 1890; NAUCK, 1938). The long flanks of the condyles are termed the epicondylus ulnaris and epicondylus radialis (lateralis). The first one is very large and reveals a canalis nervi mediani (= entepicondyloideus) in the Cotylosauria, Mesosauria, Proganochelydia, Rhynchocephalia, Araeoscelidia, Sauropterygia, Placodontia, Pelycosauria, Therapsida and Mammalia (WETTSTEIN, 1931; NAUCK, 1938). The relatively large opening on the flexor side of the humerus (foramen entepicondyloideum) is situated in the fossa supratrochlearis (cubitalis anterior). The epicondylus radialis is only perforated in th Chelonia, Rhynchocephalia, Lacertilia s. l., Araeoscelidia, Thecodontia, Pelycosauria and rudimentarily in the Australian bird *Casuarius* (s. WETTSTEIN, 1931). Both channels are only present in the Rhynchocephalia, Araeoscelidia and Edaphosauria (Pelycosauria); they appear together with a distal broadening of the humerus. A fossa olecrani is lacking in the ancestral reptiles and the lacertilians.

A foramen entepicondyloideum is described of *Bavarisaurus macrodactylus* (WAGNER, 1852) (s. COCUDE-MICHEL, 1963; HOFFSTETTER, 1964). COCUDE-MICHEL (1963) states the foramen entepicondyloideum in a figure of the humerus of *Bavarisaurus,* but describes in the text: «Le foramen ectépicondylien est seul présent». Further the concerned figure offers a completely preserved distal end of the right humerus, although WAGNER (1852) and MEYER (1860) have already noted an outbreak in the epicondylus ulnaris dexter. HOFFSTTETER (1964) has also recognised these two mistakes made by COCUDE-MICHEL (1963). After HOFFSTETTER on the contrary the distal part of the left humerus of *Bavarisaurus macrodactylus* is completely preserved; there only exists a small pit (obviously a foramen nutricium) in the flexor side of the epicondylus ulnaris sinister. A foramen ectepicondyloideum should also be lacking as HOFFSTETTER's plates of *Bavarisaurus* show. The presence of a distinct fossa supratrochlearis is important, which has been seen by COCUDE-MICHEL (1963) and by HOFFSTETTER (1964). In recent lizards the fossa supratrochlearis is associated with a vessel-opening, directed proximalwards. Its presence has either not been noticed until now or been taken to be

the perforation of the bone corresponds with a permanent muscle action, while in the contraction a tuberosity or an apophysis projects on the humerus by the muscle pull and a regression of the bone is caused on the clavicle by the pressure of the muscle. After CAMP (1923) the further development of the deltoid muscle produces the reduction of the clavicle, at first hook-like, and finally a road-shaped form.

The clavicle of the Anguimorpha is generally simply rod-shaped; the bone is only lacking in the dolichosaurids and many mosasaurids. The iguanids usually have a long and simply formed clavicle, whereas in the chamaeleonids the bone is completely reduced in common with the interclavicle. All tetrapod and many limbless Scincomorpha have a broadened clavicle, which can be perforated or hook-like, too. In the scincids, cordylids and gerrhosaurids, this bony element is unusually broad and generally perforated (CAMP, 1923).

The dermal elements of the shoulder girdle of the «lower tetrapods» are the paired cleithra and clavicles, as the medial interclavicle. Because of the isolated medial position and of the slender structure, the interclavicle of the Sauria is only seldom fossilized, and therefore has not been found in the Guimarota material.

1mm
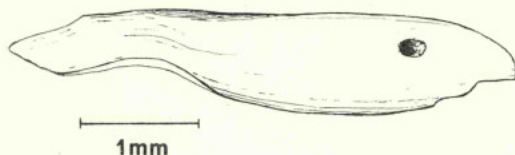
Fig. 57 — Gui. L. 198, right clavicle, medially broadened.

The specimen Gui. L. 198 is probably to be regarded as a scincomorphian right clavicle, which is medially broadened. It corresponds with the situations of Scincomorpha, described by CAMP (1923). The fossil clavicle is postmortem situated beside a badly preserved elongated sternal skeleton, which was present only as an impression. At first it was conserved by being filled with palavit and later prepared as a positive form of artificial substance. The supposed paired sternocostal elements, which are obviously located close together, can be assumed to be a parasternal development. The so-called parasternum, an abdominal continuation of the real sternal apparatus, is typical of arboricolous, as of burrowing lacertilians (s. SIEBENROCK, 1895; CAMP, 1923).

After HOFFSTETTER (1964) most recent lacertilians have a co-ossified scapulo-coracoid. The suture between both parts persists in the Agamidae, Chamaeleonidae, Varanidae, Helodermatidae, Dolichosauridae, Aigialosauridae and Mosasauridae. It is also present in the juvenile Teiidae and Anguidae, as in the skink Riopa fernandi. The independence and imperforation of the scapula and the coracoid are to be considered as primary conditions.

The specimen Gui. 188 is a right fragmentary scapula, which resembles that of a recent Varanus sp. This scapula is short and does not show any lateral fenestration, as may be seen in most known lizards. Beside small foramina nutricia situated in the marginal area, a bigger scapular opening is present in the superior part of the scapula, directed medially.The scapulo-coracoid suture is straight. Because of the similar proportions, the described scapula probably belongs to a varanoid taxon.

The scapulo-coracoid fragment Gui. L. 206 reveals two distinct fenestrations; in the superior part it exists as a large scapulo-coracoid fenestration as in the lizards Draco

H. Bones of the thoracic limb

The forelimbs are connected to the trunk, articulating by a pectoral-shoulder-
-girdle.

1) The shoulder girdle

Both cartilaginously created and dermal bony elements take part in forming the
shoulder girdle. The dermal covering bone, situated on the cranial side of the scapula
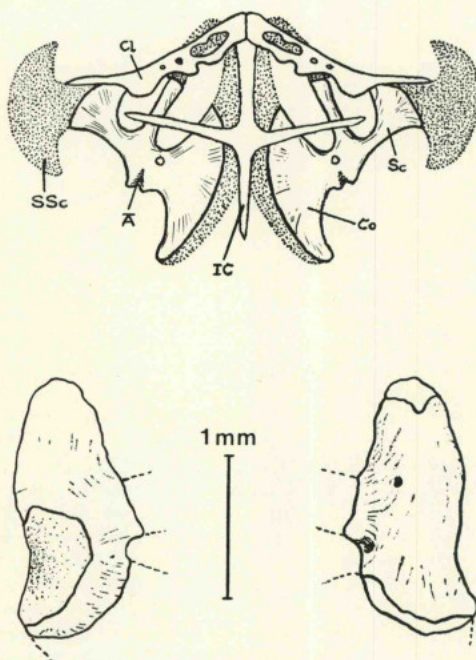in the Stegocephalia, Anura, Pelycosauria, the cleithrum, is lacking in the lepidosaurs.

Fig. 56 — Above: shoulder girdle of *Scincus scincus* [after EL-TOUBI, 1938, p. 30].
A: articulation for the humerus; Cl: clavicle; Co: coracoid; IC: interclavicle; Sc: sca-
pula; SSc: surscapular cartilage. Below: scapulo-coracoid fragment (Gui. L. 206)
from the Guimarota material, left — ventral view, right — dorsal view.

ROMER (1956) presumes that the clavicle of the ancestral Squamata is rod-shaped,
whereas CAMP (1923) supposes that the rod-shaped clavicle of saurians is derived from
a medially broadened form. Many Gekkota and Scincomorpha have clavicles broadened
towards the middle, which sometimes are perforated. The broad area of the clavicle corres-
ponds with the development of an attachment field for the musculus deltoideus (CAMP,
1923; ROMER, 1956). In the case of a nearly rod-shaped clavicle in the Gekkonidae, Xan-
tusiidae, Scincidae and Lacertidae, the bone shows distinct features of a prime breadth
and perforation. Because the deltoid muscle originates on the interior side of the clavicle,

The ribs are diversely long, the first and last ribs are the shortest. They run obliquely and ventralwards directed, whereby they show a curvature of areas and edges and a torsion. The first ribs are short and also more strongly curved than the following ones. The Guimarota material includes proximal and distal costal fragments. A prime composition of three or of two parts can not be detected. Nearly spheric costal heads are found which are distinct from the other costal bone because of a slight torsion (Gui. 199). Beside the circular articulary facts, the proximal costal fragments offer three bony ridges; the ribs seem only to be smooth, resp. without muscle insertions on the posteroventral side. The distinct ridges of the ribs indicate a bulky intercostal and levator costae musculature. In contrast all the other costal fragments have less or undeveloped ridges for the muscle insertion. Some proximal pieces (Gui. L. 195) have an oval articulary area, which is dorsoventrally broadened, and a bony crest on the anterior side.

Because the intercostal vessels and nerves run on the interior surface of the rib, sometimes a flat groove (sulcus costae) is developed; an opening for a nutritive vessel is also situated on this side. The arteria subclavia forms a very distinctive groove in the first sternal rib, providing the shoulder girdle and the anterior limbs. Because of the deep sulci costales, the specimens Gui. L. 79 can be regarded as ribs within reach of the arteria subclavia. They presumably oblong to a taxonomic costal type, which is rather smooth and rounded (Gui. 70, Gui. 78, Gui. 177, Gui. 187, Gui. L. 21, Gui. L. 78) and offers muscle insertions on the proximal part of the rib. A form with a circular articularly facet (Gui. L. 78) can be separated from a form with an oval one (Gui. 163). Six distal costal fragments (Gui. L. 196) are probably to be referred to the sternal or parasternal region because of their spheric cartilaginous ends.

Remains of associated elements of the vertebral column (cervical-lumbar), yielded by splitting the Guimarota coal, reveal smooth unicipital ribs with a circular caput costae, which is marked out by a torsion-curvature. Apart from an unimportant apophyseal development in the proximal part of the rib, no bony crests are present in these ribs.

The above named skeletal remains Gui. L. 30 indicate by a relatively short femur a beginning in the reduction of the posterior limbs (the anterior extremities are not preserved). The length of the femur (Gui. L. 30) is equal to the length of three thoracic vertebrae, whereas the one of the femur of *Lacerta lepida* corresponds to the fourfold, and of *Varanus* sp. to the fivefold length of a thoracic vertebra. The thoracic vertebrae of the skeletal remains are not elongated, but proportioned as in *Lacerta lepida* with a zygosphene-zygantrum-development. Therefore it can be assumed, that this lacertilian form had kept moving by winding in addition to the quadrupedal locomotion, similar to the cordylid *Chamaesaura aenea*.

«Thus the vertebral column of the Squamata is best studied as an entity without focusing on a single character. Some attempts have been made to elicit patterns by means of biometrical methods, or to characterize the functional basis of the morphalogical diversity.» (HOFFSTETTER & GASC, 1969)

The specimen Gui. L. 200 resembles the special caudal vertebra of *Lacerta lepida* in particulars, which is situated immediately ahead of the caudal vertebrae with an intravertebral or autotomic septum (i. e. the seventh of Lacertidae, the fifth caudal vertebra of most other lacertilian families). In this caudal region of the vertebral column, the Lacertilia and Rhynchocephalia can cast off the posterior tail part by the so-called autotomy in distress. The procoelous vertebra Gui. L. 200 reveals large, obliquely inclined zygapophyses, further slender and straight transverse processes and a reduced spina dorsalis. By the postmortem deformation, the posterior vertebral part is a little translocated into the anterior part, in the region of the potential autotomic septum (i. e. caudally of the transverse processes). A small sagittal crest on the anterior part of the neural arch, missing on the posterior one, indicates the presence of an intravertebral septum. The posterior part of the neural arch is rounded and seems to end caudally in a small process, rising dorsalwards. Because there is no known autotomy of the Varanoidea, the described specimen belongs to a non-varanoid taxon and a non-aquatic form.

The other caudal vertebrae (Gui. 136) have very compact centra, but the vertebral arches and pleurapophyses have been broken off. The centra offer a distinct ventral median crest, which caudally seems to diverge to the haemapophyseal marks. An autotomic septum is missing. A special taxonomic determination of these fragments is impossible. The Guimarota material has yielded only two fragmentary lacertilian haemal arches (Gui. L. 170), which presumably belong to two different taxa because of the appearance and bone colour.

5) The ribs (costae)

A vertebral segment primarily has one pair of ribs. The ribs are regionally discriminated. In the reptiles they are used in respiration, and for other and additional important functions in certain skeletal regions or in the case of reduced limbs. The ribs support the body wall, and are also of use in locomotion.

After REMANE (1936) the reptilian ribs are primarily separated into two of three successively situated parts: the proximal segment is named vertebrocostale, the small intercalated piece is the intercostale and the ventral, distal segment is the sternocostale. On the posterior side of the vertebrocostale, there is often present a processus uncinatus, but which is lacking in the Squamata. The tripartition of the rib exists in the Rhynchocephalia and some Lacertilia (Agamidae, Scincomorpha).

Instead of the prime dichocephal ribs in the ancestral reptiles for the articulation with the parapophysis and the diapophysis, the lacertilians only have unicipital (syncephal, holocephal) ribs, because both vertebral apophyses are fused to the synapophysis. Functionally the proximally forked rib is to be regarded as phylogenetically primary, because the double insertion of the rib creates to stability and thus has a suporting function. A dichocephaly is only presented on the cervical ribs of the Rhynchocephalia and weakly indicated in *Varanus* sp. The sometimes oblong shape of the saurian synapophysis indicates the prime dichocephaly of the reptilian rib. In contrary to the Rhynchocephalia, the Sauria do not have any processus uncinati and any wing-shaped, broad sternocostalia.

In many cases of limblessness, a so-called processus tuberculiformis appears in the front of the coastal head, which does not bear any relation to the prime dischocephally, but is of use for the insertion of the intercostal muscles. Sometimes there even exist two small costal processes, which are anteroventral and posterodorsal of the costal facet. Their lacking, resp. their size is characteristic for the degree of the limb-reduction in Scincoidea (s. HOFFSTETTER & GASC, 1969).

Two specimens (Gui. L. 182) of different bone colour (whitish and dusky) represent the forms without zygosphene-zagantrum-development. These vertebrae are stout and they have broad pleurapophyses. The light vertebra offers small prezygapophyses, which are not directed inwards, and distinct marks on the centrum for the attachment of the haemal arches. The dusky specimen has a large prezygapophysis, medialwards directed, and attachment areas, nearly intervertebrally situated, which indicate the presence of haemal arches. The two vertebrae obviously are of the anterior caudal region.
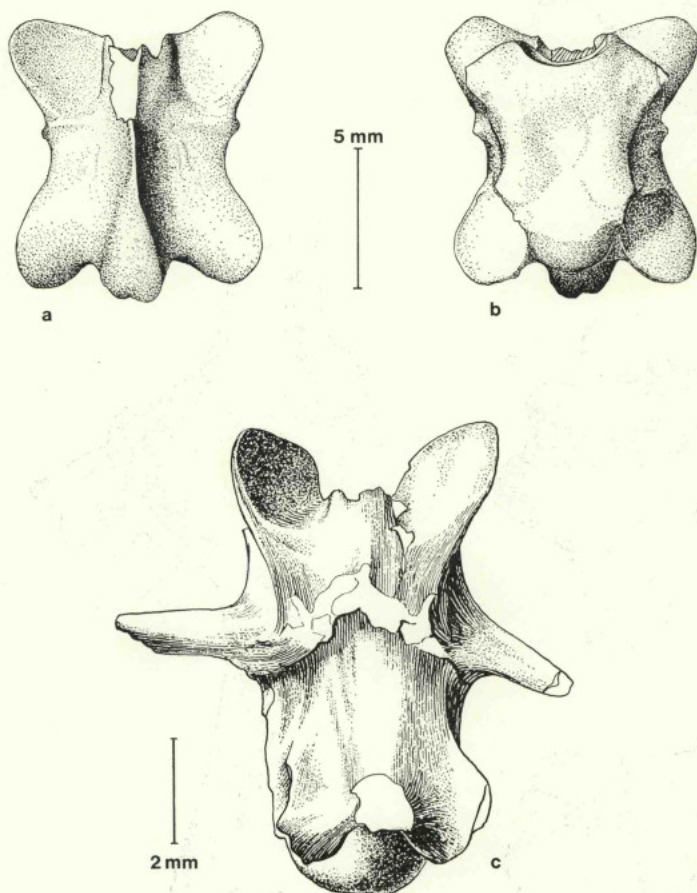
Fig. 55 — Vertebrae assumed to belong to the same lacertilian taxon (presumably *Lisboasaurus*); above: thoracic vertebra (Gui. L. 1973) with morphologic peculiarity, probably caused by the M. retrahens costarum (e. g. costal locomotion), a: dorsal view, b: ventral view (shape similar to that of *Trachysaurus* and Anguoidea); below (c): caudal vertebra (Gui. L. 200), dorsal view.
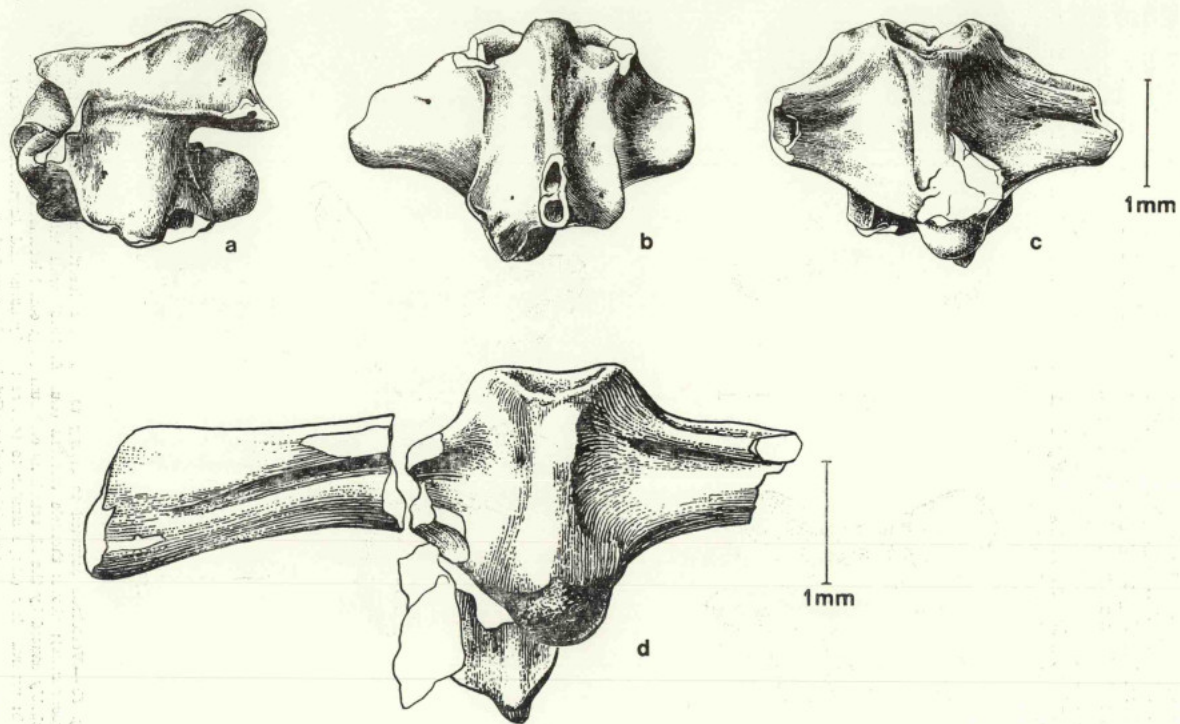
Fig. 54 — Pygal vertebrae, a-c: specimen Gui. L. 124, d: specimen Gui. L. 76; a: left lateral view, b: dorsal view, c: central view, grooving of the transverse processes is indicated; d: ventral view, distinctly grooved processus transversi.

given with a peculiarity: on the right anterior pleurapophysis, a presumable insertion mark exists as a notch for the last presacral rib, as described in the regio sacralis of the recent *Iguana* sp. after WILLISTON (s. REMANE, 1936). The distal fragmentary pleuraphyses are subcylindric and retrovert, indicating a distally larger attachment area for the ilium. The transverse processes have proximally two vessel-openings in their caudal sides. Whereas the cranial cotyle is hemispheric, the condyle seems to have an ellipsoidal form. This is obviously correlated with the breadth of the sacrum. The neural arch is slightly deformed and pressed into the neural channel. It is a little notched in the middle of the anterior part. Apparently the postzygapophyses are reduced, as an indication of a close connexion of the two sacral vertebrae (a scincomorphian habitus). There are no indications of a fusion with the second sacral vertebra.

The vertebral fragment Gui. L. 181 reveals a broad, cranially curved transverse process, which proximally has a distinct ventral foramen (for the passage of lymphatic vessels after HOFFSTETTER & GASC, 1969). Another feature is the small prezygapophysis with a zygosphene-development. In all probability the piece can be considered as a second sacral vertebra. The cranial cotyle articulates with a nearly ellipsoidal condyle.

Below the two sacral vertebrae connected with the ilia, the first vertebra already belongs to the tail region. Sometimes this vertebra can be fused with the sacrum. It has remarkably long and broad transverse processes, which usually offer a proximal ventral foramen or sometimes even a transverse channel, whereby the pleurapophyses seem to be groved on the ventral side. Further more this vertebra is characterized by the lack of ventral haemal arches, which are otherwise presented with attachment marks in the regio caudalis. The vertebra is also named pygal vertebra, because it is postsacrally and topographically situated in the collecting area of the caudal lymph, terminating in the trunk.

The vertebral specimens Gui. L. 76 and Gui. 124 bear long and broad transverse processes, which are ventrally grooved (s. palavit preparation Gui. L. 76). A zygosphene-zygantrum-articulation is developed on the apophyses of the vertebral arches. In contrast to the typic caudal vertebrae, the zygapophyseal areas of these specimens are not distinctly directed inwards, resp. outwards. The vertebral centra do not show any indication of the presence of haemal arches. This diagnosis conforms to that of a pygal vertebra. In the forms without zygosphene-zygantrum-development, any sacral- or pygal vertebra are not represented, but only posterior caudal vertebrae are found.

4) Regio caudalis

The caudal vertebrae are generally present more numerous than the prepygal vertebrae. The exceptions are correlated with the locomotion and the form of life of certain forms. In the yielded Guimarota material the caudal vertebrae are less numerous than the thoracic ones. Probably this phenomenon can be referred to the disintegration of the vertebral column by the natural, postmortem maceration, beginning in the caudal region.

The tail vertebrae are characterized by relatively long, straight transverse processes and the presence of ventral haemal arches. These arches with a paired insertion are intervertebrally situated and articulate together with two successive vertebrae. In agamids there is a tendency to shift the insertion to the posterior vertebra; in scincids, cordylids and gerrhosaurids, also some Anguimorpha (*Xenosaurus* and *Shinisaurus*), the haemal arches move to become inserted under the condyle of the preceding vertebra. In anguids, anniellids, amphisbaenids and in the snakes, the arches are fused with the centrum.

the lymphatic vessels; they also cover the lymphatic channel connecting the lymph hearts with the median perivascular lymphatic clearance. Such transverse processes are often distally forked and moreover have a proximal foramen ventrale.

The inclusion of the last presacral vertebra in the sacrum is known not only of Saurischia, but also of Iguanidae (s. REMANE, 1936). The last presacral rib (= lumbar rib) of *Iguana* sp. inserts distally in the anterior pleurapophyseal end of the first
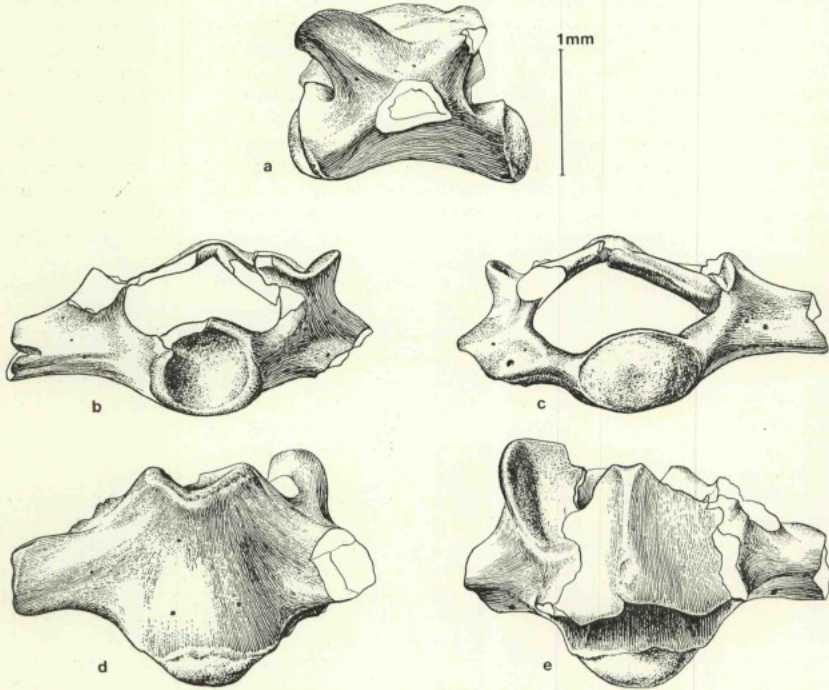

Fig. 53 — Gui. 168, sacral vertebra I; a: left lateral view; b: cranial view, distinct zygosphene formation and remarkable contact area for the last presacral rib on the right transverse process; c: caudal view; d: ventral view; e: dorsal view, zygosphene formation at the prezygapophysis.

sacral vertebra. This habitus is probably to be referred to as supporting function of the pelvis in lifting up the upper part of the body and in an arboricolous mode of life. The last presacral rib of the Anniellidae has another function in connexion with the considerable reduction of the pelvic girdle. From this lumbar rib of *Anniella* sp. connecting fibres pass to the apophyseal end of the first sacral vertebra and to the rod-shaped ilium (s. GASC, 1967).

By the stated features of the lacertilian sacral vertebrae, the specimen Gui. 168 can be determined as being a first sacral vertebra. The shape is short and stout, broad and ventrally flattened. The vertebra has remarkably large prezygaphyses with distinct zygosphene-development. Thereby a stiffening of the sacrum has been

The Guimarota material moreover comprises vertebrae and vertebral arch fragments with zygapophyses and without a zygosphene-zygantrum-forming. Most of these forms (Gui. 377, Gui. L. 18, Gui. L. 66) presumably oblong to anguimorphian taxa (cf. the diagnosis of Gui. L. 179).

A vertebral type of frail structure is remarkable (Gui. L. 134, Gui. L. 162, Gui. L. 178); the vertebra is distinguished by the partly translucent, yellow-brown bone tissue. The centrum is solid; foramina subcentralia are present; each side offers a ventrally increased articulation for the rib (s. Gui. L. 162). Therefore the corresponding rib may reveal an oblong articulary facet, which would indicate the prime double--heading of the rib. The vertebra Gui. L. 134 seems to be the last thoracic one above the pelvic girdle. The articulation areas for the ribs are lacking; the neural channel has a narrow lumen; the prezygapophyses are small, the postzygapophyses are enlarged for an articulation with the increased prezygapophyses of the first sacral vertebra. The moderate and obtuse spina dorsalis is bilaterally limited by a groove, which originates by the genuine profound dorsal musculature. In general the spina dorsalis increases caudalwards.

The specimen Gui. L. 180, determined as a lumbar vertebra, does not show any costal insertion, but offers a small, retrovert processus transversus. The centrum seems to be shortened. The prezygapophyses are very small and obliquely directed inwards in a way, which suggests the condition of opposite accessory facets. In view of the very moderate spina dorsalis, the extremely short transverse process and the missing hypapophyses, the described vertebra does not belong to thesacral or caudal region.

3) Regio sacralis

Several vertebrae (Gui. 168, Gui. L. 76, Gui. L. 124, Gui. L. 181) have special transverse processes. In the cervical and truncal vertebral column, the lacertilian vertebrae offer synapophyseal articulary headings for the insertion of ribs. Contrary to the vertebrae of the presacral region, which have short transverse processes in some groups, the sacral vertebrae bear elongated and broad transverse processes, which are also termed pleurapophyses because of their wing-shaped aspect. Free sacral ribs are lacking in the lacertilians. By the ossa ilia the pelvis is directly inserted in the first two vertebrae with pleurapophyses, which in fusion are termed os sacrum. After HOFFSTETTER & GASC (1969) the sacrum of tetrapod lizerds is formed by the 25th and 26th vertebra (in Iguanidae, Agamidae, some Lacertidae and Teiidae), in *Varanus* sp. by the 30th and 31th vertebra. Exceptionally a third vertebra functionally participates in forming the sacrum, as HOFFSTETTER & GASC (1969) have observed in *Nephrurus* sp. (Gekkonidae) and *Gerrhosaurus flavigularis* (Gerrhosauridae). Mostly the vertebral centra and arches of the two sacral vertebrae are fused, as are the ends of the pleurapophyses; an opening resists between the transverse processes (= foramen sacrale). In most of the Teiidae, Scincidae and Gerrhosauridae, the size of the sacral foramen is reduced by the close fusion of the pleurapophyses.

The first sacral vertebra is generally stronger than the second one. The pleurapophyses are subcylindric, extended and partly inclined; they form the larger part of the attachment area for the ilium. The transverse processes of the second sacral vertebra are thinner and distally forked in some forms; in this case the ilium is situated on the anterior branch.

The tendancy for limblessness influences the position and morphology of the sacrum, because the number of the presacral vertebrae increases, as the pelvis and the extremities are reduced. Thereby the function of the pleurapophyses, as a support of the ilia, is replaced by the transformation of the transverse processes for protecting

The obliteration of the sagittal crest in some vertebrae, ventrally situated, does not have any diagnostic signification. Within the thoracic vertebral column of recent Scincomorpha *(Lacerta lepida, Chalcides chalcides)*, the ventral side of the vertebrae becomes smooth, from the lumbar region to the second sacral vertebra, whereas con-
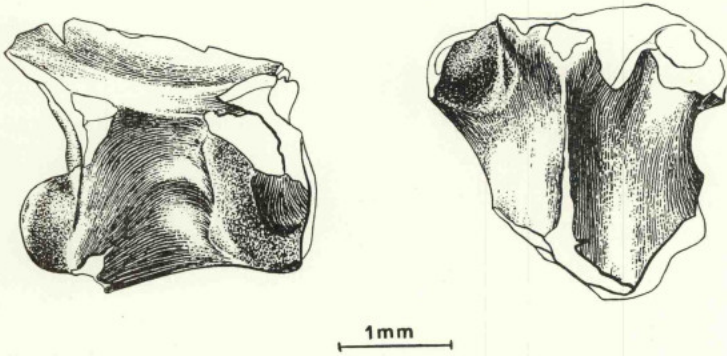

Fig. 51 — Gui. L. 162, thoracic vertebra; left: right lateral view, oblong articulary area for the rib; right: dorsal view, at the prezygapophysis the zygosphene development begins.
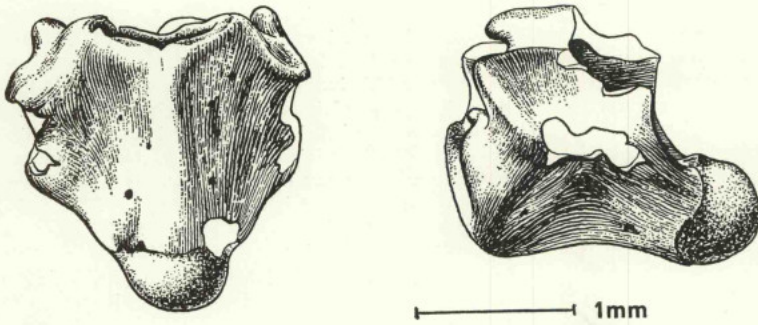
Fig. 52 — Gui. L. 180, lumbar vertebra; left: ventral view; right: left lateral view.

trary in the Anguimorpha, the ventral crest is reduced in the main part of the thoracic vertebral column and even appears again in the lumbar region.

The type of flat vertebra (Gui. L. 179), which is anteriorly broadened and ventrally smooth, reveals an anguimorphian habitus with a shortened, broad condyle and a broad, elliptic cotyle. The so-called foramina subcentralia do not have any systematic signification, as HOFFSTTETER & GASC (1969) assume for Gekkonidae and Xantusiidae. Foramina which usually appear in pairs, bilaterally of a sagittal crest, are also present in recent skinks *(Chalcides chalcides)*, lacertids *(Lacerta lepida)* and certainly in other groups. This positioning of vessel openings are found on numerous vertebrae of Guimarota.

Zonosaurus), in some lacertids and teiids, the fossil varanids *Megalania* and *Saniwa,* in the dolichosaurids and some mosasaurs (REMANE, 1936; HOFFSTETTER & GASC, 1969).

In *Sphenodon* this articulation is only suggested by an upward tendency of the prezygapophyseal facets. The specialization of the zygosphene and zygantrum in snakes, iguanids, the teiid *Tupinambis* and some mosasaurs appears with the inclination of the anterior accessory articulary areas to latero-ventral (zygosphene) and of the posterior to latero-dorsal (zygantrum), so that the area of the prezygapophysis faces that of the zygosphene, whereas those of the postzygapophysis and zygantrum are turned away mutually.
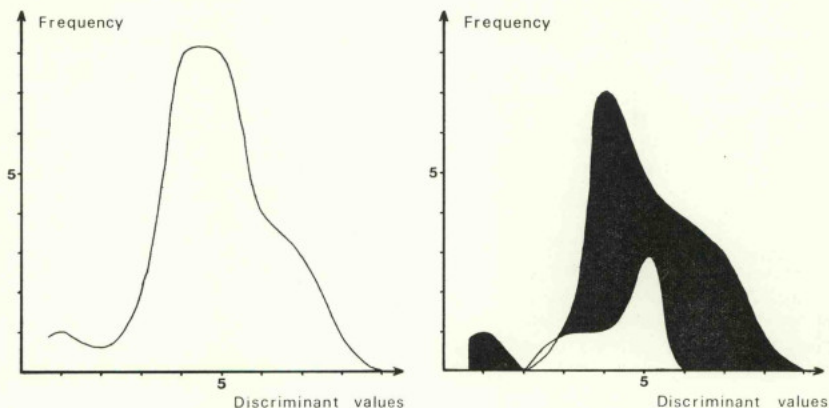
Fig. 50 — Diagram of distribution (s. text).

The zygosphene-zygantrum-articulation seems to produce a stiffening of the vertebral column by take effect of locking the torsion. Such articulation usually appears in snakelike extended forms; the presence in large forms is remarkable. Zygosphene and zygantrum offter their primary situation in the vertebrae of lacertids, cordylids, *Zonosaurus* and *Saniwa*; the described articulary areas of them are situated nearly vertically to the lightly inclined zygapophyses.

After HOFFSTTETER & GASC (1969) the zygosphenes often reveal an intracolumnar morphological variation, which stretches from a rudimentary state in the cervical region to a specialized development in the posterior truncal region; they are extinguished in the tail (e. g. *Saniwa ensidens* LEIDY, 1870). The zygosphene development is independent of a reduction of the limbs and the size of the animals.

The vertebrae of Guimarota are relatively numerous, but very fragmentary. The crocodilian vertebrae can be separated easily by their light brown, heart-wood-coloured bones. The saurian thoracic vertebrae with preserved neural arch Gui. L. 161 and Gui. L. 133 offer the well developed zygosphene-zygantrum and the described differences of the proportions in the same material. By that the systematic unity of the vertebral fragments (Gui. L. 175 and Gui. L. 176) studied with LINDER's numeric methods (1964), and of the vertebrae with the zygosphene-zygantrum-articulation (Gui. L. 161, Gui. L. 133) can be concluded. Some fragments (Gui. L. 160) have marks of an added developed articulation vertical to the zygapophyses. They are to be seen articulating vertically to the zygapophyses. They are to be regarded as related (generically or subgenerically) to the above described forms with zygosphene-zygantrum.

the centrum is determined by measuring the distance from the cotylar margin to the beginning of the condylar, the breadth is given by the distance between the two synapophyses. The discussed vertebral remains have synapophyseal articulated heads for the ribs; on the vertebral side of these vertebrae there is found no mark to suggest the presence of intercentra.

The vertebral proportions can be regarded as a function of the mode of life (e. g. the intense cotylar-condylar articulation of skinks which move on winding by reason of the reduction of limbs). Different locomotion makes specific biotops accessible. The biological and phylogenetic consequences of the selected features are appropriated in order to determine the species. But this aspect is complicated by the repeatedly apparant adaptation of the skeleton to an apod locomotion in the Squamata. Thereby after GASC (1967) a complex of features results from the modifications associated with the mode of life, from adaptive particularities and from the genetic situations, which causes one to examine the complete vertebral column. For the study of the proportional differences in the selected thoracic vertebrae, the topographic limitation meets the requirements.

The deviations of the measurement results (data of asymmetry) for the centrum-length refer to a variation within the thoracic vertebral column. By evaluating the dispersion of the differences of the mean values ($S_D = \pm 0,744$), the mean values ($M_{Gui. L. 175} = 4,951$ and $M_{Gui. L. 176} = 4,338$) and the t-datum ($t = 0,824$), the probability ($P = 0,47$) arises that both groups of measurements derive from the same basic entity. Just so the comparison of the difference of mean values with the threefold or even the twofold of their dispersion ($D_M < 3\text{-}2\ S_D$) shows that the difference is to be regarded as being accidental and that both groups of measurements descend from the same material. The so-called F-distribution for the statistical underpinning of a distance from zero does not allow a separation ($_{24}^{3}F = 4,99$; $F_{(p = 0,05)} = 4,53$).

The distribution of the discriminant values (X) of both groups does not allow any separation. The synopsis of the distributed quantities gives the diagram of a nearly standard distribution. A light asymmetry of the distribution of the breadth-measurements is to be referred to the obvious deformation of the material (s. diagenesis and tectonics of the matrix in HELMDACH, 1968). The deviation of the measurements of the centrum-length from the standard distribution depends on the variation of the vertebral length within the vertebral column, i. e. by increasing of the length from cervically to lumbarly. With the diagram both groups of vertebrae can be accounted for vertebrae of an anterior and a posterior region of the thoracic vertebrae.

Both hypothetically separated groups of measurements show a contrary asymmetry of distribution in the right diagram (Fig. 50). The additive diagram (left) of the quantities of the discriminant values (synthesis of the two separate curves) resembles that of a GAUSS's distribution of quantities. Accordingly both measure groups belong to an uniform entity, which are falsely separated after any insignificant proportional differences within the thoracic vertebral column.

In several lacertilian families the neural arch develops to a different degree the zygosphene-zygantrum-articulation. It concerns the two additional articulary areas between the prezygapophyses and between the postzygapophyses. These accessory articulations are only present within the order Squamata; they have apparently come into existence in several groups, independently of one another (a phenomenon of convergence), and they appear in like manner on the vertebrae of tetrapod and limbless forms. This described feature is characteristic of all snakes, but it is sporadically presented in the lizards as in the large iguanids, the cordylids (not gerrhosaurs, except

cervical material seems to be rightly attributed to the Scincomorpha (with C_{1-8}). The intercentra are represented by only one specimen (Gui. L. 172).

2) Regio thoracalis

The thoracic vertebrae of the lizards generally bear ribs, the first five pairs of which are usually connected with the sternal apparatus. For coastal articulation, they have developed a reniform or spherical, cartilaginous small head below the prezygapophysis of each side.

In the lumbar region of the trunk (l. e. one to three vertebrae above the first sacral vertebrae), the ribs are sometimes missing or an ankylosis of reduced ribs and corpus vertebrale is present. In the families Scincidae, Gerrhosauridae and Lacertidae, the presacral vertebrae are never ribless (after HOFFSTETTER & GASC, 1969).

As a characteristic and convergence-development the Upper Triassic eolacertilians *Kuehneosaurus, Kuehneosuchus, Icarosaurus* on the one hand and the recent agamid *Draco* have elongated synapophyses with broadened articulary areas for the long ribs, which are allowed to glide by the extended integument (ROBINSON, 1962, 1967a; COLBERT, 1966, 1970). Thoracic vertebrae with elongated, articulary transverse processes have not been found in the lacertilian remains of Guimarota.

The saurian centra mostly show a sagittal, blunt crest on the vertebral side, which is related with the ontogenetic constriction of the chorda dorsalis. The osseous material which has replaced the reduced chorda gives the vertebral conus a hourglass-shaped relief, as already described above.

In numerous Anguimorpha and some limbless Scincomorpha, the ventral surface of the vertebra is flat and the blunt median crest is obliterated. It is possible for the condyle and centrum to have been broadened. Sometimes the lateral borders of the centrum are less divergent (Scincidae).

The reduction of the limbs is correlated with an increase of the vertebral segment number and with the tendency to an uniformity of the vertebrae. The length of the vertebrae varies in relation to the function of the mechanical conditions of the vertebral column. Apart from *Varanus* and *Lanthanotus,* the lacertilians with well developed limbs possess relatively short cervical vertebrae. The vertebral length considerably increases towards the pectoral girdle and reaches its maximum in the posterior thoracic region. In the lumbar presacral region, the vertebrae are shortened again but never so short as the cervical ones.

From a part of the Guimarota vertebral material without preserved neural arches, two different groups of vertebrae with the same habitus and certain proportions are to be collated. In one group (Gui. L. 175) the breadth of the vertebra is in the ratio of the total length of 1 : 1, and the length of the centrum to the length of the condyle of 3 : 1; whereas in the other group (Gui. L. 176) a ratio of breadth to centrum-length of 1 : 1 can be stated, and a ratio of centrum-length to that of the condyle of 4 : 1. Whether this difference is a specific feature or is related to an intracolumnar increase of the centrum-length from cervically to lumbarly, has been studied biometrically with discriminating analysis.

The biometry has supplied methods which also permit an exact review of the measurement results of a moderate quantity (s. BELITZ, 1960). The presumed differences can be computed with discriminating analysis, whereby a hypothetic separation is either statistically certain or denied.

The length and breadth of the vertebral centra and the length of the condyle are taken as features for the discriminant function. By this a deviation or a conformity in proportions within the examined groups can be evaluated. The length of

tebra; on the fifth of most Agamidae and Iguanidae and of the cordylid *Chamaesaura;* on the sixth and seventh on the Varanidae (s. HOFFSTETTER & GASC, 1969).

In all probability the best preserved specimen (Gui. L. 45) is the fourth cervical vertebra of a scincomorph lizard, considering its transverse process is characteristically formed like that of the fourth cervical of *Chalcides chalcides* and equally so like the sixth one of *Varanus* sp.; the transverse processes of the ribless cervical vertebrae offer a certain obliquity to the vertebral centrum, whereas they are nearly
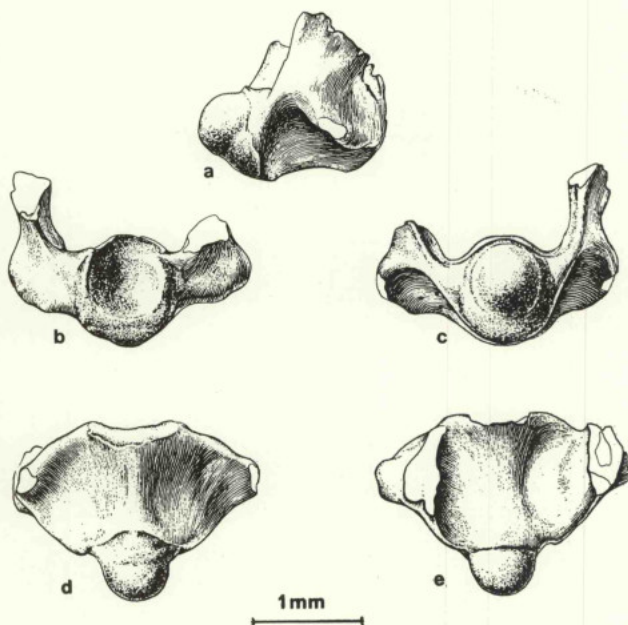
Fig. 49 — Gui. L. 45, anterior post-axial cervical vertebra (probably C₄); a: right lateral view, the intervertebral position of the intercentrum can be supposed; b: cranial view; c: caudal view, the contact area for the intercentrum has been developed; d: ventral view; e: dorsal view, the neural arch has been broken off.

vertical on the rib-bearing cervical vertebrae and have also developed a roughly spheric articulary head of the rib.

The cervical vertebra connected with the first rib has a rather oblique transverse process. The distal end is formed only as a convex chondrial articulation area, not a typical articulary head. The figured specimen shows the thinning out of the substantia compacta on the costal area of the transverse process (Fig. 49).

From the other fragmentary cervical vertebrae, one part has obliquely directed synapophyses, the other part nearly spherical ones. The ratio of the delivered anterior (C_{3-5}) and posterior (C_{6-8}) cervical vertebrae is approximately equal.

After the previous aspects and because of the above described intervertebral position of the hypocentra (therefore intercentral) with the characteristic marks, the

backwards, has been developed. The odontoid process is shaped like a small, protruding lip.

In coming to a decision over the taxonomy, it may be ascertained that the intercentra are obviously set between the vertebrae, resp. on the cranial part of the following pleurocentrum (typ: Cordylidae, the young with an intervertebral intercentrum and the adult with an antero-subsequent one, s. HOFFSTETTER & GASC, 1969). As the Anguimorpha, Scincidae and Gerrhosauridae tend to reveal a hypocentrum, caudally set on the vertebra, the presented specimens are determined probably as scincomorph, cordylid-lacertid (not teiid) axial types.
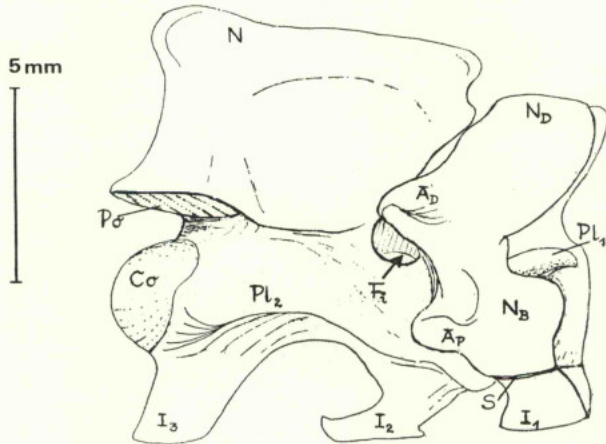
Fig. 48 — Right lateral view of the atlas and the axis of a recent varan; A_D : dorsal apophysis (diapophysis); A_P : parapophysis; Co: condyle; F_i : fenestra intervertebralis; $I_{1, 2, 3}$: intercentra; N: neural arch; N_B : base of the neural arch (pediculus arcus); N_D : tegmen of the neural channel; $Pl_{1, 2}$: pleurocentra; Po: postzygapophysis; S: synchondral joint.

b) Post-axial cervical vertebrae:

In defining cervical vertebrae, HOFFSTETTER & GASC (1969) have soundly advised one to follow that of STANNIUS (1849). Accordingly vertebrae of the cervical region are those located cranially of the vertebra, the rib of which is first connected to the sternum. As the Guimarota material has not yielded any associations of the cervical vertebral column and the pectoral girdle, other criteria have been used to characterize cervical vertebrae.

The compactness and shortness of the vertebral centra diagnose the cervical vertebrae of Sauria as do the high-rising neural arches which enclose the thick cervical medula spinalis, and also the unpaired attachment of the hypocentrum and the habitus of the synapophyseal processes.

16 of the Guimarota vertebral fragments are thought to be post-axial lacertilian cervical vertebrae (Gui. L. 45). The first rib of most lacertilians appears on the fourth cervical vertebra, of the scincomorph genus *Dibamus* on the axis itself, of some Gekkonidae, Pygopodidae, Scincidae, Anguidae, Anniellidae and of *Xenosaurus* on the third ver-
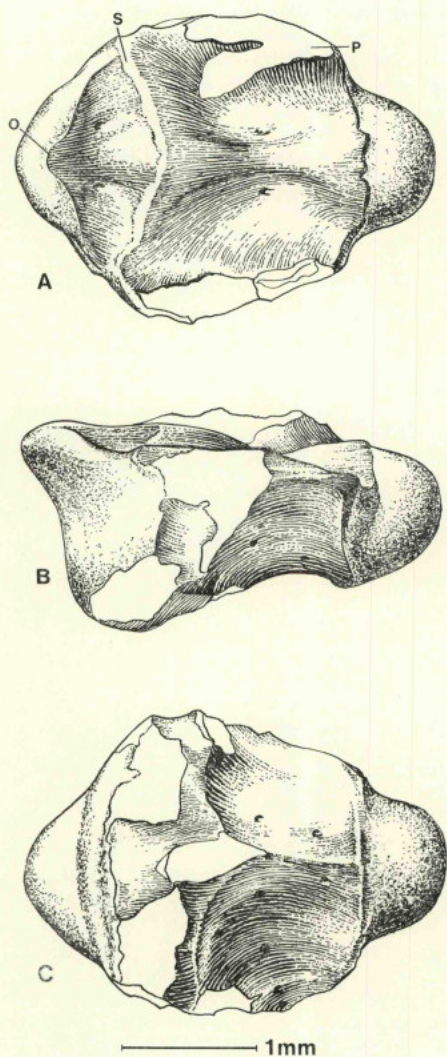
Fig. 47 — Epistropheus (Gui. L. 123); A: dorsal view, the neural arch has been broken off, the pleurocentrum of C_1 has been fused with that of C_2, O — odontoid process, P — pediculus arcus, S — sulcus intervertebralis; B: left lateral view, distinct odontoid process; C: ventral view, in the middle the regio intervertebralis.

The arch halves do not grow together dorsally as they are separated from the ventral hypocentrum on the base by a synchondral juncture. The wedge-shaped hypocentrum (Gui. L. 169) compounds the annular atlas ventrally. An anterior articulary facet is projected to the occiput to take in the medial condylar part of the basioccipital. The caudal articulary part bears the axial odontoid.

Right and left of a ventral apophysis (prominentis ventralis), each is located an opening for a vessel in the anterior part of the hypocentrum. As seen on a fragmentary hypocentrum, a third foramen can appear under the caudalarticulary area, and
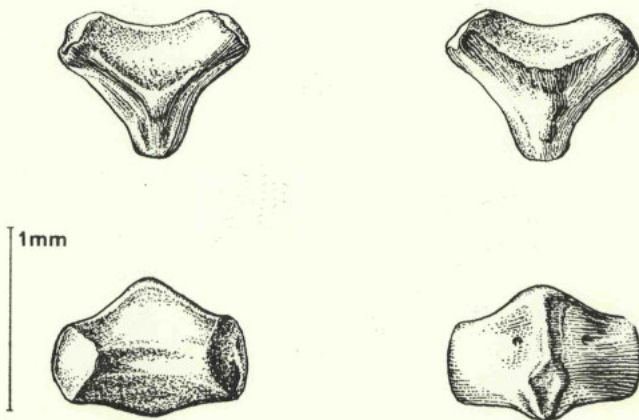
Fig. 46 — Atlantal hypocentrum (Gui. L. 169); above left: cranial view; above right: caudal view; below left: dorsal view; below right: ventral view.

is also useful in determining the facet. All five atlantal hypocentra have developed a prominentia ventralis. The atlantal articulary areas are lightly concave.

The large, cranially extended basidorsalia with postzygapophyses and the habitus of the hypocentrum are characteristic of scincomorph lizards.

In the Guimarota material the axis is represented by three specimens (Gui. L. 123) of the same type and two single odontoids. The pleurocentrum of the first cervical vertebra is fused with that of the second one; in part a weak suture is recognizable. The axis has a posterior condyle indicating the procoelian position of the following vertebrae. The second hypocentrum of the Sauria in general develops an anterior hypapophysis which is either fused with the centrum or separated by a suture and only affixed by tissues to the centrum. There is no indication of fixture point for the third intercentrum on the axial centrum, but by reason of the configuration of the ventral condylar area, a intervertebral position of the third intercentrum can be assumed, as this has also been deduced from the yielded post-axial vertebral fragments.

Both fused pleurocentra of the atlas and the axis present several foramina nutricia, which are bilaterally distributed by a cranially broadened median crest. The intravertebral compressing of the chorda is traced through the vertebral bone and reveals an hourglass-shaped relief on the dorsal side of the pleurocentrum of both atlas and axis and with bilaterally layered foramina nutricia. The neural arches of all the three specimens are broken. Below their base a synapophyseal process, which is directed
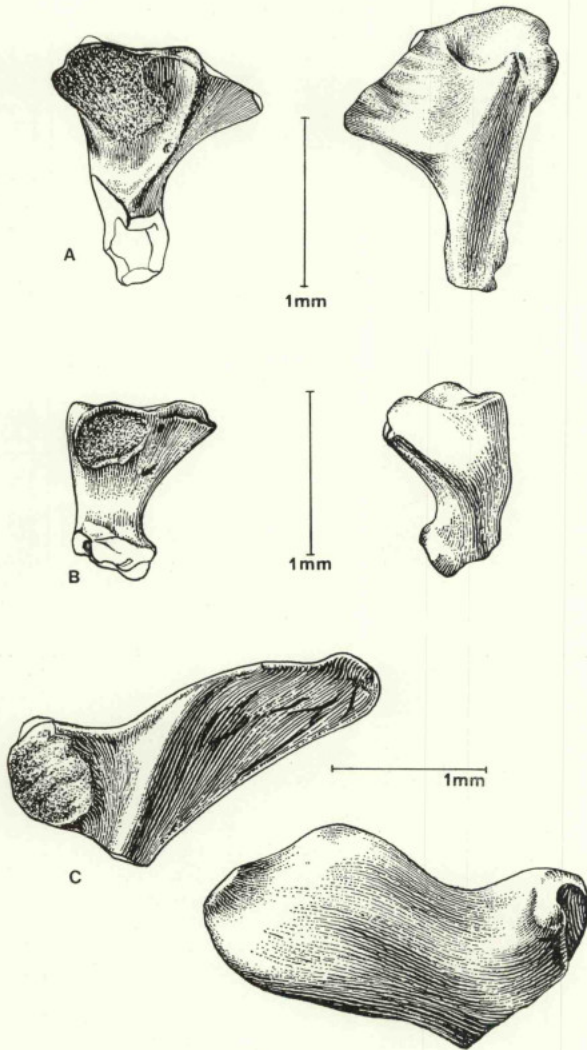
Fig. 45 — Upper parts of left halves of the atlantal arch from the Guimarota material (Gui. L. 168); A: left — medial view, postzygapophysis, right — lateral view, dorsal apophysis (diapophysis) and a diapophyseal groove; B: left — medial view, postzygapophysis, right — antero-lateral view; C: medial view and right — dorso-lateral view, dorsal apophysis.

The solid basal parts of the atlantal arch with its double-articulary facets are obviously suitable for fossification, whereas the fragile top parts and the ventral basal piece (hypo- resp. intercentrum) are often lost in the natural maceration or are broken, which I could equally well observe of *Lacerta lepida* and *Chalcides chalcides.*

The Guimarota mine yielded fourteen right (Gui. L. 165) and thirteen left (Gui. L. 131) basal parts, three right (Gui. L. 143) and four left (Gui. L. 168) dorsal parts of the atlantal arch and also five atlantal hypocentra (Gui. L. 169).

Only by the means of the four left dorsal arch fragments can three taxa be postulated. Two of these forms have distinct postzygapophyses, one specimen offers a neural arch which is anteriorly elongated in a medial direction, whereas the other can be distinguished by a relatively larger postzygapophysis and by a notch on the external side. In this way the posterior diapophysis is detached. The right arch fragments are certainly related to this described form.

The pedicels of the vertebral arches (Gui. L. 131 and Gui. L. 165) reveal that most of these fragments must have developed an arch top with a postzygapophysis. Therefore this type of atlas is numerous.

In comparison with some preparations of recent *Lacerta lepida, Chalcides chalcides* and *Varanus* sp., two foramina on the internal side of the arch next to the postzygapophysis are identified as the openings for blood-vessels.

As the second spinal nerve (N. cervicalis II) of lacertilians exits through the foramen intervertebrale between atlas and axis, the dorsal foramina in the diapophyseal groove are suited for the entry of blood-vessels. From comparative anatomy, it is known that the paired vertebral artery branches off rami spinales to the spinal cord, running between the long cervical muscles and the vertebrae. Beneath the spinal cord these accompany the Arteria spinalis anterior and the two lateral Arteriae spinales posteriores, all of which originate cranially in the A. vertebralis. As an important paired vessel, the occipito-vertebral artery runs from the aorta to the cervical vertebral column; on the atlas it bifurcates into an ascending arteria and a recurrent A. vertebralis dorsi, which runs along laterally the zygapophyses, and caudally units with the lumbal artery. This A. vertebralis dorsi gives nutritive rami for the dorsal cervical musculature and the spinal cord and anastomoses with the collaterals of the vertebal arteries. From these a vessel passes ahead of the postzygapophysis between the atlas and axis into the vertebral channel; there a connection can be suggested to the both described internal foramina. Externally a ramus branches off to the diapophyseal groove.

The Squamata generally have only one transverse process (synapophysis) on each side of the vertebra. The mode and position of the vertebral processes are embryonically induced by the arrangement of the muscles, the connective tissue and the ribs. This function conditions the differences in the location of the apophyses and also within the vertebral column. The external side of the basal fragments of the atlantal arch bears an apophysis, which is probably formed by the insertion of a trace of connective tissue like that in recent lizards. If an additional apophysis (diapophysis) is found to exist on the dorsal arch above the postzygapophysis, then this can be named parapophysis. The parapophyses are accompanied by foramina nutricia, usually by a larger posterior opening and a minute anterior one. However the latter is sometimes lacking.

The sides of the fragments are easily determined, considering that the posterior articulary facet of the basidorsale is only a little bigger than the anterior one, — the fact results from the articulation with the anteriorly tapered dens epistrophei. The atlanto-occipital articulation is smaller. Moreover both halves of the atlantal arch extend cranially.

1) Regio cervicalis

a) Atlas and axis:

The two anterior cervical vertebrae have certain characteristics; the lacertilian atlas consists only of the neural arch and a ventral hypocentrum, which corresponds with the intercentra between the other vertebrae (centra). The true centrum of the atlas is constructed as a typical pleurocentrum, but co-ossifies with the second cervical vertebra (axis or epistropheus) and forms the anterior part of it, the odontoid.
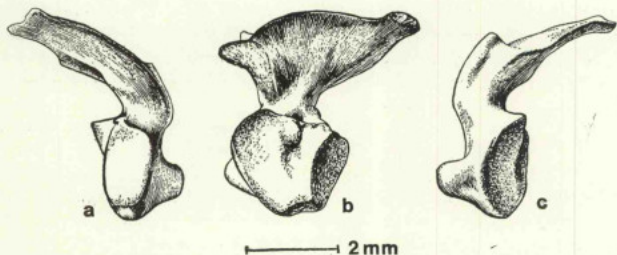

Fig. 43 — Left part of the atlantal arch of a recent *Lacerta lepida* DAUDIN, 1802; a: cranial view; b: medial view, left above the postzygapophysis; c: caudal view, left below the parapophysi.s

A complication in the construction results from the development of the cranial sclerotome half ahead of the atlas. This rudimentary vertebral design is termed proatlas. Whereas the hypochordal strap (hypocentrum) of the proatlas grows together with the occiput, parts of the neural arch are annexed to the atlas. The pleurocentrum of the proatlas becomes a small trunnion (processus odontoideus) on the odontoid (pleurocentrum of the atlas) of the axis.
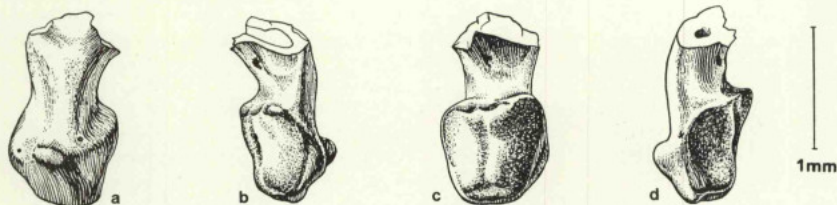
Fig. 44 — Basal part of the right part of the atlantal arch (Gui. L. 165); a: lateral view, parapophysis; b: caudal view, articulary face for the odontoid of the axis and the beginning of the postzygapophysis (above); c: medial view; d: cranial view, articulary face for the occipital condyle.

Both halves of the neural arch of the annular atlas generally remain disconnected from the ventral hypocentrum, nor do they unite above the neural channel. The articulary area for the occipital condyle is formed by the basal parts of the arches, the hypocentrum and in the middle, by the tip of the odontoid process. A septum interarticulare (ligamentum transversum) running transversally separates the processus odontoideus from the neural channel and two synergetic articulations, the atlanto-occipital and the atlanto-axial, from each other.
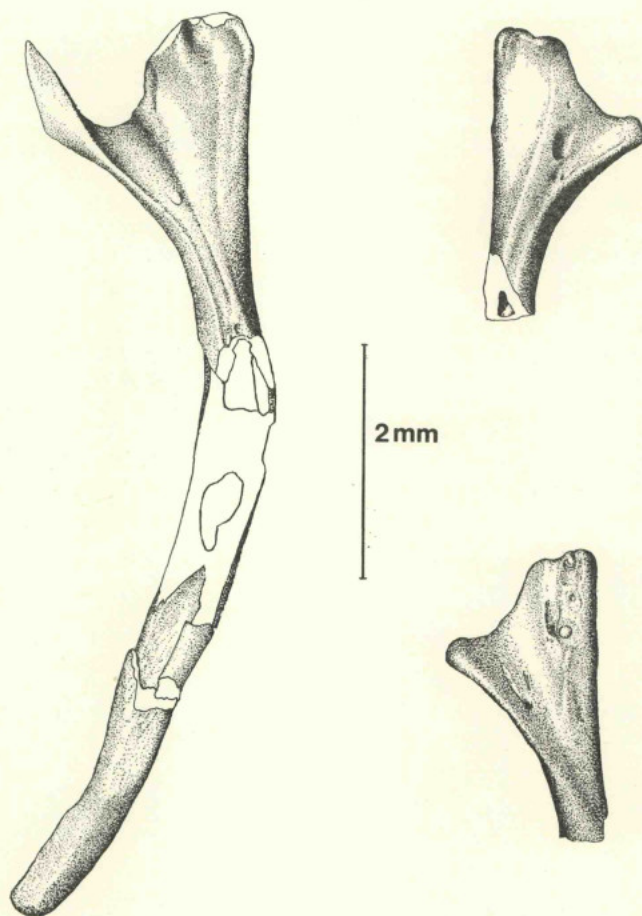
Fig. 42 — Pterygoids from the Guimarota material; left: Gui. L. 202, dorsal view
of a left pterygoid; right: Gui. L. 135, fragment of a right pterygoid (above:
dorsal view; below: ventral view, toothed processus palatinus).

perichordal vertebra is most important in the discrimination of the features in the
axial skeleton of the different vertebrate groups.

As a result of the presence of the lacertilian vertebral fragments, one can now
discuss the vertebral column under the following headings: cervical, trunk, pelvic and
tail region.

Fig. 41 — Gui. L. 149, supraoccipital; above: postero-dorsal view, anteriorly in the middle the processus ascendens; below: cerebral view.

Fig. 40 — Gui. L. 130 basioccipital; above: dorsal view, with fragmentary beginnings of the exoccipitals; below: atlanto-axial view, tripartite condylus condylus occipitalis.

Gui. L. 35

5 mm

2 mm
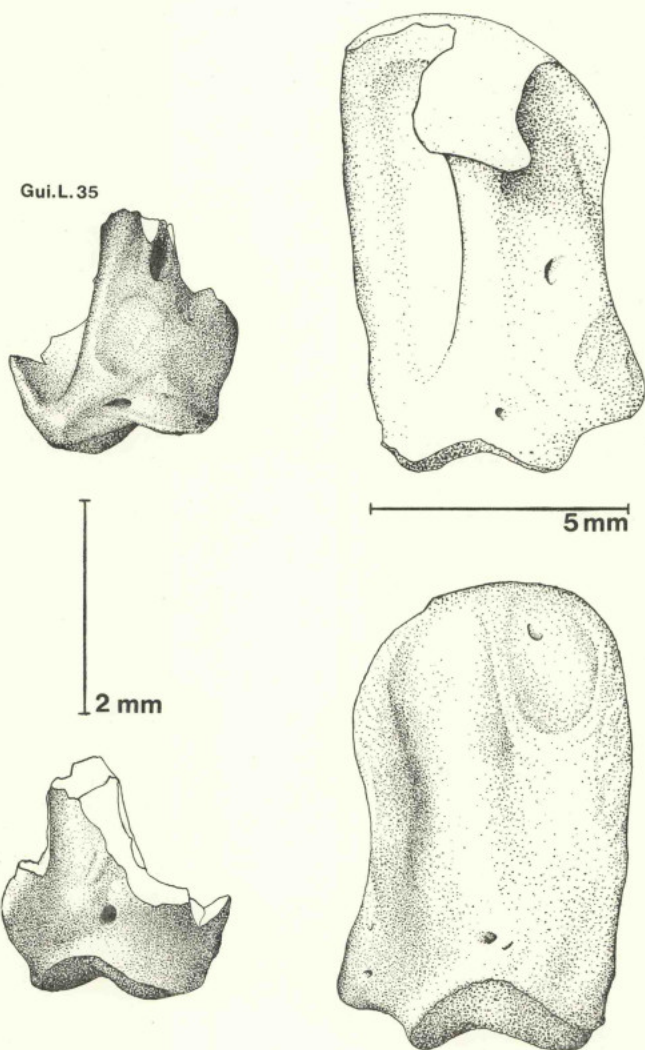
Fig. 39 — Gui. L. 35, fragment of a left quadrate from the Guimarota material in comparison with a left one of the recent *Lacerta lepida;* above: facies posterior; below: facies anterior.

5) Ossa occipitalia

The supraoccipital bone constitutes the occipital roof and also supports the parietal bone. From Guimarota a typical lacertilian supraoccipital is found (Gui. L. 149); on the dorsal side it offers a merial crest, which anteriorly continues into the processus ascendens supraoccipitalis. The configuration of the lateral processes indicates the connection with the posttemporal arch (i. e. with the processus paroticus of the exoccipital bone) and the presence of a transversal oval posttemporal opening.

The basioccipital bone Gui. L. 130 presents a tripartite occipital condyle and the fragmentary beginnings of the ascending exoccipitals on the upper sides. The piece Gui. L. 126, prepared with palavit, reveals a part of the capsula sphenoccipitalis. The occipital condyle of this specimen is not tripartite but small and hemispheric. The supraoccipital roof is broken by the intense deformation of the pieces. The processus paroticus (or paroccipitalis after EL-TOUBI, 1938) of the exoccipital bone seems to be extended laterally in a straight line. A sphenoid process of the basioccipital is preserved. The anatomical features of the presented occipital bones are best compared with those of the Scincidae.

6) Os pterygoideum

In the Guimarota material the pterygoid is represented by more than 50 fragments, which, if they have been preserved, are toothed. The pterygoids seem to extend backwards considerably (s. Gui. L. 89 and Gui. L. 202). When the jaws are in occlusion, level with the coronoid, a process of the pterygoid branches off for the connec-
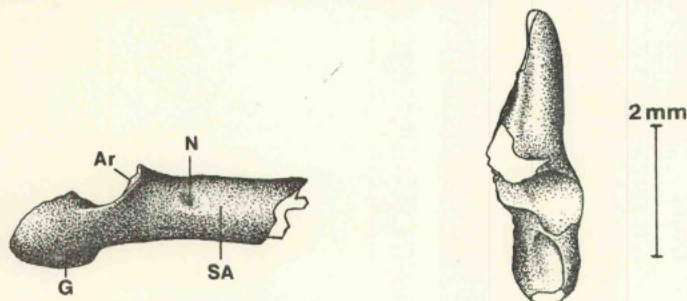

Fig. 38 — Gui. L. 2, posterior end of a right lower jaw; left: lateral view, Ar — Articular, G — Gonial (=Pre-articular), N — For. nervi auriculo-temporalis (N. V₃), SA — Surangular; right: dorsal view, articulary area for the quadrate.

tion with the ectopterygoid (or os transversum after HAAS, 1936 and VERSLUYS, 1936). At this junction point of the pterygoid with the processus ectopterygoidalis and the processus palatinus with mince teeth, there are some differences in the shape, the thickness, the broadness and the quantity of the pterygoid teeth. These features imply the existence of at least four taxa.

G. The vertebral column

From the history of development, we know that the axial skeleton of the vertebrates consists of two components derived from different germinal cells: the entodermal Chorda dorsalis and the mesodermal perichordal skeleton. The genesis of the

and on the anguid *Diploglossus;* but these lacertilians reveal another run of the groove. There are some frontalia fragments (Gui. L. 237) with a smooth surface and a long, small, incurved lateral ridge, too.

3) Os jugale

The jugal is represented by 30 angled specimens, which present, without exception, the entire characteristic reduction of the inferior temporal arch. The piece Gui. 193 (a left jugal fragment) indicates a mince process directed to the quadrate; it documents the primary quadrato-jugal junction of the ancestral lepidosaurs. The same is to be seen in a lower degree on the jugals Gui. L. 125, Gui. 143, Gui. L. 239.

The processus maxillaris, which is directed forwards, is differently developed; on the specimen Gui. L. 125 it shortly becomes thin to the maxilla, whereas on Gui. 143 and Gui. L. 239, it is rather more long than broad. The external side of the processus maxillaris jugalis presents a linear row of several foramina on most of the jugals; the specimens Gui. 107 and Gui. 193 do not have them.

By the prominent orbital margin on the internal side, a sulcus is developed in the angle of the jugal but not so on the specimen Gui. 193. The different jugalia forms certainly suggest that five lacertilian taxa exist.

4) Squamosal, quadrate and articular

Regarding their angled shape, the squamosals Gui. 94, Gui. 149 and Gui. L. 240 could be mistaken for the jugals, but in contrast to the jugal, the squamosal bones have a short posterior, rounded end forming the articulation with the quadrate and an anterior one with a medial attachment area for the postorbital.
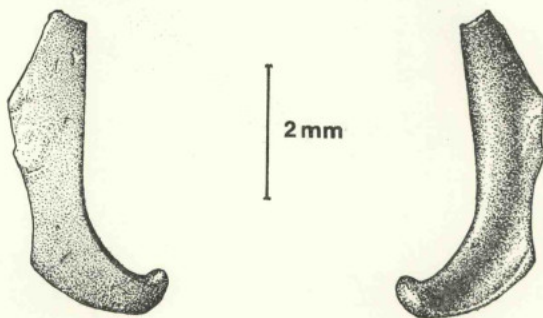

Fig. 37 — Gui. 94, right squamosal, showing the shape of a hockey stick
[cf. ROBINSON, 1967b].

The numerous quadrate fragments indicate the free motility (streptostyl of these bones. The basal ends are developed for a saddle-articulation with the articular of the dentary. The mobile junction to the pterygoid is marked (s. Gui. 53).

46 articulation pieces of the articular are presented; on several of them the channel for the auriculo-temporal nerve (N. V.$_3$) is to be seen running from the external side into the fossa Meckeli. The processus retro-articularis does not bend downwards (s. Gui. L. 2).
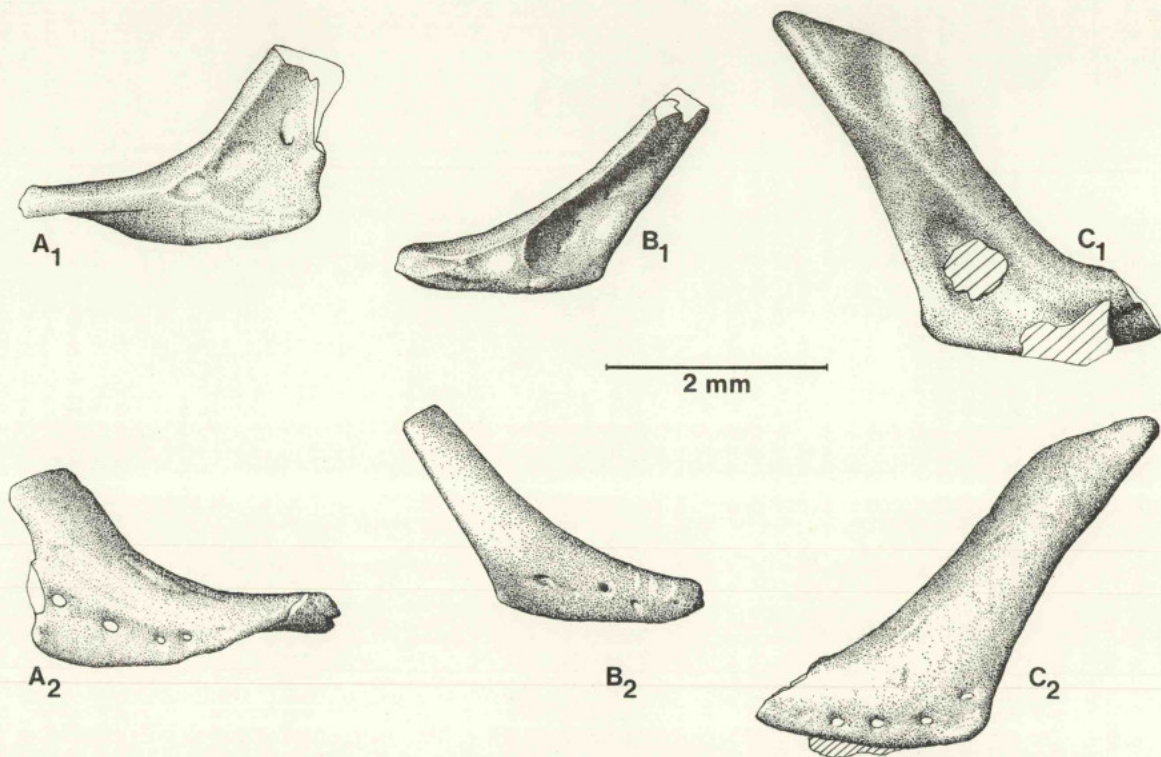
Fig. 36 — Different lacertilian jugals from the Guimarota material; A: Gui. L. 125, right jugal with a relatively short maxillary process; B: Gui. L. 239, right jugal; C: Gui. 143, left jugal; 1: medial view; 2: lateral view.
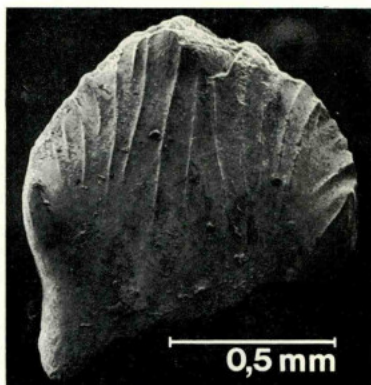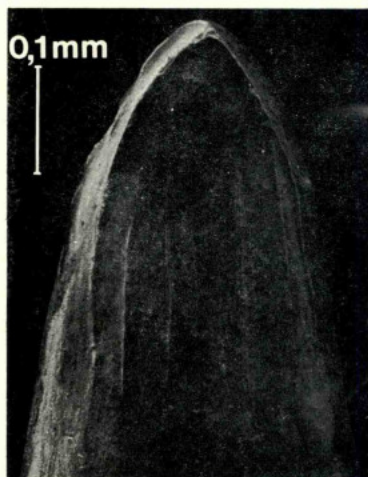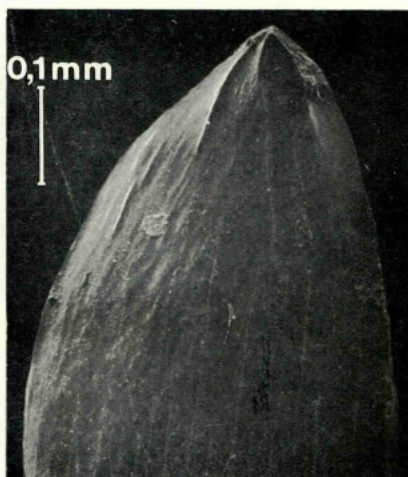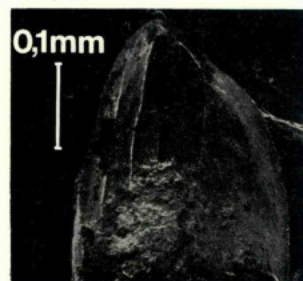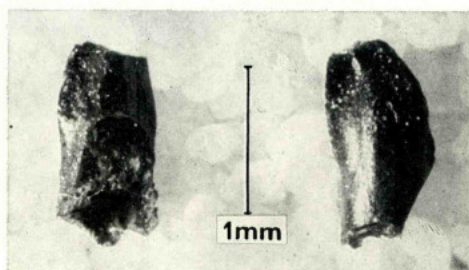
Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 1

Fig. 2
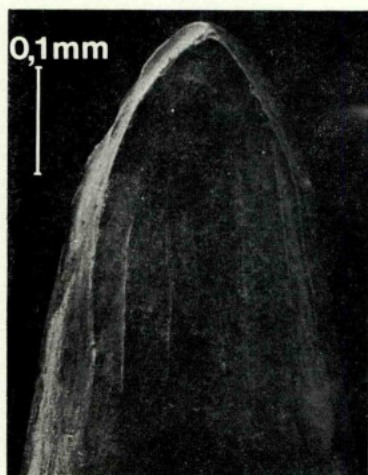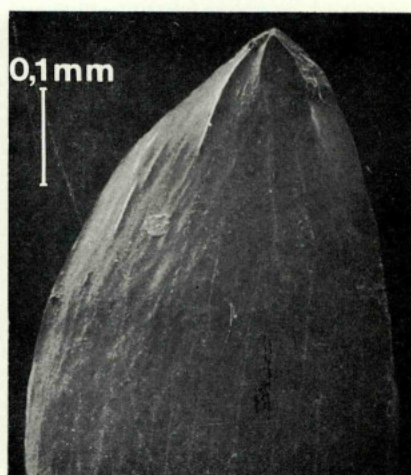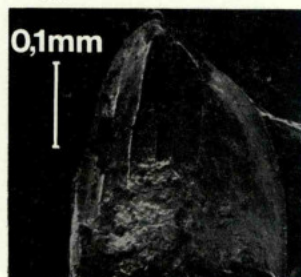

Fig. 3

Fig. 4

Fig. 5
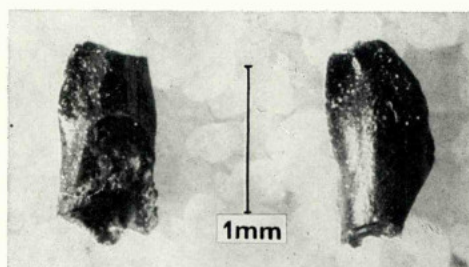

Fig. 6

Fig. 1 — Gui. L. 34, right maxilla of *Becklesisaurus hoffstetteri*, labial view, with osteodermal relief.
Fig. 2 — Gui. L. 31, right maxilla of *Becklesisaurus hoffstetteri*, labial view, smooth surface with foramina maxillo-facialia.
Fig. 3 — Gui. A. 56, *Becklesisaurus hoffstetteri*, left dentary (holotype), lingual view.
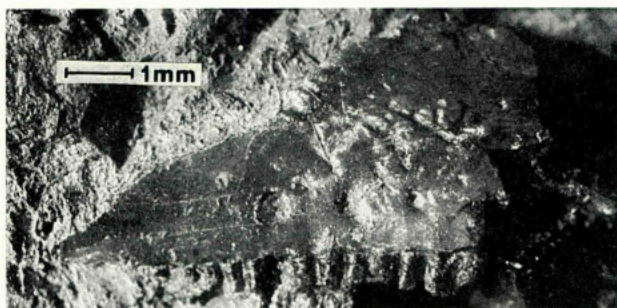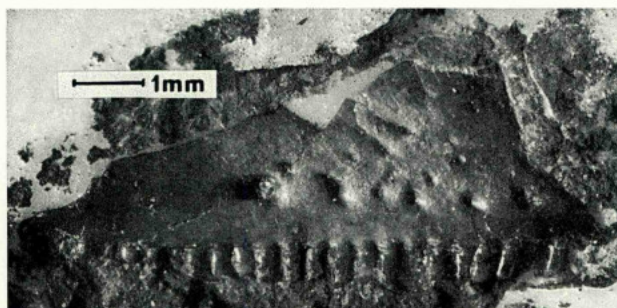
Fig. 1

Fig. 2

Fig. 3

Fig. 1

Fig. 2

Fig. 3

Fig. 1

Fig. 2

Fig. 3

Fig. 4

TEETH OF ORNITHISCHIAN DINOSAURS FROM THE UPPER JURASSIC OF PORTUGAL

WITH DESCRIPTION OF A HYPSILOPHODONTID (*PHYLLODON HENKELI* GEN. ET SP. NOV.) FROM THE GUIMAROTA LIGNITE

by

RICHARD A. THULBORN (*)

INTRODUCTION

The only comprehensive study of the dinosaurs of Portugal is that by LAPPARENT and ZBYSZEWSKI (1957). These authors recognized four Portuguese representatives of the order Ornithischia («ordre des Avipelviens»), namely:

Omosaurus armatus OWEN 1875.
Omosaurus lennieri NOPCSA 1911.
Lusitanosaurus liasicus LAPPARENT & ZBYSZEWSKI 1957.
Iguanodon mantelli MEYER 1832.

Both species of *Omosaurus* come from the Upper Jurassic and they are usually regarded as relatives of the North American *Stegosaurus* on account of their spiny (and possibly plate-like) dermal armour. LUCAS (1902) pointed out that the name *Omosaurus* is preoccupied (having been applied by LEIDY in 1856 to a crocodilian) and suggested the replacement name *Dacentrurus*. The first two ornithischians listed above should therefore be referred to as *Dacentrurus armatus* (OWEN, 1875) and *D. lennieri* (NOPCSA, 1911).

Lusitanosaurus is a problematical form which is known from a single jaw fragment. This specimen cannot be referred with absolute certainty to any particular horizon; but LAPPARENT and ZBYSZEWSKI (1957)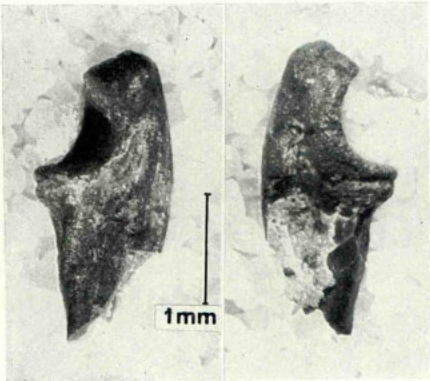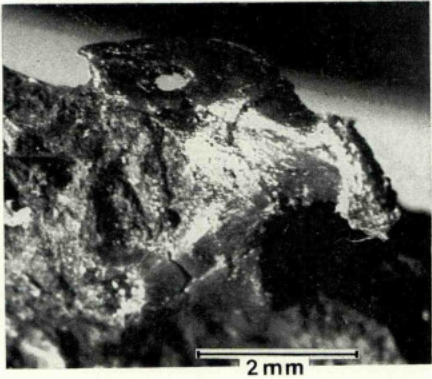 have inferred, from the evidence of matrix adhering to the holotype, that *Lusitanosaurus* is probably Lower Jurassic (? Sinemurian) in age. These authors regard *Lusitanosaurus* as an ally of *Scelidosaurus*, an armoured ornithischian from the English Lias (see OWEN, 1861a, 1862; NEWMAN, 1968). Unfortunately the systematic position of *Scelidosaurus* is far from clear; this dinosaur has often been allied with the stegosaurs (for example by SWINTON, 1934, and by ROMER, 1956) but it has recently been compared with the ankylosaurs (ROMER, 1968). It does not seem possible to determine the systematic position of *Lusitanosaurus* until the relationships of *Scelidosaurus* have been clarified.

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The Lower Cretaceous *Iguanodon mantelli* is the only ornithopod which has yet been reported from Portugal.

These four ornithischians are represented by a small number of relatively large specimens. The apparent rarity of ornithischian material may be attributed to two factors:

1) Prevalent collecting conditions. The main sources of dinosaur material are coastal exposures — where large and conspicuous fossil bones, which are resistant to wave action, persist on the beaches whilst many smaller fossils are destroyed. KÜHNE (1968) concludes that «...the whole of the Lusitanian ([1]) is rife with fossil bones but they can be observed and collected only under optimal conditions...».

2) The persistence of traditional collecting techniques. Searching by eye and breaking up promising rock has tended, once again, to yield small numbers of large specimens.

This paper deals with ornithopod teeth from the Upper Jurassic rocks of Portugal. These teeth have come from three localities: Porto Pinheiro, Guimarota and Pedrógão (see the maps provided by KÜHNE, 1968, and by SEIFFERT, 1970). Each locality is at a different stratigraphic level. The Pedrógão horizon is probably of Callovian age whilst the Guimarota fossils have been dated as early Kimmeridgian. The Porto Pinheiro specimens seem to be a little younger than those from Guimarota and are probably late Kimmeridgian in age. These various dates are based on the evidence of microfossils.

The numerous specimens forming the basis for this study (218 teeth) are the product of an intensive search which employed several specialized techniques. Material from all three localities was collected and concentrated by the «Henkel method» (see HENKEL, 1966). Details of this screening process have also been described by KÜHNE (1968). The Guimarota and Porto Pinheiro materials were further concentrated by the use of heavy liquids (a technique explained by KERMACK, LEES & MUSSETT, 1965). The material from Pedrógão was also concentrated by means of the photoelectric separation technique described by KÜHNE (1971). Material from all three localities was sorted by hand-picking under a binocular microscope.

Though the material which is described below is very fragmentary it amplifies knowledge of European ornithischians to a considerable degree. The material represents four genera and permits critical reappraisal of the history of the ornithischians in the family Hypsilophodontidae. The ornithischian teeth from Pedrógão, Guimarota and Porto Pinheiro are considered in turn.

THE PEDRÓGÃO ORNITHISCHIAN

Alocodon kuehnei gen. et sp. nov.

LOCALITY

Map reference: Carta Militar de Portugal, Sheet 272 (Vieira de Leiria), 0° 11' E., 39° 55' N. The locality is a small pit south of the coastal village of Pedrógão. Here the beds dip to the south-west and form a natural sea wall which shields the exposure. The fossiliferous rocks are soft grey and brownish-grey marls.

([1]) The term Lusitanian was coined by CHOFFAT (1885) to cover the late Oxfordian and early Kimmeridgian rocks of central Portugal. In later work (KOBY & CHOFFAT, 1904-5) it was admitted that this name had little more than local significance and I have followed ARKELL (1956) in dispensing with the term Lusitanian.

FLORAL AND FAUNAL LIST

PLANTAE

    Chareae:
        Porochara sp. (oogonia)
        Praechara sp. (oogonia)

PROTOZOA

    Foraminifera:
        Frondicularia sp.
        Lenticulina sp.
        Nodosaria sp.

MOLLUSCA

    Gastropoda:
        3 genera (very common)
    Lamellibranchia:
        Trigonia sp. (single valve)
        ?*Unio* sp.

ARTHROPODA

    Ostracoda:
        Bisulcocypris spp.
        Cytherella sp.
        Darwinula sp.
        ?*Klieana* sp.
        Lophocythere composita
        Lophocythere cf. *flexicosta*
        Monoceratina trepti
    Monoceratina aff. *ungulina*
        Schuleridea sp.
        Theriosynoecum wyomingense var. *pedrogaoense*

PISCES

    Selachii:
        Asteracanthus sp.
        A small hybodontid
    Holostei:
        Caturus sp.
        Lepidotes sp.
        Proscinetes (Microdon) sp.

AMPHIBIA

    Urodela

REPTILIA

    Chelonia.
        Shell fragments
    Squamata:
        A kuehneosaurid
        Another lizard (jaw fragment)
    Crocodilia:
        Goniopholis sp.
        Another genus
    Saurischia:
        Theropod teeth
    Ornithischia:
        Alocodon kuehnei gen. et sp. nov.
    Pterosauria:
        Rhamphorhynchus sp. (teeth)

The ostracods include cosmopolitan marine types and direct comparisons with ostracod faunas elsewhere in Europe indicate an Upper Callovian age for the Pedrógão horizon.

THE ORNITHISCHIAN TEETH

The Pedrógão locality has yielded 158 ornithischian teeth. Eleven of these were collected during preliminary investigations in 1960; the others were collected in 1970. The teeth are black or dark brown in colour and most are rolled and somewhat damaged. Every example lacks the root. In a few instances the root seems to have been lost
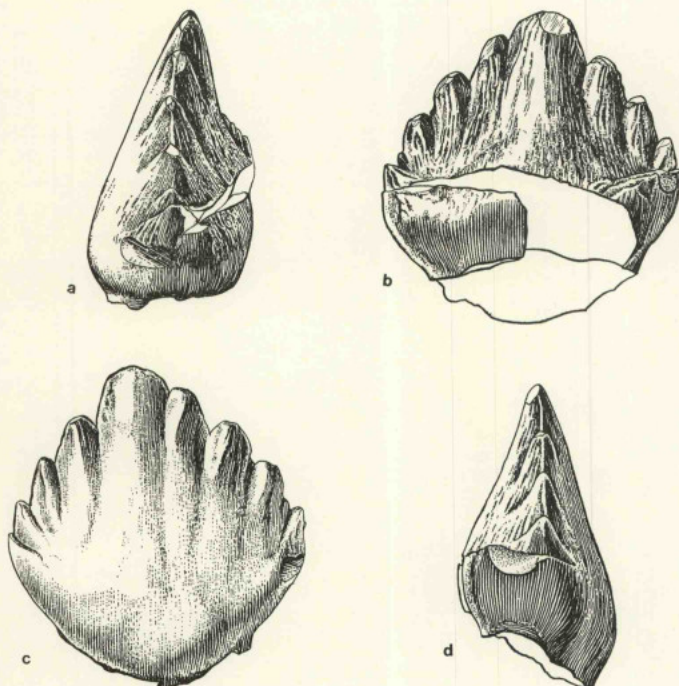
Fig. 1 — *Alocodon kuehnei* gen. et sp. nov. Holotype. Crown of a cheek tooth in mesial (a), lingual (b), buccal (c) and distal (d) views. × 14.

through breakage, but in most cases the base of the crown is excavated into a crater which is marked with fine pits. This pitting may be interpreted as evidence of root resorption and it implies that most of the Pedrógão specimens are shed crowns. At least 20 % of the crowns bear distinct wear facets and many others have blunted margins. These worn surfaces indicate that the teeth were once functional and that they are not just replacement crowns freed by post-mortem decay.

The teeth vary considerably in size and in proportions (see fig. 13). Despite this diversity there are good reasons (discussed below) to assume that the teeth represent a single species of ornithischian dinosaur.
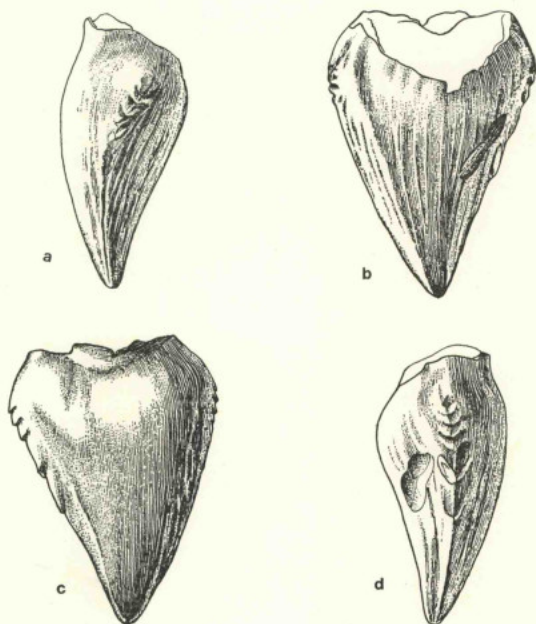
Fig. 2 — *Alocodon kuehnei* gen. et sp. nov. Designated paratype. Crown of a tooth from the middle part of the right premaxilla in mesial (a), lingual (b), buccal (c) and distal (d) views. × 14.

SYSTEMATICS

Class REPTILIA

Order ORNITHISCHIA

Suborder ORNITHOPODA

Family HYPSILOPHODONTIDAE

Genus *Alocodon* gen. nov.

Species *A. kuehnei* sp. nov.

Etymology: Greek ἀρότρου (a furrow) and ὀδούς (tooth), in allusion to the ornament of ribs and furrows on the lingual sides of the teeth. The specific epithet is to honour Professor W. G. KÜHNE, whose endeavours secured the material described in this paper.

Type material: The holotype is a single cheek tooth crown (numbered P × 2). A single premaxillary tooth crown (numbered P × 1) is designated paratype.

Referred material: The hypodigm of *Alocodon kuehnei* comprises the holotype and the designated paratype together with 156 teeth or parts of teeth. All these specimens are preserved in the collection of the Lehrstuhl für Paläontologie at the Free University, Berlin.

Horizon and locality: All specimens were collected from marls of Upper Callovian age near the village of Pedrógão, west coast of Portugal.

Diagnosis (for genus and monotypic species): Ornithischian dinosaur with heterodont dentition. Tooth crowns fully and uniformly enamelled, with smooth and inflated buccal surfaces; lingual surfaces ornamented with fine vertical ribs. Anterior premaxillary crowns tall, acutely conical, recurved, often with shoulder-like swelling of distal margin near cervix. Posterior premaxillary crowns similar, but with small denticles on distal margin (sometimes on mesial margin in addition). Cheek crowns triangular in profile, about as high as long, with occlusal tip formed by a single large denticle; lingual ribbing often irregular; mesial and distal edges with large bluntly rounded denticles; lingual surface with short cingulum near distal margin, sometimes with cingulum near mesial margin in addition. Posterior cheek crowns depressed, much longer than high, but still with large marginal denticles; cingula weak or absent. All cingula irregular, often elaborated into small denticles.

DESCRIPTION (¹)

The premaxillary crowns are readily identified by virtue of their conical form and are described first. The maxillary and mandibular crowns cannot be separated (except through their patterns of wear) and the remainder of the description refers to «cheek

Fig. 3 — *Alocodon kuehnei* gen. et sp. nov. Lingual (a) and buccal (b) views of a crown from the anterior part of the left premaxilla. Scale indicates 1 mm.

(¹) No standard descriptive nomenclature has yet been devised for reptilian teeth. The descriptions involve terms used in human odontology. The tooth surface directed outwards, towards the lips, is termed *buccal;* the surface facing inwards, towards the tongue, is *lingual.* That tooth surface facing the jaw symphysis is *mesial* whilst the opposite surface, directed towards the jaw articulation, is *distal.* The line of junction between root and crown is the *cervix.* The tip of the root is the *apex* of the tooth and structures or surfaces directed towards it are termed *adapical;* the other, masticatory, end of the tooth is defined as *occlusal.*

The following terms also require definition: crown *height* (a maximum adapical-occlusal measurement), crown *length* (a maximum mesio-distal measurement), crown *width* (a maximum bucco-lingual measurement). The *denticle count* expresses the number of marginal denticles on any crown in two figures. The first figure refers to denticles on the mesial margin, the second figure to those on the distal margin. *N. B.* The denticle count does *not* include the denticle which forms the occlusal tip of the crown.

teeth» in general. Every crown in the heterodont dentition of *Alocodon kuehnei* seems to have been fully and uniformly enamelled.

Crowns from the front of the premaxilla (figs. 3 and 4) are tall, acute and recurved cones which are gracefully arched to the exterior. Each crown is bucco-lingually compressed and is weakly constricted at the cervix. In buccal or lingual view the mesial margin forms an uninterrupted curve (convex forwards); the distal margin forms a corresponding curve but frequently swells, near the cervix, into a pronounced «shoulder». Both mesial and distal edges tend to a definite sharpness as they are traced away from the cervix. The lingual surface is appreciably flatter than the buccal
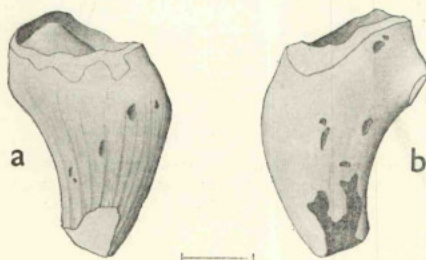

Fig. 4 — *Alocodon kuehnei* gen. et sp. nov. Buccal (a), distal (b) and lingual (c) views of a crown from the anterior part of the left premaxilla. Scale indicates 1 mm.

surface and bears a very characteristic ornament of vertical ridges. Near the cervix these ridges are numerous and ill-defined, but towards the occlusal tip of the crown they converge, decrease in number and become much sharper. The buccal surface, in contrast, is practically smooth. Every crown in the dentition of *Alocodon kuehnei* shows this striking difference between the glabrous buccal face and the ridged lingual face. The Pedrógão material includes at least 21 anterior premaxillary crowns; these range in height from 1.4 mm to 5.0 mm (estimated).

Another premaxillary crown (fig. 5c) bears a small flattened denticle on the lingual face of its inflated distal «shoulder». A second example carries at least five such denticles (fig. 5a), though these are little more than local swellings of the vertical ridges on the lingual surface. These clusters of denticles are present in most of the premaxillary crowns and may be regarded as rudimentary versions of the partial cingula which occur in the cheek teeth (see below). The crown shown in fig. 5a is also of interest in that it has a few marginal denticles; these are located on the distal edge, close to the cervix. The rest of the distal edge, like the entire mesial edge, is devoid of denticles. At least 4 such partly denticulate crowns are present in the material; they range in height from 2.0 mm (estimated) to 4.0 mm and have denticle counts of 0 : 1, 0 : 2, 0 : 3 and 0 : 5. These partly denticulate crowns probably come from the central part of the premaxilla (i. e. they are transitional between the non-denticulate anterior teeth and the fully denticulate teeth behind).
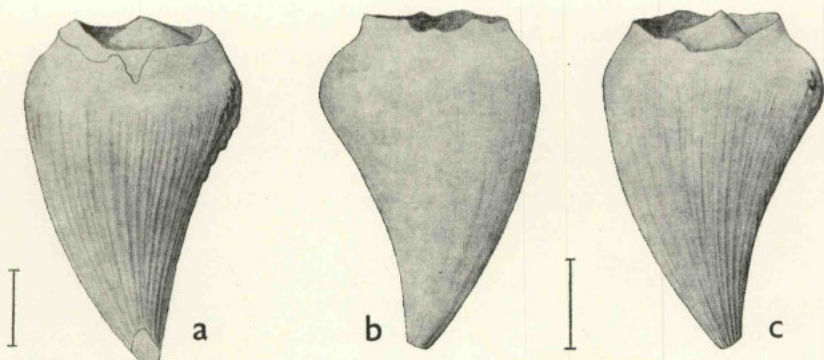
Fig. 5 — *Alocodon kuehnei* gen. et sp. nov. Lingual view of crown from the middle part of the right premaxilla (a). Buccal and lingual views (b, c) of a crown from the anterior or middle part of the right premaxilla. Both scales indicate 1 mm.

Crowns from the rear of the premaxilla are somewhat lower and longer than those described above — though they are still higher than long. They are further distinguished by having denticles on both mesial and distal edges (fig. 2). There are at least 10 such crowns in the material; their heights vary between 1.0 mm and 3.6 mm (estimated) and the best-preserved examples have denticle counts of 1 : 2, 1 : 3, 2 : 2, 3 : 2, 3 : 3 and 3 : 4.
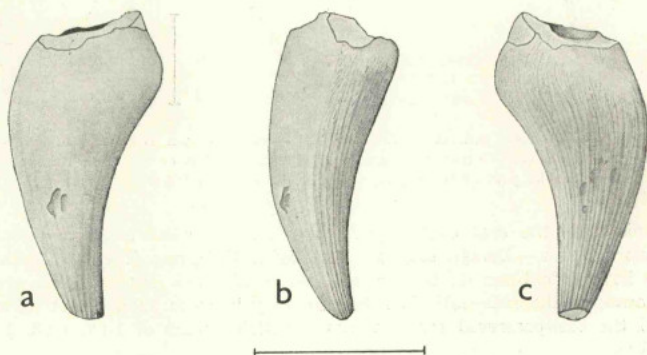

Fig. 6 — *Alocodon kuehnei* gen. et sp. nov. Lingual (a) and buccal (b) views of a crown from the anterior part of the left maxilla. Scale indicates 1 mm.

Crowns from the anterior and middle cheek regions (figs. 1, 6, 7, 8 and 9) are about as long as they are high. They appear in buccal or lingual view as broadly rounded and almost bilaterally symmetrical triangles. In each case the occlusal tip of the crown consists of a single large denticle and both mesial and distal edges are elaborated into several smaller, bluntly rounded and slightly irregular denticles. The marginal denticles are usually rather variable but in a few crowns they show a definite decrease in size towards the cervix (fig. 6). In every anterior and middle cheek crown of *Alocodon kuehnei* the most distal of the marginal denticles merges with a short cingulum on the lingual surface. And in the great majority of these crowns there is a similar, but

weaker, cingulum at the mesial margin (fig. 7). In one or two exceptional cases an almost unbroken cingulum extends across the lingual face of the crown (fig. 9). The cingula are somewhat irregular and are frequently developed into lines of small den-
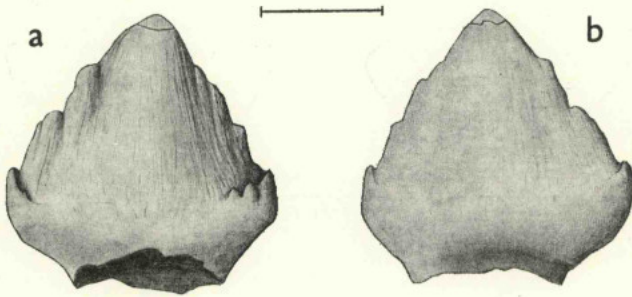
Fig. 7 — *Alocodon kuehnei* gen. et sp. nov. Lingual (a) and buccal (b) views of a crown from the anterior cheek region. Scale indicates 1 mm.

ticles. In a few of the larger crowns (such as the holotype) each cingulum is composite, being built of several small «steps» in the crown surface. Most cheek crowns have their lingual faces ornamented with ribs which are less regular and less persistent than those seen in the premaxillary crowns. The material includes at least 31 an-
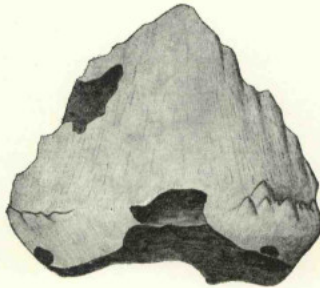
Fig. 8 — *Alocodon kuehnei* gen. et sp. nov. Lingual view of a crown from the middle cheek region. Note that the distal cingulum (at right) is better developed than the mesial one. Scale indicates 1 mm.

terior and middle cheek crowns; these range in height from 1.9 mm to 4.4 mm and have denticle counts such as 3 : 4, 4 : 4, 5 : 4, 5 : 5, 5 : 6, 6 : 5 and 6 : 6.

The hindmost cheek crowns are much longer than high and bear a superficial resemblance to the teeth of certain hybodontid sharks. Some examples retain cingula at both mesial and distal margins (fig. 10a); others, presumably from farther back
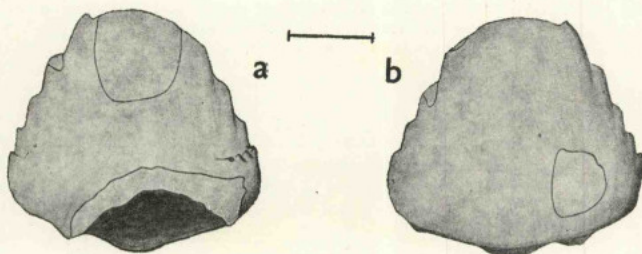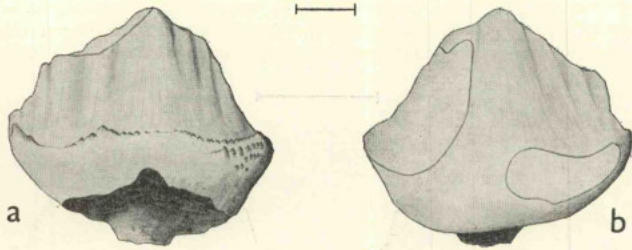
Fig. 9 — *Alocodon kuehnei* gen. et sp. nov. Lingual (a) and buccal (b) views of a crown from the middle part of the right dentary. Scale indicates 1 mm.
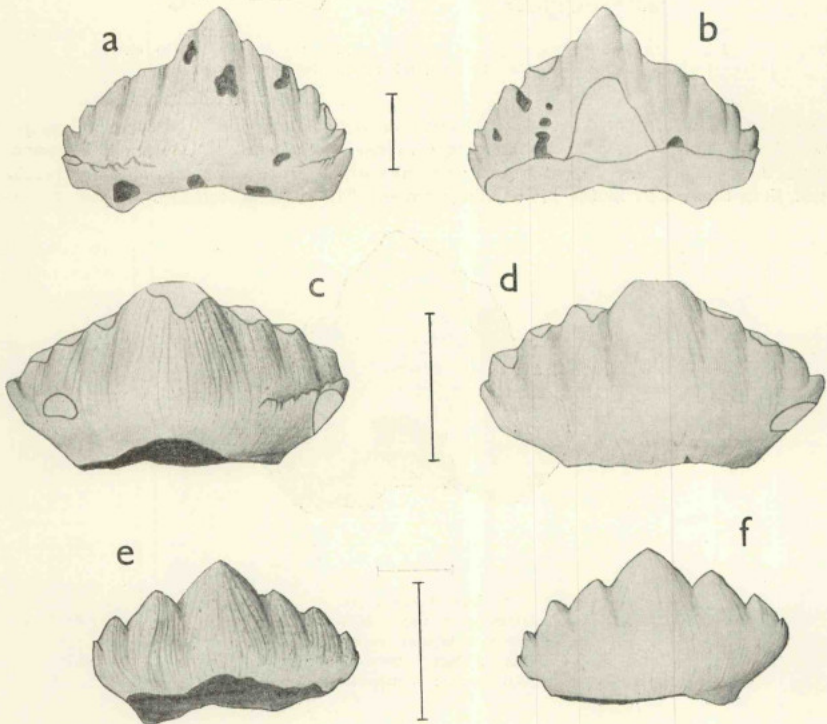
Fig. 10 — *Alocodon kuehnei* gen. et sp. nov. Lingual views (a, c, e) and buccal views (b, d, f) of three crowns from the posterior cheek region. Each scale indicates 1 mm.

in the jaws, bear only the distal cingulum (fig. 10c). Minute crowns from the posterior extremity of the tooth series have no cingula (fig. 10e). The posterior cheek crowns are represented by at least 15 good examples; these range in height from 0.8 mm to 3.0 mm (estimated) and have denticle counts such as 2 : 3, 3 : 3, 4 : 4, 5 : 4 and 5 : 5.

DISCUSSION

Systematic position

Alocodon kuehnei is clearly an ornithischian dinosaur. Its triangular and denticulate cheek teeth are typically ornithischian in appearance and are unlikely to be confused with the teeth of any other reptiles. The well-differentiated premaxillary dentition warrants assignment of *Alocodon kuehnei* to the family Hypsilophodontidae. Premaxillary teeth do occur in a few ornithischians apart from hypsilophodontids — in pachycephalosaurids, in protoceratopsians and in the iguanodontid *Thescelosaurus edmontonensis* (see STERNBERG, 1940, and GALTON, 1971) — but these dinosaurs are all, as far as I am aware, of Upper Cretaceous age. The heterodont dentition of *Alocodon kuehnei* finds convincing counterparts in a number of hypsilophodontids: in the late Triassic *Fabrosaurus australis,* in the Upper Jurassic *Echinodon becklesii;* and in the Lower Cretaceous *Hypsilophodon foxii.* General similarities between *Alocodon kuehnei* and *Fabrosaurus australis* are particularly noteworthy. One most striking resemblance concerns the transition from the premaxillary dentition to the maxillary dentition; in both animals this transition involves a change in tooth crown proportions (i. e. an increase in crown length relative to crown height) and the same gradual acquisition of marginal denticles (first on the distal edges of the crowns, then on their mesial edges). In other hypsilophodontids this changeover from premaxillary to maxillary teeth is achieved in different ways; it is often more abrupt and may even be emphasized by a short diastema (as it is in *Hypsilophodon foxii*).

It is important to note that the teeth of *Alocodon kuehnei* may be distinguished from those of any other hypsilophodontid through their finely ribbed lingual faces. The relationships of *Alocodon kuehnei* within the family Hypsilophodontidae are examined more closely in the general discussion (page 118).

Structural variation in the dentition

It has been assumed that the ornithischian teeth from Pedrógão represent a single species. There are several reasons for this assumption. First, there are general resemblances between all the tooth crowns; they are all black or dark brown in colour, they all appear to have been fully enamelled and they all (where the adapical surface is undamaged) show traces of root resorption. Second, and more important, unusual and diagnostic details of tooth structure are evident in nearly every crown; these details include the denticulate cingula and the lingual ornament of ribs. The lingual ribbing is better marked in some crowns than in others, but in no case is it entirely absent. Third, the teeth from Pedrógão seem to represent a single well-defined group when they are submitted to simple quantitative analysis. Measurements of maximum crown height and maximum crown length provide distributions approximating to normal (figs. 11 and 12), whilst a simple plot of crown height against crown length produces an acceptably coherent scatter (fig. 13). Finally it is not irrelevant to note that a selection of crowns from the hypodigm of *Alocodon kuehnei* can be fitted together to produce a realistic dentition (fig. 16).

It is not unreasonable to assume that crowns of various shapes and with various styles of marginal denticulation come from different sites within the jaws of *Alocodon*

kuehnei. To investigate this proposition (which is implicit in the description and the diagnosis of the species) I divided the crowns from Pedrógão into 5 groups on the basis of shape (i. e. crown height relative to crown length) and of the distribution of mar-
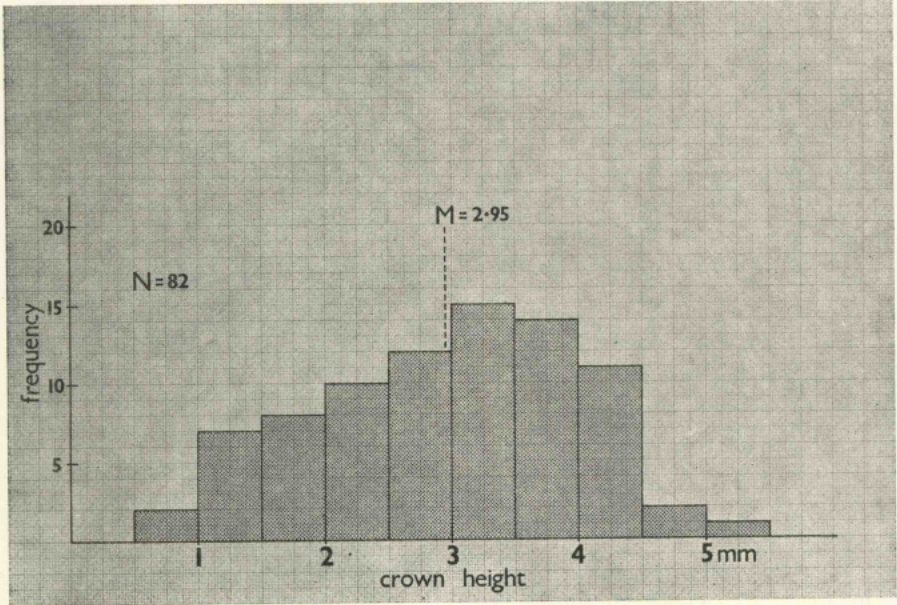
Fig. 11 — Frequency distribution of tooth crown heights in *Alocodon kuehnei* gen. et sp. nov.

ginal denticles. Each crown was assigned to one or other of the 5 groups by straightforward visual inspection. Of the 158 crowns in the hypodigm 77 were badly damaged and could not be assigned with certainty to any particular group; the remaining 81 crowns were grouped as follows:

GROUP 1 (anterior premaxillary crowns) tall conical crowns, without marginal denticles   ...   .   21 crowns

GROUP 2 (middle premaxillary crowns) tall conical crowns, with denticulate distal edge and simple mesial edge ...   .   4 crowns

GROUP 3 (posterior premaxillary crowns) conical crowns, taller than long, with denticles on both edges   ...   .   10 crowns

GROUP 4 (anterior and middle cheek crowns) triangular crowns, about as high as long, with large denticles on both edges ...   31 crowns

GROUP 5 (posterior cheek crowns) triangular crowns, distinctly longer than high, with large denticles on both edges   ...   ...   15 crowns

Total ...   .   81 crowns
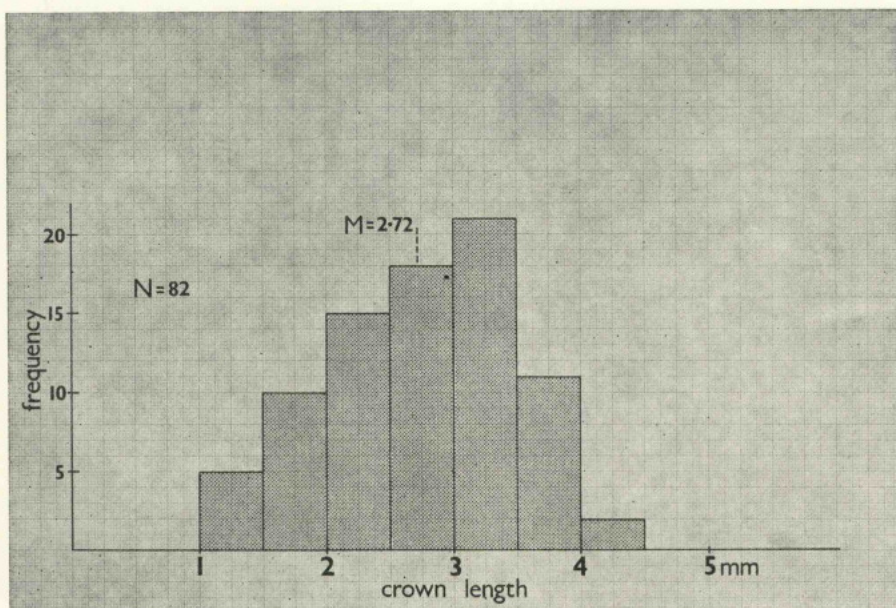
Fig. 12 — Frequency distribution of tooth crown lengths in *Alocodon kuehnei* gen. et sp. nov.

Groups 1 to 3 represent the premaxillary dentition; groups 4 and 5 represent the maxillary and mandibular dentitions.

Analysis of crown proportions and of marginal denticulation in each of these 5 groups yields the following figures:

		1	2	3	4	5
a)	arithmetic mean for maximum crown height (mm)	3.4	3.9	2.9	3.0	1.9
b)	arithmetic mean for maximum crown length (mm)	2.1	2.8	2.7	3.1	2.7
c)	arithmetic mean for maximum crown height expressed as a percentage of maximum crown length (%)	159	138	113	95	68
d)	arithmetic mean for number of denticles on mesial edge	0	0	3.5	4.1	3.9
e)	arithmetic mean for number of denticles on distal edge	0	2.0	3.6	4.0	3.7
f)	arithmetic mean for total number of denticles	0	2.0	7.3	8.0	7.5

The figures listed above are also expressed diagrammatically (figs. 14 and 15), together with indications of the observed range of variation in each group of crowns.

These simple analyses are, however, somewhat imperfect. Group 2, for example, consists of only four certainly assigned crowns (and one of these is damaged); inade-
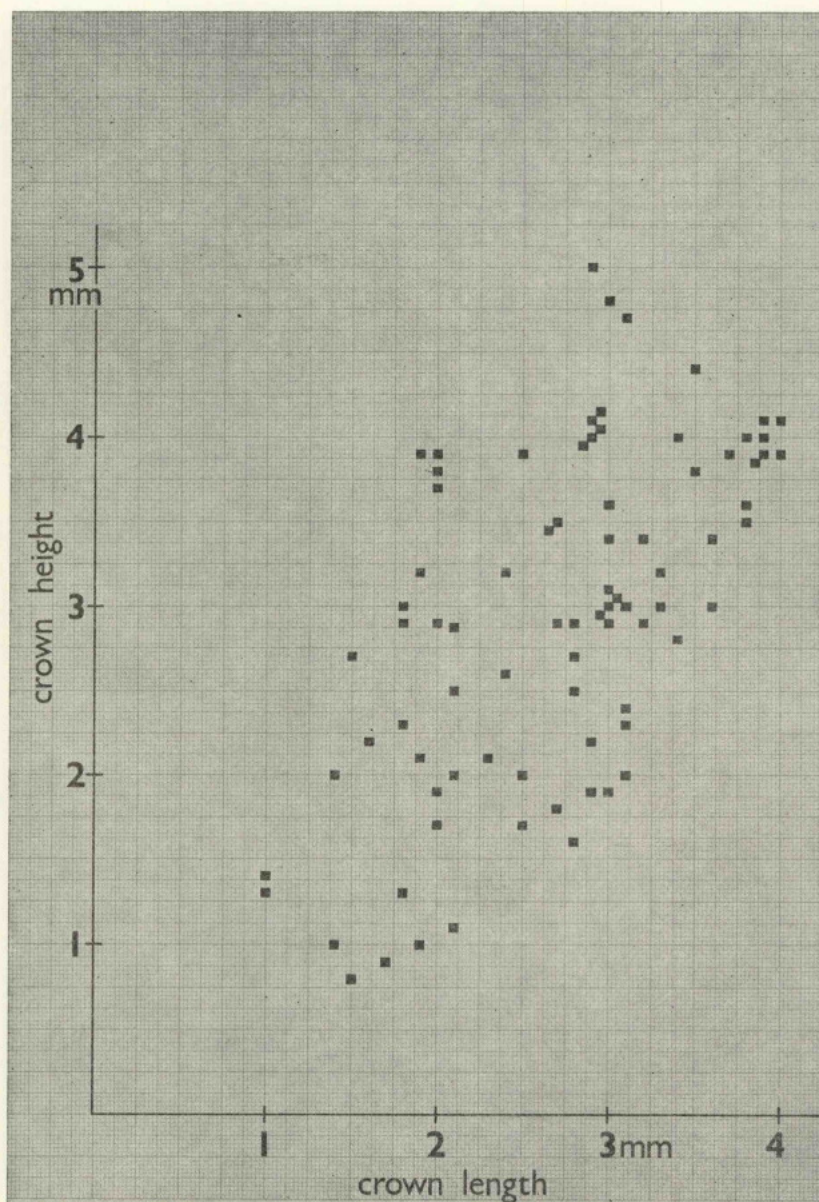
Fig. 13 — Relationship between tooth crown height and tooth crown length in *Alocodon kuehnei* gen. et sp. nov.
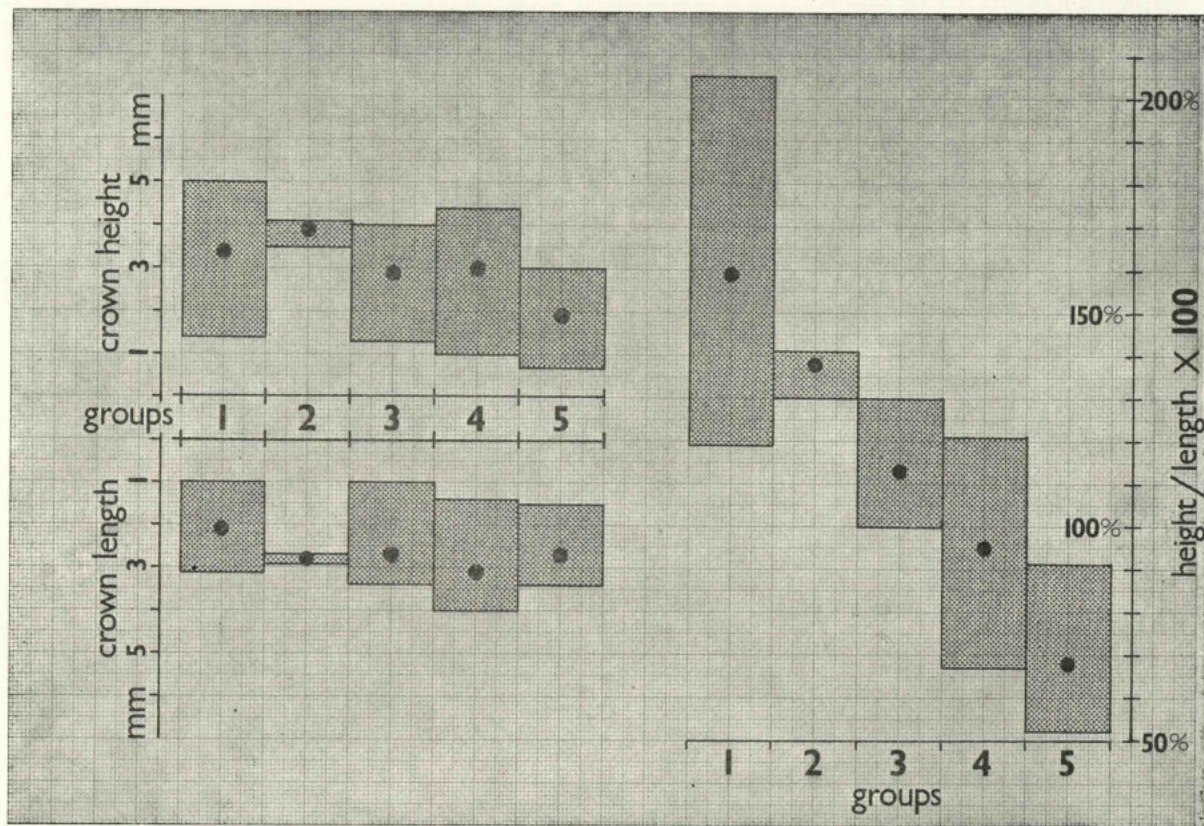
Fig. 14 — An analysis of tooth crown proportions in *Alocodon kuehnei* gen. et sp. nov. Column height indicates observed range of variation in each of the five groups of crowns; in each group the arithmetic mean is indicated by a dark spot.
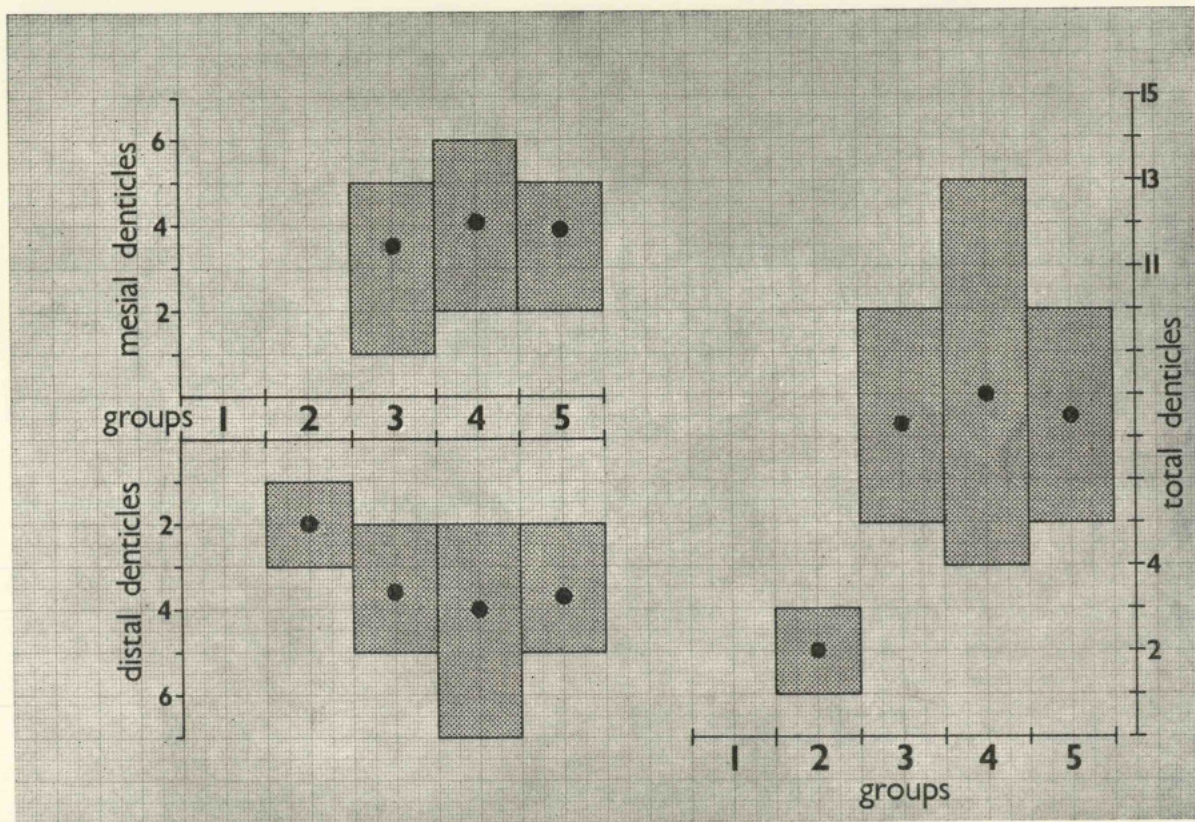
Fig. 15 — An analysis of tooth denticulation in *Alocodon kuehnei* gen. et sp. nov. Column height indicates observed range of variation in each of the five groups of crowns; in each group the arithmetic mean is indicated by a dark spot.

quate numerical representation may well be a factor influencing the rather large figures for crown height and crown length in this particular group. Group 4 is represented by 31 crowns but is clearly a heterogeneous assortment. In the first place it includes both upper and lower crowns (as does group 5). Aside from this group 4 probably comprises three types of tooth crown: (a) «typical» cheek crowns (from the central parts of maxilla and dentary), (b) anterior «transitional» crowns (grading into the premaxillary crowns), and (c) posterior «transitional» crowns (grading into the depressed crowns of group 5). It has not proved possible to separate these three types of tooth crown.

Despite such imperfections groups 1 to 5 do seem to form a definite series (at least as far as crown proportions and numbers of marginal denticles are concerned). Groups 1 to 5 represent, in effect, a backwards progression through the dentition of *Alocodon kuehnei*. In this backwards progression a number of changes in tooth structure is readily observed. Figure 14 indicates that there is a slight, but perceptible, decrease in crown height through groups 1 to 5. Crown length appears to remain fairly constant along the entire tooth row but may increase very slightly towards the rear. Figure 14 also demonstrates a correlation between crown shape and tooth site; anterior crowns are higher than long (and acutely conical) whereas posterior crowns are longer than high (and obtusely triangular in profile). Between these two extremes of crown shape (exemplified by groups 1 and 5 respectively) there appears to be an almost perfect gradation. Figure 15 shows that the number of marginal denticles per tooth tends to increase through groups 1 to 4 and then to decrease slightly in group 5.

Reconstruction of the dentition

The conclusions presented above permit reconstruction of the dentition, for they enable one to allocate crowns to particular sites in the jaws on the basis of crown shape and of marginal denticulation. The reconstruction (fig. 16) also utilises information from the dentitions of other hypsilophodontids.

PREMAXILLA   MAXILLA

PREDENTARY   DENTARY
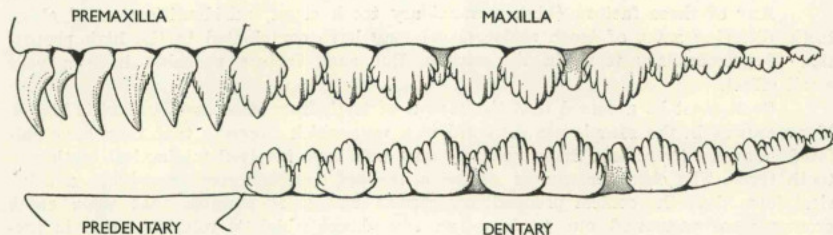
Fig. 16 — *Alocodon kuehnei* gen. et sp. nov. Left lateral view of the reconstructed dentition.

It has been assumed that the mandibular symphysis was formed by a toothless predentary bone and that teeth were implanted only in the premaxilla, maxilla and dentary. A similar arrangement obtains in other hypsilophodontids. The posterior extent of the predentary is, of course, unknown; in the reconstruction this bone is shown reaching back almost to the suture between maxilla and premaxilla (i. e. it is intermediate in extent between the predentaries of the Triassic *Fabrosaurus australis* and of the Wealden *Hypsilophodon foxii*).

The next step in reconstructing the dentition is to estimate the numbers of teeth in the various jaw bones. *Fabrosaurus australis* and *Hypsilophodon foxii* are the only hypsilophodontids in which the dental formula is known in great detail and these two forms constitute the entire basis for analogies. The *Fabrosaurus* dentition comprises 64 to 68 teeth, of which up to 12 (18 %-19 % of the total) are located in the premaxillae (THULBORN, 1970a). GALTON (in press) figures the *Hypsilophodon* dentition with 62 teeth, of which 10 (16 %) are sited in the premaxillae. One might reasonably expect any unbiased sample of 100 hypsilophodontid teeth to contain between 15 and 20 premaxillary teeth (the theoretical limits of occurrence — calculated as $Np - 3\sqrt{Npq}$ and $Np + 3\sqrt{Npq}$ — being 5 and 31) [1]. But in the selection of 81 crowns from the hypodigm of *Alocodon kuehnei* (see preceding discussion) 35 crowns have been assigned origins in the premaxillae — i. e. 43 % of the sample. If the sample is unbiased there are several factors which might account for this unexpectedly high proportion of premaxillary crowns. First, it is possible that *Alocodon kuehnei* did have a relatively large number of premaxillary teeth; it might conceivably have had more than 6 teeth in each premaxilla (the maximum recorded for a hypsilophodontid) but it is unlikely that these teeth were numerous enough to represent some 40 % of the dentition. Second, it is possible that some crowns which are supposed to have come from the rear of the premaxilla (group 3) actually came from the anterior part of the maxilla. But even if one assumes that *all* the crowns in group 3 came from the cheek regions the percentage of premaxillary teeth in the sample still remains inordinately high (31 %). Third, there is the possibility that premaxillary teeth did constitute 15 %-20 % of the dentition, but that these teeth were lost and replaced at a faster rate than the cheek teeth. This is not an unreasonable proposition when one considers the rather exposed position of the premaxillary teeth. EDMUND (1969) suggests that there is no continuity of the dental lamina across the maxilla/premaxilla suture in reptiles and there seems no reason why rates of tooth replacement should not differ in these two bones. But an unbiased sample with 43 % premaxillary crowns would require the premaxillary teeth to be replaced twice as fast as the cheek teeth (assuming the dentition of *Alocodon kuehnei* to be of fairly normal hypsilophodontid type); this seems highly improbable.

Any of these factors (high premaxillary tooth count, misidentification of cheek teeth, differing rates of tooth replacement) may have contributed to the high proportion of premaxillary teeth in the sample. But such factors probably have a very small effect.

So it must be assumed that the sample of teeth from *Alocodon kuehnei* is biased. Many crowns in the sample are damaged in a way which suggests that they have suffered transport by rolling. Such transport may well have involved mechanical sorting of tooth types. The cheek crowns of *Alocodon kuehnei* approach more nearly to a spherical form than the conical premaxillary crowns and it is possible that some cheek crowns were winnowed out to leave an assemblage which is relatively rich in premaxillary crowns.

The «bias of identifiability» which is mentioned by SIMPSON and ROE (1939) must also be taken into account. The sample under consideration comprises 81 crowns which were selected from the hypodigm (158 crowns), and bias has undoubtedly entered the process of selecting this sample. The premaxillary crowns are readily identified and classified; damage may have removed the occlusal tip of the crown but this does not obscure the conical crown shape or reduce the number of marginal denticles (which are small and are in a sheltered position near the cervix). Broken cheek crowns are

[1] The lower limit of occurrence is calculated on the lowest recorded occurrence (16 % in *Hypsilophodon*); the upper limit is calculated on the highest recorded occurrence (19 % in *Fabrosaurus*).

much less easily classified; damage usually accounts for loss of the large marginal denticles and makes it difficult to estimate the original crown shape. In short, broken premaxillary crowns are more easily identified than broken cheek crowns; damage does not affect the criteria by which premaxillary crowns were sorted into groups 1, 2 and 3 but it *does* affect the single criterion (i. e. crown shape) by which cheek crowns were assigned to group 4 or group 5. This factor of «identifiability» has certainly contributed to the seemingly large number of premaxillary crowns in the sample.

It is also worth noting that the hindmost cheek crowns resemble the teeth of hybodontid sharks such as *Acrodus* and *Hybodus*. This resemblance is so close that it has led to misidentifications; Professor KÜHNE and I have re-examined samples of fish teeth from Pedrógão and have discovered several cheek teeth of *Alocodon kuehnei*. Briefly, the posterior cheek crowns of *Alocodon kuehnei* may be distinguished from associated teeth of hybodontids by the following characters: (a) *lustre of enamel* (silky in *A. kuehnei*, shiny and glossy in hybodontids); (b) *ornament of ribs* (on one side only in *A. kuehnei*, but on both sides in hybodontids); (c) *cingula* (sometimes present in *A. kuehnei*, but never in hybodontids). The misidentification of posterior cheek crowns may also have contributed to the high proportion of premaxillary crowns in the sample.

Evidently the sample of teeth from *Alocodon kuehnei* is biased by a number of factors. Such a sample cannot safely be used to estimate the numbers of teeth in the various jaw bones and in reconstructing the dentition (fig. 16) I have necessarily had recourse to the dentitions of other hypsilophodontids. The premaxilla is shown with 6 teeth, the maxilla with 13 and the dentary with 14. The dental formula is closely comparable in the Upper Triassic *Fabrosaurus australis* and in the Wealden *Hypsilophodon foxii*. Numbers of maxillary and dentary teeth remain fairly constant throughout the family Hypsilophodontidae and the figures suggested for *Alocodon kuehnei* are probably quite accurate. But the number of premaxillary teeth is much more variable; the premaxilla of *Fabrosaurus australis* has up to 6 teeth whilst that of *Dysalotosaurus lettow--vorbecki*, from the Upper Jurassic of East Africa, is edentulous (JANENSCH, 1955). The premaxillary crowns of *Alocodon kuehnei* are of three distinct types (non-denticulate, with one edge denticulate and with both edges denticulate) and this variation in structure certainly implies that the premaxilla carried more than 3 or 4 teeth.

The diastema which separates the premaxillary and maxillary teeth in *Hypsilophodon foxii* (see GALTON, in press) would seem to be a specialization; neither *Fabrosaurus australis* nor the Purbeck *Echinodon beckesii* (see OWEN, 1861b, Plate VIII, fig. 1) has such a diastema and it has not been incorporated in the reconstruction of *Alocodon kuehnei*.

The cheek teeth were probably arranged in a simple row, rather than in complex batteries. The tooth rows have been reconstructed in irregular fashion, with large and small crowns mixed together; this irregularity is intended to convey some impression of waves of tooth replacement (zahnreihen) traversing the tooth rows.

Wear and replacement of the teeth

About one-fifth of the crowns in the hypodigm of *Alocodon kuehnei* bear distinct wear facets. Some wear facets may be attributed to interdental pressure; such facets occur on the mesial or distal margin and well away from the occlusal tip of the crown (figs. 1, 3 and 10). This wear indicates that the teeth were very tightly packed into the jaw bones. In some examples facets produced by interdental pressure extend on to the lingual or buccal face of the crown (fig. 6) and imply that the teeth were arranged *en echelon* or in roughly overlapping fashion (see reconstruction, fig. 16). Overlapping of the teeth probably served three purposes: (a) to afford some pro-

tection to the periodontal membranes, (b) to prevent rotation of teeth in their sockets, and (c) to increase the number of functional teeth in the jaws.

Some crowns show larger facets produced by tooth-on-tooth wear. These facets occur on the lingual faces of the maxillary crowns (fig. 6) and on the buccal faces of the mandibular crowns (fig. 9) and they are decidedly uneven in appearance — some are more steeply inclined than others; some are almost flat whilst others are concave from top to bottom (fig. 9). This irregularity of the wear facets may be correlated with tight packing and overlapping of the teeth. Evidently there was no fixed pattern of occlusion in *Alocodon kuehnei;* occlusion between the irregular upper and lower tooth rows would have produced a «crushing» effect in some parts of the jaws (with low-angle wear facets) and a «shearing» effect elsewhere (with steep wear facets).

Every tooth which is available lacks the root; and every well preserved specimen shows definite traces of resorption at the base of the crown. These facts seem to indicate that each tooth broke at the cervix once it had reached the end of its functional life; the crown would have been shed and the root was presumably resorbed. Similar processes of tooth loss have been described in mammal-like reptiles (KERMACK, 1956) and in the hypsilophodontid *Fabrosaurus australis* (see THULBORN, 1971a). KERMACK has suggested (op. cit.) that root resorption may have reduced the loss of calcium salts and might have assisted in preventing infection of the alveoli.

THE GUIMAROTA ORNITHISCHIAN

Phyllodon henkeli gen. et sp. nov.

LOCALITY

Map reference: Carta Militar de Portugal, Sheet 297 (Leiria), 0° 20' E., 39° 44' N. The locality is a small coal pit south of the town of Leiria. The fossiliferous rocks are lignitic marls and the history of collecting at this site has been described in detail by KÜHNE (1968).

FLORAL AND FAUNAL LIST

PLANTAE

Chareae:
Porochara raskyae (oogonia)
Porochara westerbeckensis (oogonia)

PROTOZOA

Foraminifera:
3 genera

MOLLUSCA

Gastropoda:
8 genera
Lamellibranchia:
5 genera

ARTHROPODA

Ostracoda:
Bisulcocypris sp.
Cetacella inermis
Darwinula sp.
Leiria paucistriata

    Leiria striata
    Oertliana kimmeridgiensis
    Poisia clivosa
    Theriosynoecum hemigymnon
    Theriosynoecum wyomingense
    Timiriasevia mackerrowi
  Cirripedia:
    1 genus

ECHINODERMA

  Echinoidea:
    Spines

PISCES

  Selachii:
    Acrodus sp.
    Asteracanthus sp.
  Holostei:
    Lepidotes sp.
    3 other genera

AMPHIBIA

  Urodela
  Anura

REPTILIA

  Chelonia:
    Shell fragments
  Squamata:
    Becklesisaurus hoffstetteri
    Cteniogenys reedi
    Introrsisaurus pollicidens
    Lisboasaurus estesi
    Lisboasaurus mitracostatus
    Macellodus cf. *brodiei*
    Saurillus henkeli
    Saurillus cf. *obtusus*
    Saurillus proraformis
  Crocodilia:
    Machimosaurus hugii
    2 other genera
  Saurischia:
    ?Bothriospondylus sp.
    3 other genera
  Ornithischia:
    Phyllodon henkeli gen. et sp. nov.
  Pterosauria:
    Pterodactylus sp. (teeth)
    Rhamphorhynchus sp. (teeth)

MAMMALIA

  Docodonta:
    3 genera
  Paurodontidae and Dryolestidae:
    6 genera
  Multituberculata:
    3 genera

The characean oogonia indicate an early Kimmeridgian age for the Guimarota horizon. KÜHNE (1968) points out that this age is supported by the evidence of the ostracod assemblage and gives a list of works dealing with the Guimarota locality and its fauna. Important works include those by KREBS on *Machimosaurus* (1967, 1968) and on the mammals (1969, 1971), and that by SEIFFERT (1970) on the lizards.

THE ORNITHISCHIAN TEETH

The Guimarota locality has yielded 56 ornithischian teeth. Only two of the teeth, which are black or dark brown in colour, retain roots; in every other case the base of the crown shows traces of root resorption. The teeth are generally well preserved, but many are cleanly broken; only a few are rounded in a way that might suggest prolonged transport or rolling. The teeth vary considerably in size and in shape but there are, as in the case of *Alocodon kuehnei*, good reasons to suppose that they represent a single species of ornithischian dinosaur.

SYSTEMATICS

Class REPTILIA

Order ORNITHISCHIA

Suborder ORNITHOPODA

Family HYPSILOPHODONTIDAE

Genus *Phyllodon* gen. nov.

Species *P. henkeli* sp. nov.

Etymology: Greek φύλλον (a leaf) and ὀδούς (tooth), in allusion to the leaf--shaped cheek teeth. The specific epithet is to honour Dr. SIEGFRIED HENKEL, who developed the collecting technique employed at Guimarota.

Type material: The holotype is a single cheek tooth crown (numbered G 5). A single premaxillary tooth crown (numbered G 2) is designated paratype.

Referred material: The hypodigm of *Phyllodon henkeli* comprises the holotype and the designated paratype together with 54 teeth or parts of teeth. All these specimens are preserved in the collection of the Lehrstuhl für Paläontologie at the Free University, Berlin.

Horizon and locality: All specimens were collected from lignitic marls of early Kimmeridgian age at the Guimarota mine, near Leiria, central Portugal.

Diagnosis (for genus and monotypic species): Ornithischian dinosaur with heterodont dentition. Tooth crowns fully and uniformly enamelled, bucco-lingually compressed, higher than long, deflected lingually. Buccal faces of crowns smooth and convex, occasionally with shallow divergent furrows; lingual faces similar, but slightly flatter. Anterior premaxillary crowns broadly triangular, weakly recurved, without definite marginal denticles. Posterior premaxillary crowns similar in shape, but with small denticles on mesial margin (sometimes on distal margin in addition). Cheek crowns lozenge--shaped, higher than long, with bluntly rounded denticles which are deflected to the rear; marginal denticles grow larger away from the cervix, then decrease in size near occlusal tip of crown; occlusal tip formed by several small denticles. Definite cingula absent, but cheek crowns may carry a few small denticles at postero-internal margin.
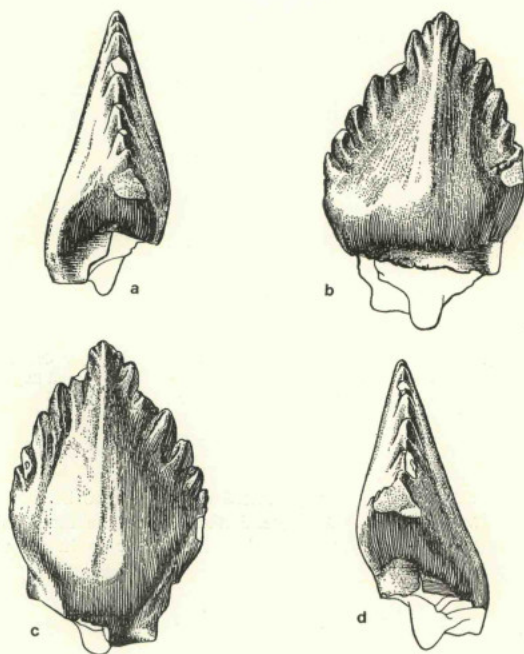
Fig. 17 — *Phyllodon henkeli* gen. et sp. nov. Holotype. Crown of an anterior cheek tooth in mesial (a), lingual (b), buccal (c) and distal (d) views. × 14.

DESCRIPTION

The premaxillary crowns are readily identified by their triangular shape and, in some cases, by their small marginal denticles; the premaxillary crowns are described first and the remainder of the description refers to «cheek teeth» in general. Every crown in the dentition of *Phyllodon henkeli* seems to have been fully and uniformly enamelled.

The anterior premaxillary crowns are triangular in profile, bucco-lingually compressed and distinctly taller than long (see fig. 18). Each crown is constricted at the cervix but lacks any trace of the prominent distal «shoulder» which is seen in the premaxillary crowns of *Alocodon kuehnei*. The distal margin is fairly thin and sharp and tends to a definite straightness. The convex mesial edge is somewhat thicker and may be elaborated into a series of feeble swellings (though none is distinct enough to be termed a denticle). Both buccal and lingual faces of the crown are smooth and rather featureless; the lingual face is slightly flattened (as it is in every crown of *Phyllodon henkeli*) and bears an extremely shallow groove at each margin. The material from Guimarota includes at least 4 such anterior premaxillary crowns; these range in height from 1.7 mm to 4.0 mm.
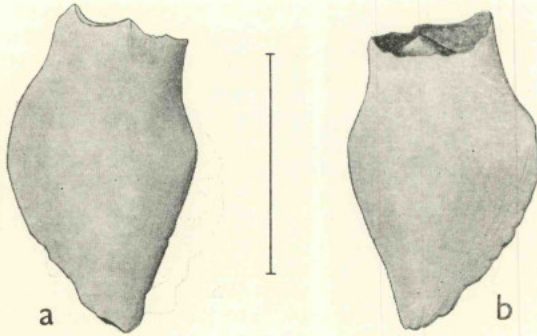
Fig. 18 — *Phyllodon henkeli* gen. et sp. nov. Designated paratype. Crown of a tooth from the anterior part of the left premaxilla in buccal (a) and lingual (b) views. Scale indicates 1 mm.

Crowns from the middle part of the premaxilla have several small denticles on their mesial edges (fig. 19b). Both buccal and lingual faces are marked with faint vertical furrows; the furrows are widely spaced and appear to be more strongly developed on the lingual faces of the crowns (particularly near the margins). It should be noted that this furrowing is always very weak and that it is in no way comparable
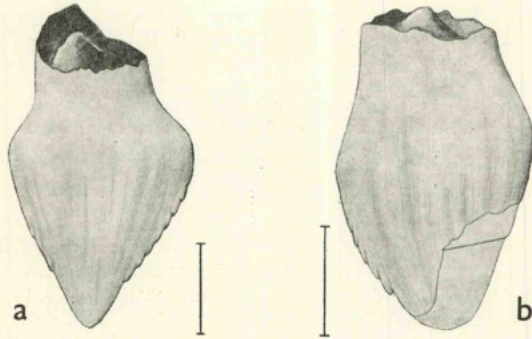
Fig. 19 — *Phyllodon henkeli* gen. et sp. nov. Lingual view of a crown from the posterior part of the left premaxilla (a). Lingual view of a crown from the middle part of the right premaxilla (b). Each scale indicates 1 mm.

with the ornament seen on the premaxillary crowns of *Alocodon kuehnei*. There are at least 5 such partly denticulate crowns in the material; they range in height from 2.0 mm (estimated) to 5.0 mm and have denticle counts such as 3 : 0, 4 : 0 and 5 : 0.

The hindmost premaxillary crowns merge imperceptibly with the anterior cheek crowns and it is difficult to draw any firm line of distinction between the two types. Nevertheless a few crowns can be assigned, with a fair degree of certainty, to either the premaxilla or the cheek regions — mainly on the basis of their marginal denticu-

lation. Any crown which shows marked disparity between the numbers of denticles on mesial and distal edges is almost certainly from the rear of the premaxilla (fig. 19a). Crowns which are generally similar in shape but which have approximately equal numbers of denticles on mesial and distal edges are probably from the anterior cheek region (fig. 17).

Every cheek crown appears to be higher than long, there being no trace of the depressed posterior crowns which were encountered in *Alocodon kuehnei*. It seems that such depressed crowns were not present in the dentition of *Phyllodon henkeli* (though their absence might be attributed to the smallness of the sample which is available). Each cheek crown of *Phyllodon henkeli* is roughly lozenge-shaped in profile and is deflected to the rear. The edges of the cheek crowns are developed into large, blunt and slightly divergent denticles. On each edge the largest denticles are found near the middle, those towards the occlusal tip of the crown and towards the cervix being distinctly smaller. The denticles are confluent with feeble ridges on the lingual and buccal faces of the crown (those on the lingual side being a little more pronounced). In each case the occlusal tip of the crown is formed by a cluster of small denticles. None of the crowns has any step-like cingulum, but some carry a few small denticles on the lingual face, close to the hindmost marginal denticle (fig. 17).

The root is preserved in two specimens. The better preserved example (fig. 20a-b) shows that the root is considerably taller than the crown and that it is almost perfectly straight. The root is bucco-lingually compressed and is barely constricted at the cervix.
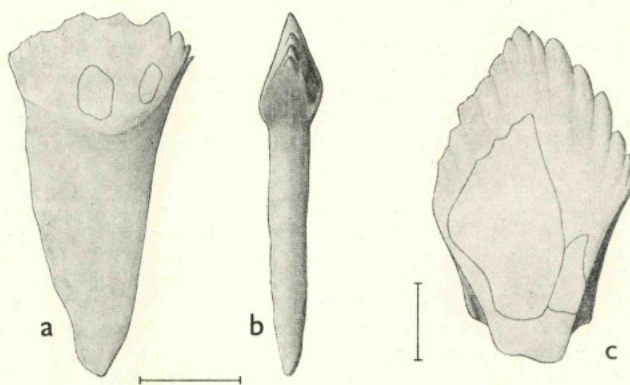
Fig. 20 — *Phyllodon henkeli* gen. et sp. nov. Buccal (a) and mesial or distal (b) views of a cheek tooth. Buccal view of a worn cheek crown (c). Each scale indicates 1 mm.

DISCUSSION

Systematic position

The denticulate and leaf-shaped cheek of *Phyllodon henkeli* are typically ornithischian in appearance. The dentition resembles that of *Alocodon kuehnei* in its basic construction and there seems little doubt that *Phyllodon henkeli* is another hypsilophodontid. Assignment of the species to the family Hypsilophodontidae is warranted, once again, by the well-differentiated premaxillary dentition.

Tooth crowns of *Phyllodon henkeli* may be distinguished without difficulty from those of *Alocodon kuehnei* — principally through their weaker ribbing and their lack of cingula. The premaxillary crowns are further distinguished by lacking any distal «shoulder» and by the straightness of the distal margin. The cheek crowns differ in shape (being higher than long), in the structure of the occlusal tip (a cluster of small denticles as opposed to a single large denticle), and in the radiating arrangement of the marginal denticles.

There seems to be no particularly close relationship between *Phyllodon henkeli* and *Alocodon kuehnei*. Indeed, certain features of the dentition set *Phyllodon henkeli* apart from all other hypsilophodontids. Perhaps the most distinctive of these features is the junction between the non-denticulate premaxillary teeth and the fully denticulate cheek teeth: in *Phyllodon henkeli* marginal denticles appear first on the mesial edges of the premaxillary crowns, and then on their distal edges. This sequence of denticle development cannot be matched in any other hypsilophodontid; in *Alocodon kuehnei* (and in *Fabrosaurus australis*) the marginal denticles are developed in reverse order. The relationships of *Phyllodon henkeli* within the family Hypsilophodontidae are examined more closely in the general discussion (see p. 125).

Structural variation in the dentition

The assumption that the ornithischian teeth from Guimarota represent a single species is sustained by a noticeable uniformity in structure. The teeth are all black or dark brown in colour; their crowns are fully and uniformly enamelled and the great majority of the teeth show traces of root resorption at the base of the crown. Every crown is higher than long and all but the premaxillary crowns are marked with feeble ribs arranged in a divergent pattern. None of the crowns has any definite cingulum.

Measurements of maximum crown height and of maximum crown length provide distributions approximating to normal (figs. 21, 22) and may be plotted to produce a closely coherent scatter (fig. 23). In addition a selection of crowns from the hypodigm may be used, as in the case of *Alocodon kuehnei,* to produce a realistic reconstruction of the dentition (fig. 24).

The teeth of *Phyllodon henkeli* show much less variation in structure than those of *Alocodon kuehnei*. Consequently it is difficult to assign individual teeth to particular sites in the jaws. The middle and anterior premaxillary crowns are readily distinguished by the lack of denticles on one or both edges (respectively), but it has proved impossible to draw any firm line of distinction between the hindmost premaxillary crowns and the cheek crowns. Nor is it possible to divide the check crowns into anterior and posterior types. In other words variation along the tooth row in *Phyllodon henkeli* cannot be investigated or described as thoroughly as it was in the case of *Alocodon kuehnei*. Nevertheless a general account is possible.

Crown height exceeds crown length along the entire tooth row in *Phyllodon henkeli*. There is no trace of the decrease in crown height, relative to crown length, which is observed in a backwards progression through the dentition of *Alocodon kuehnei*. If this backwards change in crown proportions does occur in *Phyllodon henkeli* it is certainly very insignificant and it has remained undetected. The surface ornament of the tooth crowns increases in strength towards the rear of the dentition. The anterior premaxillary crowns are practically smooth whilst the middle and posterior premaxillary crowns are marked with faint ribs and furrows. In the cheek crowns this ornament is even more pronounced, the ribs being confluent with the marginal denticles. None of the crowns has any true step-like cingulum, but some have a few small denticles on the lingual surface, close to the hindmost marginal denticle. Crowns which possess these
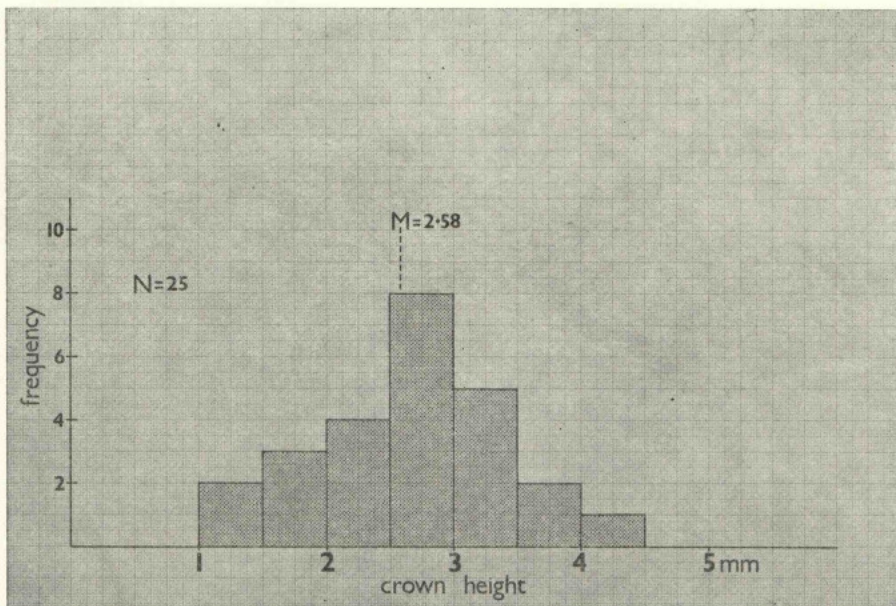
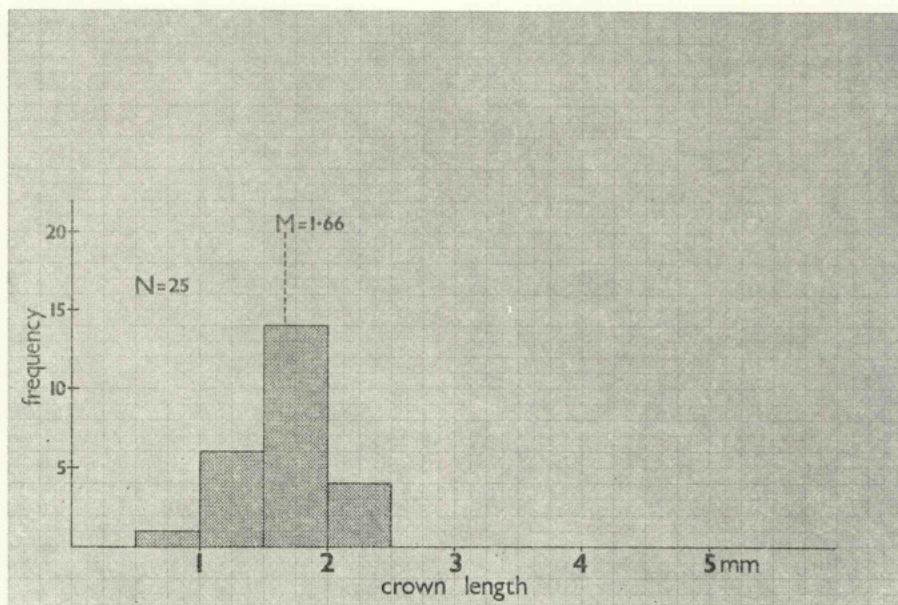Fig 21 — Frequency distribution of tooth crown heights in *Phyllodon henkeli* gen. et sp. nov.

Fig. 22 — Frequency distribution of tooth crown lengths in *Phyllodon henkeli* gen. et sp. nov.
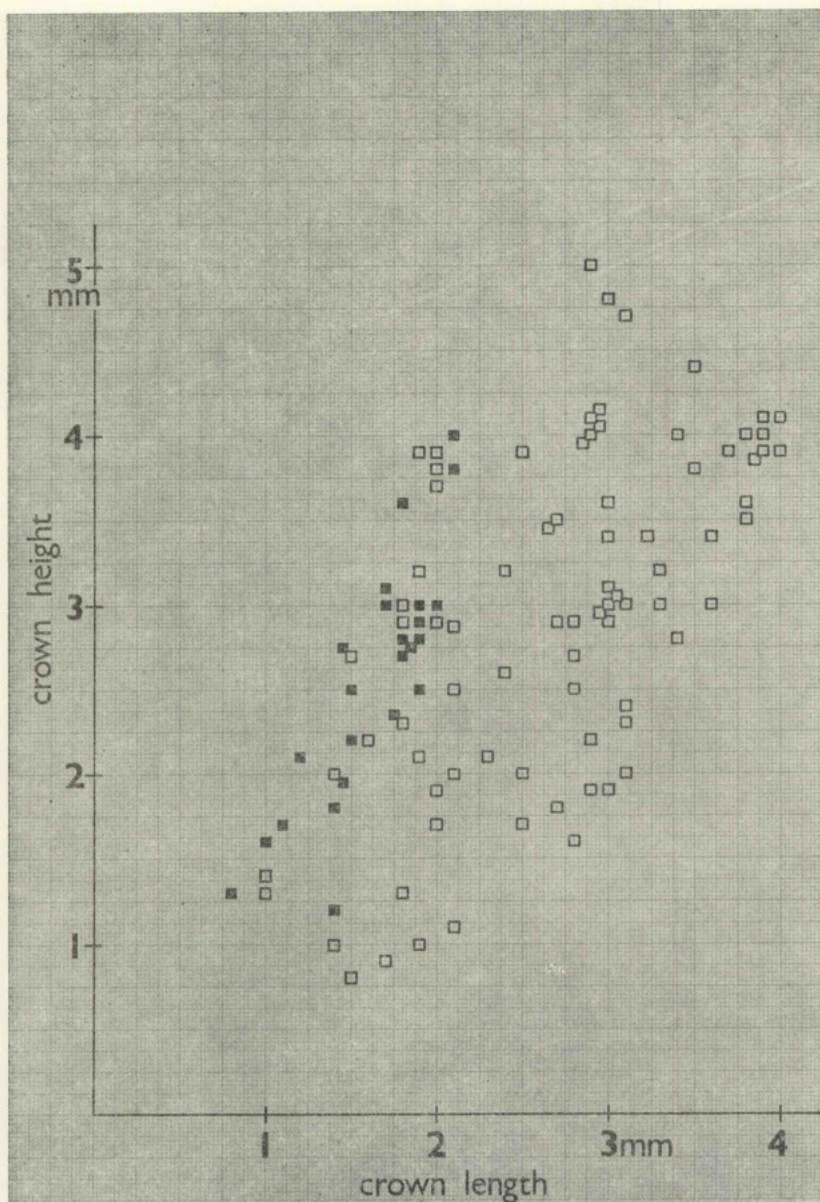
Fig. 23 — Relationship between tooth crown height and tooth crown length in *Phyllodon henkeli* (solid squares) compared with the same relationship in *Alocodon kuehnei* (open squares).

lingual denticles might tentatively be assigned to the anterior and middle cheek regions. Finally there is an increase in the number of marginal denticles per tooth from front to back in the jaws. But it cannot be determined if the number of denticles per tooth decreases slightly at the hindmost extremity of the tooth row (as it does in *Alocodon kuehnei*).

Reconstruction of the dentition

The dentition of *Phyllodon henkeli* has been reconstructed (fig. 24) using analogies with other hypsilophodontids. It must be emphasized that this reconstructed dentition is rather more conjectural than that given for *Alocodon kuehnei*. The speculative nature of the reconstruction stems from two factors: first, the limited amount of evidence which is available and, second, the lack of any marked structural variation in the teeth (making it difficult to relate particular tooth types with specific sites in the jaws.
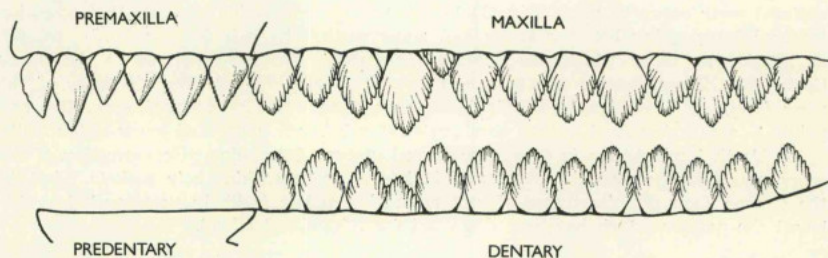
Fig. 24 — *Phyllodon henkeli* gen. et sp. nov. Left lateral view of the reconstructed dentition.

The teeth of *Phyllodon henkeli* are generally well preserved and appear to have suffered relatively little transport. In consequence it may be presumed that there was only slight preferential sorting of tooth types during transport and that the percentage of premaxillary teeth in the sample is a fair reflection of the proportion of such teeth in the entire dentition. Fifty-six tooth crowns have been examined. Three of these are merely fragments and cannot be assigned either to the premaxilla or to the cheek regions. Of the remaining 53 crowns 10 (i. e. 19 %) are almost certainly from the premaxillae. In the Triassic *Fabrosaurus australis* 18 %-19 % of the entire dentition consists of premaxillary teeth and in the Wealden *Hypsilophodon foxii* the figure is 16 %. The former has up to 6 teeth in the premaxilla (the maximum recorded in a hypsilophodontid) whilst the latter has 5; the dentition of *Phyllodon henkeli* has been reconstructed with 6 teeth in the premaxilla. The premaxillary teeth are shown opposing a toothless predentary bone (designed to be intermediate in extent between the predentaries of *Fabrosaurus australis* and *Hypsilophodon foxii*). The maxilla is shown with 13 teeth and the dentary with 14; these figures are probably quite accurate since the numbers of teeth in maxilla and dentary remain fairly constant throughout the hypsilophodontids.

Eleven crowns bear distinct wear facets. Only a few cheek crowns carry the small facets which may be attributed to interdental pressure (fig. 17). Such facets occur at the mesial or distal margin, well away from the occlusal tip of the crown, and their rarity implies that the teeth were not very tightly packed into the jaw bones. The facets produced by interdental pressure are very restricted in extent; in no case can they be traced on to the buccal or lingual surface of the crown. This indicates that the cheek teeth were disposed in a simple line, rather than in an overlapping series.

Broad, steeply inclined and almost flat wear surfaces, which are the product of occlusion, are much more common. Facets of this type are present on the lingual face of one premaxillary crown (fig. 19b) and are clearly the result of the tooth working against the horn-sheathed predentary. This particular tooth is of interest in that it shows two distinct wear facts — one superimposed upon, and cutting into, an older one. This double wear may reflect spasmodic tooth eruption or it may point to damage, and subsequent regrowth, of the predentary. In some cheek crowns the facets produced by occlusal wear occur in pairs (fig. 20c) — an arrangement which suggests that occlusion involved interlocking between upper and lower teeth. The paired wear facets are not as regular as those which are observed in *Fabrosaurus australis* and in the Upper Cretaceous *Thescelosaurus edmontonensis* (see THULBORN, 1971a). The steepness of the wear facets in *Phyllodon henkeli* indicates that there was a pronounced «overbite» and points to a shearing (rather than crushing) action between upper and lower cheek teeth.

Tooth implantation is of normal thecodont type. Bucco-lingual compression of the roots would have prevented rotation of individual teeth within their sockets. Most of the crowns show definite traces of root resorption and it is likely that tooth loss followed the pattern which has been described for *Alocodon kuehnei*.

THE PORTO PINHEIRO ORNITHISCHIANS

Trimucrodon cuneatus gen. et sp. nov.

Hypsilophodon sp.

LOCALITY

Map reference: Carta Militar de Portugal, Sheet 349 (Lourinhã), 0° 13′ W., 39° 13′ N.

FLORAL AND FAUNAL LIST

PLANTAE
> Chareae:
>> *Porochara* sp. (oogonia)

ARTHROPODA
> Ostracoda:
>> *Bisulcocypris* cf. *pahasapensis*
>> *Bisulcocypris* sp.
>> *Cetacella armata*
>> *Cetacella inermis*
>> *Cypridea* sp.

REPTILIA
> Ornithischia:
>> *Hypsilophodon* sp.
>> *Trimucrodon cuneatus* gen. et sp. nov.

THE ORNITHISCHIAN TEETH

The Porto Pinheiro locality has yielded 4 ornithischian teeth. These teeth represent two distinct taxa.

Trimucrodon cuneatus gen. et sp. nov.

This ornithischian is represented by three small tooth crowns — the largest being barely 2 mm high. Two of the crowns show traces of root resorption on the adapical surface; the third is much rolled but retains part of the root. Each crown appears to have been fully and uniformly enamelled and is light yellow-brown in colour.

SYSTEMATICS

Class REPTILIA

Order ORNITHISCHIA

Suborder ORNITHOPODA

Family HYPSILOPHODONTIDAE

Genus *Trimucrodon* gen. nov.

Species *T. cuneatus* sp. nov.

Etymology: From the Latin *tri* (threefold) and *mucro* (point) in allusion to the three prominent denticles on each tooth crown. The specific epithet refers to the triangular shape of the tooth crowns.

Type material: The holotype is a single tooth crown (see fig. 25).

Referred material: The hypodigm of *Trimucrodon cuneatus* comprises the holotype together with two similar tooth crowns. All three specimens are preserved in the collection of the Lehrstuhl für Paläontologie at the Free University, Berlin.

Horizon and locality: All specimens were collected from the marls of late Kimmeridgian age at the headland of Porto Pinheiro, west coast of Portugal.

Diagnosis (for genus and monotypic species): Triangular and bucco-lingually compressed tooth crowns, about as long as high and slightly deflected to rear. Crowns fully and uniformly enamelled, with smooth faces; lingual face a little flatter than buccal face. Mesial and distal edges almost straight, intersecting at right angles, ornamented with short, blunt denticles which increase in size towards cervix. Foremost and hindmost of marginal denticles are strongly divergent, salient and sharply pointed.

DESCRIPTION

The description is based upon the holotype (fig. 25), the other crowns differing only in their poorer preservation and smaller size. All three crowns appear to have come from the cheek regions. The smallest, and least well preserved, example retains part of the root and indicates that tooth implantation was of normal thecodont type. In the other crowns the adapical surface is excavated into a crater and the root would seem to have been lost by resorption.

Each crown is broadly triangular in profile, about as high as long, and strongly compressed in a bucco-lingual direction. The lingual face is slightly flatter than the

buccal face; both faces are smooth and featureless, the sole ornament consisting of extremely fine vertical wrinkles in the enamel. Mesial and distal edges intersect at a right angle to form the obtuse occlusal tip of the crown. A slight arching of the mesial edge contrasts with the straightness of the distal edge and imparts a perceptible asymmetry to the crown. This asymmetry is emphasized by the backwards inclination of the occlusal tip. There are 6 denticles, which increase in size towards the cervix, on the distal edge. The most distal of these denticles is strongly divergent, salient and decidedly angular; it is confluent with a feeble ridge which extends for a short distance on to the lingual face of the crown. The other five denticles on the distal edge are shorter, blunter and much less conspicuous. The denticles on the mesial edge resemble those on the distal edge but are slightly better defined.
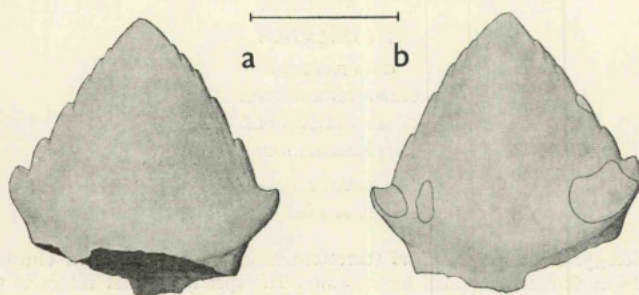
Fig. 25 — *Trimucrodon cuneatus* gen. et sp. nov. Holotype. Crown of a cheek tooth in lingual (a) and buccal (b) views. Scale indicates 1 mm.

There are three small wear facets on the buccal face of the holotype. These facets are rounded in otline and are situated at the level of the salient foremost and hindmost denticles. The largest facet lies near the distal margin and the other two are close to the mesial margin. These steeply inclined facets may be attributed to interdental pressure and they indicate that the teeth were tightly packed into the jaw bones.

DISCUSSION

Systematic position

Trimucrodon cuneatus is referred to the order Ornithischia on account of its leaf-shaped and denticulate tooth crowns. Amongst the ornithischian dinosaurs *Trimucrodon cuneatus* may be compared most closely with *Echinodon becklesii* — a hypsilophodontid from the Purbeck beds of Dorset, England [1].

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[1] *Echinodon becklesii* was originally described as a lizard (OWEN, 1861b) but comparisons with the Triassic ornithischian *Fabrosaurus australis* have shown that it is almost certainly a hypsilophodontid (see THULBORN, 1970a). OWEN's account gives the type locality for *E. becklesii* as a «...thin, fresh-water stratum at Durdleston Bay, Isle of Purbeck...». In this area the Purbeck beds attain a thickness of nearly 400 feet and the horizon which yielded *E. becklesii* cannot be identified with certainty. It is possible that the material was collected from the «Mammal Bed» at the base of the Middle Purbeck — this being a thin dirt bed which has yielded mammals and reptiles. But it seems more probable that *E. becklesii* was taken from somewhere within the Upper Building Stones,

The teeth of *Trimucrodon cuneatus* match the cheek teeth of *Echinodon becklesii* in nearly every respect. In both animals the tooth crowns are strongly compressed, triangular in profile, with an obtuse occlusal tip. In each case the crowns are fully and uniformly enamelled and they tend to a slight asymmetry (though this is not well shown in OWEN's figures (1861b) of *Echinodon becklesii)*. The surfaces of the crowns are smooth and featureless in both animals. The teeth of *Trimucrodon cuneatus* have a very characteristic pattern of marginal denticulation and this is closely approached in *Echinodon becklesii;* in each case the mesial and distal edges of the crowns are practically straight and are ornamented with denticles which decrease in size away from the cervix. The hindmost and foremost of the denticles are enlarged, salient and sharply pointed in both instances.

Detailed resemblances in tooth structure suggest that *Trimucrodon cuneatus* is a fairly close relative of *Echinodon becklesii*. It is on account of these similarities that *Trimucrodon cuneatus* has been referred to the family Hypsilophodontidae. The teeth of the two animals may be distinguished by a few differences in the style of the marginal denticulation. In *Echinodon becklesii* the denticles are very numerous and extend right to the occlusal tip of the crown; in *Trimucrodon cuneatus* there are fewer marginal denticles and these stop well short of the occlusal tip. The enlarged foremost and hindmost denticles are more strongly divergent in *Trimucrodon cuneatus*.

Hypsilophodon sp.

The second ornithischian from Porto Pinheiro is represented by a single specimen (fig. 26). This consists of a heavily worn tooth crown with part of the root still attached and it has a total height of 3 mm. Much of the crown has been removed by wear on the buccal side and it is difficult to estimate the original shape of the crown. The mesial margin of the crown runs straight into the root without interruption, but at the distal margin the crown swells into a rounded «shoulder» just above the cervix. The root is slightly arched to the exterior and the crown retains a few patches of light yellow-brown enamel. The lingual face of the crown is rather flat and bears a feeble vertical rib near the mid-line. This rib is flanked by even weaker vertical ribs (three towards the distal margin and one towards the mesial). Planar wear surfaces extend right across the buccal face of the crown and clearly indicate that this is a lower tooth. The buccal surface carries two distinct wear facets; a broad and steeply inclined facet occupies that part of the crown adjacent to the cervix whilst a slightly steeper facet is present towards the occlusal margin. The two facets intersect in a straight line which runs down and forwards from the distal margin. This double wear may point to spasmodic eruption of the tooth; alternatively it may reflect intermittent eruption, or replacement, of the opposing maxillary tooth.

Dr. P. M. GALTON has made a thorough study (in press) of the Wealden *Hypsilophodon foxii* and assures me that the worn mandibular teeth of this animal are very similar indeed to the specimen from Porto Pinheiro. In each case the flattened lingual face of the tooth crown is ornamented with vertical ribs and the root is slightly arched to the exterior. Tooth wear is planar in both cases. The crown from Porto Pinheiro appears to have been fully enamelled, but it is not clear if the enamel was thicker

which overlie the «Cinder Bed». It would seem most reasonable to follow APPLEBY *et al* (1967) in referring *E. becklesii* to the Middle Purbeck; greater stratigraphic precision is not possible.

The illustrations provided by OWEN (1861b, Plate VIII, figs. 1 to 9) are somewhat unreliable. Through the courtesy of Dr. A. J. CHARIG I have examined the material of *E. becklesii* in the British Museum (Natural History) and have found the following of OWEN's illustrations to be the least inaccurate: figs. 1, 1a, 2, 2a, 3, 3a, 3b and 4.

on one side of the tooth than on the other (as it is in *Hypsilophodon foxii*). The characteristic straightness of the mesial margin and the distinctive distal «shoulder» of the crown can also be matched in the lower cheek teeth of *Hypsilophodon foxii*. In view of these pronounced similarities (in tooth shape, in tooth ornament and in tooth wear) the specimen from Porto Pinheiro has been referred to the genus *Hypsilophodon*. It would seem, from the limited evidence which is available, that the Porto Pinheiro *Hypsilophodon* is a fairly direct antecedent of *Hypsilophodon foxii* itself.
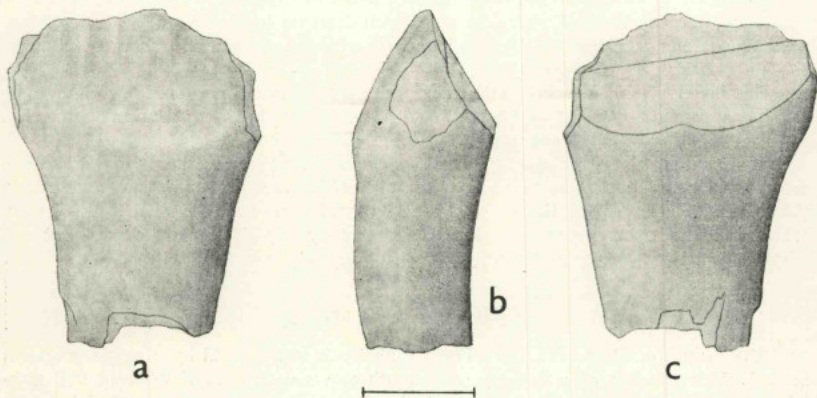
Fig. 26 — *Hypsilophodon* sp. from the late Kimmeridgian of Porto Pinheiro. Worn tooth from the left dentary in lingual (a), mesial (b) and buccal (c) views. Scale indicates 1 mm.

DISCUSSION

The following is a complete list of the ornithischian dinosaurs which are at present known from Portugal:

Alocodon kuehnei gen. et sp. nov.;
    hypsilophodontid; Upper Jurassic.

Hypsilophodon sp.;
    hypsilophodontid; Upper Jurassic.

Phyllodon henkeli gen. et sp. nov.;
    hypsilophodontid; Upper Jurassic.

Trimucrodon cuneatus gen. et sp. nov.;
    hypsilophodontid; Upper Jurassic.

Iguanodon mantelli MEYER 1832;
    iguanodontid; Lower Cretaceous.

Dacentrurus armatus (OWEN, 1875) *(Omosaurus)*;
    stegosaur; Upper Jurassic.

Dacentrurus lennieri (NOPCSA, 1911) *(Omosaurus)*;
    stegosaur; Upper Jurassic.

Lusitanosaurus liasicus LAPPARENT & ZBYSZEWSKI 1957;
    ?stegosaur; Lower Jurassic.

The ornithischians from the Kimmeridgian of Porto Pinheiro (i. e. *Hypsilophodon* sp. and *Trimucrodon cuneatus*) are assigned to the family Hypsilophodontidae because their cheek teeth approximate very closely to those of undoubted hypsilophodontids (*Hypsilophodon foxii* and *Echinodon becklesii* respectively). The teeth of *Alocodon kuehnei* and of *Phyllodon henkeli* do not find such convincing counterparts among known hypsilophodontids and these two forms are referred to the Hypsilophodontidae on account of their well-differentiated premaxillary teeth. It may be pointed out that premaxillary teeth do occur in a few ornithischians apart from hypsilophodontids — in pachycephalosaurids, in protoceratopsians and in the Cretaceous iguanodontid *Thescelosaurus edmontonensis*. But none of these ornithischians is very far advanced beyond the hypsilophodontid grade of organization and it seems safe to conclude that any ornithischian with premaxillary teeth is one of the «lower» ornithopods. On this basis it may be stated that *Alocodon kuehnei* and *Phyllodon henkeli* are certainly ornithopods; and while there is no incontrovertible proof that these forms are members of the Hypsilophodontidae they may be accommodated most conveniently, and most logically, within this particular family.

Hypsilophodontids constitute the persistent and rather conservative basal stock of the ornithischian dinosaurs (ROMER, 1945; THULBORN, 1970a; GALTON, 1971). This stock of hypsilophodontids ranges from the late Trias through the Cretaceous and is fundamental to the whole pattern of ornithischian history; it represents the ancestry, ultimately at least, of groups as diverse as the hadrosaurs, pachycephalosaurids and ceratopsians. It has been suggested that this succession of hypsilophodontids at the core of ornithischian phylogeny might best be envisaged as a plexus, or rope, in which each species represents a single strand (THULBORN, 1971b). This concept of a plexus, rather than a simple linear series, lacks the implication that any one hypsilophodontid might be directly related to another (an important qualification, since the fossil record of hypsilophodontids is decidedly sporadic).

The ornithischians described in this paper permit some elaboration upon this theme of a hypsilophodontid plexus at the heart of ornithischian history and, more important, they give some clues to relationships and to evolutionary trends within the Hypsilophodontidae. In this context the stratigraphic setting of of Portuguese hypsilophodontids is particularly favourable; they are conveniently intermediate in age between the hypsilophodontids of the Cretaceous and the ornithopods which have recently come to light in the Trias (see THULBORN, 1971b, for a review of these). A number of hypsilophodontids (*Dryosaurus* spp., *Laosaurus* spp., *Nanosaurus* spp.) are recorded from from the late Jurassic and early Cretaceous of North America (GILMORE, 1925; LULL, 1911; MARSH, 1877a, 1877b, 1878a, 1878b, 1894). Unfortunately these forms are still very poorly known and their systematics are in a most confused state; and until these ornithopods have been thoroughly revised they will be of little use in any study of relationships within the Hypsilophodontidae. In consequence it is necessary to consider the Portuguese hypsilophodontids apart from (and not in conjunction with) their North American contemporaries.

Before proceeding to investigate relationships within the Hypsilophodontidae it is desirable to establish criteria for assessing the closeness, or remoteness, of the relationship between any two hypsilophodontids. The degree of affinity between two hypsilophodontids might be reflected by pronounced resemblances, or pronounced differences, in the following characters:

    I)   the extent of the premaxillary dentition;
    II)   the transition between premaxillary and maxillary teeth;
    III)   the structure of the cheek teeth;

IV) the degree of change (if any) in crown shape from front to back in the cheek dentition;

V) the pattern of tooth wear;

VI) the presence or absence of cheeks.

These six characters are considered in turn.

I) *The extent of the premaxillary dentition*

The primitive condition, seen in the Upper Triassic *Fabrosaurus australis*, is that in which the premaxillary tooth row extends without interruption to the tip of the snout. More advanced conditions are seen in the Wealden *Hypsilophodon foxii* (where the premaxillary tooth row is preceded by a toothless space) and in the Upper Jurassic *Dysalotosaurus lettow-vorbecki* (where the premaxilla is edentulous). Such variations in the extent of the premaxillary dentition may reflect different feeding mechanisms and different types of jaw action. In *Fabrosaurus* the crowded premaxillary teeth probably bit against the horn-sheathed predentary to produce an efficient «cropping» action. This food-gathering technique is paralleled (but in inverted fashion) in the living artiodactyls, where the lower incisors bite against a horny pad in the upper jaw. In *Fabrosaurus* the anterior premaxillary teeth overhang the front of the predentary and would have prevented any protraction of the mandible; this arrangement, together with evidence from worn teeth, indicates that the jaw action in this primitive hypsilophodontid was essentially vertical (THULBORN, 1971a). In *Hypsilophodon* the abbreviated premaxillary dentition was probably preceded by a horny beak (opposing that at the mandibular symphysis) and in *Dysalotosaurus* this beak replaces the entire premaxillary tooth row. The acquisition of a premaxillary beak might have facilitated use of a prehensile tongue in food-gathering; it would also have permitted some forwards sliding of the mandible — to produce a grinding action between upper and lower cheek teeth.

It seems safe to conclude that any hypsilophodontid which retains a complete premaxillary dentition is a fairly direct descendant of the primitive Triassic hypsilophodontids (best exemplified by *Fabrosaurus australis*). On the other hand it is dangerous to infer that two hypsilophodontids are closely related because their premaxillary dentitions are reduced to the same extent. This is because the premaxillary dentition appears to have suffered reduction, or loss, at different times in several independent stocks of hypsilophodontids. The ornithopod family Iguanodontidae is an artificial assemblage which probably arose from the hypsilophodontids through iterative phases of evolution (THULBORN, 1971b). And since the iguanodontids (with the exception of *Thescelosaurus edmontonensis*) lack premaxillary teeth it is clear that each of their several lines of hypsilophodontid ancestry must have shown some independent trend towards loss of the premaxillary dentition.

II) *The transition between premaxillary and maxillary teeth*

In no hypsilophodontid is this transition in the upper dental series smooth and uninterrupted. There seems, without exception, to be some more or less obvious change in tooth structure across the premaxilla/maxilla suture. This changeover from non-denticulate premaxillary teeth to fully denticulate cheek teeth is accomplished in various ways. In *Fabrosaurus australis* this transition involves a change in crown shape (from conical to broadly triangular) combined with the gradual acquisition of marginal denticles — first on the distal edges of the crowns, and then on their mesial edges. The arrangement seen in *Fabrosaurus australis* seems to be the primitive one and it per-

sists in the Callovian *Alocodon kuehnei*. Other hypsilophodontids show different types of transition between premaxillary and maxillary teeth. In the Kimmeridgian *Phyllodon henkeli* there is a less marked change in crown shape and the marginal denticles make their appearance in reverse order (first on the mesial edges of crowns, and then on their distal edges). The Purbeck *Echinodon becklesii* shows a very abrupt changeover from acute and non-denticulate premaxillary crowns to obtuse and fully denticulate maxillary crowns (see Owen, 1861b, Plate VIII, fig. 1). In *Hypsilophodon foxii* the premaxillary and maxillary crowns differ only slightly in shape but they are separated by a wide diastema (Galton, 1970). There is no evidence to suggest that any one style of changeover between premaxillary and maxillary teeth has appeared in more than a single stock of hypsilophodontids. So it is not unreasonable to postulate a fairly close relationship between hypsilophodontids which show the same pattern of change in tooth structure at the premaxilla/maxilla suture.

III) *The structure of the cheek teeth*

The cheek teeth of hypsilophodontids have never been subjected to intensive study and a search of the literature might lead one to assume that there is a distressing uniformity of tooth structure within the Hypsilophodontidae. But this is not the case, for the cheek teeth of hypsilophodontids show a diversity in structure which seems to be unrivalled among the dinosaurs. A detailed comparison of cheek tooth structure is probably the surest method for assessing the closeness, or remoteness, of the relationship between two hypsilophodontids. This comparative approach is fundamental to the study of Mesozoic mammals and there is no reason why it should not be applied with equal vigour to the teeth of fossil reptiles.

In examining and comparing the teeth of hypsilophodontids there are numerous factors to be taken into account. The more important of these factors are indicated below.

Enamel. Most hypsilophodontids resemble the Triassic *Fabrosaurus australis* in having tooth crowns which are fully and evenly enamelled. But in *Hypsilophodon foxii* the enamel is exceptionally thick on the buccal faces of the maxillary teeth and on the lingual faces of the mandibular teeth; elsewhere on the tooth crowns of *Hypsilophodon foxii* the enamel coat becomes very thin and may disappear (Galton, in press).

Crown shape. The cheek crowns are often triangular in profile (e. g. *Fabrosaurus australis, Echinodon becklesii*). In other hypsilophodontids the crowns may be lozenge--shaped (e. g. *Phyllodon henkeli*) or ovate (e. g. *Laosaurus consors*). Crown height may exceed crown length or *vice versa*; and in several forms (such as *Alocodon kuehnei*) the crowns may be higher than long in some parts of the dentition and longer than high elsewhere.

Crown margins. The mesial and distal edges of the crown may be straight, convex or concave. The two edges may be similar (to give symmetrical crowns like those of *Echinodon becklesii*) or they may differ (as in the asymmetrical crowns of *Trimucrodon cuneatus*).

Surface ornament. The crown surfaces may be smooth or they may show an extremely fine wrinkling of the enamel (e. g. *Echinodon becklesii*). In many cases the crowns are ornamented with ribs; these may be irregular and discontinuous (e. g. *Alocodon kuehnei*), roughly parallel (e. g. *Hypsilophodon foxii*), or divergent (e. g. *Phyllodon henkeli*). The ribs often vary in their strength and distribution but in many hypsilophodontids there is a pronounced vertical rib near the mid-line of each tooth (e. g. *Dysalotosaurus lettow-vorbecki*). The style of ribbing may within a single dentition and it may even vary from lingual to buccal sides in a single tooth (as it does in *Alocodon kuehnei*).

Marginal denticles. These show considerable diversity in number, size and shape. The denticles may be divergent (e. g. *Phyllodon henkeli*) or parallel (e. g. *Echinodon becklesii*); they may remain constant in size along the crown margin (e. g. *Fabrosaurus australis*) or they may grown smaller towards the occlusal tip of the crown (e. g. *Trimucrodon cuneatus*). In some cases the denticles barely project beyond the crown margin but in others they are extended and salient (both types being found in a single cheek crown of *Echinodon becklesii).* The style of the denticulation may vary from tooth to tooth within the dentition (e. g. *Alocodon kuehnei*) or even from mesial to distal margins on a single crown.

Occlusal tip. The occlusal tip of the crown may be angular (e. g. *Trimucrodon cuneatus*), rounded (e. g. *Alocodon kuehnei*), or mucronate (e. g. *Dysalotosaurus lettow- -vorbecki*); it may consist of a single large denticle (e. g. *Alocodon kuehnei*) or of a cluster of small denticles (e. g. *Phyllodon henkeli*).

Cingula. Some hypsilophodontid teeth are without cingula (e. g. those of *Echinodon becklesii*), but others may have cingula developed as «steps» in the crown surface or as rows of denticles (e. g. those of *Alocodon kuehnei*). Each cingulum is usually quite short; but in extreme cases a cingulum may extend right across the lingual face of a crown or may be represented only a single denticle. Where a crown has one short cingulum this is normally situated at the postero-internal margin (an arrangement which is of considerable use in orientating isolated crowns). There are often two short cingula on the lingual surface of a crown; in such instances the cingula may be equally developed or (more commonly) that at the distal margin may be slightly stronger than its mesial counterpart. It should be noted that the size and appearance of cingula may vary from tooth to tooth in a single animal.

Any comparative study of hypsilophodontid cheek teeth should take into account all the characters mentioned above. It must be emphasized that several of these characters may show a considerable range of variation within a single dentition. And for this reason it is advisable to base comparisons upon complete dentitions (or, at least, upon reliable reconstructions or large numbers of isolated teeth).

While it is possible that the teeth of distantly related hypsilophodontids might show some fortuitous resemblance in one or two characters (perhaps crown shape and crown ornament) it seems extremely unlikely that convergence alone could account for more than a few similarities in tooth structure. In other words, a passing resemblance between the cheek teeth of two hypsilophodontids might indicate some affinity or it might, equally well, be coincidental; but numerous and detailed points of similarity are almost certainly indicative of close relationship.

The value of these comparisons in elucidating relationships within the Hypsilophodontidae is best illustrated by an example. The ornithischian teeth from the Callovian marls of Pedrógão were, upon their discovery, provisionally designated «cf. *Echinodon*» (KÜHNE, 1971). Yet the cheek teeth of this animal differ from those of *Echinodon becklesii* in very many respects (in shape, in ornament, in the structure of the occlusal tip, in the style of marginal denticulation and in having cingula). This wealth of differences in cheek tooth structure implies that there is no particularly close relationship between *Echinodon becklesii* and the Pedrógão ornithischian (i. e. *Alocodon kuehnei*). And by means of similar comparisons it may be deduced that *Alocodon kuehnei* is more nearly related to *Fabrosaurus australis* and that the closest Portuguese relative of *Echinodon becklesii* is *Trimucrodon cuneatus.*

IV) *Changes in crown shape from front to back in the cheek dentition*

Where complete dentitions (or reliable reconstructions) are available it is possible to compare changes in crown proportions along the tooth row. Briefly, there seem to be two distinct conditions among the hypsilophodontids. In the first of these the posterior cheek crowns are much longer (relative to their height) than the anterior cheek crowns. The second condition is that in which crown length remains fairly constant (relative to crown height) along the entire cheek tooth series.

The first of these conditions, where the cheek tooth row decreases in height posteriorly, is encountered in the Triassic *Fabrosaurus australis* (see THULBORN, 1970a, fig. 3) and may be regarded as a direct inheritance from the thecodontian ancestors of the Ornithischia. This primitive condition persists in *Echinodon becklesii* (see OWEN, 1861b, Plate VIII, figs. 3 and 5) and, probably, in *Alocodon kuehnei*. In these animals the jaw articulation is set nearly in line with the tooth row and the jaws would have closed with a scissors-like action. This shearing type of jaw action is patently ill-suited to herbivores such as the hypsilophodontids and the backwards decrease in crown height may be interpreted as an adaptation to remedy this situation. The backwards lowering of the tooth row would have ensured that upper and lower tooth rows met in parallel — in spite of the scissors-like jaw action. This modification of the tooth row, together with the retention of the primitive thecodontian-like jaw action, characterizes the more conservative members of the Hypsilophodontidae.

The second condition, where the cheek teeth are fairly constant in height, is seen in advanced hypsilophodontids such as *Hypsilophodon foxii* and *Dysalotosaurus lettow-vorbecki*. In these forms the jaw articulation is set well below the line of the tooth row in order to ensure parallel closure between upper and lower teeth — without the necessity for any backwards decrease in crown height. This modification, which affects the jaw joint rather than the dentition, may well have appeared independently in several progressive lines of hypsilophodontids.

V) *Tooth wear*

Traces of planar tooth wear are encountered in many hypsilophodontids. But more distinctive patterns of tooth wear, such as the paired wear facets attributed to interlocking between upper and lower teeth (see THULBORN, 1971a), may be identified in ornithischians which are only distantly related (e. g. the Triassic hypsilophodontid *Fabrosaurus australis* and the Cretaceous iguanodontid *Thescelosaurus edmontonensis*). Resemblances in tooth wear cannot, therefore, be taken as reliable indications of close affinity between hypsilophodontids. This contention is supported by observing that tooth wear may be extremely variable within even a single species of hypsilophodontid (e. g. *Alocodon kuehnei*).

VI) *Cheeks*

GALTON (1973) suggests that the acquisition of cheeks may account, to a very large degree, for the successful history of the ornithischian dinosaurs. Evidently the Triassic hypsilophodontid *Fabrosaurus australis* lacked cheeks (the lateral faces of the maxilla and mandible being rather flat) and this primitive condition seems to have persisted in *Echinodon becklesii*. In more advanced hypsilophodontids the former presence of cheeks may be inferred from the development of a recess in the lateral face of the maxilla and of a conterpart shelf in the flank of the mandible.

Of the six criteria discussed above one (i. e. the comparative study of tooth wear) is of little use in the investigation of hypsilophodontid interrelationships. Three others (the extent of the premaxillary dentition, the degree of change in tooth shape along the tooth row, and the presence or absence of cheeks) may be used to distinguish conservative hypsilophodontids from their more progressive relatives. The remaining two criteria (comparative studies of cheek tooth structure and of the junction between premaxillary and maxillary teeth) are the most important since they give reliable indications of hypsilophodontid interrelationships at species level.

By means of these criteria it is possible to investigate relationships within the hypsilophodontid plexus which lies at the core of ornithischian phylogeny. It is proposed to examine the better known hypsilophodontids in turn and to indicate the probable relationships of each. These relationships are are expressed in diagrammatic from (fig. 27).

Hypsilophodontids first appear in the late Trias. *Fabrosaurus australis,* from the Red Beds of southern Africa, is perhaps the best known of these early hypsilopho-
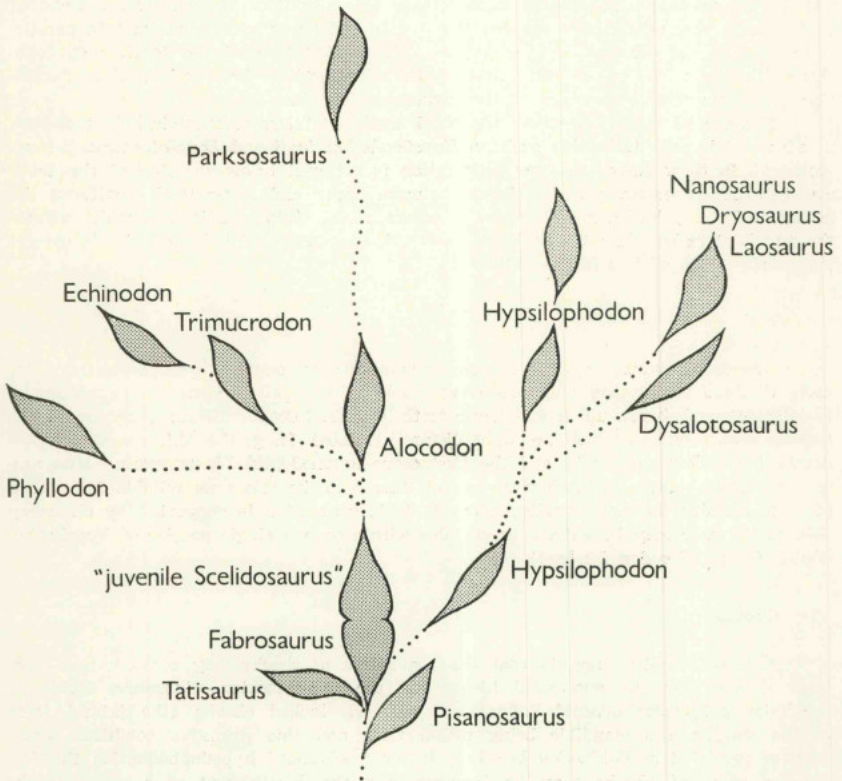

Fig. 27 — Relationships of the hypsilophodontids.

dontids and fulfils the role of a very useful ornithischian «archetype» (THULBORN, 1970a, 1972). *Tatisaurus oehleri,* from the late Trias of Yunnan, China, is represented only by a fragment of jaw with the stumps of several teeth (SIMMONS, 1965). The relationships of *Tatisaurus* are obscure, but ROMER (1966) classifies it as a hypsilophodontid and it may be regarded, with some caution, as an ally of *Fabrosaurus. Pisanosaurus mertii* is represented by teeth, cranial fragments and post-cranial bones from the Ischigualasto formation of Argentina (CASAMIQUELA, 1967). *Pisanosaurus* is still rather poorly known and is currently being restudied by Dr. J. F. BONAPARTE; and until the results of this work are published it may be best to regard *Pisanosaurus* as a hypsilophodontid allied to *Fabrosaurus.* CASAMIQUELA's suggestion (1967) that *Pisanosaurus* should be separated from the hypsilophodontids at family level does not seem to be justified by the evidence which is at present available.

Several ornithopods from from the late Trias of southern Africa (*Geranosaurus atavus, Lycorhinus angustidens* and *Lycorhinus tucki*) have highly specialized dentitions which include very large «canine» teeth (see CROMPTON & CHARIG, 1962; THULBORN, 1970b). For the purposes of this paper, and for the sake of brevity, I have followed ROMER (1966) in excluding these forms from the Hypsilophodontidae.

NEWMAN (1968) has recorded fragmentary remains of a hypsilophodontid from the Lower Lias of Dorset, England. Certain of the limb bones are quite similar to those of the Wealden *Hypsilophodon foxii* and it may not be unreasonable to postulate a fairly direct relationship between the two forms. The species of *Hypsilophodon* which has come to light in the Kimmeridgian of Porto Pinheiro may then represent a very convenient intermediate. This succession of progressive hypsilophodontids, which culminates in *Hypsilophodon foxii,* seems to be quite distinct from the conservative central stock of the Hypsilophodontidae (which is represented by *Fabrosaurus* and its successors).

Parts of a second ornithischian from the Lower Lias of Dorset have been described and figured under the name «juvenile *Scelidosaurus*» (see RIXON, 1968; ROMER, 1968; CHARIG, 1972). But this animal would seem, from the published illustrations of its pelvic and hindlimb bones, to be a fairly direct descendant of the Triassic *Fabrosaurus.*

Dysalotosaurus lettow-vorbecki, from the Tendaguru formation of East Africa, has edentulous premaxillae and cheek teeth which are not unlike those of iguanodontids (see JANENSCH, 1955). *Dysalotosaurus* has often been regarded as an iguanodontid but the postcranial skeleton is decidely hypsilophodontid-like in structure and I have followed GALTON (1971) in including *Dysalotosaurus* within the Hypsilophodontidae. The unusual dentition finds no exact counterpart in any other hypsilophodontid; but the teeth and the skull are, on the whole, more like those of *Hypsilophodon* than those of *Fabrosaurus. Dysalotosaurus* probably represents a specialized divergence from the succession of already progressive hypsilophodontids which leads to *Hypsilophodon foxii* (though it might conceivably have arisen from the more conservative line springing from *Fabrosaurus*).

Alocodon kuehnei, from the Callovian of Pedrógão, has a dentition which resembles that of *Fabrosaurus* in many respects (even though the cheek teeth of the two animals are not immediately reconcilable in structure). Though its teeth do show a few specializations (such as denticulate cingula) *Alocodon* is probably not too far removed from the conservative main line of hypsilophodontid evolution. On the other hand *Phyllodon henkeli,* from the Kimmeridgian of Guimarota, seems to be more distantly related to this same conservative stock, for it shows a unique style of transition between premaxillary and maxillary teeth.

Pronounced resemblances in tooth structure point to a close relationship between *Trimucrodon cuneatus,* from the Kimmeridgian of Porto Pinheiro, and *Echinodon beck-*

lesii, from the Purbeck beds of Dorset. The persistence of primitive features (such as the high-level jaw articulation) in *Echinodon* suggests that these two forms are not very remote from the hypsilophodontid stock which includes *Fabrosaurus* and *Alocodon*.

The hypsilophodontids which are recorded from the late Jurassic and early Cretaceous of North America (*Dryosaurus* spp., *Laosaurus* spp. and *Nanosaurus* spp.) cannot be discussed in any detail since their anatomy and their systematics are both far from clear. These forms are considered only for the sake of completeness; they are tentatively allied with the progressive hypsilophodontids leading to *Hypsilophodon foxii* (fig. 27) because the skulls of *Dryosaurus altus* and of *Laosaurus gracilis*, which are figured by GILMORE (1925), seem to resemble that of *Hypsilophodon*.

GALTON (1971) has suggested that the family Hypsilophodontidae may best be defined on the basis of limb proportions (the hypsilophodontids being characterized by elongated epipodial and metapodial segments in the hind limb). By this means the cursorial hypsilophodontids may be neatly separated from the graviportal iguanodontids. This scheme requires the transfer of the Upper Cretaceous *Thescelosaurus* from the Hypsilophodontidae to the Iguanodontidae but permits retention of the contemporary *Parksosaurus* within the former family. *Parksosaurus* is separated from the rest of the hypsilophodontids by a very great hiatus in the fossil record. And this hiatus, which extends through the greater part of the Cretaceous period, makes it difficult to assess the relationships of the genus. *Parksosaurus* might best be regarded as a descendant from the conservative main line of hypsilophodontid evolution (though it might possibly have been derived from the progressive line which includes *Hypsilophodon*).

The whole of the preceding discussion may be condensed into a single diagram (fig. 27). The most firmly established part of this phylogeny is the line which includes, or leads to, *Fabrosaurus*, *Alocodon* and *Echinodon*. The more progressive line which includes *Hypsilophodon* seems to be quite distinct; it certainly extends back into the Upper Jurassic and may possibly have made its appearance as early as the Lower Lias.

Finally, it must be emphasized that the fossil record of the Hypsilophodontidae is very discontinuous. The hypsilophodontid interrelationships which are outlined above are mostly very tentative and it is likely that future discoveries will lead to modifications in the phylogeny which has been suggested.

SUMMARY

The application of specialized palaeontological techniques has brought to light a number of small dinosaurs in the Upper Jurassic of Portugal. This paper deals with four of these dinosaurs. These are referred to the family Hypsilophodontidae of the order Ornithischia and they are represented only by isolated teeth. The earliest of the Portuguese hypsilophodontids comes from the Callovian at Pedrógão; this animal (*Alocodon kuehnei* gen. et sp. nov.) seems to be a fairly direct descendant of the Triassic *Fabrosaurus australis*. The second hypsilophodontid (*Phyllodon henkeli* gen. et sp. nov.) was discovered in the early Kimmeridgian of Guimarota and seems to represent a rather specialized divergence from the main line of hypsilophodontid evolution. The two remaining dinosaurs come from the late Kimmeridgian of Porto Pinheiro. The first of these (*Trimucrodon cuneatus* gen. et sp. nov.) is probably a close relative of *Echinodon becklesii* from the English Purbeck. The other is a species of *Hypsilophodon* which is directly antecedent to the Wealden *Hypsilophodon foxii*. Though these Portuguese fossils are very fragmentary they do permit critical reappraisal of relationships, and of evolutionary trends, within the hypsilophodontid plexus at the heart of ornithischian history.

RÉSUMÉ

L'emploi des techniques paléontologiques spécialisées a fait connâitre plusieurs petits dinosauriens dans le Jurassique supérieur du Portugal. Cette étude s'occupe de quatre de ces dinosauriens. Ces animaux appartiennent à la famille Hypsilophodontidae de l'ordre Ornithischia et ils sont représentés seulement par les dents isolées. Le plus ancien des hypsilophodontidés portugais provient du Callovien à Pedrógão; cet animal (*Alocodon kuehnei* gen. et sp. nov.) paraît descendre en ligne assez directe de *Fabrosaurus australis* du Trias. Le deuxième hypsilophodontidé (*Phyllodon henkeli* gen. et sp. nov.) s'est découvert dans le Kimmeridgien inférieur à Guimarota et paraît indiquer une divergence plutôt spécialisée de la grande ligne d'évolution parmi les hypsilophodontidés. Les deux dinosauriens de reste proviennent du Kimmeridgien supérieur à Porto Pinheiro. L'un d'entre eux (*Trimucrodon cuneatus* gen. et sp. nov.) est vraisemblablement une forme voisine d'*Echinodon becklesii* du Purbeck d'Angleterre. L'autre est espèce d'*Hypsilophodon* qui est antécédent assez direct d'*Hypsilophodon foxii* wealdien. Quoique ces fossiles portugais sont très fragmentaires ils admettrent l'appréciation critique des liens, et des cours évolutionnaires, dans le plexus hypsilophodontidé au coeur de «l'arbre généalogique» des Avipelviens.

RESUMO

A utilização de técnicas paleontológicas especializadas levou à descoberta de alguns dinossauros pequenos no Jurássico Superior de Portugal. Este artigo trata de quatro destes dinossauros. Estes pertencem à família Hypsilophodontidae da espécie Ornithischia e são tipificados sòmente pelos dentes isolados. O mais antigo dos hypsilophodontides portugueses vem do Caloviano de Pedrógão; este animal (*Alocodon kuehneli* gen. et sp. nov.) parece descender bem directamente do *Fabrosaurus australis* triásico. O segundo hypsilophodontide (*Phyllodon henkeli* gen. et sp. nov.) foi descoberto no Kimmeridgiano antigo de Guimarota, e parece simbolizar uma divergência um tanto especializada da linha principal de evolução dos hypsilophodontides. Os dois outros dinossauros são do Kimmeridgiano Superior de Porto Pinheiro. O primeiro destes (*Trimucrodon cuneatus* gen. et sp. nov.) é provável que seja parente próximo do *Echinodon becklesii* do Purbeck inglês. O outro é uma espécie de *Hypsilophodon* que é um antecedente directo do *Hypsilophodon foxii* wealdiano. Embora estes fósseis portugueses sejam muito fragmentários, permitem um nova avaliação crítica de parentescos e de tendências evolucionárias, dentro da teia hypsilophodontido ao centro da história de Ornithischia.

ACKNOWLEDGEMENTS

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Since this paper went to press (1972) there has been considerable revision of views regarding the classification of ornithopod dinosaurs. Most importantly, GALTON (1972) has advocated separation of *Fabrosaurus australis* and its relative *Echinodon becklesii* into a new family (Fabrosauridae) on the grounds that these forms lacked the fleshy cheeks which were presumably present in the great majority of ornithischian dinosaurs.

Alocodon kuehnei and *Trimucrodon cuneatus* appear to be relatives of *Fabrosaurus australis* and *Echinodon becklesii* (respectively) and might best be referred to the family Fabrosauridae. The species of *Hypsilophodon* reported from Porto Pinheiro should clearly be retained in the family Hypsilophodontidae (s. s.). The systematic position of *Phyllodon henkeli*, from the Guimarota lignite, is not immediately obvious. From the preponderance of crown height over crown length along the entire dental series of *P. henkeli* it may be deduced that the jaw articulation lay well below the level of the cheek teeth. This low-level jaw articulation is matched in hypsilophodontids (s. s.) but not in fabrosaurids (where the jaw joint is at the level of the tooth rows). On the basis of this (admittedly slight) evidence I would recommend retention of *P. henkeli* in the family Hypsilophodontidae (s. s.).

The systematic position of *Lusitanosaurus liasicus* may also be reviewed. It transpires that the (presumed) relative of *L. liasicus,* the English *Scelidosaurus harrisonii,* may be an ornithopod — rather than an ankylosaur or a stegosaur (see THULBORN, 1974).

I present an updated classification for the ornithischian dinosaurs of Portugal:

SUBORDER ORNITHOPODA

Grade DOLICHOPODA

Family Fabrosauridae
Alocodon kuehnei (Upper Jurassic)
Trimucrodon cuneatus (Upper Jurassic)

Family Hypsilophodontidae (s. s.)
Hypsilophodon sp. (Upper Jurassic)
?Phyllodon henkeli (Upper Jurassic)

Grade BRACHYPODA

Family Scelidosauridae
?Lusitanosaurus liasicus (Lower Jurassic)

Family Iguanodontidae (s. s.)
Iguanodon mantelli (Lower Cretaceous)

SUBORDER STEGOSAURIA

Family Stegosauridae
Dacentrurus armatus (Upper Jurassic)
Dacentrurus lennieri (Upper Jurassic)

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CHELONIA FROM THE UPPER JURASSIC
OF GUIMAROTA MINE (PORTUGAL)

by

H. BRÄM

The turtles can mainly be authenticated by remains of the shell. Other recognizable parts of the skeleton, e. g. vertebrae, or bones of the girdles and the extremities, are very rare. These remains of the shell chiefly consist of little fragments; very few bones of the shell which are complete or almost complete have been found. In one case only, there are a neural and a pleural still in a natural connexion on one plate (1).

This degree of preservation of turtle fossils is frequent; shells to some extent complete are a rare exception. The cause thereof is a late growing together of the sutures. Only very old turtles show a total coalescece. Moreover there are types which have all their lives persisting fontanelles, and such with joints in their shell. Whenever the coalescence is incomplete, a fast postmortem decay follows. The slightest movement caused by wind or water, or by the activity of carcass easters results in the shell falling to pieces. After the organic substance has decayed, the plate-like bones are usually rather brittle. The slightest vibrations of transportation cause them to fall apart easily into smaller fragments.

The shells of the turtles show great individual modifications. Among the turtles of one species there are always specimens whose theca shows characteristics of closely related species. To be able to get a positive picture of a fossil turtle you have at least to find a shell which is to some extent complete.

For these reasons it isn't possible to identify the remains of Guimarota exactly. Evenso there are different types which can be positively distinguished. The question is, whether there are one or several species within each group of types. This question cannot be determined by means of the material known at present. Most likely each group belongs to another family. More complete findings only could lead us to a more positive certainity.

In the following shall be demonstrated, that one type (Plesiochelys) settled in the sea near the coast, which it sometimes left, at least to lay eggs. The two other types lived in fresh water and its immediate surroundings.

1st type :

Family PLESIOCHELYIDAE

The majority of all the fragments belongs to this type. The fragments of the theca are from one to a few square centimetres large, and four to seven millimetros thick. The smallnessof the fragments usually makes an exact anatomic identification impos-

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(1) Further small remains, which have been found recently, are to be described in a later paper.

sible. The remains on one rock (No. T1) are an exception. There is a neural plate and a not quite complete pleural plate whose inner surface is visible. On the same plate there is a left hyoplastron, also visible on the inner surface. The state of preservation of this bone is so bad, that it isn't advisable to lay it open. Therefore the course of the suture of the shields is not visible. For this reason the neural and the pleural plate cannot positively be identified anatomically. It must be a neural plate 2 or 3 and its appertai-
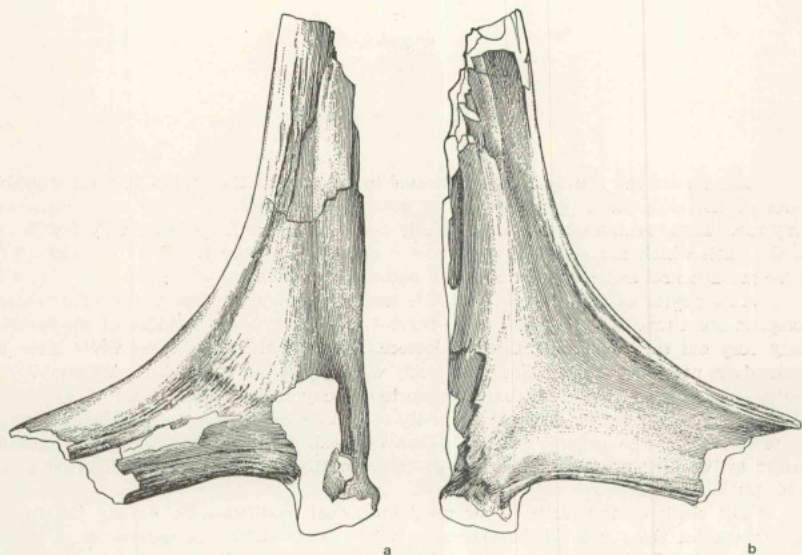

a   b

Fig. 1 — No. T3. Left scapula. a) Anterior view. b) Posterior view.

ning left side of a pleural plate. The neural plate is rounded off and hexagonal; its shortest sides are in the front, laterally. Its dimensions are: length 45 mm, width 22 mm. The pleural plate is 35 mm long, and about 100 mm wide. The horizontal plate of the left hyoplastron is 42 mm long; its width can no longer be ascertained, as it is destroyed through the middle. Very pobably these three bones come from the same carcass. Their forms and their dimensions refer to *Plesiochelys* RUETIMEYER. This supposition is supported by the finding No. T3 (Fig. 1), which is a fragment of a scapula. Both branches, the scapula s. s. and the acromial process are distally broken off. The angle formed by the two can be determined all the same, it is 123°. Though a little deformed, the central part is rather well preserved. A processus glenoidalis, 8 mm long, can be recognized. The seize and the sum of these characteristics also refer to the genus *Plesiochelys* RUETIMEYER.

The genus *Plesiochelys* RUETIMEYER belongs to the turtles which are most often found in the Upper Jurassic of Europe. The latest knowledge about them supports the supposition that it is probably a marine type, which lived in the coastal waters and on its coast.

2nd type:

Family CARETTOCHELYIDAE?

With the reservation of newer knowledge that may present better information, many fragments can be allied with early representatives of the Carettochelyidae. They are remains of the carapace and plastron, whose thickness is between 2 mm and 4 mm. On their exterior fine vermicular to fine humpy sculptures are sometimes very clear and sometimes hardly visible. There between them the suture of shields are clearly incised.

Carapaces: As a result of the very few, only to some extent complete pleural plates (e. g. No. T2, T4) it can be recognized that the possibly once existing peripheral plates were separated from the pleural plates by fontanelles. The neural plates were very wide and consequently the pleural plates narrow. The dimensions of the pleural plate No. T2 are: average length 11 mm; total width 50 mm; largest width of a neural scute recognizable on it 35 mm.
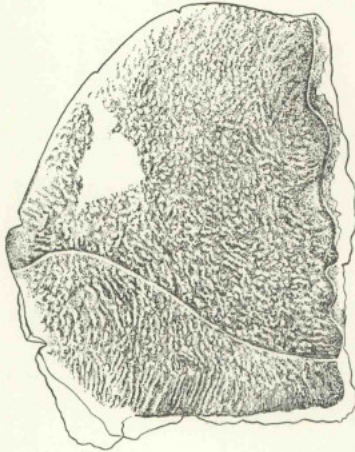

Fig. 2 — No. T8. Right forepart of a plastron.
Outer view.

Plastron: Beside some badly kept remains there are the better kept fragments No. T8 and T9 (Fig. 2 and 3), which can give some information. No. 8 is the right forepart of a plastron lobe. No sutures of the bones are visible on it. Therefore epiplastron, entoplastron and hyoplastron are not visible. On the outside there are only the sutures of shields visible, namely that between the humeral shield and pectoral shield, and the median one. The latter one shows strong lateral curves. No gular shields are perceptible.

No. T9 is a right-hand hyoplastron. The surface of the rupture, lateral in front, hints at a possible osseous connection with the peripheral plate. The plastron doesn't become narrower behind the inguinal buttresses, but it narrows evenly towards the end. The suture of shields between adbominal and femoral shield is visible on the exterior surface.
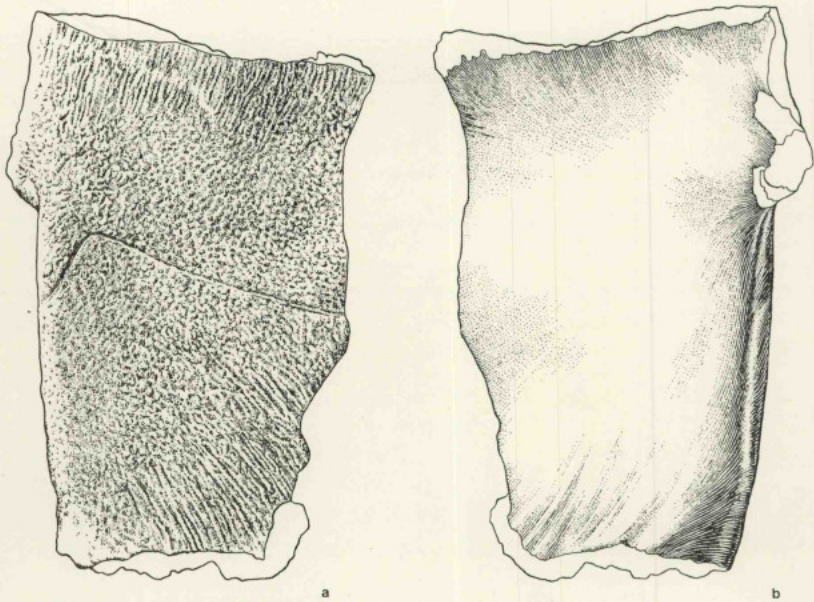
Fig. 3 — No. T9. Right hyoplastron. a) Outer view. b) Inner view.

Dimensions: No. T8: Lobe of plastron

length: 40 mm; greatest width: 31 mm.

No. T9: Hypoplastron

length: 52 mm; greatest width: 32 mm.

On the whole, these fragments of the shell look rather delicate. It could be assumed that all fragments come from young animals. But this supposition is contradicted by the fact that fragment. No. T8 has no sutures at all. More complete findings only can give greater certainty about their age. From the material in question the total length of the plastron, about 12 cm to 15 cm, can be calculated. Hence it follows that the supposed total length of the shell is at the most 20 cm.

The attribution of these fragments to the Carettochelyidae is only a supposition. Compared with similar types it is the Carettochelyidae which shows the closest likeness. The most important criterion that supports this supposition is the texture of surface in combinationwith the form of the suture of shields. Besides, there is no visible characteristic that is contradictory to this assumption. If one day this interpretation should prove correct, then these fragments are the oldest findings of Carettochelyidae. Until now only Carettochelyidae from the Upper Cretaceous have been known certainly.

As is yet known, the Carettochelyidae live in and near fresh water.

3rd type:

CHELONIA INDET.

A few of the remains of shell have exceptionally strong and irregular tubercles. If the bones are about 2 mm to 6 mm thick the tubercles rise up to 3 mm above the surface.

Few fragments only are anatomically definable. One of them is an almost complete neural plate (No. T6, Fig. 4). Its rims are a little damaged, therefore it can't be clearly decided whether it was tetragonal or hexagonal (Length: 25 mm, width: 15 mm).
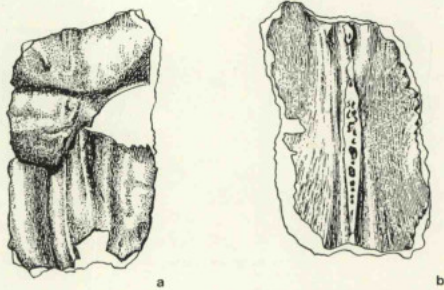

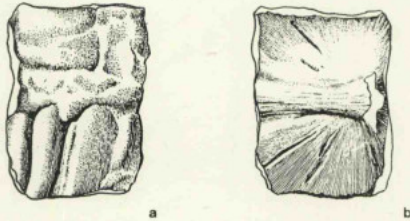Fig. 4 — No. T6. Neural plate. a) Outer view. b) Inner view.

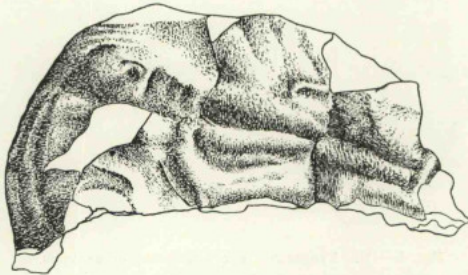Fig. 5 — No. 10. Fragment of a coastal plate. a) Outer view. b) Inner view.

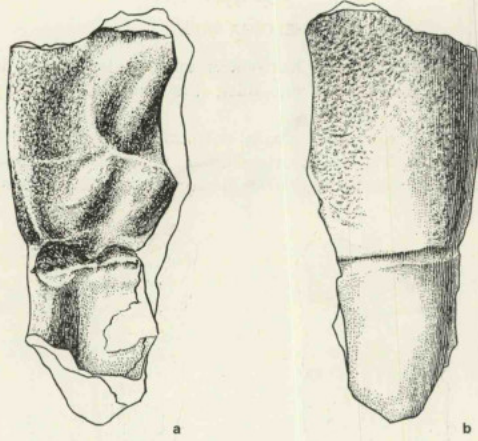Fig. 6 — No. T11. Fragment of a coastal plate; outer view.

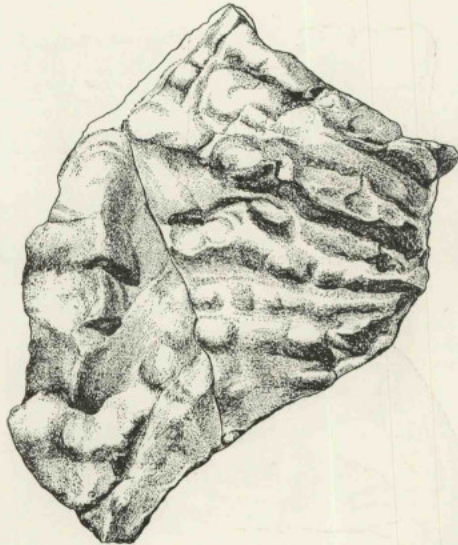Fig. 7 — No. T12. 1 ½ marginalia. a) outer view.
b) inner view.

Fig. 8 — T8. Fragment of a carapace; outer view.

The remains of the pleural plates show, that the rib merged with them immediatly at the border with the neural plate. Fragment No. T7 (Fig. 8) shows that the neural plates were very wide. A piece of bone, formed by 1 ½ peripheral plate No. T12 (Fig. 7), indicates that the shell had a strong rim of peripheral plates.

A somewhat bigger part of a carapace is on stone plate No. T1. This one is so badly preserved that it doesn't furnish any new knowledge.

The fragments in question suggest that it was a rather small turtle, its carapace 15 to 20 cm in length. Because of the scantiness of the remains, nothing can be said taxonomically. The design of the shell surface somewhat resembles that of the *Platychelys* WAGNER, which is of about the same age. The anatomical details, above all the connection of rib and pleural plate, show that no relation exists. Presumably the fragments come from an animal that belongs to the suborder of the Amphichelydia.

Because the bones which in spite of the tubercles are rather light, the sea or the open coast are excluded as their living space. For the same reason it isn't a pure terrestrial type either. Because of its probably very bizzare appearance, the turtle was well screened. It probably lurked for its prey in shallow pools or in slow-flowing streams.

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