

MINISTÉRIO DA ECONOMIA
SECRETARIA DE ESTADO DA INDÚSTRIA
DIRECÇÃO-GERAL DE MINAS E SERVIÇOS GEOLÓGICOS
SERVIÇOS GEOLÓGICOS DE PORTUGAL



MEMÓRIA N.º 17 — (NOVA SÉRIE)

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

III — THE DENTITION OF THE PAULCHOFFATHIDAE
(MULTITUBERCOLATA, UPPER JURASSIC)

by

GERHARD HAHN

IV — STRATIGRAPHY AND OSTRACOD-FAUNA FROM THE
COALMINE GUIMAROTA (UPPER JURASSIC)

by

FRIEDRICH-FRANZ HELMDACH

LISBOA
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COMP. E IMP. DA
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ALCOBAÇA

THE DENTITION OF THE PAULCHOFFATIIDAE (MULTITUBERCULATA, UPPER JURASSIC). (1)

by

GERHARD HAHN (2)

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INTRODUCTION.

In 1969 the author erected a new family of the Multituberculata, the Paulchhoffatiidae, which contains four genera ranging from the Kimmeridgian of Portugal to the Purbeckian of England. The type-genus, *Paulchhoffatia* W. G. KUEHNE, 1961 and a second genus, *Kuehneodon* G. HAHN, 1969, were found in the Guimarota coal pit near Leiria, Portugal; the two others, *Plioprion* COPE, 1884 and *Bolodon* OWEN, 1871 come from the Purbeckian of Durdleston Bay, Swansea, Dorset, England. The rich Portuguese collection — containing not only associated elements of the dentition and many isolated teeth, but also important parts of the skull — has been described in detail by the author in 1969, where the differences between the Paulchhoffatiidae and the Plagiaulacidae are also discussed. In this paper an attempt will be made to explore the evolutionary tendencies within the Paulchhoffatiidae as known to day. For this purpose only the dentition can be used successfully, because this part of the skeleton is the only one known in all four genera. The dentition of the Plagiaulacidae — which does not descend from the Paulchhoffatiidae but represents a parallel evolutionary branch — can be used for comparison.

(1) Manuscript received on September 1970.

(2) Prof. Dr. GERHARD HAHN, 1 Berlin 33, Altensteinstr. 34a, Geologisch-Palaeontologisches Institut der Freien Universitaet.

The Plagiaulacoidea as defined now includes the following taxa ^(*):

- Plagiaulacoidea (SIMPSON, 1925), G. HAHN, 1969.
 Plagiaulacidae GILL, 1872.
 Plagiaulax FALCONER, 1857.
 Pl. becklesi FALCONER, 1857.
 Pl. ? dawsoni SMITH WOODWARD, 1891.
 Otenacodon MARSH, 1879.
 O. serratus MARSH, 1879.
 O. laticeps (MARSH, 1881).
 O. scindens SIMPSON, 1928.
 O. ? falconeri (OWEN, 1871).
 Psalodon SIMPSON, 1926.
 Ps. potens (MARSH, 1887).
 Ps. fortis (MARSH, 1887).
 Ps. ? marshi SIMPSON, 1929.
 Loxaulax SIMPSON, 1928.
 L. valdensis (SMITH WOODWARD, 1911).
 Paulchoffatiidae G. HAHN, 1969.
 Paulchoffatiinae n. subfam.
 Paulchoffatia W. G. KUEHNE, 1961.
 P. delgadoi W. G. KUEHNE, 1961.
 Kuehneodontinae n. subfam.
 Kuehneodon G. HAHN, 1969.
 K. dietrichi G. HAHN, 1969.
 K. guimaratensis G. HAHN, 1969.
 K. simpsoni G. HAHN, 1969.
 Phoprion COPE, 1884.
 Ph. minor (FALCONER, 1857).
 Bolodon OWEN, 1871.
 B. crassidens OWEN, 1871.
 B. osborni SIMPSON, 1928.
 B. ? elongatus SIMPSON, 1928.
 Plagiaulacoidea?, fam. indet.
 Guimaratodon G. HAHN, 1969.
 G. leiriensis G. HAHN, 1969.

Of these two families included in the Plagiaulacoidea the Paulchoffatiidae are not only the older but, moreover, the group with a more complicated structure of the upper i^3 and the lower m_2 . In addition one can see a very large, perplexing diversity among the same type of tooth (for example the i^3) which renders more difficult the focusing of systematic units. These facts and the expectation that more complex isolated teeth will be found by application of modern field methods ^(*) necessitates intensification of the study of the several types of teeth found in the dentition of the multituberculates.

In this paper all text-figures not marked otherwise are taken from G. HAHN, 1969. Photographs of the discussed taxa are published there and in SIMPSON, 1928 and 1929. They are not repeated here. The materials of *Paulchoffatia* and *Kuehneodon* are stored in the Museu dos Serviços Geológicos in Lisboa, Portugal.

I thank Dr. W. A. CLEMENS, Department of Paleontology, University of California, Berkeley, for reading the manuscript and revising the text.

(*) The diagnoses of the families and genera are given on pp. 35-39.

(*) See HENKEL, 1966.

THE COMPLETE DENTITION.

Among the Paulchoffatiidae the complete—or nearly complete—dentition is known in *Paulchoffatia* and *Kuehneodon*; among the Plagiaulacidae in *Psalodon*. In *Ctenacodon* the upper incisors are missing. *Plioprion* and *Plagiaulax* are known only by their lower dentition. *Bolodon* is known only by parts of the upper dentition. *Loxaulax* and *Guimarotodon* are founded on isolated teeth. The species of the Plagiaulacoidea with notations of the teeth found in situ are compiled in table I. It is possible that *Ctenacodon serratus* and *C. laticeps* on one hand and the three species of *Psalodon* on the other may belong to the same species in each case, but this can not be proved. In the same way *Kuehneodon simpsoni* and the lower jaw of *K. dietrichi* or *K. guimarotensis* may be conspecific; however it is impossible again to prove this assumption.

TABLE I

Genus and species		i ₁	p ₁	p ₂	p ₃	p ₄	m ₁	m ₂	i ¹	i ²	i ³	p ¹	p ²	p ³	p ⁴	p ⁵	p ⁶	m ¹	m ²
Plagiaulacidae	<i>Plagiaulax becklesi</i> . . .	+	—	+	+	+	+	+											
	<i>Plagiaulax?</i> <i>dawsoni</i> . .						?+												
	<i>Ctenacodon serratus</i> . . .	A	+	+	+	+	+	+											
	<i>Ctenacodon laticeps</i> . . .											+	+	+	+	+	—	+	+
	<i>Ctenacodon scindens</i> . . .		A	A	+	+	+	+											
	<i>Ctenacodon?</i> <i>falconeri</i> . .	+	A	+	+	+													
	<i>Psalodon potens</i>											+	+	+	+	+	—		
	<i>Psalodon fortis</i>								A	+	+								
	<i>Psalodon?</i> <i>marshi</i>	+	+	+	+	+	+												
	<i>Loxaulax valdensis</i> . . .						?+												
Paulchoffatiidae	<i>Plioprion minor</i>	+	+	+	+	+	+	(+)											
	<i>Bolodon crassidens</i>								A	A	(+)	+	+	+	+				
	<i>Bolodon osborni</i>											+	A	+	+	+	—	+	+
	<i>Bolodon?</i> <i>elongatus</i>											+	+	+					
	<i>Kuehneodon dietrichi</i> . . .	+	+	+	+	+	A	A											
	<i>Kuehneodon guimarotensis</i>	+	—	+	+	+	A	A											
	<i>Kuehneodon simpsoni</i> . . .								+	+	+	+	+	+	+	+	—	+	
	<i>Paulchoffatia delgadoi</i> . .	+	+	+	+	+	A	A	A	A	A	+	+	+	+	+	+	+	+

The species of the Plagiaulacoidea and distribution of their known teeth.—Teeth marked by + are known with their crowns in situ in the concerned species. Teeth marked by (+) were present when the species were first described but are now lost; they have been described by earlier students. Teeth marked by A are only represented by their roots or by their alveoli. Teeth marked by — have been lost by biological reduction in the concerned species.—Isolated teeth are identified only in *Plagiaulax?* *dawsoni* and *Loxaulax valdensis*, because these species are founded solely on isolated teeth.

In the Plagiaulacoidea as in all other Multituberculata the dentition is divided into incisors, premolars and molars. Canines are not thought to be present, but it is not out of the question that the so-called upper p^1 is a premolariform canine (see p. 21-22). In the lower jaw the canines are indeed lost. The distinction between «premolars» and «molars» in multituberculates was originally founded on morphological attributes, not on evidence of tooth replacement as in placentales. In the lower jaw this morphological difference — cutting premolars and grinding molars — is well marked in all Plagiaulacoidea; however in the upper dentition such a pure morphological separation fails, in *Paulchoffatia* the last premolars are very similar to the molars, combining characters of both groups of teeth. However SZALAY, 1965 has proved tooth replacement in multituberculates and among the Guimarota materials isolated teeth were found which, because of their root structure, are very probably deciduous teeth (see G. HAHN, 1969: 48-50). Such ejected teeth could come from the premolar region, not the molar. Therefore it seems probable that a real separation is present between the cheek teeth and that the morphological differentiation seen in the lower jaw is combined with tooth replacement in the premolars and the lack of such a replacement in the molars.

The normal tooth formula found in both families of the Plagiaulacoidea is $\frac{3.0.5.2.}{1.0.4.2.}$. Two types of deviation from this formula are known: 1) in the lower jaw the first premolar can disappear (one species in the Paulchoffatiidae and one species in the Plagiaulacidae); 2) in *Paulchoffatia* the number of upper premolars is six instead of five. Correlated with this higher number of upper premolars is a marked difference in the group-formation among these teeth (see pp. 20) which gives *Paulchoffatia* a unique position in comparison to all other Plagiaulacoidea. The number of incisors and molars does not vary among the known species of the suborder.

The direction of the lower tooth row in respect to the border of the jaw must be mentioned. In all hitherto known multituberculates this tooth row runs in a very distinctive way diagonally across the jaw, the molars situated near the lingual border and the anterior premolars near the outer border (see fig. 1a). This arrangement allowed enlargement of the lower incisor and its root without disturbance of the roots of the premolars. In order to compensate for the inward shift of the lower molars, in the Plagiaulacoidea the second upper molar was also shifted inward in respect to the m^1 , whereas in the Ptilodontoidea and the Taeniolabidoidea the upper molars become broadened by a third row of cusps, in this way compensating for the modified position of the lower and upper molars.

The only known genus that does not show this arrangement of the lower tooth row is *Paulchoffatia*. Here the tooth row runs nearly parallel to the border of the jaw, with neither a marked shift of the molars inward nor the anterior premolars outward (see fig. 1b). Accordingly the last upper molar is not moved inward but is situated directly behind m^1 . In this character *Paulchoffatia* shows the most primitive situation known among multituberculates, one to be expected in the forerunners of the order.

Summarizing one can state that in number of teeth, in group-formation of the upper premolars, in inward shifting of the m^2 and in the diagonal course of the lower tooth row three of the four known genera of the Paulchoffatiidae agree with the Plagiaulacidae. However in all these respects *Paulchoffatia* shows remarkable differences that must be taken into consideration in discussion of the phylogenetic tendencies found in the Paulchoffatiidae.

THE INCISORS.

The number of incisors, $\frac{3}{1}$, is — as far as known — constant in all Plagiaulacoidea. Not a single species of multituberculates with more than one incisor in the lower

jaw has ever been found. In the Plagiaulacoidea the lower incisor is enlarged, more or less procumbently inserted, and has a pointed crown covered by enamel. This tooth is separated from the premolars by a long diastema. In the Ptilodontoidea this structure is not fundamentally altered; the incisor grew larger in respect to the lower jaw, the diastema lengthened, and the crown of the *i* became more strongly curved. But in the Taeniolabidoidea the incisors are transformed into gnawing instruments with the enamel reduced to a band on the outer side of the crown. To which of the three upper incisors the one lower incisor corresponds cannot be determined with certainty; in the upper jaw the *i*² is the dominate one. Perhaps the lower incisor also corresponds to the original *i*².

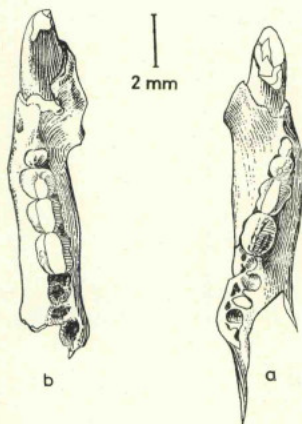
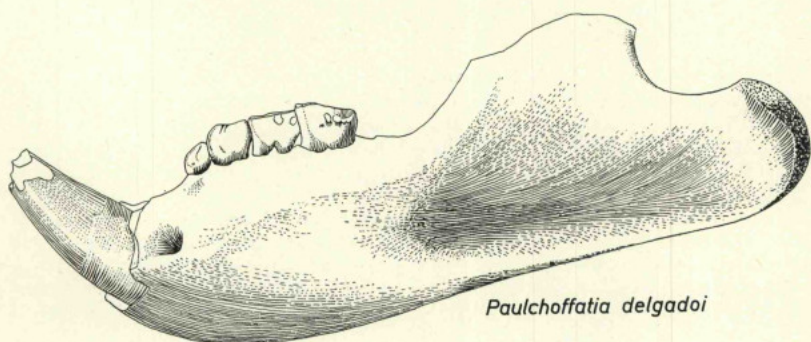


Fig. 1.—The course of the lower tooth row in relation to the border of the jaw in the Paulchoffatiidae.

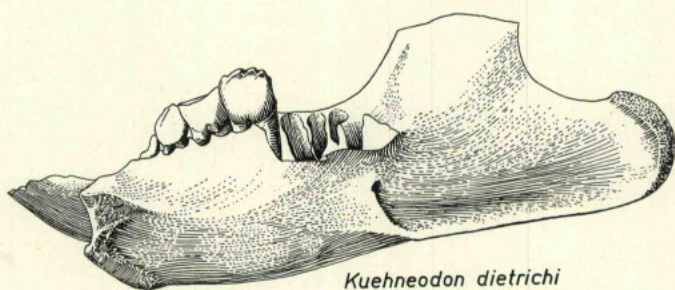
- a) *Kuehneodon dietrichi*.—The tooth row runs diagonally across the jaw as in all known Purbeckian and younger multituberculates.
- b) *Paulchoffatia delgadoi*.—The tooth row is directed nearly parallel to the border of the jaw. This is the most primitive evolutionary stage known among the multituberculates.

In the Paulchoffatiidae the lower incisors are relatively short, their crown is only slightly curved. The upper face is separated from the outer by a relatively distinct, longitudinal angulation; a similar angulation separates the inner from the inferior face. The inner face shows a slight serration in the region near the apex. These morphological features help to distinguish the right incisors from the left when found out of the jaw. Near the root these angulations disappear and the section of the tooth becomes oval.

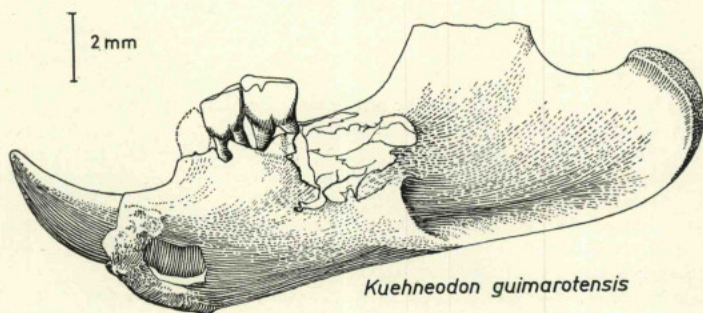
In details the lower incisors of the known Paulchoffatiidae — *Paulchoffatia delgadoi*, *Kuehneodon dietrichi*, *K. guimarotensis* and *Plioprion minor* — show differences in such a way that *P. delgadoi* represents the most primitive, *K. guimarotensis* the most specialised species (see fig. 2). In *P. delgadoi* the incisor is very steeply implanted, its crown is inclined about 40° from the front of the premolars, and is scarcely curved. The proximal part of its root is partially situated beneath the roots of the *p*_{1,2}, not lin-



Paulchoffatia delgadoi



Kuehneodon dietrichi



Kuehneodon guimarotensis

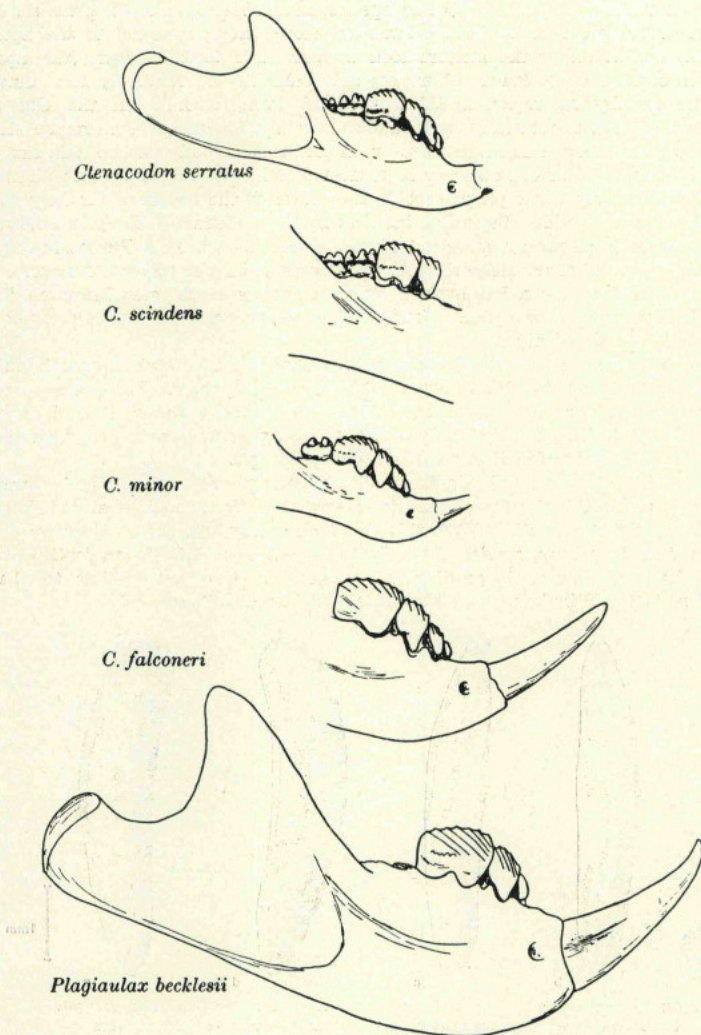


Fig. 2—Comparative view of the mandibular rami of the Paulchoffatiidae and the Plagiaulacidae, showing the incisors and the premolars.

a) *Paulchoffatia delgadoi*.—b) *Kuehneodon dietrichi*.—c) *Kuehneodon guimarotensis*.
—d) *Ctenacodon serratus*.—e) *Ctenacodon scindens*.—f) *Plioprius minor*.—g) *Ctenacodon? falconeri*.—h) *Plagiaulax becklesii*.—a, d-h external view, b-c internal view.
d-h after SIMPSON, 1928, 1929.

gually beside them as in the three other species. In *Kuehneodon* and *Pliopriion* the lower incisors are more procumbent, their crowns are more strongly curved to the apex. In *K. dietrichi* and *P. minor* the incisors look similar each to the other (the apex is unknown in both species). Minor differences are found in the relatively long diastema and slender symphyseal region in the Purbeckian form, whereas in the Guimarota species the diastema is relatively somewhat shorter and the symphyseal region stouter. *Kuehneodon guimarotensis* is much more specialised than the other species: In this form the p_1 is lost and the alveolar border is separated from the diastema by a well marked step not found in any other plagiaulacoid. The crown of the incisor is strongly curved. Among the Plagiaulacidae *Plagiaulax becklesi* is most similar to *K. guimarotensis* in the loss of p_1 and the strong curvature of the incisor crown. This Purbeckian species shows a higher evolutionary stage than *K. guimarotensis* in the larger extension of the incisor from the jaw, but a less evolved stage in absence of the step before p_2 . Therefore *Plagiaulax* can not be a descendant of *K. guimarotensis*; the loss of p_1 must have occurred twice independently.

The upper incisors of the Paulchoffatiidae show singular structures not found in any other multituberculate. The crown of i^1 is known only in *Kuehneodon simpsoni*, i^2 in this species and — among the Plagiaulacidae — in *Psalodon fortis*, i^2 in both these species and in *Bolodon crassidens*. Knowledge of the upper incisors is also derived from nearly 100 isolated teeth found in the Guimarota coal pit.

The i^1 (fig. 3) are small, pin-like teeth closely appressed between the enlarged i^2 . The crown is unicuspid. Its lingual face is somewhat flattened and separated from the anterior by a slight angulation. With this the i^1 show nearly a «normal» crown similar to the structure in other mammals. In *Bolodon crassidens* and *Psalodon fortis* only the alveoli of the i^1 are known; in position and proportions they are similar to that of *Kuehneodon*. In the Ptilodontoidea and Taeniolabidoidea the i^1 are lost.

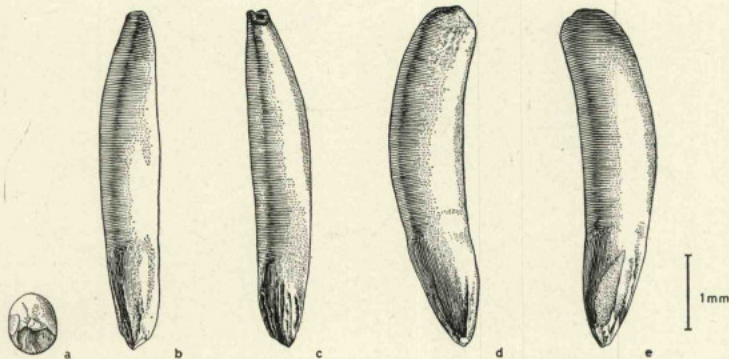


Fig. 3 — An isolated left i^1 of the Paulchoffatiidae from the Guimarota coal pit.

a) Crown view. — b) Front view. — c) Posterior view. — d) Right view. — e) Left view.

The i^2 of the Paulchoffatiidae (fig. 4) are about three times as large as the i^1 ; they are the most prominent of the anterior teeth. The crown is divided into a large, projecting anterior cusp and a less prominent but distinct posterior cusp. Whereas the anterior cusp shows no unusual variability in its shape the posterior cusp varies in an unexpected manner. In some of the isolated Guimarota- i^2 it shows a transversally

situated, depressed, ridge-like shape; in others this ridge is divided in 2 to 4 serially orientated little cuspsules. In one tooth (fig. 4c) even 5 little, irregularly arranged cuspsules are present. This diversity in the posterior region of the crown is perplexing and—as in the i^2 —its systematic implications are unknown. Does each of these crown patterns represent a different species or does this remarkable diversity represent intra-specific variation among a few species? This question cannot be solved till more complete dentitions are known which will help to estimate the meaning of the morphological diversity. It is worthy to note that CLEMENS, 1963 has illustrated an i^2 of the Paulchoffatiid pattern from the Wealden which suggests that members of the family survived into the Lower Cretaceous.



Fig. 4—Several isolated i^2 of the Paulchoffatiidae from the Guimarota coal pit with the posterior cusp divided into cuspsules.

- a) Left i^2 with 2 posterior cuspsules arranged serially.—b) Left i^2 with 4 posterior cuspsules arranged serially.—c) Right i^2 with 5 posterior cuspsules not arranged serially.

In the Plagiaulacidae—*Psalodon fortis*—the posterior cusp of the i^2 is small, much less distinct, and does not make up an important part of the crown. SIMPSON, 1929, p. 27 calls it «a small accessory cusp». The great difference in respect to the i^2 in the Paulchoffatiidae is also seen in SIMPSON, 1929, pl. 5 fig. 3.

The i^2 are in the Paulchoffatiidae even more specialised than the i^1 . The highly complicated structure of their crowns is distinctly different from the simple pattern in the Plagiaulacidae. This is one of the reasons for separation of the Paulchoffatiidae. At their bases the i^1 , which are rather smaller than the i^2 , are built stouter and their crowns are lower than those of i^2 . They are known in situ in *Kuehneodon simpsoni* and *Bolodon crassidens* (the crown of the last named species was described by SIMPSON, 1928, but is missing now). Additionally, 37 isolated Guimarota- i^1 are available. Essentially the crown of the i^1 consists of a main cusp which is compressed to a ridge-like structure running from antero-lingual to postero-buccal corners of the crown. As a rule a distinct cusp is situated at the antero-lingual end of the main ridge (fig. 6a-b); sometimes, an additional cusp is visible at the postero-buccal corner (fig. 6b-c). In this way the main ridge tends to be divided into three units. Moreover, cuspsules independent from the main ridge can be present at its base on the antero-buccal and the postero-lingual slope. In this way the antero-buccal corner can carry 1-2 cuspsules and the postero-lingual corner 0-2 cuspsules. By permutation of the number of these cuspsules and those of the main ridge a great diversification arises; some of the realized patterns are illustrated in the fig. 6a-d. The systematic value of this diversification remains to be determined. In *Bolodon crassidens* the main ridge is not subdivided; one antero-basal and one postero-lingual cuspule are present (fig. 5). In *Kuehneodon simpsoni*

(fig. 13) the main ridge is subdivided into a central main cusp and a antero-lingual cusp; in the antero-buccal corner 2 cuspules are present, but in the postero-lingual corner only a cingulum is visible. In this species the i^3 is separated by a short diastema from the i^2 as well as from the p^1 .

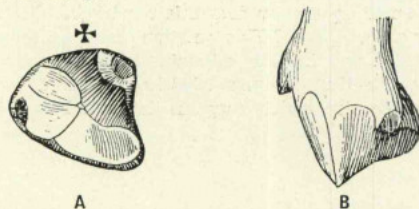


Fig. 5 — Right i^3 of *Bolodon crassidens*, after SIMPSON, 1928.
a) Crown view. — b) Buccal view.

The structure of i^3 in the Paulchoffatiidae is one of the most complicated among mammals and is not repeated in the Plagiaulacidae or in the younger multituberculates. In the Plagiaulacidae the i^3 — known in *Psalodon marshi* — is smaller and similar to

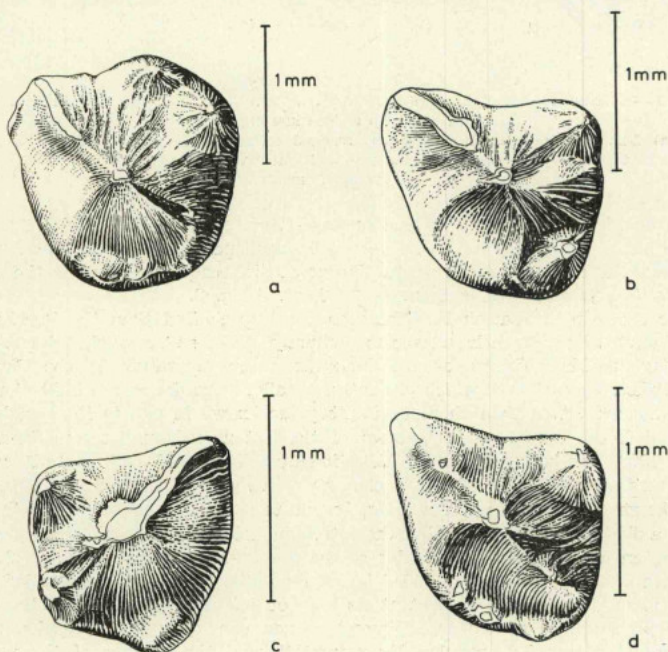


Fig. 6 — Isolated i^3 of the Paulchoffatiidae from the Guimarota coal pit, showing different patterns in the subdivision of the main cusp and in the number of cuspules in the antero-buccal and postero-lingual corner of the tooth. a, b, d are left i^3 , c is a right i^3 .

the i^2 . SIMPSON, 1929, p. 27 describes that tooth as follows: « i^2 is about half as large as i^1 and nearly parallel to it. The tip is rounded, subspatulate and there is a very small accessory cusp». In the Ptilodontidae and Taeniolabidoidea i^1 is a very small, unicuspid tooth no longer significant in the function of the dentition.

In the Paulchoffatiidae the incisors were not only used in grasping the food but they were also included in the chewing process. This is shown by the very deep wear on the right i^1 of *Kuehneodon simpsoni* (fig. 13) and by a fragment of a lower jaw from the Guimarota coal pit with the incisor worn to a spatulate-like nub (G. HAHN, 1969, pl. 2, fig. 7a-b). Therefore in the Paulchoffatiidae—at least in the Kimmeridgian forms—the incisors took part in mincing the food, a function taken over from Purbeckian time by the cutting premolars.

Differences among the Paulchoffatiid genera are visible in the inclination of the incisors. Whereas in *Bolodon crassidens* and in *Kuehneodon simpsoni* the upper incisors are implanted relatively steeply (inclined about 20° forward from the vertical plane), in *Paulchoffatia delgadoi* (as is seen by their alveoli) the inclination is greater, increasing to $30-35^\circ$. The inclination in the last named species is similar to that in the plagiaulacids *Psalodon fortis* and *Ctenacodon laticeps*, expressing not a phylogenetic relationship but an ecological adaption to a similar method of grasping the food.

THE PREMOLARS.

The number of premolars in the Paulchoffatiidae is $\frac{6-5}{4-3}$. The full set of premolars is known in *Paulchoffatia* and *Kuehneodon*; among the Plagiaulacidae in *Ctenacodon* and *Psalodon*. In *Pliopriion* only the lower p, in *Bolodon* only the upper p are known.

The structure of the lower premolars is similar in all Plagiaulacoidea. Their crowns form a cutting edge which includes $p_{2,4}$, whereas the p_1 (lost in *Kuehneodon guimarotensis* and *Plagiaulax becklesi*) remains low crowned and retains its conical shape. This cutting edge can be interpreted as the homologue of the lingual row of cusps in a lower molar. In all the lower cheek teeth the tendency to elevate the inner row of cusps and to lower the outer one is clearly visible. Whereas in the upper cheek teeth, in the reverse way, the outer row of cusps is elevated in respect to the lingual one. In the cutting edge of the lower premolars the original differentiation into cusps and valleys is still visible: the cusps are marked by the projections, the valleys by the notches of the saw-like blade of the transversely compressed crown; the ribs are located on the flanks of the original cusps (fig. 7). What has happened to the outer row of cusps? These are reduced to basal cuspules which are well preserved on $p_{3,4}$ of the Guimarota species; on $p_{1,2}$ they are lost. The cuspules are only a quarter as high as the cutting edge and each of them corresponds to one of the projections on its edge. Between the cutting edge and the row of basal cuspules the original longitudinal valley is retained. It is closed at the posterior end by a slightly elevated rim.

The evolutionary change visible in the lower premolars among the Plagiaulacoidea is important in two respects: the morphological alterations, and the change in use of these teeth.

The morphological alterations of the lower premolars visible from Kimmeridgian time to early Tertiary are the most «orthogenetic» trend known among multituberculates. In *Paulchoffatia* and *Kuehneodon* (fig. 8-10) only a slight difference in length between $p_{2,4}$ is visible. The maximum number of projections on the cutting edge is limited to four; the tendency to evolve a fifth projection is weakly represented. The number of projections corresponds to that of basal cuspules as far as known.

In the latest Jurassic (Purbeck and Morrison faunas) the lower premolars are much more differentiated in length (fig. 2d-h); p_4 is twice as long as p_3 and the shearing edge contains 6 to 8 projections, whereas the projections on p_3 are limited to 3-5. In table II the number of projections in the Plagiaulacoid taxa is compiled. The basal cuspules are much more reduced than in Kimmeridgian species. Only in *Psalodon? marshi* does their number correspond with that of the projections on the cutting edge

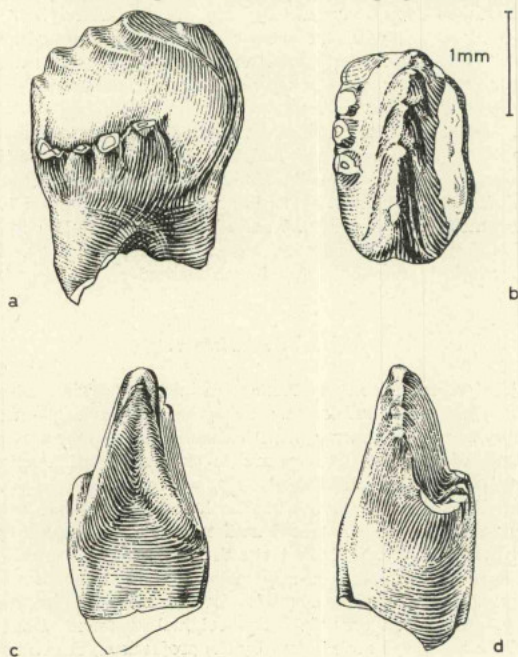


Fig. 7—An isolated right p_4 from the Guimarota coal pit with an unworn cutting edge and a very well preserved row of basal cuspules.

a) Buccal view.—b) Crown view.—c) Front view.—d) Posterior view.

(see SIMPSON, 1929, pl. 4 fig. 2); in all other species fewer basal cusps than projections are visible. This is shown best in *Plagiaulax becklesi* (fig. 2h). In the Ptilodontidae and Taeniolabidoidea (with exception of the Taeniolabididae themselves which have lost cutting premolars completely) the shearing function is confined to the large, multi-serrated p_4 , whereas all other lower premolars are either entirely lost or at most p_3 is preserved as a pin-like tooth no longer in shearing function. Basal cuspules are fully lost, and the origin of the lower premolars from molar-like teeth can no longer be recognized.

Whilst the reduction of the anterior premolars and the extension of p_4 evolved continuously, change in the use of the premolars occurred suddenly with an unexpected rapidity. After Purbeckian and Morrison time all multituberculates which have pre-

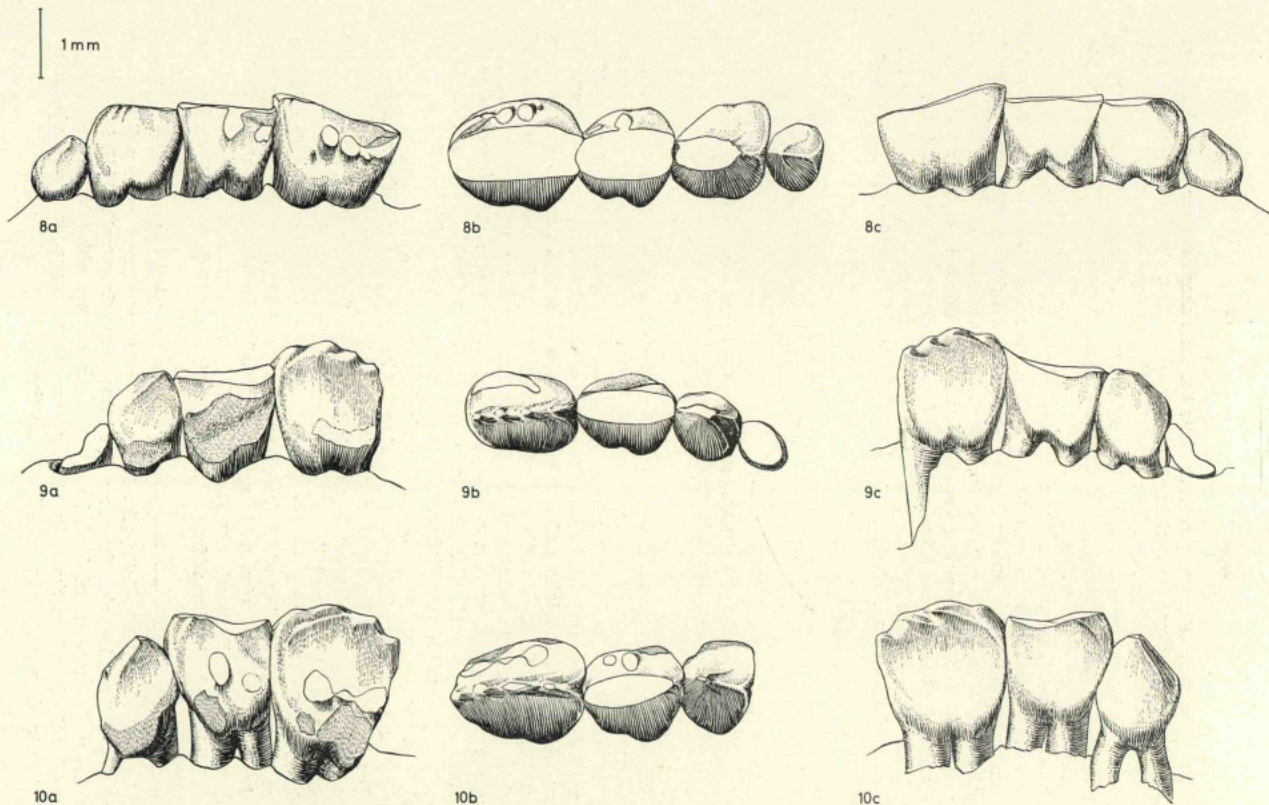


Fig. 8-10 — Lower premolars of the Paulchoffiatiidae from the Guimarota coal pit. The cutting edge and the basal cuspules are slightly worn.

- 8 — *Paulchoffatia delgadoi*. — a) Buccal view. — b) Crown view. — c) Lingual view.
 9 — *Kuehneodon dietrichi*. — a) Buccal view. — b) Crown view. — c) Lingual view.
 10 — *Kuehneodon guimarotensis*. — a) Buccal view. — b) Crown view. — c) Lingual view.

served their cutting edge use it in cutting their food. Not so in *Paulchoffatia* and *Kuehneodon*; although the lower premolars show the same shape as their younger relatives they are used grinding, not cutting! In the young tooth first the basal cuspules were eroded, then the cutting edge itself became more and more lowered. In fig. 8-10 different stages of this process are represented. The highest degree of erosion is seen in fig. 11. In this stage the original shape of the tooth has been completely lost, its function now is the same as the worn molars.

This very perplexing use of the premolars is confined to Kimmeridgian time as far as known. In the Purbeckian members of the Paulchoffatiidae the cutting use has come into function in the same manner as in the Plagiaulacidae. This change in use must have happened very suddenly, and it is understood only in relationship to the transformation of the upper premolars (see p. 23). For the cutting edges in *Paulchoffatia* and *Kuehneodon* are fully evolved and the reason for their grinding use can be found only in the upper premolars. The structure of the lower premolars in the Kimmeridgian Paulchoffatiidae is one of the best examples for pre-adaption known among mammals.



Fig. 11 — ?*Paulchoffatia delgadoi*. — Buccal view of $p_{1.4}$ in an extreme stage of wear.

This change from grinding to cutting premolars is one of the most important evolutionary modifications in the multituberculates only comparable with the transformation of the incisors into gnawing instruments. The change brings establishment of the «multituberculate» type of dentition with grasping incisors, cutting premolars and grinding molars. *Paulchoffatia* and *Kuehneodon* show a much more primitive functional stage: not only are all cheek teeth used in grinding, but also the incisors were involved. Here we see the multituberculates at the very beginning of a new adaption, for it is obvious that the cutting function of the premolars made new sorts of food (for instance hard seeds) available which had been inaccessible to *Paulchoffatia* and *Kuehneodon*. In these genera the «multituberculate» type of dentition is visible in statu nascendi, evolved to a pre-adaptive stage but not realised in function. In this respect the Kimmeridgian genera represent the most primitive habit known in multituberculates.

Very probably the change from grinding to cutting premolars occurred independently in the Paulchoffatiidae and in the Plagiaulacidae. Both families differ so much in the structure of the i^1 and the m_2 that it seems impossible to derive the second from the first. The Guimarota coal pit has delivered only members of the Paulchoffatiidae; no i^1 or m_2 of Plagiaulacid pattern has come to light. It seems that biogeographical borders otherwise unknown to us are responsible for the circumstance that in the Kimmeridgian of Portugal only Paulchoffatiidae are present, in the Morrison of North America only Plagiaulacidae. In the Purbeckian of England both families are represented.

The number of the upper premolars is 6 in *Paulchoffatia* and 5 in all other known Plagiaulacoidea. In *Paulchoffatia* (fig. 12) not only the number of upper p differs from that of its relatives, but also the group-formation among these teeth. While in *Kuehneodon*, *Bolodon*, *Ctenacodon* and *Psilonodon* p^{1-3} form one group which is clearly separated from p^{4-5} by the length of the teeth and arrangement of cusps, in *Paulchoffatia* p^{1-5} are similar in shape and only p^6 differs from them.

TABLE II

	Genus and species	P ₁	P ₂	P ₃	P ₄
Plagiaulacidae	<i>Plagiaulax becklesi</i>	—	1	5	8
	<i>Ctenacodon serratus</i>	1	?2	3	6
	<i>Ctenacodon? falconeri</i>	?	3	4	8
	<i>Ctenacodon scindens</i>	?	?	3	6
Paulchoffatiidae	<i>Pliopriion minor</i>	1	3	4	7
	<i>Kuehneodon dietrichi</i>	1	1	3-4	4
	<i>Kuehneodon guimarotensis</i>	—	1	3-4	4
	<i>Paulchoffatia delgadoi</i>	1	1	3-4	4

The number of projections on the cutting edge of the lower premolars in the Plagiaulacoidea. *Psalodon? marshi* is not included in this table, because the number of projections is not stated in SIMPSON, 1929, p. 28.

The anterior upper premolars (p¹⁻⁵ in *Paulchoffatia*, p¹⁻³ in all others) are rounded in shape with 3-4 cusps. A tricuspid crown, not otherwise complicated, is found in *Bolodon crassidens* (fig. 14a), *B. osborni* (fig. 14b) and *Ctenacodon laticeps* (fig. 15b). In these species the cusps are arranged in a triangular pattern and all the teeth are set close together. In «*Bolodon*» *elongatus* (fig. 14c) p¹⁻³ are also tricuspid, but they are lengthened and each shows a distinct heel unknown in other Plagiaulacoid species. Therefore grouping of this species with *Bolodon* seems to be wrong and it may be better to regard *elongatus* as a member of an independent, inadequately known genus. p¹⁻² of *Psalodon potens* (fig. 15a) resemble those of the other mentioned species, but p³ shows unique features. SIMPSON, 1929, p. 26 describes that tooth as follows: «The posterointernal cusp is much smaller, while the external cusp is smaller still—a mere projection on the confluent slopes of the other two. It is also more anterior in position than in the preceding teeth».

In the Kimmeridgian genera not three but four cusps are present on the anterior upper premolars—a very unexpected feature. In p¹ of *Paulchoffatia delgadoi* and in p² of *Kuehneodon simpsoni* (fig. 12-13) the fourth, antero-buccal cusp is still in a rudimentary stage but nevertheless these teeth are tetracuspid. In p³ of *K. simpsoni* and in p² and p⁵ of *P. delgadoi* a tendency to evolve a fifth cusp is indicated.

If one understands the addition of cusps on the anterior premolars as a derived evolutionary stage in respect to a primitive unicuspid or bicuspid pattern, the known Kimmeridgian Paulchoffatiidae are more specialised than their Purbeckian relatives and they cannot be ancestral to them. In addition to the well known species of *Paulchoffatia* and *Kuehneodon* in the Guimarota coal pit some isolated p¹ have been found with only three or even two cusps on the crown (fig. 16). From these otherwise unknown taxa the structure of the p¹⁻³ in the younger Paulchoffatiidae and the Plagiaulacidae may be derived. Whereas in *Paulchoffatia delgadoi* all premolars are arranged close together, in *Kuehneodon simpsoni* p¹ is separated from p² by a short diastema.

p¹ deserves special attention. This member of the tooth row differs from all other premolars in having only one, very large root. This feature is well known in *Paulchoffatia*, *Kuehneodon* and some isolated teeth from the Guimarota coal pit; in the Purbeckian and Morrison taxa the number of roots is not reported, but I think that the p¹ may be one-rooted in them also. W. G. KUEHNE, 1961, p. 378-379—having at

hand only a palate with the alveoli but lacking teeth—was the first to interpret the large first alveolus of the maxillary as that for the canine. Remembering the highly complicated structure of the i^3 , not seen in other mammals, it seems possible that in a similar way the canine may have become premolariform and therefore the « p^1 » is not a true premolar.

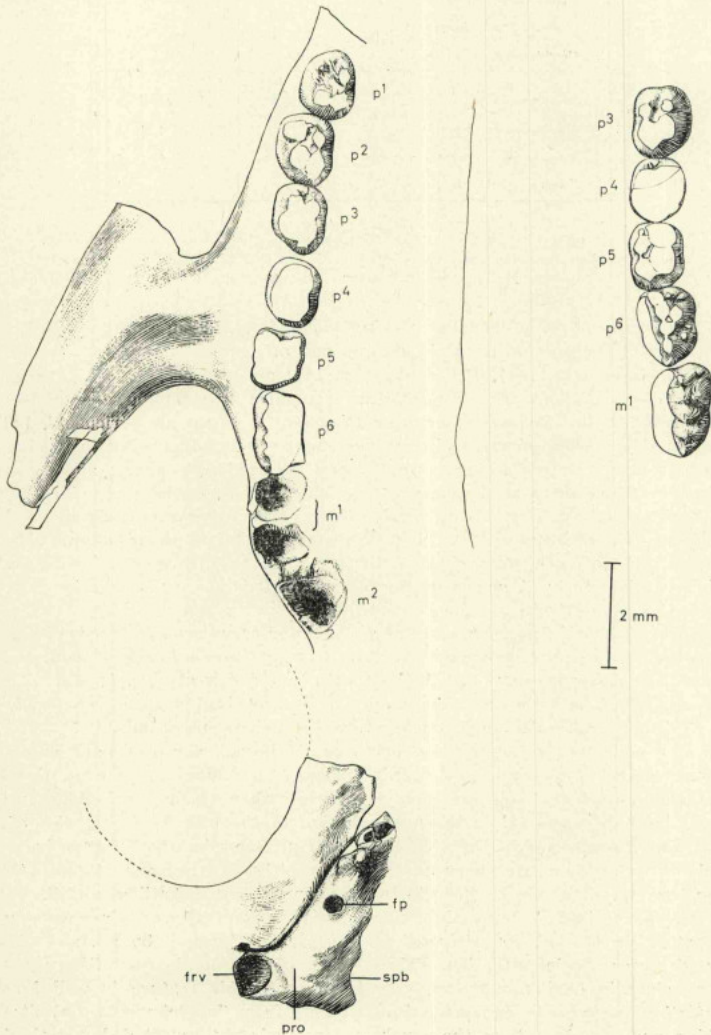


Fig. 12 — *Paulchoffatia delgadoi*. — The teeth of the upper jaw.

The posterior premolars (p^{4-5}) resemble the molars and carry two rows of 2-4 cusps. In *Kuehneodon simpsoni* the lingual row of cusps is similar in structure to the outer one; they both were used in grinding. But in *Psalodon* and *Ctenacodon* the cusps of the lingual row are depressed laterally, producing a steep, abraded slope which worked against the shearing edge of the lower premolars in the cutting process. In *Bolodon* these morphological features are not so clearly expressed (the lingual faces

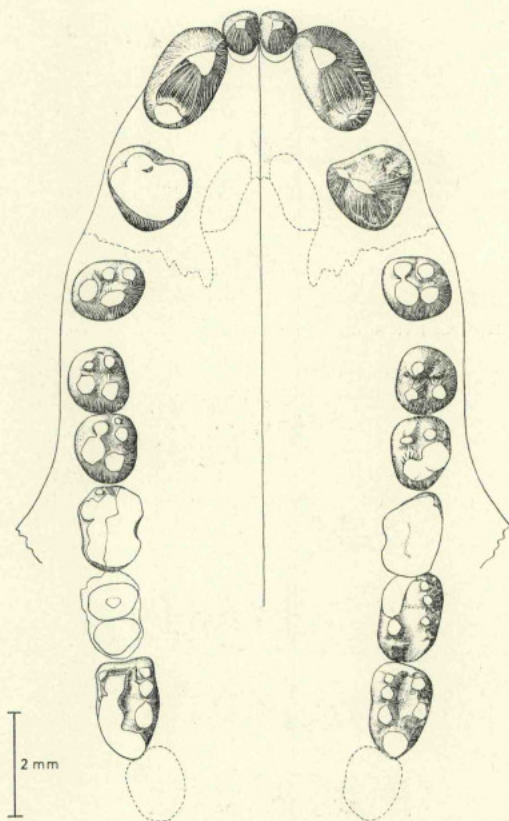


Fig. 13 — *Kuehneodon simpsoni*. — The teeth of the upper jaw.

of p^{4-5} are hardly eroded in *B. crassidens* and *B. osborni*) but their function is the same as the aforementioned North American taxa. This relatively slight morphological distinction in structure of the lingual row of cusps on the p^{4-5} reflects an important difference in use of the premolars between the Kimmeridgian and the younger Plagiolacoidae.

The p^6 of *Paulchoffatia* differs from the posterior premolars of all other Plagiaulacoidae in the presence of a third, buccal row of cusps. This additional row consists of 5 cusps, the central one being the largest, the two anterior and the two posterior are much smaller. No tendency to form a lingual slope as an antagonist to the cutting edge of the lower p is visible. The development of a third cusp row is unique among the Plagiaulacoidea. It is not comparable to the third rows in the upper molars of Cre-

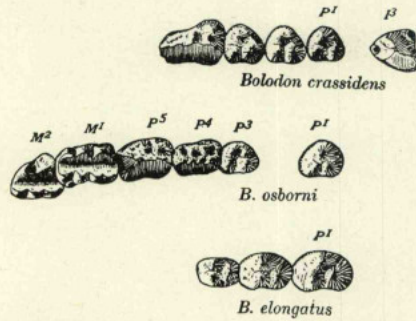


Fig. 14 — The teeth of the upper jaw in *Bolodon*, after SIMPSON, 1928.

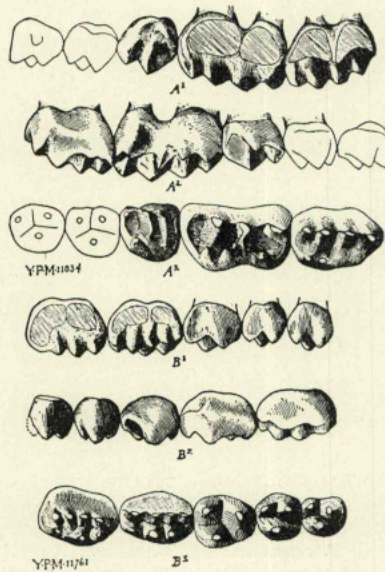


Fig. 15 — The upper premolars of the North American Plagiaulacoids, after SIMPSON, 1929.

- a) *Psalodon potens*, in lingual, buccal and crown view.
- b) *Otenacodon laticeps*, in lingual, buccal and crown view.

taceous and Tertiary multituberculates. In those the third cusp row is evolved in order to compensate for the diagonal course of the lower tooth row, whereas in *Paulchoffatia* this row is evolved on the last upper premolar, increasing the chewing function of that tooth!

The described patterns of upper and lower premolars show specialisation in various directions. This diversity is enriched by some isolated teeth from the Guimarota coal pit which do not correspond to any of the known Plagiaulacoid species, thus showing that our knowledge of these animals is by no means complete. The most puzzling of those strange teeth is *Guimarotodon leiriensis*, described by the author 1969, p. 83-85 and figured there on pl. 10 fig. 50 a-c and in text-fig. 84.

The number of cusps in the Plagiaulacoid upper premolars is compiled in table III.

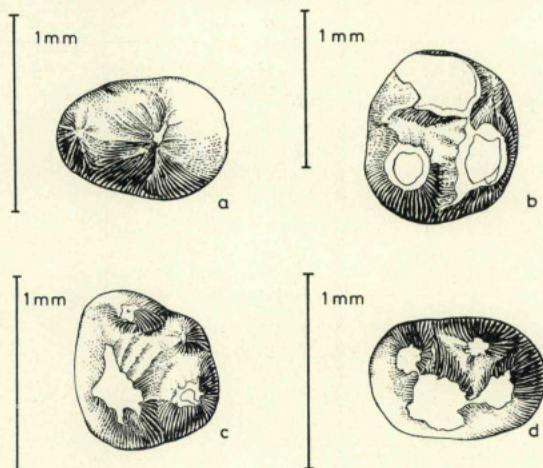


Fig. 16—Isolated upper p^1 of the Paulchoffatiidae from the Guimarota coal pit. The number of cusps is 2-4. All teeth are characterised by having only one root. The left lower tooth (c) resembles the p of *Paulchoffatia delgadoi*, the right lower one (d) that of *Kuehneodon simpsoni*. The right upper tooth (b) is similar to the p^1 in the Purbeckian and Morrison forms, whereas teeth similar to the left upper p^1 (a) are unknown in situ.

THE MOLARS.

The number of molars, $\frac{2}{2}$, is constant in all multituberculates from the Kimmeridgian to the Eocene. In all Plagiaulacoidea the crowns of the upper m and m_1 have two longitudinal rows of cusps; in the Plagiaulacidae m_2 shows the same morphology. However in the Paulchoffatiidae this tooth has a completely different form. This is one of the reasons for erecting a new family for *Paulchoffatia* and its relatives. The number of cusps in Plagiaulacoid molars is compiled in table IV.

In the first lower molar the number of cusps in the outer row is 2-4, in the lingual row 2-3. In the Paulchoffatiidae the outer row has more cusps than the lingual one (3 to 2 in *Plioprius minor*, 3-4 to 2-3 in the Guimarota forms); in the Plagiaulacidae the number of cusps is equal in both rows (3 to 3 in *Ctenacodon serratus* and *C. scindens*) or the inner row has more (2 to 3 in *Plagiaulax becklesi*). Besides number of cusps,

minor differences are seen in height and distinctness of the cusps of the Guimarota teeth (fig. 17-18) ^(*).

The second lower molar of the Paulchoffattidae is known by 19 isolated specimens from the Guimarota coal pit and by m_2 of *Pliopriion minor*. In the latter the m_2 — formerly present — is now missing. The structure of the crown in the Paulchoffatiid- m_2 is quite different from that of m_1 : There are no rows of cusps, but the crown is deeply basined, bordered by an elevated rim. Only the antero-lingual corner does one cusp arise, which is not separated from the anterior part of the elevated rim. This

TABLE III

	Genus and species	p^1	p^2	p^3	p^4		p^5		p^6	
					b	l	b	l	b	
Plagiulacidae	<i>Otenacodon laticeps</i>	3	3	3	3	4	2+	4	—	—
	<i>Psalodon potens</i>	3	3	3	3	4	2	4	—	—
Paulchoffatiidae	<i>Bolodon crassidens</i>	3	3	3	4	?				
	<i>Bolodon osborni</i>	3	?	3+	3	4	2	?4	—	—
	<i>Bolodon? elongatus</i>	3	3	3						
	<i>Kuehneodon simpsoni</i>	4	4	4+	?	?	3+	3?	—	—
	<i>Paulchoffatia delgadoi</i>	3+	4	4	?		4		5+4	5

The number of cusps on the upper premolars of the Plagiulacidae.

b = buccal, l = lingual.

rim bears — if uneroded — a number of denticles on its anterior and outer parts. It is interrupted only behind the antero-lingual cusp by a narrow but deeply incised valley. Posterior to the valley the ridge is somewhat swollen, and, if eroded, it resembles a little worn cusp. A remarkable diversity occurs in shape and length of m_2 (fig. 19).

This singularly constructed type of m_2 was long known in *Pliopriion minor*. It was described and figured by many of the older students but not noted as a new, unique type of multituberculate tooth. In 1928, when SIMPSON re-examined the English Mesozoic mammals, this tooth was lost! Therefore one does not wonder that SIMPSON did not accept such a great morphological difference between m_1 and m_2 , and explained the structure of the m_2 as the product of erosion (1928, pp. 39-40):

«It is extremely unfortunate that the crown of the m_2 , which seems at one time to have been present and essentially complete, is now entirely missing, only the roots remaining. As described by FALCONER, OWEN and OSBORN, the tooth has a broadly basined interior with an elevated rim, the outer part of the rim appearing to bear a number of denticles, the inner part with one prominent anterior cusp, followed by a prolonged ridge not divided into cusps. This concurrence of high authority can leave no question as to the general morphology of the tooth, despite its unfortunate loss, but a great deal of doubt still remains as to the interpretation of these facts. The following considerations seems to lead to a rather different conclusion from that hitherto held:

(*) In *Paulchoffatia* and *Kuehneodon* the lower molars are not present in situ, but 15 isolated m_1 and 19 isolated m_2 are known. It must be repeated that all known m_2 without exception belong to the Paulchoffatiid-type as characterised below and that no m_2 of the Plagiulacidae-pattern has been found. From this it follows that both the named genera agree in the principal structure of the m_2 (as they do in the p^1) and that they both must be grouped with the Paulchoffatiidae.

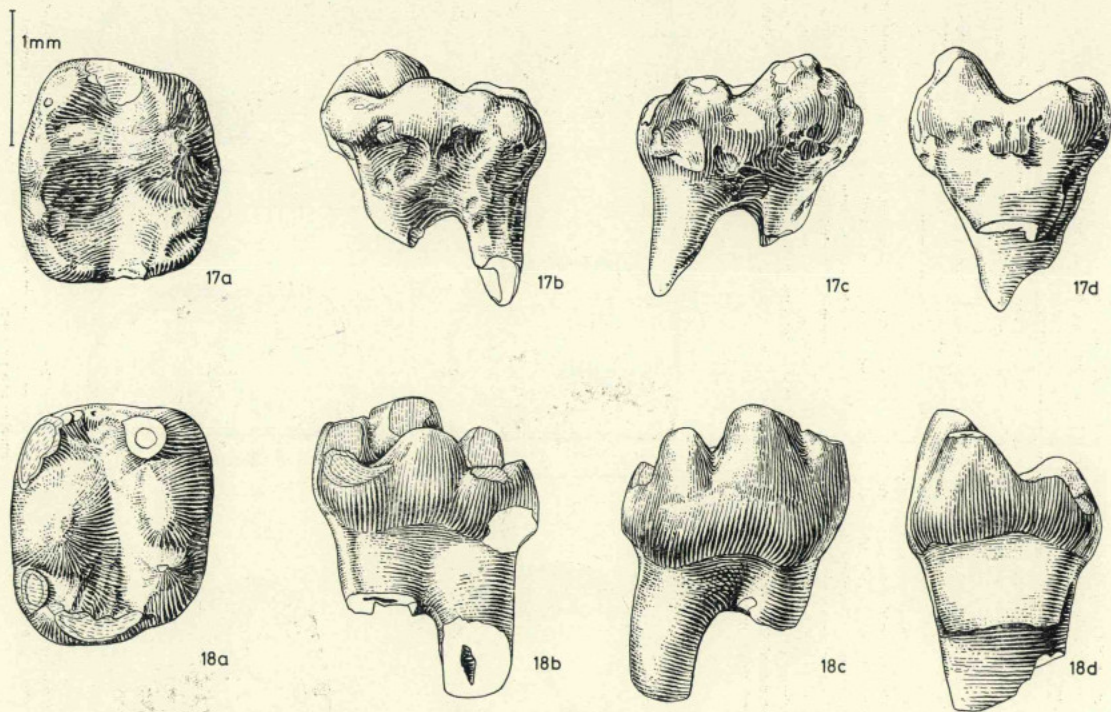


Fig. 17-18 — Two different left Paulchoffatiid-m, from the Guimarota coal pit. The tooth in the upper row is characterised by low, blunt cusps, that of the lower row by better differentiated, higher cusps.
a) Crown view. — b) Buccal view. — c) Lingual view. — d) Anterior view.

1. The individual is fully adult and the teeth are much worn, m_2 being, among plagiaulacids, the tooth which receives the most severe usage of all.

2. The broadly basined nature of the crown, as figured and described, clearly indicates advanced wear.

3. Except for this tooth, the jaw agrees in all essential features with those of the American species of *Ctenacodon*, but in the latter m_2 is positively known to have had a simple pattern of six cusps in two rows of three each. Its seems extremely improbable that the English form would agree so well in other respects and differ so violently in this one point.

4. In some worn American specimens of *Ctenacodon*, however, an apparently multicuspidate outer row is developed by the wearing through the enamel, and it seems at least possible that this had happened in *C. minor*, making it seem that there were many small cusps in the outer row whereas there may have been originally but three.

5. These considerations are further strengthened by the improbability that m_2 would differ so much from m_1 . While not identical, these two teeth are at least built on the same plan in all other Jurassic multituberculate jaws, upper and lower, in which the facts are known.

While it is necessary to recognize that only a reasonable probability can be established in the absence of the original tooth, yet it seems a just conclusion that the apparently unique form of m_2 of this specimen was simply due to wear, and that originally it was a simple tooth with five or six cusps arranged in two parallel rows. At least, this appears to be the hypothesis upon which we must proceed until more material is secured.

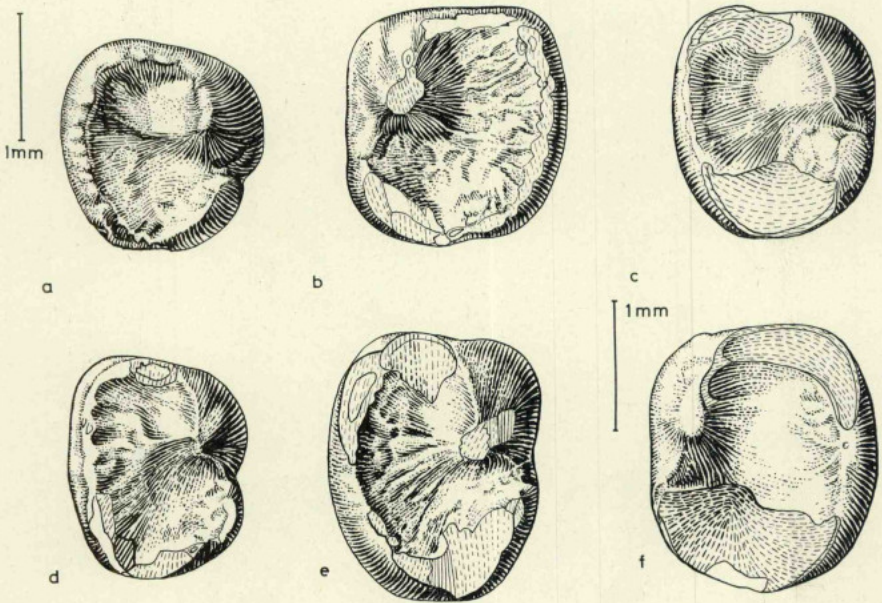


Fig. 19.—Different isolated Paulchoffatiid- m_2 from the Guimarota coal pit, belonging to *Paulchoffatia* and *Kuehneodon*. The remarkable difference in shape suggests that the teeth of several species are present.

a, c, d, e are left m_2 , b and f are right m_2 .

The Guimarota material now at hand proves that this singular type of tooth really exists and that it is confined to m_2 , whereas the associated m_1 shows a «normal» construction as in all other Plagiaulacoids. With this a very important diagnostic feature is recognized, marking a hitherto unknown phylogenetic line in multituberculate evolution, which is set apart systematically as the family Paulchoffatiidae.

In comparison to the multicuspitate m_2 of the Plagiaulacidae the basin-shaped m_2 of the Paulchoffatiidae seems to be highly specialised. Despite of the fact that no connecting link between normal crowned molars and the Paulchoffatiid- m_2 is known to day, it seems inevitable that the structure of the last must have evolved from that of the first. In order to change the structure of the crown so fundamentally, a long time of evolution must have passed. Therefore the common root of the Plagiaulacidae and the Paulchoffatiidae can be expected in the Middle Jurassic at the earliest, perhaps only in the Liassic. Further discoveries of the multituberculates older than Kimmeridgian in age are needed to solve this problem.

TABLE IV

	Genus and species	Lower jaw				Upper jaw			
		m_1		m_2		m^1		m^2	
		b	l	b	l	b	l	b	l
Plagiaulacidae	<i>Plagiaulax becklesi</i>	2	3	?	?				
	<i>Ctenacodon serratus</i>	3	3	3	3				
	<i>Ctenacodon scindens</i>	3	3	3	3				
	<i>Ctenacodon laticeps</i>					4+	4+	2	3
Paulchoffatiidae	<i>Pliopriion minor</i>	3	2	0	1				
	<i>Bolodon osborni</i>					3	4	2	3
	<i>Kuehneodon simpsoni</i>					2	4		
	<i>Paulchoffatia delgadoi</i>					1/4-5	3	2	3-4
	Isolated m of the Guimarota coal pit, belonging to <i>Paulchoffatia</i> and <i>Kuehneodon</i>	3-4	2-3	0	1			2-3+	3-6

The number of cusps on the molars of the Plagiaulacoidea.
b = buccal, l = lingual.

In the upper jaw both m^1 and m^2 have two rows of cusps. In both these teeth the lingual row consists of more cusps (3-6) than the buccal one (2-5). The number of cusps in the known species can be seen in table IV.

In m^1 the crown pattern differs in some details. In *Bolodon osborni* (fig. 14b) as in *Ctenacodon laticeps* both rows of cusps run straight from front to back without any other complication. But in *Kuehneodon simpsoni* the lingual row is curved in such a way that its last cusp bars the posterior end of the longitudinal valley between the cusp rows, as the row turns toward the postero-buccal border of the tooth (fig. 21). In *Paulchoffatia delgadoi* both the rows are parallel as in the first mentioned taxa, but in this species the tendency to develop a third row of cusps (as in the p^0) is introduced by a large cusp situated antero-buccal to the outer row of cusps. This feature is unknown in the other Plagiaulacoidea (fig. 20).

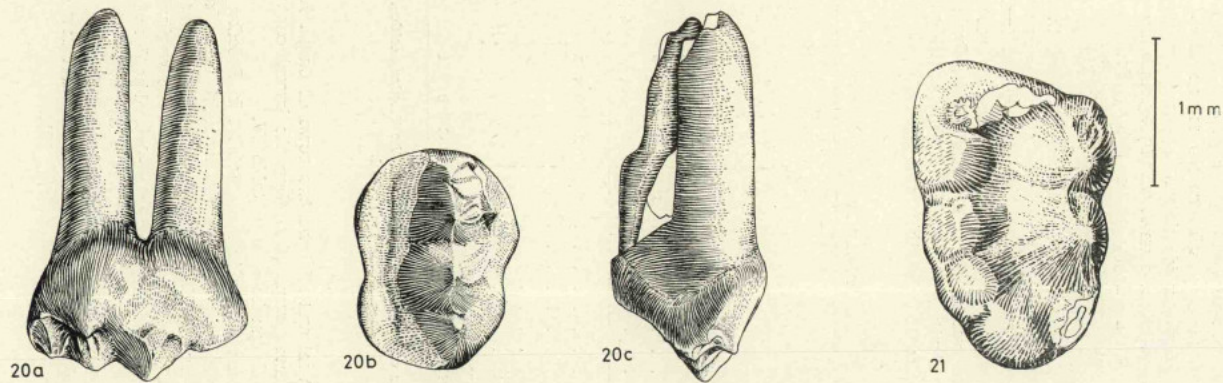


Fig. 20-21 — Upper m¹ of the Kimmeridgian Paulchoffatiidae.
 20 — Left m¹ of *Paulchoffatia*, characterised by the tendency to develop a third row of cusps. — a) Buccal view. — b) Crown view. — c) Anterior view.
 21 — Left m¹ of *Kuehneodon*, characterised by the curved course of the lingual row of cusps which blocks the median valley at its posterior end.

There is a remarkable difference in position of m^2 in respect to m^1 between *Paulchoffatia* and other genera. In *P. delgadoi* this tooth is situated directly behind m^1 (G. HAHN, 1969, pl. 5 fig. 20), in the other genera it is shifted inwards. The reason for this change in position is discussed on p. 10. In *Paulchoffatia* the anterior border of the m^2 is rounded similar to all other teeth; in the other Plagiaulacoidea this border is angulated because only the antero-buccal corner of m^2 contacts the posterior wall of m^1 , the antero-lingual does not. This difference in structure of the anterior border is most important in order to recognize the systematic position of the isolated Guimarota- m^2 . Some have a rounded anterior border while others have an angulated anterior border (fig. 22). As the first kind may belong to *Paulchoffatia*, the second can be grouped with *Kuehneodon* (where the m^2 is missing in situ). In this genus the lower tooth row runs diagonally across the jaw and consequently an inward-shifted m^2 should be expected.

Besides the structure of the anterior border, the Guimarota- m^2 show a remarkable diversity in shape, number of cusps and construction of the antero-buccal cusp. In some of the specimens this cusp is conical as in other Plagiaulacoidea, but in the majority of isolated m^2 it is complicated by a shelf-like broadening (fig. 22c), by a ridge running into the antero-buccal corner of the tooth (fig. 22b) or by the existence of a secondary cusp which evolves from a ridge-like structure projecting back from the anterior border (fig. 22a). These different peculiarities found in the structure of the first outer cusp are discussed and figured in detail in G. HAHN, 1969, pp. 81-83 and fig. 82a-e. They show that in the Paulchoffatiidae the m^2 — which is not so strongly differentiated as the m_2 — is nevertheless of more complicated build than in the Plagiaulacidae. This again emphasises the independent evolution of the Paulchoffatiidae. In *Bolodon osborni* the antero-buccal cusp of the m^2 shows a prominent shelf-like extension similar to that shown in fig. 22c.

Finally it should be mentioned that the roots of both the upper and lower second molars often tend to grow together; in some specimens they become confluent. In the premolars and the first molars of the Guimarota multituberculatus this tendency is not developed. Therefore this feature helps in identification of isolated m^2 when the crown pattern is eroded or destroyed by postmortem influence.

THE RELATIONSHIP OF THE PAULCHOFFATIID TAXA.

Having discussed in the preceding chapters the details of the Paulchoffatiid dentition, one can try now to compile the morphological features in order to draw the outlines of the Paulchoffatiid evolution as known today. This family is distributed in time from the Kimmeridgian to the Purbeckian (and perhaps the Wealden); geographically it is confined to Europe. The referred taxa are known from the following localities:

1. Kimmeridgian of the Guimarota coal pit near Leiria, Portugal: *Paulchoffatia delgadoi*, *Kuehneodon dietrichi*, *K. guimarotensis*, *K. simpsoni*; also many isolated teeth and *Guimarotodon leiriensis* are present.
2. Middle Purbeckian of Durdlestone Bay, Swanage, Dorset, England: *Plioprius minor*, *Bolodon crassidens*, *B. osborni* and «*B.*» *elongatus*.
3. Wealden of Cliff End Bone Bed, England: perhaps one or several of the isolated teeth grouped by CLEMENS, 1963 with *Loxaulax valdensis* belong to a Paulchoffatiid genus, for instance the P^1 (text-fig. 5 in CLEMENS) or the tetracusp upper p (text-fig. 4 in CLEMENS).

These taxa of the Paulchoffatiidae represent three evolutionary stages. *Paulchoffatia delgadoi* persisted from the most primitive level. This genus is characterised by the following primitive features:

1. In contrast to all other known multituberculates the lower tooth row runs parallel to the border of the jaw; the molars are not shifted inwards, the anterior premolars are not shifted outwards.
2. The lower premolars are little differentiated in length, they are used grinding, not cutting.
3. The lower incisor is implanted very steeply; its root rests immediately below the roots of the anterior premolars.
4. In the upper jaw 6 premolars are present, only the last being oblong and molar-like in shape.
5. The m^2 is not shifted inward but is situated immediately behind m^1 .

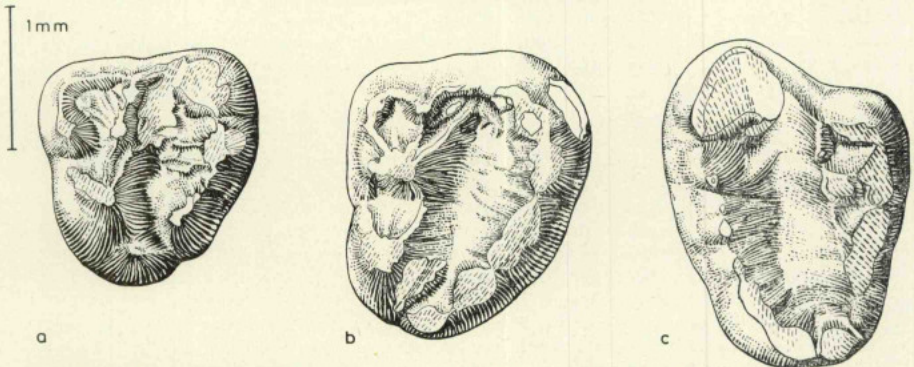


Fig. 22 — Different isolated *Paulchoffatiid*- m^2 from the Guimarota coal pit. — a and b are right m^2 ; they show a rounded anterior border and may belong to *Paulchoffatia*. c is a left m^2 ; it shows an angulated anterior border and may belong to *Kuehneodon*. The different structures of the anterior buccal cusp are visible.

With these characteristics *Paulchoffatia* can be regarded as a structural model, from which all other multituberculates may have derived. This genus is a model, but not a real forerunner. First *Paulchoffatia* shows the specialisations in the i^3 and m^2 , which are diagnostic for its family and which exclude it from the evolutionary lineages of all non-paulchoffatiid multituberculates. Secondly, the presence of tetracuspoid anterior premolars in the upper jaw and the tendency to evolve a third row of cusps on p^3-m^1 also exclude *Paulchoffatia* from the direct ancestry of *Bolodon*, and finally, the last mentioned feature and the temporal distribution exclude it also from the ancestry of *Kuehneodon*.

Unfortunately this most primitive known multituberculate genus is not part of the ancestry of all other multituberculate genera! *Paulchoffatia* can be best understood as a remnant of a pre-Kimmeridgian radiation, persisting on a very primitive level but equipped with some peculiar specialisations. It was a «living fossil» in Kimmeridgian time. This singular position among the multituberculates — also among the remaining *Paulchoffatiid* genera — should be given greater emphasis than the author gave it in 1969. Therefore I propose to erect a new subfamily for *Paulchoffatia* — *Paulchoffatiinae* — in contrast to the *Kuehneodontinae* including *Kuehneodon*, *Pliopriion* and *Bolodon*.

The second evolutionary stage is represented by *Kuehneodon*. This genus shows — in contrast to *Paulchoffatia* — progressive tendencies in the following features:

1. The lower tooth row runs diagonally in respect to the border of the jaw.
2. The lower incisor is implanted more procumbently, its root is situated beside rather than directly below the roots of the anterior premolars.

3. In the upper jaw only 5 premolars are present, p_{1-3} are rounded in shape; p_{4-5} are oblong, similar to the molars.
4. The upper m^2 is shifted inward in respect to m^1 .

In all these features *Kuehneodon* resembles the younger, Purbeckian and Morriston multituberculates, not only members of the Paulchoffatiidae but also the Plagiaulacidae. Differences from these forms — being unequivocally primitive ones — are found in the structure of the lower premolars:

1. These teeth are little differentiated in length, as in *Paulchoffatia*.
2. They are used in grinding, not cutting, again as in *Paulchoffatia*.
3. The basal cusps are very well marked, also as in *Paulchoffatia*.

With these characteristics *Kuehneodon dietrichi* is perhaps a real ancestor for younger members of the Paulchoffatiidae (*Pliprion minor*). It is excluded from the ancestry of the Plagiaulacidae by only the structure of the m_2 . *Kuehneodon guimaroensis*, specialised by the loss of the p_1 and the presence of a step on the alveolar border in front of p_2 , represents a side branch not ancestral to any other known Plagiaulacoid.

In the upper jaw *Kuehneodon simpsoni* is similar to *Bolodon crassidens* and *B. osborni*. But a direct ancestry is again impossible, because the anterior upper premolars in *Bolodon* are tricuspid, whereas in *Kuehneodon* they are tetracuspid. Besides, the arrangement of cusps on the i^3 is different in *K. simpsoni* and *B. crassidens*.

The third, youngest known evolutionary stage among the Paulchoffatiidae is represented by the Purbeckian and Wealden species. They most clearly differ from *Kuehneodon* in the more progressive structure of the lower premolars:

1. These teeth are well differentiated in length, p_1 being much longer than p_2 .
2. They are used cutting.
3. The basal cusps are reduced to a greater degree than in *Kuehneodon*, but they are still present.

With this the Purbeckian Paulchoffatiids have reached the same evolutionary level as the contemporaneous Plagiaulacidae, differing from them in the structure of i^3 and m_2 . *Pliprion minor* is much smaller than *Kuehneodon dietrichi*, but otherwise it shows no features which hinder suggestion of its descent from that species. The species of *Bolodon* — also being smaller than the Kimmeridgian forms (*) — can not have descended from *Kuehneodon simpsoni*, as is shown above. But among the isolated teeth of the Guimarota coal pit tricuspid anterior premolars of the upper jaw as well as i^3 of the *Bolodon* pattern are present. This shows that the ancestors of *Bolodon*, perhaps already belonging to this genus, may have existed in the surroundings of Leiria with *Kuehneodon*. It has been shown that because of its heeled p_{1-3} «*Bolodon*» *elongatus* may belong to another genus (p. 21).

Loxaulax valdensis from the Wealden requires a short discussion. This taxon is now known by seven teeth doubtfully referred to the same species. The type specimen, a peculiar lower molar with subselenodont cusps in one of the cusp rows, does not resemble any of the Paulchoffatiid molars. Its subselenodont pattern is a progressive feature and should be expected in Plagiaulacids rather than in the Paulchoffatiids. Among the teeth describes by CLEMENS, 1963 and referred to *valdensis* are a tetracuspid upper premolar and a i^2 with a divided posterior cusp, which can be grouped much better with the Paulchoffatiidae than with the Plagiaulacidae. Therefore the grouping of all

(*) It is a remarkable fact that all known Kimmeridgian Plagiaulacoida are larger than their younger relatives.

these teeth with *Loxaulax valdensis* may be wrong. It seems more acceptable to suppose that—as in the Jurassic deposits—in the Wealden more than one multituberculate species is present and that some of the teeth belong to the Paulchoffatiids, others to the Plagiaulacids.

Summarising the facts on the evolution of the Paulchoffatiidae one can state that the materials now at hand are sufficient to give an interesting insight into the principal problems of the evolution of that family, but that they fail to bring to light the individual evolutionary lineages. In fig. 23 the results of the preceding discussion are shown graphically. The reason for this incomplete knowledge is clearly visible in the small number of known mammal-bearing deposits in the Jurassic and Cretaceous. Remembering that the multituberculates were the ecological forerunners of rodents one will not be wrong to suppose that this group of mammals may have produced a similar great diversity of different species. If so, there is only a very small chance that ancestors and descendants of distinct evolutionary lineages are present in the material known today. The materials stored up in our museums are nothing but a minute sample of the great diversity of forms which must have lived in the days of the Jurassic. We can hope that by use of new methods in field-work—as that invented by HENKEL for instance—the remaining gaps may be closed and that knowledge of the evolution of this most interesting group of little mammals will be rapidly increased.

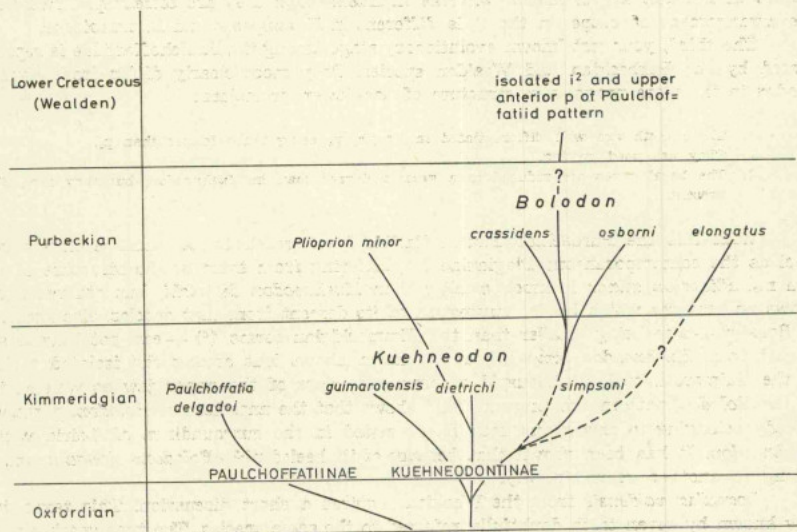


Fig. 23 — The supposed phylogenetic relationships of the known Paulchoffatiid taxa.

DIAGNOSES.

Suborder *Plagiaulacoidea* (SIMPSON, 1925), G. HAHN, 1969

Diagnosis. — A suborder of the Multituberculata with the following characteristics: Tooth formula $\frac{3.0.6-5.2}{1.0.4-3.2}$. i^1 unicuspid, i^2 enlarged, bicuspid, i^3 either similar to i^2 (but

smaller) or of different construction, tri- to tetracuspoid. Lower i more or less procumbently inserted, enlarged, with a conical crown curved upwards. Posterior p of the upper jaw morphologically similar to m, no distinct separation between these two kinds of teeth. p^{1-3} rounded, with 3-4 cusps; p^{4-6} and m^{1-2} with two longitudinal rows of cusps, 3-4 cusps in each; some tendency to evolve a third row of cusps on p^6-m^1 . Cheek teeth of the lower jaw well separated morphologically into p and m. Crowns of the p transformed into a high, transversally compressed cutting edge; number of serrations 3 to 8 on p_{3-4} ; $p_{1,4}$ with several buccally placed basal cuspules that are the last remains of the original buccal row of cusps. Use of the premolars in grinding or cutting. m_1 always with two rows of cusps, each with 2-4 cusps; m_2 either built similarly to m_1 or of different construction with a basin shaped interior surrounded by an elevated rim bearing only one antero-lingually situated cusp. All cusps of the upper p and m conical. p^4-m^2 and $m_{1,2}$ slightly different in length.—Skull retained lacrimal, but perhaps lacked jugal. Nasal bones relatively narrow. Petrosal with anterior lamina through which the nervus mandibularis passed. Brain cavity enlarged, mammal-like. Cerebellum and postotic portion of skull short, but something longer as in *Ptilodus*.

Formation and locality: In the Kimmeridgian of Portugal, in the Purbeckian and Wealden of England, in the Morrison Formation and Lower Cretaceous of the USA.

Included families: Plagiaulacidae GILL, 1872 and Paulchoffatiidae G. HAHN, 1969.

Family Plagiaulacidae GILL, 1872

Type genus: Plagiaulax FALCONER, 1857.

Diagnosis.—Typical family of the Plagiaulacoidea with the following characteristics: Tooth formula $\frac{3.0.5.2.}{1.0.4.3.2.}$. i^3 bicuspid, similar to i^2 in structure of the crown. m_2 with two longitudinal rows of cusps, similar to m_1 . Lower premolars used in cutting. p_4 distinctly longer than p_5 .

Formation and locality: In the Purbeckian and Wealden of England, in the Morrison Formation and the Lower Cretaceous of the USA.

Included genera: Plagiaulax FALCONER, 1857, *Otenacodon* MARSH, 1879, *Psalodon* SIMPSON, 1926 and *Loxaulax* SIMPSON, 1928.—The isolated teeth from the Trinity Sandstone, Texas, Lower Cretaceous, are not yet allocated to a genus.

Plagiaulax FALCONER, 1857

Type species: Plagiaulax becklesii FALCONER, 1857.

Diagnosis.—Type genus of the Plagiaulacidae, known only from the lower jaw, which has the following characteristics: Tooth formula $\frac{3.0.5.2.}{1.0.3.2.}$. p_1 missing, p_2 small, conical, not taking part in the cutting edge; p_3 with 5, p_4 with 8 serrations; serrations not confined to the cutting edge but running down on the flanks of the crown. m_1 with 2 buccal and 3 lingual cusps; on m_2 cusps eroded by wear. Jaw stout in its anterior part.

Formation and locality: In the Purbeckian and Wealden? of England.

Included species: *P. becklesi* FALCONER, 1857 and *P. dawsoni* SMITH WOODWARD, 1891.—Diagnosis and description of *P. becklesi* see in SIMPSON, 1928, pp. 33-36 and in RIDE, 1957, pp. 397-399, of *P. dawsoni* in SIMPSON, 1928, pp. 51-52.

Ctenacodon MARSH, 1879

Type species: Ctenacodon serratus MARSH, 1879.

Diagnosis. — A genus of the Plagiaulacidae with the following characteristics: Tooth formula $\frac{37.0.5.2.}{1.0.4.2.}$. p_1 small, conical, not taking part in the cutting edge; p_2 larger, included in the cutting edge. Number of serrations 2 on p_2 , 3-4 on p_3 and 6-8 on p_4 ; serrations confined to the cutting edge, not expanded on the flanks of the crowns. m_1 and m_2 each with 3 cusps buccal and 3 lingual in position. Lower jaw more slenderly built than in *Plagiaulax*. — Upper jaw with p^{1-3} tricuspid; number of cusps on p^4 , 3 buccal and 4 lingual, on p^5 , 2 buccal and 4 lingual, on m^1 , 4 buccal and 4 lingual, on m^2 , 2 buccal and 3 lingual. m^2 shifted inwards in respect to m^1 . Upper i unknown.

Formation and locality: Morrison Formation, USA; perhaps also in the Purbeckian of England.

Included species: *Ctenacodon serratus* MARSH, 1879 (lower jaw), *C. laticeps* (MARSH, 1881) (upper jaw, probably belonging to *C. serratus*, see SIMPSON, 1929, p. 15) and *C. scindens* SIMPSON, 1928 (lower jaw). — The systematic position of «*Ctenacodon*» *falconeri* (OWEN, 1871) remains doubtful, because the m_2 is unknown. — With this modification the genus *Ctenacodon* is restricted to 2 species, both from the Morrison Formation of the USA, whereas the European species formerly included in the genus are of doubtful systematic position (*falconeri*) or belong to the Paulchoffatiidae (*minor*). — Diagnosis and description of *C. serratus* in SIMPSON, 1929, pp. 16-20, of *C. laticeps* in SIMPSON, 1929, pp. 21-25, of *C. scindens* in SIMPSON, 1929, p. 20 and of *C.?* *falconeri* in SIMPSON, 1928, p. 41.

Psalodon SIMPSON, 1926

Type species: Ctenacodon potens MARSH, 1887.

Diagnosis. — A genus of the Plagiaulacidae with the following characteristics: Tooth formula $\frac{3.0.5.2.}{1.0.4.2.}$. i^2 enlarged, bicuspid; i^3 only half as large as i^2 , bicuspid. p^{1-2} with three conical cusps, crown of p^3 differently constructed with a transversely prolonged posterior cusp; p^{4-5} with 4 lingual cusps and 2-3 buccal cusps; buccal cusps smaller than lingual ones. Upper m unknown. Lower jaw (systematic position not certain) similar to *Ctenacodon*.

Formation and locality: Morrison Formation, USA.

Included species: *Psalodon potens* (MARSH, 1887) (upper jaw with p^{1-5}), *Psalodon fortis* (MARSH, 1887) (upper jaw with the incisors) and *P.?* *marshi* SIMPSON, 1929 (lower jaw). It is probable that all three parts of the dentition belong to one species [see SIMPSON, 1929, p. 15]. — Diagnosis and description of *P. potens* in SIMPSON, 1929, p. 26, of *P. fortis* in SIMPSON, 1929, pp. 26-27 and of *P.?* *marshi* in SIMPSON, 1929, pp. 27-28.

Loxaulax SIMPSON, 1928

Type species: Dipriodon valdensis SMITH WOODWARD, 1911.

Diagnosis. — A plagiaulacid genus, known only from isolated teeth with the following characteristics: Lower m with two rows of cusps 3 lingual and 4 buccal. Lingual cusps bunodont, buccal cusps, in contrast to all other Plagiaulacoidea, subselenodont.

Formation and locality: Wealden of England.

Included species: Only *L. valdensis* (SMITH WOODWARD, 1911). — The systematic allocation is secured for only the type specimen. As is discussed on p. 33-34 some other teeth grouped by CLEMENS with *L. valdensis* may belong to the Paulchoffatiidae.

Family Paulchoffatiidae G. HAHN, 1969

Type genus: Paulchoffatia W. G. KUEHNE, 1961.

Diagnosis. — A family of the Plagiaulacoidea with the following characteristics:

Tooth formula $\begin{smallmatrix} 3.0.6-5.2 \\ 1.0.4-3.2 \end{smallmatrix}$. i^3 enlarged, specialised, tricuspid or tetracuspid, dissimilar to i^2 . m_2 basin shaped, with an elevated rim and only one antero-lingual cusp, dissimilar to m_1 , which has two rows of cusps. Lower p used in grinding in the Kimmeridgian genera, but in cutting in *Plioprion*. p_4 (except in *Plioprion*) scarcely longer than p_3 .

Formation and locality: In the Kimmeridgian of Leiria, Portugal and in the Purbeckian of Swanage, England; perhaps also in the Wealden of England.

Included subfamilies: Paulchoffatiinae n. subfam. and Kuehneodontinae n. subfam.

Subfamily Paulchoffatiinae n. subfam.

Type genus: Paulchoffatia W. G. KUEHNE, 1961.

Diagnosis. — The typical subfamily of the Paulchoffatiidae with the following characteristics: Tooth formula $\begin{smallmatrix} 3.0.6.2 \\ 1.0.4.2 \end{smallmatrix}$. Lower tooth row, in contrast to all other Plagiaulacoidea, arranged parallel to the border of the lower jaw. Lower p functioned in grinding, p_{3-4} little differentiated in length with 3-4 serrations. Upper premolars 6 in number, of different morphology than in all other Plagiaulacoidea (p^{1-5} short and oval, only p^6 oblong and similar to m^1). m^2 not shifted inwards, situated directly behind m^1 .

Formation and locality: Kimmeridgian of the Guimarota coal pit near Leiria, Portugal.

Included genera: Only Paulchoffatia W. G. KUEHNE, 1961.

Paulchoffatia W. G. KUEHNE, 1961

Type species: Paulchoffatia delgadoi W. G. KUEHNE, 1961.

Diagnosis. — The only known genus of the Paulchoffatiinae.

Formation and locality: As given for the subfamily.

Included species: Only Paulchoffatia delgadoi W. G. KUEHNE, 1961.

Paulchoffatia delgadoi W. G. KUEHNE, 1961

Holotype: A left mandibular ramus, V. J. 1-155, Museu dos Serviços Geológicos, Lisboa, Portugal.

Diagnosis. — The only known species of Paulchoffatia with the following characteristics: Lower i steeply inserted, proximal part of the root below the roots of p_{1-2} . p_1 small, conical; p_{3-4} with 3-4 serrations and 2-4 basal cusps. Lower m only known from isolated teeth, not separable from those of *Kuehneodon*. Forward inclination of upper i about 30-35°. p^{1-5} tetracuspid, p^6 oblong, with a well developed third row of cusps. m^1 also with the tendency to evolve a third row of cusps. — For detailed description see in G. HAHN, 1969, pp. 11-34.

Formation and locality: As given for the subfamily.

Subfamily *Kuehneodontinae* n. subfam.

Type genus: *Kuehneodon* G. HAHN, 1969.

Diagnosis. — A subfamily of the Paulchoffatiidae with the following characteristics: Tooth formula $\begin{smallmatrix} 3.0.5.2. \\ 1.0.4.3.9. \end{smallmatrix}$. Lower tooth row arranged diagonally in respect to the border of the lower jaw, the lower m shifted inwards, the anterior lower p shifted outwards. Lower p functioned in grinding or cutting. p^{1-3} short, rounded, tri- or tetracuspoid; p^{4-5} oblong, similar to m^1 ; lacking third row of cusps. m^2 shifted inwards in respect to m^1 .

Formation and locality: In the Kimmeridgian of Leiria, Portugal and in the Purbeckian of Swanage, England; perhaps also in the Wealden of England.

Included genera: *Kuehneodon* G. HAHN, 1969, *Pliopriion* COPE, 1884 and *Bolodon* OWEN, 1871.

Kuehneodon G. HAHN, 1969

Type species: *Kuehneodon dietrichi* G. HAHN, 1969.

Diagnosis. — The typical genus of the *Kuehneodontinae* with the following characteristics: Tooth formula $\begin{smallmatrix} 3.0.5.2. \\ 1.0.4.3.2. \end{smallmatrix}$. Lower p grinding; $p_{3,4}$ with 3-4 serrations and 2-4 basal cuspules, little differentiated in length. Lower m only known from isolated teeth, not separable from those of *Paulchoffatia*. i^1 small, i^2 enlarged, with a large anterior cusp and a not completely separated smaller posterior cusp; i^3 slightly smaller than i^2 , with a central ridge divided into 2 cusps and 2 antero-buccal situated cuspules; no postero-lingual cuspule. p^{1-3} tetracuspoid, p^{4-5} and m^{1-2} with two longitudinal rows of cusps.

Formation and locality: In the Kimmeridgian of Leiria, Portugal.

Included species: *K. dietrichi* G. HAHN, 1969, *K. guimarotensis* G. HAHN, 1969 and *K. simpsoni* G. HAHN, 1969.

Kuehneodon dietrichi G. HAHN, 1969

Holotype: A right mandibular ramus, V. J. 4-155, Museu dos Serviços Geológicos, Lisboa, Portugal.

Diagnosis. — The type species of *Kuehneodon*, known only from the lower jaw, with the following characteristics: Tooth formula $\begin{smallmatrix} 3.0.5.2. \\ 1.0.4.2. \end{smallmatrix}$. p_2 longer than p_1 , but shorter than p_3 ; diastema between $i-p_1$ without step in front of the premolars. — For detailed description see in G. HAHN, 1969, pp. 35-39.

Formation and locality: As given for the genus.

Kuehneodon guimarotensis G. HAHN, 1969

Holotype: A right mandibular ramus, V. J. 5-155, Museu dos Serviços Geológicos, Lisboa, Portugal.

Diagnosis. — A species of *Kuehneodon*, known only from the lower jaw, with the following characteristics: Tooth formula $\begin{smallmatrix} 3.0.5.2. \\ 1.0.3.2. \end{smallmatrix}$. p_1 missing, p_2 small, as p_1 in *K. dietrichi*; diastema between $i-p_2$ with a distinct step in front of the premolars. — For detailed description see G. HAHN, 1969, pp. 39-41.

Formation and locality: As given for the genus.

Kuehneodon simpsoni G. HAHN, 1969

Holotype: A portion of the upper jaw with the i, p and m¹ in situ, V. J. 112-155, Museu dos Servicos Geológicos, Lisboa, Portugal.

Diagnosis. — A species of *Kuehneodon*, known only from the upper jaw, with the following characteristics: Tooth formula $\frac{3.0.5.2}{1.0.4.2}$. Forward inclination of i about 20°. p¹ isolated from i³ as well as from p² by a short diastema. Number of cusps on p⁴ unknown, on p³ 3 buccal and 3? lingual, also a small antero-buccal cuspule is present. m¹ with 2 buccal and 4 lingual cusps; cusps of the lingual row curved, blocking the median valley at its posterior end. m² not known in situ. — For detailed description see G. HAHN, 1969, pp. 41-44.

Formation and locality: As given for the genus.

Pliopriion COPE, 1884

Type species: *Plagiaulax minor* FALCONER, 1857.

Diagnosis. — A genus of the Kuehneodontinae, known only from the lower jaw, with the following characteristics: Tooth formula $\frac{1.0.4.2}{1.0.4.2}$. Lower p cutting, p₄ distinctly longer than p₃; p₃ with 4, p₄ with 7 serrations; basal cuspules more reduced than in *Kuehneodon*. m₁ with 3 cusps buccal and 2 + cusps lingual in position; m₂ with the characters of the family.

Formation and locality: In the Purbeckian of Swanage, England.

Included species: Only *Pliopriion minor* (FALCONER, 1857). — Description in SIMPSON, 1928, pp. 38-41.

Bolodon OWEN, 1871

Type species: *Bolodon crassidens* OWEN, 1871.

Diagnosis. — A genus of the Kuehneodontinae, known only by parts of the upper jaw, with the following characteristics: Tooth formula $\frac{3.0.5.2}{1.0.4.2}$. i³ with a ridge-like undivided central cusp and 1 postero-lingual cuspule. p¹⁻³ tricuspid, p⁴⁻⁵ and m¹⁻² with two rows of cusps.

Formation and locality: In the Purbeckian of Swanage, England.

Included species: *B. crassidens* OWEN, 1871 and *B. osborni* SIMPSON, 1928. — «*Bolodon*» *elongatus* probably does not belong to that genus. — Diagnosis and description of *B. crassidens* in SIMPSON, 1928, pp. 43-45, of *B. osborni* in SIMPSON, 1928, pp. 45-48 and of «*B.*» *elongatus* in SIMPSON, 1928, p. 48.

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A more detailed list of references is given in G. HAHN, 1969.

STRATIGRAPHY AND OSTRACOD-FAUNA FROM THE COALMINE GUIMAROTA (UPPER JURASSIC) ⁽¹⁾

by

FRIEDRICH-FRANZ HELMDACH

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⁽¹⁾ Manuscript received on September 1970.

1. PREFACE

In connection with the exploration of the vertebrate fauna of the coalmine Guimarota near Leiria, arose the necessity of an exact stratigraphical integration of the fossil-bearing layers. Stratigraphy, sedimentological research and determination of age of the layers in the pit were necessary to carry this out. The ostracods appearing in nearly all horizons offered suitable material for this task. The brackish and fresh-water ostracods will be discussed in this paper.

I wish to express my thanks to my teacher Prof. Dr. W. G. KÜHNE for the inspiration and support given to me during the work on this paper, to Dr. H. J. OERTLI (SNPA, Pau, France) for hints and advice concerning the palaeontological side, to Dr. H. J. BELITZ (Genetical Institute of the Freie Universität, Berlin) for the critical revision of the statistical side of this work and to all my friends in Leiria for their hospitality and assistance.

A part of the photographic illustrations were made possible by the friendly co-operation of Prof. J. G. HELMCKE (Max-Planck Institute for Micromorphology, Berlin).

The holotypes and the illustrated paratypes are preserved in the collection of the Serviços Geológicos de Portugal, Lisboa, under the numbers: GO 3; GO 6; GO 10; GO 16; GO 17, No. 4; GO 17, No. 7; GO 23 and GO 26.

The paratypes which are not illustrated remain in the Lehrstuhl für Paläontologie, Freie Universität Berlin, under the numbers: GO 4-5; GO 7-9; GO 11-13; GO 17, No. 1, 2, 3, 6, 10, 11, 26; GO 18-19; GO 25 and GO 27.

2. THE COALMINE GUIMAROTA.

2.1. Introduction.

The coalmine of Guimarota is situated about one km. south of the Portuguese district capital, Leiria (Fig. 1).

The limestones, marls and coaly seams of this mine have, on an average, an inclination of 22° S.

The coal-bearing horizons consist mainly of a mixture of coal and marl. Pure coal layers can be found only to a thickness of a few centimetres. Therefore all coal-bearing units will henceforth be described as marly coal seams.

Today the mine is closed, caused by the low quality of this coal. To a great extent the marly coal was used in the past to produce burnt lime.

To Dr. W. Süss, Essen, is due a maceral analysis of a marly coal layer (FA, see facies profile) it shows the following composition:

Vitrinite	47
Exinite	2
Inertinite	22
Minerals	29
						<hr/>
						100 Vol. %

The coal can be defined as a gas coal.

2.2. The age of the layers

The age of the Guimarães layers have, up to now, been determined as Kimmeridge sensu lato: The gyrogonites of the charophytes *Porochara raskyae* MÄDLER, 1952 and *Porochara westerbeckensis* MÄDLER, 1952 indicate, by courtesy of Dr. K. MÄDLER, Hannover, an age between Kimmeridge and Lower Portland. This determination can now be stated more specifically by the appearance of a species of the ostracod genus *Cetacella*. The best conserved sample of these specimens seems to be almost surely an example of *Cetacella inermis* MARTIN, 1958 (by courtesy of Dr. G. P. R. MARTIN). The age of the Guimarães layers can, therefore, be determined as Kimmeridge sensu

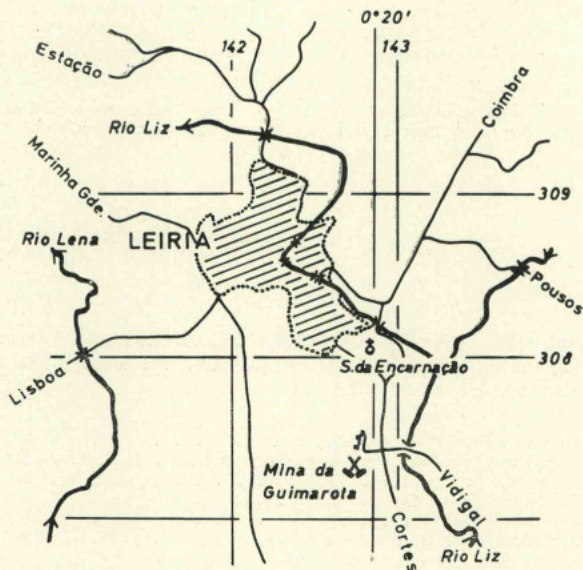


Fig. 1—Position of the coalmine Guimarães (according to Carta Militar de Portugal. Leaf Leiria, No. 297).

stricto. Finally the ostracod species *Oertliana kimmeridgensis* KILENYI, 1965 allows a determination of the relevant deposits as Lower Kimmeridge.

The Guimarães layers can be arranged in the Alcobaça beds. Their marly coal layers belong to the second series of the so-called Lignites which appear in the Portuguese Upper Jurassic. The first of these series is contained in the region of Alcobaça-Fátima in the Valle Verde beds and in Cabo Mondego in the *Zement Kalk*. Both of these stratigraphical units are said to have an age of Lower Oxford [RUGET-PERROT, 1959; ZIEGLER in HÖLDER, 1964]. The Alcobaça beds are correlated with the Abadia beds which in the type region have an age of Lower Kimmeridge, recorded by Ammonites [RUGET-PERROT, 1959].

An exact distinction between the Alcobaça beds and the overlying Pterocerien is, however, not possible.

In the Torres Vedras region
(according to B. ZIEGLER)

In the Leiria region

Tithon	Couches de Freixial		
	Corallien and Pterocerien		Pterocerien ?
Lower Kimmeridge	Marnes d'Abadia		Alcobaça beds with the second series of «Lignites» (Guimarota)
Upper Oxford	Couches de Montejunto	Lusitanien	Beds with <i>Pholadomya protei</i>
Lower Oxford	Couches de Cabaco		?

Fig. 2—Arrangement of the Upper Jurassic in the middle and southern part of Portugal (according to B. ZIEGLER in HÖLDER, 1964 and F. F. HELMDACH, 1966).

3. STRATIGRAPHY OF THE COALMINE

3.1. Introduction.

The components of the Guimarota layers can be distinguished from one another by their varying contents of marl, limestone and coal. The following terms, therefore, are used for the description of the layers:

Layers with dominant marly-limy constituents	KM
Layers with dominant argillaceous-marly contents	TM
Marly coal	FA
Dominant limy layers	K
Flat marls	P
Layers with numerous shells of pelecypods	M

Furthermore, combinations of these terms are also used. For the overall view of the Guimarota layers, five sequences can be distinguished in which limy-marly series alternate with marly-coaly ones.

This rough arrangement appears as follows (compare Guimarota facies profile):

- Limestone and marl of K_0 and H_1 . The vertical extensions of this sequence are not known because this sequence is on the top of the Guimarota layers and therefore is known only in its lowermost decimetres.
- Marly coal from FA_3 to H_2 .
- Limestone and marl from KM_{9a} to KM_{9b} .
- Marly coal from P_1 to TM_3 .
- Limestone and marl from K_{2a} to K_2 . This sequence forms the base of the Guimarota layers. Its vertical extension is unknown as in a.

3.2. Stratigraphy

3.2.1. Limestone and marl from K_2 to K_{2a} (e)

3.2.1.1. K_2 and K_{2a}

In the stratigraphical connection K_2 is only exposed in the lowermost 40-50 centimetres. A larger sequence of K_2 exists in the western parts of the galleries Q_2 and Q_3 (see mine section).

The exposed thickness in this part of the mine is between 4 and 6 metres. However, a stratigraphical integration of this material into the profile is not possible; because of the fault S_1 , only a part out of K_2 can be seen. But it is evident that the minimum thickness of K_2 is 7 to 8 metres. K_2 consists of a hard, light yellowish lime in which no fossils were found. In the uppermost 10 to 15 cm. the material becomes more marly and for this reason is separated from K_2 . This stratum is called K_{2a} . Only a weak banking can be recognized in K_2 and K_{2a} .

The following ostracods were found in K_{2a} .

Darwinula sp.

Poisia bicostata n. sp.

Leiria paucistriata n. sp.

3.2.2. Marly coal from TM_5 to P_1 (d)

3.2.2.1. TM_5

The thickness oscillates between 78 and 105 cm. TM_5 consists of an argillaceous brownish-grey marl which also reveals a finely spread coaly material. TM_5 can also be termed as marly coal. Singular coal-lenses also appear occasionally. Small fragments of shells which cannot be determined appear at intervals. The lowermost part of this layer is very similar to a marly coal layer. In this part *Isognomon* sp. was often present.

The microfauna consists of:

Theriosynoecum wyomingense (BRANSON, 1935).

Darwinula sp.

Leiria striata n. sp.

Bisulcocypris sp.

Leiria paucistriata n. sp.

Timiriasevia mackerrowi BATE, 1965.

3.2.2.2. KM_{11}

This layer has a thickness of 98-100 cm. It consists of a marly coal in which coal-lenses and bands of fine fragments of shells are embedded. In some parts the coaly components become so frequent that a separation from the overlying bank FA_{11a} is not possible. The above mentioned thickness is already applied to FA_{11} . FA_{11} is one of the two dismounted layers which are exposed in the Guimarota pit. In 1961 and 1962 it was dismounted especially in order to obtain fossils.

The following fossils were found there:

Representatives of the Vertebrate orders:

Crocodylia with *Machimosaurus hugii* H. v. MEYER.

Pterosauria

Saurischia with *Megalosaurus* sp.

Bothriospondylus sp.

Chelonia

Urodela

Squamata

Multotuberculata

Pantotheria with *Docodon* sp.

Semionotoidea with *Lepidotes* sp.

Selachii

Furthermore Otoliths and egg-shells are represented.

Invertebrates:

Isognomon sp.

?*Leda* sp.

Unio sp.

Discohelix sp.

Cerithium sp.

The microfauna consists exclusively of Ostracods:

Theriosynoecum wyomingense (BRANSON, 1935).

Leiria striata n. sp.

Leiria paucistriata n. sp.

Timiriasevia mackerrowi BATE, 1965.

Bisulcocypris sp.

Darwinula sp.

Gyrogonites of Charophytes are numerous. Two species could be determined:

Porochara westerbeckensis MÄDLER, 1952.

Porochara raskyae MÄDLER, 1952.

3.2.2.3. FA_{11a}

The thickness is 11-15 cm. The layer consists of an almost pure coal. Remains of dark, hard wood are often represented.

3.2.2.4. TM₄

60-70 cm. marl with a brownish-grey uniform hue. 14-18 cm. above the basement, a thin layer 2 cm. thick is embedded. This thin layer consists of shells and fine shell fragments. Sporadic shell fragments can always be found in TM₄.

Ostracods:

Darwinula sp.

Bisulcocypris sp.

3.2.2.5. FA₁₀

The thickness is mostly between 10 and 20 cm. Bands of dull hard coal are embedded in a dark grey matrix of coal marl. The matrix contains numerous small

fragments of shells which, however, were not able to be determined. As in many marly coal layers no microfauna is present.

3.2.2.6. TM_3

Consists of a hard, yellow-greyish marl. This horizon seems to have a uniform yellow-grey hue. Shell fragments and pieces of wood are rare. A thin layer of a thickness of 2 cm. consisting of very fine shell fragments appears to be typical of TM_3 , and can always be found 40 cm. above the basement. The total thickness of TM_3 is very variable. Towards the end of the gallery Q , the thickness reaches a maximum of 240 cm. and at the beginning of Q_0 only 68-70 cm.

Ostracods:

Poisia clivosa and *Poisia bicostata* are very rare. Other presumably marine forms are abundant. They belong to the Cytheridae.

3.2.2.7. KM_{10}

Towards the top this layer is represented by a grey coaly marl. Pelecypods are rare. The lower half has a darker hue, which has its origin in a concentration of small pieces of coal. Larger shells can often be found here (*Isognomon* sp.). The thickness of KM_{10} is between 27 and 40 cm. The surface can be slightly wavy.

3.2.2.8. TM_2

40-50 cm. Marl with a uniform dark greyish hue. Only towards the top can some thin, light bands be found to exist. Shell fragments are not rare and are especially numerous near the basement. In most cases, the shells belong to the species *Isognomon*.

The Ostracods of this horizon consist of:

Darwinula sp.

Poisia bicostata n. sp.

Poisia clivosa n. sp.

Bisulcocypris sp.

3.2.2.9. FA_0

Has a thickness of between 15 and 25 cm. Pure coaly components are numerous, for which reason the colour of this layer is a dull black. The superficies of FA_0 is slightly to heavily wavy. Presumably these waves are ripple marks. No fossils have been found in this horizon.

3.2.2.10. M_4

The sediments of M_4 also fill out the valleys of the superficies of FA_0 . Therefore, the thickness of M_4 oscillates, the maximum being 25 cm. This horizon consists of a dark-grey to brown marl, in which smaller and larger shells of pelecypods are embedded. These shells are partly broken into small pieces. In nearly all cases the larger shells belong to *Isognomon* sp. The smaller ones are and being badly conserved could not be determined. A slight increase in the number of fossils towards the basement could be observed.

Microfossils:

Darwinula sp.

Poisia bicostata n. sp.

Bisulcocypris sp.
Porochara sp.
 ?*Cytheropteron* sp.

3.2.2.11. P₁

10-15 cm. dark-grey thin marl. P₁ exists only in the NE. parts of the mine. The only fossils found were small mostly broken ostracods presumably of a juvenile form.

?*Bisulcocypris* sp.
 ?*Darwinula* sp.
Leiria sp.

3.2.3. Limestone and marl from KM_{ob} to KM_{oa}

3.2.3.1. KM_{ob}

The thickness cannot be fixed exactly, because this layer extends continuously into the overlying limestone of K₁. Presumably, the thickness varies between 50 and 100 cm. KM_{ob} is a hard yellow-greyish marl. The transition into K₁ is optically signified by the disappearance of the darker hue of KM_{ob}.

Microfossils are very rare:

Darwinula sp.
Bisulcocypris sp.

At 20-30 cm. above the basement, fragments of shells appear. Their number increases towards the basement.

3.2.3.2. K₁

420 cm. of hard, shelly breaking impure lime without banking. The colour is light grey to yellowish. Secretions of calcite sometimes appear. No fossils were found in K₁.

3.2.3.3. KM_{oa}

180 cm. of hard limey marl in a yellow-greyish colour. Remains of wood, small coal-lenses and gypsum in clefts are not rare. Locally, the coaly components exist in an independent layer of a thickness up to 10 cm. (Gallery 1b).

A clear separation from the underlying K₁ does not exist. Macrofossils were not found.

Microfossils:

Darwinula sp.
Bisulcocypris sp.
 ?*Leiria* sp. *Cetacella inermis* MARTIN, 1958 (see chapter 2.2).

3.2.4. Marly-coal from FA_s to H₂ (b)

3.2.4.1. FA_s

5-20 cm. marly coal-layer.

The superficies shows a strong wavy structure, thus making the thickness very variable.

3.2.4.5. KM_s

The thickness oscillates between 3 and 10 cm. as a result of sedimentation on the wavy top of the layer FA_s.

M_s contains numerous shells, especially towards the top. Nearly all shells belong to the genus *Isognomon*. In several parts of the mine, especially in the Northern ones, M_s is totally lacking. No microfauna was found.

3.2.4.3. KFM

This layer consists of a marl which often contains small coal lenses. Therefore its colour varies between dark brown in dominant coal-bearing parts and brownish grey to yellowish grey in dominant marly parts. Macrofossils are rare. Near the top appear some indeterminable shells of pelecypods. Small gastropods are not so rare. They seem to be juvenile forms which are also indeterminable. Microfossils are more numerous.

Ostracods are:

Darwinula sp.

Poisia clivosa n. sp.

Poisia bicostata n. sp.

Leiria striata n. sp.

Leiria paucistriata n. sp.

Bisulcocypris sp. *Timiriasevia mackerrowi* BATE, 1965.

In addition to these, appear several gyrogonites of charophytes. They belong nearly all to the species:

Porochara raskyae MÄDLER, 1952 and *Porochara westerbeckeensis* MÄDLER 1952.

The thickness of KFM oscillates between 40 and 80 cm

3.2.4.4. FA_{7a}

Exists in some parts of the mine between KFM and KM_s.

In consists of a marly coal layer with the following microfossils:

Darwinula sp.

Poisia bicostata n. sp.

Poisia clivosa n. sp.

Leiria striata n. sp.

Bisulcocypris sp.

Timiriasevia mackerrowi BATE, 1965

Porochara sp.

3.2.4.2. M_s

The whole layer appears to have a wavy form in the cross section. It consists of a limy marl of light yellowish-grey colour, but some dark bands also exist. Small coal lenses which also appear in the form of long, small bands can be present. Sporadically, small indeterminable shells and some broken shells of *Isognomon* species exist. The thickness is between 15 and 25 cm. The microfossils in KM_s are the same as in KFM.

3.2.4.6. FA₇

Is a marly coal layer with coarsely wavy or furrowed superficies. This appearance can be ascertained in many marly coal layers. Presumably, this is the result of the effects of erosion after a changing of sedimentation from flat water sediments with dominant plant material (FA₇) to marly sediments of deeper and more agitated water. The total absence of FA₇ in the galleries 11, 1b, 2, 5 and 7 can be for the same reason.

The thickness of this layer is therefore very variable being between 2 and 55 cm. Dark brownish to yellowish coloured marly lenses can be concentrated locally. This means that often FA₇ cannot be signified as a marly coal layer. In FA₇ no fossils were found.

3.2.4.7. M₂

This layer fills out the top of the wavy and furrowed superficies of FA₇. The thickness therefore oscillates between 3 and 35 cm. M₂ consists of a medium light brownish-grey marl. M₂ can be characterized by its great number of embedded shells of *Isognomon* species, which have a length of between 2 and 4 cm.

A red-brownish shell colouring is nearly always recognizable. In the southern parts of the mine with a northern limitation of the galleries 8 and 7 the shells are concentrated in the upper part of the layer. Their number decreases towards the basement, but their presence is always visible. In the galleries 1a and 2 the shells seem to be evenly distributed in a vertical manner, an enrichment at the basement is partly evident.

Microfossils:

- Theriosynoecum hemigymnon* n. sp.
- Darwinula* sp.
- Poisia bicostata* n. sp.
- Leiria striata* n. sp.
- Leiria paucistriata* n. sp.
- Bisulcocypris* sp.
- Timiriasevia mackerrowi* BATE, 1965.
- Porochara* sp.

3.2.4.8. TM₁

25 cm. of a dark greyish argillaceous marl which contains small isolated coal-strips. In the galleries 1a and 7 appear isolated shells which could not be exactly determined. The colour of TM₁ is rather uniform.

Microfossils:

- Theriosynoecum hemigymnon* n. sp.
- Darwinula* sp.
- Bisulcocypris* sp.
- Leiria striata* n. sp.

3.2.4.9. FA₈

Consists of a marly coal with a dull black hue; the thickness is 30 cm. Various bright coal stripes are embedded in a matrix of black marl. Typical of this layer seems to be a horizon of a thickness of 10 cm. mostly situated in its centre. This ho-

rizon shows a lighter colour and can appear as a uniform brownish band or as yellowish stripes of marl in a dark coaly matrix.

Microfossils:

Theriosynoecum hemigymnon n. sp.

Darwinula sp.

Leiria striata n. sp.

Leiria paucistriata n. sp.

Timiriasevia mackerrowi BATE, 1965.

3.2.4.10. KM₇

This layer can be characterized by its different colours. The upper part (6-9 cm.) consists of a dark marl which contains light stripes. The middle part is very dark as a result of a high portion of coaly material. In the lower third, light stripes dominate again in which a 4 cm. horizon of numerous *Isognomon* species is embedded locally. KM₇ has a thickness of 30 cm.

Microfossils:

Darwinula sp.

Leiria paucistriata n. sp.

Bisulcocypris sp.

Timiriasevia mackerrowi BATE, 1965

Porochara sp.

3.2.4.11. FA₅

In the SE parts of the mine, this layer is represented by a thickness of 10-15 cm. In most other parts it is only a few centimetres. As in FA₇, the different thickness can be the result of erosion. At the basement, small fragments of shells can be found. Other fossils could not be observed.

3.2.4.12. M₁

Consists of a medium light grey-brownish marl which is very bituminous. An enrichment of small to greater *Isognomon* species (length 4-5 cm.) which are specially dominant in the lower part is typical. The shells are represented as larger pieces and complete shells in a matrix which consists of small fragments of *Isognomon* species and marl. In general M₁ has a thickness of 25 cm.

Microfossils:

Darwinula sp.

Leiria striata n. sp.

Leiria paucistriata n. sp.

Bisulcocypris sp.

Timiriasevia mackerrowi BATE, 1965

Porochara sp.

3.2.4.13. TM₆

This layer is present only in the NE part of the mine. It consists of a dark grey bituminous marl. Fragments of shells (small samples of *Isognomon* species) are always present but not in great numbers. The thickness is mostly 25 cm.

Microfossils:

Theriosynoecum hemigymnon n. sp.*Darwinula* sp.*Poisia bicostata* n. sp.*Leiria striata* n. sp.*Leiria paucistriata* n. sp.*Bisulcocypris* sp.*Timiriasevia mackerrowi* BATE, 19653.2.4.14. FA₄

Is a marly coal layer consisting of hard dull shining coal and dark brown pieces of wood. FA₄ can be interspersed locally by many small stripes of marl (Gallery 5). No fossils were found except for fragments of carapaces of turtles. The thickness of FA₄ is mostly 20 cm.

3.2.4.15. KM_{4,5}

Consists of a little consolidated, dark greyish bituminous marl of a thickness of 45-50 cm. Bits of coal are often embedded in it.

In the uppermost parts of this layer thin pure coal stripes are present. Above the basement the colour is lighter than in the other parts of the layer. Numerous fragments of shells are also to be found here.

Microfossils:

Theriosynoecum hemigymnon n. sp.*Darwinula* sp.*Poisia bicostata* n. sp.*Poisia clivosa* n. sp.*Leiria striata* n. sp.*Bisulcocypris* sp.*Timiriasevia mackerrowi* BATE, 1965*Porochara raskyae* MÄDLER, 1952*Porochara westerbeckensis* MÄDLER, 1952

3.2.4.16. A

This layer has a constant thickness of 15 cm. in all its outcrops. The light yellowish-grey colour is very conspicuous. This horizon therefore demonstrates a very good guide layer for the upper part of the Guimarota layers. Furthermore, the furrowed lower edge is typical for this hard bituminous marl. Plant stalks are common and in most cases are situated vertically in relation to the bedding. It is very probable that this is a rootlet bed. Small gastropods are frequent. Presumably they belong to the Valvataceae. Microfossils are abundant. Nearly all of them are Gyrogonites of Charophytes. As well as this, *Darwinula* species could be found.

3.2.4.17. KM₃

17-22 cm. of dark grey-brownish marl. In this matrix, hard yellowish bands of lime and lenses, as well as thin stripes of coal in the form of lenses are embedded. Macrofossils are rare and only isolated shell fragments appear.

Microfossils:

Darwinula sp.*Leiria striata* n. sp.

Leiria paucistriata n. sp.

Bisulcocypris sp.

Timiriasevia mackerrowi BATE, 1965

Porochara sp.

3.2.4.18. FA₃

Is presented in a thickness of 10 cm. This layer consists of a coal which is heavily interspersed by marl. Only locally does one find almost pure coal. In several parts of the mine, this layer is lacking or it is represented very sparsely (Q₁₁).

Microfossils:

Darwinula sp.

Leiria striata n. sp.

Leiria paucistriata n. sp.

Bisulcocypris sp.

Timiriasevia mackerrowi BATE, 1965

Porochara sp.

3.2.4.19. KM₃

Is a medium hard marl with a thickness of between 10 and 20 cm. Coal lenses often occur. Fragments of shells are never lacking; partly they form a thin band in the middle of this layer.

Ostracods:

Darwinula sp.

Poisia clivosa n. sp.

Furthermore, but very rarely a representative of the? Discorbidae occurs.

3.2.4.20. FA₂

Marly coal with a thickness of between 25-30 cm. and some embedded thin calcitic bands. Macrofossils are very rare and only represented by fragments. In the samples pieces of amber of a size of $\pm 1 \text{ mm}^3$ often appear.

Microfossils:

Darwinula sp.

Poisia bicostata n. sp.

Poisia clivosa n. sp.

Leiria paucistriata n. sp.

Porochara sp.

3.2.4.21. KM₁

10-12 cm, of limy marl, which occurs dominantly in irregular light grey layers. A small band (2 cm.) consisting of fragments of shells situated near the top of the layer seems to be typical. Size, thickness and form of the shells point to *Isognomon* species.

Microfossils:

Darwinula sp.

Poisia clivosa n. sp.

Leiria paucistriata n. sp.

Bisulcocypris sp.

Timiriasevia mackerrowi BATE, 1965

Porochara sp.

These microfossils, however, have been found very rarely. On the contrary appear numerous forms that belong to the Cytheridae. These ostracods are almost certainly marine forms. KM_1 therefore seem to be sedimented in a dominantly marine environment.

3.2.4.22. FA_1

10-15 cm. of hard marl heavily interspersed by dull coal. No fossils were found.

3.2.4.23. MA

60 cm. of soft dark grey marl which shows towards the basement a strong enrichment of shells. Presumably all these shells are representatives of *Isognomon* species. The numerous appearances of pieces of wood may be classed as typical for this layer.

Microfossils:

Darwinula sp.

3.2.4.24. H_2

30-35 cm. of hard light grey marl which is interspersed by small shell. These forms may be shells of *Leda* sp. and juvenile forms of *Isognomon* sp.

3.2.5. Lime and marl from K_0 and H_1 (a)

3.2.5.1. H_1

100 cm. of hard limey marl which is enriched by shells. The colour is light grey to yellowish. The shells, probably only? *Leda* species become dominant especially near the basement. A sharp petrographical limitation to the overlying layer K_0 does not exist. But the complete lack of macrofossils in K_0 allows a clear distinction.

3.2.5.2. K_0

The thickness is not known. K_0 seems to be a sequence of impure lime with a thickness of several metres. A similar sequence was found in K_1 and K_2 . K_0 shows outcrops at the top of the Guimarota layers in only two places in the mine. The lowermost 110 cm. are exposed. Equivalent to the character of the layers K_1 and K_2 a total thickness of 5-6 m. can be supposed.

4. SEDIMENTOLOGY.

The sedimentary basin in which most of the deposits of the Guimarota layers were formed was presumably a lagoon. Layers of little thickness and frequent wavy furrows, which can be interpreted as ripple marks (known from the superficies of FA_1 , FA_3 , FA_7 , FA_8 , FA_9 , KM_2 , KM_3 and KM_{9a} , see Pl. I) point to shallow water and a small water basin [RUCHIN, 1958].

The formation of a lagoon seems also to have been favoured by a continent that extends only a little in height above sea level. The almost total lack of coarse clastic

sediments points to a continent of little relief energy. Sandy deposits could not be found. In the samples too, grains of sand are very rare. A delta-like sedimentary basin can therefore be eliminated [RUCHIN, 1958].

The fauna of invertebrates which is poor in species but very rich in individuals, as, for example (?*Leda* species in H₁, *Isognomon* species in M layers and gastropods in A) points to a brackish water and to a lagoon like a sedimentary basin. The fauna of vertebrates shows influences from the sea and from the continent. As well as representatives of the Selachii, Semionotoidea and Crocodilia (*Machimosaurus hugii* v. MEYER) as marine forms, freshwater and terrestrial animals as Chelonia, Urodela, Anura, Lacerilia, Dinosaurs and Mammals are present. The Chelonia appear presumably in 3 species

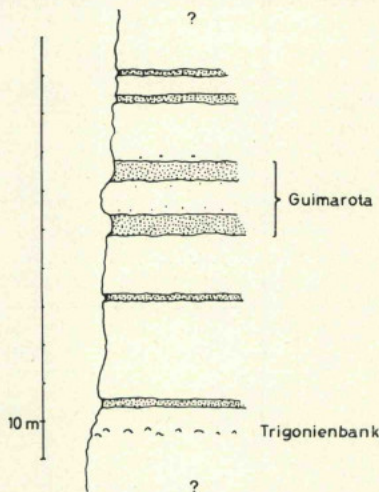


Fig. 3 — Coal-bearing beds (punctuated) in the Guimarota region.

(by courtesy of Dr. H. BRÄM, Zürich). One of them lived in the steppe or wood and another could have been an inhabitant of brooks and ephemere pools. The microfossils show a dominant freshwater character. The appearance of *Darwinula* sp., *Bisulcocypris* sp., *Theriosynoecum* sp. and Gyrogonites of Charophytes can be significant for this. Only isolated marine ostracods (representatives of ?Paracypridinae and several other not determinable forms and foraminifera (a few individuals of Lagenidae in KM_{9a}, Lituolidae in KM_{4,5}, and ?Discorbidae) are present. Most of these microfossils exist in badly preserved singular individuals. Only one layer (KM₁) shows presumably pure marine Ostracods. Also macrofossils of invertebrates demonstrate influences of freshwater. Especially the *Isognomon* sp. which in parts are numerous, exist in a stunted fauna which could have lived in a nearly sweetened water. It is almost sure therefore, that the sedimentary basin in which the Guimarota layers were deposited was a lagoon, shore lake or shore swamp-like structure.

It seems possible that the sedimentary basin was a lagoon with a freshwater junction which was now and again flooded by the sea and which afterwards became freshwater again. As well as paleontological statements, also certain rhythms in the

sedimentation (see facies profile) point to that possibility. Roughly viewed, the following rhythm of sedimentation can be seen:

limy marl,
marl and marly coal,
limy marl,
marly lime.

This sequence occurs twice in the Guimarota layers. But this rhythm of sedimentation is also present in the over and underlying deposits of the Guimarota layers as shown by prospection drillings in the surroundings of the mine. A sequence of coaly

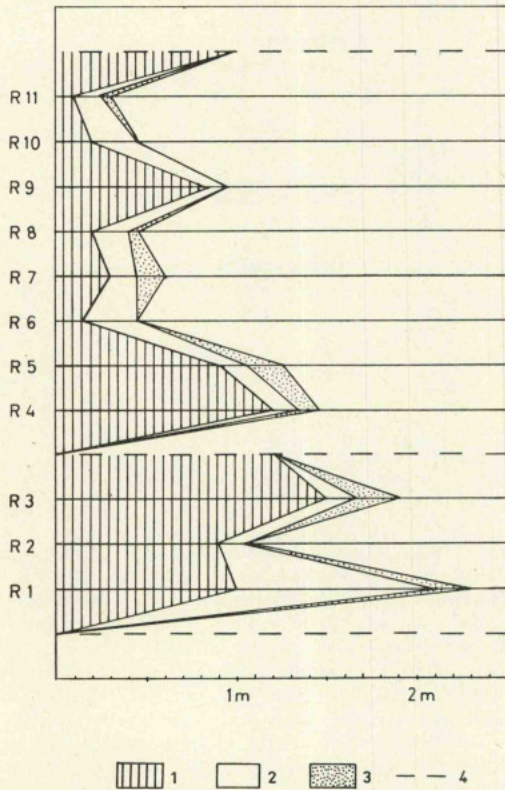


Fig. 4—This rhythmogram shows a rhythmical series of the sequence:

- 1—marl
- 2—marly coal layer
- 3—bed largely enriched with shells
- 4----- marly lime of K₂, K₁, and K₀

marl which is situated between marl and marly lime occurs twice both upwards and downwards of the Guimarota layers.

But also within the marl and marly coals which are inserted between the marly limestones, a repetition of a sequence is evident.

The following sequence occurs eleven times.

marl, enriched with shells,
marly coal,
marl.

This rhythm is only twice interrupted by the marly lime of K₁. The illustrated rhythmogram shows a rhythmical series of this sequence. A decrease in the thickness off the marly layers is thereby evident. The other two beds also show a decrease but a less distinct one.

(The rhythms are marked on the ordinate, the thickness of the layers on the abscissa).

5. TECTONICS.

The fault system that occurs in the area of the Guimarota can be derivated from the movements of a salinar. Therefore, this area can be termed as a «pseudotectonic» region because almost all the tectonics do not depend on orogeny. Tectonics can only be derived from the heightening of a salinar [M. RICHTER, 1962].

This salinar, the so-called Dagorda belongs primarily to the Trias. This piercement presumably began its ascent in the Lower Jurassic. It has influenced nearly all later deposited sediments. So the deposits of the Jurassic with its marl and limestones are turned over and broken. Mine drawings and profile of the Guimarota show the following effects of these tectonics: parallel to the length of the piercement several synthetic normal faults are presumably a phenomenon of strain which are the effects of a raising of rocks. In the Leiria region these faults are never definitely disclosed. But the disclosed tectonics in the mine could be typical for the whole region which is influenced by the Dagorda piercement. Four faults in NS directions which tip towards E are exposed. Consequently they strike about parallel to the heightening of the Dagorda piercement. Prospections for coal in the region of the mine show towards W and E other faults which agree in character with those exposed in the Guimarota mine. In all probability therefore, the ascent of the Dagorda piercement after its mobilisation by static loads has caused the faults. These faults strike about parallel to the length of the Dagorda heightening. They are staggered normal faults which dip towards E (compare Guimarota mine section and profile).

6. PALAEONTOLOGICAL SECTION

6.1. Preliminary note.

The ostracods described in the following chapters presumably have lived in a lagoon-like basin containing mostly \pm pure freshwater (compare the chapter on sedimentology).

Marine influences can be seen only very little in the explored sediments. In a few layers a marine character appears to be dominant. In the layers KM₁, TM₈, TM₂ and M₄ the following ostracods have been found in large quantities:

?*Macrocypri* sp.
 ?*Paracypris* sp.
 ?*Cytheropteron* sp.

and also not exactly determinable representatives of the Cytheridae.

These forms point to a marine environment. The sedimentary basin therefore could have been flooded by the sea for some time. In all other layers marine ostracods are partly represented, but only by single specimens. These individuals have presumably been transported into the lagoon by intermittent floods from the sea. All other ostracods show only a little tendency to a brackish water environment. The genera *Poissia* n. gen. and *Leiria* n. gen. seem however to be adapted to a life in \pm brackish water.

6.2. *Leiria* n. gen.

Order	<i>Ostracoda</i>	LATREILLE, 1802
Suborder	<i>Podocopa</i>	SARS, 1866
Family	<i>Cyprididae</i>	BAIRD, 1845
Subfamily	<i>Cypridinae</i>	BAIRD, 1845
Tribus	? <i>Cyprinotini</i>	BRONSTEIN, 1947
Genus	<i>Leiria</i> n. gen.	

Type species: *Leiria striata* n. sp.

Derivatio nominis: after the city of Leiria: the Guimarota coalmine is situated in its neighbourhood.

Diagnosis:

A genus of the? Cyprinotini with the following peculiarities: The ornamentation shows thin ribs running almost parallel to the dorsal margin. These ribs are set out at equal distances \pm parallel to one another. They rarely show a branching off. L is distinctly larger than R. The posterior end is moderately narrow-rounded. The ventral margin in the posterior third is straight to distinctly concave. The greatest height of the carapaces is demonstrated at the dorsum by the R valve. The R valve shows a denticulation which runs from the middle of the anterior margin to the ventral margin and further on to the middle of the anterior margin.

Description:

The carapaces from a lateral view are well-rounded triangularly. The anterior margin is nearly half circled broadly rounded. The posterior margin bends to the ventral margin moderately narrow rounded. A concavity is in front of the anterior cardinal angle and is especially exposed in the right valve. The other anterior margin is equally broadly rounded. The ventral margin is anteriorly straight to convex. In the posterior third appears mostly a weak concavity. The surface shows a pattern of weak to well-developed ribs.

Dorsal view: carapaces slightly lanceolate, anteriorly and posteriorly ended in a point but posteriorly less marked.

L overlaps R especially strongly in front of the anterior and in the region of the posterior cardinal angle.

Ventral view: L overlaps R in a wide arch. The hinge is simply built: L. has a thin rib; R has a weak furrow. The muscle scars consist of six different large scars. Four of them are situated in a slightly bent vertical row. In size they diminish inconsistently from top to bottom. Little higher than the third and fourth scar, counted from above, two other scars are situated behind this row. Sexual dimorphism is scarcely recognizable. Among the small number of adult individuals a few more elongated and narrowed forms are present from the side view demonstrating a more narrowly rounded posterior end. These forms could be males.

Measurements:

maximum length	0.9 mm.
maximum height	0.6 mm.
maximum width	0.32 mm.

Occurrence: In nearly all layers of the Guimarota mine whose sediments do not originate from marine deposits.

Affinities:

Distinguished from *Cetacella* MARTIN 1958 by the partly concave ventral margin and the more pointed posterior end. The surface ribs of *Cetacella* show a stronger meandering.

Petrobrasia KRÖMMELBEIN 1965 is represented by a much more pointed posterior end and by a very weak overlapping of L over R. As well as this the pattern of the ribs in the anterior third and an unsculptured part near the dorsum of *Petrobrasia* are different from *Leiria* n. gen. Finally, the Brazilian and the African species of *Petrobrasia* are said to have a rather «geknickten» (bent) dorsal margin. (By courtesy of Prof. Dr. K. KRÖMMELBEIN, Kiel).

Remarks:

Muscle scars, the number of pore canals and the size of the inner lamella are very similar to representatives of the Cyclocypridinae. But the carapaces of *Leiria* n. gen. are ventrally not smoothed; R shows denticulation of the margin and L overlaps R, though the greatest height is formed by the R. A connection to the Cypridinae seems therefore to be more probable.

6.3. *Leiria striata* n. sp.

Derivatio nominis: striatus (latin) = striped.

Holotypus: 1 Garapace GO 3, Fig. 5.

Locus typicum: Layer M₂.

Paratypes: 24 valves and carapaces GO 7-9.

Diagnosis:

A species of the genus *Leiria*; the valves of which are equally decorated with thin ribs. These ribs run about parallel to the dorsal margin. They meander only scarcely and branch off rarely. The greatest height is formed by R. R has a denticulation.

Description:

The outline from a lateral view is well rounded triangularly. L is larger than R. The greatest height is anterior to the middle. The anterior margin is nearly half circled widely rounded. It runs gradually into the ventral margin. In front of the anterior cardinal angle a straight to concave part is to be seen. This concavity is specially well developed at the R. The dorsal margin runs backwards from the anterior cardinal angle in a weak bending downwards.

It forms an indistinct posterior dorsal angle. The outline then runs rapidly downwards almost to the ventral margin and passes fairly narrowly rounded into the ventral margin. The ventral margin of the L in the anterior half is slightly convex; in the posterior third it is always with a concavity of a different strength. The ventral margin of the R shows in nearly all its length an equally concave line. The R possesses a denticulation beginning in the middle of the anterior margin, extending over the ventral margin up to half the height of the posterior margin. These small teeth decrease in size from the back to the front; their number increases. The surface of both valves is ornated with ribs almost up to the anterior and posterior margin. These ribs can branch off at acute angles. At the anterior and posterior margin the ribs turn up to the dorsum. They then run a little more weakly parallel to these margins. Extending nearly parallel to the dorsal margin, the ribs get their normal size again. In the uppermost third, about in the middle of the valve, a small pointed oval «window» is formed by the ribs (Pl. II, fig. 2).

From the dorsal view the carapaces are meagrely lanceolate. L overlaps R, especially in front of the anterior and in the region of the posterior cardinal angle. From the ventral view L overlaps R in a wide curve for almost the whole length. The hinge is a simple desmodont. A ridge of the L interlocks a weak furrow of the R. The test is thin; the zone of conrescence is narrow. A broad inner lamella and normal pore canals could only be seen in juvenile valves. The pore canals occur fairly often and are simple and straight. Radial pore canals could also be seen solely in juvenile valves; they are numerous (± 40 at the anterior margin) straight and simple.

The exact position of the muscle scars in adult valves cannot be given. In juvenile valves the muscle scars are situated almost exactly in the middle in the region of the greatest inflation. The central muscle scars consist of six slightly elliptic to longish scars; four of them lie, weakly bent, to the anterior margin in a vertical row. Behind the undermost two scars, two other scars occur; being arranged respectively a little bit higher than the anterior ones. Further muscular insertions (mandibular and antennal scars) could not be seen with certainty. The greater percentage of the discussed material consists of juvenile carapaces and valves. They are slimmer, less high and show a more concave ventral margin than adult specimens.

Occurrence:

In nearly all layers of the Guimarota mine (see table).

Affinities:

Leiria striata can be distinguished from *Leiria paucistriata* by the more pointed posterior end; from the lateral view by the nearly totally ribbed surface and by stronger ribs.

6.4. *Leiria paucistriata* n. sp.

1951 ?*Cyprinotus* sp. — STEGHAUS, Ostracoden als Leitfossilien des Kimmeridge. — *Paläont. Z.* 24, pp. 208-209, table 14, fig. 7.

1958 *Cetacella* sp. — MARTIN, Cetacella, eine neue Ostracoden-Gattung aus dem Kimmeridge Nordwestdeutschlands. — *Paläont. Z.* 32, pp. 194-195, table 18, fig. 7a-b.

Derivatio nominis: paucus (latin) = little, striatus (latin) = striped.

Holotypus: 1 Carapace GO 6, Pl. III, fig. 1.

Locus typicus: Guimarota coalmine.

Stratum typicum: layers TM₀ and M₃ with the exception of the coal layers.

Paratypes: 47 valves and carapaces GO 4-5.

Diagnosis:

A species of the genus *Leiria* with the following peculiarities:

The surfaces of the valves are ornamented only partly with very weak thin ribs. These ribs run about parallel to the dorsal margin. At the margin of the undermost half R has a denticulation. The greatest height in the carapaces is formed by the R.

Description:

The outline in the lateral view is broadly rounded triangularly. The greatest height is almost central. A well-rounded anterior cardinal angle is in front of it with a distinct concavity. In the same region L shows a weak concavity up to a straight part.

The rest of the anterior margin forms about a half-circle. It runs gradually into the ventral margin. The ventral margin of the L is almost straight in all its length. The ventral margin of the R shows a weak concavity in the middle. The dorsal margin goes downwards in a feeble convex line to a little marked posterior cardinal angle. The outline at the posterior margin falls steeply and forms a moderately well rounded posterior end. The very feebly developed ribs are mostly present only in the region of the strongest inflation of the valves. In many cases, they are only visible under inflation of the valves. In many cases, they are only visible under or behind this region. The ribs never extend to the margin. From the dorsl view the carapaces are longish oval. The greatest width is to be seen posteriorly. L overlaps R especially widely at the posterior end. From a ventral view there is also a wide overlapping of the L. The hinge is desmodont. A ridge of the L interlocks a furrow of the R. The valves are thinly shelled; the zone of concrescence is narrow. A large anterior and a smaller posterior vestibulum are present. Normal pore canals are simply built. In the back valve quarter and near the venter they do not appear very often. Radial pore canals are straight and simple. Their number could never be seen totally. At the anterior margin the quantity presumably reaches between 35 and 40. Only juvenile valves show clear muscle scars. The pattern is the same as in *Leiria striata* (Pl. III, fig. 2). Juvenile valves are relatively shorter and look therefore more compact. Partially they show stronger ribs than adult ones.

Occurrence:

Guimarota coalmine (see table). Possibly also in the Kimmeridge of northern Germany (Kimmeridge 1a, Wietze) see remarks.

Affinities:

Leiria paucistriata can be distinguished from *Leiria striata* by its weak and incomplete ornamentation and by its diverse shape.

Remarks:

Cyprinotus? sp. STEGHAUS 1951 is interpreted by G. P. R. MARTIN [MARTIN, 1958] as possibly belonging to *Cetacella inermis* MARTIN, 1958. This form shows however almost the same shape and almost the same muscle scars, and after MARTIN 1958 largely unornamented parts of the valves. According to this an attachment to *Leiria paucistriata* n. sp. seems to be possible.

6.5. Genus *Theriosynoecum*

Family: *Cytheridae* BAIRD, 1850.

Subfamily: *Limmocytherinae* SARS, 1925.

Type species: *Theriosynoecum wyomingense* [BRANSON, 1935]

1935 *Morrisonia*, BRANSON.

1936 *Theriosynoecum*, BRANSON (pro *Morrisonia* GROTE 1874 = Lepidoptera).

1958 *Theriosynoecum*, SOHN.

1962 *Theriosynoecum*, PINTO & SANGUINETTI.

1963 *Theriosynoecum*, VAN MORKHOVEN.

1964 *Theriosynoecum*, SOHN & ANDERSON.

1965 *Theriosynoecum*, BATE.

1960 *Theriosynoecum*, BRANSON.

Genus diagnosis of PINTO & SANGUINETTI 1962:

«Carapace thick-walled, irregularly oval to ovoid in dorsal view and sub-rectangular in side view; with a strong sulcus from the dorsum to the ventrum just in front of the midlength, practically dividing the valves into two portions, the anterior one being highly depressed; a second small sulcus a little in front of the main sulcus. Ornamentation consists of a reticulate surface with nodes in the anterior and posterior portion, with the posterior nodes ornamented with a net of thin ridges at the top, looking like and old castle tower; presenting also ventrally velate ridges. Hingement lophodont with a laminate anterior tooth and a stronger posterior tooth in a crescentic form, slightly bent dorsally; muscle scars in a vertical row of 4 adductors; marginal areas regular with fairly numerous straight radial canals. Accomodation groove present. Jurassic».

This diagnosis will be extended thus: the ornamentation can be smooth or reticulate.

6.6. *Theriosynoecum wyomingense* [BRANSON, 1935]

1935 *Morrisonia wyomingensis* BRANSON 1935—*Jour. Pal.*, Vol. 9, 6, pp. 521-522, pl. 57, figs. 17-21.

1936 *Theriosynoecum wyomingense* (BRANSON) BRANSON—*Jour. Pal.*, Vol. 10, 4, p. 323 (pro *Morrisonia wyomingensis*).

1961 *Theriosynoecum wyomingense* (BRANSON) HOWE—*Treatise on Invertebrate Paleontology*, Part Q, p. 312, figs. 239a-c.

1962 *Theriosynoecum wyomingensis* (BRANSON) PINTO & SANGUINETTI—*Esc. Geol. Porto Alegre*, Publ. Esp. 4, pp. 73-74, pl. I, figs. 7a-d, pl. II, figs. 7a-e.

1963 *Theriosynoecum wyomingensis* (BRANSON) VAN MORKHOVEN—*Post Paleozoic Ostracoda*, Vol. 2, pp. 412-416, fig. 690.

1964 *Theriosynoecum wyomingense* (BRANSON) SOHN & ANDERSON—*Palaeontology*, Vol. 7, pp. 72-73, text-fig. 18j.

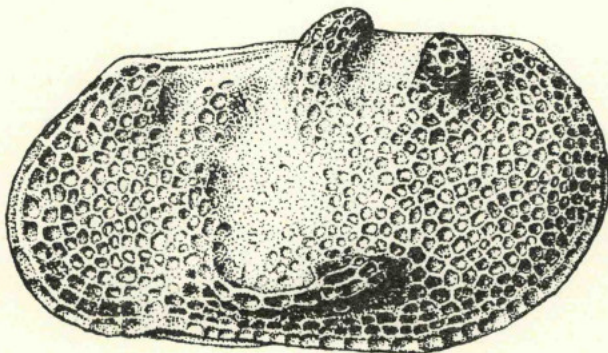
1966 *Theriosynoecum wyomingense* (BRANSON) BRANSON—*Okla. Geology Notes* 26, 4, pp. 88-89, figs. 1-15.

Material: over 70 carapaces and single valves (Figs. 5, 6, 7) GO 1-2.

Diagnosis: see PINTO & SANGUINETTI 1962, pp. 73-74.

Description:

From the lateral view a trapeze type outline with irregularly rounded anterior and posterior. The dorsal and ventral margins run almost parallel to each other. They converge slightly near the anterior. The shells are roughly sculptured. In the middle of the valves behind an anteromedian sulcus near the dorsal margin is a swollen hump. This hump rises towards the back beyond the dorsal margin.



1 mm

Fig. 5 — *Theriosynoecum wyomingense* (BRANSON, 1935).

L extern, male, GO 1.

Layer TM₀.

Almost in the middle of a line, which extends between the basis of this swelling and the posterior parallel to the dorsal margin, is a raised knot similar to a stalk. Between the front dorsal angle and the anteromedian sulcus, a second narrower sulcus extending itself slightly towards the ventrum, can be found. The anteromedian sulcus stretches far down and ends there in the region between the side surface and venter in a strong longitudinal ridge. This longitudinal ridge begins as a flat wide elevation at about half the height of the valve as a front limitation of the middle sulcus and bends near the ventral margin to the back at right angle. It can be described as a longitudinal ridge only after the bending over from the dorso-ventral direction in the length direction. It spreads itself in form of a clube to the back and ends under the back knot shortly before the basis of the latter. The valve surfaces are decorated with clearly formed grooves with the exception of the Sulci. These

grooves usually have a rounded-polygonal outline, but can appear oblong on the ribs, swellings and the ventral margin. From the dorsal view the carapaces appear wide at the back and narrow at the front. Clearly upraised, small swellings can be recognized in the dorsal angle region of the L. The dorsal margin of the R projects over that of the L. From a ventral view can be seen 3 to 4 longitudinal ribs near the outside margin which partly run together in the front valve quarter. The L overlaps the R

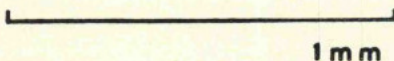
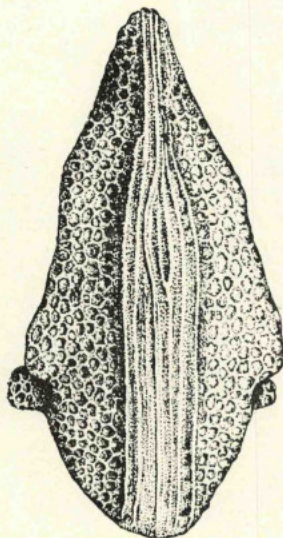


Fig. 6 — *Theriosynoecum wyomingense* (BRANSON, 1935).
Male from the ventral view. GO 1.

clearly here. The hinge is lophodont. R carries a longish narrow tooth at the front and a somewhat wider and higher one at the back of the hinge. Between them is a furrow, which is very well-developed in the front half. The L is accordingly furnished with a middle rib and tooth cavity at the front and at the back. The inner lamella is narrow, and moderately wide at the front.

A small vestibulum is present. Radial pore canals are not very numerous. (16-20) straight and simple. The muscle scars consist of 4 uneven longish scars lying under one another. A sexual dimorphism is clear. From a ventral view the females are posteriorly very wide and pointed in the form of hearts anteriorly. The posterior humps

cannot be seen. The ventral rib is only a little removed; it moves into the posterior valve part with a small step. The males are essentially slimmer from the ventral view; the two posterior humps project clearly on the sides. The ventral rib ends sharply in its posterior limitation (Figs. 6 and 7). Juvenile forms of this type show their greatest height in the anterior third; contrary to the adult forms. The polygonal cavities



1 mm

Fig. 7 — *Theriosynoecum wyomingense* (BRANSON, 1935).

Female from the ventral view. GO 2.

Layer TM₅.

of ornamentation in juvenile valves in relation to the entire length of the animals are bigger than in adults; they have almost the same diameter as the cavities belonging to the adult valves. Because of this, the cavities become only minutely enlarged in the course of ontogeny; the number of these cavities increases in growth.

Occurrence:

U.S.A. (Wyoming, Morrison Formation), and Portugal (Guimarota layers TM₆-FA₁₁).

6.7. Attempt at a distinction of 2 types of *Theriosynoecum* according to a statistical method

6.7.1. Introduction

Theriosynoecum wyomingense [BRANSON, 1935] appears in the layers TM_6 to FA_{11} in the Guimarota mine. In the layers lying above this there are no ostracods of this type to be found up to and including FA_7 . In the M_2 layer a type of ostracod makes an appearance and belongs with certainty to the genus *Theriosynoecum*. This form, moreover, looks very similar to *Theriosynoecum wyomingense*. Only in the formation of one feature, the ornamentation, do we find obvious differences. Because of this it is impossible either to state that it clearly belongs to *Theriosynoecum wyomingense* or to separate it completely from the same. However, perhaps with the help of a statistical process, a well-defined separation of both ostracod forms could be reached. In doing this, minor differences could be established which are scarcely perceptible in a morphologically descriptive manner.

Let us assume that 2 types of ostracods are similar in most features. Only a few characteristics show distinct differences. A clear demarcation of these forms appears scarcely possible due to this. With sufficiently large material, statistically comprehensible differences in many features could be present, and with this a separation of both groups from each other could be facilitated. The application of a statistical examining process of the following material appears to have a purpose.

With the help of a discriminant analysis the following should reveal whether *Theriosynoecum?* n. sp. can be separated from *Theriosynoecum wyomingense* [BRANSON, 1935]. With a positive result of this examination, that is, with sufficiently large differences between both forms, the specification of the form in question as a new subspecies of species could be justified.

For the calculations the following 3 features were chosen: height, length and number of cavities on one part of the valve (see below). A comparison of these three pairs of features is shown in the diagrams below. The abscissa with the scales for length, and height and the number of cavities, put into groups respectively, has been transferred (the scales for length and height are given in graduations of a measuring ocular. Division of these quantities through 48.5 gives the scale in mm.).

The ordinate shows the number of scales for length and height, and the number of cavities per group. In this comparison of features, differences show themselves only in the number of cavities. Lengths and heights intersect clearly. In both diagrams for the quantities and scales of *Theriosynoecum?* n. sp. the dotted lines are applicable, and for *Theriosynoecum wyomingense* [BRANSON, 1935] the broken lines are applicable.

6.7.2. Discriminant analysis

Different entities can, by reason of a certain number of features, be separated from one another by their single members and a specific function. This function — also called discriminant function, decides therefore on the classification of the single members. As one feature is scarcely sufficient for the separation of two entities, [WEBER, 1967] three features will be used in the following division process. These ought to be characteristic and easily measurable.

For measuring the following 3 features have been chosen:

1. The length of the valves.
2. The height of the valves.
3. The quantity of cavities in the anterior part of the valves (see below).

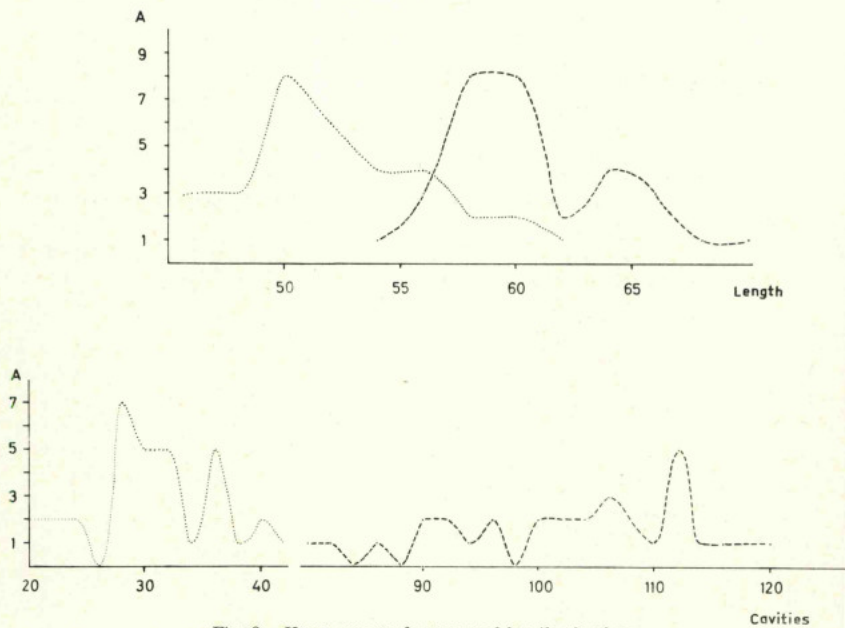


Fig. 8—Upper curves: frequency of length of valves.
Lower curves: frequency of number of cavities.

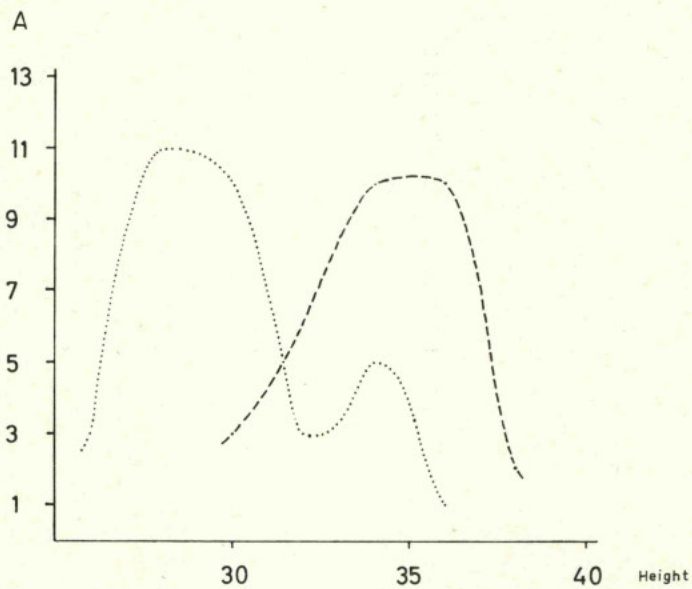


Fig. 9—Frequency of height of valves.

The measuring of the quantity of cavities took place in the region between the anterior margin and a line, which goes horizontally to the straight part of the ventral margin from the centre of the first lobus. An approximate equivalent of these measurable characteristics seems to be present. Not only the proportions of the carapaces, that is, length and height, but also the type of ornamentation in question apply as genotypical and therefore as essential criterion to a systematic classification [POKORNY, 1958; VAN MORKHOVEN, 1963].

The calculation follows a dividing process from LINDER 1964: «Statistische Methoden».

Measuring quantities:

First group: *Theriosynoeum?* n. sp.

Division of the measuring quantities through 48.5 gives the measures in mm.

	Height	Length	Number of cavities
(1)	30	51	37
(2)	30	52	36
(3)	29	51	31
(4)	26	50	20
(5)	26	48	29
(6)	33	59	24
(7)	28	49	28
(8)	27	49	27
(9)	28	45	32
(10)	30	50	24
(11)	27	50	22
(12)	33	58	34
(13)	31	53	30
(14)	35	60	28
(15)	31	52	22
(16)	28	46	36
(17)	27	48	35
(18)	29	55	30
(19)	28	49	32
(20)	30	51	31
(21)	28	48	39
(22)	30	51	32
(23)	27	55	27
(24)	33	56	39
(25)	34	53	35
(26)	30	61	28
(27)	26	58	19
(28)	32	56	36
(29)	30	46	30
(30)	29	50	41
(31)	28	54	27
(32)	33	54	30
(33)	28	49	28
	x_1^1	x_2^1	x_3^1

$$\text{Sum } x_1^1 \cdot x_3^1 = 29604$$

$$\text{Sum } (x_1^1)^2 = 28938$$

$$\text{Sum } x_1^1 = 974$$

$$\bar{x}_1^1 = 29,515$$

$$\text{Sum } x_2^1 \cdot x_3^1 = 51838$$

$$\text{Sum } (x_3^1)^2 = 31225$$

$$\text{Sum } x_3^1 = 999$$

$$\bar{x}_3^1 = 30,273$$

$$\text{Sum } x_1^1 \cdot x_2^1 = 50854$$

$$\text{Sum } (x_2^1)^2 = 89887$$

$$\text{Sum } x_2^1 = 1717$$

$$\bar{x}_2^1 = 52,03$$

$$n_1 = 33$$

Second Group: *Theriosynoecum wyomingense* B.

Conversion into mm. as above.

	Height	Length	Number of cavities
(1)	35	62	105
(2)	36	64	110
(3)	36	64	112
(4)	32	56	96
(5)	43	59	106
(6)	36	60	89
(7)	33	61	82
(8)	35	55	117
(9)	34	68	105
(10)	32	65	100
(11)	37	57	111
(12)	32	59	112
(13)	32	58	104
(14)	29	54	90
(15)	33	58	95
(16)	30	58	100
(17)	33	60	113
(18)	36	60	112
(19)	32	66	94
(20)	34	60	112
(21)	37	70	86
(22)	34	57	103
(23)	31	58	79
(24)	29	58	108
(25)	36	65	92
(26)	33	64	119
(27)	35	56	116
(28)	34	57	102
(29)	35	60	92
(30)	33	60	101
(31)	35	63	107
	x_1^2	x_2^2	x_3^2

Sum $x_1^2 \cdot x_3^2 = 107743$	Sum $x_1^2 \cdot x_2^2 = 63605$
Sum $(x_1^2)^2 = 35924$	Sum $(x_2^2)^2 = 113494$
Sum $x_1^2 = 1052$	Sum $x_2^2 = 1872$
$\bar{x}_1^2 = 33,935$	$\bar{x}_2^2 = 60,387$
Sum $x_2^2 \cdot x_3^2 = 191290$	
Sum $(x_3^2)^2 = 327488$	
Sum $x_3^2 = 3170$	$n_2 = 31$
$\bar{x}_3^2 = 102,258$	

From the above measuring results and the results obtained from the calculation operations which took place with, a linear discriminant function can be calculated.

In order to calculate the dividing formula the totals and products within the groups will be used first.

$$Sx_p x_s = S (x_3^1)^2 - \frac{(Sx_3^1)^2}{n_1} + S (x_3^2)^2 - \frac{(Sx_3^2)^2}{n_2} = 4312,4810$$

In the same way are calculated:

$$Sx_p x_s = 1000,3246 \quad \text{and} \quad Sx_s x_1 = 414,1135$$

These quantities are classified according to their size. The resulting sequence:

1. Cavities 2. Length 3. Height is retained in all further calculations.

$$Sx_p x_s = Sx_2^1 \cdot x_3^1 - \frac{Sx_2^1 \cdot Sx_3^1}{n_1} + Sx_2^2 \cdot x_3^2 - \frac{Sx_2^2 \cdot Sx_3^2}{n_2} = -277,3694$$

In the same way are calculated:

$$Sx_p x_1 = 285,8799 \quad \text{and} \quad Sx_s x_1 = 254,2591$$

Furthermore the differences of the averages are needed:

$$d_1 = \bar{x}_3^1 - \bar{x}_3^2 = 71,985$$

$$d_2 = \bar{x}_2^1 - \bar{x}_2^2 = 8,357$$

$$d_3 = \bar{x}_1^1 - \bar{x}_1^2 = 4,420$$

In the following three equations now the b_j can be determined:

$$b_1 \cdot S_{11} + b_2 \cdot S_{12} + b_3 \cdot S_{13} = d_1$$

$$b_1 \cdot S_{21} + b_2 \cdot S_{22} + b_3 \cdot S_{23} = d_2$$

$$b_1 \cdot S_{31} + b_2 \cdot S_{32} + b_3 \cdot S_{33} = d_3$$

The determination of the b_j results from a scheme of calculation from LINDER 1964, 613, 3. As well as this the S_{jk} and d_j are divided by 1000, in order to retain quantities which possibly may be between 0,5 and 2,0. The coefficients b_j will not be influenced by this and the calculations will be more exact.

For the S_{jk} and d_j which have been changed to such a degree the following quantities result:

$$\begin{aligned}
 Sx_3x_3 &= 4,3124810 = S_{11} \\
 Sx_3x_2 &= 1,0003246 = S_{23} \\
 Sx_2x_1 &= 0,4141135 = S_{23} \\
 Sx_3x_1 &= 0,2858799 = S_{13} \\
 Sx_2x_1 &= 0,2542591 = S_{23} \\
 Sx_3x_3 &= -0,2773694 = S_{12} \\
 d_1 &= -0,071985 \\
 d_2 &= -0,008357 \\
 d_3 &= -0,004420
 \end{aligned}$$

From this results the following scheme of calculation:

	1. Cavities	2. Length	3. Height	d	Q	Probation
01	4,3124810	— 0,2773694	0,2858799	— 0,071985	4,2490065	
02		1,0003246	0,2542591	— 0,008357	0,9688573	
03			0,4141135	— 0,004420	0,9498325	
04						
05					0,084762	
10	1,0	— 0,0643178	0,0662912	— 0,0166922		0,9852812
11	— 0,0643178	0,9824849	0,2726462	— 0,0129869	1,1778264	1,2421442
12	0,0662912		0,3951622	0,0003519	0,7344515	0,6681603
13						
14	— 0,0166922			— 0,0012015	— 0,0305287	0,0138365
20	— 0,0654644	1,0	0,2775067	— 0,0132184		1,1988239
21	0,0841398	0,2775067	0,3195011	0,0039558	0,6851028	0,4075961
22						
23	— 0,0175423	— 0,0132184		— 0,0013731	— 0,0281780	— 0,0149596
30	0,2633474	0,8685625	1,0	0,0123811		2,1442893
31						
32	— 0,0185840	— 0,0166542	0,0123811	— 0,0014220	— 0,0242791	— 0,0366602

From these quantities we now obtain the required dividing formula:

$$X = -0,0185840 \text{ Cavities} - 0,0166542 \text{ Length} + 0,0123811 \text{ Height}$$

For simplification $L = -1$ will be applied:

$$X = 1,115874 C + L - 0,743422 H$$

This equation represents the final form of the discrimination function. If the measuring quantities of both animal groups are applied in this dividing formula we obtain the following measures of calculation.

1. Group (*Theriosynoecum?* n. sp.)

(1)	69.9	(12)	71.4	(23)	65.0
(2)	69.8	(13)	63.4	(24)	74.9
(3)	64.0	(14)	65.2	(25)	66.7
(4)	52.9	(15)	53.5	(26)	69.9
(5)	61.0	(16)	65.3	(27)	59.8
(6)	61.2	(17)	66.9	(28)	72.3
(7)	59.4	(18)	66.9	(29)	57.1
(8)	59.0	(19)	63.8	(30)	74.1
(9)	59.8	(20)	63.2	(31)	63.3
(10)	54.4	(21)	70.7	(32)	62.9
(11)	54.4	(22)	64.4	(33)	59.4

2. Group (*Theriosynoecum wyomingense* B).

(1)	153.1	(12)	127.9	(23)	150.2
(2)	159.9	(13)	127.0	(24)	132.8
(3)	162.2	(14)	159.8	(25)	139.4
(4)	139.3	(15)	152.7	(26)	147.2
(5)	145.3	(16)	153.3	(27)	161.5
(6)	132.5	(17)	160.1	(28)	158.2
(7)	147.1	(18)	156.9	(29)	136.6
(8)	159.7	(19)	140.8	(30)	148.1
(9)	138.4	(20)	172.2	(31)	156.3
(10)	146.6	(21)	145.5		
(11)	123.1	(22)	159.4		

If these measures of calculation are summarised into groups, their distribution looks as the following:

Group 1:

51	to	55	=	4
56	to	60	=	6
61	to	65	=	12
66	to	70	=	7
71	to	75	=	4

Group 2:

121	to	125	=	1
126	to	130	=	1
131	to	135	=	2
136	to	140	=	5
141	to	145	=	2
146	to	150	=	5
151	to	155	=	3
156	to	160	=	9
161	to	165	=	2
166	to	170	=	0
171	to	175	=	1

In the graphic representation of the distribution of the scales of calculation of booth groups, the following two curves are obtained:

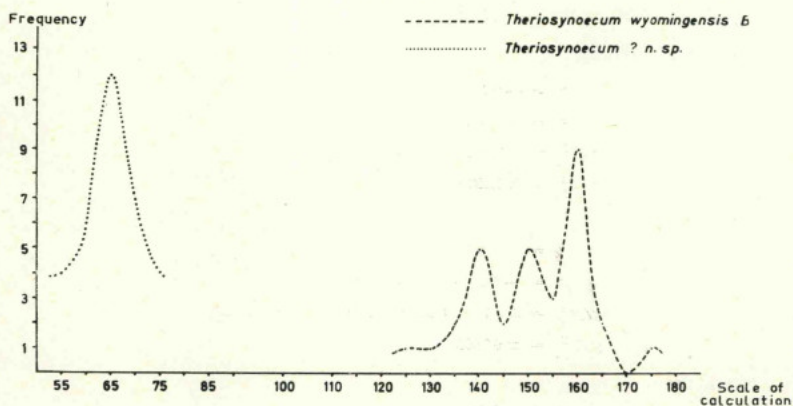


Fig. 10

According to this a complete division of both animal groups is present; both curves are widely separated from each other. Furthermore it must now be ascertained how strongly this division is assured. To do this, it will be tested to see whether the single features are normally distributed. This is necessary, since the exactness of the significance examination to follow later depends on a normal distribution of the features.

In the normality test the following quantities have been obtained (calculating scheme of LINDER 1964 pp. 85-90).

Theriosynoecum n. sp.

Number of cavities:

$$\begin{aligned} g_1 &= 0,1145 \\ g_2 &= -0,4422 \\ g_1/S_{g1}^2 &= \pm 0,6857 \\ g_2/S_{g2}^2 &= \pm 0,6930 \end{aligned}$$

Length:

$$\begin{aligned} g_1 &= 0,4914 \\ g_2 &= -0,4568 \\ g_1/S_{g1}^2 &= \pm 2,942 \\ g_2/S_{g2}^2 &= \pm 0,716 \end{aligned}$$

Height:

$$\begin{aligned} g_1 &= 0,5241 \\ g_2 &= -0,5266 \\ g_1/S_{g1}^2 &= \pm 3,138 \\ g_2/S_{g2}^2 &= \pm 0,826 \end{aligned}$$

Theriosynoecum wyomingense B.

Number of cavities:

$$g_1 = -0,48150$$

$$g_2 = -0,55735$$

$$g_1/S_{g1}^2 = \pm 2,722$$

$$g_2/S_{g2}^2 = \pm 0,8272$$

Length:

$$g_1 = 0,6702$$

$$g_2 = -0,0265$$

$$g_1/S_{g1}^2 = \pm 3,789 \text{ (the curve is not symmetrical)}$$

$$g_2/S_{g2}^2 = \pm 0,0393$$

Height:

$$g_1 = 0,8470$$

$$g_2 = 2,9498$$

$$g_1/S_{g1}^2 = \pm 4,378 \text{ (deviation in the height)}$$

$$g_2/S_{g2}^2 = \pm 4,7893 \text{ (the curve is not symmetrical)}$$

$$g_1 = \text{measurement for the skewness}$$

$$g_2 = \text{measurement for the elevation}$$

$$S_{g_i} = \text{dispersion}$$

The preserved quantities show only slight deviations from a normal distribution, with the exception of the length and height of *Theriosynoecum wyomingense*. In all probability however, these deviations can be traced back to external effects. Deformation of the valves, caused by diagenese or tectonics can be so weakly formed that they are not always recognizable a such. Changes in the height of the valves and carapaces occur very slightly and also in weak deformations. Deviations from the normal distribution especially in features of *Theriosynoecum wyomingense* are very distinctly marked. This may be due to the strong ornamentation of this type and also to the difficult recognition of any valve distortions or fractures. The total picture of the quantities shows, however, no essential deviations from a normal distribution.

From the scheme of calculation of the discriminant analysis we get furthermore, the size: dx to 1,422 (scheme of calculation 32/d). Since the quantities in the scheme of calculation were divided through 1000 this size has been multiplied again with 1000. dx shows how strongly the function of discrimination separates both groups from each other.

$$\text{Moreover } dx = b_1 \cdot d_1 + b_2 \cdot d_2 + b_3 \cdot d_3$$

Now can be tested whether the dj deviates from 0, or whether both groups belong to the same normal three dimensional basic entity.

For this is calculated:

$$F = \frac{n_1 \cdot n_2 (n_1 + n_2 - m - 1)dx}{m (n_1 + n_2)}$$

$\chi^2 F = 454,595$ that is, it can be assumed that
60 at least one dj deviates from O.

Therefore highly significant differences exist between the two groups of ostracods. We can be safely assured that the discrimination function effected a clear division of both groups. However, this dimorphism alone is not sufficient to allow for a separation of the form *Theriosynoecum?* n. sp. as a new species. But further criteria for such a division are present.

Stratigraphically, between both groups of forms yawns a gap cohabitation does not seem to have taken place. No differing facies can be given as the cause for the dimorphism, as the accompanying fauna of both groups has the same composition. For a so-called season dimorphism are no signs either. The climate seems to have been \pm the same in all layers in which *Theriosynoecum wyomingense* and *Theriosynoecum?* n. sp. appear.

A distinct morphological division of both groups is revealed by the discrimination analysis. Furthermore, we can be assured that the form *Theriosynoecum?* n. sp. does not appear to be dimorph through the effects of facies influences. Due to this, clear signs of a phyletic transformation of species are present.

It appears therefore as justifiable to separate *Theriosynoecum?* n. sp. from *Theriosynoecum wyomingense* as a new species. This occurs in the following chapter.

6.8. *Theriosynoecum hemigymnon* n. sp.

Derivatio nominis: hemigymnos (gr.) = half-naked; according to the only partly present ornamentation.

Holotypus: left valve of a female, GO 26, Fig. 17.

Locus typus: Guimarota mine near Leiria.

Stratum typicum: layer M₂.

Paratypoids: 39 single valves and carapaces.

Diagnosis:

A type of the genus *Theriosynoecum* with a long anteromedian sulcus, two large dorsolateral humps and a ventro-lateral rib.

The surface is partly smooth, and partly covered with small polygonal cavities. This ornamentation covers mostly only the part between the anterior margin and the first small sulcus.

Description:

The valves are decorated with the same coarse sculpture as in the wyomingense type. From the side view the outline is almost completely the same as in *Theriosynoecum wyomingense*. A part of the valve surface is decorated with small polygonal cavities. This ornamentation is found mostly only on the surface between the anterior margin and the first sulcus. The pattern does not continue over the large anteromedian sulcus. Cavities in the back third, in the region of the highest inflation of the valves are found only very rarely. Both humps and the «Langsrippe» are proximally smooth. In the distal region longish formed cavities are mostly present.

Sexual dimorphism is clear: from the ventral view the females appear heart-formed because of the bloated back part. The back side humps are not visible due to the spreading of the back valve parts. The males appear slimmer from the ventral view than the females; they are longish and egg-shaped.

The posterolateral humps are clearly recognizable from this view. The hinge is lophodont. The R has a longish, narrow tooth at the front and a higher and wider one at the back. Between them is a furrow which is deeper and broader in the front half. The L is also equipped with tooth cavities and different higher and wider middle ridges. The inner lamella is moderately wide at the anterior margin. A small vestibulum is present.

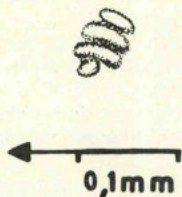


Fig. 11 — *Theriosynoecum hemigymnon* n. sp.
Muscle scars of the internal R.

Radial pore canals are not rare: there are 16 to 18 at the anterior margin and 18 to 20 at the posterior margin. They are partly irregularly arranged, mostly straight and do not seem to branch off. At the anterior margin false radial canals are not rare. The muscle scars consist of 4 scars; the 3 upper scars are situated in the length direction and are kidney-shaped and somewhat slanted under one another. The lowermost scar is smaller, oval and is situated under the front half of the one lying above it.

Juvenile animals of this type still show in the early skinning stage an almost complete ornamentation; that is, the valves are almost totally covered with polygonal cavities. Early youth stages of this type can, because of this, scarcely be differentiated from juvenile animals of the *Theriosynoecum wyomingense* type.

This ornamentation disappears in the course of further growth. The dissolution begins in the large anteromedian sulcus, stretches over the dorsal side parts and effects a smoothing out of the cavity in the real part of the valve. The front third retains this ornamentation the longest. Some remains of the anterior margin decoration are present in all adult animals. Between juvenile and adult carapaces the following changes have formed in the proportions:

The greatest height, which is situated in the front third in juvenile carapaces, shifts to the back during further growth.

This means that the ventral and dorsal margins converge slightly towards the back in young animals, whereas with adult animals the opposite is the case.

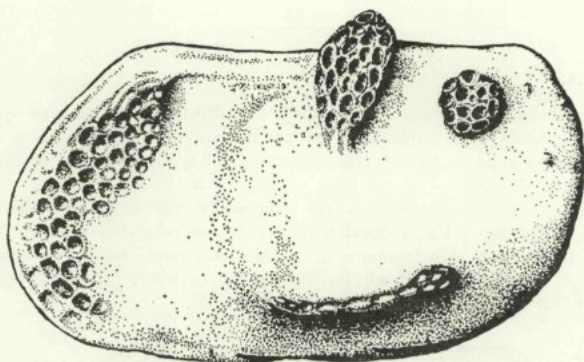
Measurements:

length 0,92-1,25 mm.

height 0,53-0,72 mm.

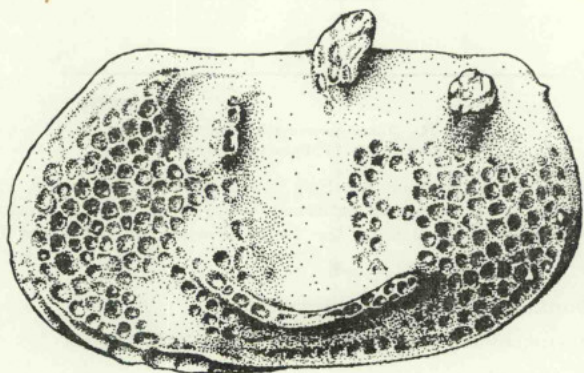
Occurrence: Until now only known from the Portuguese Kimmeridge. (see table).

Affinities: see chapter 6.7.



1 mm

Fig. 12.—*Theriosynoecum hemigymnon* n. sp.
L of a female, Holotyp GO 26. Layer M.
Measurements: length 1,11 mm., height 0,63 mm.



1 mm

Fig. 13.—*Theriosynoecum hemigymnon* n. sp.
L external, juvenile valve GO 24. Layer KM₄₋₆.

Remarks:

The illustrated form shown by PINTO & SANGUINETTI 1962 as type species appears on almost the whole valve surface to be not reticulated. In view of this it can belong to the *hemigymnon* type or to a further development of this species; a form completely lacking in ornamentation.

Theriosynoecum hemigymnon n. sp. supposedly represents a further development of the *wyomingense* type. The reduction of decoration indicates this [POKORNY, 1958].

In *Theriosynoecum hemigymnon* n. sp. the ontogeny shows the appearance of a reduction in ornamentation with all the stages in between. These in-between stages are lacking as evolutive witnesses.

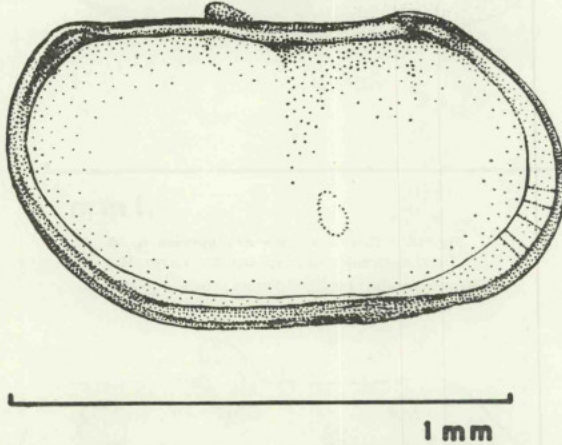


Fig. 14.—*Theriosynoecum hemigymnon* n. sp.
L internal GO 23. Paratype. Layer KM_{4,6}

No type of *Theriosynoecum* has been found between the layers TM₄ and FA₇.

In the layer M₂ the sparsely patterned hemigymnon type is present. This type retains the sparse ornamentation on the front valve also in the layers TM₁, FA₆ and KM_{4,6} which lie above it.

6.9. Genus *Bisulcocypris* PINTO & SANGUINETTI 1958

Type species: *Bisulcocypris pricei* PINTO & SANGUINETTI 1958.

The *Bisulcocypris* genus is represented with certainty in several species of the examined layers. In these types, thinness of the shells and size of the valves (± 1 mm.) diagenetic, tectonic or refrained mechanical strenght have offered little resistance. Complete valves therefore are rare, if they are present they seem to be exclusively juvenile valves. Because of this, description and illustrations must be dispensed with. The following types could be present according to the numerous fragments:

Bisulcocypris? forbesii [JONES, 1885].

Bisulcocypris? verrucosa [JONES, 1885].

And another type which is similar to *Bisulcocypris forbesii*.

6.10. Genus *Timiriasevia* MANDELSTAM 1947

Type species: *Timiriasevia epidermiformis* MANDELSTAM 1947.

Timiriasevia mackerrowi BATE 1965 Table III, figs. 2-12).

Material: over 40 single valves and carapaces (Pl. IV, figs. 1 and 2).

Description: compare BATE 1965.

From the side view oval. In the front third slightly tied up. L is larger than R. From the dorsal view heart-shaped. The surfaces are ornamented with irregularly running fine ribs. These ribs follow the outline approximately.

Occurrence:

In the middle to upper Bathonian of England. In the Portuguese Kimmeridge they appear in many layers of the Guimarota mine (see table).

Remarks:

After a comparison with the illustrations of BATE 1965 there scarcely exists a doubt that the species found in the Guimarota is identical to *Timiriasevia mackerrowi*.

6.11. *Poisia* n. gen.

Family: *Cytheridae* BAIRD 1850.

Sub-family: *Progonocytherinae* SYLVESTER-BRADLEY 1948 sensu MALZ 1961.

Type species: *Poisia bicostata* n. gen., n. sp.

Derivatio nominis: after a Portuguese adverb pois = natural.

Diagnosis:

A genus of the Progonocytherinae with dorso-ventral running ribs, which through cross ridges are partly joined in a honeycomb pattern. The side surfaces are limited underneath by a strong double rib.

Description:

L is clearly larger than R. In the region of the two hinge-angles L overlaps R, otherwise L lies against R, but, with the exception of the ventral region, is always clearly set apart from it. The inner lamella is moderately wide. The inner margin runs parallel to the outer margin. The radial pore canals are straight and simple; they are not very numerous. The central muscle scars consist of a row of 4 scars lying above one another at regular intervals. These scars are longish oval and show slight elevations. In front of these scars is also an approximate V-form impression.

The hinge is antimerodont. The front hinge part shows 4 to 5, the back 6 to 7 teeth. The central hinge is clearly subdivided. Well-formed ornamentation is present. It consists of dorso-ventral running ribs, which are partly joined together by cross-ridges. Ribs and ridges form a honeycomb pattern. A strong to weak appearing double ridge separates the lateral from the ventral surface. Eye swellings are present.

Affinities:

Similarities in the ornamentation with *Macrodentina* (Polydentina) MALZ 1958 and *Macrodentina* (Macrodentina) MARTIN 1940 are present. But these two sub-genera show no tooth ridges in the central hinge. *Fastigatocythere* WIENHOLZ 1967 is longer-stretched, and shows with an approximately equal hinge, a pointed posterior end and a partly convex dorsal margin projected through valve inflation. It is furthermore distinguishable from this and other genera by the characteristic ornamentation and the distinct latero-ventral rib.

Occurrence:

Until now only known from the Portuguese Kimmeridge.

Remarks:

Poisia n. gen. is delgated to the extended Progonocytherinae following a suggestion of SYLVESTER-BRADLEY 1948, from MALZ 1961 et. al.

Deviation from *Fastigatocythere* WIENHOLZ 1967 is possible because of the weaker grooved front hinge part.

6.12. *Poisia bicostata* n. sp.

Derivatio nominis: bicostatus (latin) = double-ribbed; named after the double latero-ventral rib.

Holotypus: a right valve, GO 16, fig. 22.

Paratypoids: 17 valves and carapaces GO 17-19.

Locus typicus: Guimarota coalmine.

Stratum typicum: layer M₂.

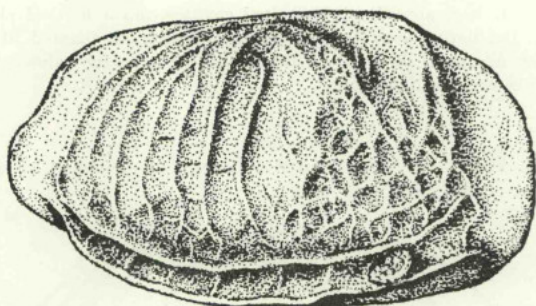
Diagnosis:

A species of the genus *Poisia* with rather wider doubled ventral rib. From the side view can be seen dorso-ventral running ribs, which going away from the centre of the valve, approximately parallel to the anterior and posterior margins, are bent. Almost all these ribs meet in a part of the valve which is situated a little underneath the dorsal margin, shortly before its middle. Thin ridges form a net with approximately 6 cornered meshes between the coarse ribs in the lower anteromedian region.

Description:

L from the side view slanted and trapeze shaped with a slightly convex dorsal margin. Behind a weak dorsal angle, a concave part of the posterior margin appears. The posterior margin transfers itself finally into the ventral margin in an almost half-circle. Contrary to this, the R has an almost straight dorsal margin and a distinct back dorsal angle.

Near the finely-formed honeycomb patterned ridges in the lower anteromedian region the coarse sickle ribs and the double ventral ribs are partly joined together by thin ridges. The hinge construction is amphidont-merodont. The anterior terminal element of the R consists of 5 teeth, the posterior of 6 teeth. The central hinge is formed of cavities lying next to one another, which generally become smaller from the front to the back. However, this does not occur regularly; the first 5 cavities are still approximately the same size; only after this does a decrease in size continue weakly.



0,5 mm

Fig. 15—*Poisia bicostata* n. gen. sp. Holotypus:
GO 16. R external. Layer H_2 (in the front in the
double ridge is a tightly encased piece of calcite).

Measurements: length 0,59 mm. Height 0,35 mm.



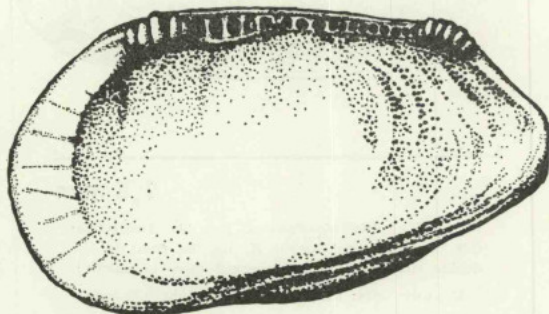
0,5 mm

Fig. 16—*Poisia bicostata* n. sp. Paratype
L external GO 17 Nr. 4. Layer M.

The hinge of the L has, accordingly terminal cavities and a toothed ridge in the central hinge. From the dorsal view the carapaces appear oval, pointed at the front and at the back. From a ventral view 3 to 4 thin length ribs on each valve can be recognized. Radial pore canals are not numerous.

Occurrence:

Up to now known only from the Kimmeridge of Portugal. Appears in many layers of the Guimarota mine (see table).



0,5 mm

Fig. 17 — *Poisia bicostata* n. sp. Paratype
R internal GO 17 Nr. 7. Layer M₂.

Affinities:

Poisia bicostata resembles some types of the sub-species *Macrodentina* (*Polydentina*) MALZ 1958, but can be distinguished from it by its hinge construction.

6.13. *Poisia clivosa* n. sp.

Derivatio nominis: clivus (latin) = hill.

Holotype: 1 R valve, GO 10.

Paratypoids: 21 valves and carapaces GO 11-12.

Locus typicus: Guimarota mine.

Stratum typicum: layer FA₂.

Diagnosis:

A species of the *Poisia* genus with a well-formed hill behind the centre of the valve near the dorsal margin.

Description:

The outline is slanted and trapeze-formed from the side view. The dorsal margin is almost straight with a slight concavity before the centre. The R shows a blunt, well-rounded anterior dorsal angle. In front of this is an almost straight part, which in the L can even be slightly concave. The remaining widely-rounded anterior margin goes into the ventral margin with a slight break. The back dorsal angle is especially clearly formed at the R. The posterior margin decreases sharply after this, forms a concavity shortly above the centre of the valve and goes gradually into the ventral margin almost in a half circle. Contrarily, the back dorsal margin at the L is slightly convex and forms a widely-rounded posterior dorsal angle. The outline then continues falling almost straight to a well-rounded point at the back end.

At the border between the side surface and the venter is a length rib, which shows a weak length furrow in the middle. On the front part of the valve some narrow ribs can be seen, which run approximately parallel to the anterior margin. Below the centre of the front dorsal angle is a broad moderately high eye-hump from which stretches \pm parallel to the anterior margin, a swelling free of decoration, to about half the height of the valve.

Behind the middle line, beginning with the feet, is an ornamented hill, the diameter of which at the feet amounts to about one fifth of the length of the valve. Between swelling and hill is a mostly weakly ornamented broad sulcus, which shows in its upper part a weak sometimes longish rib-typed swelling running down to the bottom.

Both valves are evenly ornamented. The ornamentation consists of polygonal, mostly six-cornered cavities below the swelling and below as well as behind the hill. Between the anterior margin ribs can be seen approximately right-angled cavities, which have formed themselves through short ridges which connect these ribs with one another. A clear differentiation between these two types of cavities is not always possible. Especially on the back of the valve and on the hill there seem also to be weak ridges with cross-ridges, although not always recognizable as such, and which also form polygonal cavities. From the side view the hill usually shows one, rarely two ribs, which copy its outline. The outline is determined by the two latero-ventral ribs in the dorsal view. The carapaces are not very broad and longish-oval and show points clearly set apart at the front and the back. The L is clearly larger than the R.

From the ventral view can be seen a few very thin length ridges close to the outer margin. Similarly a ridge pattern is barely visible near the lateral ventral hill. The hinge is amphidont-merodont. The right valve carries 4-5 teeth at the front, 5-6 at the back. The central hinge of the R consists of a row of cavities, which lie in a furrow which becomes narrower from the front to the back. Approximately, the L has cavities for the front and back hinge teeth and a toothed differently broad ridge of the central hinge. The melted zone is moderately broad, the inner lamella is very narrow.

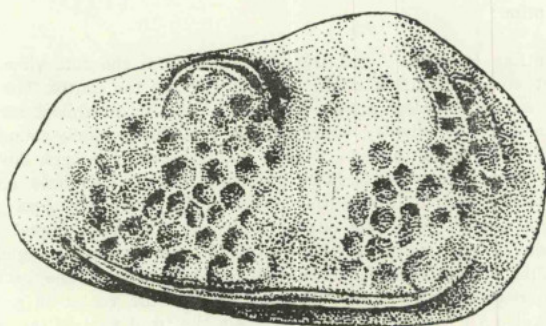
Juvenile shells are numerous. In sculpture and outline, they are much the same as adult ones: only the valve is clearly thinner.

Occurrence:

Up to now known only from the Kimmeridge of the Guimarota coalmine (see table).

Affinities:

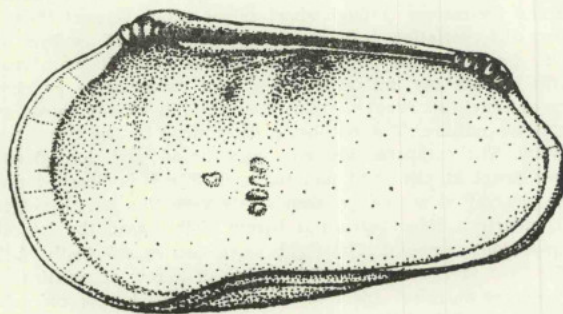
The noticeable sculpture enables a clear distinction from other species.



0,5 mm

Fig. 18 — *Poisia clivosa* n. sp. Holotype: GO 10.
R external. Layer: FA₂.

Measurement: Length 0,62 mm. Height 0,37 mm.



0,5 mm

Fig. 19 — *Poisia clivosa* n. sp. R internal GO 11.
Layer: FA₂. (Example was severely destroyed
after the illustration).

6.14. *Darwinula* sp.

Super family *Darwinulacea* BRADY and NORMAN 1889.

Family *Darwinulidae* BRADY and NORMAN 1889.

Genus *Darwinula* BRADY and ROBERTSON 1870.

Type species *Polycheles stvensoni* BRADY and ROBERTSON 1870.

It most layers of the Guimarota mine *Darwinula* sp. makes an appearance (see table). However, completely preserved valves or carapaces are very rare due to their thin shells; they are almost always broken. From small pieces can be seen that these fractures are primarily present; probably they originated from the embedding resp. the diagenesis.

Probably two types are present, a small grower and a rather large type. Because of the badly preserved conditions estimations of size could not be made. For the same reason an illustration is missing.

6.15. *Oertliana kimmeridgensis* KILENYI, 1965

Family *Cytheridae* BAIRD 1850.

Subfamily unknown.

Genus *Oertliana* KILENYI 1965.

Oertliana kimmeridgensis KILENYI 1965.

GO 13, fig. 27.

1957 *Cytherideinarum?* sp. 1. — OERTLI, Ostracodes du Jurassique Supérieur du Bassin de Paris (Sondage Vernon 1), p. 661, pl. III, figs. 86-91.

1965 *Oertliana kimmeridgensis* — KILENYI, *Oertliana*, a new Ostracod Genus from the Upper Jurassic of North-West Europe. pp. 573-574, text-fig. 1, pl. 79, figs. 1-12.

Description:

From side view slanted and trapeze formed. The approximately straight dorsal and ventral margins are parallel or converge lightly against the anterior margin. The greatest height is behind the mid-point. The back end is formed as a coarse point, the outline of which resembles a rounded right angle. The anterior margin is bent far round.

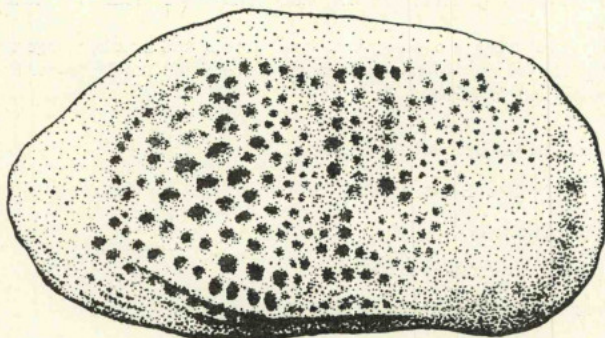
A thin length rib represents the border to the venter in the centre part of the valve. The valve surfaces are decorated with cavities of varying sizes. These cavities are largest in the rear third of the valve. They lie there mostly between weak ridges, which partly copy the valve outline. The size of these cavities decreases in the front half in the direction of the anterior margin. At the rear end, in the lower half of the front valve quarter, as well as on the edges, can be found surfaces occupied with uniform small cavities. In front of the centre can be a flat sulcus, which is broad at the top and narrows towards the bottom. A moderately broad inner lamelle shows itself on the anterior part of the the margin. Radial pore canals are rare front: 8-11) straight and simple. The muscle region can never be seen com- in a row. The L is larger than the R. The hinge is adont with a curved ridge on the right and a groove on the left valve.

Occurrence:

Evident in almost all layers of the Guimarota mine. *Oertliana kimmeridgensis* occurs in the lower Kimmeridge of Dorset and the Paris Basin [KILENYI, 1965].

Remarks:

The present material does not be sufficient for a clear separation of juvenile and adult forms or males and females. But in almost all shell details it seems to be evident that the described Guimarota-Ostracod belongs to the species *Oertliana kimmeridgensis* KILENYI 1965.



0,25 mm

Fig. 20 — *Oertliana kimmeridgensis* KILENYI 1965

R external, GO 13

Layer FA₂

Measurements: Length 0,40 mm.

Height 0,22 mm.

7. SUMMARY

Stratigraphy and microfossils of the layers of the coalmine Guimarota near Leiria (Portugal) are discussed. The age of the sediments can be assessed as Lower Kimmeridge.

The described sediments have probably been formed in a lagoonlike basin mostly containing \pm pure freshwater. The ostracods found in fresh- to brackish water sediments are described. Among them are two new genera: *Leiria* n. gen. and *Poisia* n. gen. With the help of a discriminant analysis, *Theriosynoecum hemigymnon* n. sp., a very similar form to *Theriosynoecum wyomingense* (BRANSON) is separated from the latter.

ZUSAMMENFASSUNG

Stratigraphie und Mikrofossilbestand der in der Kohlengrube Guimarota bei Leiria (Portugal) aufgeschlossenen Schichten werden vorgestellt. Das Alter dieser Gesteine kann als Unter Kimmeridge angegeben werden.

Die untersuchten Sedimente sind vermutlich in einem lagunen-ähnlichen, meist \pm reines Süßwasser enthaltenden Becken gebildet worden. Die gefundenen Süß- bis Brackwasserostrakoden werden beschrieben. Dabei werden zwei neue Gattungen: *Leiria* n. gen. und *Poisia* n. gen. aufgestellt.

Mit Hilfe einer Diskriminanzanalyse wird eine der Art *Theriosynoecum wyomingense* (BRANSON) sehr ähnliche Form von dieser abgetrennt und als neue Art *Theriosynoecum hemigymnon* n. sp. beschrieben.

RÉSUMÉ

La stratigraphie et les microfossiles des couches exposées dans la mine de charbon Guimarota près de Leiria (Portugal) sont présentés. L'âge de ces sédiments peut être déterminé comme Kimmérien inférieur.

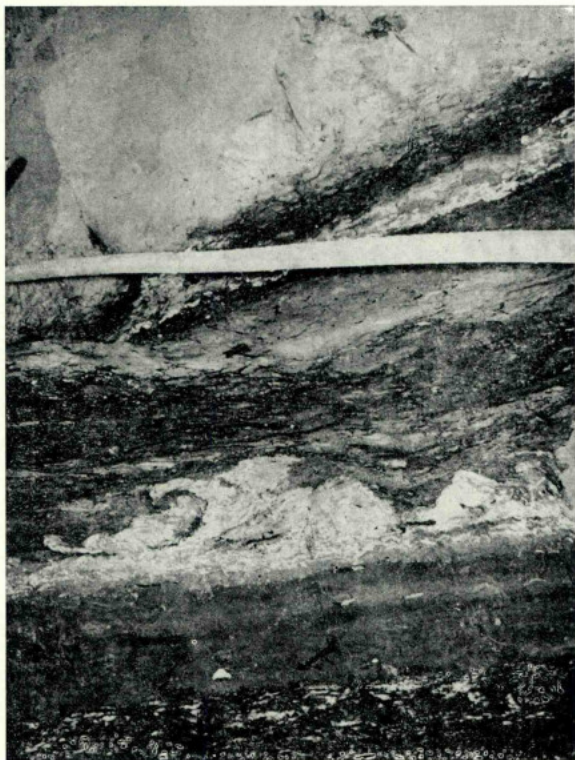
Les sédiments étudiés se sont déposés probablement dans un bassin de type lagunaire, contenant généralement de l'eau douce plus ou moins pure. Les ostracodes d'eau douce à saumâtre sont décrits et deux nouveaux genres sont établis: *Leiria* n. gen. et *Poisia* n. gen. A l'aide d'une analyse discriminante l'espèce *Theriosynoecum hemigymnon* n. sp., très voisine de *Theriosynoecum wyomingense* (BRANSON), a pu être séparée de celle-ci.

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PLATES

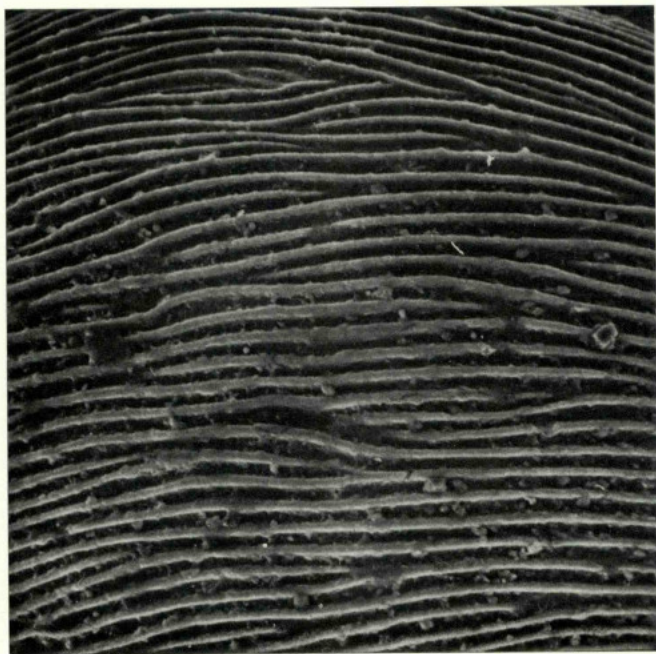


Guimarota layers from KM_6 to FA_4 . From above. FA_4 , TM_1 , M_2 (FA_1), KM_4 , KFM , M_2 , FA_2 and KM_{2a} .



0,5 mm

Fig. 1—*Leiria striata* n. sp. Holotypus, Carapace seen from the left.
Measurements: Length 0,80 mm. Height 0,49 mm. Width 0,35 mm.



0,2 mm

Fig. 2—*Leiria striata* n. sp. Holotypus. Part of the left valve
seen from outside.



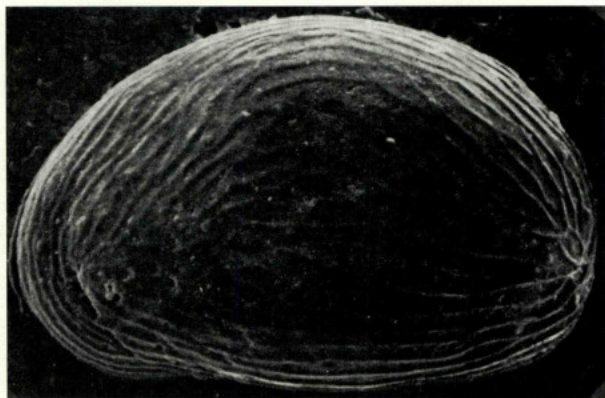
0,5 mm

Fig. 1—*Leiria paucistriata* n. sp. Holotypus, Carapace, view from left GO 6. Layer TM₁. Measurements: Length 0.89 mm. Height 0.60 mm.



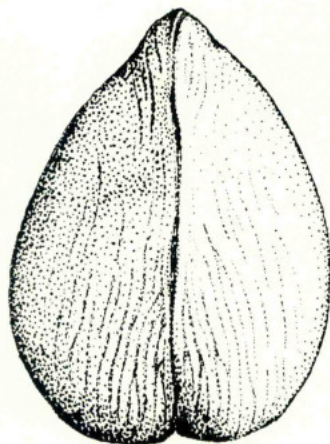
0,05 mm

Fig. 2—*Leiria paucistriata* n. sp. Muscle scars, outside view of a right valve.



0,25 mm

Fig. 1 — *Timiriasevia mackerrowi* BATE 1965. L external GO 32.
Layer M₂.



0,5 mm

Fig. 2 — *Timiriasevia mackerrowi* BATE 1965.
Carapace from above GO 30. Layer M₂.

TABLES

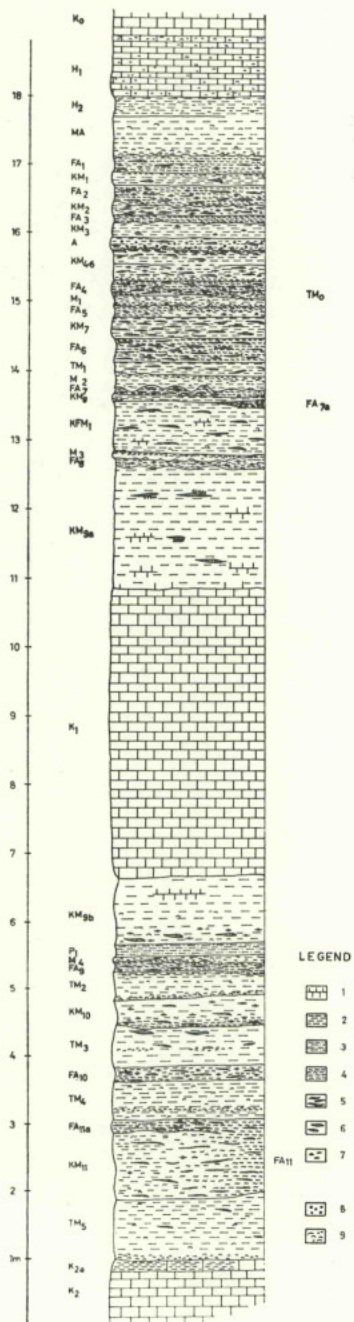


Table 1—Guimarota mine. Facies profile.

1—Lime. 2—Marl. 3—Flat Marl.
4—Impure coal. 5—Coal lenses.
6—Driftwood. 7—Fusite. 8—Charophyta. 9—Shells.

Layer	<i>Theriosynoec. wyomingense</i>	<i>Theriosynoec. hemigymnon</i>	<i>Darwinula</i> sp.	<i>Poisa bicostata</i>	<i>Poisa clivosa</i>	<i>Leiria striata</i>	<i>Leiria paucistriata</i>	<i>Timiriasevia mackerrowi</i>	<i>Disulcocypis</i> sp.	<i>Porochara</i> sp.
K ₀ - H ₂										
MA			■							
FA ₁										
KM ₁			■		■		■	■	■	■
FA ₂			■	■	■		■		■	■
KM ₂			■		■					
FA ₃			■			■	■	■	■	■
KM ₃			■			■	■	■	■	■
A			■							■
KM ₄₋₆		■	■	■	■	■		■	■	■
FA ₄										
TM ₀		■	■	■		■	■	■	■	
M ₁			■			■	■	■	■	■
FA ₅										
KM ₇			■				■	■	■	■
FA ₆		■	■			■	■	■		
TM ₁		■	■			■			■	
M ₂		■	■	■		■	■	■	■	■
FA ₇										
KM ₈			■	■	■	■	■	■	■	■
FA _{7a}			■	■	■	■		■	■	■
KFM			■	■	■	■	■	■	■	■
M ₃			■			■				
FA ₈										
KM _{9a}			■						■	
K ₁										
KM _{9b}			■						■	
P									■	
M ₄			■	■			■		■	■
FA ₉										
TM ₂			■	■	■				■	
KM ₁₀			■	■	■		■	■	■	■
TM ₃				■	■					
FA ₁₀										
TM ₄			■						■	
FA ₁₁	■		■			■	■	■	■	■
KM ₁₁	■		■			■	■	■	■	■
TM ₅	■		■			■	■	■	■	
K _{2a}			■	■			■			
K ₂										

■ = rare ■ = frequently ■ = abundant

Table 2—Microfossil distribution.

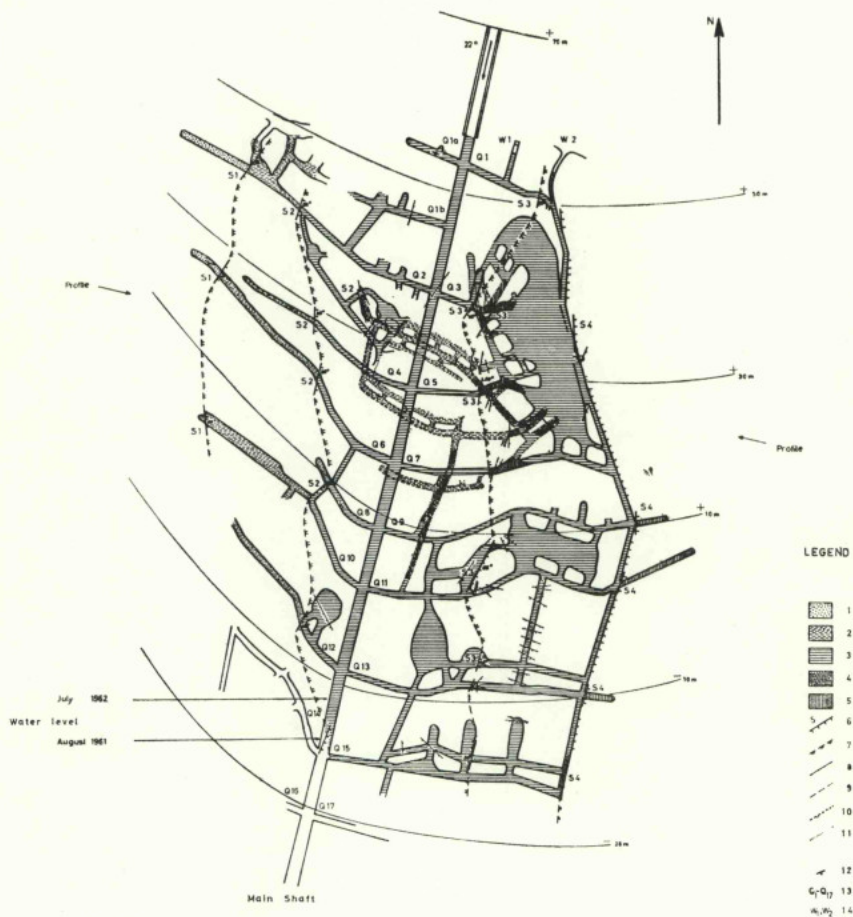


Table 3 — Guimarota mine plan.

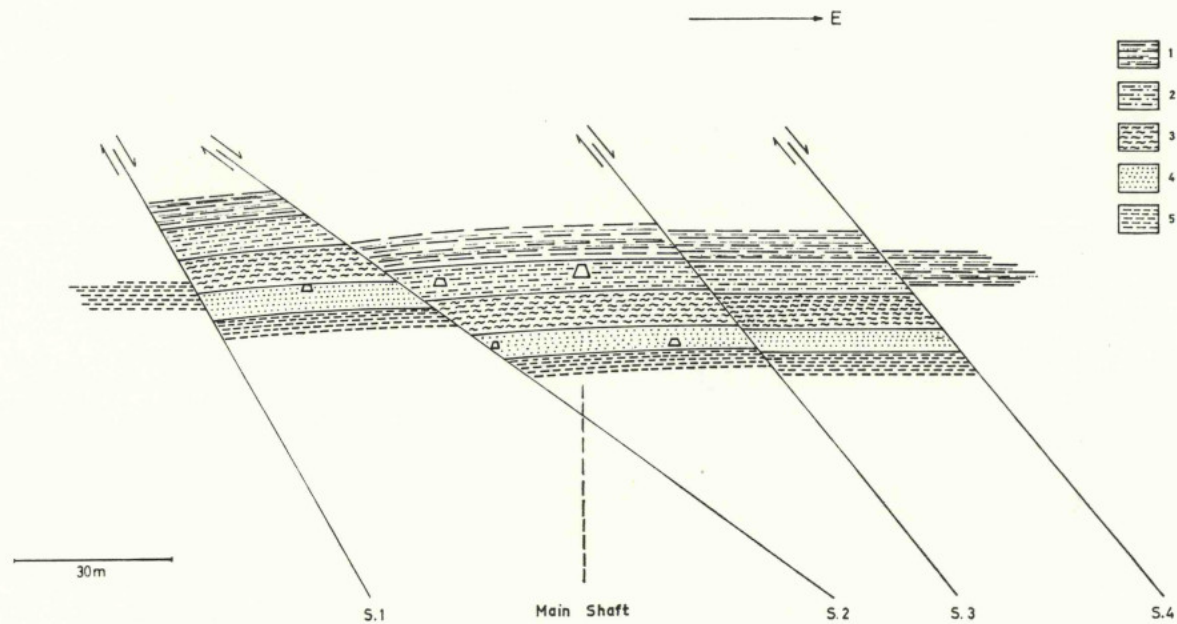


Table 4 — Gulmarota mine. E-W profile (adapted from HELMDACH, 1963).

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