LOWER PALEOGENE CROCODILIANS FROM SILVEIRINHA, PORTUGAL

by

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SOMMAIRE

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ABSTRACT

The presence at Silveirinha of one of the earliest, ?Late Paleocene or Lowermost Eocene, european representatives of the genus *Diplocynodon* is based mostly on isolated bones and teeth (often from juveniles). This small-sized form is the only crocodilian so far recognized in this site. The longevity of *Diplocynodon* in Portugal becomes much extended; the genus survived there until the Middle Miocene at least.

A discussion on the possible affinities with other eocene *Diplocynodon* and especially those from Cubillos-Valdegallina (Zamora, Spain) is presented. On the other hand, differences have been detected in comparison with: *Diplocynodon tormis*, from the middle Eocene of the Douro basin in Spain, which may belong to another phyletic line; and the aff. *Diplocynodon* from Dormaal (Belgium) and Le Quesnoy (France), nearly contemporaneous of Silveirinha.

The Silveirinha *Diplocynodon* and many other data strongly suggests moist, subtropical, quite limited in space environments related to an alluvial plain crossed by small, meandering channels.

RESUMO

A presença em Silveirinha de um representante do género *Diplocynodon*, um dos primeiros (?Paleocénico superior ou Eocénico basal) na Europa, foi demonstrada com base em numerosos restos ósseos e dentários, muitos de jovens. Trata-se de crocodilos de pequeno porte. Nenhum outro crocodilo foi aí reconhecido. A longevidade de *Diplocynodon* em Portugal fica, assim, muito ampliada, pois é conhecido pelo menos até o Miocénico médio.

São discutidas possíveis afinidades com representantes eocénicos, em particular de Cubillos-Valdegallina (Zamora, Espanha). Por outro lado, foram verificadas diferenças relativamente a: *Diplocynodon tormis*, do Eocénico médio da bacia do Douro, possivelmente de outra linha filética; bem como ao aff. *Diplocynodon* de Dormaal (Bélgica) e Le Quesnoy (França), aproximadamente contemporâneo do de Silveirinha.

O *Diplocynodon* de Silveirinha, em conjunto com muitos outros dados, sugere ambientes húmidos, subtropicais, certamente limitados em espaço, associados a uma planície aluvial atravessada por canais relativamente pequenos e meandrizados.

RESUME

La présence d'un représentant du genre *Diplocynodon*, l'un des plus anciens (?Paléocène supérieur ou Éocène basal) en Europe, a été démontrée d'après un matériel osseux et dentaire nombreux, souvent de jeunes sujets. Il s'agit de crocodiliens de petite taille. Aucun autre crocodilien n'a été reconnu à Silveirinha, important site à mammifères, etc. La longévité du genre au Portugal devient ainsi très amplifiée; le genre y a survécu au moins jusqu'au Miocène moyen.

On discute les affinités possibles avec des représentants éocènes du genre en cause, et particulièrement avec ceux de Cubillos-Valdegallina (Zamora, Espagne). D'autre part, on a reconnu des differences par rapport à: *Diplocynodon tormis* de l'Eocène moyen du basin du Douro en Espagne, qui appartient peut-être à une autre lignée phylétique; au aff. *Diplocynodon* de Dormaal (Belgique) et Le Quesnoy (France), presque contemporain de celui de Silveirinha.

Le *Diplocynodon* de Silveirinha suggère, en ensemble avec bien d'autres données, des environnements humides, subtropicaux, en des aires restreintes, en rapport avec une plaine alluviale traversée par d'assez petits chenaux méandrisés.

INTRODUCTION

The K-T crisis is related to the extinction of the latest non-avian dinosaurs, among other groups. Although many explanations have been proposed, there is one general key factor that must be taken into account: a distinct drop of temperatures during uppermost Cretaceous times.

The crisis had effects on crocodilians. Some taxa apparently became extinct but others survived. Improving environmental situations between the Middle Paleocene and the Middle Eocene undoubtedly favoured crocodilian radiation and diversity. Temperature and aquatic environments are of paramount importance, as has been recognized for long. According to Berg (1964), extant crocodilians cannot live normally and reproduce below 10 degrees Celsius. This would be a lower limit for those that are the most tolerant, requirements being much higher for other species. *Alligator mississipiensis* "are affected much less severely by adverse conditions of cold for brief periods than they are by adverse conditions of heat" and "is better able to withstand adverse low temperatures above freezing than adverse high temperatures and presumably the same holds for other crocodilians" (Colbert *et al.*, 1946). "Probably recent and fossil crocodiles are restricted in their geographic range by the same temperature limits" ["up to the 10 or 15° C isothermal line of January/N. Hemisphere or July/S.Hemisphere] (Berg, id.). *Alligator mississipiensis* and the Yangtse *Alligator sinensis* can withstand brief periods of freezing (I. L. Brisbin, Jr. in Ross *et al.*, 1990: 50).

Large-sized crocodilians inhabit adequate tropical, humid areas (large rivers, bogs, lakes, even coastal sea areas). The long-snouted gharials, tomistomines, *Crocodylus cataphractus* and *C. johnstoni* are mostly fish-eaters. Most *Crocodylus* and the largest alligatorines as *Melanosuchus* prefer large prey. Smaller crocodilians, either young individuals and smaller species, may thrive on secondary or small rivers, on creeks or rain forests (Ross *et al.*, 1990). The most tolerant taxa may occupy areas that are marginal to the optimum ones.

Excluding the longirostrine, supposedly partly marine forms, the following taxa are represented in the European Paleocene-Eocene (Systematics mostly according Brochu, 1997):

SEBECOSUCHIA

Family Iberosuchidae

Genus *Iberosuchus* - Large-sized, with robust, ziphodont, laterally compressed teeth, mostly terrestrial, archaic crocodilians/ Middle to early Upper Eocene - prior to the appearance of large enough carnivore mammals (see Antunes, 1975, 1986a, 1986b; Buffetaut, 1982: 1104, 1986: 105-106 and Buffetaut in Ross *et al.*, 1990: 32-33; Jiménez-Fuentes *et al.*, 1987: 375-376; Ortega and Buscalioni, 1992: 68).

NEOSUCHIA

Family Pristichampsidae

Genus *Pristichampsus* - ziphodont eusuchians (Paleocene - Middle to early Upper Eocene; Europe, Asia, N. America; ? Quaternary, Australia).

Super-Fam. ALLIGATOROIDEA

Family Diplocynodontidae

Genus *Diplocynodon* - small to medium-sized (maximum adult length about 2 m), brevirostrine crocodilians with a pair of nearly the same size, mandibular "pseudo-caniniforms" (third and fourth teeth) – an essential character referred in all textbooks, diagnostic of the genus and unknown in any other genera (Jehenne, 1970: 6) (Paleocene - Middle [?until early Upper] Miocene of Europe; its presence in N. America has been denied – Brochu, 1994: 695). *Diplocynodon* has been ascribed to the Alligatorinae; however by some skull and other characters it seems closer to the Crocodylinae. According to Ginsburg and Bulot (1997: 108-112), *Diplocynodon* should be included among the latter, unless it would be justified to segregate it in a distinct subfamily.

Genus indet., aff. *Diplocynodon* - a new species with dental characters that look similar to those of eocene ziphodont crocodilians (represented in the Lower Eocene MP7 of Dormaal in Belgium; at Le Quesnoy, France - see Nel *et al.*, 1999; and maybe the same was referred as cf. *Diplocynodon*, from Meudon, Sparnacian – Russell *et al.*, 1990).

Family Indeterminate

Genus *Baryphracta*, very small (scarcely 1 m long adult size), brevirostrine crocodilians with a particularly developed osteoderm armour until the tail's end and on the limbs, from the middle Eocene (Lutetian) Messel Mine near Darmstadt in Germany (Frey *et al.*, 1987; von Koenigswald and Storch, 1998: 38-39). In the original description, the type species *Baryphracta deponiae* has been ascribed to an Eusuchian "?Familie" (Frey *et al.*,1987: 16). The classification of *Baryphracta* at the familial level does not seem clear in later papers, as in Koenigswald and Storch (1998).

Family Alligatoridae

Genus *Allognathosuchus* - small to middle-sized, very brevirostrine crocodilians with typical rear crushing teeth with low and round crowns (Lower Paleocene-Middle Eocene; Europe, N. America, ?Asia) (see Berg, 1966).

Super-Family CROCODYLOIDEA

Family indeterminate

Genus *Asiatosuchus* - large, brevirostrine, robust crocodilians (Paleocene - Middle Eocene; Europe, Asia).

The study of the crocodilians from the scarce late Palaeocene or lowermost Eocene sites is particularly interesting. It has been done for Dormaal (Belgium), the Reference Locality for the MP7 level, lowermost Eocene (Buffetaut, 1985). Brief references have been included in papers on other Sparnacian sites (Russell *et al.*, 1990; Nel *et al.*, 1999).

The study of the even earlier crocodilians from Silveirinha along with comparison with its Spanish counterparts is our current aim.

Although account is taken on recent developments in crocodilian systematics, general systematics and phylogeny are beyond our goals and will not be discussed here. Anyway it would not add much to the progress of knowledge about the westernmost and earliest European *Diplocynodon* representatives.

THE SILVEIRINHA SITE

Crocodilian remains are very common among the fossils from Silveirinha, a large clay pit for tile production in the Lower Mondego area, West-Central Portugal (Topographic co-ordinates, x = 141.300 and y = 357.375, Carta Militar de Portugal 1: 25 000, Sheet 261).

The concerned lithostratigraphical unit, the "Areias e argilas de Taveiro" whose lower levels are Late Cretaceous in age, mainly comprises greenish, clayey beds crossed by fluviatile channels.

Sedimentation occurred in an alluvial plain, maybe in bogs that often (seasonally?) were flooded through crevasse-splay, rather narrow channels filled by fossil-rich microconglomerates that do not exceed 1 meter in thickness (Reis and Soares, 1981).

Fossil-rich channels are less than 30 m wide at most (our own observations).

On the other hand, the clays outside of the channels are nearly devoid of fossils, except for some possible worm bioturbation. Only a few remnants from a single crocodilian and the partial skeleton of a wader bird (Harrison, 1983) have been recorded by us in these clays, close by the margin of one channel.

The channel-infilling fossils underwent transportation by running waters and became more or less abraded. However, no granulometric sorting was detected.

The first fossils were sent by our Coimbra University Colleagues, A. Ferreira Soares and R. Pena dos Reis to M.T. Antunes, who recognized a Lower Eocene mammal assemblage (Antunes, 1981; Antunes and Russell, 1981).

A research Program on Silveirinha has been developed since then under our (M.T.A.) direction. Field work, washing and screen scanning of more than 10 tons of sediments allowed us to collect thousands of vertebrate and other fossils (table 1).

Silveirinha is one of the Europe's richest sites for those times. It yielded a rich mammalian fauna (Antunes *et al.*, 1997) that is critically important for dating (table 2). It is older than that from Dormaal.

Similar but poorer mammal assemblages from the Pyrenean region were shown to lay stratigraphically below marine Paleocene (Gheerbrant *et al.*, 1997). An upper

Paleocene age cannot therefore be excluded for Silveirinha.

The understanding of environmental characters requires geological and palaeontological (Tables 1-2) evidence to be taken into account.

Tables: Data have in part been contributed by: J. Riveline (Charophytes)*; J. Pais (other plant material); J.-P. Colin (Ostracods)*; P. Callapez (Molluscs)*. A. Nel (Insect); J. Gaudant and M.T.Antunes (Fishes)*; J.-C. Rage and M. Augé (Amphibians, Squamata)*; F. de Lapparent de Broin (Chelonians)*; C. J. O. Harrison (1983) (*Fluviatilavis*); D. E. Russell, M.T. Antunes and C. Estravís (Mammals); M. T. Antunes (other fossils).

* included in *Ciências da Terra (UNL),* N   15 (in print; for 2002).

- **PLANTAE**
  - **CHAROPHYTA**
    - * *Nitellopsis (Tectochara)dutemplei minor*
  - GYMNOSPERMAE
    - * Amber
  - DICOTYLEDONEAE
    - * *Vitis* sp.
    - * Seeds, several types
- ANIMALIA
  - MOLLUSCA
    - Cl. **GASTROPODA**
      - * *Bithynia soaresi* n. sp.
      - * *Gyraulus antunesi* n. sp.
    - Cl. **BIVALVIA**
      - * *Chlamys* sp.
      - * Cardiacea, gen. sp. indet.
  - ?ANNELIDA
    - * Borings
  - **ARTHROPODA**
    - Cl. **OSTRACODA**
      - * *Iliocypris lusitanicus* n.sp.
      - * *Cyclocypris?* sp.
      - * *Cypria?* sp.
      - * *Cypris silveirinhaensis* n. sp.
      - * Indet. Cypridacea sp. 1
      - * Indet. Cypridacea sp. 2
      - * Indet. Cypridacea sp. 3
      - * Indet. Cypridacea sp. 4
    - Cl. **INSECTA**
      - * Lepidophidae indet. (coleophore)
      - * ?Bioturbations ("trace fossils")
  - **VERTEBRATA**
    - Indet. - Coproliths
    - Cl. **OSTEICHTHYES**
    - Subcl. **ACTINOPTERYGII**
    - Ord. **Perciformes**
      - Fam. Perchichthyidae
        - * Gen. sp. indet.
      - Fam. Phyllodontidae
        - * *Egertonia* sp.
    - Cl. AMPHIBIA
    - Subcl. **LISSAMPHIBIA**
    - Superord. CAUDATA
    - Ord. **Urodela**
      - Fam. Salamandridae
        - * Gen. sp. indet.
    - Ord. **Anura**
      - Fam. ?Pelobatidae
        - * Gen. sp. indet.
    - Cl. **REPTILIA**
    - Ord. **Testudines**
    - Subord. **Pleurodira**
      - Fam. Pelomedusidae
        - * *Neochelys* sp.
    - Ord. **Squamata**
    - Subord. **Lacertilia**
    - Infraord. IGUANIA
      - Fam. Iguanidae
        - * *Geiseltaliellus* sp.
      - Fam. Agamidae
        - * Cf. *Tinosaurus* sp.
    - Infraord. GEKKOTA
      - Fam. Gekkonidae
        - * Gen. sp. indet.
    - Infraord. SCINCOMORPHA
      - Fam. indet.
        - * Gen. sp. indet. 1
      - Fam. indet.
        - * Gen. sp. indet. 2
    - Infraord. ANGUIMORPHA
      - Fam. Anguidae
      - Subfam. Glyptosaurinae
      - Glyptosaurini
        - * Gen. sp. indet
      - Melanosaurini
        - * Cf. *Melanosaurus* sp.
        - * Gen. sp. indet
      - Subfam. ?Anguinae
        - * Gen. sp. indet
      - Infraord. PLATYNOTA
        - Fam. ?Varanidae
          - * Gen. sp. indet.
    - Infraord. AMPHISBAENIA
      - Fam. Amphisbaenidae
        - * Gen. sp. indet.
    - Subord. **Serpentes**
      - Fam. Boidae
        - * Gen. sp. indet.
      - Fam. Tropidophiidae
        - * *Dunnophis matronensis*
      - Fam. indet.
        - * Gen. sp. indet.
    - Infracl. **ARCHOSAUROMORPHA**
    - Ord. **Crocodylia**
    - Subord. **Eusuchia**
      - Fam. Diplocynodontidae
      - * *Diplocynodon* sp.
    - Cl. **AVES**
    - Subcl. **NEORNITHES**
    - Ord. **Charadriiformes**
      - Fam. Recurvirostridae
        - * *Fluviatilavis antunesi*
    - Ord. **indet.**
      - Fam. indet.
        - * Small indet. bird

Tableau 1.— List of taxa (mammals excepted) from the Silveirinha locality (Upper Paleocene or basal Eocene)

Cl. MAMMALIA
Subcl. **ALLOTHERIA**
Ord. **Multituberculata**
* Fam. gen. indet.
Subcl. **THERIA**
Infracl. **METATHERIA**
Ord. **Didelphiomorphia**
Subord. **Didelphia**
Fam. Didelphidae
* *Peratherium* cf. *constans*
Infracl. **EUTHERIA**
Ord. **Apathotheria**
Fam. Apatemyidae
* *Apathemys* sp. 1
* Cf. *Apatemy* sp. 2
* *Heterohyus* sp. 1
* *Heterohyus* sp. 2
* *Russellmys denisae* sp. 1
Ord. **Lipotyphla**
Subord. **Soricomorpha**
Fam. Nyctitheriidae
* *Leptacodon nascimenti*
* Cf. *Leptacodon* sp.
* Gen. sp. indet.
* ?Nyctitheriidae or Doormaliidae indet.
Subord. **Erinaceomorpha**
* *Talpavus* sp.
Ord. **Chiroptera**
* Fam., gen. and sp. indet.
Ord. **Cymolesta**
Fam. Cymolestidae
* *Didelphodus* sp.
Fam. Conoryctidae
* *Eurodon silveirinhensis*
Ord. **Dermoptera**
Fam. Paromomyidae
* *Arcius zbyszewskii*
Ord. **Primates**
Subord. **Strepsirhini**
Infraord. ADAPIFORMES
Fam. Adapidae
* *Donrussellia lusitanica*
* Cf. *Cantius* sp. and/or *Donrussellia* sp.
Ord. **Creodonta**
* Fam., gen. and sp. indet.
Ord. **Carnivora**
Subord. **Arctoidea**
Fam. Canidae
* *Miacis* cf. *latouri*
* Cf. *Miacis* sp.
Subord. **Aeluroidea**
Fam. Viverravidae
* Cf. *Viverravus* sp.
Subord. **indet.**
* Gen. sp. indet.
Ord. **Rodentia**
Subord. **Protrogomorpha**
Fam. Ischyromyidae
* *Microparamys paisi*
* *Microparamys* cf. *nanus*
* *Meldimys cardosoi*
Ord. **Condylarthra**
Subord. **Arctocyonia**
Fam. Hyopsodontidae
* *Paschatherium marianae*
* *Microhyus reisi*
Ord. **Artiodactyla**
Subord. **Hypoconifera (= Palaeodonta)**
Fam. Dichobunidae
* *Diacodexis antunesi*
Ord. **Perissodactyla**
Subord. **Hippomorpha**
Fam. Equidae
Subfam. Hyracotheriinae
* *Hyracotherium* cf. *vulpiceps*
Subord. **Ceratomorpha**
Fam. Lophiodontidae
* Cf. *Lophiaspis maurettei*
Ord. **indet.**
Fam. indet.
* *Ilerdoryctes* cf. *sigei*
Ord. **indet.**
Fam. indet.
* Gen. spp. indet.

Tableau 2.— List of mammals from the Silveirinha locality (Upper Paleocene or basal Eocene)

SYSTEMATICS

The most meaningful specimens are described. A detailed description of other specimens may not be justified, and therefore are only summarily referred. These specimens give nevertheless a more complete view of the available material, and that is useful.

Mostly isolated skull and mandible elements, vertebrae and limb bones are scarce, osteoderms being common. Tiny (not rearmost) teeth, bones and osteoderms correspond to very young individuals. Even the larger, certainly from adults, are rather small for crocodilians.

Fossils often present a black, manganese oxide patina or a diagenetic silica coating.

All measurements are in mm.

Systematics – For older viewpoints, see Steel (1973). Further developments have been presented (Benton and Clark, 1988; Norell, 1989; Clark, 1994), including a synthesis by Brochu (1997). In a simplified version and by phylogenetic order prepared by us on the basis of the above referred references:

CROCODYLOMORPHA
➘**CROCODYLIFORMES** *sensu* CLARK, 1994
➘**MESOEUCROCODYLIA** *sensu* CLARK, 1994
➘**NEOSUCHIA** *sensu* CLARK, 1994
➘**EUSUCHIA** *sensu* CLARK, 1994;

and among the Eusuchia:

➘**Crocodylia** LAURENTI, 1768 *sensu* CLARK, 1994
➘**GAVIALOIDEA**
Gavialidae
➘† Borealosuchidae?
➘† Pristichampsidae
➘**BREVIROSTRES** BROCHU, 1997
➘**ALLIGATOROIDEA**
† Diplocynodontidae [Diplocynodontinae]
➘**GLOBIDONTA** BROCHU, 1999
➘Alligatoridae
➘**CROCODYLOIDEA**
Crocodylidae

In this classification, the genus *Diplocynodon* (which is specially dealt with in this paper) is obviously to be included among the Diplocynodontidae and clearly out of the Alligatoridae. It is even farther away from the Crocodyloidea.

According to Benton (2000: 395-397), the classification is as follows:

Class REPTILIA, Infraclass Archosauromorpha, Division Archosauria, Subdivision Crurotarsi, Infradivision Crocodylotarsi, Superorder Crocodylomorpha, Order Crocodylia, Division Mesoeucrocodylia, Subdivision Metasuchia, Infradivision Neosuchia, Suborder Eusuchia.

Assuming that controversy on Systematics is far from being settled, we will adopt provisionally the following classification.

Order **CROCODYLIA** LAURENTI, 1768 *sensu* CLARK, 1994

Super-family **ALLIGATOROIDEA** GRAY, 1844 *sensu* BROCHU, 1997, table 1)

Family **DIPLOCYNODONTIDAE** (unnamed taxon, according to Brochu, idem)

Genus *DIPLOCYNODON* POMEL, 1847

Diplocynodon sp.

(Plates 1-4)

Previous references concerning Silveirinha:

Cfr. *Diplocynodon* sp., in Antunes (1981: 257).

Cf. *Diplocynodon* sp., in Antunes and Russell (1981: 1100).

Skull

* Right maxillary - A fragment of the expanded, mesial part just after the constriction near the praemaxillary-maxillary border has been collected. There is a space for the mandibular "two caniniforms" (as in *Diplocynodon*) that is followed by the bases or alveoli of the first to the fourth maxillary teeth, the last being somewhat larger. All this matches the situation in *Diplocynodon*, where the maxillary teeth 4 and 5 are the largest and nearly the same size, as verified directly in specimens from St. Gérand-le-Puy and Artenay (Muséum, Paris). The internal border follows in part the maxillo-nasal suture. Max. length as preserved, 20.2; max. breadth, 16.4. Estimated alveole's length between 2.5 and 4.

* Right squamosal - The upper, distal part is broken and does not attain the border of the supratemporal fenestra; width as preserved is ca. 7.8.

* Supraoccipital - Incomplete; the contact surface for the parietal is preserved, as well as a large portion of the rear, caudal surface. Max. width may be estimated (half x

2) in ca. 12.8.

* Basioccipital - Incomplete, reduced to the condyle and a part of the descending process; it shows the ventral border of the foramen magnum, and a portion of the dorsal surface for the spinal chord. Condyle max. width, 6.4; heigth, 4.3.

* Left jugal - Incomplete caudal process. Length as preserved, ca. 25.8.

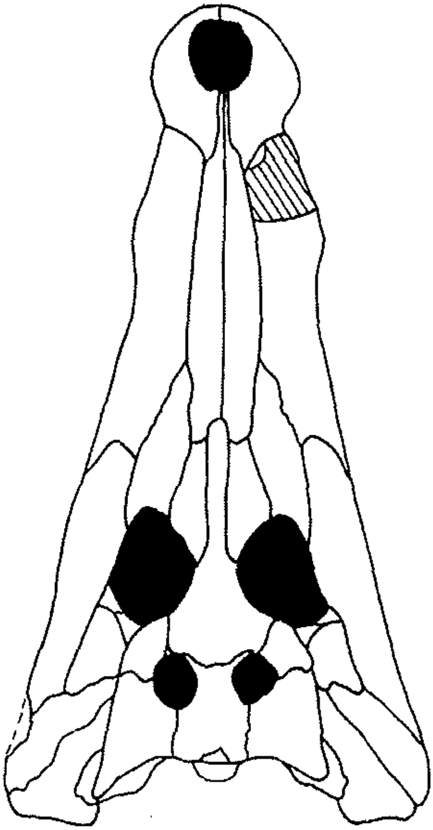

Figure 1.— *Diplocynodon*, reconstruction of skull after Ginsburg and Bulot (1997): dorsal view to show the position of the maxillary fragment under study, hatched.

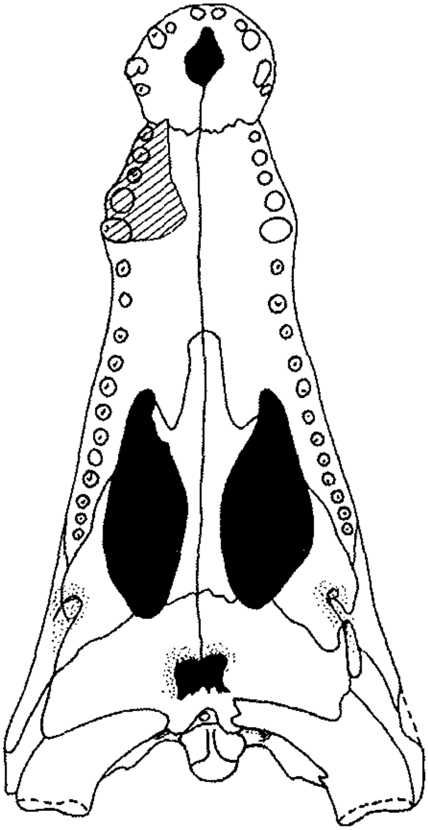

Figure 2.— *Diplocynodon*, reconstruction of skull after Ginsburg and Bulot (1997): the same, ventral view, id.

Mandible

* Left dentary - It comprises the symphyseal part and a small part of the incomplete mandibular ramus. There are the alveoli and the basal parts of mandibular teeth 1 to 6. The 3th and 4th teeth are larger than the other ones and very close by, i.e. the "two caniniform" set that is diagnostic of *Diplocynodon* (see also Norell and Clark, 1990: 119). The splenial does not reach the symphysis. Medial length, a little more than 16. Whole length of the 3th + 4th alveoli, 6.7. An important character is that the symphysis reaches the rear part of the 5th mandibular tooth.

* Left hemimandible – caudal part, comprising parts of the angular, surangular, the incomplete caudal part of the splenial and the caudalmost part of the dentary (with a displaced incomplete tooth, maybe the last mandibular one, and part of the external cast of another tooth). The specimen shows the medial and ventral parts of the large external mandibular opening. No useful measurements are possible.

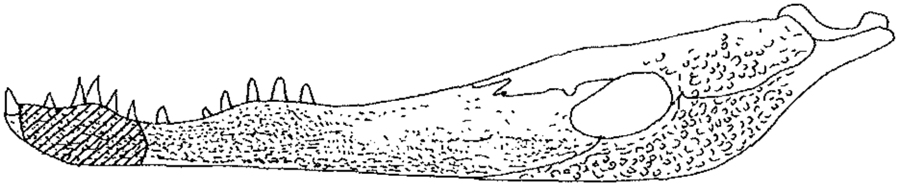

Figure 3.— *Diplocynodon*, left hemimandible, reconstruction after Ginsburg and Bulot (1997): text-fig. 3 (external)

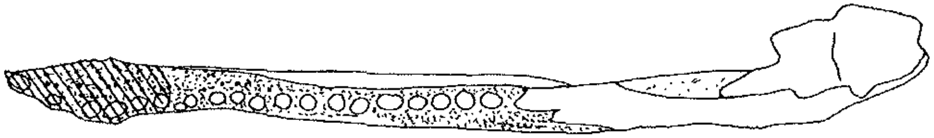

Figure 4 .— (dorsal) views to show the position of the studied dentary fragment].

Teeth

* We selected more than 500 teeth plus a large lot of fragments. Most are reduced to the often incomplete crown and are undoubtedly shed teeth. The root is preserved in a few specimens.

The teeth correspond to different positions in the premaxillaries, maxillaries and dentaries. The shape is conical (not slender as it is generally the case in longirostrine crocodilians) and shorter in teeth from the rear part of the maxillaries and the dentaries. The section is less round in the rearmore teeth, that are somewhat laterally compressed and shorter. No close similarities with eocene ziphodont crocodilian teeth can be recognized. See also the introduction for comparison with teeth from Dormaal and Le Quesnoy reported as aff. *Diplocynodon* (Nel *et al.*, 1999).

Enamel does not present any marked striations or ridges. There are two smooth carinae on the anterior and posterior parts of the tooth.

The length of the crown attains ca. 9.3 in the largest teeth. Teeth are often tiny (crown length < 2 mm). Young individuals were frequent; there is no confusion with smaller teeth from adults.

Nothing suggests the presence of more than one taxon.

Axial skeleton

* Vertebrae – 11 small-sized, procoelous vertebrae were collected: 3 cervicals, 1 anterior with hypapophysis and 2 posterior dorsals (one nearly complete), 1 sacral and 4

caudals.

8 have lost the still unfused neural arch and therefore keep the neurocentral sutures. This situation corresponds to not yet fully adult specimens.

Maximum length of centra attain or slightly exceeds 16.5.

Limbs

Fore limb

* Radius - A nearly complete right radius was collected. The almost complete proximal, articular surface is well preserved . Max. length, 91.1; transversal, proximal diameter, 18.9; idem, distal diameter, 21.3.

* Ulna – A small fragment from the distal part of what could probably be a crocodilian ulna has been collected. Its size seems compatible with the radius. Distal surface is well preserved. The max. length as preserved is 16.4, the transversal, distal diameter being 12.5.

Hind limb

* Femur - A right femur whithout both articular extremities may be referred to a probably young crocodilian.

No useful length measurements can be obtained.

The diameter about the middle of the shaft is ca. 6; max. length of the fragment, 27. Two further specimens found in probable anatomical position and in association to bone (basin?) fragments consist in the proximal part of the left and right femora, maybe from the same individual. The right one is very well preserved: max. width, 24.9, max. anteroposterior diameter, 13.8.

Osteoderms

* Osteoderms – Are very well represented; 45 specimens have been selected. They correspond to the basic types of the Miocene *Diplocynodon styriacus* (see Ginsburg and Bulot, 1997: 120-122, fig. 9): dorsals, laterals and ventrals.

The osteoderm pattern is distinct from those of *Crocodylus* and *Alligator*: in those genera, dorsal osteoderms are densely sculpted in the whole external surface and do not seem to overlap, while in *Diplocynodon* as well as in Silveirinha's (and plenty of other specimens and even in some other species) there is an anterior, smooth surface that was placed under the rear part of the next, anterior osteoderm.

Some osteoderms are very small. They seem to correspond to very young, juvenile individuals, even if some could perhaps be smaller osteoderms from the tail or from the legs of not so young animals.

Dimensions (mm) of the largest specimens: (a) 2 dorsal osteoderms, 19.5 (length) x 19.0 (width); 16.9 (l) x 15.8 (w); (b) 1 lateral osteoderm, 20.6 (l) x 16.4 (w); (c) 1 nearly complete ventral osteoderm, ca.16.2 (l) x 14.0 (w).

Similar osteoderms from the Eocene of the Duero basin (Spain) have been ascribed to *Diplocynodon* (see Martín de Jesús *et al.*, 1987, lám. 1).

Remark: The skeletal data as a whole show that the larger Silveirinha *Diplocynodon* adults seem to be ca. 20% smaller than the composite skeleton (max. length, ca. 1.7 m) from St.-Gérand-le-Puy (Oligocene) at the Galerie de Paléontologie, Muséum national d'Histoire naturelle (Paris). The maximum length for Silveirinha would not exceed ca. 1.4 m (just like the *Diplocynodon* from Messel, according to E. Frey, written statement).

DISCUSSION

Remnants from Silveirinha undoubtedly show the presence of brevirostrine, small-sized eusuchians. Hence it is possible to eliminate the following time-compatible hypotheses (see Introduction): - the Pristichampsines, whose teeth are serrated; - the robust, much larger *Asiatosuchus,* as we could directly verify in comparison with specimens from Eocene units of the Duero Basin ("Sala de las Tortugas" collection, Salamanca University). The research domain is therefore restricted to *Allognathosuchus* and *Diplocynodon,* since there are not any other known possibilities.

Allognathosuchus is easily recognizable because of the laterally-compressed, low-crowned, crushing teeth (Berg, 1966; Buffetaut, 1985). No such teeth were collected at Silveirinha, even if hundreds of crocodilian teeth were obtained there. Hence *Allognathosuchus* remains unknown at this site: a single crocodilian taxon seems to be represented at Silveirinha.

On the other hand, the presence of *Diplocynodon* can be recognized beyond any doubt by the occurrence of a very typical dentary that shows the diagnostic "two caniniform" pattern; this specimen is utmost important for classification. Although they are not very diagnostic, other bones and teeth are compatible with *Diplocynodon,* as we could verify in comparison with French and Spanish material. A further (if needed) confirmation is offered by the large number of osteoderms, and especially by the shape of the dorsal ones with its smooth anterior part.

As we have shown, the Silveirinha crocodilian material is diagnostic enough to ascertain its classification at the rank of the genus: it undoubtedly belongs to *Diplocynodon.*

Opinions about this genus systematics shifted often, *Diplocynodon* being ascribed either to the Alligatorinae, to the Crocodylinae or even segregated in another family, Diplocynodontidae. The Crocodylinae hypothesis was discussed and adopted by Antunes and Ginsburg (1989), and by Ginsburg and Bulot (1997: 108-112). However the overwhelming evidence points out to its closest relationships with the Alligatoridae.

The Silveirinha *Diplocynodon* may perhaps belong to a new species, especially if account is taken that no more or less synchronic species has so far been described. However the available material is too incomplete to establish an adequate diagnosis.

This is the also the case of the paleocene *Diplocynodon* from Cernay (Ginsburg and Bulot, 1997:123-124).

The lowermost Eocene, MP7 *Diplocynodon* sp. from Dormaal (Buffetaut, 1985: 54-55) is slightly later than Silveirinha's. The symphyseal length is short, its caudalmost extremity attaining the level of the mesial extremity of the 4th tooth (Buffetaut, id., Pl. I fig. F, G, H). Hence it is clearly different from the Silveirinha specimen.

According to Nel *et al.* (1999: 71), there is an aff. *Diplocynodon,* a new species, at Le Quesnoy (Sparnacian, MP7) and Dormaal. Its dentition "se singularise par une ressemblance superficielle avec celle des crocodiliens ziphodontes éocènes". If so, it is different from the Silveirinha *Diplocynodon.* On the other hand, little can be said of the undescribed cf. *Diplocynodon* from the Sparnacian of Meudon (Russell *et al.,* 1990). The *Diplocynodon* sp. from Silveirinha seems smaller than its nearly contemporary, ca. 1.7 m maximum length *Diplocynodon* from Meudon (Russell *et al.,* 1990: 23).

Although we verified directly that the material from Silveirinha and the available specimens from Cubillos-Valdegallina - teeth and osteoderms – practically look as identical, this does not seem enough to ascertain if all belong to the same indeterminate *Diplocynodon* species (see also Gil-Tudanca, 1992: 30-31; Jiménez-Fuentes, 1992: 40-41; Ortega and Buscalioni, 1992: 68-69). The age of the Cubillos-Valdegallina sites is less accurate; as the concerned sedimentary units underlie the Middle Eocene, MP 13-14, Sanzoles level, age may be Lower to Middle Eocene, MP 9? to 14 (Jiménez-Fuentes, 1993, p. 18, 23, 27, 28). Hence the above referred occurrences are time compatible.

Comparison between the *Diplocynodon* from Silveirinha and Cubillos-Valdegallina is especially tempting because they also seem compatible by geographic neighbourhood and stratigraphic reasons. *Diplocynodon* is represented in both sites by remnants of small-sized individuals only (for Cubillos-Valdegallina, "de talla muy pequeña" according to E. Jiménez-Fuentes, *in litt.).*

The chronologically next species is *D. darwini* (Ludwig, 1877) from the middle Eocene of Messel and the Geiseltal in Germany. This species is represented by complete skeletons, and especially by the excellent material from Messel. However, detailed comparisons between the *Diplocynodon* from Messel (quite far away geographically and chronologically later) with the very incomplete material from Silveirinha most probably would not be conclusive, except at the level of the genus.

Upper Middle Eocene MP 15 or 16, geographically close specimens were collected at the "Escarpes del Tormes" near Salamanca (Jiménez-Fuentes, 1993: 19). More complete skull material allowed the description of a new species, *Diplocynodon tormis* (see Buscalioni *et al.,* 1992). The size of *D. tormis* clearly exceeds the maximum size that has been observed in specimens from Silveirinha.

As in *D. tormis,* the Silveirinha form presents a strong indentation close to the premaxillary-maxillary suture. However, the long symphyseal length in the Silveirinha specimen is markedly different from the short one in *D. tormis.* A moderately long symphysis also occurs in the Miocene *D. styriacus* (Ginsburg and Bulot, 1997), a character that may be related to a longer snout.

According to Ginsburg and Bulot (1997: 123-126), who discussed the

Diplocynodon phylogeny, there is an acceptable, anagenetic line *D. darwini* →*D. hantoniensis* →*D. gervaisi* →*D. styriacus*. Another, less known line would comprise *D. tormis* Duero basin, Spain) and maybe *D. levantinicum* (Middle to Upper Miocene, Bulgaria, see von Huene and Nikoloff, 1963).

- Would the Silveirinha *Diplocynodon* sp. be a short-snouted ancestor of *D. tormis* and hence of this last line?

- Or may it, perhaps more probably, be an ancient member of the *D. darwini* evolutionary line?

These questions apparently cannot be settled in the present status of knowledge. Trying to answer them would require a more thorough comparison work that certainly is not possible on the available incomplete material under study.

In Portugal, scarce crocodilian remnants were found in the Middle to Upper Eocene (Antunes, 1975; 1986 a,b). However, data are not enough for detailed comparisons with the *Diplocynodon* from Silveirinha.

DISTRIBUTION OF EUROPEAN (ESPECIALLY IBERIAN) *DIPLOCYNODON*

Let us recall that Silveirinha's age is accurately known after mammals: MP7, lowermost Eocene. However, if correlations with mammal assemblages from the Pyrenean region **under marine Paleocene beds** are correct, an upper Paleocene age cannot be excluded for Silveirinha (this is a matter of marine-continental correlations and Period limits, not of mammal-zones nor the corresponding dating, which is not ambiguous at all).

Even if the lack of mammals does not afford an accurate dating of Cubillos-Valdegallina, there is an apparent compatibility of its fossil contents with that from Silveirinha. Evidence as a whole seems to be enough as a basis for correlation:

(a) the only chelonian from Silveirinha is a small Pelomedusid that once was described as *Neochelys* cf. *arenarum* (de Lapparent in Antunes and Russell, 1981: 1100) and now as *Neochelys* sp. (de Broin, in the press). This could perhaps be the same as the Cubillos-Valdegallina *Neochelys zamorensis* (see Jiménez-Fuentes, 1993: 147). (According to F. de Lapparent de Broin, personnal communication, the *Neochelys* from Silveirinha and *Neochelys zamorensis* are not identical);

(b) the very common perciform fish remains from Silveirinha have been reported to cf. *Prolates? doormalensis* (Antunes and Russell, 1981: 1100). This occurrence may be compared to the situation of the Zamora area Paleogene sites, including Cubillos-Valdegallina, from where perciform fish remnants were described by Gaudant (1984) as a Percichthyid and named by Peña-Zarzuelo (1992) as *Vixperca corrochani*. This and the Silveirinha perciforms seem to represent but a single taxon, and also suggest that the sites can be correlative;

(c) the absence at Silveirinha and Cubillos-Valdegallina of other crocodilians as

Asiatosuchus and *Iberosuchus,* that are well represented in later Eocene beds in Portugal and in Spain (where many intensive excavations have been made) is obvious (see Ortega and Buscalioni, 1992; Jiménez-Fuentes and Andrés, 1994); it therefore points out in favour of the validity of more or less approximate correlations between the concerned lower Eocene units;

(d) recent washing and sieving of sediments from Cubillos-Valdegallina yielded *Bithynia* opercules identical to those from Silveirinha and unknown in later beds.

Taking into account the discussion above, the European time distribution of the genus *Diplocynodon* may be summarized as follows (Table 3).

Remarks: Data from Ginsburg and Bulot (1997, tableau 3, modified); * the older than Dormaal site of Silveirinha has been regarded as Lowermost Eocene, but may instead be upper Paleocene in age; data from the Duero Basin according to papers by Antunes *et al.* (1997, fig. 2), Jiménez-Fuentes (1992 a), Ortega and Buscalioni (1992) and Tudanca (1992); ** "Escarpes del Tormes" comprising Cabrerizos (Los Caenes and Teso de la Flecha), San Morales, Babilafuente, Aldealengua and Aldearrubia.

The presence of *Diplocynodon* in North America has been denied because the formerly reported american forms have been ascribed to another genus, *Borealosuchus* Brochu, 1997 (see Brochu, 1997: 694-695), and therefore *Diplocynodon* is only known in Europe. Yet the North Atlantic was not entirely open at Lower Eocene times and terrestrial migrations were still possible. Close american affinities have been detected among squamates and mammals. Crocodilian migrations would have been easy as they are good swimmers, and because some can tolerate salt waters. Similarities between Lower Paleogene crocodilian associations in Europe and North America are to be expected.

Tableau 3.— Distribution of *Diplocynodon* in Portugal and in the Paleogene of the Duero basin in Spain.

→

Period	Subdivisions (MP, Paleogene; MN, Neogene units)	European species	Sites in Portugal	Sites in Duero basin, Spain (Paleogene only)
Miocene	upper Middle to lower Upper, MN7-10	*D. levanticum*	? *D.* sp./ Aveiras de Baixo	-
	Middle, MN6	*D.* cf. *styriacus*		
	upper Lower to early Middle, MN4-5	*D. styriacus*	*D.* sp./ Amor, Leiria, MN5; ? *D.* sp./ from Vb - Va units, Lisbon (MN 5 - 4)	
	Lower, MN3		? *D.* sp./ Horta das Tripas, Lisbon	
	Lower, MN2	*D. ratelii*		
	Lowermost, MN1			
Oligocene		*D. gervaisi*		*D.* sp.? / Los Barros (Ávila)
Eocene	Upper, MP 17-20	*D. hantoniensis,* *D. tormis*		*D.* sp./ Molino del Pico and Escarpes del Guareña, MP18 or higher
	Middle, MP 11-16		*D.* sp.?/ Vale Furado, MP 13-14	*D. tormis* TYPE from Teso de la Flecha MP16 (as **Escarpes del Tormes, Mazaterón and Deza) *D.* sp./ Jambrina, Sanzoles, Corrales, Casaseca, MP 13-14
	Lower, MP 7-10	*D. darwini* Aff. *D.* sp. from Dormaal and Le Quesnoy, MP 7	**D.* sp./ Silveirinha, MP 7 ↕	*D.* sp./ Cubillos and Valdegallina, MP9?-14
Paleocene	MP 1-6	*D. sp.* from Cernay, MP 6	↕*/ idem, MP 7	

ECOLOGICAL REMARKS

Silveirinha yielded a wealth of geological and palaeontological data. It points out to an alluvial plain, eventually flooded and where bogs (and oxbows?) developped, crossed by channels depending on a river system that drained higher areas more north or eastwards. Most fossils were deposited in the channels after short transportation. Vegetation should have been rich in nearby areas, supporting a rich fauna. Ostracoda, Gastropoda, Amphibia and Pelomedusid chelonians indicate freshwaters, although rare Bivalvia (see Table 1) show that salt or at least brackish waters were not very far away. Chelonians and Squamatans (as Iguanidae, Anguids, Platynota and Boids) are largely enough to show tropical to perhaps prevailing subtropical environments. The common presence of *Diplocynodon* is in agreement with these conditions.

The Silveirinha *Diplocynodon* are small. Many specimens belong to juveniles that died nearby and suggest an high juvenile mortality rate. Small size can perhaps be explained through phylogeny and/or environmental conditions: (a) they seem to belong to a small-sized species, (b) they lived in far from optimal environments and hence did not reach a long enough individual age and the maximum possible body size. This can also result from living in restricted ecological niches, where crowding can lead into cannibalism; as far as extant species are concerned, cannibalism may be either rare or common, according to specialists. Parents do not seem to attack their offspring, who are protected by their mothers. However, young crocodilians are known to prey on smaller, next generation individuals (Ross *et al.*, 1990: 100-101). All these behaviours could have been possible.

On the other hand, larger crocodilians require as habitat large water masses as lakes, large rivers and coastal sea areas. The remarkable absence at Silveirinha of large crocodilians as *Asiatosuchus*, that is known in the Douro basin in Spain later in the Eocene, suggests that there were then no close-by large river at this place, as stratigraphy and sedimentology also show.

Most crocodilians depend on suitable waters in all seasons although a few may predominantly be rain-forest dwellers. Another key requirement is tropical to subtropical environments, and temperature (see Introduction). Climate in the concerned area must have been warm and humid enough. All extant crocodilians do not possess sex chromosomes; sex is determined by the incubation temperature. Nearby successful reproduction also required a rather high insolation rate. Reproduction is possible between thermic limits from 28° to 34° C. For *Alligator missipiensis* and *Caiman crocodilus,* at lower (28° to 31° C) temperatures only females eclode; both sexes in different proportions between 31° and 32° C; and only males above this last value until the upper limit. For five species of *Crocodylus,* the females-only pattern is the same for the lower temperature gap; males and females are determined between 31 and 33°C; and females again from 33° to 34° C (Ross *et al.*, 1990). If these results can be approximately extrapolated to the past, as it seems, and taking into account that there is evidence of close-by hatching of *Diplocynodon* eggs at Silveirinha, environmental conditions would be at least seasonally adequate. Eventually, more or less long dryness or excessive rain events can introduce disequilibria through excessive production of one sex. This may explain the impoverishment of crocodilians in numbers of individuals and taxa related to climate crises and even extinction (see Lang in Ross *et al.*, 1990: 120). As far as the K-T crisis is concerned, and even if crocodilian losses were lesser than representatives of other groups as non-avian dinosaurs, not less than ca. 35% crocodilian families became extinct (Benton, 1993).

Diplocynodon probably was the most tolerant tertiary crocodilian genus - the only one that survived in Europe after the general decline of climate conditions in Upper Eocene. It corresponds to moderately warm and subtropical, maybe somewhat marginal for crocodilians environments. This could have been the Silveirinha case.

CONCLUSIONS

1. The presence at Silveirinha of one of the earliest, ?Late Paleocene or Lowermost Eocene european representatives of the genus *Diplocynodon* at Silveirinha is shown.

2. A small-sized, indeterminate *Diplocynodon* species is the only crocodilian so far recognized there, mostly on (often juvenile) isolated bones and teeth.

3. We may provisionally admit that the small *Diplocynodon* from Silveirinha and that from the lower Paleogene units in the Duero basin (Cubillos-Valdegallina) may perhaps belong to the same indeterminate species.

4. The absence at Silveirinha as well as at Cubillos-Valdegallina of all other crocodilians from later Eocene beds as *Asiatosuchus* and *Iberosuchus* seems to support this (3) conclusion; the common occurrences of the same gastropod *Bithynia,*apparently the same percomorph fishes, and of similar Pelomedusid chelonians, as well as the stratigraphic context seem to corroborate it.

5. On the other hand, the Silveirinha *Diplocynodon* is different from the middle Eocene *D. tormis* and does not seem to be an ancestor of it; the *Diplocynodon* from Silveirinha may therefore be an element of another phyletic line.

6. The Silveirinha *Diplocynodon* also differs from its approximately contemporary or slightly later aff. *Diplocynodon* sp. from Dormaal and Le Quesnoy.

7. The longevity of *Diplocynodon* in Portugal becomes therefore much extended, since it survived there at least until Middle Miocene.

8. The small *Diplocynodon* from Silveirinha is compatible with moist, subtropical, maybe marginally adequate environments, certainly quite restricted in space; these environments can be characterized by other, rich evidence and correspond to an alluvial plain crossed by meandering, quite narrow channels.

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REFERENCES

ANTUNES, M. Telles (1975). — *Iberosuchus*, crocodile Sebecosuchien nouveau, l'Eocène ibérique au Nord de la Chaîne centrale, et l'origine du canyon de Nazaré. *Comunic. Serv. Geol. Port.*, t.LIX: 285-330, 5 fig., 3 tab., 9 pl.

ANTUNES, M. Telles (1981). — As areias e argilas de Silveirinha II - Aspectos paleontológicos. *Memórias e Notícias, Publ. Mus. Lab. Mineral. Geol., Univ. Coimbra*, n^{os} 91-92: 255-267.

ANTUNES, M. Telles (1986a). — *Paralophiodon* cf. *leptorhynchum* (Tapiroidea, Mammalia) à Vale Furado: contribution à la connaissance de l'Eocène au Portugal. *Ciências da Terra (UNL)*, n°8: 87-98, 2 tab., 1 pl.

ANTUNES, M. Telles (1986b). — *Iberosuchus* et *Pristichampsus*, crocodiliens de l'Éocène/ données complémentaires, discussion, distribution stratigraphique. *Ciências da Terra (UNL)*, n°8: 111-122, 1 tab., 1 pl.

ANTUNES, M. Telles, CASANOVAS, M. L., CUESTA, M. A., CHECA, L., SANTAFÉ, J. V. and AGUSTI, J. (1997). — Eocene mammals from Iberian Peninsula. Actes du Congrès BiochroM'97, J.-P. Aguilar, S. Legendre and J. Michaux (Eds.), *Mém. Trav. E.P.H.E., Inst. Montpellier*, 21: 337-352, 2 fig.

ANTUNES, M. Telles and GINSBURG, L. (1989). — Les Crocodiliens des faluns miocènes de l'Anjou. *Bulletin du Muséum national d'Histoire naturelle,* Paris, série 4, C 11 (2): 79-99, 3 pl.

ANTUNES, M. Telles and RUSSELL, D. E. (1981). — Le gisement de Silveirinha (Bas Mondego, Portugal): la plus ancienne faune de Vertébrés éocènes connue en Europe. *C. R. Acad. Sc. Paris,* t. 293 (21 Décembre 1981), Série II: 1099-1102.

BENTON, M. J. (1993). — The Fossil Record 2. Chapman & Hall, London.

BENTON, M. J. (2000) - *Vertebrate Palaeontology.* Second Edition. Blackwell Science Ltd.

BENTON, M. J. and CLARK, J. (1988). — Archosaur phylogeny and the relationships of the Crocodylia. In *The Phylogeny and Classification of the Tetrapods.* Volume 1, *Amphibians, Reptiles, Birds* (ed. M. J. Benton). Systematics Association Special Volume, 35A: 295-338. Clarendon Press, Oxford.

BERG, D. E. (1964). — Krokodile als Klimazeugen. *Geologischen Rundschau, Bodenforsch.,* Bd. 54: 328-333 , 1 fig. Stuttgart.

BERG, D. E. (1966). — Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus?,* aus dem Eozän von Messel bei Darmstadt/ Hessen. *Abh. hess. L.-Amt Bodenforsch.,* Heft 52: 105 p., 11 fig., 6 pl. Wiesbaden.

BROCHU, C. A. (1997). — A review of "Leidyosuchus" (Crocodyliformes, Eusuchia) from the Cretaceous through Eocene of North America. *Journal of Vertebrate Paleontology,* vol. 17, 4, pp. 679-697, 15 fig, 1 tab., 1 appendix.

BROIN, F. de Lapparent de (in print). — *Neochelys* sp. (Chelonii, Erymnochelyinae), from Silveirinha, early Eocene, Portugal. *Ciências da Terra (UNL),* n°15, 2 tab., 1 pl.

BUFFETAUT, E. (1982). — Un problème de paléobiogéographie continentale: les Crocodiliens mésosuchiens ziphodontes de l'Eocène européen. *Bull. Soc. Géol. France,* 1982, (7), t. XXIV, n° 5-6: 1101-1107, 2 fig.

BUFFETAUT, E. (1985). — Les Crocodiliens de l'Eocène inférieur de Dormaal (Brabant, Belgique). — *Bull. Soc. belge de Géol.,* t. 94, fasc. 1: 51-59, 2 fig., 1 pl.

BUFFETAUT, E. (1986). — Un Mésosuchien ziphodonte dans l'Éocène supérieur de La Livinière (Hérault, France). *Géobios,* n°19, fasc.1: 101-108, 2 pl.

BUSCALIONI, A. D., SANZ, J. L. and CASANOVAS, M. L. (1992). — A new species of the eusuchian crocodile *Diplocynodon* from the Eocene of Spain. *Neues Jahrbuch für Paläontologie Abhandlungen,* Stuttgart, 187 (1): 1-29, 11 fig.

FREY, E., LAEMMERT, A. and RIEß, J. (1987). — *Baryphracta deponiae* n. g. n. sp. (Reptilia, Crocodylia), ein neues Krokodil aus der Grube Messel bei Darmstadt (Hessen, Bundesrepublik Deutschland). *N. Jb. Geol. Paläont. Mh.,* 1987, H. 1: 15-26, 4 fig., 2 tab.

GAUDANT, J. (1984). — Sur la présence de Percichthyidae (Poissons Téléostéens) dans l'Eocène moyen du Bassin du Duero (Province de Zamora, Espagne). *Acta Geológica Hispánica,*t. 19 (1984), n°2: 139-142.

GHEERBRANT, E., ABRIAL, C. and CUENCA, G. (1997). — Nouveau mammifère condylarthre du Paléocène supérieur de Campo (Pyrénées aragonaises, Espagne). *C. R. Acad. Sc. Paris,* t. 324, Série IIa: 599-606, 3 fig., 1 pl.

GIL-TUDANCA, S. (1992). — Yacimientos de vertebrados paleógenos de Castilla y León. *Vertebrados fósiles de Castilla y León* (Coord., E. Jiménez-Fuentes): 27-37, 1 fig. Museo de Salamanca, Junta de Castilla y León, Consejería de Cultura y Turismo.

GINSBURG, L. and BULOT, Ch. (1997). — Les *Diplocynodon* (Reptilia, Crocodylia) de l'Orléanien (Miocène inférieur à moyen) de France. *Geodiversitas,* 19 (1): 107-128, 9 fig., 3 tab.

HARRISON, C. J. O. (1983). — A new wader, recurvirostridae (Charadriiformes), from the early Eocene of Portugal. *Ciências da Terra (UNL),* 7: 9-16, 2 fig.

HUENE, F. von and NIKOLOFF, I. (1963). — Ein pliozänes Krokodil in Bulgarien. *N. Jb. Geol. Paläont. Abh.*, 118, 3: 266-271. Stuttgart.

JEHENNE, Y. (1970). — Etude de restes de Crocodiliens stampiens du Bassin d'Aquitaine. *Bulletin des Sciences de la Terre de l'Université de Poitiers,* Tome XI.

JIMÉNEZ-FUENTES, E. (1992). — Las dataciones del Paleógeno de Castilla y León. *Vertebrados fosiles de Castilla y León* (Coord., E. Jiménez-Fuentes), 39-41, 2 fig. Museo de Salamanca, Junta de Castilla y León, Consejería de Cultura y Turismo.

JIMÉNEZ-FUENTES, E. (1993). — Aclaraciones sobre el *status* de *Neochelys zamorensis,* Pelomedúsido (Reptilia, Chelonii) de pequeña talla del Eoceno de Zamora (España). *Studia Geologica Salmanticensia,* XXVIII: 141-153, 2 fig. Ed. Univ. Salamanca.

JIMÉNEZ-FUENTES, E. and ALONSO ANDRÉS, L. (1994). — Nuevos hallazgos de Trionychidae (Chelonii) en el Eoceno de Salamanca y Zamora. Consideraciones sobre los ecosistemas fluviales durante el Eoceno en la Cuenca del Duero. *Studia Geologica Salmanticensia,* XXIX: 95-113, 5 fig. Ed. Univ. Salamanca.

JIMÉNEZ-FUENTES, E., MARTÍN de JESÚS, S., FINCIAS, B., PRADO J. M. Del and MULAS ALONSO, E. (1987). — La Herpetofauna paleogena de la cuenca del Duero: distribución cronoestratigráfica y consideraciones paleoecológicas. *Acta zool. Lilloana,* 41: 371-380, 4 fig.

JIMÉNEZ-FUENTES, E. and GIL TUDANCA, S. (1993). — Vertebrados fosiles de Zamora. Instituto de Estudios Zamoranos Florian de Ocampo, *Anuario* 1992: 17-29, 3 fig.

KOENIGSWALD, W. von and STORCH, G. [coll. work under the Direction of] (1998). — Messel/ La mémoire de la Nature. SEUIL (Ed. of the French translation).

MARTÍN de JESÚS, S., JIMÉNEZ-FUENTES, E., FINCIAS, B., PRADO, J. M. Del and MULAS ALONSO, E. (1987). — Los Crocodylia del Eoceno y Oligoceno de la Cuenca del Duero, dientes y osteodermos. *Revista Española de Paleontología,* 2: 95-108.

NEL, A., de PLÖEG, G., DEJAX, J., DUTHEIL, D., de FRANCESCHI, D., GHEERBRANT, E., GODINOT, M., HERVET, S., MENIER, J.-J., AUGÉ, M., BIGNOT, G., CAVAGNETTO, C., DUFFAUD, S., GAUDANT, J., HUA, S., JOSSANG, A., de LAPPARENT de BROIN, F., POZZI, J.-P., PAICHELER, J.- Cl., BEUCHET, F. and RAGE, J.- Cl. (1999). — Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Eocène basal, MP7): Le Quesnoy (Oise, France). *C. R. Acad. Sc. Paris,* Sciences de la Terre et des Planètes, 1999, 329: 65-72, 1 tab., 1 pl.

NORELL, M. A. (1989). — The higher level relationships of the extant Crocodylia. *Journal of Herpetology,* 23 (4): 325-335, 7 fig., 1 tab.

NORELL, M. A. and CLARK, J. M. (1990). — A reanalysis of *Bernissartia fagesii,* with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique,* Sciences de la Terre, 60: 115-128, 2 fig., 1 tab.

NORELL, M. A., CLARK, J. M. and HUTCHINSON, J. H. (1994). — The Late Cretaceous Alligatoroid *Brachychampsa montana* (Crocodylia): new material and putative relationships. *American Museum Novitates,* Number 3116: 1-26, 10 fig., 1 tab.

ORTEGA, F.J. and BUSCALIONI, A.D. (1992). — Cocodrilos fósiles de Castilla y León. *Vertebrados fosiles de Castilla y León*(Coord., E. Jiménez-Fuentes): 59-70, 8 fig. Museo de Salamanca, Junta de Castilla y León, Consejería de Cultura y Turismo.

PEÑA-ZARZUELO, A. de la (1992). — Peces del Paleógeno de Castilla y León. *Vertebrados fosiles de Castilla y León* (Coord., E. Jiménez-Fuentes): 43-45, 1 fig. Museo de Salamanca, Junta de Castilla y León, Consejería de Cultura y Turismo.

REIS, R. Pena dos and SOARES, A. F. (1981). — As areias e argilas de Silveirinha I - Aspectos sedimentológicos. *Memórias e Notícias,* Publ. Mus. Lab. Mineral. Geol., Univ. Coimbra, 91-92: 245-255, 8 fig.

ROSS., C. A. (Scientific Counselor) *et al.* (1990). — Crocodiles, Alligators et Caimans. *Encyclopedie visuelle,* Bordas, Paris.

RUSSELL, E., BROIN, F. de, GALOYER, A., GAUDANT, J., GINGERICH, D. and RAGE, J.-Cl. (1990). — Les Vertébrés du Sparnacien de Meudon. *Bulletin d'information des Géologues du bassin de Paris,* 1990, 27 (4): 21-31, 3 fig., 1 pl.

STEEL, R. (1973). — Crocodylia. *Handbuch der Paläoherpetologie,* Teil 16/Part 16: 116 p., 33 fig. Gustav Fischer Verlag. Stuttgart. Portland-USA.

CAPTIONS OF PLATES

PLATE 1

Diplocynodon sp. from Silveirinha (?Upper Paleocene or Lowermost Eocene).

[Fig. 1-3, drawings by Mário Estevens; 4-5, unretouched photographs].

Fig. 1, right maxillary, lateral view.

Fig. 2 and 3, left dentary from Silveirinha, dorsal (fig. 2) and external (fig. 3) views, showing the characteristic close pair of "caniniforms".

Fig. 4, the same right maxillary, lateral view.

Fig. 5, the same left dentary, dorsal view.

Scale in millimeters.

PLATE 2

Diplocynodon sp. from Silveirinha (?Upper Paleocene or Lowermost Eocene).

Unretouched photographs.

Fig. 1, cervical vertebra having lost the neural parts, left view.

Fig. 2, incomplete anterior dorsal vertebra, left view.

Fig. 3-5, posterior dorsal vertebra, fig. 3 (left), 4 (cranial) and 5 (distal) views.

Fig. 6-7, incomplete (dorsal parts lacking) caudal vertebrae, 7 being one of the rearmost vertebrae.

Scale in millimeters.

PLATE 3

Diplocynodon sp. from Silveirinha (?Upper Paleocene or Lowermost Eocene).

Unretouched photographs.

Fig. 1-2, right radius, dorsal and external views.
Fig. 3-6, dorsal osteoderms.
Scale in millimeters.

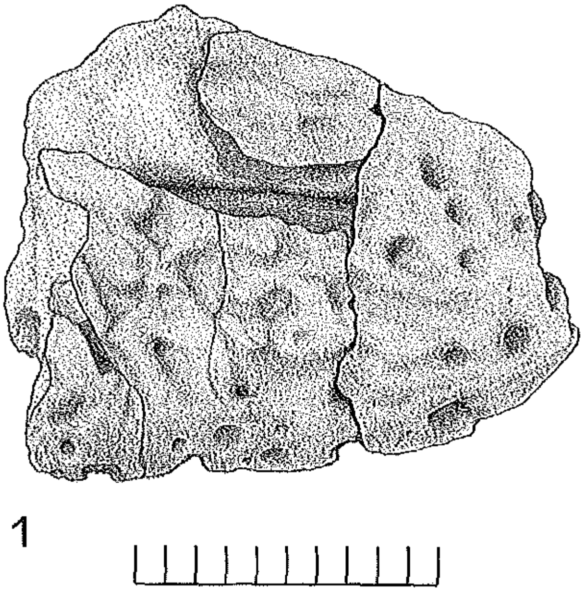
PLATE 4

Diplocynodon sp. from Silveirinha (?Upper Paleocene or Lowermost Eocene).

Unretouched photographs.

Fig. 1-3, lateral osteoderms.
Fig. 4, ventral dermal scute.
Scale in millimeters.

PLATE 1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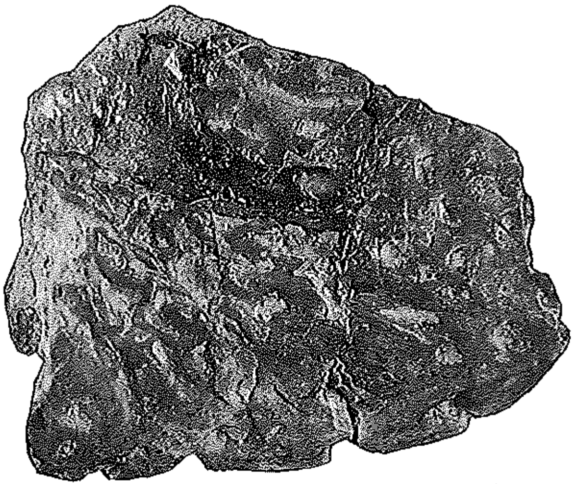
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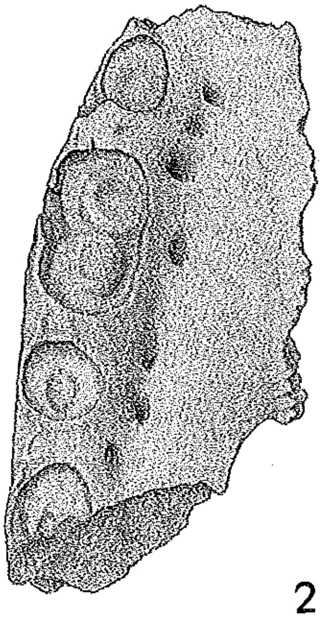
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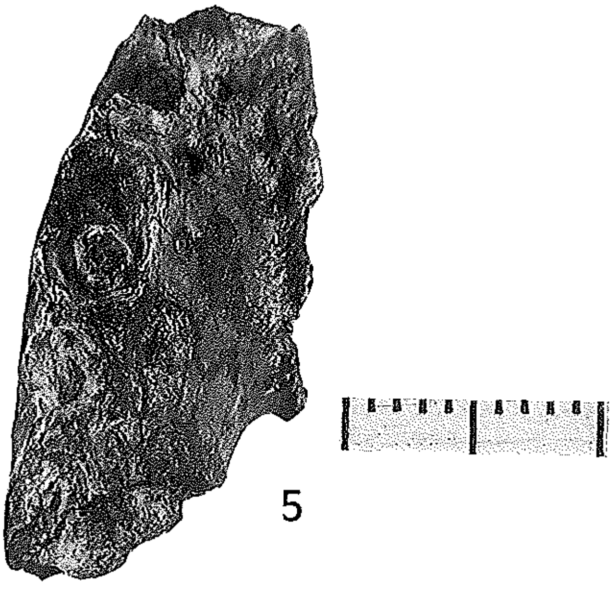
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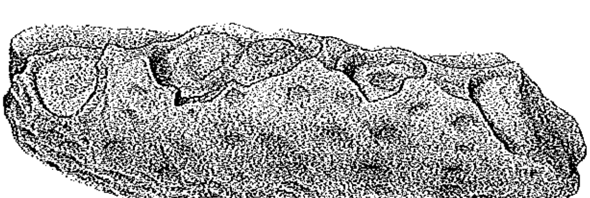
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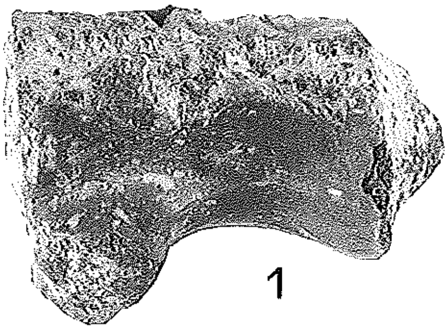

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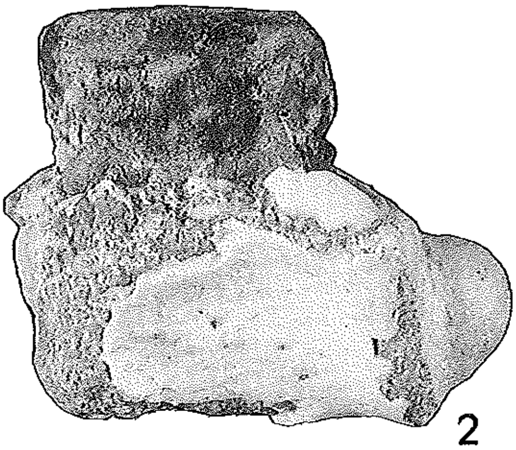

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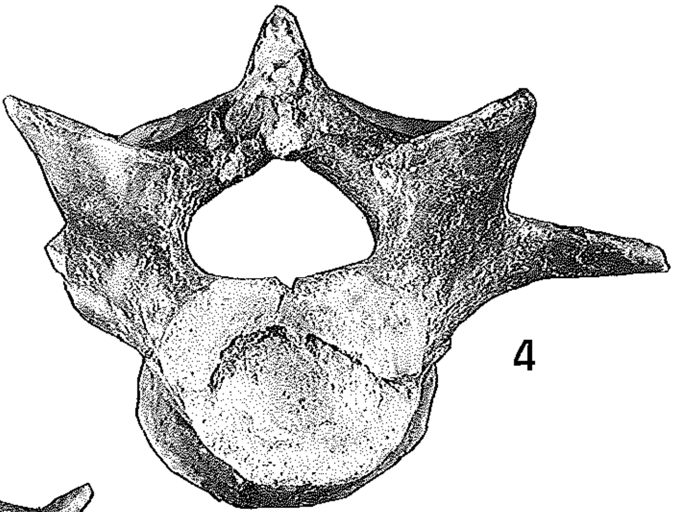

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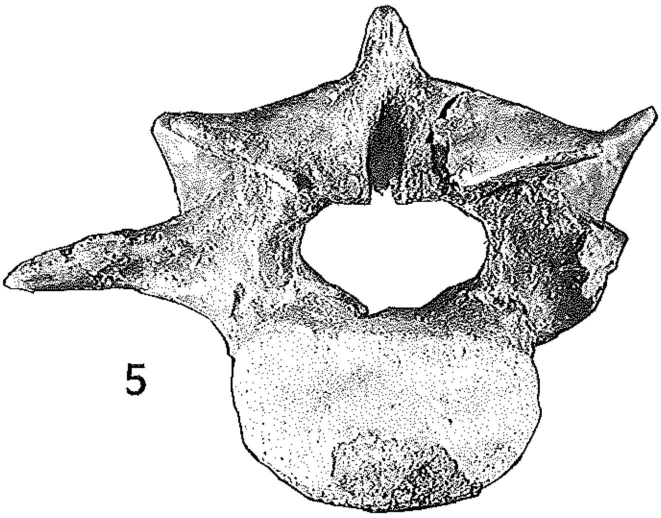

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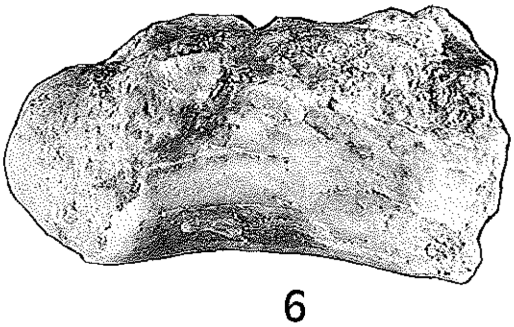

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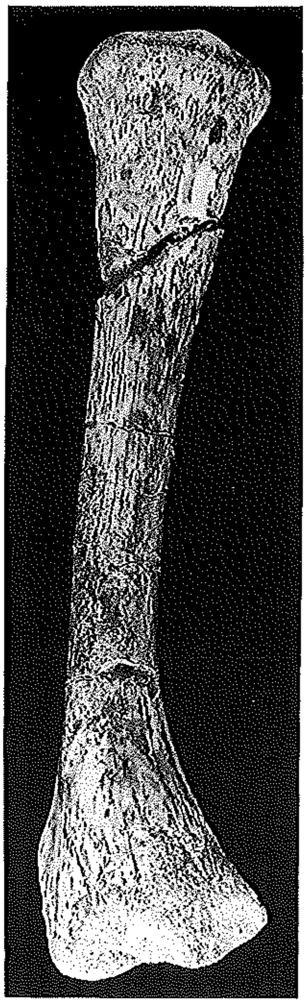
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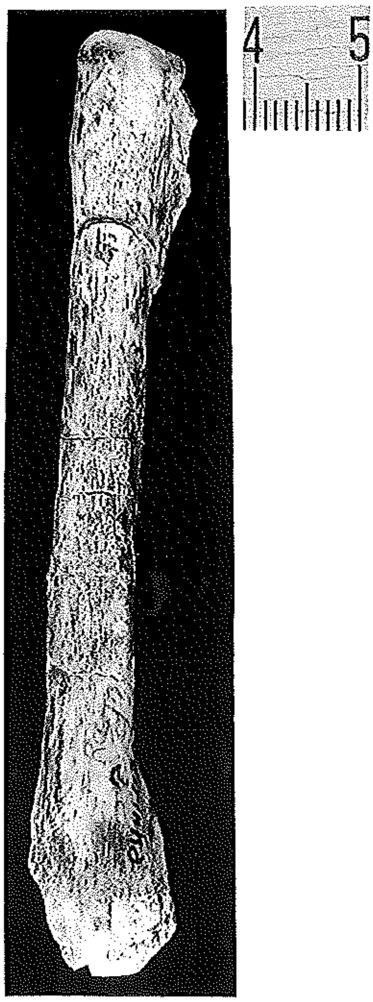

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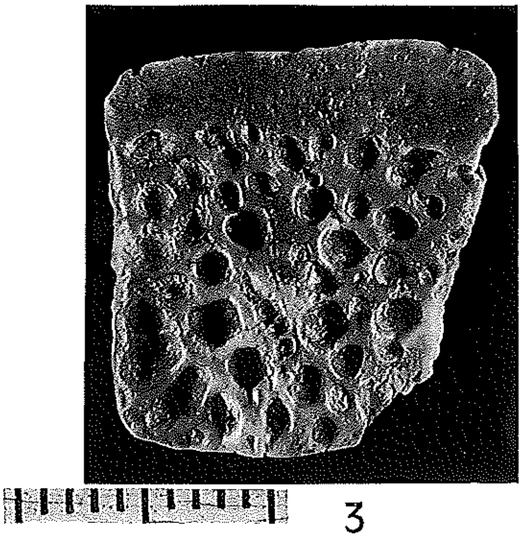
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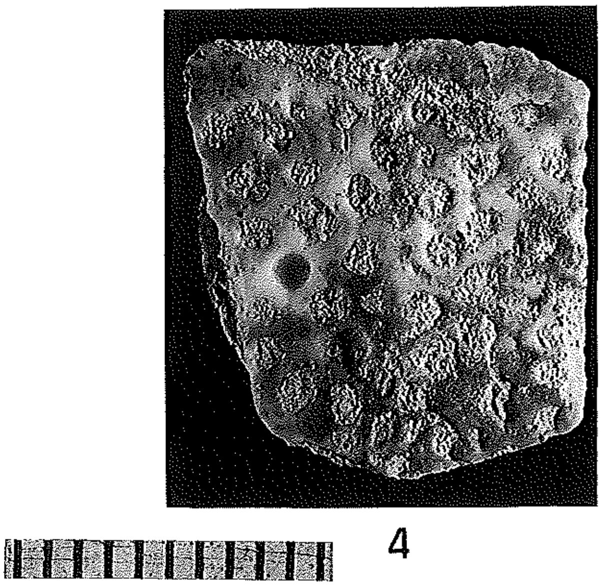
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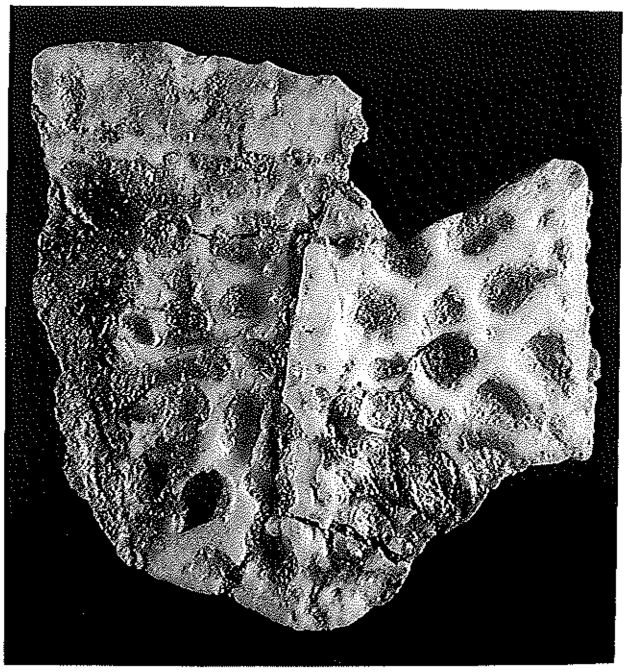
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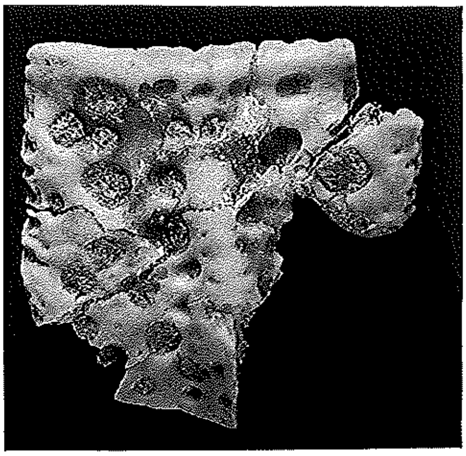

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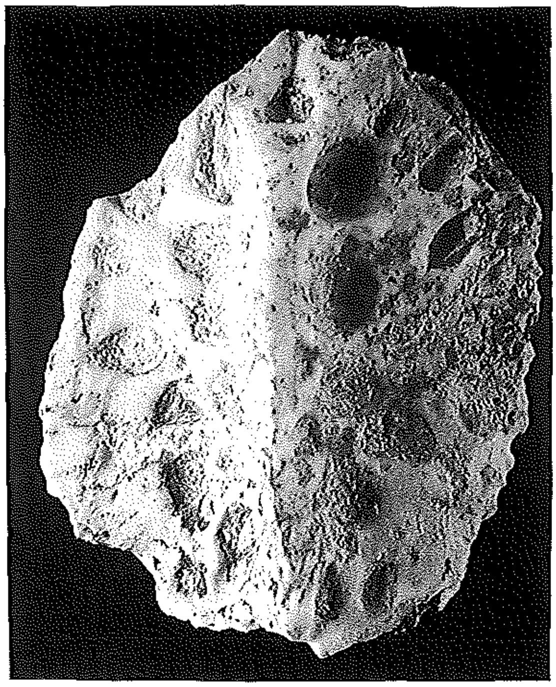

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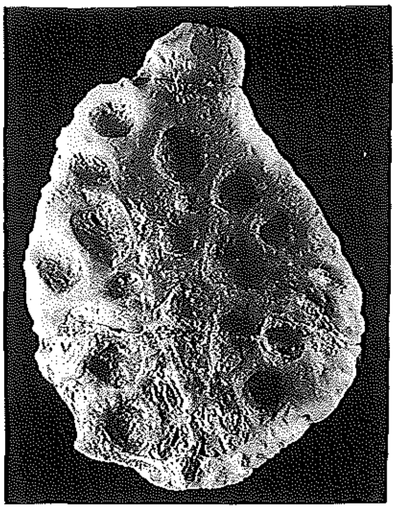

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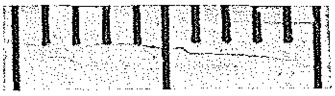

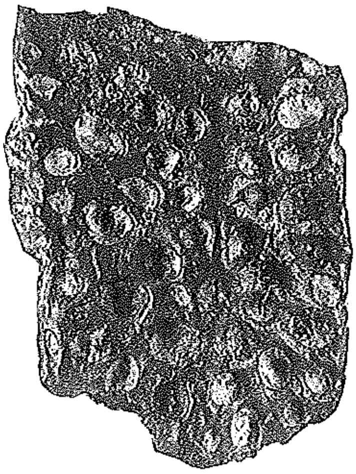

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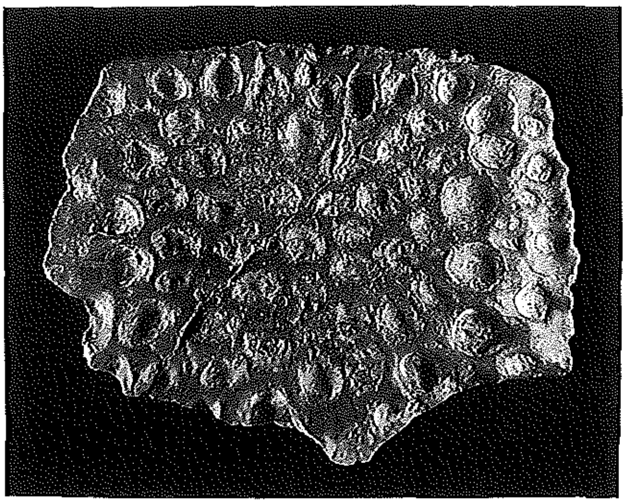

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