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THE SERRATED TEETH OF *SEBECUS* AND THE IBEROCCITANIAN CROCODILE, A MORPHOLOGICAL AND ULTRASTRUCTURAL COMPARISON

O. LEGASA (*)
A. D. BUSCALIONI (*)
Z. GASPARINI (**)

RESUMEN:- Se compara la morfología y ultraestructura del esmalte de dientes aserrados de cocodrilos. La muestra está compuesta por coronas aisladas atribuídas a la forma iberoccitana (Eoceno de la cuenca del Duero) y *Sebecus* (*S. ?huilensis* y *S. icaeorhinus* del Mioceno medio de Colombia y Eoceno inferior de Argentina). Se examinaron caracteres cuantitativos y cualitativos de la corona y sus márgenes aserrados. En este sentido, se han explorado todas las variables que caracterizan la simetría de la corona dentaria, diferenciando los dientes más grandes de *Sebecus ?huilensis* de los de la forma iberoccitana.

El análisis de la ultraestructura evidencia una organización pseudoprismática del esmalte de *Sebecus ?huilensis*, contrastando con el modelo aprismático del cocodrilo iberoccitano.

En este artículo se definen los dientes aserrados como aquellos que poseen carenas con dentículos aislados. Un dentículo aislado es una unidad morfológica discreta. Esta definición excluye los dientes con carenas crenulados formadas por crestas anastomosadas convergentes, que proceden de la ornamentación del esmalte.

También, se evaluan aspectos funcionales de los dientes considerando los microdesgastes observados en los dentículos aislados.

ABSTRACT:- The morphology and enamel ultrastructure of serrated teeth of crocodiles is compared. The sample is composed by isolated teeth attributed to the iberoccitanian form (Eocene of the Duero basin, Spain) and *Sebecus* (*S. ?huilensis* and

(*): Unidad de Paleontología. Dpto. Biología. Universidad Autónoma, Cantoblanco 28049 Madrid, Spain.
(**): Museo de La Plata, Paseo del Bosque s/n. 1900 La Plata. R.Argentina.

S. icaeorinus, Eocene of Argentine and middle Miocene of Colombia). Quantitative and qualitative characters of the tooth crown and serrations are examined. Exploration of new significant morphological characters of the tooth crown is essayed. In this sense, it has been raised several variables that discern symmetry of the tooth crown, differentiating the larger teeth of *Sebecus ?huilensis* from the iberoccitanian ones.

Ultrastructural analysis also evidenced a pseudoprismatic organization of the enamel of *S. ?huilensis* contrasting with the aprismatic pattern of the iberoccitanian crocodile.

Here serrated teeth is defined as those that posses carinae with isolated denticles. An isolated denticle is a discrete morphological unit. This definition excludes teeth with coarse carinae, builded from convergent anastomosed ridges that coming from the ornamentation of the crown enamel.

Functional aspects of the teeth are evaluated considering the microware patterns observed on the isolated denticles.

Palabras clave: Cocodrilos zifodontos, Dientes aserrados, Esmalte, Microdesgaste.

Key words: Enamel, Microware, Serrated teeth, "Ziphodont" crocodiles.

INTRODUCTION

Much work has been done on the functionality, morphology and ultrastructure of compressed and serrated teeth with (LANGSTON, 1956; ANTUNES, 1975; BUFFETAUT, 1986; BUFFETAUT *et al.*, 1986; ARGAST *et al.*, 1987; DAUPHIN, 1987a; FARLOW & BRINKMAN, 1987; ABLER, 1992). Among archosaurs, members of the linage Pseudosuchia and Ornithosuchia show this tooth morphology, being the diversity of theropod dinosaurs one of the best known (CURRIE *et al.*, 1990; FARLOW *et al.*, 1991).

Among crocodiles the presence of this pattern distantly related taxa, have produced a vast literature (LANGSTON,1956, 1975; BUFFETAUT, 1986; LI, 1976; MOLNAR, 1981). The Spanish Eocene record has yield abundant compressed isolated crowns, mostly known in the Duero Basin outcrops (MARTÍN DE JESÚS *et al.*, 1987). In the Iberian Peninsula preliminary studies were carried out by ANTUNES (1975, 1986) trying to differentiate the Duero Basin Sebecosuchia with the Eocene Eusuchia *Pristichampsus*. However, any morphological comparison have been done comprising the Duero basin compressed teeth with the South american ones of Sebecosuchia. This study intend a first approach for a better understanding on the morphology and ultrastructure of Sebecosuchia, contrasting isolated teeth of *Sebecus* (*S. ?huilensis*) and those from the Duero basin form.

Due to the similarity between the teeth of "ziphodont" crocodiles and theropod dinosaurs (ABLER, 1992; CURRIE *et al.*, 1990), we intent also to discuss some functional aspects on the serration morphology and its microware patterns.

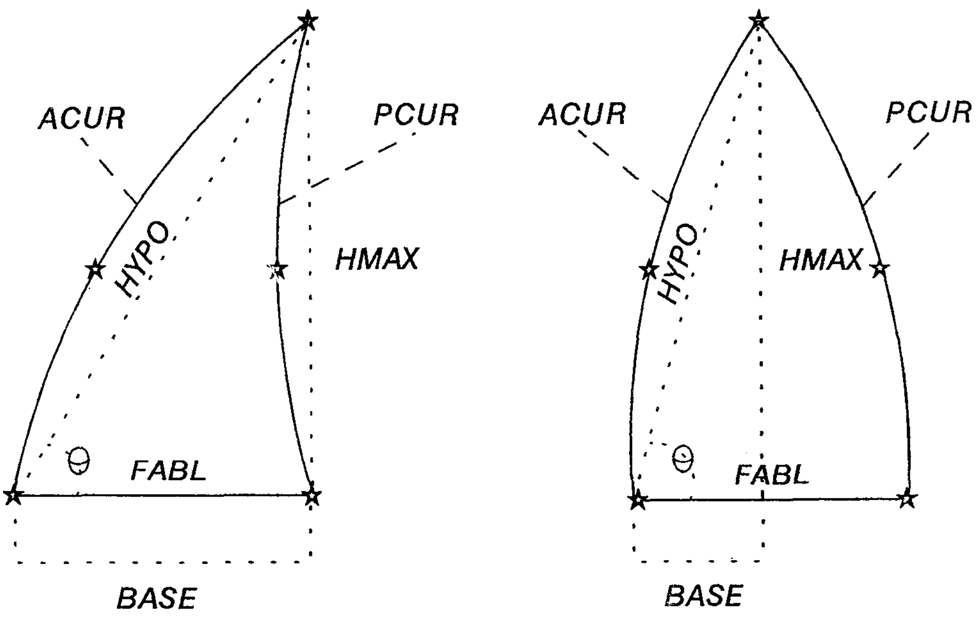


Fig.1.- Schema of the lingual view of an isolated tooth of the iberoccitanian crocodile (left) and *Sebecus huilensis* (right). In the schema is represented different variables used for measuring the tooth crown using MTV software: **HYPO**, cord of the anterior tooth margin; **FABL**, fore-aft basal length of the crown; **HMAX**, apical-base maximal orthogonal length; **PCUR**, radius of curvature of the posterior margin; **ACUR**, radius of curvature of the anterior margin; **ANG**, angle formed by **HYPO** and **FABL**. On the schema also is evidenced the symmetry of the *Sebecus* tooth with respect to the iberoccitanian one.

MATERIAL AND METHODS

About 40 isolated teeth have been examined. The Spanish specimens came from diverse Eocene outcrops of the Duero basin (Salamanca, Soria and Zamora provinces). The southamerican specimens came from the Eocene of Colombia and Argentina.

Most of the specimens lack the root. The selected crowns for morphometric objectives were not badly crush or flattened. Fragmentary crowns were used for morphological details and ultrastructural analysis.

Specimens from the Eocene of Spain were first assigned to *Iberosuchus macrodon* (ANTUNES, 1975). However, a recent revision, gather the fragmentary record of the Iberian Peninsula and Southern France under the denomination of Iberoccitanian crocodile (ORTEGA *et al.*, in press). Up to know, this study on isolated mandibles has allowed a preliminary approach, allying the iberoccitanian crocodile with the Sebecosuchia (GASPARINI, 1972; BENTON & CLARK, 1988). The isolated teeth from Southamerica belong to *Sebecus ?huilensis* (Colombia) and *Sebecus icaeorhinus* (Argentina).

All measures were taken in lingual view, using MTV software, and defining the following variables (Fig. 1): **HYPO**, cord of the anterior tooth margin; **FABL**, fore-aft basal length of the crown; **HMAX**, apical-base maximal orthogonal length with respect to FABL; **PCUR**, radius of curvature of the posterior margin; **ACUR**, radius of curvature of the anterior margin; **ANG**, angle formed by **HYPO** and **FABL**. A triangle is defined by the variables HYPO, BASE and introducing a new variable

BASE, former by the projection of HYPO on FABL (Fig. 1).

Meristic data are referred to the number of denticles per 1mm or 3mm on the anterior (**DENA**) and posterior keels (**DENP**). It has also been used for comparison isolated teeth of theropod dinosaurs that came from the Upper Jurassic fossil site of Lourinhá (Portugal).

Morphological details and ultrastructural examination was done using a Scanning Electron Microscope (SEM). For ultrastructural porpoise teeth have been cleaned with ultrasonic (60s), and etched with HCl (3.5%) and formic acid (85%) following the methodology of DAUPHIN (1987a, b). The observations was done on fresh sections of the enamel.

DESCRIPTION AND COMPARISON OF *SEBECUS* AND THE IBEROCCITANIAN TEETH.

The ziphodont crowns has been characterized by its compression and the presence of marginal serrations. Both groups of teeth have other similarities as well: -absence of a basal constriction at the base of the crown, enamel not ornamented, apex sharply ended, crowns relatively height with respect to its basal width (fore-aft basal length), two serrated carinae mesial and distally placed at the geometrical margins of the crown, and serrated carinae running from the base to the apex. However, the comparison of these two groups, the iberoccitanian crocodiles and *Sebecus*, has revealed a number of differences concerning the magnitude of the crown compression and their general curvature.

Sebecus teeth are almost symmetrical. A mesio-distal symmetry is raised regarding a longitudinal plane (that has been denominated **linguo-labial cutting plane**, fig. 2) sectioning the crown through the middle of its FABL length. The tooth is divided in two subequal half (Fig. 1b). In a basal view of the tooth crown the anterior (mesial) and posterior (distal) parts are equally compressed (specially the largest teeth of *S. ?huilensis*, fig. 2b). The iberoccitanian teeth are, however, asymmetrical. In basal view the crown is more compressed posteriorly (Fig. 2b), and the position of the apex is displaced distally with respect to this longitudinal plane (Fig 2b).

The largest sized teeth of *S. ?huilensis* tends also to be linguo-labially symmetrical, that is a longitudinal plane through the crown margins will divide the tooth into two linguo-labial subequals half. The iberoccitanian teeth have a greater lingual curvature.

Metric data have been explored for an preliminary approach of the variation observed in the original data including not only crocodilian teeth but theropod dinosaurs (Table 1). A principal component analysis (PCA) was essayed, using standardized variables and selecting those combinations of variables that provided best result in ordering the cases (Fig. 3 and Table 2) (MAINLY, 1989). The figured result reinforces our observation on the symmetry of the tooth crown described for *Sebecus* with respect to the iberoccitanian crocodile and theropod dinosaur. However, the volume of data does not allow us further significant conclusions.

The first principal component explains 72% of the variation in the data related predominantly to size differences (Table II). The second principal component explains the 24% of the variation. The value of this latter component is mainly affected by the variable ANGLE dealing with shape. As the ANGLE between the

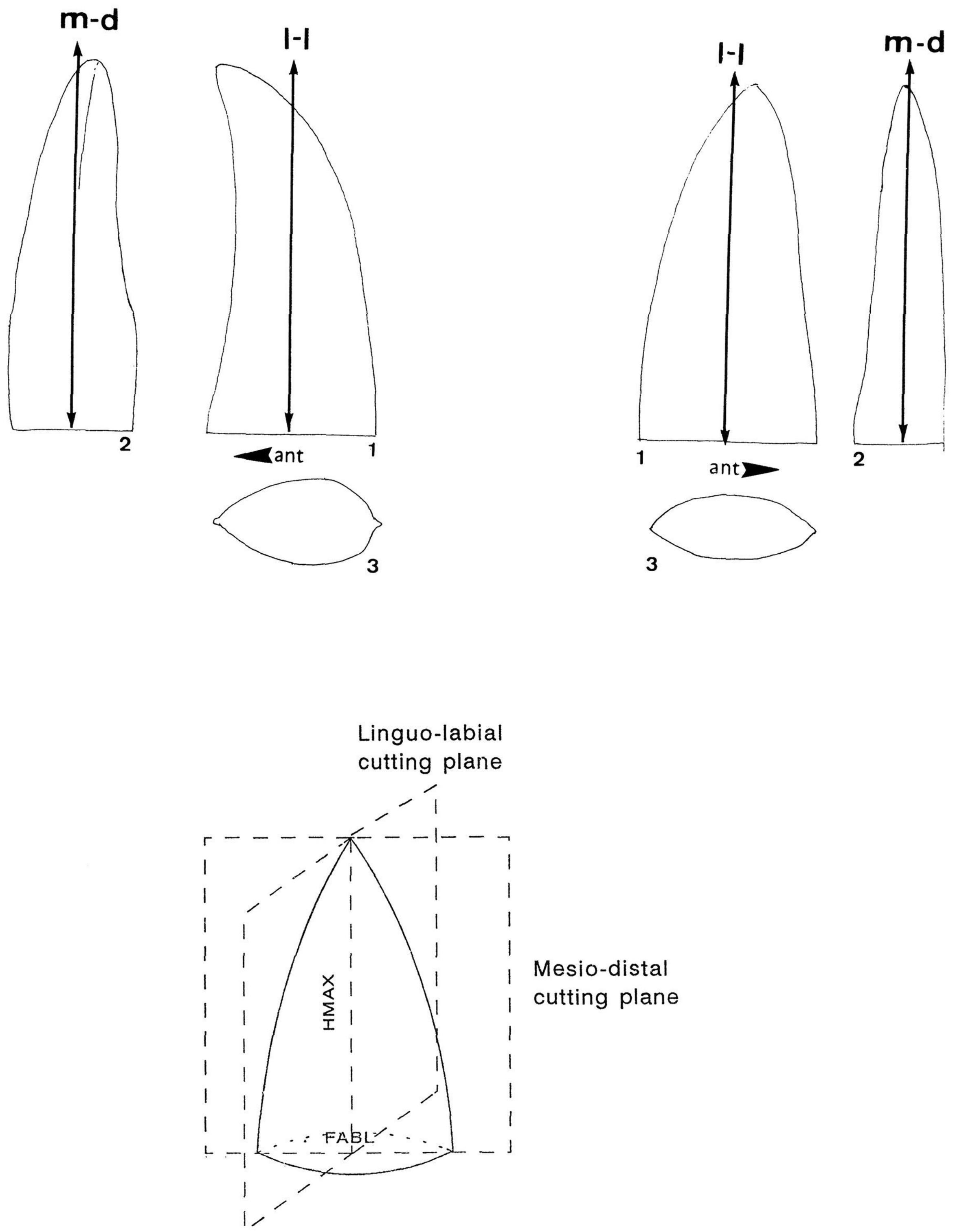


Fig.2.- Below; schema showing the two defined planes of symmetry with respect to the HMAX and FABL variables (see Fig. 1). The linguo-labial cutting plane defines the mesio-distal symmetry, and the mesio-distal cutting plane does the linguo-labial symmetry. Above, left; iberoccitanian tooth (1, lingual view; 2, mesial or anterior view; 3, basal section of the tooth crown). Right, *Sebecus huilensis* (1,2, and 3 represents the same views). The lines figured are the intersections with the planes of symmetry, l-l, with the linguo-labial cutting plane, and m-d, with the mesio-distal one.

CASES	ACUR	ANGLE	BASE	FABL	HYPO	HMAX	PCUR
I.1	139	64.36	85.5	111.5	168.2	140	821.9
I.2	161.6	66.8	76.5	96	213.7	192	1326
I.3	134	59.49	87	96.3	163.1	138	547.4
I.4	114.6	64.11	49.5	69	119.9	105	954.4
I.6	281.8	56.94	169.5	145.5	305.4	253	1210
I.7	264.8	60.61	148.5	132	303.6	259	586.8
S.1	290.6	69.44	88.5	123	263.4	242	735
S.2	262.6	68.63	102	126	245.2	223	523
PMGI6	89.86	53.57	67.5	67.5	128.2	105	448.9
PERic	33.5	62.51	76.5	72	162.7	141	491.7
PMGI256	133.8	63.43	69	81	167	145	250.8
PMGI5	97.57	57.48	72	70.5	143.2	118	257.6

Table 1.- Measurements (in mm) of the variables represented in Fig. 1. and used in the PCA analysis. Measurements were taken using MTV software. Signature of the cases are: I, iberoccitanian crocodile from the Duero basin (I1, 13701STUS; I2, 13701STUS; I3, 13701STUS, I4, DI5 and I6, 342TF); S, *Sebecus huilensis* (S1, IGM-184427; S2, IGM-184378); PMG and PER, megalosaurid dinosaur.

HIPO line and the BASE line (Fig. 1) became greater, the BASE lenght becomes reduced. Teeth with a mesio-distal symmetry tend to have a reduced BASE lenght (Fig. 1, compare both schemas). So, the variable BASE is somehow included in Factor 2 with a negative correlation.

The two *Sebecus* specimens introduced in the analysis show this tendency toward the reduction of the BASE, with greater ANGLE values, differing from all the remaining teeth (Fig. 3). This tendency is more evident in large sized tooth of *S. ?huilensis*, so a better resolution of the analysis is expected with a larger sample of these specimens.

MORPHOLOGICAL DETAILS: THE MARGINAL SERRATIONS

"Serrated margins" is a common term used for defining a rather diverse sort of tooth morphotypes. We prefer using the term serrated margins designating those teeth that posses carinae with isolated denticles. An "isolated denticle" is a discrete morphological unit, clearly individualized by an interdenticle groove or notch. The denticles extend in series along the carinae, frequently from the base to the apex. The isolated denticles posses an equivalent size throughout the carinae, except at the base and apical ends of the crown, where they become smaller. Defining teeth with serrated margins in such a way allows us to differentiate them from those teeth that

VARIABLES	FACTOR SCORES COEFFICIENTS FACTOR(1)	FACTOR(2)
HMAX	0.257	0.096
ACUR	0.47	0.154
ANGLE	-0.048	0.822
FABL	0.265	0.016
BASE	0.289	-0.358
EIGENVALUES	3.658	1.180

VARIABLES	ROTATED LOADINGS FACTOR(1)	FACTOR(2)
HMAX	0.960	0.201
ACUR	0.944	0.270
ANGLE	0.096	0.991
FABL	0.964	0.107
BASE	0.928	-0.343
VARIANCE EXPLAINED	72%	24%

Table 2.- Results of the principal component analysis.

has coarse carinae, builded from convergent anastomosed ridges coming from the ornamentation of the crown enamel. We prefer in this latter case using the term "crenulated teeth". So, the crenulations are not individualized units, and they are heterogeneous in size and shape.

The isolated denticles in *S. ?huilensis* and the iberoccitanian teeth show the same morphological pattern. The body of the denticle has a subrectangular shape, "chisel-shaped". Its maximal volume is at its middle and in its base (Fig. 4). Their interdenticular edges are almost straight. The exposed edge of the denticle is dome-shaped. The interdenticle groove extends from its base towards its exposed edge. The unit is not oriented toward the apex of the crown, differing of the maniraptoran dinosaur *Troodon*. The unique distinction between *Sebecus* and the iberoccitanian denticle morphology consist on their development. The denticles of the iberoccitanian crocodile are bulky, being those of *Sebecus* flatter. In few cases, when the denticle series is well preserved, it can be appreciated, on the iberoccitanian teeth, that the base of the interdenticular groove projects slightly towards the base of the crown. The observations with SEM has also revealed a probable pattern of microware on the denticle surface (Fig. 5). Along the interdenticular groove predominates series of parallel scratches disposed from the apex to the base of the

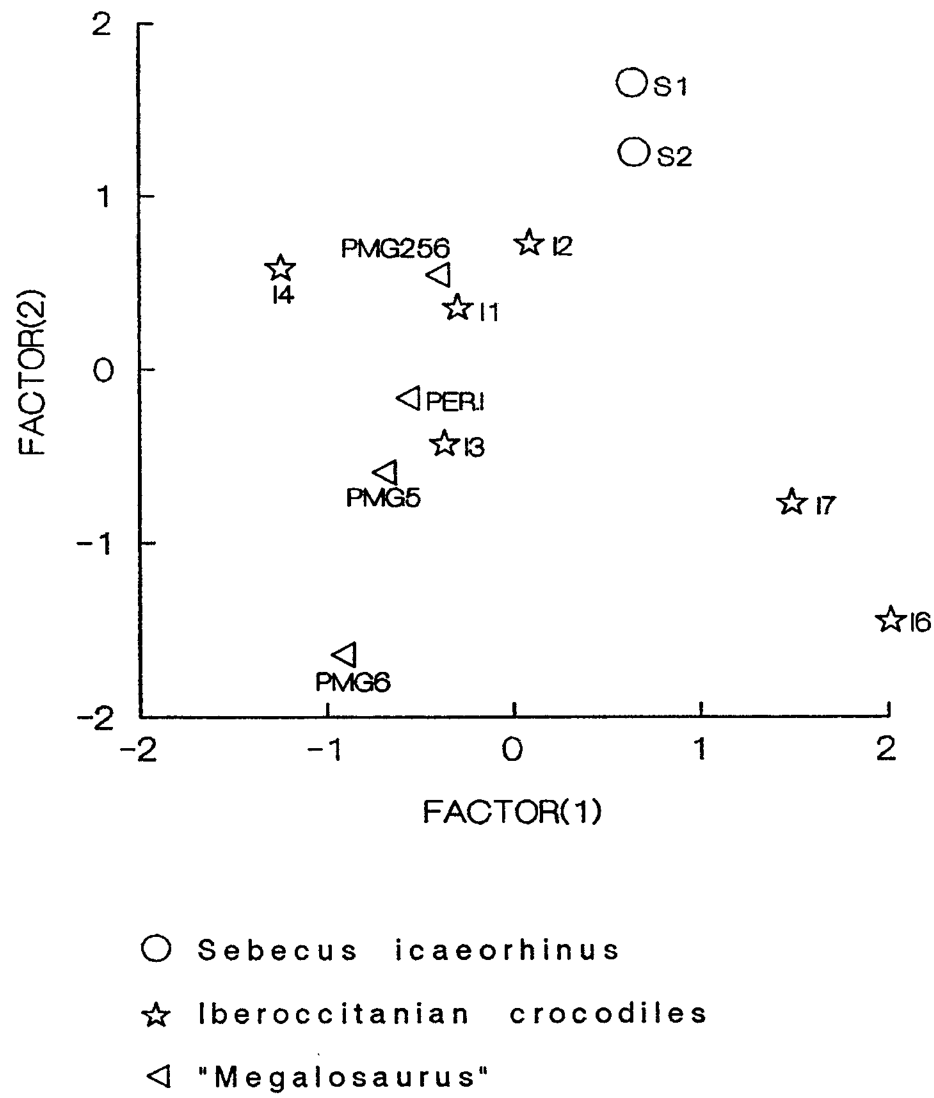


Fig.3.- Bidimensional plot of the PCA analysis. Factor (2) (second principal component) is mainly affected by the variables ANGLE and BASE, separating the two specimens of *Sebecus huilensis* from the remaining teeth:-"*Megalosaurus*" and iberoccitanian crocodile.

denticle, while on its body the scratches are pararell to its exposed edge.

One of the most debatable feature for differing ziphodont taxa has been the denticle density. Our observations deal with no differences between the iberoccitanian crocodile and *Sebecus* when the number of denticles are referred per 1 mm (Table 3, see also the median values in Fig. 6). However, the range of variability of the denticle density on the anterior margin is probably greater in the iberoccitanian crocodile, while in *Sebecus* seems to be rather stable. Small teeth of *Sebecus ?huilensis* or the iberoccitanian crocodile have as many as 11-15 denticles/3 mm of the anterior margin and 6-7 denticles/3mm of the posterior margin. As in theropod dinosaurs teeth, tooth serrations declines when increasing tooth size, and there is a lesser number of posterior denticles too (FARLOW & BRINKMAN, 1987; FARLOW *et al.*, 1991).

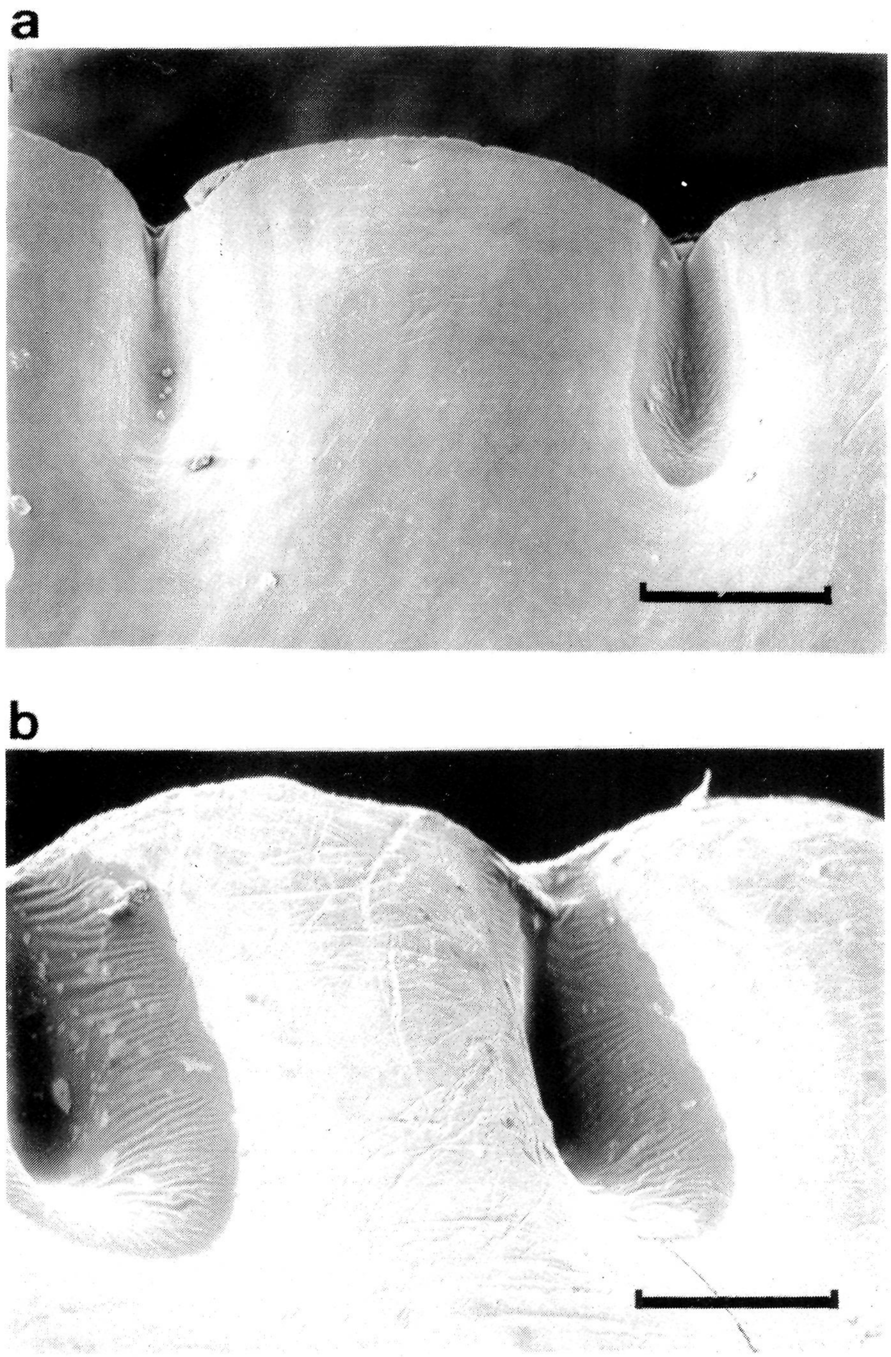


Fig.4.- Electron microscope photograph of an isolated denticle of *Sebecus huilensis* (**a**), and the iberoccitanian crocodile (**b**). Scale bar 100 micrometers.

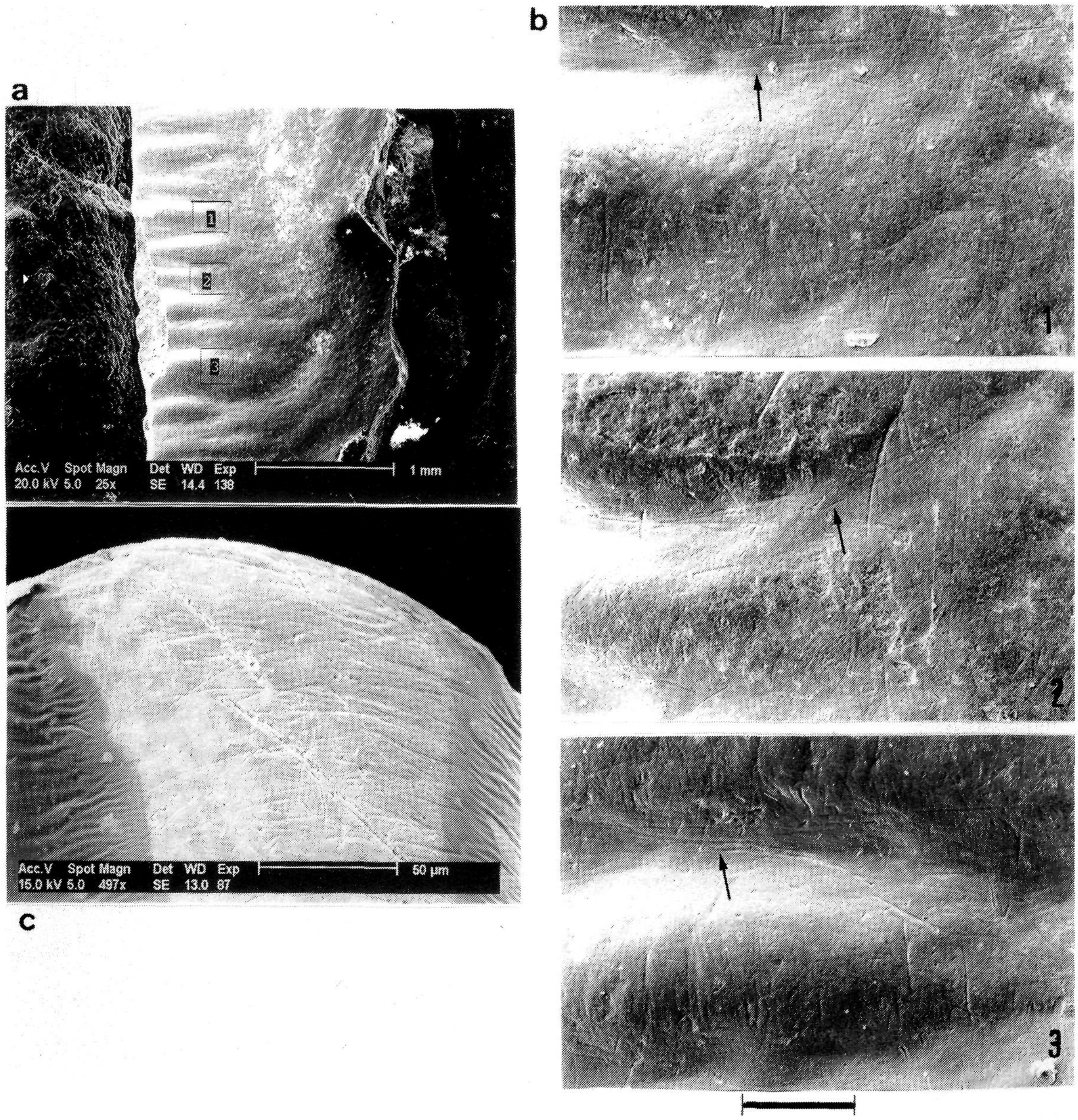
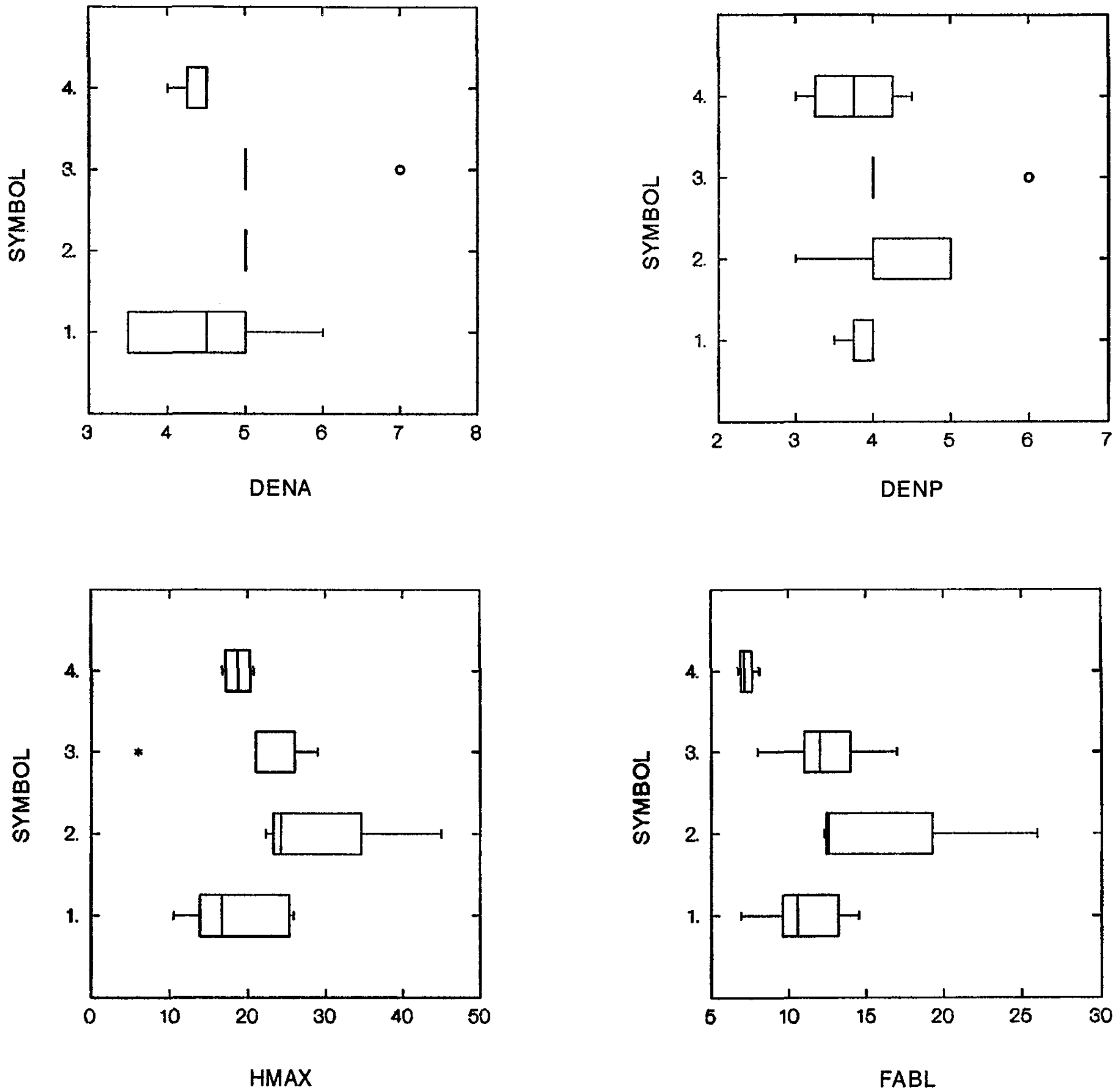


Fig.5.- Microware pattern of an isolated teeth of *Sebecus huilensis*. **a**. Fragment of the tooth crown showing a series of isolated denticles, the numbers 1, 2 and 3 correspond to the partial areas magnified in **b**. In these three zones the arrows show the bunch of pararell scratches is appreciated on the interdenticular area. All are 200x magnified, scale bar 100 micrometers. **c**. Isolated denticle showing a series of scratches on the body of the denticle parallel to its exposed or outer edge.

ULTRASTRUCTURAL ANALYSIS.

A preliminary ultrastructural analysis has revealed some details of the enamel of *Sebecus* and the iberoccitanian crocodile. The enamel thickness is greater in *Sebecus* (57 micrometers) than in the iberoccitanian ones (33 micrometers). The enamel outer surface is irregular for both taxa (Fig. 7), without polygonal cells, as is frequent in *Tarbosaurus* or *Alligator missipienssis* (BUFFETAUT *et al.*, 1986; DAUPHIN, 1988).

In the teeth enamel of iberoccitanian sample the c-axes apatite crystallites are



1= Iberoccitanian form.
2= S. huilensis.
3= S. icaeorhinus.
4= "Megalosaurus".

Fig.6.- Distribution of the values of DENA and DENP. Below, distribution of HMAX and FABL variables. 1, iberoccitanian crocodile, 2, *Sebecus huilensis*, 3, *Sebecus icaeorinus*, and 4, "megalosaur". Each rectangular box contains the 50% of the values for each group, and the vertical line within the box is the median value. The whiskers (horizontal lines emanating from each box) extends to the smallest and the amplest values. The asteric represents outside value and the circle the far outside value. In the DENA box the 50% of the values in each taxa is occupies the same range, but in DENP the range that shows the iberoccitanian crocodile diverge slightly of that of *Sebecus*.

CASES	DENA	DENP
I.1	5	4
I.2	3.5	3.5
I.3	5	4
I.4	6	-
I.6	3.5	-
I.7	4	4
S.1	5	5
S.2	5.5	6
IGM250541	5	3
AMNH3160	5	-
AMNH3160	-	4
AMNH3160	5	4
AMNH3160	5	4
AMNH3160	5	4
AMNH3160	5	4
AMNH3160	7	6
MMP754M	5	4
MMP2070M	-	4
PMGI6	4.5	4.5
PERic	4.5	3.5
PMGI256	4	3
PMGI5	4.5	4

Table 3.- Number of denticles per 1mm at the half of the mesial (DENA) and distal (DENP) carinae.

orthogonal arranged with respect to the enamel surface. No prismatic enamel was observed along all its thickness being the enamel compact and uniform. In few specimens growth lines were appreciated close to the dentine-enamel junction (Fig. 8).

The *Sebecus* (*S. ?huilensis*) sample presents a pseudoprismatic organization. The external enamel area is aprismatic, while its inner part shows a pattern of divergent crystallites from a possible origin centra. This divergence seems to be more evident on one side of the longitudinal axis of the prism (Fig. 9). Growth lines are appreciated close to the dentine-enamel junction, being the enamel compact and uniform.

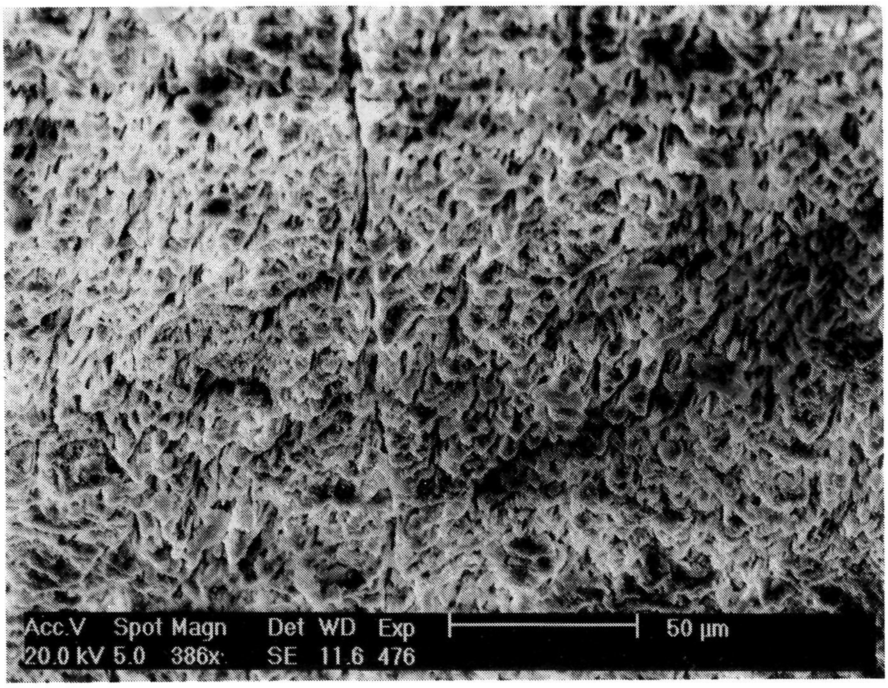


Fig.7. *Sebecus huilensis*. Fresh cut cleaned with ultrasonic (1 min.) and etched with HCl (3.5%, 1 min). Enamel surface showing no polygonal cells.

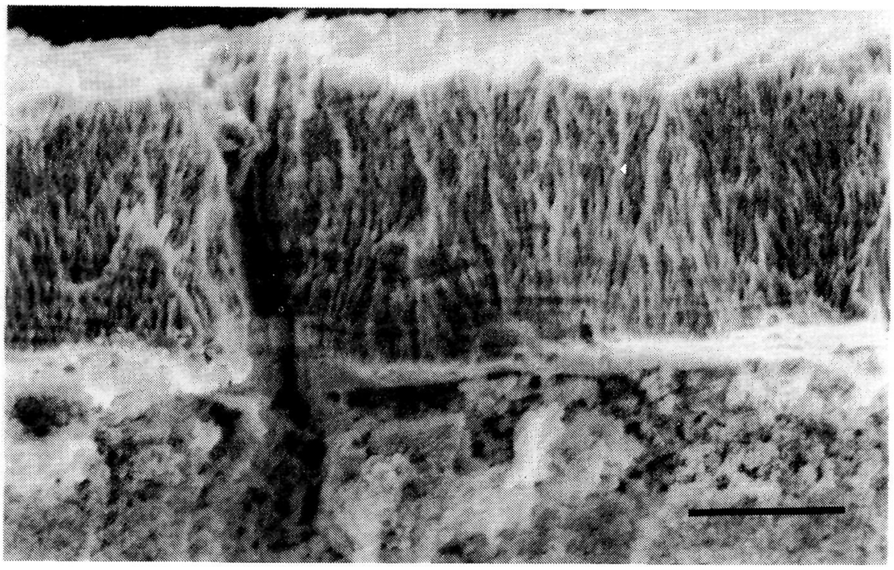
DISCUSSION

The morphology of ziphodont crowns, that is, lateral compressed crowns with no basal constriction, sharp distally recurved tooth, and the presence of serrations (isolated denticles) seem to be the primitive pattern, regarding Archosaur phylogeny. Up to now, only compression, and distally curved tooth crowns have been considered sinapomorphies defining the node Prolacertiforms + Archosauria (BENTON, 1990). However, the "crocodylotarsi" linage (phytosaurs, rauisuquids and crocodylomorphs) contains taxa possessing the primitive dentition pattern described above, as well as other basal members of the Ornithosuchia linage (*Ornithosuchus*, *Euparkeria*). Thus, we think that serrated teeth, with lateral compressed crowns and distally recurved is a probable sinapomorphy of Archosauria.

Nevertheless, this pattern disappear and subsequently reappear along the different subclades of Archosauria, generating a number of reversions and parallelism.

The morphology of the tooth crown differs mainly when large sized teeth are compared. Symmetrical crowns of *S. ?huilensis* versus asymmetrical crowns of the iberoccitanian form is remarkable. When teeth of other *Sebecus* (*S. icaeorhinus*, COLBERT, 1946) are compared, the same tendency is observed (symmetry of tooth crowns). We think that these teeth would be placed at the middle of the maxilla or mandible, probably where the biting force is maximal.

The enamel ultrastructure of Archosauria seems to be independent of tooth morphology, diet, and phylogeny (DAUPHIN, 1988). The enamel ultrastructural



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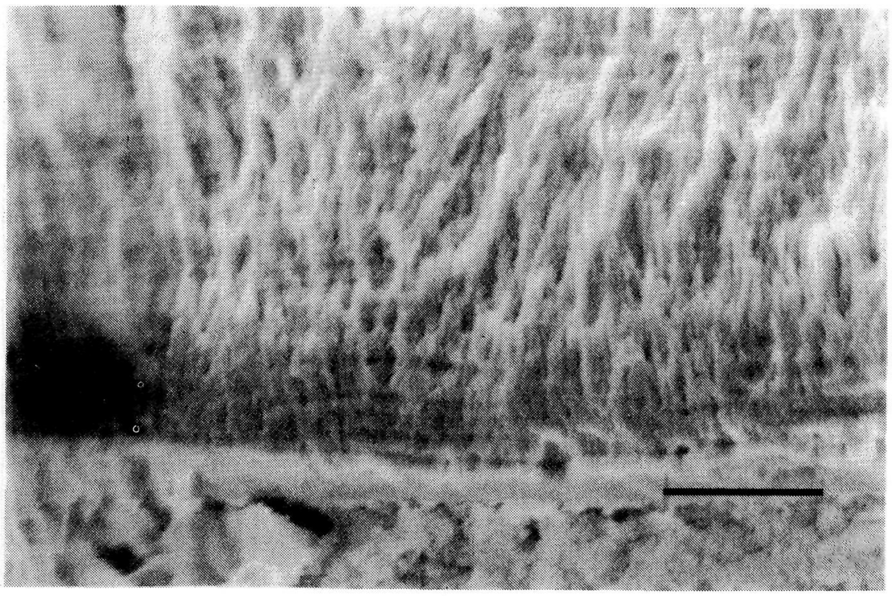

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Fig.8.- Enamel ultrastructure of "*Iberosuchus*". **1**) General view. Scale bar 20 micrometers, magnification 808x. **2**) Detail of the inner layer showing growth lines close to enamel-dentin junction. No prismatic organization is appreciated. Scale bar 10 micrometers, magnification 1617x.

analysis require the observation of a large sample and diversity for characterizing the organization of the enamel prism, and delimits its variability. The study of isolated teeth introduce an additional problem related with its taxonomic attribution. For instance, the tooth morphology of the "ziphodont" *Pristichampsus* and the Sebecosuchia may be confuse. Furthermore, among crocodiles it has been described a variability within the same genera, or even within different ontogenetic stages of the same species (*Gavialis*, SAHNI, 1987), or exist partial organizations in the enamel

Fig.9. *Sebecus huilensis*, fresh cut just cleaned with ultrasonic (1 min). In the section the outer layer is aprismatic, while the inner layer is dense, and pseudoprismatic organized with divergent crystallites. Growth lines are also appreciated.

structure in the same tooth (SAHNI, 1987; DAUPHIN, 1988). Thus, it is not strange that the enamel of *Sebecus* were considered aprismatic (Dauphin, 1988) differing from our results on *Sebecus ?huilensis*. Up to now, there is no criteria for resolving this type of uncertainty (DAUPHIN, 1987, 1988; DAUPHIN *et al.*, 1988; SAHNI, 1987). In this sense, crocodiles seem to exhibit a greater dispersion of results in comparison, for instance, with theropod dinosaurs. All studied theropod dinosaurs present prismatic enamel except *Velociraptor* (BUFFETAUT *et al.*, 1986). Among crocodiles, Eusuchia show aprismatic enamel (*Crocodylus palustris*, *Paleosuchus trigonatus*, *Pristichampsus*, *Diplocynodon*) or prismatic (*Alligator mississipiensis* and *Allognathosuchus*), also the metasuchian here described (*Sebecus* and the iberoccitanian crocodile) and within the Thalattosuchia the same dispersion has been quoted (DAUPHIN, 1988).

Compressed crowns with serrations will show similar functional device. Some theropod dinosaurs and the ziphodont crocodiles can be interpreted with similar functional patterns of the tooth crown (ABLER,1992). The relative height of the tooth is related with the deepness and the force of the bit, and the compression is related with a lesser resistance of pushing into, acting as a sharp blade. Serrations, however, will provoke a distribution of the resistance along the surface of the denticles, increasing the pressure upon the flesh with respect to the isolated denticles surface.

The drawing force is converted into cutting force, providing the motion for ripping the material on the interdenticular groove producing a cut, and also providing the force that accomplishes the split and cut of the flesh, by the body and edge of the denticle. The direction of the rip mechanism is consistent with direction of the interdenticular microwares, while the microware observed on the body of the denticle seems to be consistent with the splitting-cutting mechanism (Fig. 5). Among theropod dinosaurs, probably tyrannosaurids, show the greater (functional and morphological) similarity with these crocodiles: tooth crown and denticles morphology, and microware patterns (ABLER, 1992).

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APPENDIX

The Spanish specimens belong to collections of: a) Universidad de Salamanca ("Sala de las Tortugas") (references: TF342; C-936; C-926; C-929; C-931; C-1025; C-1027; C-1026; 11643; 1246; 11859; 11857; DMIJ2; DMIJ4; (teeth in situ in the STUS 349 mandible), b) Universidad Autónoma de Madrid (reference: DI1-5). The southamerican specimens belong to: d) Museo Mar del Plata (Argentina) (references: MMP754m; 755m; 756m; 2070m; 295m); e) American Museum Natural History (New York) (references: AMNH3160) f) INGEOMINAS (Colombia) (references: IGM184165; IGM184378; IGM 84427; IGM 250457; IGM250541).

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