

# *Elosuchus*, a new genus of crocodile from the Lower Cretaceous of the North of Africa

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**Abstract** – ‘*Thoracosaurus*’ *cherifiensis* Lavocat, 1955, a longirostrine from the late Lower Cretaceous of Morocco and Algeria, is attributed to *Elosuchus*, n. g., with another species, *E. felixi* n. sp., from In Abangarit (Niger), of the same age. *Stolokrosuchus* from the Lower Cretaceous of Niger is also referred to the new family Elosuchidae. Synapomorphies and grades are indicated for the families of ‘mesosuchian’ longirostrine crocodiles, but no synapomorphy has been found to unite the families, except perhaps for the Thalattosuchia. **To cite this article:** F. de Lapparent de Broin, C. R. Palevol 1 (2002) 275–285. © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Crocodylia / Cretaceous / North of Africa / new taxa / mesosuchian / longirostrine

**Résumé** – *Elosuchus*, nouveau genre de crocodile du Crétacé inférieur du Nord de l’Afrique. « *Thoracosaurus* » *cherifiensis* Lavocat, 1955, fin du Crétacé inférieur du Maroc et d’Algérie, est décrit et attribué à *Elosuchus* n. g., avec une autre espèce d’âge voisin, *E. felixi* n. sp. d’In Abangarit, Niger. À la nouvelle famille des Elosuchidae est aussi référé *Stolokrosuchus*, du Crétacé inférieur de Gadoufaoua, Niger. Des synapomorphies et les grades sont donnés pour les familles de « mésosuchiens » longirostres, mais aucune synapomorphie n’a été trouvée entre elles, sauf peut-être pour les Thalattosuchia. **Pour citer cet article :** F. de Lapparent de Broin, C. R. Palevol 1 (2002) 275–285. © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Crocodylia / Crétacé / Nord de l’Afrique / nouveaux taxons / mésosuchien / longirostre

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## Version abrégée

### 1. Introduction

Grâce à la redécouverte du syntype complet de *Thoracosaurus cherifiensis* Lavocat, 1955 [17] et de nouveau matériel du Maroc, du Niger (« *Eleiosuchus africanus* » in Broin [3], inédit) et d’Algérie [4], cette espèce s’avère appartenir, non à l’Eusuchien *Thoracosaurus*, mais à un nouveau genre de crocodile de grade mésosuchien progressif, qui est défini ici sous le nom d’*Elosuchus*, avec deux espèces différentes. Le genre *Stolokrosuchus* Larsson & Gado, 2000 [14] est aussi rapporté aux Elosuchidae, et non aux Peirosauridae [10].

### 2. Systématique

Crocodylia Gmelin, 1788

Elosuchidae n.f.

La famille, créée pour le genre *Elosuchus* n. g. et pour *Stolokrosuchus* Larsson & Gado, 2000 [14], est distribuée dans la moitié nord de l’Afrique (Algérie, Éthiopie, Maroc, Niger, Soudan, Tunisie), dans le « Continental intercalaire » supérieur du Sahara, Crétacé inférieur, de l’Aptien terminal à la base du Cénomani. Apomorphies : présence de deux dents prémaxillaires en avant et entre les deux premières dents mandibulaires (droite et gauche) ; les prémaxillaires sont allongés devant le rostre, lui-même allongé (de type platyrostral *Tomistoma*, ondulé et non tubulaire), s’élargis-

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sant aux dents 2–3, puis s'étrécissant en avant, avec festons autour des dents 2–3 et 4–5 ; plus grand espace entre les dents maxillaires 1 à 10–12 qu'entre les postérieures. Crânes de 50 cm à plus de 1 m. D'autres caractères diagnostiques sont donnés. Possible apomorphie de la famille (Fig. 2A) : présence d'une fosse « élosuchienne », dépression de la partie postérieure palatine du palais, étendue primitivement jusqu'au bord orbitaire, de chaque côté des conduits respiratoires et des chambres sinusiennes médiales et important cloisonnement osseux préfrontal et lacrymal postérieur de ces cavités. Le coude lacrymal que forme le bord orbitaire en s'abaissant dans sa partie latérale est un caractère primitif, présent également chez *Sarcosuchus* [4, 13, 22] et d'autres formes. La famille est située à un grade progressif des « mésosuchiens ».

### 2.1. *Elosuchus n. g.*

Le nouveau genre est réparti dans la partie supérieure du « Continental intercalaire » supérieur du Sahara, de l'Albien supérieur jusqu'à la transgression cénomaniennne, au Maroc (localité de l'espèce type, la Gara Sba, Kem-Kem) et en Algérie (Gara Samani, sables inférieurs [3, 7] avec *E. cherifiensis* (Lavocat, 1955) [17], à In Abangarit (Niger) [11] avec *F. felixi* n. sp. et dans d'autres localités d'Algérie, de Tunisie, d'Éthiopie et du Soudan (espèce indéterminée) [1–3, 6, 11–13, 17, 22, 23]. Apomorphies : les quatre dents antérieures prémaxillaires sont alignées transversalement (en arrondi chez *Stolokrosuchus*), entre les foromens des deux premières dents mandibulaires, les prémaxillaires sont très élargis aux dents 3–4, le rostre est plus court et plus large, la table crânienne, l'espace interorbitaire et les fosses temporales sont plus larges. D'autres caractères homoplasiques sont donnés ; certains de ceux de la mandibule sont examinés et comparés [18]. Par comparaison avec les autres formes, la région basicranienne postérieure montre la réalisation apparemment homoplasique ou synapomorphique de caractères, mais, en fait, avec des particularités pour chacune dans le détail des éléments pour l'évolution du basisphénoïde, du basioccipital, des exoccipitaux et de la place des tubes et foromens d'Eustache. L'appartenance de *Stolokrosuchus* aux Peirosauridae (sensu [10]) est écartée pour ces points, comme pour la présence d'une prolongation des maxillaires jusqu'au foramen incisif, non homologue [9], et pour d'autres caractères additifs. *Stolokrosuchus* apparaît plus ou moins progressif qu'*Elosuchus*. Ses particularités sont envisagées et celle de la crête dorsale du carré est mise en doute [5]. Références sur les genres comparés in [8–10, 14, 18, 20, 21, 24]. Les deux genres sont d'eau douce.

### 2.2. *Elosuchus cherifiensis* (Lavocat, 1955)

Synonymie : *Thoracosuchus cherifiensis* Lavocat, 1955 [17] : 340. Localité type: la Gara Sba, Hamada des Kem-Kem, Sud du Maroc [15, 16]. L'espèce est connue aussi en Algérie (Gara Samani) [3, 7 (Fig. 7), 13]. Âge : Albien supérieur jusqu'à la transgression cénomaniennne. Matériel :

lectotype, MNHN, MRS 340–25, un basioccipital avec fragments d'os adjacents [17: 338] (Fig. 1I et J, Fig. 2J) Le reste du syntype (MRS 340) : 59 pièces, la plupart d'un même individu, certaines décrites par Lavocat [17] et figurées ici (Fig. 1F, H et M, avec d'autres, Fig. 1G et K–N) [2]. Autre matériel du Maroc : Gara Sba (coll. Lavocat) : environ 200 fragments, dont ceux figurés (Fig. 1D, Fig. 2I, K et L) ; d'ailleurs, au Maroc (Guir-Kem Kem), environ 200 spécimens (coll. Lavocat), dont ceux représentés sur la Fig. 1O, P, T et U et sur la Fig. 2G, et environ 100 d'autres collections, d'Erfoud (Fectay-Bidaut, MNHN) et de Taouz (Escuillé) : restes de crânes (dont un crâne presque complet), de mandibules (Fig. 2D–F), dents, vertèbres amphicoeles, plaques, os des membres ; d'Algérie, Gara Samani, coll. MNHN, plusieurs centaines de pièces, dont un crâne (Fig. 1A–C et Fig. 2A, B, Q, R, S, V et W) [3 (Fig. 1)] et des parties de mandibules (Fig. 2C et H). Apomorphies : bord antérieur prémaxillaire plus arrondi et plus long, en avant de la narine externe que chez *E. felixi* n. sp. Dix-huit dents maxillaires, 23 dents par dentaire. Bord antérieur mandibulaire élargi aux dents 2–3, en spatule arrondie. Splénial contactant la rangée dentaire postérieure. Dents costulées, crénelées en réseau à l'apex, à carène plate ou à « faux » festons chez la jeune dent [20].

### 2.3. *Elosuchus felixi* n. sp.

Dédiée à Albert-Félix de Lapparent, inventeur du site, In Abangarit, Tamesna, Niger, Albien supérieur jusqu'à la transgression cénomaniennne [11, 12]. Holotype : MNHN INA 25, dentaire gauche avec splénial, Fig. 2, M [2 (pl. 12, 3)] et tout ou partie de 50 fragments, de prémaxillaires avec partie nasale [2 (pl. 11, 2–3)], d'autres restes de mandibules (Fig. 1N) [2 (pl. 12, 1–2)], de rostre, dents, plaques, vertèbres amphicoeles [2 (pl. 12, 7–15, pl. 12, 1–11, pl. 12, 4–6)] (Fig. 2O–Q). Apomorphies : partie prémaxillaire antérieure à la narine courte et presque verticale, symphyse mandibulaire peu élargie, même chez l'adulte, à la dent 4, et étrécie en avant, 19 dents par dentaire. Mandibule plus robuste et plus sinueuse en vue latérale que chez *E. cherifiensis*.

## 3. Discussion

Des résultats préliminaires sont donnés d'après l'examen d'environ 60 genres de crocodiles et des phylogénies des crocodiles ([8, 14, 21, 24] et références incluses). *Stolokrosuchus* Larsson & Gado [14, 21], premier longirostre mésosuchien non tubulaire décrit, a été rapproché des Peirosauridae argentins brévirostrés [10], les longirostres à rostre tubulaire étant généralement regroupés par ailleurs, du fait de la tubularité et en fonction du niveau évolutif. Les caractères des analyses phylogénétiques sont insuffisamment définis : les clades se révèlent ainsi être des grades. Les longirostres sont trop spécialisés par rapport aux brévirostrés pour qu'on puisse établir des parentés entre eux. Grâce à l'emploi de plusieurs taxons par familles de longirostres et l'utilisation de caractères plus précis pour chacun, les synapomorphies les

plus importantes des familles sont données pour les Thalattosuchia, méso-suchiens longirostres très primitifs (groupe éventuellement monophylétique), les Teleosauridae et les Metriorhynchidae (premier grade), les méso-suchiens progressifs – les Pholidosauridae (deuxième grade), les Elosuchidae

n. fam. et les Dyrosauridae (troisième grade proche du précédent) – partageant de nombreux caractères homoplasiques ou faussement homoplasiques. À défaut de synapomorphies, les groupes de crocodiles, brévirostrés compris, doivent être placés en irrésolution les uns par rapport aux autres.

## 1. Introduction

When the ‘Lavocat collection’ was given to the ‘Museum national d’histoire naturelle’ of Paris and subsequently registered, the recovered type specimen of *Thoracosaurus cherifiensis* Lavocat, 1955 [17] revealed to be conform to the undefined form from the Gara Samani, Algeria [3] and also to that from Morocco and Niger, previously described as ‘*Eleiosuchus africanus*’ in Broin, 1965 (unpublished) [2], late Lower Cretaceous. The genus is not the Eusuchian *Thoracosaurus*, but a new ‘mesosuchian’ genus, *Elosuchus*, with two recognised species. A new family is given to this genus along with *Stolokrosuchus lapparenti* Larsson & Gado, 2000 [14], from the Early Cretaceous from Niger. The latter does not belong to the Argentine Peirosauridae from the Late Cretaceous [10]. Both Elosuchidae are continental fluviatile forms.

## 2. Systematics

Crocodylia Gmelin, 1788

Elosuchidae n.f.

**Etymology.** From the genus name *Elosuchus* n. g.

**Type genus and species.** *E. cherifiensis* (Lavocat, 1955).

**Distribution and age.** Cretaceous, northern part of Africa. *Elosuchus* n. g., late part of the Upper ‘Continental intercalaire’ of Sahara, Late Albian to the Cenomanian transgression, from Algeria, Niger, Morocco, Ethiopia, Sudan. *Stolokrosuchus lapparenti* Larsson & Gado, 2000 [14], Lower Cretaceous (Late Aptian), lower part of the Upper ‘Continental intercalaire’, Gadoufaoua area, Niger.

**Diagnosis and comparisons.** Apomorphies: premaxillaries with two teeth before and between the two first mandibular teeth, elongated before their narrow basis, which prolongs the narrowed rostrum, elongated and widened before the narrowed anterior border; festoons around the teeth 2–3 and 4–5, wider space between teeth 1 to 10–12 than between the posterior teeth. Other characters: Longirostrine platyrostral–*Tomistoma* type (undulating), ‘mesosuchian’ large forms (skull from

50 cm to more than 1 m long), with external nare in a dorsoanterior position, slightly anteriorly inclined, long nasals up to the nare, maxillary teeth 4–5 broadened and 10–12 slightly broadened; 5 premaxillary teeth, at least 17 maxillary teeth; trapezo-rectangular wider than long skull table, orbitae approximately as long as supratemporal fenestrae and both moderate, oval jugal bar section; pits, ridges and vermiculations more (rostrum) or less (table) elongated or marked. Possibly shared by *Stolokrosuchus* and *Elosuchus* are the imbricated dentary teeth 4 to 15, with the corresponding maxillary teeth, the other dentary teeth being primitively medial with respect to the corresponding upper teeth. Elosuchidae have an undulating rostrum as the Eusuchian (i.e. with pterygoidian choanae, procoelous vertebrae, etc.) *Tomistoma* and many brevirostrines, while most of the longirostrines have a tubular rostrum, such as the Eusuchians *Gavialis* and *Thoracosaurus* and the ‘mesosuchians’ Pholidosauridae, including *Sarcosuchus imperator* Broin & Taquet, 1966 [4, 13, 21, 22], known from the Late Aptian of Niger (Gadoufaoua with *Stolokrosuchus*), Algeria (Aoulef area) and Tunisia (Remada Kamboute area), the Thalattosuchia and the Dyrosauridae. Possible familial apomorphy: preserved in *E. cherifiensis* (Fig. 2A), hypothesised for *Stolokrosuchus* from the original drawings, the flat palate (primitively prolonged up to the orbitae) is apomorphically depressed on each side of the ventral part of the palatine air ducts of the secondary palate, producing a ‘elosuchid’ fossa in ventral view.

The superposed sinusal medial chambers and air ducts are laterally enclosed, separated from the lateral acrian sinusal chambers up to the back by a complete bony wall, medially sinuous in two circles: a dorsal division, toward the middle, forms two dorsal dilata-tions of the inner cavity, particularly wide, medially open on each side of the soft septum descending from the domed frontal ventral side (medially roofing the olfactive nerves) and joining the vomer (ventrally separating the air ducts up to the choanae); the posterior dilatation constitutes a rounded fossa at the top of the prefrontal pillar. A prefronto-lachrymal vertical wall, posteriorly limiting the prefrontal fossa just below the front of the orbitae, partly encloses the cavity posteriorly (as in *Dyrosaurus*, known from a Moroccan specimen, which shows a wider and higher concave

lacrimal part); the cavity opens medioposteriorly and was closed by a soft septum in the living, beside the prefrontal pillar. The lacrimal chamber is laterally isolated, communicating anteriorly with the posteriorly depressed sinusal chamber. The prefrontal fossa may exist in other fossil crocodiles (most of them are unprepared) and, in extants, it is either very weak to variably strong (*Alligator*, *Crocodylus*, *Osteolaemus*, *Caiman*), sometimes with a lowered prefrontal wall (*Caiman*) but it is not enclosed anterolaterally and not as much dilated and the sinusal chambers are only anteriorly separated by bone. In *Sarcosuchus*, there is no prefrontal fossa, the sinusal chambers are not posteriorly separated by bone; they widely open posteriorly, as in the *Thalattosuchia* [9] and in extants, below the prefronto-lacrimal border, thickened in *Sarcosuchus* but not lowered in a vertical wall. In *Elosuchus*, a sulcus below the postorbital indicates that the quadrate-laterosphenoid contact was made by the quadrate cartilagineous extremity as in *Sarcosuchus* (unknown in *Dyrosaurus*). The elbow, which is situated on the anterior orbital border (which gave the name to *Stolokrosuchus*), and which is laterally followed by a short smooth part, is a primitive character compared to the primitive brevirostrine ‘mesosuchians’. It also occurs in *Sarcosuchus*, in a weaker condition on a more elevated border. The elbow is variably shaped in several other forms. See references on genera in [4, 8–10, 14, 18, 21, 22, 24].

Based on characters found in *Elosuchus* characters (partly hypothesised for *Stolokrosuchus*), it is stated

that the Elosuchidae belong to a grade corresponding to ‘Mesosuchia’ auctorum (i.e. with palatino-pterygoidian choanae, amphicoelous vertebrae etc.). They are progressive mesosuchians as *Dyrosauridae*, *Pholidosauridae* and several brevirostrines in various degrees, due to homoplastic characters: antorbital fenestra reduced to a depression, moderately arched rostrum, heterodonty in relative mensurations (diameter and height) conical teeth which are posteriorly shorter and not serrated (Fig. 1U–W), although newly grown teeth possibly have a false serration (Fig. 1T) [20], frontal weakly contributing to the supratemporal fenestrae, moderate inner choanae, which are well posterior with respect to the posterior rear of the palatine fenestrae, interiorised postorbital-jugal pillar, reduced basisphenoid to a transversal bar, thick wide ventral border of the verticalised exoccipitals–basisoccipital (but differently situated and related with the basisphenoid in both genera (see below) etc. (see Figs. 1 and 2) [8]. Other derived characters, probably familial (partly known in *Stolokrosuchus*) and homoplastic: rounded and relatively narrow edge of the anterior border of the inner choanae, (which are however here primitively as deep all along and completely divided), anteriorly and posteriorly elongated ectopterygoids and elongated pterygoids all along their width, pterygoid wings not much curved upward and with thickened lateral border.

## 2.1. *Elosuchus* n. g.

**Etymology.** From the Greek *Elos*, swamp, and *soukos*, crocodile.

Fig. 1. *Elosuchus* n. g. *cherifiensis* (Lavocat, 1955), late Lower Cretaceous, MNHN coll. Gara Samani: **A, B, C**, SAM 129, skull, posterior, dorsal and ventral views. Gara Sba; MRS: **D, E**, 334, right premaxillary, ventral and dorsal views; syntypes (lectotype, paralectotypes): **F**, 340–1, fronto-parieto-postorbital parts, dorsal view; **G**, 340–11, left postorbital-squamosal part, dorsal view; **H**, 340–7, rostrum with posterior part of nasals and adjacent maxillary parts, dorsal view; **I, J** (lectotype), 340–25, basioccipital with exoccipital, basisphenoid and pterygoid parts, posterior and dorsal views; **K**, 340–12, left jugal bar part, lateral view; **L**, 340–32, right squamosal part, lateral view; **M**, 340–2, ventral maxillaries between teeth 4 to 10 with the suture with the palatines, ventral view; **N**, 340–30, right quadratojugal, dorsal view. Tabroumit; **O, P**, MRS 1112, young grown adult tooth, medial and anterior or posterior view. Gara Samani, SAM 129, from the skull: **Q**, left maxillary tooth 10, posterior view; **R, S**, right maxillary tooth 2, anterior and medial views. Guir, MRS 3107, young grown tooth: **T**, false serrations on the carina, at mid-height, and costulations,  $\times 30$ ; **U**, anastomosed ridges and flat carina at the apex,  $\times 30$ . Gara Samani, SAM 129, from the skull: **V**, maxillary left tooth 10, detail of the apex, anastomosed ridges and flat carina,  $\times 7$ ; **W**, maxillary right tooth 2, detail on the costulations,  $\times 10$ .

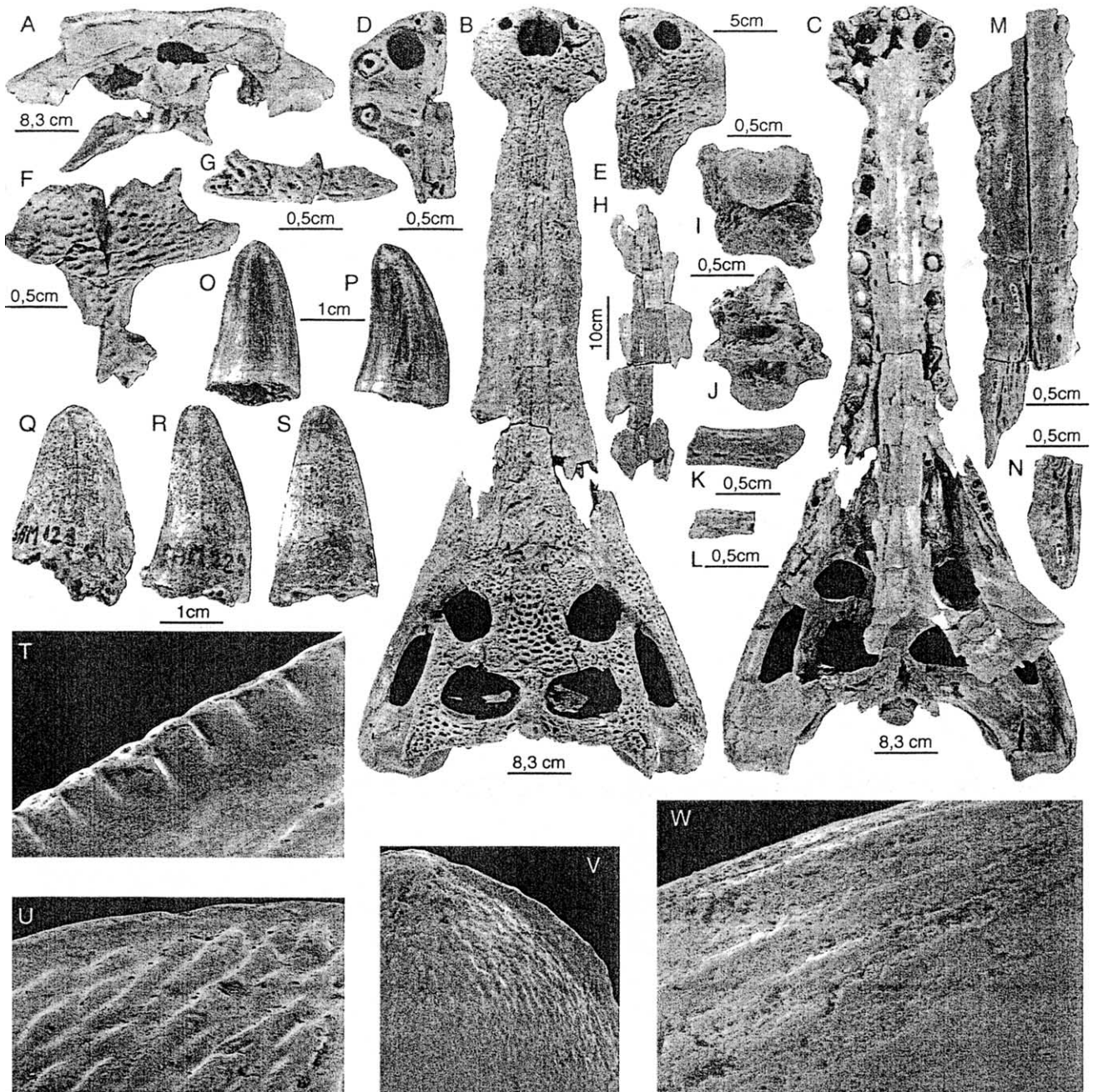
Fig. 1. *Elosuchus* n. g. *cherifiensis* (Lavocat, 1955), Crétacé inférieur terminal, coll. MNHN. Gara Samani : **A, B, C**, SAM 129, crâne, vues postérieure, dorsale et ventrale. Gara Sba ; MRS : **D, E**, 334, prémaxillaire droit, vues ventrale et dorsale ; syntypes (lectotype, paralectotypes) : **F**, 340–1, fragment fronto-pariétéo-postorbitaire, vue dorsale ; **G**, 340–11, fragment postorbital-squamosal gauche, vue dorsale ; **H**, 340–7, partie rostrale avec partie postérieure des nasaux et parties adjacentes maxillaires, vue dorsale ; **I, J** (lectotype), 340–25, basioccipital avec parties d'exoccipitales, basisphénoïde et ptérygoïdes, vues postérieure et dorsale ; **K**, 340–12, fragment de barre jugale gauche, vue latérale ; **L**, 340–32, fragment de squamosal droit, vue latérale ; **M**, 340–2, plancher maxillaire entre les dents 4 à 10 avec la suture avec les palatins, vue ventrale ; **N**, 340–30, quadratojugal droit, vue dorsale. Tabroumit ; **O, P**, MRS 1112, dent nouvelle d'adulte, vues médiale et antérieure ou postérieure. Gara Samani, SAM 129, extraites du crâne : **Q**, dent maxillaire 10 gauche, vue postérieure ; **R, S**, dent maxillaire 2 droite, vues antérieure et médiale. Guir, MRS 3107, dent nouvelle d'adulte : **T**, festons de fausse zipodontie sur le bord de la carène à mi-hauteur de la dent et costulations,  $\times 30$  ; **U**, crêtes anastomosées et carène plate à l'apex,  $\times 30$ . Gara Samani, SAM 129, extraites du crâne : **V**, dent maxillaire 10 gauche, détail de l'apex avec crêtes anastomosées et carène plate,  $\times 7$  ; **W**, dent maxillaire 2 droite, détail des costulations,  $\times 10$ .

**Type species.** *Thoracosaurus cherifiensis* Lavocat, 1955 [19]: 340.

**Referred species.** *E. cherifiensis* (Lavocat, 1955), *E. felixi* n. sp.

**Distribution and age.** Hamadas of Kem Kem and Guir, South Morocco [17]. Algeria: La Gara Samani, Oued Boudjihane, Timimoun, others; Tunisia; northern Niger; Ethiopia; see turtles localities in [12]. Late part of the Upper ‘Continental intercalaire’ of Sahara, late Early Cretaceous (Late Albian) to the base of the Late Cretaceous (prior to the Cenomanian transgression) [1–3, 6, 7, 11–13, 17, 21, 23].

**Diagnosis and comparisons.** Apomorphies: the four premaxillary teeth, which are situated before and between the foramina of the two first mandibular teeth lay in a transversal line (instead of curved in *Stolokrosuchus*); rounded premaxillaries much widened, more at the teeth 3–4 (instead of 4) beyond their basis and the anteriorly narrowed long rostrum. Wider and shorter rostrum with more space between the anterior maxillary teeth and relatively wider skull table with wider interorbital space and wider supratemporal fenestrae with respect to *Stolokrosuchus*. Other characters: undivided nares; nasals contacting the nares on a narrow



width or not or partly dorsally covered by the premaxillaries; mandibular symphysis 13–16 teeth long, splenial participation: 6 teeth long.

Characters possibly shared with *Stolokrosuchus* (unpreserved): rectangular dorsal osteoderms (less wide than in pholidosaurids), arranged in two rows, with a flat straight anterior face and strong lateral keels (less lateral than in *Sarcosuchus*) and without anterolateral spur; complete ventral armour of polygonal plates, amphicoelous vertebrae. In *Elosuchus*, as in *Dyrosaurus* (known from the Morocco specimen), there is an anterior post-symphysal foramen in each splenial, leading to the lateral Meckel canal. This becomes medial two teeth after, between the splenials and between the dentaries, and it finishes before the extremity; there is no median foramen at the posterior symphysis border as in the Eusuchia. In *Sarcosuchus*, the anterior splenial foramina are very close, at the symphysis posterior border, and reach the lateral Meckel canals inside the

symphysis (probably also in *Thalattosuchia*). In *Gavial* and *Tomistoma*, a median foramen (double in the former) opens on a medial canal, which receives the lateral Meckel canals a little forward in the symphysis (more forward in *Tomistoma* ([18, Fig. 5]). In Eusuchians without a splenial symphysis, the lateral canals finish before the posterior symphysis border and the medial Meckel canal is either very short in the back of the symphysis of the short snouted forms, or long in *Crocodylus cataphractus*. In *E. cherifiensis*, the dentary is externally prolonged below the angular, and along the splenial medially, and beyond the exterior mandibular fenestra. The articular is well curved upward, slightly medially depressed, differently and not as much as in the dyrosaurids.

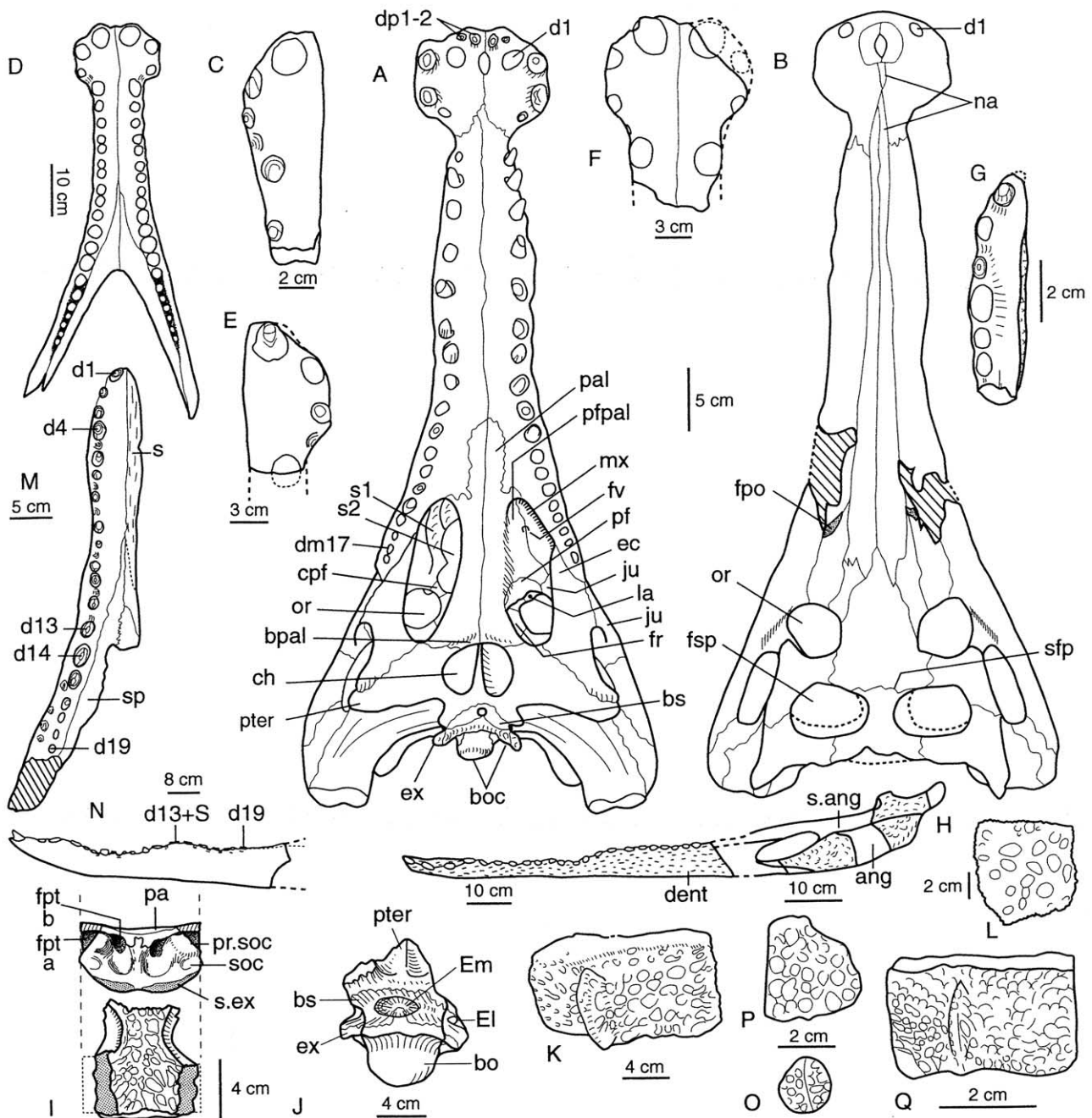
*Stolokrosuchus* differs from *Elosuchus* by the nearly completely divided nare (primitive or reversive division?), the narrower supratemporal fenestrae, not prolonged postorbital angle, narrower and more elongated

Fig. 2. *Elosuchus* n. g. *cherifiensis* (Lavocat, 1955), late Lower Cretaceous, Gara Samani (MNHN coll., SAM), Morocco (MNHN, MRS; Escuillé coll., E): **A, B**, SAM 129, skull, ventral and dorsal views; the floor of the 'elosuchid' palatal fossa (pfpal) is reconstructed with the help of E 1, from Taouz. **C**, SAM 141, dentary, part of left anterior symphysis. Taouz area: **D**, E 43, dentaries with splenials; **E**, E 45, dentary, part of right anterior symphysis; **F**, E 44, dentaries, anterior symphysis, dorsal views. Taouz, **G**, MRS 330, dentary, part of left anterior symphysis of a young, dorsal view. **H**, reconstructed lower jaw, from the dentary E 43 (Taouz), the angulo-splenial part SAM 138 (Gara Samani) and the angulo-articular part SAM 137–157 (Gara Samani), left lateral view. Gara Sba, MRS: **I**, 336, partial parietal, posterior and dorsal views; **J**, 340–25 (lectotype), basioccipital with pterygoid, basisphenoid and exoccipital parts, dorsal view; **K**, 339, dorsal osteoderm, dorsal view; **L**, 3100, ventral osteoderm, dorsal view. *Elosuchus felixi* n. sp., late Early Cretaceous, In Abangarit (Niger), MNHN, INA-; **M**, holotype, 25, left dentary and partial splenials, dorsal view; **N**, 21, right dentary-partial corresponding splenial part transposed in left view to compare with Fig. 1H; **O**, 41, nugal osteoderm; **P**, 40, ventral osteoderm; **Q**, 38, dorsal osteoderm, dorsal view. ang, angular; bo, basioccipital; bpal, rounded anterior choanal border; bs, basisphenoid; ch, choanae; cpf, prefrontal vertical wall; dent, dentary; d1, mandibular tooth 1 or its foramen in the premaxillary; dm17, maxillary tooth 17; dp 1–2, premaxillary teeth 1 and 2; d4, d13, d14, d19, mandibular teeth 4, 13, 14, 19; d13+S, mandibular tooth 13 and symphysis posterior limit; ec, ectopterygoid; Em, El, medial, lateral Eustachian foramen; ex, exoccipital; fpo, antorbital fenestra; fpta, fptb, posttemporal fenestrae; fr, frontal; fsp, supratemporal fenestra; fv, vascular foramen; ju, jugal; la, lachrymal foramen; mx, maxillary; na, nasal; or, orbit; pa, parietal; pal, palatine; pf, prefrontal; pfpal, reconstructed floor of the depressed 'elosuchid' palatal fossa; pter, pterygoid; s. ang, surangular; s.ex, supraoccipital-exoccipital suture; soc, supraoccipital; sp, splenial; s1, s2, maxillary lateral and medial sinus chambers in the roof of the maxillary, above and medially to the "elosuchid" fossa; sfp, fronto-parietal suture.

Fig. 2. *Elosuchus* n. g. *cherifiensis* (Lavocat, 1955), Crétacé inférieur terminal, Gara Samani (coll. MNHN, SAM), Maroc (MNHN, MRS; coll. Escuillé, E) : **A, B**, SAM 129, crâne, vues ventrale et dorsale ; le plancher de la fosse « élosuchienne » palatale (pfpal) est reconstruit à l'aide du crâne E 1, Taouz. **C**, SAM 141, partie antérieure symphysaire du dentaire gauche. Taouz : **D**, E 43, dentaires avec spléniaux ; **E**, E 45, partie antérieure symphysaire de dentaire droit ; **F**, E 44, partie antérieure symphysaire des dentaires, vues dorsales. Taouz, **G**, MRS 330, partie antérieure symphysaire de dentaire gauche d'un jeune, vue dorsale. **H**, mandibule reconstruite à l'aide des dentaires E 43 (Taouz), l'angulaire-splénial partiel SAM 138 (Gara Samani) et le fragment angulo-articulaire SAM 137–157 (Gara Samani), vue latérale gauche. Gara Sba, MRS : **I**, 336, pariétal partiel, vues postérieure et dorsale ; **J**, 340–25 (lectotype), basioccipital avec parties de ptérygoïde, basisphénoïde et exoccipital, vue dorsale ; **K**, 339, ostéoderme dorsal, vue dorsale ; **L**, 3100, ostéoderme ventral, vue dorsale. *Elosuchus felixi* n. sp., Crétacé inférieur terminal, In Abangarit (Niger), coll. MNHN, INA-, **M**, holotype, 25, dentaire gauche et spléniaux partiels, vue dorsale ; **N**, 21, dentaire droit transposé en vue gauche pour comparer avec la Fig. 1H ; **O**, 41, ostéoderme nugal ; **P**, 40, ostéoderme ventral ; **Q**, 38, ostéoderme dorsal, vue dorsale. ang, angulaire ; bo, basioccipital ; bpal, bord palatin antérieur arrondi de la choane ; bs, basisphénoïde ; ch, choane ; cpf, cloison postérieure préfrontale verticale ; dent, dentaire ; d1, dent mandibulaire 1 et son foramen dans le prémaxillaire ; dm17, dent maxillaire 17 ; dp 1–2, dents prémaxillaires 1 et 2 ; d4, d13, d14, d19, dents mandibulaires 4, 13, 14, 19 ; d13+S, dent mandibulaire 13 et limite postérieure de la symphyse ; ec, ectoptérygoïde ; ex, exoccipital ; fpo, fenêtre antorbitaire ; fpta, fptb, fosses post-temporales ; fr, frontal ; fsp, fosse supratemporale ; fv, foramen vasculaire ; ju, jugal ; la, foramen lacrymal ; mx, maxillaire ; na, nasal ; or, orbite ; pa, pariétal ; pal, palatin ; pf, préfrontal ; pfpal, plancher reconstruit de la fosse palatine « élosuchienne » déprimée ; pter, ptérygoïde ; s. ang, surangulaire ; s.ex, suture supraoccipital-exoccipital ; soc, supraoccipital ; sp, splénial ; s1, s2, chambres sinuales maxillaires latérale et médiale, sous le toit maxillaire, au-dessus de et médialement à la fosse palatine « élosuchienne » ; sfp, suture fronto-pariétale.

rostrum, slightly compressed teeth, ventrally and medially protruding maxillaries up to the foramen incisivum (which is longer anteriorly) in a narrow strip and not in a wide and short triangle as in *Peirosaurus* [10]: it is not homologous and therefore not a synapomorphy; an incomplete protrusion in a triangle exists in *E. cheri-fiensis* and in various taxa (*Dyrosaurus* and *Metriorhynchidae*), and in an anteriorly more rounded line in *Teleosauridae* ([9] and MNHN coll.) – foramen incisivum not present in *Thalattosuchia* –; there is not even a protrusion tendency in *E. felixi* n. sp. *Stolokrosuchus* is

also progressive by the dorsally very elongated premaxillaries, the verticalised basisphenoid and the more elevated basioccipital and exoccipitals with respect to the pterygoids with the thicker ventral part of the exoccipitals (see below) – unknown in *E. felixi* n. sp. *Stolokrosuchus* also differs by the dorsal projection on the posterior extremity of the quadrate (which could be similar to that of *Trematochampsia taqueti* Buffetaut, 1974 and *Libycosuchus* sp. in [5]). As in *Dyrosaurus*, the descending process of the prefrontal are firmly united with the palatines, while it is united together



with the palatines and pterygoids in *Elosuchus* and in *Sarcosuchus*.

In *E. cherifiensis*, the ventral border of the basioccipital and the adjacent lowered exoccipital extremities are thick, with a thin basisphenoid participation on each side, which forms a ventrally thickened wide collar (arc of a circle posteriorly open, Fig. 1C, I and J, Fig. 2A, J) at the basal level of the choanae, just behind the remaining part of the basisphenoid, ventrally reduced to a transversal groove containing the Eustachian foramina on the same level. In *Stolokrosuchus*, the thickened ventral border of the basioccipital, the posterior border of the basisphenoid and the median Eustachian foramen are elevated, posteriorly to the much reduced in length and thin anterior border of the basisphenoid, which becomes vertical, posteriorly facing, and itself elevated with respect to the choanae. The exoccipitals are laterally more elevated and more thickened. In brevirostrine mesosuchians, such as *Notosuchus* and ‘*Araripesuchus patagonicus*’ Ortega et al., 2000 [19], the posterior face of the wide basioccipital and adjacent exoccipitals are posteriorly oblique, descending forward toward the base of the palate (level of the choanae) with a thin suture with the basisphenoid in a slightly rounded transversal line, the exoccipitals being higher than the basioccipital; there is a longitudinal median crest on the lower part of the basioccipital; in front of the basioccipital, the basisphenoid is largely exposed ventrally on the palate, with the Eustachian foramina posteriorly. From this primitive condition, which is approximately that of the very juvenile *Caiman*, each element can evolve with variations (which play a role in the muscle attachment) according to the taxa, eventually depending of the longirostry and partly ontogenetically. Evolutionary variations with respect to the basisphenoid (ventral reduction in width and length, verticalisation, elevation), the exoccipitals (narrowing or ventral widening, further elevation, or lowering with variable participation to the ventral border), the basioccipital (verticalisation with basisphenoid suture becoming a thickened ventral border, elevation, widening or narrowing); the formation of a median basioccipital sulcus (weak or accentuated) and other variations (sinuosity of the ventral outline collar, accentuated basioccipital crest etc.). A collar similar to that of *Elosuchus*, but slightly slender, exists in *Brillianceausuchus* Michard et al., 1990 and *Crocodylimus robustus* Gervais, 1873 (which cannot be placed in the Eusuchians or the Atoposauridae), while that of the Pholidosauridae is thick, but medially thin, with a slight median sulcus; there is a deep median sulcus in the short and uncrested basioccipital of *Gavialis* and *Thalattosuchia* producing the homoplastic ‘pendulous

tubera’. These are slender and more longitudinal in the *Thalattosuchia*, behind a largely ventrally exposed basisphenoid and a basioccipital that is not verticalised (the basisphenoid is reduced and the basioccipital are verticalised in all the other Eusuchians). In *Dyrosaurus*, the basisphenoid is ventrally reduced, the ventral basioccipital border is narrow and thickened, medially thinner for the median Eustachian foramen, and the exoccipitals are less lowered; there is a reduction of the choanal medial crest, an elevation together of the posterior border of the choanae and basisphenoid and a sulcus between the choanae and the basisphenoid is present. *Tomistoma* differs from the latter by the slightly elevated basioccipital and by the basisphenoid and posterior border of the choanae that are not elevated. The Eustachian lateral tubes are in a groove, more or less laterally closed in the above-mentioned longirostrine forms, except in the Pholidosauridae, where they are well enclosed between the pterygoid and the basioccipital (possible apomorphy). The lateral Eustachian foramina are elevated or not with the exoccipitals according to the taxa. *Thoracosaurus* has a hardly thickened basioccipital collar, medially basal at the Eustachian median foramen and choanae level, relatively narrow, with high exoccipitals similar to *Diplocynodon*. The basisphenoid verticalisation and elevation of *Stolokrosuchus* recall that of ‘*Sebecus querejazus*’ Buffetaut & Marshall, 1991 and *Lomasuchus* Gasparini et al. 1991 [10], which, however, have a basioccipital thinner border (differently in both). The various verticalisations and elevations occurred by homoplasy with *Stolokrosuchus*, which is supported by other characters (teeth, rostrum, palate, choanae, etc.).

## 2.2. *Elosuchus cherifiensis* Lavocat, 1955

**Synonymy.** *Thoracosuchus cherifiensis* Lavocat, 1955 [17]: 340.

**Type locality and age.** Collected by R. Lavocat in 1951 at the bottom of the northern side of the ‘Gara Sba’ (or southwestern ‘Signal Chute’ of Kem-Kem, see [15]), Hamada of Kem-Kem, southern Morocco, close to the type locality of the dinosaur *Rebbachisaurus garasbae* Lavocat, 1954b [16], from the southern side of the Gara Sba. Late Albian–base of Cenomanian prior to the transgression [1, 2, 13, 17].

**Distribution and age.** Morocco (Kem-Kem, Guir) from base to upper levels. Algeria (Gara Samani), lower sands [7 (Fig. 7)]. Age: as in the type locality.

**Material.** MNHN MRS: Lectotype: MRS 340–25, basioccipital with exoccipital, basisphenoid and pterygoid small parts, Fig. 1I and J, Fig. 2J [17]: 338. Syntype (lectotype, paralectotypes) MRS 340: 59 pieces, collected together on a restricted area, most of which



probably belong to the same individual, with three undetermined fragments. Described specimens in this order by Lavocat [17]: 340–25 (lectotype) (Fig. 1I and J, Fig. 2J), 340–1, 340–7 and 340–2 (paralectotypes) (Fig. 1F, H and M). Other syntype parts (paralectotypes): 340–12, 340–32, 340–30 (Fig. 1K, L and N) [2]. Other material from Gara Sba and other localities from North to South Guir/Kem Kem (ca 250 km) (MNHN, Lavocat and Fectay-Bidaut coll., Escuillé coll., E) and from Algeria, Gara Samani (MNHN SAM), several hundreds of fragments of skull (Fig. 1I), a skull SAM 129 (Fig. 1A–C, Q, R, S, V and W) and a nearly complete skull E1, without the premaxillaries, dentaries (Fig. 2C–H), teeth and osteoderms (Fig. 1O–P, T and U, Fig. 2K and L), amphicoelous vertebrae.

**Diagnosis and comparisons.** Apomorphies: Longer rounded premaxillary dorsal border before the nare with respect to *E. felixi* n. sp. 18 maxillary teeth, 23 dentary teeth. Spatulated-rounded anterior mandibular symphysis widened at teeth 2–3, more rounded in adults. Other characters: anteriorly prolonged ornamented postorbital angle, descending above the flat external jugo-postorbital pillar face, ornamented posterior lobe of the squamosal (maybe of genus level). Larger maxillary teeth: 3–4–5 and 10–11–12 (5 and 13 in *Stolokrosuchus*). Splenial contacting the posterior tooth rows.

The postorbital angle is more or less as prolonged as in *Sarcosuchus* and *Rhabdognatus*, much less than in *Dyrosaurus*, less than in *Terminonaris*. In the three former taxa, the projection is prolonged below the angle in a forward sharp angle of the pillar and, in *Dyrosaurus*, it is engaged deep in the orbit. The forward prolongation of the angle accompanied by the downward inclination of the lateral face of the skull table was achieved, earlier, in the Teleosauridae, by the apomorphic jugo-postorbital pillar and the angle fusion. The maxillary tooth 18 may be replaced by a small rounded ossification (Fig. 1C, Fig. 2A). The anterior symphysis of a Gara Samani specimen (Fig. 2C) is less widened than in the larger specimens from Morocco (Fig. 2D–F and others). A symphysis part from Taouz (Fig. 2G) possibly belongs to a young of the species: it is more similar to the specimens from *E. felixi* n. sp. (symphysis anteriorly narrow in the adult). The other elements from Kem-Kem/Guir and Gara Samani do not indicate other variations than individual. Scanning electron micrographs (Fig. 1) of the teeth show costulations (T, W), anastomosed ridges at the apex (U, V), false serration on the lateral border of the young grown teeth (T), but flat carina at the apex (U) and all along the border in older tooth (W) [20].

### 2.3. *Elosuchus felixi* n. sp.

**Etymology.** From Albert-Félix de Lapparent, who discovered the locality and fossils.

**Type locality and age.** In Abangarit, Tamesna, Niger. Late part of the upper ‘Continental intercalaire’ of Sahara, upper level, late Early Cretaceous (Late Albian to Cenomanian transgression) [15, 16].

**Material.** Holotype: MNHN INA 25, left dentary and partial splenials (Fig. 2M) [2 (pl. 12, 3)]. Other material: among ca 50 specimens, some very fragmentary possibly belong to another small taxon. Paratypes: INA 30, premaxillaries with nasal anterior part [2 (pl. 11, 2–3)]; 11 fragments of lower jaw including a right dentary-partial left and corresponding splenial part, Fig. 2N, INA 21 [2 (pl. 12, 1–2)]; fragment of rostrum, teeth [2 (pl. 12, 7–15)], amphicoelous vertebrae including a partial cervical and dorsal column [2 (pl. 12, 1–11)], dorsal and ventral osteoderms (Fig. 2O–Q), INA 41, 40, 38[2 (pl. 12, 4–6)].

**Diagnosis.** Short nearly vertical premaxillary part before the nare. Nineteen dentary teeth. Just slightly widened symphysis at teeth 4, forward narrowed, even in the large adult. Jaw with more accentuated waves in lateral view than in *E. cherifiensis*.

## 3. Discussion

Preliminary results are given based on a comparison of over 60 taxa, from the Jurassic to the Present, either a genus with one species or genera with several species (many of them not enough preserved or described). Previous crocodile phylogenies ([8, 24] and included references) integrate longirostrine forms at the genus or family or group (such as Thalattosuchia) level. The non-Eusuchian longirostrine forms either constitute only one grouping within brevirostrines, or the Thalattosuchia are isolated in a more basal place, or even before all crocodiles. Alternative proposals integrate the Eusuchian *Gavialis* beside *Pholidosaurus*. Larsson and Gado [14] add the undulating longirostrine *Stolokrosuchus*, referring it to the Peirosauridae from Argentina [10], short snouted forms. Except for this grouping, the other mesosuchian groupings are partly based on characters produced by the longirostry in tubular longirostrine forms. Actually, the groupings do not represent clades, but grades and the families are not well individualised. The addition of several genera and species of one family and a more refined definition of the characters allow us to recognise synapomorphies within the longirostrine ‘mesosuchian’ families. The crocodile families or groups (monophyletic or not) of several families may be separated in grades. In longi-

rostrine forms: as a first grade, the Thalattosuchia group, with the Lower–Upper Jurassic marine Teleosauridae with *Teleosaurus*, *Steneosaurus*, *Machimosaurus*, and *Pelagosaurus* (downward inclined lateral border of the skull table and union of the descending postorbital angle with the jugo-postorbital pillar in a flattened widened area) and the Middle Jurassic–Early Cretaceous marine Metriorhynchidae with *Metriorhynchus*, *Geosaurus* and *Dakosaurus* (dilated prefrontal above the lachrymal, heterocerqual tail and paddle like extremities); as a second grade, the Cretaceous continental (Africa, Brazil, Europe)-littoral marine (USA) Pholidosauridae with *Pholidosaurus*, *Terminonaris* and *Sarcosuchus* (conjunction of rake shaped premaxillaries and a corresponding spatulated anterior jaw, wide rectangular dorsal osteoderms with an anteriorly rounded anterolateral spur and a very lateral keel); as a third very close grade, but clearly more progressive as a whole, the Lower (–Upper?) Cretaceous Elosuchidae n. fam., and the Late Cretaceous–Palaeogene littoral Dyrosauridae, with mainly the *Dyrosaurus*–*Congosaurus*–*Rhabdognathus* group (fused nasals, extremely developed exoccipitalo-supraoccipital protuberances, posteriorly shortened palate, anteriorly shortened pterygoids at the palatine fenestrae and drawn back posterior position of the back of the long ectopterygoids, accom-

panying the elongation of the temporal fenestrae). Each family is also characterised by relationships and proportions of the skull bones and openings. The Thalattosuchia may be considered as a monophyletic group because of the thin rounded jugal bar and the thin posterior bar of the supratemporal fenestrae: however, it could be possible that these characters are inherited from a more basal taxon and the two families basically diversified, completely apart. The temporal fenestrae are large, as in Dyrosauridae, but not similar in the three families; with the ‘pendulous tubera’ (as in gavial but differently shaped) and the short nasals not contacting the premaxillaries (as in gavial and more or less in *Thoracosaurus* spp.); they constitute equivocal characters because falsely homoplastic or homoplastic; nevertheless, the union of the two families may be considered in an early diversified line (one proposal of Clark [8]). No synapomorphies are found between the other families and between them and the Thalattosuchia. Once better defined, most of the characters appear as the different expression of evolutionary trends common to crocodiles. No synapomorphy has been found with brevirostrine groups because, besides these common trends, the longirostrine characters separate them. Actually these three families appear as diverging at the same node as many brevirostrine fossil forms, in an unresolved position.

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