A new genus for the Dipnoan species *Ceratodus tuberculatus* Tabaste, 1963

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ABSTRACT
A tooth plate of the large lungfish referred to *Ceratodus tuberculatus* Tabaste, 1963 from Kharga Oasis, Egypt, allows reconsideration of its generic status. Comparisons with fossil *Ceratodus* and living *Neoceratodus* demonstrate the generic distinction of this taxon and *Retodus* n. gen. is proposed for this large dipnoan. Tooth plates of *R. tuberculatus* n. comb. are characterised by four transverse ridges, broadly rounded crests, a reticular pattern of ridges and hollows, and large adult size. The stratigraphic time span for specimens assigned to *R. tuberculatus* n. comb. is Albian-Early Cretaceous of southern Algeria, to Campanian-Late Cretaceous of Dakhleh and Kharga Oases, Egypt, and Maastrichtian Late Cretaceous of Niger.

KEY WORDS
Dipnoi,
Retodus n. gen.,
Ceratodus tuberculatus,
Albian-Maastrichtian,
Late Cretaceous,
Egypt,
new genus.

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RÉSUMÉ
Un nouveau genre de dipneuste pour l'espèce Ceratodus tuberculatus *Tabaste, 1963.*
Une plaque dentaire bien conservée du dipneuste *Ceratodus tuberculatus* Tabaste, 1963 de l'oasis de Kharga (Égypte) permet une révision de son statut générique. Des comparaisons avec les plaques dentaires du genre fossile *Ceratodus* et celles du genre actuel *Neoceratodus* montrent des différences morphologiques significatives. En conséquence, la création du genre *Retodus* n. gen. est proposée. Les plaques dentaires de *R. tuberculatus* n. comb. sont caractérisées entre autres par quatre crêtes transversales arrondies et des spécimens adultes de grande taille. L'extension stratigraphique de *R. tuberculatus* n. comb. s'étend de l'Albien (Crétacé inférieur, sud de l'Algérie) au Campanien (Crétacé supérieur de Dakhleh et Kharga, en Égypte). Des restes connus au Niger datent du Maastrichtien (Crétacé supérieur).

MOTS CLÉS
Dipnoi,
Retodus n. gen.,
Ceratodus tuberculatus,
Albien-Maastrichtien,
Crétacé supérieur,
Égypte,
nouveau genre.

INTRODUCTION

A partial right upper (or less likely, a left lower) tooth plate of *Ceratodus tuberculatus* (Fig. 1) was retrieved from a gravel-covered terrace surface in the Piedmont below the Libyan Escarpment in the Western Desert of Egypt, north of Ain Umm Dabadib, 35 km north of Kharga City, Kharga Oasis, in New Valley (Wadi el-Gedid) Province (Fig. 2). It was collected on March 7, 1998 by Kleindienst while surveying terrace surfaces for earlier Middle Stone Age artifacts. Its provenience lies near the head of the middle terrace, of a series of three, high-elevation terraces of probable Pleistocene age (cf. Gardner 1952), *c.* 4 km north of the ruined Romano-Byzantine "fort" known as Ain Umm Dabadib. The terraces are formed on flaggy sandstones and shales, probably of the Campanian Taref Formation, of Late Cretaceous (Maastrichtian) age (El Deftar *et al.* 1978; Hermina 1990).

The specimen has no *in situ* stratigraphic context but is presumed to be a lag derived from the underlying local Campanian Baris Formation (= Qusseir Fm., Variegated Shales or "Qusseir Clastic Member"), which overlies the Taref Formation and is exposed in the Escarpment to the north (El Deftar *et al.* 1978: 61) (Fig. 1). The specimen is eroded around its margins showing its denteon structure and some supporting bone. It preserves the third and fourth ridges, with vestiges of the second, and has lost the protuberant crests (Fig. 1).

A previously recovered lower tooth plate with prearticular bone still adhering (ROM 44609) assigned to *C. tuberculatus* also derives from this formation, but some 5 km southeast of Baris, about 100 km south of Kharga City (Churcher 1995). Other fragments of *C. tuberculatus* tooth plates have been collected from the equivalent Mut Fm. in the neighbouring Dakhleh Oasis, 150 km to the west (Churcher & De Iuliis 2001).

The species *C. tuberculatus* comprises a separate genus on the basis of crest morphology and size, and is easily separable from both *Ceratodus*, the genus to which Tabaste (1963) originally assigned it, and *Neoceratodus* to which Martin (1981, 1982a, b, 1984a, b) assigned it, on these characters.

Abbreviations

Acronyms for Saharan localities that yielded dipnoan tooth plate materials are used in Martin (1984a, b) and reviewed in Churcher & De Iuliis (2001).
Those cited here are:
MNHN Muséum national d'Histoire naturelle, Paris;
ROM Royal Ontario Museum, Toronto.
HG series-Ahoggar Massif or Hoggar Mountains:

HGO West (Ouest);
HGN North (Nord);
HGS South (Sud).

TERMINOLOGY
The terminology for features of lungfish tooth plates is not consistent and we use that previously used by us (Churcher & De Iuliis 2001: 309, text-fig. 3). It is reproduced here as Figure 3.

SYSTEMATICS

Order CERATOFORMES Berg, 1937
Family CERATODONTIDAE Gill, 1872
Subfamily CERATODONTINAE Gill, 1872

Genus *Retodus* n. gen.

TYPE SPECIES. — *Ceratodus tuberculatus* Tabaste, 1963.

ETYMOLOGY. — From the Latin, *rete*, net; *-odus*, Latinised Greek -όδούς, toothlike, referring to a network of ridges on the occlusal surface of a tooth plate.

DIAGNOSIS. — The same as *Retodus tuberculatus* n. comb.

REMARKS
The new lungfish tooth plate (ROM 47638) reported here preserves features unknown in the species previously known as *Ceratodus tuberculatus* and indicates that the species cannot be referred to an already described genus. Although insufficient material of the species is known to permit a phylogenetic analysis, it is apparent that it forms a distinct clade, and thus merits generic distinction as *Retodus* n. gen.

Retodus tuberculatus (Tabaste, 1963) n. comb.

Ceratodus tuberculatus Tabaste, 1963: 444, 445, fig. 3, 448, pl. 2, figs 3, 4, pl. 3, figs 1-6, pl. 4, figs 1-3. — Cappetta 1972: 185. — Kemp 1997a: 729; 2001: 430, 434, fig. 16. — Lehman 1966: 271, fig. 27B, 291. — Martin 1984b: 233. — Schultze 1992: 192.

Neoceratodus tuberculatus – Martin 1982a: 612; 1982b: 56, 60, 61; 1984b: 225, 226, 243, fig. 44 *non* 46, 244, 245, fig. 49, 246, fig. 50, 248, 251-253, fig. 53, 257, 258. — Schaal 1984: 44-46. — Churcher & De Iuliis 2001: 305.

"*Neoceratodus*" *tuberculatus* – Churcher 1999: 64, table 2.2.

LECTOTYPE. — Mandibular tooth plate HGO 49 (Ct_2) (Tabaste 1963: pl. II, fig. 3a, b), designated by Martin (1984a: 244). (See also Fig. 4B).

REFERRED SPECIMENS. — Ct_1, Ct_3-Ct_6 (Tabaste 1963: pl. II, fig. 3a), Albian-Early Cretaceous age.
ROM 44609 (Churcher 1995: figs 2, 3), Campanian-Late Cretaceous age.
ROM 47638, probably Campanian-Late Cretaceous age. (See also Fig. 4D).

TYPE LOCALITY. — Rouaix (Algeria). Albian-Lower Cretaceous.

TYPE STRATA. — Erg Iller (Algeria) and Mt. Igdaman (Niger): Albian-Lower Cretaceous.

DIAGNOSIS. — Same for genus and species. Four ridges oriented almost transversely across the plate, concave distally (not straight) when unworn, and cross-linked by smaller lunate secondary ridges into a network of crests and hollows, best seen in the Egyptian Campanian form. Tooth plate size is considerably larger than those of coeval *Ceratodus* or *Neoceratodus*. Length 76-100 × breadth 32.0-48.5 mm.

REFERRED STRATA. — Baris and Ain Umm Dabadib, Kharga Oasis, Egypt: Baris (= Qusseir) Formation shale, Campanian-Upper Cretaceous. Dakhleh Oasis, eastern area, Egypt: Mut (= Qusseir) Formation shale, Campanian-Upper Cretaceous. Bahariya Oasis, Egypt: Bahariya Formation shale, Albian-Lower Cretaceous (probable occurrence).

DESCRIPTION AND COMPARISONS
Upper right tooth plate (Figs 1; 4)
When compared to other species placed within the genus *Neoceratodus*, the Ain Umm Dabadib fragment, representing the unworn condition of tooth plates of its taxon, does not fit easily within the previously observed tooth plate morphotypes. Compared with other dipnoan tooth plates from Saharan Africa, those of *Ceratodus africanus* (Haug, 1905) most closely resemble those of *R. tuberculatus* n. comb. in that their six or seven ridges are arranged in a poorly radiating pattern, and the central ones, i.e. nos 2 and 3, are concave distally, and are oriented approximately across the axis of the plate *fide* Tabaste (1963: pl. I, figs 2-7) and Martin (1981: pl. 1, figs 6, 12, 17, 18; 1982a: fig. 1.10), *contra* Martin (1984a: 273, figs 24 [HGN 28], 26

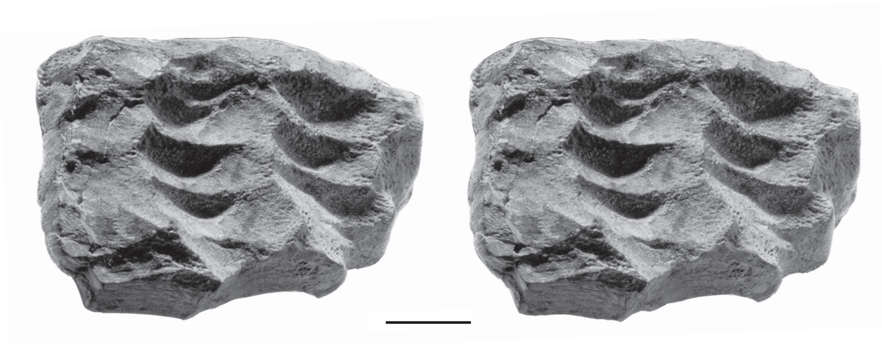

Fig. 1. — Stereoscopic image of a partial tooth plate of *Retodus tuberculatus* (Tabaste, 1963) n. comb. (ROM 47638), from the surface of a Pleistocene terrace on the Libyan Escarpment near Ain Umm Dabadib, Kharga Oasis, Wadi el-Gedid, Egypt. It is presumed to derive from the underlying Campanian Baris Formation, of Late Cretaceous (Campanian) age. Compare with those illustrated by Tabaste (1963: fig. 3, pl. II, fig. 3a, b, pl. III, figs 1, 2, 4) and Churcher (1995: fig. 2). Scale bar: 12 mm.

[HGO 7?]); 275, fig. 30 [HGN 30]) who assigns specimens from north and west of the Ahoggar Massif (Hoggar Mountains) with only four crests to *N. africanus.* (N.B. HGS 114, from In Abangarit, south of the Ahoggar ["Hoggar Sud"] is given as HGN 114 in text [Martin 1984a: 238, 241, fig. 38]). These plates fit best within *Ceratodus humei* (Priem, 1914) on the basis of size, crest orientation, and in possessing only four crests.

As *R. tuberculatus* n. comb. tooth plates have only four ridges which run almost transversely across the plate, are bowed rather than straight, may be cross linked by smaller cross ridges into a network of crests and hollows, at least in the Egyptian Campanian form, and are considerably larger than tooth plates of all African species of *Ceratodus* or *Neoceratodus*, these plates differ strongly from *Ceratodus* and *Neoceratodus*. Unobservable diagnostic characters considered by Martin (1982b) are the position of the palatine process relative to the ridges (currently unknown) and resorption at the internal angle during growth (not deducible on isolated specimens or from the material illustrated by Tabaste 1963).

Discussion

Distribution and age of Retodus tuberculatus *n. comb. and* Ceratodus humei *in the Central Sahara*

Tabaste's (1963) species *Ceratodus tuberculatus* was founded without a designated holotype on a collection of 36 specimens. Tabaste (1963: 444) states: "Presque toutes les pièces (32) rapportées à cette espèce proviennent du gisement Rouaix (Soudan). trois ont été trouvées à l'Erg Iller et une au Niger (Mt. Igdaman) où elle était accompagnée d'un échantillon de *Ceratodus humei*". This extralimital specimen of *C. humei* unfortunately is not illustrated as it is possibly its most southerly occurrence in Saharan Africa. Rouaix and Erg Iller (Ilafehr), both in southern Algeria west of Tamanrasset and the Hoggar Mountains, are exposures of Albian-Early Cretaceous age ("Crétacé inférieur continental", *fide* Tabaste 1963), and Mt. Igdaman in Niger is of Late Cretaceous ("Maastrichtien") age.

Martin (1984a: 244) lists numbers for 25 specimens of "*N.*" *tuberculatus* from Rouaix (22), and Erg Iller (3) and designates as the lectotype a lower plate (HGO 49) recorded by Tabaste (1963: pl. II, fig. 3a, b) as "Ct_2" (Fig. 4B). This appears not to be the tooth plate discussed as "Ct_1" by Tabaste. In effect, Martin designated as the lectotype a specimen that Tabaste did not consider typical (see below).

The 10 entire and six fragmentary tooth plates of *C. humei* discussed by Tabaste (1963: 443) derive from "trois zones : la dépression du Djoua [Algeria], le Sud marocain [Algeria], le Niger". All the specimens are not listed but the entire ones comprise five upper and four lower plates from Rouaix, of which a lower (Ch_1) is described and illustrated, and an upper from In Afarag also illustrated (Tabaste 1963: pl. II, figs 1, 2, respectively). The Djoua Depression lies to the east of Fort Flatters (now Bordj Omar Driss), Algeria (Fig. 2B), and

TABLE 1. — Comparative measurements of tooth plates of *Retodus tuberculatus* n. comb. from deposits at Rouaix, West Hoggar, Algeria, and Kharga Oasis, Wadi el-Gedid, Egypt. Measurements from Tabaste (1963: 444) for Ct_1 shown in parentheses with asterisks; Tabaste designates tooth plate ridges as 3-6 whereas we use 1-4; Ct_1 and Ct_2 appear confused in Tabaste's account (see text); and measurements for Ct_2, Ct_4, and Ct_7 are calculated from Tabaste's (1963) plates II, fig. 3a and III, figs 1 and 2. From its measurements, Ct_7 is a small individual. Measurements for ROM 44609 are from Churcher (1995: 846). Tabaste's specimen numbers are her published field numbers: Ct_2 is identified as HGO 49 by Martin (1984b: 244); others numbers are not equated. Measurements in mm; **e** indicates estimated values; length dimensions are minimal as specimens' extremities are broken or abraded.

	Tabaste (1963) Rouaix, Algeria				**Churcher (1995)** Kharga Oasis, Egypt	**This paper**
	Ct_1	Ct_2	Ct_4	Ct_7	ROM 44609	47638
Length of tooth plate	76*	83.3	90.0	48	100e	70-100e
Width of tooth plate	32*	33.3	48.5	22	36	34e
Distance between crests						
1 & 2		16.0	21.5	10	20	-
(3 & 4	15*)					
2 & 3		16.0	15.4	9	30	-
(4 & 5	16*)					
3 & 4		15.3	13.9	8	29	14.7
(5 & 6	12*)					

contains no *C. tuberculatus* sites. Its "gisements" are given as Lower Cretaceous by Tabaste (1963: 440). However, the figured plate from Rouaix is of Albian-Early Cretaceous age and that from In Afarag is of Maastrichtian-Late Cretaceous age. Thus the *C. humei* plate noted as associated with *R. tuberculatus* n. comb. may be from either the Early or Late Cretaceous! We therefore are concerned with the ages assigned to these materials.

MORPHOLOGY OF THE TOOTH PLATES OF *CERATODUS TUBERCULATUS*, AND IDENTITY OF THE TYPE SPECIMEN

The first tooth plate of *C. tuberculatus* discussed by Tabaste (1963: 444) is the mandibular "Ct_1 (pl. II, fig. 3)" and may be considered as the intended holotype. However, the specimen figured in "planche II, fig. 3" is identified in the legend as "Ct_2" (Tabaste 1963). Measurements of Ct_1 given by Tabaste are length 76 and width 32 mm, but measurements of Ct_2 taken from pl. II, fig. 3 give length as 83 and width as 32 mm. Tabaste (1963) gave no measurements for Ct_2. The 9.2% discrepancy in the length measurements suggests that the figured specimen is not Ct_1, as stated in the text, but Ct_2 (= HGO 49; Martin 1984a: 244), and that the Ct_1 or Ct_2 confusion may involve conflated descriptions of two specimens. Ct_1 is the first discussed by Tabaste and should be considered the lectotype for the species *tuberculatus*: the figured Ct_2 is a specimen referred to the species by Tabaste and is not described except in that it (and Ct_3) "coïncident avec cette description", i.e. it agrees with the general description also applicable to specimens Ct_4-Ct_6 (Tabaste 1963: 445). Martin (1984a), however, designated Ct_2 (HGO 49) as the lectotype for the species.

Tabaste's (1963) pl. II, fig. 3a shows a tooth plate of low relief, presumably the result of wear, with subparallel arcuate ridges and low ripples linking them approximately at right angles.

The specimen from Baris, Kharga Oasis, Egypt (ROM 44609; Churcher 1995: figs 2, 3; Fig. 4A) is a plate of about the same shape and size as Tabaste's Rouaix Ct_1 but penetrated by atypical circular conical pits arranged along the summits of the ridges (Table 1). Kemp (2001: 430, 434, fig. 16) discusses and illustrates tubercles and denteons united on the plate surface in *C. tuberculatus* where the arrangement of denteons appears similar to those in ROM 44609. She shows tubercles in HGO 52 situated on the crest of the ridge as are the pits in ROM 44609. As HGO 52 is from Early Cretaceous sediments of Rouaix and ROM 44609 is from the Late Cretaceous sediments of Kharga, Egypt, the occurrence of tubercles on the summits of the crests may be a character that is lost in Late Cretaceous "*tuberculatus*" lungfish plates. Tabaste's descriptions make no mention of it and her illustrations show no similar pits. Both specimens have well developed buccal crests although those on the Baris specimen have damaged extremities. A distal fragment from a probable left upper plate collected from the surface west of Bee's Friday Site, Dakhleh Oasis (Churcher & De Iuliis 2001) is so worn that no vestiges of ridges or crests remain. However, its size (37 wide × 35 mm broken length) indicates its probable origin from a large specimen of *Retodus tuberculatus* n. comb. Its worn condition resembles that of Ct_4 shown by Tabaste (1963: pl. III, fig. 1, distolingual shelf).

A fragmentary tooth plate of *R. tuberculatus* n. comb. was observed among the *C. africanus* tooth plates seen on the surface of Lower Cretaceous Bahariya Formation deposits during a field visit to Bahariya Oasis by Churcher in February, 2001. Thus this taxon or its genus probably existed from Early to Late Cretaceous times within the now Saharan region, if Tabaste's (1963: 440), Churcher's (1995), and Churcher & De Iuliis's (2001) observations are substantiated.

The new north Khargan specimen (ROM 47638) is unworn on the occlusal surface when compared to Tabaste's Rouaix plate Ct_2 and the Baris Formation lower plate from southern Kharga Oasis. It preserves two main ridges and crests, possibly nos 3 and 4, as on the Baris specimen, and indications of the second crest, and shows ridges and secondary cross ridges linking the main ridges in a network (Figs 1; 4D). The major crests are arcuate and oriented approximately transversely as in the Baris specimen; there is a fragment of bone adhering to the aboral surface beneath the major left hand crest (Fig. 1), and the buccal margin is sinuous with denticulations and sulci as in the Baris specimen. There is minor wear on the tooth plate where ridges on the opposing upper plate occluded.

The low cross ridges that connect the main ridges across the furrows show as two or three lunate swells in Ct_2 (= HG0 49) and Ct_4 (Fig. 4B, C, respectively), which are only indicated by shallow rises in ROM 44609 (Fig. 4A), are present as sharp-edged lunate ridges in ROM 47638 (Figs 1; 4D). The variations in the development of these secondary ridge features as seen in these specimens suggest that ROM 47638 exhibits an unworn condition and ROM 44609 a mature state of wear, with the two Rouaix specimens, Ct_2 and Ct_4, exhibiting intermediate wear states. Martin (1984b: 243, fig. 44 *non* 46) illustrates the well worn plate HGO 26 where all traces of ridges are absent and only three crests remain. ROM 47638 shows three sharp lunate cross ridges, Ct_4 two swells linking main ridges 1 and 2, and 2 and 3, and three swells joining ridges 3 and 4. In ROM 44609, the swells are poorly developed or preserved, and two or three may be discerned.

This new specimen is considered to exhibit an unworn condition of a typical plate from which those figured by Tabaste (1963: pls II, III) may represent more wear or, as the complete plates figured by Tabaste derive from a Lower Cretaceous deposit, may represent a less derived condition of unknown taxonomic status. The pitted condition of the Baris plate (Churcher 1995: fig. 2) is currently inexplicable in function or ontogeny (see below), although diagenesis or disease are possible causes. The pattern of major ridges with low connecting cross swells at present is also not amenable to functional interpretation.

The variations in size of the tooth plates (Fig. 4; Table 1) may represent stages in the progress through life of the animal, with tooth plates becoming worn flat in old age. In which case, ROM 47638 would represent a newly functional plate and ROM 44609 a well worn plate. Should this be the case, the specimens collected by Tabaste represent well worn and moderately worn plates, but do not include moderately worn or pristine specimens. Ct_7 is a complete tooth plate but of smaller size than the larger ones (Table 1) and it and Ct_8, as shown by Tabaste (1983: pl. III, figs 2, 4, respectively), probably represent wear stages of upper plates.

The mode of function of the *R. tuberculatus* n. comb. tooth plates requires some interpretation as modern lungfish have plates with radiating series of ridges which occlude with the furrows of the opposing plate and interlock labially or buccally

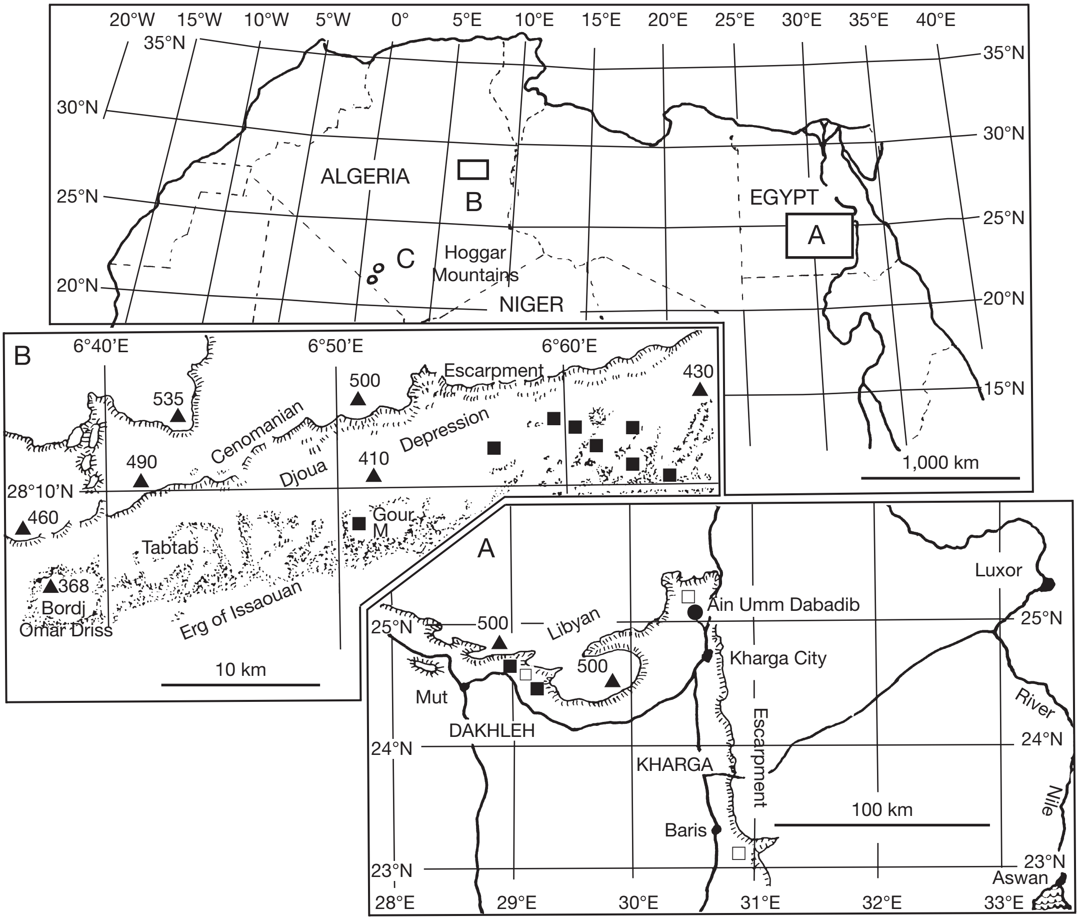

FIG. 2. — Map of North Africa showing sites from which *Ceratodus africanus* (Haug, 1905), *C. humei* (Priem, 1914), and *Retodus tuberculatus* (Tabaste, 1963) n. comb. have been recovered, with inset maps of the oases of Kharga and Dakhleh (**A**, after Vivian 1990) and the Djoua Depression (**B**, after Foureau 1904). *R. tuberculatus* n. comb. was first described from Erg Iller and Rouaix (**C**), west of the Hoggar Mountains (Ahoggar or Hoggar Massif), and from Mt. Igdaman, south of the Hoggar Mountains in Niger (Tabaste 1963). National borders as dashed lines. Escarpments in A and B hatchured, dune areas in B stippled, Ain Umm Dabadib indicated by ●, *Retodus tuberculatus* n. comb. recovery sites indicated by □ in A, *Ceratodus humei* sites by ■ in A, and *C. africanus* sites by ■ in B, and trig points by ▲ with heights in metres. In A roads and the River Nile are shown as solid lines. In B, Bordj Omar Driss (= Fort Flatters = Timassânine) lies near ▲ 368. Information on *Ceratodus* sites in A after Churcher & De Iuliis (2001).

(Kemp 2003: 520, fig. 3). The crushing actions involve an early closure when the prey is caught between the plates, followed by a closing motion with the ridges sliding past each other in a shearing action, and ending with a final crushing when an upper ridge meets the bottom of the furrow between two lower ridges. A very small "subterminal rotational grinding" motion is possible as the crests enter the locked appositional state (Kemp 1996: 18; 1998: 47), and may be provided by flexibility within the jaw joint.

In *R. tuberculatus* n. comb. the situation is different. The tooth plates' arcuate ridges basically run transversely across the plate and rotary motion is prevented by their parallel spacing. When closing, there is the early closure with the prey caught between the plates, followed by effective shearing motions when the mesial face of an upper ridge slides past

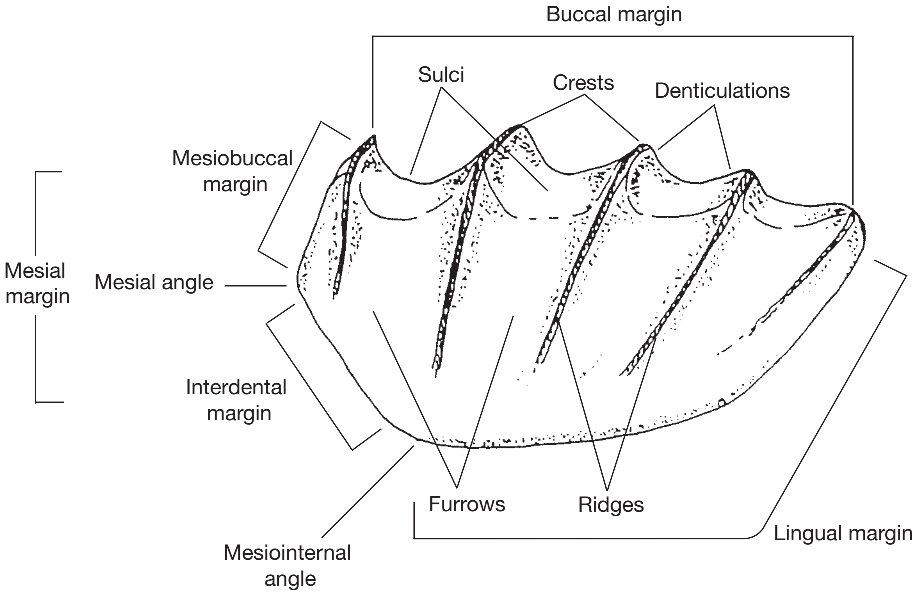

FIG. 3. — Diagram of generalised right upper dipnoan tooth plate (based on ROM 47628), showing dimensions and terminology, from Churcher & De Iuliis (2001: 309, fig. 3A).

the distal face of an opposing lower ridge, and final crushing occurs when an upper ridge meets the bottom of a lower furrow or *vice versa*. Thus a small mesial displacement occurs during occlusion as the distal faces of the lower ridges slide over the mesial faces of the upper ridges. Clearly, translational movement at the jaw joint would have been impossible if *R. tuberculatus* n. comb. possessed typical dipnoan jaw joint surfaces between Meckel's cartilage and the quadrate, and consisting of medial and lateral sockets separated by a ridge on the cartilage (e.g., as in modern *Neoceratodus* and Devonian *Dipterus*, see Jarvik 1967: pl. 1, figs 6, 8) and condyles on the quadrate. As the orientation and wear of the ridges on the tooth plates of *R. tuberculatus* n. comb. are unique within Dipnoi, it is not unreasonable to suppose that some jaw joint modification had taken place.

Previously, Churcher (1995: 847) speculated on the lack of grinding potential, concluding that shearing and crushing appeared to be the only motions that were possible. The crescentic conformation of the small linking cross ridges implies possible transverse motion with the ridges meeting in a shearing action when the plates are in full occlusion (similar to that in some mammalian herbivores). As no jaw joint of *R. tuberculatus* n. comb. has been recovered, motion, transverse or buccolingual, cannot be confirmed. As orientation of and wear on the ridges of the tooth plates of *R. tuberculatus* n. comb. are unusual within Dipnoi, some modification of the joint had probably occurred. However, if some transverse or oblique lateral motion was possible, then lateral displacement of lower plates relative to upper plates would allow the main ridges to be honed by friction, and result in a reduction of the relief of the connecting cross ridges within the valleys, both upper and lower, and make it possible that the specimens shown in Figure 4 represent a wear series. Plate HGO 26 illustrated by Martin (1984b: 243, fig. 44 *non* 46) would represent a very worn tooth plate. The angle of the ridges to the long axis of the tooth plate may reflect the angle that the plate makes to the sagittal plane; in the case of Ct_4 (Fig. 4C) *c.* 67°

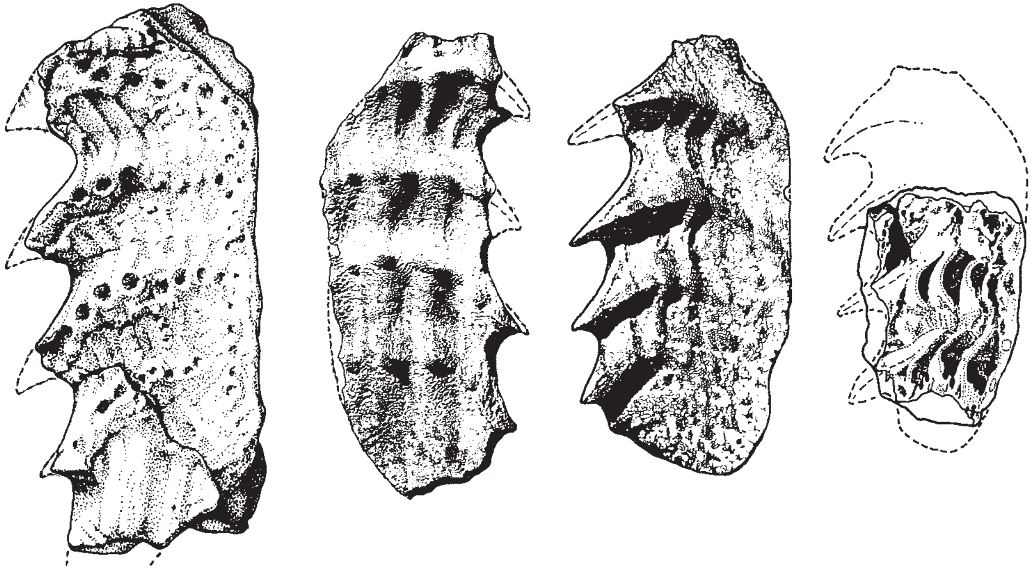

FIG. 4. — Comparisons of tooth plates of *Retodus tuberculatus* (Tabaste, 1963) n. comb.: **A**, left lower plate (ROM 44609) from Baris, Kharga Oasis, Western Desert, Egypt, modified from Churcher (1995: fig. 2), max. length *c.* 100 mm; **B**, left upper plate Ct_2 = HGO 49, from Rouaix, NW of Tikarkas, Southern Algeria, modified from Tabaste (1963: pl. II, 3a), overall length 83.3 mm; **C**, right upper plate Ct_4, from Rouaix, NW of Tikarkas, Southern Algeria, modified from Tabaste (1963: pl. III, 1), overall length 90 mm; **D**, partial right upper plate (ROM 47638) from Ain Umm Dabadib, Kharga Oasis, Western Desert, Egypt, estimated overall length 76-100 mm. Diagrams not drawn to same scale but to show ridges to similar sizes.

if the ridges align approximately transversally to the sagittal plane.

The diet of *R. tuberculatus* n. comb. thus required shearing, crushing and possibly grinding. The likely diet would then have been of soft bodied invertebrates that could be sheared into portions between the ridges, crushed at the end of the shearing stroke (and triturated in a mesiodistal motion of the lower jaw). Food that had a hard shell such as molluscs or large arthropods could have been preferred as an animal as large as *Retodus* n. gen. could have processed prey items with thick shells or carapaces which were within the power of *Retodus* n. gen. jaws and large tooth plates. Modern lungfish have immensely powerful bites: in *Ceratodus* s.l. (incl. *Neoceratodus*): "The jaw articulation is strong and the tooth plates broad and flat. These characters set this genus [*Ceratodus*] apart from other contemporaneous dipnoans" (Kemp 1998: 61).

TAXONOMIC HISTORY OF *NEOCERATODUS* DE CASTELNAU, 1876, *CERATODUS* AGASSIZ, 1838, AND *RETODUS* N. GEN., AND PHYLOGENETIC IMPLICATIONS

Haug (1904) was the first to note the occurrence of a *Ceratodus* in North Africa in a short report on the Cretaceous geological deposits of the Djoua Depression or Wadi Ohanet (Ouad Ohanet), east of Timassânine, Algeria, where he names the sandstone beds ("grés albiens à *Ceratodus*") after the occurrence of this dipnoan. The age of the type specimen of *C. africanus* is given by Haug (1904, 1905) as Albian or latest Early Cretaceous. Tabaste (1963: 440) groups all the deposits of the Djoua Depression, except those at Taouratine, as Continental Early Cretaceous. Foureau (1904: 1527) also gives the age of the fossiliferous deposits of the Djoua Depression ("long thalweg") as early Late

Cretaceous (Cenomanian) and maps eight localities that produced *Ceratodus* tooth plates on a sketch map (Fig. 2B).

Haug (1905) described the first African species of *Ceratodus*, *C. africanus*, from the Timassânine beds, from a left upper (palatine), and two complete and one partial right upper tooth plates, and one complete, one damaged and one posterior fragmentary right mandibular plates. These are not located to the sites shown by Foureau (1904: sketch map; Fig. 1B). Haug (1905: 820) characterised the new species by its six crests on both upper and lower plates which "rapproche *Ceratodus africanus* n. sp. d'*Epiceratodus Forsteri* (Krefft) Teller...". He noted the presence of more than five crests as rare in Triassic *Ceratodus* (cf. Teller's [1891] report of *C. sturii* with only four crests, below) and that the Late Cretaceous *Ceratodus* described by Cope (1876: 259) has six crests and "weak transversal ridges". The forwardly oriented crests in the modern Australian lungfish, now known as *Neoceratodus forsteri*, contrast with the backwardly directed crests of the Triassic species. Haug (1904, 1905) considered *C. africanus* intermediate between the Triassic species and extant *N. forsteri*. He refrained from identifying its genus, or from creating a new genus, and only provisionally assigned the Timassânine, Djoua, lungfish to *Ceratodus*.

Tabaste (1963: 439-440, fig. 1), in her review of the Saharan Cretaceous fossil fish, did not refer to Haug's Timassânine locality, confirm its age, or show the fossiliferous Timassânine site on her map of localities near Fort Flatters and Edjeleh. We do not find Timassânine on current maps but it is shown by Foureau (1904: sketch map; Fig. 2) as lying at the western end of the Djoua Depression, and *c*. 9 km west of Tabtab, mentioned by Tabaste (1963: 440) in reference to site "18" "entre Tabtab et Mazoula". Seven of the eight *Ceratodus*-yielding localities are at the eastern end of the Depression, *c*. 44 km to the east and one is central, near Gour M, *c*. 25 km east of Timassânine.

Foureau (1904: 1528) located the Djoua Depression between "le méridien 4°17' et 4°45' de longitude est, et par les parallèles 28°05' et 28°13' de latitude nord". This longitude is reckoned from the Paris Meridian and not from the Prime Meridian through Greenwich, 2°20' to the west. Thus Foureau's longitudes are corrected to 6°37' and 7°05'E.

The corrected positions agree with the area indicated by Tabaste (1963: fig. 1) for the depression, with the seven *Ceratodus* sites grouped at about 28°13'N and between 6°37' and 7°05'E (corrected longitudes) and the isolated "Gour M" site at 28°09'N, 6°51'E. Fort Flatters, now Bordj Omar Driss, lies at 28°04'N, 6°39'E, which agrees within seconds of latitude and longitude to that of the western end of the depression mapped by Foureau (1904). Foureau seemingly located an elevation of 368 m in a dune-free area of the "Erg d'Issaouan" labelled "Timassânine". It therefore appears that Foureau's geological locality "Timassânine" may include the modern Bordj Omar Driss (Fort Flatters) at long. 006°39'E and extend easterly 26' to 7°05'E.

Tabaste (1963) described *Ceratodus tuberculatus* on 36 whole or partial tooth plates collected from Rouaix, and Erg Iller (Ilafehr), both west of the Ahoggar Massif (Hoggar Mountains), Algeria and both deposits of Early Cretaceous age, and Mt. Igdaman, 80 km north of Tahoua and south of the Ahoggar Massif, of Maestrichtian Late Cretaceous age, in Niger. No holotype is designated but specimen "Ct_1", from Rouaix, is the first discussed with measurements (see above for discussion of these finds).

Krefft (1870) named the living Australian lungfish *Ceratodus forsteri*. De Castelnau (1876) erected the genus *Neoceratodus* for this fish as *N. forsteri* (Krefft, 1870). The differences between fossil *Ceratodus* and living *Neoceratodus* were established for cranial material by Teller (1891) on evidence of the cranial elements of *C. sturii*. There is no evidence to support differentiation on tooth plates (Kemp 1979). *Ceratodus africanus* and *C. tuberculatus* were placed in *Neoceratodus* by Martin (1982a: 612), together with the Australian *N. forsteri*, *N. eyrensis*, *N. palmeri* (now *Metaceratodus palmeri* [Kemp 1997b]) but without reasons. Martin (1982a: 612) also modified ("a émendé") Miles' (1977) characterisation of the family Neoceratodontidae to "Dipneustes portant des plaques dentaires à six à huit crêtes tranchantes, parallèles et perpendiculaires au bord lingual (au moins les premières) chez les adultes ; processus palatin au-dessus de la 3e crête (ou plus en arrière)". In addition, he gave resorption of the internal angle during growth, reduction of the bony roof in the rostral region, and the presence of a single lung as familial characters but, in fossil taxa, these are not observable and are thus arguable.

All "*tuberculatus*" tooth plates carry only four bowed shearing ridges, contrary to Martin's diagnosis, more or less parallel to each other and at right angles to both lingual and buccal borders. The position of the palatine process relative to the ridges on the upper tooth plates is not given by Tabaste (1963) and its position is unknown on the Ain Umm Dabadib specimen (ROM 47638; Fig. 1), if it is indeed an upper plate. As this process is absent from the Baris lower plate (ROM 44609), it is not available as a character. Thus neither Tabaste's Western Saharan nor the Egyptian New Valley (Wadi el-Gedid) specimens fit Martin's diagnosis for inclusion within the Neoceratodontidae. Teller's (1891) description of a skull and jaw of *Ceratodus sturii* ("*T. sturii*" in Martin 1982a) from the schists of Lower Austria near Lunz did not indicate a palatine process in relation to the upper tooth plate, though the palatopterygoid is indicated in his pls II and IV as "*ppt.*", and thus what might be the earlier position is unknown. It therefore appears that the position of the palatine process in African Cretaceous fossil lungfish is essentially unknown, despite previous authors' assertions (e.g., Martin 1982b).

Kemp (1977) gave the maximum number of ridges as seven in *N. forsteri*, with the seventh often either small or absent, and demonstrated that there is little variation in ridge number in the living species. Pause (1979) recorded *C. africanus* from Baris Formation (= Qusseir Formation or Variegated Shales) shales south of Baris, Kharga Oasis, Egypt. Pause (1979: fig. 18) illustrated a right lower plate with only four radiating ridges, and thus probably from *C. humei*.

Churcher & De Iuliis (2001) consider Late Cretaceous African *Ceratodus*, based mainly on *C. humei* and, following Priem's (1914) description and illustration, to have an occlusal surface with typically five radiating ridges and crests or denticulations, the anterior four being robust and equally developed. A small incipient sixth denticulation may occur at the distal root of the fifth ridges denticulation in upper plates. Domnik & Schaal (1984: 163) give "the number of ridges of [the] tooth plates [as] four ridges on the pre-articular [= lower or mandibular] tooth plates and five ridges on the palatine [= upper] plate" in *C. humei*. Accordingly "*C. humei* differs from *C. africanus* Haug which always has fice [*sic*], six or seven ridges". The condition in upper plates of *C. africanus* observed by Haug (1905) and Tabaste (1963) shows six ridges as normal, or five ridges plus one or two reduced ridges joined lingually as possible variants. It is probable that the number of ridges in upper plates has been reduced from six or seven in the Early Cretaceous African *Ceratodus* to five or six in Late Cretaceous members of the genus. The Late Triassic *C. sturii* Teller, 1891 (Teller 1891: pls II-IV) has only four and apparently represents a lineage that underwent ridge reduction early in its phylogeny. The lineage leading to the Cretaceous *R. tuberculatus* n. comb. underwent reduction in the number of ridges to four earlier than some species in the *Ceratodus* group and may be related to *C. sturii* or *C. latissimus*. Two *Ceratodus* lineages starting from a Triassic four crested tooth plate are thus possible. One leads by elaboration of ridges distally to the four to five, or rarely six, radiating crested plates of *C. humei* and the other retains the four crested condition but enlarges the plate (and the animal) and changes the ridge orientation to across the plate, leading to the *R. tuberculatus* n. comb. conformation.

CONCLUSIONS

The recovery of tooth plates of the large Cretaceous lungfish originally described as *Ceratodus tuberculatus*, and here considered the separate genus, *Retodus* n. gen., from Niger, southern Algeria and Egypt establish the existence of a fish larger than the coeval species of the genus *Ceratodus.* This is the largest species of ceratodont affinity in which four crests are normal, and the only one in which the crests are oriented across the tooth plate's long axis. Its crests are bowed, arched or arced, subparallel, both distinct characters, and, together with a series of lunate cross ridges linking the main crests, form a network of interconnected crests. Individual plates measure approximately 70-100 mm in length by 32-48.5 mm in breadth (Table 1). Tooth plates of *Ceratodus humei* measure 45.3-51.8 (6 plates) by 19.0-50.6 (9 plates) (Churcher & De Iuliis 2001: 311, table 1) and of *C. africanus* 54.1 by 26.5 (1 plate) (Churcher & De Iuliis 2001: 311, table 2). The *Retodus* n. gen. plates are robust, varying between 10 and 15 mm in thickness: those of *C. humei* and *C. africanus* are thinner, between 5 and 7 mm in thickness.

The mode of mastication in *Retodus tuberculatus* n. comb. is unique for dipnoans, and involves a closing shearing bite with a small mesial motion, and crushing at the end of the shearing action. Some buccolingual motion is possible to sharpen the major ridge crests and to triturate the food between opposing lunate secondary ridges.

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