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THE MADAGASCAN MESOZOIC PTYCHOCERATODONTIDS (DIPNOI) SYSTEMATIC RELATIONSHIPS AND PALEOBIOGEOGRAPHICAL SIGNIFICANCE

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Abstract : The Mesozoic continental deposits of Madagascar have yielded a lot of Dipnoan tooth plates which have been described a long time ago, on the bases of new data they are revised inside. Dipnoan tooth plates yielded by the madagascan continental Upper Triassic are referred to *Ptychoceratodus* cf. *hislopianus* and to *P. acutus*. These species are closely related to *P. hislopianus* and to *P. virapa* respectively (continental Late Triassic, India). They possess an obtuse inner angle on the tooth plates which could be an apomorphic character. These species provide evidences for good terrestrial connection between Madagascar and India during the Late Triassic. The Late Cretaceous lungfish cf. *Ferganaceratodus madagascariensis* is related to a special group of ptychoceratodontids worldly recorded since the Late Triassic (apart from Africa), frequently these ptychoceratodontids do not show a clear apex of the inner angle on the tooth plates. In the Late Cretaceous these latter ptychoceratodontids have no longer paleogeographical significance. During the Mesozoic they are recorded everywhere apart from Africa and several landroutes are possible in order to explain their distribution during the Late Cretaceous.

Keywords : Malagasy Republic, India, Triassic, Cretaceous, Dipnoi, Ptychoceratodus, Ferganaceratodus, freshwater environment

Les Ptychoceratodontidés (Dipnoi) mésozoïques malgaches : systématique et signification paléogéographique.

Résumé : Les formations mésozoïques continentales malgaches ont fourni de nombreuses plaques dentaires de Dipneustes décrites pour la dernière fois il y a un demi-siècle. A cause des données acquises depuis cette époque la révision de ce matériel était nécessaire. Des plaques dentaires inédites en provenance du Trias supérieur continental malgache sont rapportées à *Ptychoceratodus* cf. *hislopianus* et à *P. acutus.* Ces espèces sont voisines de *P. hislopianus* et de *P. virapa* du Trias supérieur continental indien. Toutes ces espèces possèdent un caractère commun: un angle interne très obtus qui pourrait être un caractère apomorphe. De nouveau ce matériel du Trias supérieur malgache indique des affinités entre les faunes indiennes et malgaches et suggère des communications terrestres faciles entre ces deux masses continentales. La révision des plaques dentaires de cf. *Ferganaceratodus madagascariensis* montre que cette espèce du Crétacé appartient à un groupe réparti mondialement, sauf en Afrique, et connu depuis le Trias supérieur en Allemagne avec cf. *Ferganaceratodus concinnus*. Dans ce groupe souvent les plaques dentaires des adultes ne montrent plus de sommet de l'angle interne net et les bords mésial et lingual forment une courbe continue. L'un d'entre nous avait suggéré en 1981 et 1982 une introduction de cette espèce via 1'Afrique et 1'Amérique du sud mais la présence d'espèces voisines en Mongolie dès le Jurassique supérieur et en Australie au Crétacé interdit de privilégier actuellement une origine géographique plutôt qu'une autre pour ces Dipneustes. L'espèce malgache du Crétacé supérieur n'a plus dans l'état actuel des connaissances de signification paléogéographique.

Mots Clés : Madagascar, Inde, Trias, Crétacé, Dipneustes, Ptychoceratodus, Ferganaceratodus, milieu d'eau douce

INTRODUCTION

When reading the "lexique stratigraphique international" (Bessairie and Collignon, 1960) it appears that the Middle and Upper Triassic of Madagascar has yielded many lungfish tooth plates. However only two fragmentary remains have been described and published: the holotype of *Ptychoceratodus acutus* (Priem, 1924) and a remain determined as *Ceratodus* sp. by Dechaseaux (1949). We have found in the collection of the Laboratory of Paleontology (Muséum national d'Histoire naturelle, Paris) some remains (MAT 2-12) collected a long time ago. We will give the description of this material and a revision of cf. *Ferganaceratodus madagascariensis,* the typical ptychoceratodontid species of the continental Upper Cretaceous of Madagascar.

Geographical and geological setting :

By comparison with the South African Karroo, the geologists have described a Madagascan Karroo, Lower Permian to Middle Jurassic in age, comprising from the base to the top: the Sakoa Group, the Sakamena group and the Isalo Group. The Isalo Group was divided into three parts: the Isalo I, Isalo II and Isalo III. However the stratigraphy of this Karrroo was completely revised by Razafimbelo (1987). He integrated the former Isalo I as the topmost part of the Sakamena Group and he replaced the Isalo II by the Makay Formation.

According to palynological studies (Razafimbelo, 1987), the Makay Formation is Triassic in age, and probably restricted to the Carnian. Buffetaut (1983), on account of the evolutionary level of the Rhynchosaurian *Isalorhynchus genovefae*, gave to the base of the Makay Formation (= Isalo II) a Ladinian age. Later however, this rhynchosaur was recognized as a hyperodapedontine and not as a rhynchosaurine as stated by Buffetaut (Benton, 1987, 1990 ; Hunt & Lucas, 1991). New discoveries made by Barbieri and Cuny in 1996 near the Isalo river confirm that *Isalorhynchus genovefae* is indeed very close to *Hyperodapedon goroni* (Lossiemouth Formation, Scotland) and *H. huxleyi* (Maleri Formation, India), which corroborates a Carnian age of the Makay Formation (Cuny & Barbieri, in prep.). Moreover, Barbieri and Cuny discovered also a jaw fragment belonging to a highly derived procolophonid, which confirms the Upper Triassic age of this Formation (Cuny & Barbieri, in prep.) Other vertebrate discoveries made in the Makay Formation in the Folakara area (West of Madagascar) comprise metoposaurid amphibians and phytosaurs, a typical Upper Triassic assemblage (Buffetaut, 1983; Dutuit, 1978; Guth, 1963; Westphal, 1970). The marine Eotriassic has yielded two dipnoan genera but we do not deal with these remains since one of us has previously studied this material (Martin, 1981). In the Morafenobe region (West central part of Madagascar, see the map fig. 1: B) the Makay Formation has yielded many tooth plates which will be studied below. The localities are not precisely located but there are at least two different localities (according to the original old labels and to the matrix).

On the other hand the continental Upper Cretaceous (Campanian) Mahajanga basin (fig. 1: C) has yielded cf. *Ferganaceratodus madagascariensis* tooth plates. This basin lies on the North-Western coast about 300 km from Antsiranana (Diego Suarez).

The latter tooth plates have been collected in the Marovoay sandstones and in the Ankazomihaboka clays and sandstones. The faunistic assemblage of the Mahajanga basin includes sharks, actinopterygians, presumably frogs, turtles, snakes, lizards, crocodilians, birds, theropods, sauropods, ornithopods and mammals (see Russell *et al.*, 1976 ; Sues, 1980 ; Krause *et al.*, 1994 ; Forster *et al.*, 1996).

Fig. 1 Map of Madagascar / Carte de Madagascar
A: Antananarivo,
B: Morafenobe, C: Mahajanga.

Terminology (fig. 2)

The lungfish tooth plates are almost always triangular in shape. One ridge forms the mesial edge of this triangle. It is the first ridge. The other ridges radiate from the apex of an angle, the inner angle, which is subtended by the lingual edge and the mesial edge. The third edge of the tooth plate is the labial edge. On occasion a continuous curve begins at the labial end of the mesial edge and finishes at the labial end of the lingual edge without any indication of apex of the inner angle, this character could be apomorphic (Martin, 1982) but it is not a general condition in a single species.

This character could depend on the ontogenic age and the diet (environment).

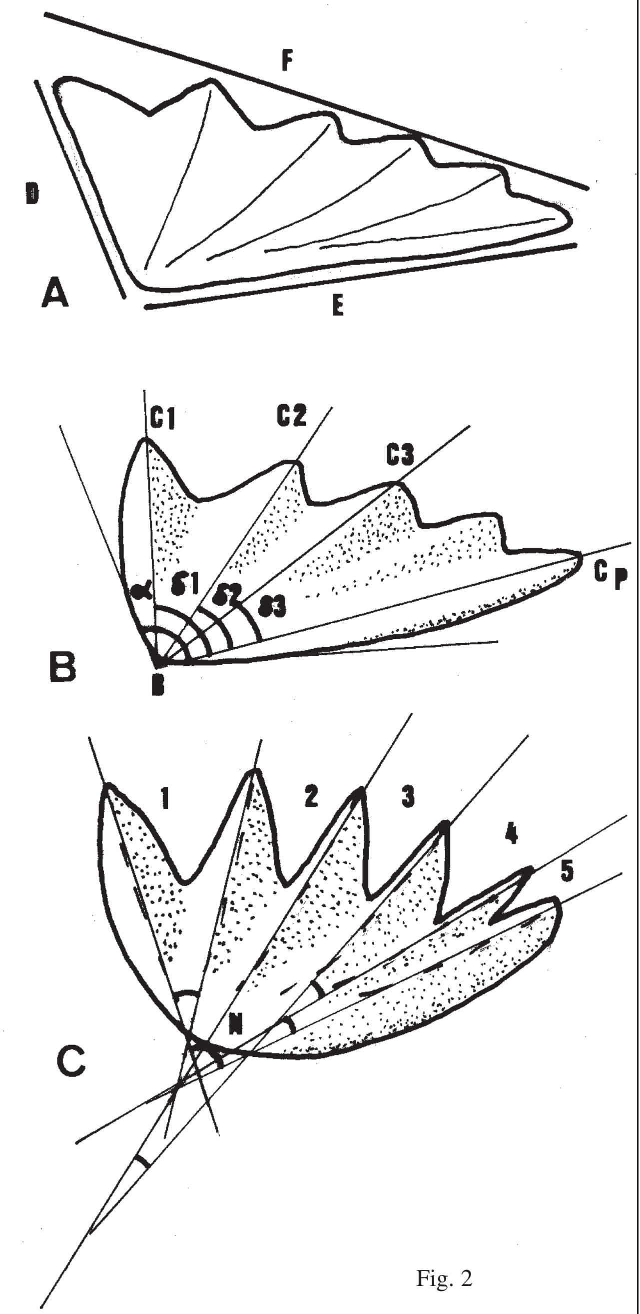


Fig. 2

Fig. 2A Terminology - D: mesial edge, E: lingual edge, - F: labial edge.

Fig. 2B Biometry (Vorobjeva and Minikh's method) - Cl, C2...Cp: tip of the first, the second... and the last ridge, B: apex of the inner angle, α : inner angle, δ1: inner angle of the first ridge, δ2: inner angle of the second ridge, δ3: inner angle of the third ridge.

Fig. 2C Biometry (Kemp's method) - N: angle between the first and the last ridge, 1: angle between the first and the second ridge...

Fig. 2A Terminologie - D: bord mésial, E: bord lingual, F: bord labial. - Fig. 2B Biométrie (méthode de Vorobjeva et Minikh) Cl, C2... Cp: apex de la première, deuxième... et de la dernière crête, B: sommet de l'angle interne, α : angle interne, δ1: angle interne de la première crête, δ2: angle interne de la deuxième crête, δ3: angle interne de la troisième crête. - Fig. 2C Biométrie (méthode de Kemp)
N: angle entre la première et la dernière crête, 1: angle entre la première et la deuxième crête, etc.

Systematic foreword

The tooth plates studied here are typical tooth plates of ptychoceratodontids (see Martin, 1982) but the generic referral to a precise genus is not always clear because even if in Australia the different tooth plates exhibit generic characters (Kemp, 1993; 1997) on the bases of remains housed in European collections it is not always possible to find these indications. The different Mesozoic tooth plates from Madagascar have been previously referred to the genus *Ceratodus* by different authors and later to *"Ptychoceratodus"* by Martin (1982). At the moment, after the description of *Ferganaceratodus* by Kaznyshkin and Nessov (1985) and the discovery of *Ptychoceratodus phillip*si in South Africa (Kemp, 1996) a more precise referral to these genera is possible. However the referral of Austral remains to the species *phillipsi* is not sure. The small tooth plates of the specimen described by Kemp do not resemble at all the holotype of *P. phillipsi* (Agassiz, 1838) which is neither lost nor destroyed as claimed by Kemp since it is housed in the Museum of Natural History in Neuchâtel (Martin, Cuny and Cavin, in prep.). These differences can be due to a difference of ontogenetic age but the juvenile tooth plates of the different species of ptychoceratodontids are more similar than the adult ones (Martin *et al.*, 1981) whereas this holotype is very similar to specimens referred to *P. phillipsi* from the European Upper Triassic described by Martin *et al.* (1981). The designation of a holotype or a lectotype for *P. phillipsi* by Kemp is meaningless. However the discovery of a skull roof clearly belonging to *Ptychoceratodus* in Southern continents demonstrates the validity of generic referrals of some tooth plates to *Ptychoceratodus* or to a closely related genus by one of us (Martin, 1982). For this reason the tooth plates of Triassic Madagascan ptychoceratodontids are referred to *Ptychoceratodus* Jaeckel 1923, and to cf. *Ferganaceratodus* Kaznyskhin and Nessov, 1985. We do not compare the Indian and Madagascan species to other species from austral continents since the designation by Kemp of the specimen of *P. phillipsi* from the Lower Triassic of South Africa both as the holotype (sic -Kemp, 1996 : p. 412, 413) and lectotype (sic -Kemp, 1996 : p. 410, 411) has changed the orientation of our revision of the true holotype of *P. phillipsi*. It must be pointed out that it was only possible to designate a neotype. The different austral Triassic species will be discussed on this occasion.

THE TRIASSIC SPECIES

Systematics

Dipnoi Müller, 1844
Ceratodontiformes Berg, 1940
Ptychoceratodontidae Martin, 1982
Ptychoceratodus Jaeckel, 1923.

Description of *P. hislopianus*

Oldham (1859) erected four new species for several remains from the Triassic Maleri Formation: *Ceratodus hislopianus* Oldham, *C. oblongus* Oldham, *C. hunterianus* Oldham and *C. virapa* Oldham. *Ceratodus hislopianus* is valid since it has been firstly erected by Oldham, but according to Oldham's plates and to specimens kept in the Museum of Natural History (London) this species cannot be referred to the genus *Ceratodus* since even on the large tooth plates the labial part of the ridges is not crushing (see also Martin, 1982 and Kemp, 1993 for the generic characters of *Ceratodus*). On the other hand these tooth plates resemble very much tooth plates of *Ptychoceratodus*. There is at least some doubt about the validity of the other species erected by Oldham (Miall, 1878; Jain, 1968).

According to the material housed in London and to Oldham's paper (1859) *P. hislopianus* possesses 5 cutting radiating ridges. The inner angle is obtuse (pl I., figs 6, 12) and the lingual edge is straight or slightly curved. The size of tooth plates depends probably on the ontogenetic age of the animals. The 5th ridge is wide and crushing, the tip of this last ridge is much more posterior than the tip of the 4th ridge. Some denticles are present on the labial unworn part of the ridge of small, young tooth plates and the first notch is broad. The shape of the ridges is variable. Sometimes the ridges slope progressively (pl I, fig. 16) or sometimes the labial part is almost perpendicular to the occlusal part and vertical (pl I, fig. 18). According to these features this species is clearly related to *Ptychoceratodus* (see also Martin, 1982).

Validity of the other Triassic Indian species

Always on the base of specimens housed in London and on Oldham's figure (except Oldham, 1859: pl. 15, figs. 9, 10) the species described as *C. hunterianus* is a junior synonym of *P. hislopianus*. A single difference is recorded which results from the range of variability: some lower tooth plates of the so-called *C. hunterianus* possess only four ridges. The single fragmentary tooth plate referred to *C. oblongus* (Oldham, 1859: pl. 15, figs. 7, 8) fits rather well *P. hislopianus* but only the posterior part is preserved and it is impossible to be absolutely sure that the two species are synonyms. In this condition it is best to consider the former species as a *nomen dubium*.

About *C. virapa*, Oldham (p. 305) wrote "the tooth is broader and more massive, as compared with its length; the upper face exhibits a much larger proportion of flat surface; the ridges and furrows are less sharp and defined, but more rounded and open. The anterior inner edge of the tooth (upper jaw) is straight or nearly straight for two thirds of its whole length, when it curves rapidly round..." It is possible to add that two remains referred to *C. virapa* (Oldham, pl. 13, figs. 9, 10) exhibit the loss of the radiating pattern of ridges, which could be the result of a specific way of wear. Moreover on these remains the lingual edge is very curved posteriorly (Oldham, 1859 : pl. 14, fig. 9, herein pl. I, fig. 9). On these bases (more rounded ridges, functionnal loss of the radiating pattern, posteriorly curved lingual edge) it could be possible to distinguish *C. virapa* from *P. hislopianus*. The former species exhibits the ptychoceratodontid features and pending the revision of this Indian material it is possible to consider it as a valid species provisionnaly referred to the genus *Ptychoceratodus*. The small tooth plate (Oldham, 1859: p. 308, pl. 15, figs 9-10, herein pl. I, fig 4) exhibits an incipient loss of radiating pattern, and for this reason it must be referred to *P. virapa* (Oldham thought that it was a young tooth plate of *C. hunterianus*).

The genuine truly obtuse inner angle which is present on these Triassic Indian tooth plates must be pointed out. It could be an apomorphic character. At the moment we accept the validity of two species of ptychoceratodontids in the Indian Triassic: *P. hislopianus* and *P. virapa.*

Description of **P.** *cf.* **hislopianus** *from Madagascar*

Ptychoceratodus cf. *hislopianus* (Oldham, 1859)

1949 *Ceratodus* sp., Dechaseaux p. 75-86, pl. I fig. 3.
1981 *Ceratodus hislopianus*, Martin p. 281, fig. 2a.

Material MNHN MAT 2, 4, 8, 10, 11, 12 (tooth plates, and for MAT 11 with entopterygoid).
Locality : Morafenobe region (at least two different localities).

Description of MAT 11 (pl I, fig. 17)

This left upper tooth plate is large in size (length of the lingual side: 40 mm) and the inner angle is clearly obtuse (120°). It possesses 5 cutting ridges arranged in a radiating pattern. The lingual edge and the ridges are almost straight. The breadth of the notches decreases gently from the second to the last one. The occlusal part is smooth. The pterygopalatine process arises above the second ridge on the labial edge and the notches are deep.

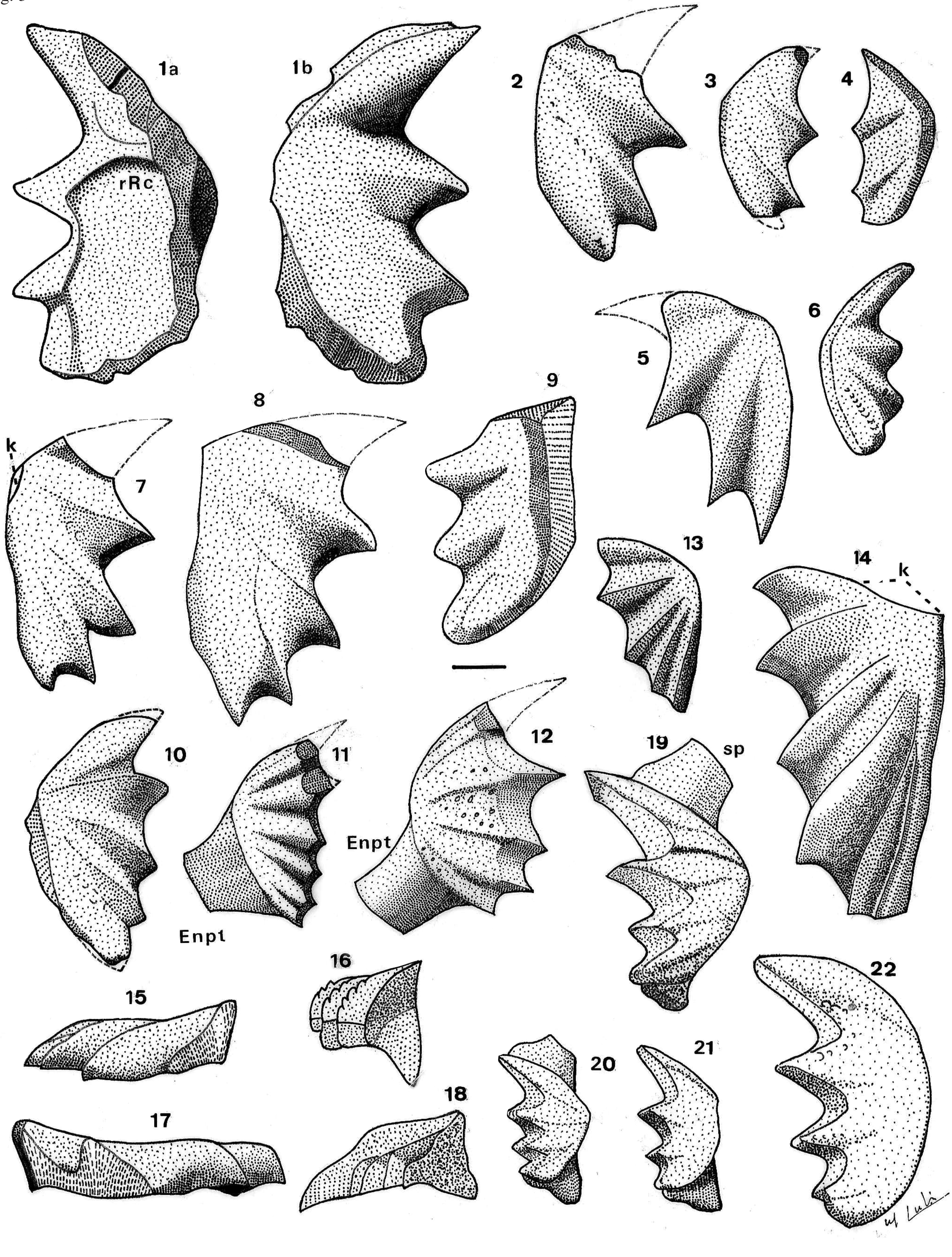
Range of variability

The radiating pattern is clearly preserved on 5 remains (MAT 4, 8, 10, 11, 12 - pl I, figs. 7, 8, 15, 17). The enameloid tissue is preserved on a single tooth plate (MAT 4), which has been surely collected in a different locality or level. The shape of the ridges is variable (on the same specimen). Generally the labial part slopes gently and progressively (MAT l l, pl I, figs. 3,15). In some cases the labial edge of the ridge (MAT 10- r. ut.-, pl I, fig. 17) is straight and almost perpendicular to the occlusal part of the ridge. The tooth plates are thick (4 to 15 mm) the size is not variable in this sample (length of the lingual edge from 40 to 50 mm).

Comparison

A similar morphology occurs in the European species referred to the ptychoceratodontids but in these species the obtuse inner angle (when present) is mainly caused by the articulation between the symetrical tooth plates (pl I, fig. 14). In the Madagascan

Fig. 3


1a
rRc
1b
2
3
4
6
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10
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17

species the articular surface between the tooth plates is visible on a single specimen (MAT 11, pl. I, fig. 7) and its position is not the same : it lies on the lingual side instead of the mesial one in European ptychoceratodontids. The same obtuse inner angle is recorded in several ptychoceratodontids for instance *P. ornatus* (Broom, 1909, herein pl. I, fig. 13) an Early Triassic South African species. However the relationships of *P. ornatus* with the species from India and from Madagascar are not clear. These problems will be studied on occasion of the revision of the holotype of *P. phillipsi* in another paper.

Comparison between **P. hislopianus** *from India and* **P.** *cf.* **hislopianus** *from Madagascar*

The Madagascan remains now referred to *P*. cf. *hislopianus* fit the Indian *P. hislopianus* very well, except for the shape of the posterior part of the tooth plate. On Indian remains, the 5th ridge is much more posterior than the 4th ridge. It is not the case on the Madagascan tooth plates. This difference is recorded in other species of Mesozoic lungfish as a character related to the individual variability (for example in *Neoceratodus africanus* (Haug), the common Jurassic and Cretaceous species of Northern Africa : pl. II, fig. 16). But at the moment, on Indian specimens the 5th ridge is always longer than the 4th one whereas the last two ridges are always as long on Madagascan specimens. For this reason it is more convenient to refer these Madagascan remains to *Ptychoceratodus* cf. *hislopianus*. One of us (Martin, 1981) previously referred the fragmentary MAT 2 (l. ut., pl. II, fig. 15) to *C. hislopianus* (on this tooth plate the posterior part is broken off).

Ptychoceratodus acutus **(Priem, 1924)**

1924 *Ceratodus acutus*, Priem; p. 17-21, pl. 7 fig. 11
1981 *Ceratodus acutus*, Martin; p. 580-581, fig. 2c.

Material: holotype MAT 1, and 4 tooth plates MAT 5 (with the prearticular), 6, 7, 9.
Locality: probably Morafenobe region.

Description of the holotype

It is a large sized tooth plate (length of the lingual edge 40 mm, MAT 1, pl. I, fig 5, pl. II fig. 17) which bears 4 cutting radiating ridges. The first ridge is broken off. The others are quite sharp. The value of the inner angle is about 120°. The ridges are straight. The lingual edge is slightly curved. The holotype seems very narrow. The breadth of the notches decreases gently. This remains is not easy to determine either as lower or upper tooth plate.

Plate I
1, 2, 3, 5 : *Ptychoceratadus acutus*; 4-6 : *P. virapa*; 7, 8, 15, 17 : *P. cf. hislopianus;* 13 : *P. ornatus*; 14 : *P. serratus*; 6, 10: *P. hislopianus*; 11: *Ceratodus wollastoni*; 12, 19, 20: cf *F. madagascariensis*; 16-18 : *P. hislopianus*; 21 *Ceradodus sp*.; 22: *Ceratodus sp*.
1: MAT 5 (r. 1t.); 2: MAT 6 (1. ut.); 3: MAT 9 (l. ut.); 4: redrawn from Oldham 1859 pl. 15, fig. 10; 5 : MAT 1 (?); 6 : redrawn from Oldham 1859 pl. 14, fig. 1; 7: MAT 11 (l. ut.); 8: MAT 12 (l. ut.); 9: redrawn from Oldham 1859 pl. 14, fig. 1; 10: BM(NH) P 3400(l. ut.); 11: BM (NH) P 13678-cast-(l. ut.); 12: MAJ 1 (r. ut.); 13: BM(NH) P 11271 (l. ut); 14: SMNS without number (r. ut.); 15: MAT 11 (l. ut.- side view); 16: redrawn from Oldham 1859 pl. 16 fig. 2; 17 : MAT 10 (r.ut.) (side view); 18 : redrawn from Oldham 1859 pl. 16, fig. 4; 19: MAJ 17 (l. lt.); 20 : MAJ 12 (l. lt.); 21: redrawn from Pascual and Bondesio 1976 pl. I, fig. 5 (l. lt.); 22 : redrawn from Wichmann 1928 pl. 1, fig. 3 (l. lt.). Scale bar 1: cm.
Abbreviations. l: left; r: right; lt: lower tooth plate; ut: upper tooth plate; k: symphyseal articular surface; entp: entopterygoid; rRc: ridge of Ruge's canal; SMNS: Staatliches Museum für Naturkunde Stuttgart; BM(NH) Museum of Natural History London.

Planche I
1 : MAT 5 (d. i); 2: MAT 6 (g. s.); 3 MAT 9 (g. s.); 4 d'après Oldham 1859 pl. 15, fig. 10; 5 : MAT 1 (?); 6 : d'après Oldham 1859 pl. 14, fig. 1; 7: MAT 11 (g. s.); 8: MAT 12 (g. s.); 9: d'après Oldham 1859 pl. 14, fig. 1; 10: BM(NH) P 3400 (g. s.); 11 : BM(NH) P 13678-moulage-(d. s.); 12: MAJ 1 (d. s.); 13: BM(NH) P 11271 (g. s.); 14: SMNS sans numéro (g. s.); 15: MAT 11 (g. s.-vue latérale); 16: d'après Oldham 1859 pl. 16, fig. 2; 17: MAT 10 (d. s.-vue latérale); 18 : d'après Oldham 1859 pl. 16, fig. 4; 19: MAJ 17 (g. i.); 20 : MAJ 12 (g. i.); 21: d'après Pascual et Bondesio 1976 pl. I, fig. 5 (g. i.); 22 : d'après Wichmann 1928 pl. 1, fig. 3 (g. i.). Barre d'échelle 1 cm.
Abréviations. d: droit; g: gauche; i: inférieur; s: supérieur; k: articulation symphysaire; rRc: ride du canal de Ruge; SMNS: Staatliches Museum für Naturkunde Stuttgart; BM(NH): Museum of Natural History London.

Description of new material

The lower tooth plate MAT 5 (r. lt.) is complete (pl. I, fig 1). It possesses ridges arranged in a radiating pattern. Because of the wear this pattern has partly disappeared and the 3rd and 4th ridges look blunt. The first ridge is larger than the lingual side. The first notch is broader than the others and the mesial edge is strongly curved posteriorly. This tooth plate is large (length of the lingual edge 50 mm), its inner angle reaches 120° and is still fixed to the prearticular which is stout. The tooth plate and this bone are thick. In the Meckelian groove there is, under the first notch, a ridge (pl. I fig. 1a), which is the remain of Ruge's canal. The left smaller upper tooth plate MAT 6 (pl. I, fig. 2) is rather large (40 mm as length of the lingual edge).

This remain is less worn and the ridges are more cutting but the radiating pattern of the 4 ridges is no longer obvious. A small difference with the former tooth plate is recorded: the shape of the lingual side is almost straight. Its inner angle was probably very obtuse. The smallest tooth plate MAT 9 (l. ut., pl. I, fig. 3) possesses a very obtuse inner angle. The tip of the first and 4th ridges are broken off. Its occlusal surface is almost smooth and the radiating pattern is not very visible, however the labial part of the unbroken ridges is still rather sharp. The lingual side is convex. The variation in size is large, from 23 mm to 50 for the lingual edge.

Comparison

The last tooth plate MAT 9 (pl. I, fig. 3) is quite similar to the Indian tooth plate (pl. I, fig. 4) which we refer to *P. virapa*. Moreover, the complete tooth plate MAT 5 looks very similar to the Indian tooth plate (pl. I, fig. 9) referred by Oldham to *P. virapa*. Without a revision of Indian species the systematical determination of Madagascan species is impossible. Pending this revision we suppose that *P. virapa* is valid. Several possibilities do exist : 1 *P. virapa* is a junior synonym of *P. hislopianus*, in this case because of the range of variability *P. acutus* will be another junior synonym of *P. hislopianus*; 2 *P. virapa* is a valid species, in this second case on the base of the range of variability *P. acutus* could be a junior synonym of *P. virapa*; 3 *P. acutus* is a valid species, the demonstration will depends on the discovery of new material in Madagascar. However the resemblance between Indian and Madagascan tooth plates is fairly good and suggests close relationships if not identity between *P. virapa* and *P. acutus.*

THE LATE CRETACEOUS DIPNOANS

Ptychoceratodontidae Martin, 1982
Ferganaceratodus Kaznyshkin and Nessov, 1985
cf. *Ferganaceratodus madagascariensis*
(Priem, 1924)

1924 *Ceratodus madagascariensis*, Priem; p. 15-17, 20-21, pl. 7, figs 4 to 10.
1949 *Ceratodus madagascariensis,* Dechaseaux; p. 75-86, pl. figs 5, 7, 8.
1949 *Ceratodus sp.*, Dechaseaux; p. 75-86, pl. l figs. 2, 4.
1981 *Ceratodus madagascariensis,* Martin; p. 581-583, figs. 3a-c, 3f.
1982 *"Ptychoceratodus" madagascariensis*, Martin; p. 59-62, fig. 5a.
1997 cf. *Ferganaceratodus madagascariensis,* Martin *et al.* figs. 10, 14.

Lectotype : laboratoire de paléontologie (Museum national d'Histoire Naturelle, Paris) MNHN MAJ 1 1 (Priem 1924, pl. 7, fig. 4, herein pl. II, fig. 1).
Material: MNHN MAJ 11-33, BM(NH) P 15664-15677, 15682. (Museum of Natural History, London).
Locus typicus: Mahajanga Basin (Madagascar)
Stratum typicum: Marovoay sandstone and Ankazomihaboka clays and sandstone (Campanian).

Description of the lectotype (pl. II, fig 1)

This right lower tooth plate is still fused to the prearticular (which is the general condition). It exhibits 4 cutting, straight and radiating ridges. The first ridge is broken off about 5 mm before its tip. The 4th ridge is worn whereas the 3rd one bears some denticles on its labial and occlusal parts. The apex of the inner angle, which measures about 105°, is rounded.

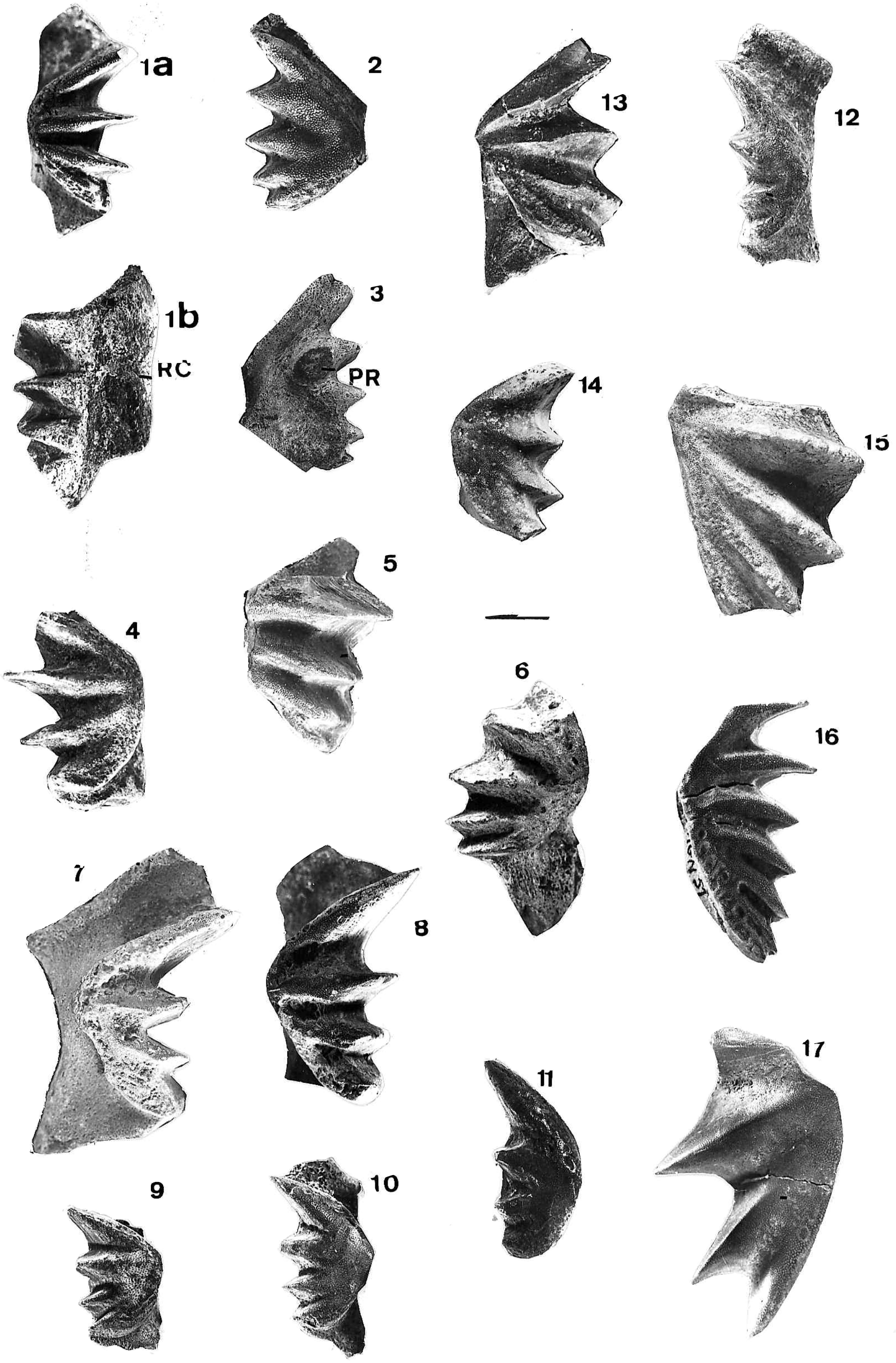

Plate II
1-12: cf. *F. madagascariensis*;
13, 14: *F. concinnus*;
15: *P. cf. hislopianiu*;
16: *N. africanus;*
17: *P. acutus*.
1: Lectotype MAJ 1 1 (r. lt), a: occlusal face, b: basal face, Rc: ridge of Rudge's canal,
2 : MAJ 29 (r. ut.) occlusal face;
3 : MAJ 29 basal face, pr: palatine process;
4 : BM(NH) P 15676 (l. lt.);
5 : MAJ 28 (?) fragmentary tooth plate;
6 : MAJ - (r. ut.);
7 : BM(NH) P 15667 (r. lt.) tooth plate with broad symphyseal process;
8 : MAJ 22 (r. lt);
9 : MAJ 32 (l. lt.) small tooth plate;
10 : MAJ 12 (l. lt.);
11 : MAJ 13 (1. lt.) tooth plate with smooth occlusal face;
12: MAJ 13 (l. lt.);
13: SMNS without number (r. lt.);
14: SMNS 51110 (r. lt.);
15: MAT 2 (l. ut.);
16 : MNHN-HGN 52 (l. ut.);
17: MAT 1 (?).
Scale bar 1: cm.
Abbreviations: see pl. I.

Planche II
1 : lectotype MAJ ll (d. i.), a: face occlusale, b: face basale, Rc: ride du canal de Ruge; 2 : MAJ 29 (d. s.) face occlusale; 3 : MAJ 29 face basale, pr: processus ptérygopalatin; 4: BM(NH) P 15676 (g. i.); 5 : MAJ 28 (?) plaque fragmentaire; 6: MAJ - (d. s.); 7 : BM(NH) 15667 (d. i.) plaque dentaire possédant un processus symphysaire large; 8 : MAJ 22 (d. i.); 9 : MAJ 32 (g. i.) petite plaque dentaire; 10: MAJ 11 : MAJ 13 (g. s.) plaque dentaire à la face occlusale émoussée par usure; 12 (g. i.); 12: MAJ 13 (g. i.); 13: SMNS sans numéro (d. i.); 14: SMNS 51110 (d. i.); 15 : MAT 2 (g. i.);16: MNHN-HGN 52 (g. s.); 17: MAT 1 (?).
Barre d'échelle 1 cm. Abréviations voir pl. I.

The prearticular, relatively thick, bears a ridge (remains of Ruge's canal) under the first notch (fig. 4.26b). There is no contact between the symetrical tooth plates and a stout symphyseal process for the articulation of the two prearticulars is present. This tooth plate is medium sized for the species (length of the lingual side 22 mm).

Range of variability. (pl. II, figs 2-12)

The size is not very large : the largest tooth plate does not exceed 30 mm as length of the lingual side (MAJ 14). The smallest recorded remain is the small BM(NH) P 15682, the same length of which being only 14 mm long. The upper tooth plates possess 5 ridges (MAJ 17, 18, MAJ 28, 29, pl. II figs 2, 6, 5). The inner angle is sometime right (90° in 24, 87° in MAJ 29- r. ut.-, pl. II, fig. 2). The mean reaches 104°, this angle reaches 120° as maximum value (MAJ 17-l. lt.-, pl. I, fig. 19). The lingual side which is slightly curved on the lectotype is straight on some tooth plates (MAJ 29, pl. II, fig. 2) or truly curved on some lower tooth plates (BM(NH) P 15676-l. lt.-, pl. II, fig 4). For this reason the apex of the inner angle is not always easy to determine and consequently many measurements are difficult. These tooth plates exhibit an archaic character, the first ridge is often longer than the lingual edge. Because of the wear and perhaps of the preservation some tooth plates possess an occlusal surface which is almost smooth (MAJ 12-l. lt., 13-l. lt.-, pl. II, figs. 10, 11), the labial part of the ridges is more or less rounded, the sharpness and the radiating pattern of ridges disappear. The strong curvature of the posterior part of the lingual side is surely the result of a poorly developed 5th ridges which stopped its growth - this feature and this phenomenon are recorded (Martin, 1980; 1981; 1984) in *Ceratodus kaupi* Agassiz, in *Ferganaceratodus concinnus* (Plieninger) and in *Neoceratodus africanus* (Haug).

The functionnal wear

It begins on the posterior part of the tooth plate and for this reason the last ridge is always worn even on the small, probably juvenile, tooth plates.

The lingual part of the ridges is abraded and becomes rounded. This wear reaches later the labial part and on completely worn tooth plates only the labial part of ridges is still cutting. On relatively unworn tooth plates the labial part of ridges is serrated because of the presence of small denticles, previously observed by Priem (1924) and Dechaseaux (1949). Usually the largest tooth plates (pl. II, fig. 6) are more abraded than the small ones (pl. II, fig. 1a) and the apex of the inner angle is more difficult to determine (when possible) on these former remains than on the latter tooth plates.

Biometry (figs. 2B, 2C)

We use two different methods which have been used first by Vorobjeva and Minikh (1967) (table 1) and by Kemp (1977) (table 2). In a recent paper Kemp (1997) has pointed out that on occasion the measurements (especially of angles) were meaningless because of the wear. We suspect that it is the case in this sample of cf. *F. madagascariensis*. The results are only indicative. The different indices of ridge length or notch width are perhaps more significant but this is not sure. The angles used by Kemp for the measurement of the allometric growth of the tooth plates are probably meaning1ess. We precise that because of the low number of upper tooth plates the different data from the pterygoid tooth plates are always included inside the range of variability of the lower tooth plates, for this reason the indices and angles of upper and lower tooth plates are not separated. The results of table 2 provide the evidence that there is no reduction of the inner angle during the growth (x 2 test) but because of the low number of each sample and the preservation, these results could be meaningless.

Comparison

Many species wordly recorded exhibit features which are visible in cf. *F. madagascariensis,* long first ridge, invisible apex of the inner angle and a gentle curve formed by the mesial and lingual edge in large specimens, radiating pattern of sharp ridges (when unworn), less than 7 ridges.

	α	δ1	δ2	δ3	BC2/ BC1	BC1/ BCp	C1C2/ BCp	C1C2/ BC1	C1C2/ C1Cp	C1C2/ BCp	C2C3/ C2Cp	n
le	105	77.5	48.3	23	72.2	126	109.8	52.5	47.6	66.8	53.6	29
±	9.8	7.6		4.4	7.9	18	9.7	7.5	5.3	9.5	5.7	

Table 1
Biometry, method of Vorobjeva and Minikh (1967). Tooth plates of cf. *Ferganaceratodus madagascariensis* (Priem, 1924). Abbreviations: see Fig. 2B, n: number of remains.

Table 1
Biométrie, méthode de Vorobjeva et Minikh (1967). Plaques dentaires de cf. *Ferganaceratodus madagascariensis* (Priem, 1924). Abréviations: voir Fig. 2B, n: nombre de restes.

inner angle lower tooth plates		
juvenile	subadult	adult
67 ± 7.7	66.8 ± 9.9	64 ± 6.5

Table 2
Biometry, method of Kemp (1977). Tooth plates of cf. *Ferganaceratodus madagascariensis* (Priem, 1924).

Table 2
Biométrie, méthode de Kemp (1977). Plaques dentaires de cf. *Ferganaceratodus madagascariensis* (Priem, 1924).

These characters are consistent with the referral to the ptychoceratodontids but are also indicative of close relationships (the curve in large specimens could be an apomorphic character). These species are recorded in Europe with *Ceratodus concinnus* (Plieninger, 1842), pl. II, figs 13, 14, in the Cretaceous and the Tertiary of South America and referred to *Ceratodus iheringi* Ameghino, 1916 or to *Ceratodus sp.* (Whichman, 1928; Pascual and Bondesio, 1976; Arratia and Cione, 1996 ; pl. I, figs 21, 22), in North America from the Late Jurassic to the Cretaceous with *Ceratodus guentheri* Marsh, 1878, *C. frazieri* Ostrom, 1970, *C. felchi* Kirkland, 1987 and *C. gustasoni* Kirkland, 1987 (Kirkland, 1987), in the Cretaceous of Australia with *Metaceratodus wollastoni* Chapman, 1914, pl. I, fig. 11, and *Ceratodus pattinsonae* White, 1926 (Kemp, 1997) and in Asia with *Ceratodus temporatus* Krupina, 1994 and *C. porrectus* Krupina, 1994 from the Upper Jurassic of Mongolia (Krupina, 1994). These species are recorded from the Late Triassic with *F. concinnus* to the Tertiary in South America (Kemp, 1997). Some Tertiary Australian remains, *M. palmeri* (Kreft, 1874) and *M. bonei* Kemp, 1997 seem more similar to tooth plates of neoceratodontids and herein we do not deal with these species. Most of the large tooth plates of these different species exhibit the curved formed by the lingual and the mesial edge and when the same formation or the same locality have yielded both small and large specimens the small ones possess an evident inner angle whereas the curve is present on the large ones. Kirkland (1987) has erected two new species *C. felchi* and *C. gustasoni* which could be junior synonyms of *C. guentheri*. Krupina (1994) has used Kirkland's conclusions in order to erect several species for material from the Upper Jurassic of Mongolia, but at least on the basis of the range of variability recorded in cf. *F. madagascariensis, Ceratodus porrectus* could be a junior synonym of *C. temporatus* which is a large completely worn tooth plate.

Systematic and Phyletic position of cf. *F. madagascariensis*

The description of the small holotype of *C. felchi* Kirkland, 1987 is clearly indicative of close relationships of these Dipnoans with the ptychoceratodontids; the holotype of *C. felchi* resembles very much small tooth plates of *C. concinnus* housed in Stuttgart (pl. II, fig. 13). The last year (Martin *et al.*, 1997) have referred *C. concinnus* to the genus *Ferganaceratodus* on the bases of the tooth plates and of the B bone. At the same moment Kemp (1997) referred Australian species to the genus *Metaceratodus* Chapman, 1914, but this genus is based only on tooth plates which provide evidences for the specific determination and referral to the family rank but not always to the generic one, for this reason we think that the generic referral to cf. *Ferganaceratodus*, a genus described on the basis of both dermal elements of the skull roof and tooth plates is better. This choice does not mean that *Metaceratodus* is invalid. Colleagues who have faith in cladistics will never accept these referrals. The general similarities and resemblances are provisionnaly sufficient when the polarity of character is not clear. For the tooth plates of Dipnoans (and other fossil remains) in which the discovery of derived characters is not obvious because of allometric growth, functionnal wear, diet, preservation and the individual variability it would be absolutely forbidden to use similarities. But the example of *P. phillipsi* is very demonstrative.

One of us (Martin, 1982) referred a lot of species based on isolated tooth plates to the ptychoceratodontids and to the genus *Ptychoceratodus*, the use of quotation marks being indicative of the provisionnal generic determination. Of course some authors (including A. kemp) did not accept these generic referrals. Among the species referred to *"Ptychoceratodus"* there was *P. phillipsi*. This species and the others were referred to different genera on the basis of characters listed in a table (Martin, 1982). It is possible to read in different papers that these new generic referrals were unfounded if not nonsensic.

Have a look to the present result after the description by Kemp (1996) of the South African skull roof of *P. phillipsi* : most of species referred to *Ptychoceratodus* or to *"Ptychoceratodus"* in 1982 by Martin are now referred with certainty to the genus *Ptychoceratodus* (for instance Kemp 1996, 1997). Is it necessary to add anything about the generic determination of Dipnoans tooth plates based on similarities and also on derived characters when possible ? On the base of the radiating pattern of ridges, the number of ridges (less than 7), the absence of crushing ridges the tooth plates from the Madagascan Mesozoic can be referred to the Ptychoceratodontidae. On the basis of general similarities and combinations of characters which are perhaps meaningless in cladistics it has been possible to determine two closely related species for the late Triassic *P. acutus* and *P*. cf. *hislopianus* but these tooth plates are different from those of the type species *P. serratus* Agassiz 1838. However the presence of a skull roof of *Ptychoceratodus* in South Africa provide the evidence of the dispersal of this genus. The Cretaceous tooth plates possess also characters of Ptychoceratodontidae but a common character (the absence of obvious apex of the inner angle in large tooth plates) permit the provisionnal referral of this material to the genus *Ferganaceratodus.* However the small tooth plates of the type material of *Ferganaceratodus* does not possess this character and it is only the provisionnal referral of *C. concinnus* to *Ferganaceratodus* on the basis of other characters (Martin et al. 1997) which permit the referral of *C. madagascariensis* to cf. *Ferganaceratodus*. On the basis of the available characters it is meaningless to try to find more precise data about the phyletic position of cf. *F. madagascariensis* because at the moment it is possible to find apomophic characters at the family rank, but not always at the generic one on the tooth plates of Mesozoic and Caenozoic dipnoans.

PALEOGEOGRAPHICAL CONCLUSIONS

During the Late Triassic a group of ptychoceratodontids, but maybe a single species, was present in India and in Madagascar. On the basis of their obtuse inner angle these continental dipnoans from both areas are closely related and are either indicative of easy "land routes" between India and Madagascar or indicative of a dispersal older than the Late Triassic. They are not the single evidence for the connection between India and Madagascar at that time. The vertebrate assemblage of the Maleri Formation with phytosaurs (Chaterjee, 1978) and amphibians (Roy Chowdhury, 1965) resembles the vertebrate assemblage of the Madagascan Late Triassic, where metoposaurs and phytosaurs are also present (Dutuit 1978). The connection between these different Gondwanian landmasses fits the paleogeography based on geophysical data (Smith and Briden, 1977, Smith *et al.*, 1994) or on faunal evidences (Cox, 1980; Benton, 1987). The significance of cf *F. madagascariensis* is less clear. One of us has suggested (Martin, 1982) several possibilies but the presence of ptychoceratodontids similar to this species everywhere (apart from Africa) since the Triassic suggests an early dispersal of these dipnoans. The Madagascan ones could have reached Madagascar from the South America through South Africa or via Antarctica and Australia but Rage (1996) has also recently suggested the possibility of dispersal from Laurasia via India during the Cretaceous for some Madagascan vertebrates. On the base of present paleontological data it is impossible to choose between these different possibilities of dispersal and moreover the Campanian Madagascan dipnoans are perhaps not paleogeographically significant.

CONCLUSIONS

The Late Triassic Madagascan freshwater dipnoans are referred to the genus *Ptychoceratodus*, they are closely related to the Indian Late Triassic dipnoans. They are indicative of good "terrestrial" connections between India and Madagascar during this time. The Campanian Madagascan freshwater dipnoans are related to a group of ptychoceratodontids recorded as early as the Late Triassic with *F. concinnus*. This group is worldly recorded (apart from Africa) and on the base of present data during the Late Cretaceous has probably no paleogeographical significance.

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