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First procolophonid (Reptilia, Parareptilia) from the Lower Triassic of Madagascar

Premier procolophonidé (Reptilia, Parareptilia) du Trias inférieur de Madagascar

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ABSTRACT

Lasasaurus beltanae nov. gen. nov. sp., a new procolophonid (Reptilia, Parareptilia) from the Lower Triassic of Madagascar, is represented by a single partial skeleton preserved in a ferro-calcareous nodule from the Middle Sakamena Formation, in the North of the island. This new taxon is unique in possessing peculiar, fine and dendritic crests running along the posterolateral side of the squamosal, widely spaced maxillary teeth, subparallel mesiodistal ridges connecting maxillary teeth to the tooth row, and a strongly acute anterior margin of the copula (hyoid bone). This well-preserved specimen belongs to a juvenile individual. The inclusion of *L. beltanae* nov. gen. nov. sp. in a phylogenetic analysis suggests that it is close to Theledectinae, Procolophoninae, and Leptopleurinae, though their respective relationships are uncertain. This specimen is the first procolophonid described from Madagascar and represents a minor terrestrial component of a coastal vertebrate assemblage dominated by amphibious to fully-aquatic taxa.

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RÉSUMÉ

Lasasaurus beltanae nov. gen. nov. sp., un nouveau procolophonidé (Reptilia, Parareptilia) du Trias inférieur de Madagascar est décrit. Il est représenté par un seul squelette partiel préservé dans un nodule ferro-calcaire de la Formation de la Sakamena moyenne, dans le Nord de l'île. Ce nouveau taxon est unique car il possède de fines crêtes dendritiques qui s'étendent le long du côté postérolatéral du squamosal, des dents maxillaires largement espacées, des rides mésiodistales connectant les dents maxillaires à la rangée dentaire et une marge antérieure de la copule (os hyoïde) fortement aiguë. Ce spécimen bien préservé appartient à un individu juvénile. L'inclusion de *L. beltanae* nov. gen. nov. sp. dans une analyse phylogénétique suggère qu'il est proche des Theledectinae, Procolophoninae et Leptopleurinae, bien que leurs parentés respectives soient incertaines. Ce spécimen est le premier procolophonidé décrit de Madagascar et représente une composante terrestre mineure d'un assemblage à vertébrés côtiers dominé par des taxons amphibies ou pleinement aquatiques.

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1. Introduction

The Permo-Triassic (PT) ecological crisis was the most drastic crisis in the history but the patterns of extinction in the terrestrial realm remain more poorly understood than the marine extinctions (Benton, 2003; Erwin, 1993). This is mainly because (1) most of the palaeontological data come from the marine realm (the localities with continental PT rocks cropping out are restricted to southern Africa and Russia, e.g., Jablonski, 1994; Steyer, 2009), and (2) there are few key fossil taxa that cross the PT boundary, rendering the ecological analyses of the post-crisis recovery very difficult.

Comparisons between pre- and post-crisis faunal communities showed that they underwent major structural changes (Benton et al., 2004; Nicolas and Rubidge, 2010; Roopnarine et al., 2007). This phenomenon is well exemplified in the 'main Karoo' Basin of southern Africa, where temnospondyls, cynodonts, and archosauromorphs benefited from the extinction of gorgonopsians and the decline of dicynodonts and therocephalians (Irmis and Whiteside, 2012). The supposed decline of parareptiles during the Early Triassic was recently challenged with the description and revision of procolophonoids from the South African Karoo (Botha et al., 2007; Modesto et al., 2001, 2003). These new data show that the taxonomic diversity of parareptiles was able to keep up during the PT events because the extinction of some procolophonoids, millerettids, and pareiasaurs was offset by the diversification of the remaining procolophonoids (Irmis and Whiteside, 2012; Ruta et al., 2011). Though turtles have also been considered as parareptiles (Lee, 1995; Lyson et al., 2010; Reisz and Laurin, 1991), they have been regarded, in the latest studies, as modified diapsids that are more closely related to lepidosauriforms and sauropterygians on morphological (Li et al., 2011) and molecular (Lyson et al., 2012) grounds. In this case, the only parareptiles that crossed the PT boundary would be procolophonoids. This cosmopolitan group including small to medium-sized taxa (Bartholomai and Howie, 1970; Cisneros, 2008b, 2008c; Cisneros and Schultz, 2003; Colbert, 1946; Colbert and Kitching, 1975; Gow, 1977; Li, 1989; Modesto and Damiani, 2007; Modesto et al., 2001, 2002, 2010; Piñeiro et al., 2004; Säilä, 2008, 2009, 2010a; Spencer and Benton, 2000; Sues et al., 2000; Tripathi and Satsangi, 1963) is therefore important to better understand the recovery of tetrapod faunas after the PT extinction events.

Procolophonoids, as defined by Lee (1995), comprise owenettids and procolophonids *sensu* Modesto and Damiani (2007). In Africa, they are only known from the Karoo basins of South Africa and Madagascar. An excellent record of Permo-Triassic tetrapod faunas has been produced by the extensive outcrops of the Beaufort Group, in the retroarc foreland main Karoo Basin of South Africa (Rubidge, 2005 for a review). In this basin, three owenettid and ten procolophonid genera and species are currently recognized (Cisneros, 2008a, 2008b, 2008c; Modesto and Damiani, 2003; Modesto et al., 2001, 2002, 2003, 2010; Reisz and Scott, 2002). It has also yielded most of the hundreds of specimens referred to the southern Gondwanan

Procolophon (Cisneros, 2008c). In Madagascar, however, tetrapods are restricted to the outcrops of the Sakamena and Isalo groups in the Morondava, Mahajanga, and Diego (= Antananarivo) rift basins. The Sakamena Group is especially famous for having produced abundant fossiliferous nodules, including many tetrapods (Arduini, 1993; Besairie, 1972; Currie, 1981; Ketchum and Barrett, 2004; Lehman, 1966; Maganuco et al., 2009; Meckert, 1995; Piveteau, 1926, 1955; Smith, 2000; Steyer, 2002, 2003). Though Malagasy procolophonoids are relatively common, their diversity remains very poor in comparison to South Africa. Only one has been adequately studied: the owenettid *Barasaurus besairiei* Piveteau, 1955, represented by more than a hundred specimens from the Late Permian-Early Triassic of the Lower and Middle Sakamena formations, Morondava and Diego basins (Arduini, 1993; Besairie, 1972; Ketchum and Barrett, 2004; Meckert, 1995; Piveteau, 1955; Smith, 2000; J.F., pers. obs. of MNHN specimens). Additional specimens from the Late Permian Lower Sakamena Formation of the Morondava Basin have been considered to represent two new 'procolophonids' according to Arduini (1993). There is no evidence from his brief descriptions that these specimens are actually procolophonids. In fact, the comparison of the first new taxon with the so-called 'procolophonids' *Owenetta* and *Nyctiphruretus* by Arduini (1993) suggests it might not be procolophonid at all but that it would rather belong to another procolophonian clade. More recently, a single procolophonid mandible has been mentioned, but not described, from the Middle Triassic of the Isalo Group in the Morondava Basin (Flynn et al., 1998).

Here we describe for the first time a procolophonid from the Lower Triassic of the Diego Basin of Madagascar (Discussion for a comparison with *Barasaurus*). This new taxon is represented by MNHN.F.MAE 3039, a relatively complete specimen that was briefly described by Lehman (1966) (who misidentified it as an 'Eosuchia' *sensu* Romer, 1956 at the time), and later mentioned by Kuhn (1969) and by Ketchum and Barrett (2004). This specimen had been previously examined during the early 2000s by Ross Damiani (pers. comm. to J.-S.S., 2006), who referred it tentatively to *Barasaurus*. Preliminary re-examination confirmed the procolophonoid assignment of MNHN.F.MAE 3039, though the dentition suggested procolophonid rather than owenettid affinities (Discussion). MNHN.F.MAE 3039 is the first procolophonid taxon described from Madagascar.

Institutional Abbreviations – BP: Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; MNHN: Muséum national d'Histoire naturelle, Paris, France; SAM: Iziko, South African Museum, Cape Town, South Africa.

2. Systematic palaeontology

Parareptilia Olson, 1947
Procolophonia Seeley, 1888
Procolophonoidea Lydekker in Nicholson and Lydekker, 1889 sensu Lee, 1995
Procolophonidae Lydekker in Nicholson and Lydekker, 1889 sensu Modesto and Damiani, 2007

Lasasaurus beltanae nov. gen. nov. sp.

Holotype–MNHN.F.MAE 3039, half of a ferro-calcareous nodule containing the mould of a relatively complete skeleton preserving the skull, mandible, hyoid apparatus, and presacral region. Both the nodule and its casts have been described below.

Diagnosis–Procolophonid showing several peculiar, fine and dendritic crests running along the posterolateral side of the squamosal, widely spaced maxillary teeth, subparallel mesiodistal ridges connecting maxillary teeth to the tooth row, and a strongly acute anterior margin of the copula.

Type Horizon and locality–Near the Ambodipo village, near the Mamoro River, East of Ankitokazo, Ambilobe District, Antsiranana Province, Diana Region, North of Madagascar. Middle Sakamena Formation, Diego Basin. The presence of *Magniestheria truempyi* in the same formation (Shen et al., 2002) indicates an Early Smithian (Olenekian, Early Triassic) age by correlation with the well-constrained Triassic strata of the Germanic Basin (Kozur and Weems, 2010).

Etymology–'Lasa' for 'from past' in Malagasy, 'saurus' for reptile in Latin, and 'beltanae' in honor of Laurence Beltan (former palaeoichthyologist at MNHN, Paris) who found the nodule.

3. Description

3.1. General features

The mould of the skeleton is incomplete and articulated (Fig. 1). It lies mostly on its dorsal side. The skull and the anterior region of the postcranial skeleton are well preserved. The bones have been dissolved in the ferro-calcareous nodule but a silicone cast, recently made, reveals important and new anatomical characters described below.

3.2. Skull roof

The posterior half of the right maxilla is partly visible in lateral and palatal views (Fig. 2). Its lateral surface is smooth without any foramina. The dorsal flange of the maxilla rapidly decreases in height posteriorly, then more steadily. In contrast, the ventral margin is subhorizontal. The posterior extremity of the maxilla is missing. The postorbital region was pushed in medially post-mortem, so the jugal and quadratojugal are now located medial to their anatomical position while the squamosal has rotated counterclockwise, revealing the tympanic fossa and the quadrate. The cheek region is otherwise well preserved and only visible in lateral view. The jugal is a rod-like bone with weakly dilated extremities. Its anterior end shows a laterally directed but poorly defined surface for the suture with the posterior extremity of the maxilla. In contrast, the shortness and the dilated ends of the jugal of *Procolophon trigoniceps* (Carroll and Lindsay, 1985) produce an hourglass shape. The quadratojugal is subcomplete. It is

roughly quadrangular with a smooth lateral surface. Dorsally, the quadratojugal meets the jugal along a straight suture. These two perpendicular elements form a right-angled subtemporal emargination, a configuration also known in *Coletta seca* (Modesto et al., 2002) and *Sauropareion anoplus* (MacDougall et al., in press). Morphological variation occurring in the latter (MacDougall and Modesto, 2011; MacDougall et al., in press; Modesto and Damiani, 2007) still indicates that this condition should be regarded as a variant of the broadly excavated emargination seen in most procolophonids (Cisneros, 2008a). It is distinct from the acute emargination formed by the boomerang-like jugal in *Nyctiphruretus* (Säilä, 2010b) and Owenettidae (Meckert, 1995; Reisz and Scott, 2002). In the postorbital region, the supratemporal is partly preserved. Exposed in ventral view, it is a wide blade overlying the dorsal part of the squamosal and forming the posterolateral corner of the skull. The exact shape of the supratemporal is not well defined on the silicone cast because a part of the silicone became stuck in the nodule in the course of freeing the mold from the specimen. Observation of the original print after the removal of the residual silicone suggests that the supratemporal terminates in a pointed corner, with an angle slightly lower than 90°. The squamosal and quadrate are visible in posterolateral occipital view. The squamosal presents, on its anterodorsal side, a thick tympanic flange. The temporal notch, where the tympanic membrane was attached, is represented by a shallow posterolateral depression. The quadrate is covered posteriorly by the vertical occipital flange of the squamosal. Fine parallel crests extend mediodorsally from the middle of this region toward the supratemporal–a structure unique so far in procolophonids (Fig. 2A–B). The squamosal is broken anteriorly, at the contact with the quadratojugal. The relatively high quadrate is massive and trapezoidal. The two condyles are well developed. The medial one remains in contact with the articular. The lateral condyle consists of an anteroposterior ridge located slightly dorsal to the level of the medial one. Although the quadrate is poorly preserved medially, the contact with the respective quadrate process of the pterygoid is discernible.

3.3. Palate

The palate, visible in ventral view, is articulated except for the left pterygoid. The anterior process of the pterygoid bears denticles (Dentition) along the anterolaterally directed ridge bordering the interpterygoid cavity. The basipterygoid recess of the pterygoid is short and ends in a concave surface for the basipterygoid process of the parabasisphenoid. The quadrate process forms an arcuate blade sutured extensively to the quadrate. A low, straight ridge runs anterolaterally from the centre of the pterygoid. This ridge is edentulous, in contrast with 'Owenetta' kitchingorum (Reisz and Scott, 2002: fig. 2B) and *P. trigoniceps* (Carroll and Lindsay, 1985: fig. 1B).

3.4. Mandible

The right ramus, missing its anterior tip, is visible in ventral and lateral views. The massive dentary deepens
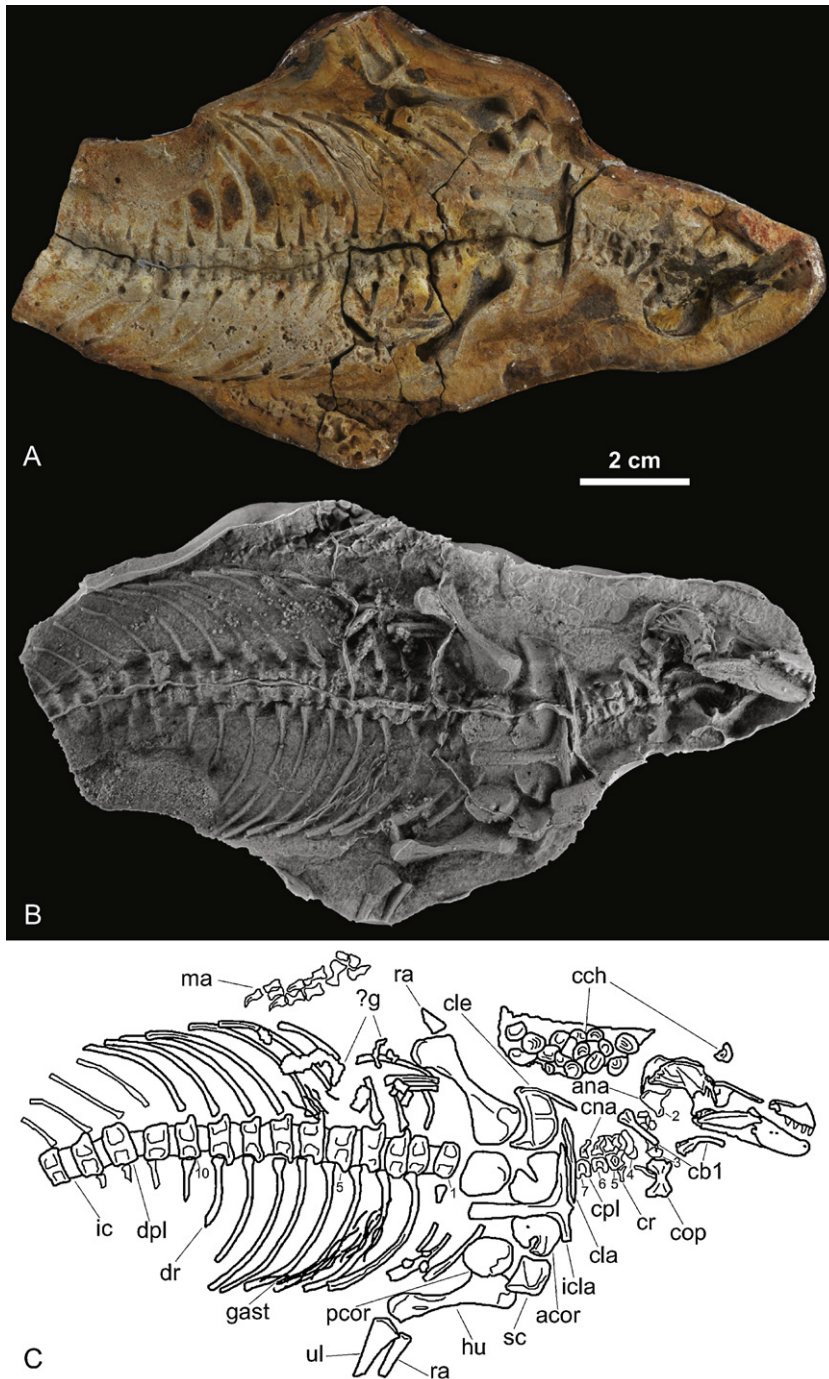
Fig. 1. *Lasasaurus beltanae* nov. gen. nov. sp. from the Lower Triassic of Madagascar. Photographs of the specimen MNHN.F.MAE 3039: original (A), cast (B), and interpretative drawing in ventral view (C). Abbreviations: acor: anterior coracoid; ana: axis neural arch; cb1: first ceratobranchial; cch: conchostracans; cla: clavicle; cle: cleithrum; cna: cervical neural arch; cop: copula; cpl: cervical pleurocentrum; cr: cervical rib; dpl: dorsal pleurocentrum; dr: dorsal rib; g: geogastroliths; gast: gastralia; hu: humerus; ic: intercentrum; icla: interclavicle; ma: manus; pcor: posterior coracoid; ra: radius; sc: scapula; ul: ulna.
Fig. 1. *Lasasaurus beltanae* nov. gen. nov. sp. du Trias inférieur de Madagascar. Photographies du spécimen MNHN.F.MAE 3039 : original (A), moulage (B) et dessin interprétatif en vue ventrale (C). Abréviations : acor : coracoïde antérieur ; ana : arc neural de l'axis ; cb1 : premier cératobranchial ; cch : conchostracés ; cla : clavicule ; cle : cleithrum ; cna : arc neural cervical ; cop : copule ; cpl : pleurocentre cervical ; cr : côte cervicale ; dpl : pleurocentre dorsal ; dr : côte dorsale ; g : géogastrolithes ; gast : gastralia ; hu : humérus ; ic : intercentre ; icla : interclavicule ; ma : main ; pcor : coracoïde postérieur ; ra : radius ; sc : scapula ; ul : ulna.
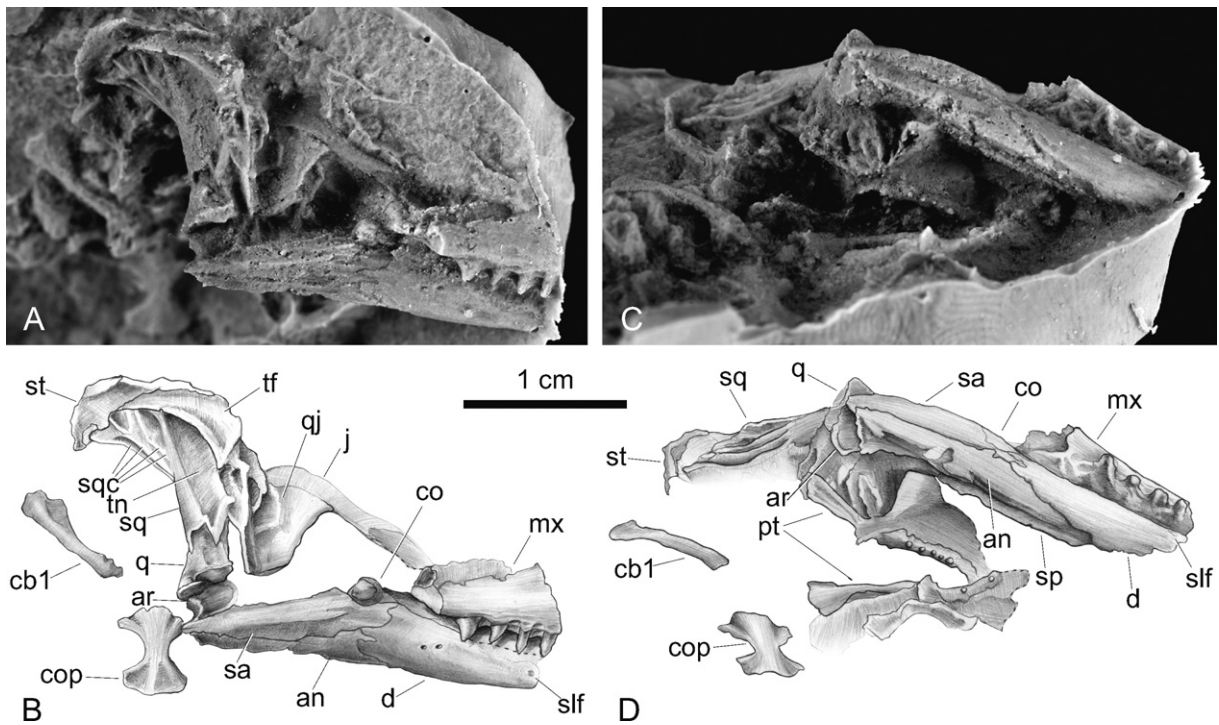
Fig. 2. *Lasasaurus beltanae* nov. gen. nov. sp. from the Lower Triassic of Madagascar. Detail of the skull. Photographs of the cast (A–C) of MNHN.F.MAE 3039 and interpretative drawings in right lateral and palatal views (B–D). Abbreviations: an: angular; ar: articular; cb1: first ceratobranchial; co: coronoid; cop: copula; d: dentary; j: jugal; mx: maxilla; pt: pterygoid; q: quadrate; qj: quadratojugal; sa: surangular; slf: supralabial foramen; sp: splenial; sq: squamosal; sqc: squamosal crests; st: supratemporal; tf: tympanic flange; tn: temporal notch.

Fig. 2. *Lasasaurus beltanae* nov. gen. nov. sp. du Trias inférieur de Madagascar. Détail du crâne. Photographies du moulage (A–C) de MNHN.F.MAE 3039 et dessins interprétatifs en vues latérale droite et palatale (B–D). Abréviations : an : angulaire ; ar : articulaire ; cb1 : premier cératobranchial ; co : coronoïde ; cop : copule ; d : dentaire ; j : jugal ; mx : maxillaire ; pt : ptérygoïde ; q : carré ; qj : quadratojugal ; sa : surangulaire ; slf : foramen supralabial ; sp : splénial ; sq : squamosal ; sqc : crêtes squamosales ; st : supratemporal ; tf : crête tympanique ; tn : échancrure temporale.

steadily posteriorly and shows a smooth lateral surface except for a labial foramen, as in *Coletta seca* (Modesto et al., 2002). The blade-like splenial occupies the medial surface of the jaw, covering the dentary medially, and reaching the angular posteriorly. The subtriangular coronoid forms, in lateral view, the eponymous prominence and is sutured ventrally to the surangular and dentary. The subtriangular surangular contributes anteriorly to the coronoid prominence. The surface of the angular and surangular, in lateral view, appears rough but only reflects tiny bubbles in the silicone cast. The articular is preserved close to the quadrate condyles. The articular region is relatively straight in lateral view, in contrast with leptopleurines in which the whole region is downturned (Li, 1989; Sues et al., 2000). The robust, subtriangular angular extends up to the level of the supralabial foramen mentioned above.

3.5. Dentition

Four teeth are preserved on the maxilla. An empty space, distal to the fourth tooth, suggests an additional tooth. In apical view, the teeth are connected by subparallel ridges running along the dental row (Fig. 3B), a condition that suggests a strong tooth attachment or even tooth ankylosis (Discussion). Although this morphology might have been

artifactual, a closer look at the mould confirms the presence of such ridges. The kind of tooth implantation is hard to identify (Discussion). The teeth are separated from each other at their bases by spaces of about the same length as the teeth, but there is no evidence for tooth replacement.

The first three mesial teeth are subconical, and this aspect becomes more pronounced distally. These teeth have a single cusp, a condition contrasting with the fourth, bicuspid tooth. In this molariform tooth, the distolabial cusp is higher and thinner than the mesiolingual one. In occlusal view, both cusps are connected by a sigmoid labiolingual crest known in some other procolophonids despite differences in the degree of curvature and sharpness (Carroll and Lindsay, 1985, fig. 14; Cisneros, 2008b). It is also broader, being as high as wide, and more bulbous than the mesial teeth. At least two tooth prints are observed on the dentary, directly on the nodule, but they are difficult to interpret. This area is unfortunately obscured by the maxilla on the silicone cast. Six large and at least three small denticles are respectively present on the anterior process of the left and right pterygoids. These denticles are scarce and widely spaced, a possible result of the poor preservation of the pterygoid area. Furthermore, both pterygoids are covered by a shagreen of denticles, close to the supposed symphyseal region, as in *Owenetta rubidgei* (Reisz and Scott, 2002).
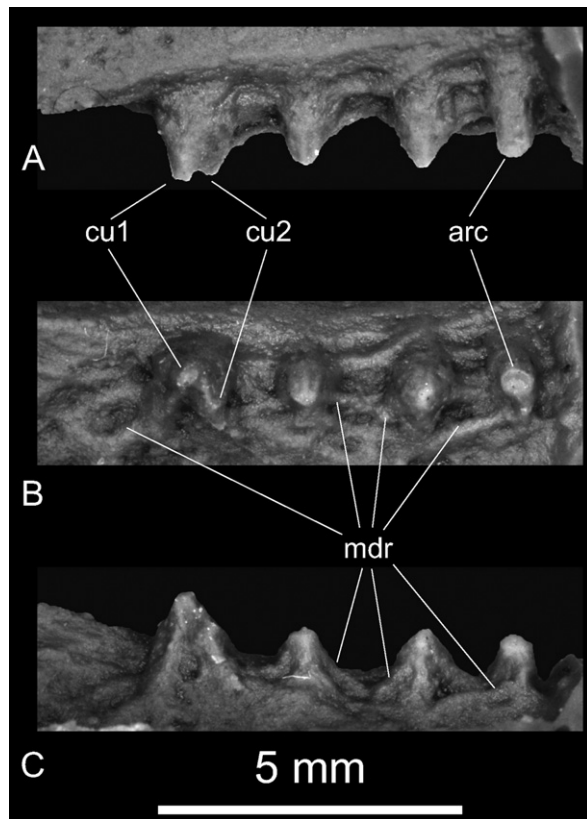
Fig. 3. *Lasasaurus beltanae* nov. gen. nov. sp. from the Lower Triassic of Madagascar. Detail of the dentition. Photographs of the cast of MNHN.F.MAE 3039 in labio-occlusal, occlusal, and lingual views (A–C). Abbreviations: arc: artefactual concavity; cu: cusp; mdr: mesiodistal ridge.

Fig. 3. *Lasasaurus beltanae* nov. gen. nov. sp. du Trias inférieur de Madagascar. Détail des dents. Photographies du moulage de MNHN.F.MAE 3039 en vues labio-occlusale, occlusale et linguale (A–C). Abréviations : arc : concavité artéfactuelle ; cu : cuspide ; mdr : ride mésiodistale.

3.6. Hyoid apparatus

The copula or *corpus hyoideum* is a thin, flat, and butterfly-shaped bone, which is wider than long. It shows two (anterior and posterior) paired processes of similar length, as in *O. rubidgei* and '*Owenetta*' *kitchingorum* (Reisz and Scott, 2002) but not in *P. trigoniceps* (Carroll and Lindsay, 1985), which has a longer posterior process. The deep concavity of the posterior margin reaches a third of the length of the bone, resulting in a U-shaped arch. Similarly, the anterior margin is V-shaped in *L. beltanae* (Fig. 2A–B), whereas that of *P. trigoniceps* (Carroll and Lindsay, 1985: figs. 9A, 13C), *O. rubidgei* (Reisz and Scott, 2002: figs. 4D, 5D), and '*Owenetta*' *kitchingorum* (Reisz and Scott, 2002: fig. 2B) is only gently concave. It differs even further from *Sauropareion*, in which the copula is bowed anteriorly (MacDougall et al., in press; Modesto and Damiani, 2007). The first ceratobranchial pair is preserved. The right one has been shifted between the pterygoids, while the left one is still connected with the copula and extends posterolaterally, overlying a part of the anterior cervical region. These ceratobranchials are slender,

rod-like elements with a ventrally bowed shaft and terminating distally in a flat, spatula-shaped end.

3.7. Vertebrae

The preserved presacral series is articulated, for a minimal vertebral count of 20 (Fig. 1C). Because the individual described here is exposed in ventral view, three to four vertebrae are obscured by the pectoral girdle. A minimal presacral count of 23 would suggest that few presacral vertebrae are missing. There are indeed 25 to 27 presacral vertebrae in procolophonoids (Broili and Schröder, 1936; MacDougall et al., in press; Meckert, 1995; Reisz and Scott, 2002; Säilä, 2010a). For convenience, the vertebral series preserved anteriorly and posteriorly to the scapular girdle of *L. beltanae* will be referred to here as the cervical and dorsal series, respectively. Six cervical vertebrae are visible in lateral view, except the missing atlas and the penultimate cervical, which is also preserved in anterior view. The third cervical is partially covered by the left ceratobranchial. The axis shows a massive neural arch with a typical hatchet-like neural spine. Its corresponding pleurocentrum could not be identified. The neural spine and the pedicel of the neural arch are relatively high. Other cervicals have shorter and more slender neural spines. The neural arches and pleurocentra have a similar height, but the latter are about twice as wide as long, resulting in a compressed aspect. The fourth cervical pleurocentrum shows a concave anterior surface suggestive of the plesiomorphic amphicoelous condition seen in procolophonids (deBraga, 2003). The pleurocentra also have a pronounced 'lip' on their anterior and posterior articular surfaces, which are connected ventrally by a strong ridge. This configuration results in a deep lateroventral excavation on the pleurocentrum. Short diapophyses are also visible anteriorly, at the junction between the neural arch and pleurocentrum. There is no trace of parapophyses, which are present on the intercentra in other procolophonoids (deBraga, 2003; Reisz and Scott, 2002).

Fourteen dorsal vertebrae are preserved in ventral view. As in the cervical series, the dorsal pleurocentra are wider than long and bear a low ventral ridge and two lateral shallow excavations. The ventral longitudinal sulcus seen in *P. trigoniceps* (deBraga, 2003) is absent. Intercentra are short, crescent-shaped, and ventrally arched. They are well developed, with a width sub-equal to that of the corresponding pleurocentra, and well ossified. This is also the case in *P. trigoniceps* (deBraga, 2003), *Nyctiphruretus acudens* (Efremov, 1940) and *B. besairiei* (Meckert, 1995). Conversely, vacant spaces between two vertebrae suggest cartilaginous intercentra in *Hypsognathus fenneri* (Colbert, 1946: pl. 27, figs. 5–6) and *Soturnia caliodon* (Cisneros and Schultz, 2003: fig. 4A–C).

3.8. Ribs

Only the presacral ribs are preserved. Two long, straight cervical ribs are located to the right of the pleurocentra of the fourth and fifth preserved vertebrae. The first one is apparently holocephalic, but the second one bears two slender articular heads separated by a depression. This

condition differs from the dichocephalic one of *P. trigoniceps* (deBraga, 2003) which has two depressions. Sixteen pairs of dorsal ribs are preserved. They are long, slender, and bowed, forming a wide rib cage. The left rib series has been slightly displaced compared to the right series, and the first ribs are broken. The ribs are flared proximally and terminate in a flat head, where the capitulum is indistinguishable from the tuberculum. The distal extremities of the ribs are also mediolaterally dilated, ending in a flat tip. From the thirteenth pair onward, they become progressively narrower and straighter, though this apparent straightening seems to be an artefact of compression.

3.9. Gastralia

Gastralia are numerous subparallel, bowed, needle-shaped elements, visible on the right side of the rib cage (Fig. 1B–C). They are thinner, shorter and slightly more curved than those of *P. trigoniceps* (deBraga, 2003) and SAM-PK-K7711 [a specimen assigned to *P. trigoniceps* by deBraga (2003), but considered later as an indeterminate procolophonid by Modesto and Damiani (2007), and as a possible *Teratophon spinigenis* by Cisneros (2008c)].

3.10. Pectoral girdle

The pectoral girdle is articulated and nearly complete, missing only the left clavicle and cleithrum. The clavicle, still in its natural position, is a slender, crescentic element ending medially in a pointed head. The shape of the dorsal process is poorly preserved. The junction of the head and branch forms an angle of about 120°. A splint-like bone, interpreted here as the cleithrum, is preserved close to its natural position on the right scapula. The cleithrum has pointed extremities and its anterior half is wider and flatter than its posterior one. This bone is rarely preserved in procolophonoids (MacDougall et al., in press; Modesto and Damiani, 2007; Reisz and Scott, 2002). The interclavicle has a typical ankyramorphan T-shape. The left lateral process of the interclavicle is missing its tip, but the right one is complete. The lateral processes are straight and the tip is recurved posteriorly, ending at the junction between the scapula and the anterior coracoid, as in *P. trigoniceps* (Colbert and Kitching, 1975: figs. 16–17). Both lateral extremities are connected by a high ridge along the anterior border of the interclavicle. A second ridge runs posteriorly along the median process. This ridge becomes gradually lower until becoming indistinguishable from the remainder of the process, at about two-thirds of the interclavicle length. Both the lateral and median ridges are approximately perpendicular and meet anteriorly on the interclavicle. The posterolateral margin of the interclavicular head is slightly concave as in *P. trigoniceps* and SAM-PK-K7711 (deBraga, 2003), whereas it forms a right angle in *Pentaedrusaurus ordosianus* (Li, 1989; Cisneros, 2008a). The anterior coracoids are flat and subcircular. A medial ridge separating the coracoid in two sub-equal parts runs along its dorsal face. A deep depression at the base of this coracoid corresponds to the opening of the coracoid foramen. The posterior coracoids, thicker and longer

than the anterior ones, are flat and subcircular too. They also present a large glenoid articular surface dorsally. The scapulae are subrectangular blades, stretched dorsolaterally. Laterally, the scapular blade presents two shallow depressions separated by a low anteroposterior ridge at mid-length. The anterior scapular margin is thin in contrast to the thick, rounded posterior margin. The latter bears a subtriangular ventral supraglenoid buttress.

3.11. Limb bones

The forelimbs are well preserved and their bones are articulated. The humerus is very robust, with broad, flat heads that are twisted at about 90° from each other, in contrast with SAM-PK-K7711 (deBraga, 2003), in which it is no more than 45°. In *L. beltanae*, the deltopectoral crest is restricted to the proximal head of the humerus in lateral view. Both humeral heads are about the same size. The entepicondyle, more prominent than the ectepicondyle, forms an angle of about 45° with the diaphyseal axis. The entepicondylar foramen, visible on both humeri, is large and elongated. The presence of an ectepicondylar foramen or groove cannot be assessed. The distal head of the humerus shows the two small lenticular surfaces for the articulation with the zeugopod.

The left ulna of *L. beltanae* is only preserved proximally. This bone is larger than the radius and has a distinct triangular proximal head with a smooth convex articular surface. The radius is a slender element showing a flat, smooth triangular articular surface for the humerus. The distal part of both radii is missing (Fig. 1C).

The autopodium is incomplete, consisting here of seven carpals, two metacarpals and ten phalanges (Fig. 4). The carpals are more or less lined up in a proximal, a medial, and a distal row. The proximal row comprises three different carpals. The lateral one, the most massive, has a pentagonal shape, with blunt edges, a large central depression, and a semicircular medial notch. The central carpal, much smaller and oval, presents a short, shallow groove in its proximal part. The medial carpal is rectangular and exhibits many rugosities. These elements are tentatively identified as the ulnare (the semicircular notch would thus border the manual perforating foramen), the intermedium, and the radiale, respectively. The medial row includes two carpals. The carpal showing a medially oriented tip and a large foramen may represent the lateral centrale. Laterally, a larger, pentagonal or round carpal with two small foramina is possibly the weakly ossified medial centrale. The distal row comprises two carpals, which may be the distal carpals 2 and 3 because they are very close to the metacarpals.

The metacarpals are recognizable by their typical hour-glass shape. The medial one presents on its medial side the typical lateral bowing of the metacarpal I seen in *P. trigoniceps*, in SAM-PK-K7711 (deBraga, 2003: figs. 3–5), and in *B. besairiei* (Meckert, 1995: figs. 24–26). Whereas its distal end is almost perpendicular to the long axis, its proximal end is deflected at 45° medially. Metacarpal II is as wide as metacarpal I, but longer. Its proximal extremity is less deflected but more developed than in the latter, however. It shows two articular surfaces, the medial one being
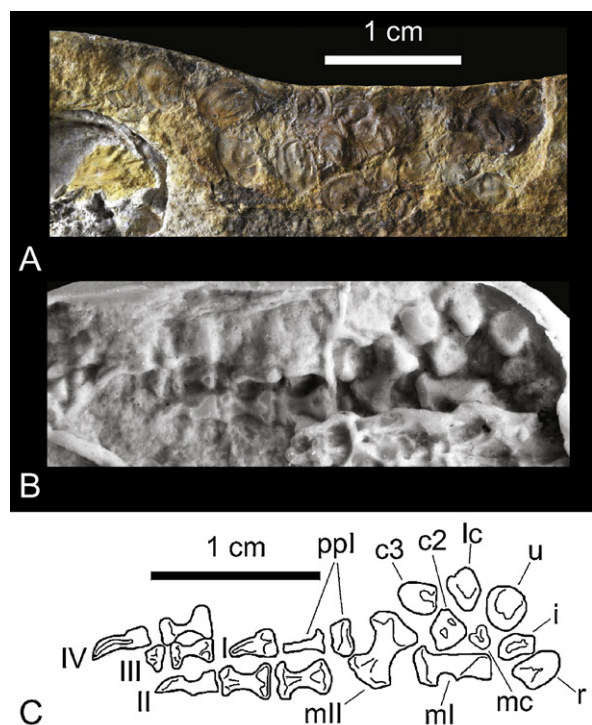
Fig. 4. *Lasasaurus beltanae* nov. gen. nov. sp. from the Lower Triassic of Madagascar. Detail of the euestheriids and right manus. Photographs of the original carapaces (A) and cast of the right manus of MNHN.F.MAE 3039 (B) and interpretative drawing in ventral view (C). Abbreviations: c: carpal; i: intermedium; lc: lateral centrale; m: metacarpal; mc: medial centrale; ppI: proximal phalanx I; r: radiale; u: ulnare; I-IV: digit number.
Fig. 4. *Lasasaurus beltanae* nov. gen. nov. sp. du Trias inférieur de Madagascar. Détail des euestheriidés et de la main droite. Photographies des carapaces originales (A) et du moulage de la main droite de MNHN.F.MAE 3039 (B) et dessin interprétatif en vue ventrale (C). Abréviations : c : carpien ; i : intermédium ; lc : centrale latéral ; m : métacarpien ; mc : centrale médial ; ppI : phalange proximale I ; r : radiale ; u : ulnaire ; I-IV : numéro des doigts.

particularly prominent. The distal end of metacarpal II bears two small and symmetrical condyles.

Four partial digits are preserved in articulation. The phalangeal formula is 2–3– > 2– > 2–?. Given the relative size, position, and articulation of the phalanges, digits III and IV may have had four phalanges each. The two elements proximal to ungual I belong to the same proximal phalanx I, artifactually separated by a break. Also, digit I overlaps digit III proximally. The print of other phalanges is possibly within the nodule. The phalanges are relatively robust, with bulbous extremities showing two distinct surfaces each. The ungual phalanges are recurved and bear a deep median lateral groove.

3.12. ?Geogastroliths

Clustered rounded pits are visible all over the rib cage, especially on the right side (Fig. 1B–C). They are considered either as sedimentary micronodules or as possible geogastroliths (*sensu* Wings, 2007) that would have been dissolved and/or removed by weathering. Though geogastroliths are so far unknown in procolophonids, quartz

pebbles (5 mm > 1 cm) are frequently found in the left ventral region of specimens of *Barasaurus* (Smith, 2000; J.F., pers. obs. of MNHN.F.MAP 88, 161, 191).

4. Discussion

4.1. Ontogenetic age

The immaturity of MNHN.F.MAE 3039 at the time of death is revealed by the weak ossification and co-ossification of its postcrania. The former phenomenon is illustrated by: (1) the nearly circular shape of the coracoids; (2) the convex but smooth and weakly developed articular surfaces of limb elements (humerus, ulna, radius, carpus); and (3) the absence of a distinct olecranon. The lack of co-ossification is also notable, given that: (4) the axial neural arch is free; (5) post-axial cervical vertebrae show an open neuropleurocentral suture–though they may be actually free because the area was left undisturbed after death; (6) the scapula and coracoids are free. In fact, this is the case in all procolophonids in which this region is preserved, even in mature specimens (Colbert and Kitching, 1975; deBraga, 2003; Li, 1989; Säilä, 2010a; Sues and Reisz, 2008), suggesting that the pectoral girdle elements did not co-ossify during ontogeny in these reptiles.

4.2. Comparison with Barasaurus

Until recently, *Barasaurus* was represented by dozens of nodules collected from the Lower Sakamena Formation only, in the Morondava Basin (Meckert, 1995; Piveteau, 1955; Smith, 2000). The description of additional material showed that this genus is also present in the Middle Sakamena Formation in the Diego Basin (Ketchum and Barrett, 2004). Thorough comparisons between MNHN.F.MAE 3039 and *Barasaurus* are therefore necessary to justify their separation. The following comparisons are based on specimens assigned to *B. besairiei* (casts of MNHN.F.MAP 88, 166, 186, 191, and an unnumbered MNHN specimen, the last two being respectively cited as 'P 1' and 'P 6' in Meckert, 1995).

In this case, the dentition is particularly informative. The most conspicuous feature is the presence of a bicuspid tooth in MNHN.F.MAE 3039, distally. Among procolophonians, bicuspidy is so far only known in procolophonids. The low, blunt conical shape of the more mesial teeth is also distinctive. The dentition of *Barasaurus* consists of slender conical teeth with a pointed apex. These teeth are furthermore tightly packed on the tooth row, where they are inserted in a distinct groove (MNHN.F.MAP, unnumbered). There is also an empty alveolus for each missing tooth. This is not the case in MNHN.F.MAE 3039. Its teeth are widely spaced, but there is neither a groove nor an indication of tooth loss or replacement explaining this pattern. The tooth row surface is covered instead by mesiodistal ridges that are connected to the teeth. These ridges might have strengthened the attachment of the teeth to the maxilla. They may even be related to tooth ankylosis, though this interpretation must remain speculative given the absence of actual bone and teeth. Interestingly, both MNHN.F.MAP (unnumbered) and MNHN.F.MAE 3039 bear the high lingual walls typical of acrodont implantation,

although the presence of a groove and alveoli in the former suggest rather a protothecodont condition. This apparent inconsistency may be the first stage of the setting of a 'pseudo-acrodont' implantation–described in detail for the procolophonids *Soturnia* by Cabreira and Cisneros (2009) and *Sauropareion* by MacDougall and Modesto (2011)–characterized by the combined presence of high lingual walls, protothecodont implantation, tooth replacement (albeit very slow), and tooth ankylosis (MacDougall and Modesto, 2011). This configuration is likely that displayed by MNHN.F.MAE 3039 (except for the speculative ankylosis). However, because the mode of tooth replacement and implantation of procolophonids remain highly disputed (Cabreira and Cisneros, 2009; MacDougall and Modesto, 2011; Säilä, 2009), it will not be discussed further.

The maxillary tooth count is also helpful to distinguish *Lasasaurus* from *Barasaurus*. That of the latter can be estimated using MNHN.F.MAP (unnumbered), on which the maxillae are adequately exposed. This specimen bears 12 teeth on the left maxilla and 13 on the right one, with respectively nine and seven empty alveoli. This suggests a total tooth count of 20–21, close to the reconstructed count of 19–20 of Meckert (1995) and to that of 20 for 'Owenetta' *kitchingorum*, (J.F., pers. obs. of BP/1/4195a). Such a count is much higher than in MNHN.F.MAE 3039 with its four teeth, considering the preserved length of the maxilla in the latter. Though its actual tooth count cannot be assessed, this likely reflects the trend to reduction of tooth count seen in procolophonids.

Other features supporting the separation of *Lasasaurus* from *Barasaurus* include the right angle (versus acute) temporal emargination, the presence (versus the absence) of dendritic crests on the squamosal, the presence (versus the absence) of an entepicondylar foramen, and the prominent (versus smooth) interclavicular medial ridge. These characters also justify the assignment of *Lasasaurus* to Procolophonidae.

4.3. Phylogeny

A phylogenetic analysis was performed to determine the position of *L. beltanae* within Procolophonidae and to test the monophyly of the group. The data matrix was taken from Cisneros (2008a) and modified following Cisneros (2008b), Modesto et al. (2010), MacDougall and Modesto (2011), and MacDougall et al. (in press). The characters are numbered here from 1 to 59. The new Malagasy procolophonid was added to the data matrix in order to test its phylogenetic position. In a recent redescription, *N. acudens* was shown having an acute temporal emargination (Säilä, 2010b). This taxon was therefore rescored accordingly as '1' for character 13. New material referred to *Sauropareion* (MacDougall et al., in press) indicates that *Coletta* should be scored as '2' for the same character (Description). Twenty-six taxa and 59 characters (42 cranial and 17 postcranial) were considered (Appendix A for data matrix and Appendix B for character list). Following Cisneros (2008a), the parareptiles *Nyctiphruretus* and Owenettidae were selected as outgroups. Owenettidae were subdivided into 'Owenetta' *kitchingorum* (Reisz and Scott, 2002; J.F. pers. obs. of BP/1/4195a and b) and *B. besairiei* (Meckert,
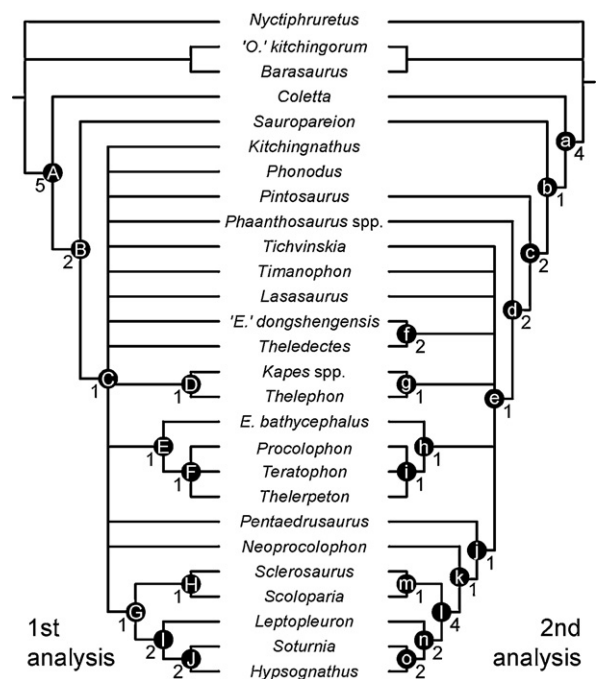

Fig. 5. Strict consensuses of the 255 and 15 equally parsimonious trees obtained by the first and second phylogenetic analyses, respectively (in the second, two taxa were deleted to improve resolution). The Bremer support is given for each clade of the strict consensus. For convenience, the letters designating clades are in upper case for the first analysis and in lower case for the second one.

Fig. 5. Consensus stricts des 255 et 15 arbres équiparcimonieux obtenus par les première et seconde analyses phylogénétiques, respectivement (dans la seconde, deux taxons ont été retirés pour améliorer la résolution). L'indice de Bremer est donné pour chaque clade du consensus strict. Par commodité, les lettres désignant les clades sont en capitale pour la première analyse et en minuscule pour la seconde.

1995; J.F., pers. obs. of MNHN.F.MAP 88, 161, 186, 191, and unnumbered). The scoring is consistent with that of Owenettidae except for three characters: character 23 was rescored as '1' for both taxa (Meckert, 1995; Reisz and Scott, 2002), character 38 as '1' for *Barasaurus* because it has no pterygoid dentition (Meckert, 1995), and character 56 as '1' for *Barasaurus* according to the femur/humerus length ratio given by Meckert (1995) (p. 75). The analysis was performed using the heuristic search of the software PAUP 4.0 beta10 (Swofford, 2002) and TNT 1.1 (Goloboff et al., 2008). Characters were considered unordered and equally weighted, and polymorphism was treated using the "uncertainty" option. Branches with a maximal length of zero were collapsed using Collapsing Rule 3.

The first analysis resulted in 255 equally optimal trees of 133 steps each (CI = 0.617; RI = 0.787) of which the strict consensus is 181 steps long (CI = 0.453; RI = 0.586). The topology of the latter (Fig. 5) is identical to that found by MacDougall and Modesto (2011) and MacDougall et al. (in press), except, of course, for the presence of *Lasasaurus*. *Coletta* and *Sauropareion* are successive sister taxa to clade #C, which contains the remaining procolophonids. This clade consists of a huge polytomy formed by clades #D, #E (=Procolophoninae), and #G (=Leptopleurinae) and 11

other terminal taxa including *Lasasaurus*. This lack of resolution is not only caused by the amount of missing data, but also by the erratic behaviour of some of the taxa included in the analysis. Using the comparative pruning option of TNT, the most erratic taxa were identified as *Phonodus* (three nodes gained) and *Kitchingnathus* (two nodes gained).

A second analysis was therefore performed without *Phonodus* and *Kitchingnathus*. It generated 15 optimal trees of 126 steps each (CI = 0.651; RI = 0.787) for a strict consensus of 137 steps (CI = 0.599; RI = 0.770). Procolophonid interrelationships were better resolved than in the first analysis. About half of the clades have a very low Bremer support (1), however. It is a bit higher in clades #c, #d, #f, #n, and #o (2) and much stronger in clades #a (=Procolophonidae) and #o (4). The strict consensus (Fig. 5) shows a monophyletic Procolophonidae as in previous analyses (Cisneros, 2008a; Modesto and Damiani, 2007; Modesto et al., 2002; Piñeiro et al., 2004; Säilä, 2008). Unequivocal synapomorphies of procolophonids include the presence of roughly circular or dorsoventrally expanded external nares (3[1*]) bordered posteroventrally by a depression of the maxilla (6[1*]), a broadly excavated temporal ventral margin (13[2*]), four premaxillary teeth (26[1*]), and vomerine teeth anteriorly (35[1*]) but not along the posteromedial suture (36[1]) (changes followed by a star are non-homoplastic). *Lasasaurus* belongs to clade #e, where it forms a polytomy with *Tichvinskia*, *Timanophon*, #f (=Theledectinae), #g, #h (=Procolophoninae), and #j (=Leptopleurinae). Clade #e is supported univocally by the presence of external nares which are anterior to the first premaxillary tooth (2[1*]), a wide internarial bar (4[1*]), an orbitotemporal fenestra of which the posterior margin is beyond the posterior border of the pineal foramen (8[2*]), enlarged mesialmost premaxillary teeth (27[1*]), both mono- and bicuspid maxillary teeth (31[1*]), eight to six maxillary teeth (32[3*]), an inset of maxillary cheek teeth (33[1*]), and two widely separated cusps on dentary molariforms (41[2*]). Among these characters, *Lasasaurus* could only be scored for characters 31 and 33. Its inclusion in clade #e is founded on the presence of mono- and bicuspid maxillary teeth (31[1]) despite the fact that they are not inset from the lateral surface of the bone (33[0]) as are those of most members of the clade. The latter feature, interpreted here as a reversion, is shared with Theledectinae. It might represent a mere convergence, a potential synapomorphy uniting *Lasasaurus* to this clade, or, more likely, a symplesiomorphy. In the last two cases, it would mean that *Lasasaurus* is not as close as *Tichvinskia* is to Procolophoninae and Leptopleurinae.

In previous analyses of procolophonid interrelationships, *Tichvinskia* was found as either a Leptopleurinae (deBraga, 2003; Modesto and Damiani, 2007) or the sister taxon of the clade (Procolophoninae + Leptopleurinae) (Cisneros, 2008a, 2008b; Modesto et al., 2001, 2002, 2010; Piñeiro et al., 2004; Säilä, 2008). In addition, Theledectinae has been suggested as the sister taxon to the clade (*Tichvinskia* (Procolophoninae, Leptopleurinae)) (Cisneros, 2008a, 2008b; Modesto et al., 2010). The discovery of new material referable to *Sauropareion* sheds light on the relationships of this genus with *Coletta* and the clade including other procolophonids, but it results in the collapse of many

branches in the latter. The phylogenetic resolution could be improved by removing *Phonodus* and *Kitchingnathus*, but the interrelationships of Theledectinae, Procolophoninae, Leptopleurinae, *Tichvinskia*, and, of course, *Lasasaurus* remain uncertain. This lack of resolution within clade #e is unfortunate because the interrelationships of its members are crucial to elucidate aspects of the evolution of procolophonids, such as their ecological adaptation, the timing of their diversification, and their biogeographical range.

4.4. Palaeoenvironment and palaeoecology

Procolophonoids are the only parareptiles that survived the PT mass extinction (Cisneros, 2008a; Modesto et al., 2001). The Early Triassic radiation of procolophonids is likely the result of diverse dietary specializations related to deep modifications of the jaw apparatus and teeth (Cisneros, 2008a). The ecological success of these reptiles appears linked to their spread across Pangaea–including Madagascar–as early as the Early Triassic. Although in some areas procolophonids are the most common reptiles (Nicolas and Rubidge, 2010; Thulborn, 1986), MNHN.F.MAE 3039 is the first procolophonid identified from the Middle Sakamena Formation, despite intensive collection of fossil vertebrates. Finally, a comprehensive palaeoclimatic study has shown promising results in investigating the geographical distribution and relative abundance of leptopleurines and traversodont therapsids in eastern North American rift basins during the Late Triassic (Whiteside et al., 2011). It showed that their respective ecological preferences have a major bearing on their biogeography. Such a study is needed for the Early Triassic, but, meanwhile, it is hard to interpret the occurrence of procolophonids in Madagascar at that time. In fact, their scarcity in the Middle Sakamena Formation can be hypothesized as the mere result of unfavourable palaeoenvironmental settings.

MNHN.F.MAE 3039 provides palaeoecological and taphonomical evidence to help reconstruct the depositional environment. This evidence includes several suboval structures bearing concentric striations, located right to the neck region of the holotype of *L. beltanae*. These remains are interpreted as carapaces of euestheriid conchostracans, identified as *Palaeolimnadia* sp. and *Euestheria* sp. or *Magniestheria* sp. by Heinz Kozur (pers. comm. to M.A., 2011). Their presence here may be explained by scavenging on *L. beltanae*, a frequent behaviour in these crustaceans (Martin and Christiansen, 1995). Euestheriids are abundant in the Middle Sakamena Formation of Madagascar (Besairie, 1972). They are represented by *M. truempyi*, which is considered euryhaline, living in brackish, estuarine, deltaic, or coastal palaeoenvironments (Shen et al., 2002). However, because most extant species live in temporary freshwater ponds, they could be also considered freshwater indicators (Vannier et al., 2003). The conchostracans preserved on MNHN.F.MAE 3039 are also associated with a wide range of facies (from freshwater ponds, shallow lakes, or floodplains to brackish estuarine deposits), but are at least indicative of a low energy depositional environment (Heinz Kozur, pers. comm. to M.A., 2011). Here, in the Middle Sakamena Formation, euestheriids are typically associated with marine interbedding,

suggesting that the palaeoenvironment was probably deltaic and under tidal influence. These conclusions are reinforced by the co-occurrence of (possibly) terrestrial, freshwater, brackish, and especially marine indicators (Maganuco et al., 2009 for a review).

Lasasaurus shows no osteological adaptation to an aquatic or even amphibious mode of life, in contrast to the temnospondyls (Lehman, 1966; Maganuco et al., 2009; Steyer, 2002, 2003) and diapsids (Ketchum and Barrett, 2004) found in the same formation. Yet, one may argue that the presence of (possible) geogastroliths in *Lasasaurus* may have been used to regulate buoyancy. This is the case, for instance, in the supposedly amphibious diapsid *Hovasaurus boulei* (Currie, 1981; Piveteau, 1926; Smith, 2000) from the Lower and Middle Sakamena formations (Ketchum and Barrett, 2004). This species displays various morphological adaptations to swimming and would have used geogastroliths as ballast (Currie, 1981; Smith, 2000). Geogastroliths are also common in *Barasaurus* (Smith, 2000; J.F. pers. obs. of MNHN.F.MAP 88, 161, 191), which shows no osteological evidence of aquatic adaptation. Surprisingly, lithological and taphonomical data suggest otherwise. According to Smith (2000), *Barasaurus* is indeed the dominant component of a fossil assemblage (comprising also actinopterygians and plant remains) that was deposited in a distal lacustrine environment. He also noted that, if the geogastroliths of *Barasaurus* and *Hovasaurus* had been used as a gastric mill, plants fragments should be expected in its pebble mass. Yet, despite the preservation of macroplant fossils next to several skeletons, Smith (2000) observed no plant remains in the pebble mass of any of the *Barasaurus* and *Hovasaurus*-bearing nodules he inspected, hence concluding that the concentration of geogastroliths should be rather interpreted as having a ballast function in these reptiles. From these data, an amphibious to mostly aquatic mode of life is inferred for *Barasaurus*. In contrast, procolophonids are considered as terrestrial. Their taphonomy and the various anatomical adaptations they exhibit even suggest that they were burrowers (MacDougall et al. (in press) for a discussion). There is currently no evidence for the need of buoyancy regulation in these reptiles. These geogastroliths would have been more likely used by *L. beltanae* to crush hard prey or to grind hard-fibre plants to help digestion, a hypothesis that is consistent with the supposed specialization toward a durophagous diet in procolophonids. Finally, the limited disarticulation of its remains indicates that it was deposited and buried shortly after death. This implies brief transport and the proximity of the terrestrial source, consistent with the supposed depositional environment.

The deltaic to coastal lagoonal environmental setting of the Diego Basin was likely the main influence on the preserved composition of the Madagascar tetrapod fauna during the Early Triassic. This depositional environment contrasts strongly with that of the contemporaneous strata of the Beaufort Group, in the main Karoo Basin, that were deposited in wide floodplains associated with braided and meandering river systems (Catuneanu et al., 1998). Additionally, the Diego Basin was closer to the Equator and had therefore a much warmer and a bit wetter climate than the main Karoo Basin (Péron et al., 2005). Although Madagascar and Africa were in contact at that time, it is therefore not surprising that the Early Triassic Beaufort Group and Middle Sakamena Formation tetrapod faunas are very different taxonomically and ecologically (Battail et al., 1987). Besides, the association of relictual Permian tetrapods (Ketchum and Barrett, 2004) alongside typical Triassic forms (Maganuco et al., 2009; Steyer, 2002, 2003; this work) in the Middle Sakamena Formation suggests that Madagascar acted as a refuge zone during the PT extinction events.

5. Conclusion

The procolophonoids represent a relatively well-known and widespread group of particular interest because they crossed the PT boundary. However, their presence and distribution in the Karoo rift basin of Madagascar has remained very limited up to now. In this article, we describe for the first time a well-preserved and relatively complete procolophonid from the Early Triassic of Madagascar. This taxon, named *L. beltanae*, is important because it is one of a few procolophonids with a preserved postcranial skeleton. It illustrates the post-extinction recovery of procolophonids by increasing their Early Triassic diversity. Finally, the description of *Lasasaurus* enlarges the distribution of Early Triassic procolophonids to Madagascar and complements existing data on the rich and diversified coastal palaeoenvironment of the Middle Sakamena Formation that comprised various aquatic 'invertebrates', actinopterygians, actinistians, dipnoans, and temnospondyls but very few plants and reptiles (Maganuco et al., 2009 for a review).

Appendix A. Supplementary data

Scripted TNT data matrix (Appendix A) and character list (Appendix B) with online version of this article available at http://dx.doi.org/10.1016/j.crpv.2012.04.001.

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