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FIRST RECORD OF THE MOSASAUR *PLATECARPUS* COPE, 1869 FROM SOUTH AMERICA AND ITS SYSTEMATIC IMPLICATIONS

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ABSTRACT – Two isolated, presumably shed, marginal tooth-crowns of the mosasaur *Platecarpus* sp. are described from the upper Turonian and Turonian-Coniacian (Upper Cretaceous) of the Sergipe Basin in northeastern Brazil. They represent the first record of the genus from South America, thus extending the geographic range of *Platecarpus* beyond Africa, Europe and North America. It is suggested that *Platecarpus* originated in the northern part of the incipient South Atlantic Ocean during the early Late Cretaceous.

Keywords: *Platecarpus*, Mosasauridae, Turonian, Coniacian, Cretaceous, Sergipe, Brazil.

RESUMO – São descritas duas coroas dentais marginais, provavelmente descartadas, do mosassauro *Platecarpus* sp., provenientes do Turoniano superior e Turoniano-Coniaciano da bacia de Sergipe, Nordeste do Brasil. Representam o primeiro registro deste gênero da América do Sul, e estendendo, assim, a sua distribuição geográfica para além da África, Europa e América do Norte. Sugere-se que o gênero *Platecarpus* tenha se originado no iníco do Neo-Cretáceo na região setentrional do incipiente Oceano Atlântico Sul.

Palavras-chave: *Platecarpus*, Mosasauridae, Turoniano, Coniaciano, Cretáceo, Sergipe, Brasil.

INTRODUCTION

The marine Cretaceous rocks exposed in the Sergipe Basin in northeastern Brazil (Figure 1) contain a rich macroinvertebrate fauna dominated by ammonites (Bengtson, 1996, 1999, and references therein), bivalves (e.g., Bengtson, 1983; Hessel, 1988; Seeling & Bengtson, 1999; 2003a, 2003b; Andrade *et al.*, 2003, 2004), gastropods (Burrer *et al.*, 2002) and echinoids (e.g., Smith & Bengtson, 1991; Manso & Souza-Lima, 2003). Vertebrate remains are locally common and mainly represented by scales, teeth, and vertebrae of bony fishes, whereas reptilian remains are rare (Bengtson, 1983). Here we describe two isolated, presumably shed, marginal tooth-crowns of the mosasaur *Platecarpus* Cope, 1869, from the upper Turonian and near Turonian-Coniacian, respectively. For biostratigraphic data and locality descriptions, see Bengtson (1983, appendix 1) and Koutsoukos & Bengtson (1993).

The Mosasauridae is geographically one of the most widely distributed groups of Cretaceous marine tetrapods, with reported occurrences from all continents, including Antarctica (e.g., Gasparini & del Valle, 1981, 1984; Martin *et al*., 1999; Novas *et al*., 2002). Among the mosasaurs, *Platecarpus* is one of the most widespread genera; it has been reliably identified from Africa, Europe and North America, (e.g., Thévenin, 1896; Antunes, 1964; Russell, 1967; Bardet *et al*., 1991), and now also from South America. Reports from New Zealand (Lingham-Soliar, 1994) are probably based on a misidentification (Bell *et al*., 1999). The vast majority of reports of *Platecarpus* are from the Santonian-lower Campanian of the Western Interior of North America (Russell, 1988). Older North American occurrences include, for example, the upper Coniacian of the Smoky Hill Chalk in Kansas (Everhart, 2003) and the Coniacian of the Austin Chalk in Texas (Thurmond, 1969).

In general, mosasaur remains from the Turonian are rare and fragmentary. *Platecarpus* is one of the few genera with a reliable Turonian record, as demonstrated by a reasonably complete skull of *P. bocagei* (Antunes, 1964) collected from the Kwanza (Cuanza) basin in Angola (Antunes, 1964; Lingham-Soliar, 1994). The presence of *Platecarpus* in Brazil widens the paleobiogeographic range of the genus beyond Africa, Europe and North America, and the Turonian age supports its inferred basal position within the evolution of the Mosasauridae.

GEOLOGICAL SETTING

The Sergipe Basin is located in the coastal and contiguous offshore part of the state of Sergipe in northeastern Brazil (Figure 1). It is one of the numerous South Atlantic continental margin basins that were formed as a result of rifting and separation of South America from Africa in late Mesozoic times. Structurally, the basin forms a half-graben, which is limited to the south-east by the continental slope and to the north-west by a system of normal faults. The sedimentary fill comprises a basal, Upper Carboniferous to middle Aptian non-marine succession and an Aptian to Miocene marine succession, which together represent one of the most complete Cretaceous sequences recorded in the South Atlantic marginal basins (Souza-Lima *et al.*, 2002, and references therein).

The marine succession consists of the carbonate Riachuelo and Cotinguiba formations and the clastic Calumbi Formation (Figure 1C). The material described herein derives from the Cotinguiba Formation, which was deposited during the Cenomanian-Coniacian interval in neritic to upper bathyal environments under moderately dysoxic to fully anoxic bottom conditions and well-oxygenated epipelagic conditions (Bengtson, 1983; Berthou & Bengtson, 1988; Koutsoukos *et al.*, 1991). The formation is dated primarily with ammonites, inoceramid bivalves and foraminifers (Bengtson, 1983; Kauffman & Bengtson, 1985; Koutsoukos & Bengtson, 1993; Seeling & Bengtson 2003a; Andrade *et al.*, 2003, and unpublished results). The age of the two mosasaur teeth described here is established as late Turonian and Turonian-Coniacian, respectively, on the basis of ammonites and inoceramids.

The geological evolution and the development of the marine Cretaceous of the Sergipe Basin have been discussed at length by several authors, e.g., Ojeda & Fugita (1976), Ojeda (1982), Bengtson (1983), Koutsoukos & Bengtson (1993), Koutsoukos *et al.* (1993), Feijó (1995) and Souza-Lima *et al.* (2002). For more detailed information on the evolution of the Cretaceous carbonate succession the reader is referred to Koutsoukos *et al.* (1993).

PREVIOUS WORK

Occurrences of early mosasauroids (apart from aigialosaurs) are based mainly on isolated remains (e.g., Lundelius & Warne, 1960; Martin & Stewart, 1977; Bell & VonLoh, 1998; Vilas Bôas & Carvalho 2001), although reasonably complete skeletons have been collected from the upper(?) Turonian of Angola (Antunes, 1964; Lingham-Soliar, 1994), the upper Turonian of Colombia (Páramo-Fonseca, 2000) and the lower Turonian of Morocco (Bardet *et al.*, 2003). A nearly complete skeleton (No. PMU R163, Museum of Evolution, Uppsala University, Sweden) of the basal mosasaur *Halisaurus sternbergi* (Wiman, 1920) from the upper Coniacian-lowermost Campanian Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA, provides a rare insight into the anatomy of early members of the mosasaur group (Bardet & Pereda Suberbiola, 2001). In this species, the most fundamental adaptations to a life in the marine realm, such as dorsally located nares and a laterally compressed tail, had already evolved, although a number of characters, including the primitive configuration and morphology of the limb elements, indicate a terrestrial origin (see, e.g., Bardet & Pereda Suberbiola, 2001, fig. 1).

Mosasaur teeth have long been known from Brazil, with records of the genera *Globidens* Gilmore, 1912 and *Mosasaurus* Conybeare, 1822 from the upper Campanian-Maastrichtian of the Pernambuco-Paraíba Basin (Price, 1953, 1957; Carvalho, 1996; Carvalho & Azevedo, 1998) and *Plioplatecarpus* Dollo, 1882 (including vertebrae) from the upper Campanian of the Sergipe Basin (Souza-Lima, 2001; Bertini, 2002). Indeterminate mosasaurine teeth from the São Luís Basin (Maranhão) were described and dated as Cenomanian on palynological grounds (Eugênio, 1994; Vilas Bôas & Carvalho, 2001), although a later age cannot be excluded (I.S. Carvalho, UFRJ, Rio de Janeiro, *in litt.*, 9 February 2004). Records from the Acre Basin in westernmost Brazil are considered doubtful (Brito *et al.*, 1992).

The genus *Platecarpus* has previously not been definitely identified from Brazil. Carvalho & Azevedo (1998) reported isolated teeth from the Pernambuco-Paraíba Basin showing features characteristic of this genus but assigned them only broadly to the subfamily Plioplatecarpinae Their brief description and sketchy drawings do not allow a generic determination.

SYSTEMATIC PALAEONTOLOGY

Dental terminology used herein follows mainly that of Lindgren & Siverson (2002, fig. 2). Institutional abbreviations: MN, Museu Nacional, Rio de Janeiro, Brazil; PMU, Museum of Evolution, Palaeontology Section, Uppsala University, Uppsala, Sweden; FHSM, Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas, USA.

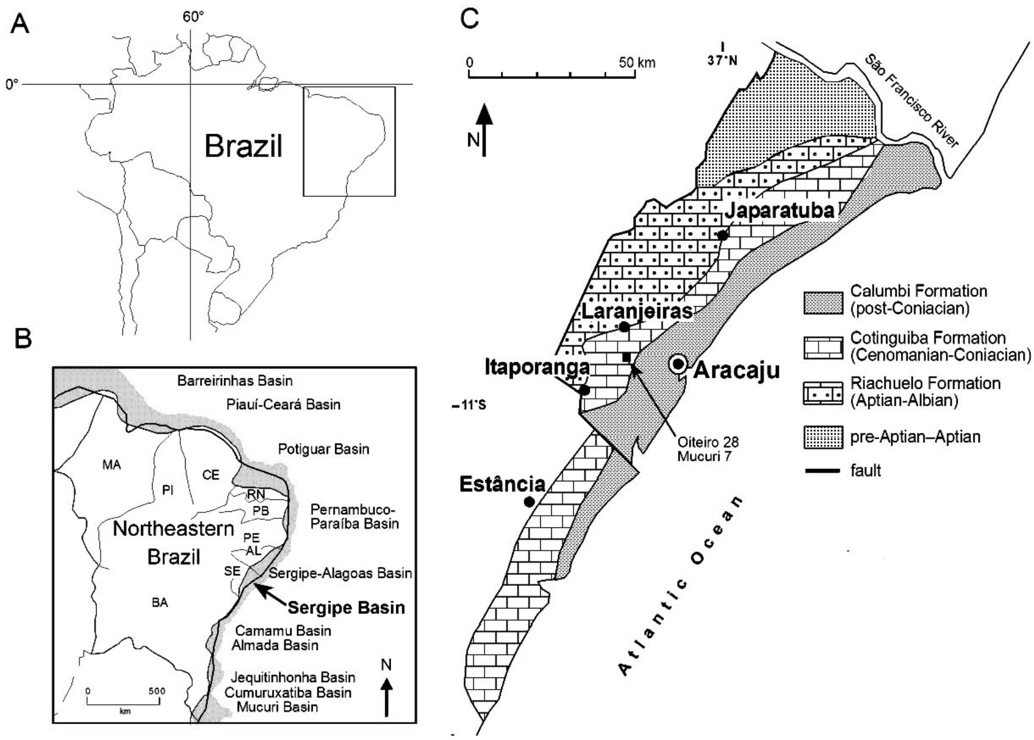

Figure 1. A- B,. Location of the Sergipe Basin and other continental margin basins in northeastern Brazil. **C**. Geology of onshore portion of the Sergipe Basin below the non-marine Cenozoic cover, with mosasaur localities Oiteiro 28 and Mucuri 7 (adapted from Bengtson, 1983 and Seeling & Bengtson, 2003). **Abbreviations**: **AL**, Alagoas; **BA**, Bahia; **CE**, Ceará; **MA**, Maranhão; **PB**, Paraíba; **PE**, Pernambuco; **PI,** Piauí; **RN**,

Order SQUAMATA Oppel, 1811
Family MOSASAURIDAE Gervais, 1853
Subfamily PLIOPLATECARPINAE Williston, 1897

Diagnosis. See Russell (1967).

Remarks. As defined by Lindgren (2004), isolated teeth of plioplatecarpine mosasaurs are readily distinguished from those of mosasaurines, tylosaurines and *Halisaurus* Marsh, 1869 on the basis of the following character state combination: (1) fine hairline striations on, at least, the basal portion of the lingual face of the crowns; (2) labial and lingual surfaces faceted, rendering the crowns a more or less prismatic appearance; (3) carinae prominent but lacking serrations; (4) crowns more or less abruptly curved distally from approximately the mid-point of their height; (5) basal cross-section elliptical to sub-circular; (6) labial and lingual surfaces on latero-posterior teeth almost equally convex, whereas anterior teeth have a gently convex labial face and a deeply U-shaped lingual surface; (7) crowns generally slender and slightly pointed in lateral view.

Genus PLATECARPUS Cope, 1869

Type species. *Platecarpus tympaniticus* Cope, 1869, from the Santonian Tombigbee Sand near Columbus, Mississippi.

Diagnosis. See Russell (1967).

Remarks. Despite being one of the best known mosasaur genera, the taxonomic status of *Platecarpus* is still unclear. In a recent phylogenetic revision of the Mosasauroidea, Bell (1997) concluded that *Platecarpus* is a paraphyletic genus and hence not a valid taxon. Moreover, the well-known *P. ictericus* (Cope, 1871) and *P. coryphaeus* (Cope, 1872) may both be junior synonyms of *P. tympaniticus*, as the characters previously used to distinguish between these three nominal species (e.g. Russell, 1967) most likely represent natural and/or ontogenic variation (Kiernan, 2002; Everhart, 2003, and references therein). Besides *P. tympaniticus*, three nominal species of *Platecarpus* are currently considered valid, i.e. *P. planifrons* (Cope, 1874) from the upper Coniacian-lower Santonian part of the Smoky Hill Chalk in Kansas, USA, *P. bocagei* (Antunes, 1964) from the upper (?) Turonian of Angola, and *P. somenensis* Thévenin, 1896 from the lower Campanian of France (e.g., Lingham-Soliar, 1994; Lindgren, 2004; but see also Everhart, 2003). In addition, Arambourg (1952) tentatively assigned his new species *ptychodon* from the Maastrichtian of Morocco to *Platecarpus*. Isolated teeth of '*P.*' *ptychodon* share a few characters with *Platecarpus*, such as faceted labial and lingual surfaces. However, the low and compressed form of the crowns (see Arambourg, 1952, pl. 39, figs. 1-7) is markedly different from that seen in marginal teeth of *P.*

tympaniticus, *P. planifrons*, *P. somenensis* and *P. bocagei*. '*Platecarpus*' *ptychodon* is here considered as a valid species although of uncertain generic affinity. This view is supported by a recent find of a nearly complete skull in the Maastrichtian phosphates of Morocco, which is currently being examined at the Muséum National d'Histoire Naturelle in Paris, France (Bardet *et al*., 2004).

With the exception of *P. somenensis* and related forms (see Thévenin, 1896, pl. 30, figs. 1-2; Lindgren, 2004, figs. 2, 4), the species of *Platecarpus* are equipped with fairly slender and pointed marginal teeth (see e.g., Cope, 1875, pl. 14, fig. 3), probably as an adaptation for piscivorous feeding (Russell, 1967). In accordance with extant members of the Gavialidae (see Massare, 1987, fig. 1b), these mosasaurs probably captured their prey by piercing it with rows of weakly differentiated teeth that were specialized for penetrating between thin but closely spaced ribs.

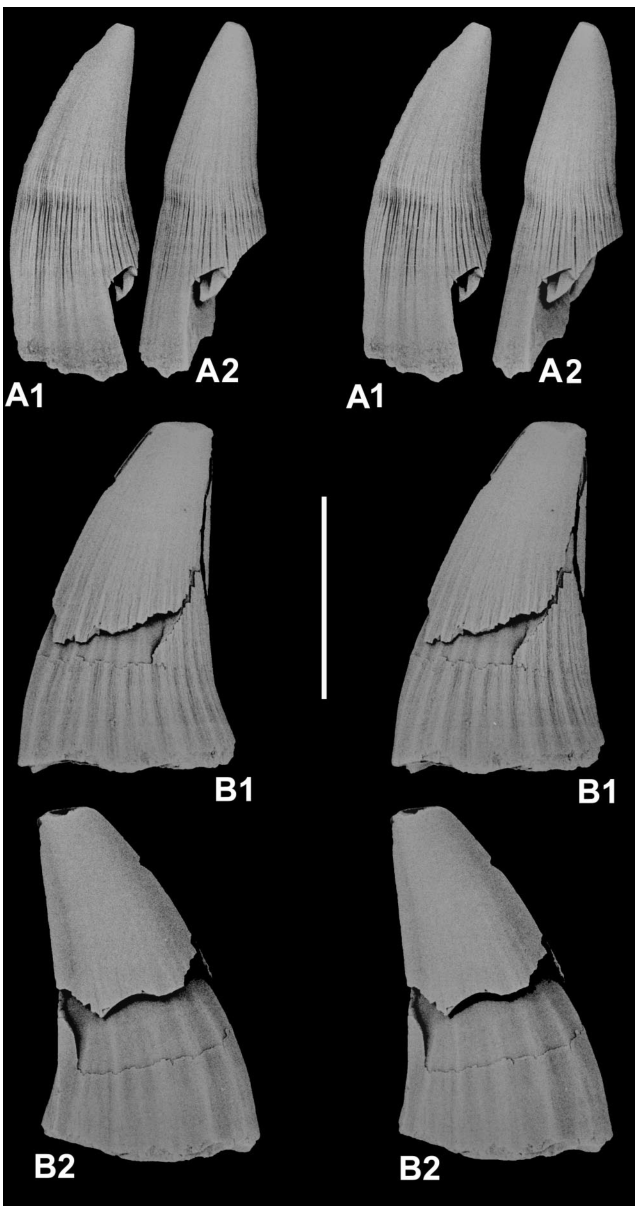

Figure 2. Stereopairs of marginal tooth-crowns of *Platecarpus* sp. from the Sergipe Basin, northeastern Brazil. **A**, MN 6940-V, from Oiteiro 28 (upper Turonian) in lingual (**A1**) and posterior (**A2**) views; **B**, MN 6941-V, from Mucuri 7 (Turonian-Coniacian), in lingual (**B1**) and labial (**B2**) views. Scale bar: 10 mm.

The dental morphology of *Platecarpus* is closer to that of *Plioplatecarpus* than to any other plioplatecarpine genus, although marginal *Plioplatecarpus* teeth can usually be distinguished by their more acute distal curvature, delicate form, and finely pointed tips (cf., e.g., Williston, 1898, pl. 13; Dollo, 1913, pl. 25, fig. 2; Kuypers *et al*., 1998, pl. 6). The overall morphology of the teeth in *Plioplatecarpus* suggests that they had an even more pronounced piercing function than those of *Platecarpus*. Moreover, the strongly backward-curved crowns of *Plioplatecarpus* probably aided in the transport of the prey towards the gullet (see Massare, 1987).

Platecarpus sp.
(Figure 2)

Material. Two isolated marginal tooth-crowns, nº. MN 6940-V from Oiteiro 28, upper Turonian, and nº. MN 6941-V from Mucuri 7 (2 km S of Oiteiro 28), lower Coniacian, Sergipe Basin, northeastern Brazil.

Description. Specimen MN 6940-V (Figure 2a) is an anteriorly situated marginal tooth-crown with a slightly worn apex and much of its labial face broken off. As preserved, the crown measures 16.2 mm in height (when measured at a right angle to the plane formed by the base of the enamel) and 6.9 mm in basal width (original width is estimated at approximately 8.5 mm). The lower half of the lingual surface displays indistinct, slightly concave facets separated by weak ridges, whereas the upper half (as well as the preserved apical portion of the labial face) is nearly smooth. The central portion of the lingual face is ornamented by fine, densely spaced hairline striations, beginning a few mm up the base of the enamel and reaching approximately to the mid-point of the height of the crown. Unserrated anterior and posterior carinae divide the crown into a narrow, almost flat (apical) labial face and a U-shaped lingual surface. In lateral view, the tooth-crown is gently curved medio-posteriorly.

The second and larger specimen, MN 6941-V (Figure 2b), is a lateroposterior tooth-crown, measuring 18.1 mm high and 11.0 mm wide. It has a worn and somewhat medioposteriorly curved apex. In basal cross-section, the crown is elliptical with a gently convex labial face and inflated lingual surface. Towards the apex, the labial surface widens at the expense of the lingual face, and the two surfaces become almost equally convex. Anterior and posterior carinae are present, both lacking serrations. Low and gently rounded crests divide the labial and lingual surfaces into gently concave facets. There are seven discernible facets on the proximal half of the labial face, whereas the lower portion of the lingual surface displays a large number of closely spaced facets. The lower two-thirds of the lingual face exhibits a fine pattern composed of anastomosing and undulating striae.

Remarks. With their delicate lingual striae, gently concave facets, and unserrated carinae, the two tooth-crowns from the Sergipe Basin agree very well in morphology with teeth of *Platecarpus* from the upper Coniacian-lowermost Campanian Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA (e.g., FHSM VP-13810 [*P. planifrons*] and PMU R198 [*P. tympaniticus*]), and with those in the dentition of *P. bocagei* from the upper(?) Turonian of Angola (Antunes, 1964, pl. 17, fig. 1, pl. 21, fig. 2). It seems, nonetheless, premature at this point either to erect a new species, or to assign the Sergipe specimens to a described species (including the approximately contemporaneous *P. bocagei*) because of the fragmentary state of the material at hand and the lack of high-quality illustrations of teeth of *P. bocagei*, which would perhaps allow this nominal species to be separated from *P. tympaniticus* and *P. planifrons* from a dental point of view. Hence, the Sergipe specimens are kept in open nomenclature, pending the discovery of more complete material. Besides their overall morphological similarity, the two tooth-crowns described herein show a few differences. These distinguishing characters (e.g., in slenderness and curvature) are probably linked to different positions on the dental ramus, although the differences in facet development may attest to intraspecific variation.

DISCUSSION

During the initial phase of the Late Cretaceous, the global marine reptile fauna underwent a profound reorganization. The highly specialized ichthyosaurs that had inhabited epeiric seas and oceans since the Early Triassic (e.g., Callaway & Brinkman, 1989) disappeared (Bardet, 1995), and many forms of marine crocodilians were on the wane (Bakker, 1993; Bardet, 1995). Among the groups that benefited from this worldwide faunal turnover were the mosasaurs. Following the demise of the last ichthyosaurs, this family of aquatic reptiles invaded coastal waters and shallow seas some time during the Turonian (or perhaps even earlier), and soon became top predators of the world's oceans.

Despite more than two hundred years of intense research, the origin and early evolution of mosasaurs are still imperfectly known. The closest inferred relative to 'true' mosasaurs *sensu* Bell (1997) is the early Turonian mosasauroid *Tethysaurus nopcasi* Bardet *et al*., 2003, which seemingly fills the gap between the mid-Cretaceous semi-aquatic aigialosaurs and the Late Cretaceous mosasaurs (Bardet *et al*., 2003). The study of the transition of mosasaurs from these primitive reptiles has contributed significantly to the understanding of large-scale evolutionary patterns (see Carroll, 1997). The relationships between mosasauroids (i.e. mosasaurs, *Tethysaurus* Bardet *et al*., 2003 and aigialosaurs) and other reptiles remain controversial. Many workers (e.g., deBraga & Carroll, 1993) favour the idea that the mosasauroids are derived varanoid lizards (i.e., within the order Sauria), although recent studies (e.g., Lee *et al*., 1999) have revived an old theory (e.g., Cope, 1869) that the mosasauroids form a sister group to modern snakes (order Ophidia). Russell (1967) suggested that two ancestral lineages of the Mosasauridae; one *Clidastes*-like and one *Platecarpus*-like, gave rise to all subsequent mosasaur taxa. In this scenario, a *Platecarpus*-like ancestor, derived from an advanced aigialosaur stock, would have diversified and eventually evolved into all mosasaur species included in the subfamilies Plioplatecarpinae and Tylosaurinae, whereas mosasaurine mosasaurs would represent derivates of a *Clidastes*-like ancestor. Recently, Bell & Polcyn (2004) suggested that the Mosasauridae might be polyphyletic. However, as their conclusions are tentative and data matrix is under development, the traditional phylogeny is adopted here.

The occurrence of the genus *Platecarpus* in late Turonian times (Angola, Brazil) is in agreement with its inferred basal position within the systematics of the Mosasauridae and further supports Russell's (1967) hypothesis of a *Platecarpus*-like ancestor for the Plioplatecarpinae and Tylosaurinae. The Brazilian occurrence extends the Turonian record of the genus from West Africa (Angola) to the opposite margin of the then narrow South Atlantic Ocean. Thus, it appears that the origin of *Platecarpus* is to be found in the northern part of the incipient South Atlantic.

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