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The first silesaurid dinosauriform from the Late Triassic of Morocco

CHRISTIAN F. KAMMERER, STERLING J. NESBITT, and NEIL H. SHUBIN


Disarticulated material from the Late Triassic Timezgadiouine Formation in the Argana Basin of Morocco represents a new taxon of silesaurid dinosauromorph, Diodorus scytobrachion gen. et sp. nov. D. scytobrachion can be distinguished from other silesaurids by the presence of anteriorly-canted teeth that decrease in size towards the anterior end of the dentary and a distinct lateral ridge running parallel to the dentary alveolar margin. In a phylogenetic analysis, D. scytobrachion is recovered as the sister-taxon to the Brazilian Sacisaurus agudoensis, nested deep within Silesauridae. This new taxon provides further evidence of a near-cosmopolitan range for basal dinosauriforms in the Late Triassic and further demonstrates the disparity of dental morphologies within Silesauridae.

Key words: Dinosauromorpha, Silesauridae, Triassic, North Africa, Morocco.

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Introduction

Long known from only fragmentary specimens from the Middle Triassic Chañares Formation of Argentina (Romer 1971, 1972a, b; Arcucci 1986, 1987; Sereno and Arcucci 1994a, b), non-dinosaurian dinosauromorphs have recently experienced an explosion in known taxonomic richness, geographic breadth, and stratigraphic range (Irmis et al. 2007a; Nesbitt et al. 2009, 2010). Particularly remarkable has been the recognition of a widespread group of long-necked, quadrupeal early dinosauriform taxa, most of which possess dentary “beaks” and leaf-shaped marginal dentition indicative of either omnivory or herbivory. This morphotype was first recognized in Silesaurus from the Upper Triassic Kraśiejów locality in Poland (Dzik 2003), and similar features were subsequently identified in new taxa such as Sacisaurus from the Upper Triassic Caturrira Formation of Brazil (Ferigolo and Langer 2007) as well as an assortment of previously described forms traditionally placed in other clades (such as the supposed “theropod” Eucoelophysis, the “ornithischian” Technosaurus, and the “lagosuchian” Pseudolagosuchus) (Irmis et al. 2007a, b; Nesbitt et al. 2007). Nesbitt et al. (2007) first listed possible synapomorphies grouping Silesaurus, Eucoelophysis, and Pseudolagosuchus together, and Silesaurus and Eucoelophysis were found to form a clade outside Dinosauria in subsequent phylogenetic analyses (Irmis et al. 2007a; although see Ezcurra [2006] and Langer and Benton [2006] for alternative views). More recently, Nesbitt et al. (2010) described a new taxon of Silesaurus-like dinosauriform, Asilisaurus kongwe, from the early Middle Triassic of Tanzania and provided increased support for the monophyly of this group, which they named Silesauridae. Here, we describe a new taxon of silesaurid, representing the first body fossil record of the group from northern Africa.

Comparisons with other silesaurid taxa are based on Arcucci (1987), Novas (1996), Dzik (2003), Ezcurra (2006), Irmis et al. (2007a, b), Nesbitt et al. (2007, 2010), Ferigolo and Langer (2007), and personal observations of the type specimens of all nominal silesaurids by SJN: MCN PV10041 (Sacisaurus agudoensis), NMMNH P-22298 (Eucoelophysis baldwinii), NMT RB9 (Asilisaurus kongwe), PVL 4629 (Pseudolagosuchus major), TTUP P9021 (Technosaurus smallii), UNLR 1 (Lewisuchus admixtus), and ZPAL Ab III/361 (Silesaurus opolensis).

Institutional abbreviations.—GR, Ruth Hall Museum of Paleontology, Ghost Ranch, New Mexico, USA; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MHN-ARG, Museum d’Histoire Naturelle de Marrakech (Argana Basin Collection), Marrakech, Morocco; NMMNH, New Mexico Museum of Natural History; SCH, T. Schlaikjer Collection, Brown University, Providence, Rhode Island; ZPAL, Museum of Paleontology, Charles University, Prague.
Systematic palaeontology

Archosaursia Cope, 1869
Ornithodira Gauthier, 1986
Dinosauromorpha Benton, 1985
Dinosauriformes Novas, 1992
Silesauridae Nesbitt, Sidor, Irmis, Angielczyk, Smith, and Tsuji, 2010

Genus Diodorus nov.

Type species: Diodorus scytobrachion gen. et sp. nov.; see below.

Etymology: Named after Diodorus, legendary king of the Berber people and son of Sufax, the founder of Tangier. Also named in honour of Diodorus Siculus, a 1st century Greek historian, who wrote about North Africa.

Diagnosis.—As for the type and only species.

Diodorus scytobrachion gen. et sp. nov.

Figs. 1–3.

Etymology: From ancient Greek scytobrachion, leathery arm, a reference both to a possible integument for this taxon and the classical mythographer Dionysius Scytobrachion, who chronicled the mythical history of North Africa.

Holotype: MNHM-ARG 30, a partial right dentary.

Type locality: Northeastern Argana Basin, 2.9 km east of Imziln, Morocco. Specific coordinate information on file at the Museum of Comparative Zoology, MA, USA, and University of Chicago, IL, USA and available on request. The holotype and all referred specimens were collected in a single quarry as part of a layer of disarticulated skeletal material that also includes phytosaur, “prolacertiform”, fish, and temnospondyl elements.

Type horizon: Base of the Irohalene Mudstone Member (t5), Timezgadiouine Formation, Late Triassic. Photographs (A1, A3), explanatory drawings (A2, A4).

Referred material.—MNHM-ARG 31, 32, and 33, isolated teeth; MNHM-ARG 34 and 35, two humeri; MNHM-ARG 36, a metatarsal; and MNHM-ARG 37, a femur. Although these elements are unassociated and probably represent different individuals, here they are all referred to Diodorus scytobrachion based either on direct comparison with the holotype (the isolated teeth), or on the identification of diagnostic silesaurid (femur, humeri) or dinosauriform (metatarsus) character states. At present, we are operating under the assumption that only a single silesaurid taxon is present in the basal t5 member of the Timezgadiouine Formation, as is the case for other silesaurid-bearing localities (the two nominal silesaurids from Los Chañares, Lewisuchus and Pseudolagosuchus, are probably synonymous [Nesbitt et al. 2010: supplementary information]).

Diagnosis.—Small silesaurid with triangular, denticulated teeth, cingula absent, and a marked decrease in size anteriorly in the dentary. All teeth preserved in place in the dentary are anteriorly directed at an angle of ~20° from the root. Meckelian groove restricted to ventral edge of dentary but expands in dorsoventral height posteriorly, reaching 40% of dentary height by the fourth tooth position. Dentary ventrally bowed. Lateral ridge present near and trending parallel to alveolar margin of the dentary.

Differential diagnosis.—Distinguished from all other archosaurs except silesaurids by the presence of a distinct notch below the femoral head (CS 207[1]) in the phylogenetic analysis [see below] and teeth rooted but firmly fused to their sockets (CS 104[0]) (termed ankylothecodont by some workers [e.g., Chatterjee 1974]). Can be distinguished from all silesaurids except Saccisaurus and Silesaurus by a straight edge to the anteromedial face of the femoral head (CS 206[1]). Can be distinguished from all silesaurids other than Saccisaurus by dental morphology. Both Diodorus and Saccisaurus exhibit a decrease in tooth size anteriorly (CS 291[1]) and possess narrow, anteriorly-directed anteriormost teeth in the dentary (CS 292[1]). Diodorus can be differentiated from Saccisaurus by a Meckelian groove that that does not extend to the anterior edge of the dentary, greater dorsoventral expansion of the Meckelian groove, lack of cingula on the teeth, greater expansion of the tooth crown at base, anterior angulation of at least the first six dentary teeth, and the presence of a lateral ridge on the dentary running parallel with the alveolar margin.

Fig. 1. Mandibular and dental material of dinosauriform Diodorus scytobrachion gen. et sp. nov., Timezgadiouine Formation, Late Triassic. A. MNHM-ARG 30, holotype right dentary, in lateral (A1, A3) and medial (A2, A4) views. Photographs (A1, A3), explanatory drawings (A2, A4). B. MNHM-ARG 31, referred isolated tooth. B not to scale.

[Image of mandibular and dental material of Diodorus scytobrachion]

[Image of Diodorus scytobrachion: A1, A3 views; A2, A4 views; MNHM-ARG 31, referred isolated tooth; MNHM-ARG 30, holotype right dentary]
Description.—The holotype of Diodorus scytobrachion (MHNMR-ARG 30; Fig. 1A) is the anterior portion of a right dentary, missing the anteriormost tip. This fragment preserves six tooth positions with four teeth in place (positions 1, 2, 4, and 6), and three with crowns intact (1, 2, and 4). A ridge is present slightly above mid-height on the lateral surface of the dentary (Fig. 1A). This ridge is well developed at the posterior end of the fragment, at the level of tooth position 6, weakening anteriorly until it disappears entirely under tooth position 2. This character is absent in all silesaurids for which the dentary is known and is here considered an autapomorphy of Diodorus. No dentary material can be referred with certainty to Pseudolagosuchus or Eucoelophysys, although it is probable that the former is synonymous with Lewisuchus and the latter is identical to the “Hayden Quarry silesaur”, both of which have dentaries preserved (Irmis et al. 2007a; Nesbitt et al. 2010). A row of nutrient foramina is present between the alveolar margin of the dentary and the lateral ridge. The Meckelian groove is located at the ventral face of the dentary (Fig. 1A), as in all silesaurids except Asilisaurus. The Meckelian groove is relatively tall in Diodorus compared with the extremely narrow grooves of Sacisaurus and Silesaurus. Although the medial surface of the dentary is poorly preserved in the holotype of D. scytobrachion, the Meckelian groove clearly does not extend anterior to tooth position 2, unlike the condition in Sacisaurus and Silesaurus in which the groove extends anteriorly through the dentary symphysis.

The four preserved teeth in the holotype have roots that are firmly fused to their sockets, as in Proterosuchus (based on NMQR 1484), non-archosauriform archosauromorphs, and all silesaurids except possibly Lewisuchus. In the three teeth for which crowns are preserved, the crowns are triangular, denticulated along the mesiodistal edges, and anteriorly cant. Within silesaurids, triangular, denticulated teeth are present in all species except Lewisuchus (which possesses the primitive archosaurian condition of blade-like, recurved teeth) and Asilisaurus (in which the teeth are peg-like). The forward cant to all the anteriormost dentary teeth is an autapomorphy of Diodorus, but the first dentary tooth of Sacisaurus (based on MCN PV10043 and MCNPV10061) is similarly angled. The three preserved crowns decrease in size anteriorly (the crown height at tooth position 1 is ~66% that of tooth position 2, which is ~60% that of tooth position 4), as is also the condition in Sacisaurus (based on MCN PV10043; Ferigolo and Langer 2007). In addition to the poorly preserved three crowns present in the holotype, several very well preserved, isolated tooth crowns from the type locality matching the holotype’s dental morphotype can be referred to Diodorus (MHNMR-ARG 31, 32, and 33; Fig. 1B). These crowns are very similar in morphology to the crown in tooth position 4 in the holotype, but are more bulbous at the base and larger in absolute size, indicating either a more posterior position in the jaw or that they come from a larger individual than the holotype. The teeth of Diodorus are more coarsely denticulated (4–5 denticles per 5 mm in Diodorus versus 6–7 denticles per 5 mm in Silesaurus [Dzik 2003]) and broader (wider crown base relative to height) than those of Silesaurus (based on ZPAL Ab III/361/26), and can also be distinguished from Silesaurus by the lack of longitudinal striations. The crown proportions of Diodorus are generally similar to those in Technosaurus (TTUP P9021), Sacisaurus, and the “Hayden Quarry silesaur” (probably Eucoelophysys [Irmis et al. 2007a]; GR 224). However, Diodorus teeth can be distinguished from those of Technosaurus by the lack of an accessory cusp, from Sacisaurus by the absence of a cingulum and a more abrupt expansion of the crown at base (resulting in a more “spade-shaped” tooth in Diodorus), and from the “Hayden Quarry silesaur” by being relatively taller and less bulbous.

Two isolated humeri (MHNMR-ARG 34 and 35; Fig. 2A) are here referred to Diodorus. As in other silesaurids, the humerus is elongate and largely featureless other than the distinct ect- and entepicondyles separated by a prominent furrow distally. The shaft of the humerus is “ramrod”-straight and the long axes of both the proximal and distal ends are in the same plane. The head of the humerus is very poorly developed and asymmetrical, with the mediolateral expansion distally. The proximal and distal ends are poorly expanded relative to the shaft, a character state shared with Silesaurus (ZPAL Ab III/362) among avian-line archosaurs. The delto-
pectoral crest extends for one-third the length of the humerus, but the apex of the deltopectoral crest is situated at the proximal tip of the humerus, similar to the condition in *Silesaurus* (ZPAL Ab III/362). This is in contrast with the condition in Dinosauria, where the apex of the crest is situated around 30% down the shaft of the humerus (Langer and Benton 2006; Nesbitt et al. 2010).

Hindlimb material is represented by an anteroposteriorly crushed femur (MHNM-ARG 37; Fig. 3) and a metatarsal (MHNM-ARG 36; Fig. 2B). The femoral head is triangular in proximal view, with a 5.5:1.8:6.3 ratio of anterior:medial:posterior edge lengths. These edges are essentially straight, as in *Sacisaurus* (based on MCN PV10019) and *Silesaurus* (based on ZPAL Ab III/361/23), rather than rounded as in most archosaurs. It is unlikely that the straightness of these edges arose from crushing of this specimen, considering that such deformation would distort the anterior/posterior and medial edges in opposite ways. The postero-medial tuber of the proximal portion of the femur is absent in *Diodorus*. A straight mediolateral groove bisects the femoral head in proximal view. The anterior trochanter is a small, dorsally pointing spike but the proximal tip is broken off. There is no evidence for a trochanteric shelf attached to the anterior trochanter. A distinct, blade-shaped dorsolateral trochanter (sensu Langer and Benton 2006) is present lateral to the anterior trochanter. It is narrow, elongate, and less visible in proximal view than in *Eucoelophysis* and PEFO 34347. The combination of a “finger-shaped” anterior trochanter, the absence of a trochanteric shelf, and the presence of a blade-like dorsolateral trochanter on the femur of *Diodorus* is also found in *Sacisaurus* (based on MCN PV10019), smaller specimens of *Silesaurus* (e.g., ZPAL Ab III/460/1), and the “gracile” morph of *Coelophys rhodesiensis* (Raath 1990). The fourth trochanter is located more distally on the femur than in *Sacisaurus* (based on MCN PV10019) and is similar in position to that of *Silesaurus* (based on ZPAL Ab III/361/23), albeit more weakly developed than in either of those two taxa. The fourth trochanter is crescent-shaped with a sharp rim, proximodistally symmetrical, and with a shallow depression to its anteromedial side. The fourth trochanter is much less expanded in *Diodorus* than in *Silesaurus* (based on ZPAL Ab III/361/23). The distal end is only slightly more expanded (in all views) than the shaft. The crista tibiofibularis and the medial and lateral condyles are rounded on the posterior side. A rounded depression occupies

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**Fig. 3.** Isolated left femur referred to *Diodorus scytobrachion* gen. et sp. nov., Timezgadiouine Formation, Late Triassic, MNHM-ARG 37 in anterior (A), lateral (B), medial (stereopair) (C), proximal (D), and distal (E) views. Phylogenetically important character states visible on this element include: 1, distal condyles of femur divided posteriorly between 1/4 and 1/3 the length of the shaft (CS 223[1], synapomorphy of all silesaurids except *Pseudolagosuchus*); 2, notch ventral to the proximal head of the femur (CS 207[1], synapomorphy of Silesauridae); 3, posteromedial tuber absent on the proximal portion of the femur (CS 204[2], synapomorphy of all silesaurids except *Pseudolagosuchus* and *Asilisaurus*); 4, flat medial articular surface of the femur head in dorsal view (CS 206[1], synapomorphy of *Silesaurus, Sacisaurus*, and *Diodorus*).
the distal surface. The lateral side of the lateral condyle is rounded like that of other dinosauriforms (Parker and Irmis 2005). The ridges dorsally extending from the crista tibiofibularis and the medial condyle extend up the shaft of the femur for more than 1/4 the length of the femur. This also occurs in Sacisaurus (based on MCN PV10019), Silesaurus (based on ZPAL Ab III/362), and Asilisaurus (Nesbitt et al. 2010).

The isolated metatarsal is a problematic element. It is elongate, with a robust rim for extensor attachment, as in Silesaurus, but the digit identity of MHNM-ARG 36 is unclear. Although compression in this specimen renders interpretation of the proportions difficult, the rectangular distal profile and mediolateral symmetry of the metatarsus suggest that it most likely represents metatarsal III.

Geographic and stratigraphic range.—Argana Basin of Morocco (Timezgadiouine Formation, Late Triassic).

Phylogenetic analysis

Diodorus was included in an expanded version of the phylogenetic analysis of Nesbitt et al. (2010), featuring 35 taxa and 292 characters (two new, see Appendix 1). The data set was analyzed using the parsimony-based phylogenetic program TNT v1.1 (Goloboff et al. 2008) using the same parameters as Nesbitt et al. (2010) to produce the consensus tree and a 10000 replicate resampling to produce bootstrap values. All characters were equally weighted and the following characters were equally weighted and the following characters were ordered: 21, 78, 89, 98, 116, 142, 159, 169, 175, 177, 195, 200, 227, 250, 281. We first scored Diodorus only from the holotype and then scored all of the material referred to Diodorus into a single terminal taxon. The results from both iterations were identical, suggesting that inclusion or exclusion of the referred material does not significantly affect the placement of the taxon. Nine most parsimonious trees of length 744 (CI = 0.469, RI = 0.708) were recovered, differing in the relative positions of the three ornithischians (Pisanosaurus mertii, Lesothosaurus diagnosticus, and Heterodontosaurus tucki) and the silesaurids Lewisuchus admixtus and Pseudolagosuchus major. Three most parsimonious trees of length 744 were found when the scores of Pseudolagosuchus and Lewisuchus were combined (these two taxa are probably synonymous, see Nesbitt et al. [2010; supplementary information]). The strict consensus of these three trees is shown in Fig. 4.

Discussion

Relationships.—Diodorus is well supported as a member of the clade including all those taxa more closely related to Silesaurus than to dinosaurs or more basal dinosauromorph groups (e.g., lagerpetids). Paul (1988) named the taxon Lewisuchinae as a monotypic subfamily (for Lewisuchus Romer, 1972) within Lagosuchidae Bonaparte, 1975. Recent phylogenetic study (Nesbitt et al. 2010, see also above) has indicated that Lewisuchus represents a basal member of the dinosauriform clade to which Diodorus and Silesaurus belong. However, as Paul (1988) provided no description or definition for Lewisuchinae, it must be considered a nomen nudum with no standing in zoological nomenclature. Article 13.5 of the International Code on Zoological Nomenclature, which covers validity conferred through the combined description of families and genera, only applies if both family and genus are established as new in the same work, and thus does not validate Paul’s (1988) family level taxon for the previously erected Lewisuchus. Olshovsky (1991) later raised Lewisuchinae to family status, but provided no new descriptive information that would render this taxon available. Langer et al. (2010) named Silesauridae as a stem-based group containing all taxa more closely related to Silesaurus opolensis than to Heterodontosaurus tucki or Marasuchus lilloensis. However, they provided no diagnosis for this taxon, rendering it unavailable under Article 13.1.1 of the Code. As such, we utilize the first validly proposed family-level taxon to refer to this clade: Silesauridae Nesbitt, Sidor, Irmis, Angielczyk, Smith, and Tsuji, 2010.

Diodorus is nested deeply within Silesauridae, as part of a clade that also includes Sacisaurus and Silesaurus (Fig. 4). A sister-group relationship between Diodorus and Sacisaurus is supported by characters 291 and 292 (dentary teeth decrease in size anteriorly and anteriormost dentary teeth canted anteriorly). The Meckelian groove in Sacisaurus and Silesaurus extends to the anterior tip of the dentary, through the beak-like dentary tip, whereas it does not extend to the anterior edge of even the dentigerous portion of the dentary in Diodorus. This is most parsimoniously interpreted as a reversal in Diodorus.

Biostratigraphy and biogeography.—Diodorus scytobrachion is part of a diverse assemblage of Triassic tetrapods found in rocks at the base of the Irihalene Mudstone Member (t5) of the Timezgadiouine Formation (hereafter referred to as the “basal t5 assemblage”). The basal t5 assemblage has previously been placed in the Otischalkian “land vertebrate faunichron” (based on the shared presence of the phytosaur Paleorhinus and the metoposaur Metoposaurus) and considered late Carnian in age (Lucas 1998). Although the basal t5 assemblage of the Argana Basin is roughly similar to the typical Otischalkian assemblages of the American southwest (including Paleorhinus-grade phytosaurs, metoposaurid and laticepid amphibians, silesaurid dinosauriforms, and kanne Meyeriform dicynodonts [Jalil 1999; Tourani et al. 2000; Irmis 2005; Parker et al. 2006]), we would caution against biostratigraphic overinterpretation of these Moroccan records. For one thing, the index taxa Paleorhinus and Metoposaurus, as traditionally circumscribed, have been shown to represent non-monophyletic units (Hunt 1993; Stocker 2010) and thus are not suitable for stratigraphic correlation (Angielczyk and Kurkin 2003; Rayfield et al. 2009). Indeed, the basal t5 representatives of Paleorhinus (P. magnoculus Dutuit, 1976) and Metoposaurus refer to taxa endemic to the Irihalene Mudstone (t5) of the Timezgadiouine Formation. Additionally, the distant relationship between the Irihalene Mudstone (t5) assemblage and other contemporaneous faunas (e.g., the famous Riojasupian Lascaux and Erzgebirge assemblages (Nesbitt et al. 2010), the “basal t5 assemblage” is expected to be distinct from that of the Irihalene Mudstone (t5). As we have pointed out above, the inclusion of Diodorus in the “basal t5 assemblage” of the Irihalene Mudstone (t5) is confirmed by multiple characters. We believe that Diodorus is a member of this Late Triassic Irishalkian assemblage and belongs to a clade that has its origins in Morocco. We will refer to this clade as the “Diodorus scytobrachion faunichron.”
Metoposaurus (*M. ouazzoui* Dutuit, 1976) have already been assigned to new genera (*Arganarhinus* Long and Murry, 1995 and *Dutuitosaurus* Hunt, 1993, respectively). Furthermore, some elements of the basal t5 assemblage confound simple correlation with other well-known Triassic assemblages. For example, the basal archosauromorph *Azendohsaurus* (represented in the basal t5 assemblage by *A. laaroussii* Dutuit, 1972) is otherwise known only from the “basal Isalo II” of southwestern Madagascar (Flynn et al. 2010), a traversodontid/rhynchosaur-dominated assemblage that may be late Ladinian or early Carnian in age (Flynn et al. 1999; Kammerer et al. 2010). Records such as this underline the complexity of Triassic biochronology: as more Triassic assemblages are discovered globally, taxa once considered tightly stratigraphically-constrained have been found to have extended temporal ranges across basins (see, for example, Abdala and Smith 2009). Additionally, a Carnian age for many Upper Triassic vertebrate assemblages in North America has recently been called into question, with radioisotopic and magnetostratigraphic data indicating that many if not all of these assemblages are actually Norian in age (Irmis et al. 2010). Comparably detailed age data is not yet available for North African Triassic sequences: given the complex and conflicting assemblage in the t5 member of the Timezgadiouine Formation, it may be Carnian or Norian in age.

The discovery of *Diodorus* in Morocco demonstrates the continued presence of silesaurids in Africa (first represented by the Anisian taxon *Asilisaurus* in Tanzania) in the Late Triassic. The presence of dinosauromorphs in the Timezgadiouine Formation was previously suggested based on footprints (Klein et al. 2011), but this is the first definitive record of silesaurids from the region. This record provides further evidence for the cosmopolitanism of basal dinosauromorphs (and silesaurids in particular) in the Middle-to-Late Triassic. Rather than being a rare, geographically and temporally restricted grade, basal dinosauromorphs appear to have been widespread, long-ranging, common elements of Triassic assemblages. The recent recognition of this pattern can likely be attributed to a combination of misidentification of specimens as true members of Dinosauria and the relatively low preservation potential of small-bodied, delicate-boned dinosauromorphs compared to coeval pseudosuchians.

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References


Dutuit, J.M. 1976. Introduction


Appendix 1

Character data for *Diodorus scytobrachion*, using the matrix of Nesbitt et al. (2010). For all characters not listed below, *Diodorus* was coded as “?”. Characters 291 and 292 are new for this analysis: *Sacisaurus* and *Diodorus* were coded as state “1” for characters 291 and 292, all other taxa were coded as state “0” where the character could be scored.

<table>
<thead>
<tr>
<th>Character</th>
<th>State</th>
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<tbody>
<tr>
<td>291</td>
<td>1</td>
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<tr>
<td>292</td>
<td>1</td>
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291. Dentition, anterior portion of the dentary, teeth remain relatively same size throughout anterior portion of dentition (0); teeth significantly decrease in size anteriorly (1).

292. Dentition, anterior portion of the dentary, long axis of the teeth, vertical (0); inclined anteriorly (1).