

## **The First Silesaurid Dinosauriform from the Late Triassic of Morocco**

Authors: Kammerer, Christian F., Nesbitt, Sterling J., and Shubin, Neil H.

Source: *Acta Palaeontologica Polonica*, 57(2) : 277-284

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2011.0015>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# The first silesaurid dinosauriform from the Late Triassic of Morocco

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



Kammerer, C.F., Nesbitt, S.J., Shubin, N.H. 2012. The first silesaurid dinosauriform from the Late Triassic of Morocco. *Acta Palaeontologica Polonica* 57 (2): 277–284.

Disarticulated material from the Late Triassic Timezgadiouine Formation in the Argana Basin of Morocco represents a new taxon of silesaurid dinosauriform, *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.

Christian F. Kammerer [ckammerer@amnh.org], Division of Paleontology and Richard Gilder Graduate School, American Museum of Natural History, New York, NY 10024, USA; current address: [christian.kammerer@mfn-berlin.de], Museum für Naturkunde, Invalidenstraße 43, 10115 Berlin, Germany;

Sterling J. Nesbitt [nesbitt@jsg.utexas.edu], Jackson School of Geosciences, The University of Texas at Austin, Austin, TX 78712, USA;

Neil H. Shubin [nshubin@uchicago.edu], Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA.

Received 24 February 2011, accepted 5 June 2011, available online 11 July 2011.

## 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 dinosauriforms 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, quadrupedal 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 Krasiejów locality in Poland (Dzik 2003), and similar features were subsequently identified in new taxa such as *Sacisaurus* from the Upper Triassic Caturrita 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 baldwini*), NMT RB9 (*Asilisaurus kongwe*), PVL 4629 (*Pseudolagosuchus major*), TTUP P9021 (*Technosaurus smalli*), 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 and Science, Albuquerque, New Mexico, USA; NMQR, National Museum, Bloemfontein, South Africa; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; PEFO, Petrified Forest National Park, Arizona, USA; PVL, Instituto Miguel Lillo, Tucumán, Argentina; TTUP, Texas Tech University Museum, Lubbock, Texas, USA; UNLR, Museo de Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

*Other abbreviations.*—CI, consistency index; CS, character state; RI, retention index.

## Systematic palaeontology

Archosauria 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* 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 1<sup>st</sup> century Greek historian, who wrote about North Africa.

*Diagnosis.*—As for the type and only species.

*Diodorus scytobrachion* 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:* MHNM-ARG 30, a partial right dentary.

*Type locality:* Northeastern Argana Basin, 2.9 km east of Imzila, 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 (?Carnian–Norian, Triassic; see discussion).

*Referred material.*—MHNM-ARG 31, 32, and 33, isolated teeth; MHNM-ARG 34 and 35, two humeri; MHNM-ARG 36, a metatarsal; and MHNM-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

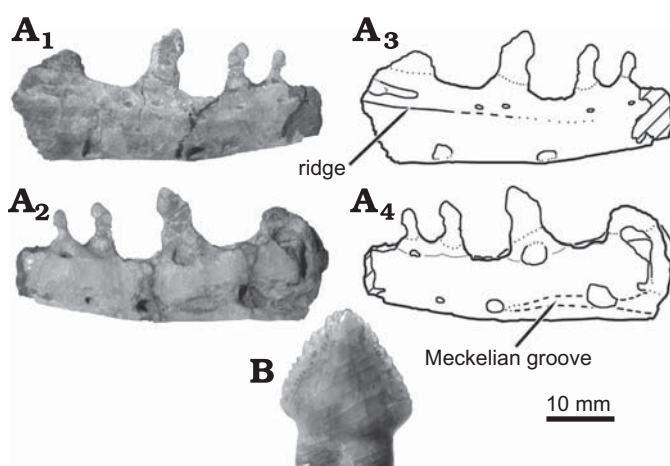


Fig. 1. Mandibular and dental material of dinosauriform *Diodorus scytobrachion* gen. et sp. nov., Timezgadiouine Formation, Late Triassic. A. MHNM-ARG 30, holotype right dentary, in lateral (A<sub>1</sub>, A<sub>3</sub>) and medial (A<sub>2</sub>, A<sub>4</sub>) views. Photographs (A<sub>1</sub>, A<sub>2</sub>), explanatory drawings (A<sub>3</sub>, A<sub>4</sub>). B. MHNM-ARG 31, referred isolated tooth. B not to scale.

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 ankylotheodont by some workers [e.g., Chatterjee 1974]). Can be distinguished from all silesaurids except *Sacisaurus* 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 *Sacisaurus* by dental morphology. Both *Diodorus* and *Sacisaurus* 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 *Sacisaurus* by a Meckelian groove 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.

**Description.**—The holotype of *Diodorus scytobrachion* (MNHM-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<sub>1</sub>). 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 *Eucoelophysis*, 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 edge of the medial dentary surface (Fig. 1A<sub>2</sub>), 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 canted. 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 MCN PV10061) 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* (MNHM-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



Fig. 2. Limb elements referred to *Diodorus scytobrachion* gen. et sp. nov., Timezgadiouine Formation, Late Triassic. **A.** MNHM-ARG 34, isolated right humerus, in anterior (A<sub>1</sub>), proximal (A<sub>2</sub>), posterior (A<sub>3</sub>), and distal (A<sub>4</sub>) views. **B.** MNHM-ARG 36, isolated metatarsal, in anterior (B<sub>1</sub>) and distal (B<sub>2</sub>) views.

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 *Eucoelophysis* [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 (MNHM-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 medial portion expanded 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-

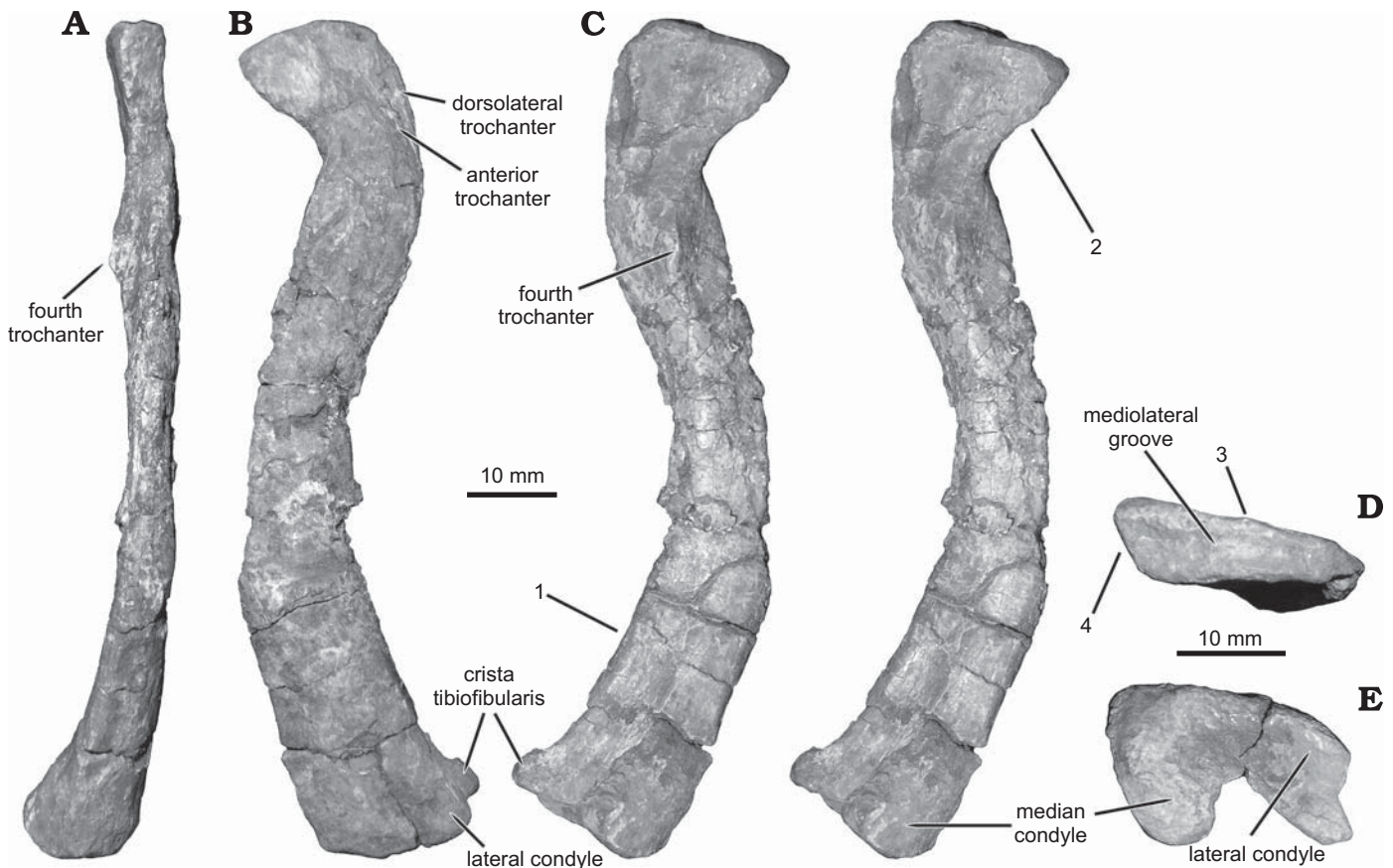


Fig. 3. Isolated left femur referred to *Diodorus scytobrachion* gen. et sp. nov., Timezgadiouine Formation, Late Triassic, MNHM-ARG 37 in anterior (A), lateral (B), medial (stereopair) (C), proximal (D), and distal (E) views. Phylogenetically important character states visible on this element include: 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*).

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 posteromedial 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 *Coelophysis 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

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 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 dinosauriform groups (e.g., lagerpetids). Paul (1988) named the taxon Lewisuchinae as a monotypic subfamily (for *Lewisuchus* Romer, 1972) within Lagosuchidae Bonaparte, 1975. Recent phylo-

genetic 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*. Olshevsky (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 Irohalene 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 faunachron” (based on the shared presence of the phytosaur *Paleorhinus* and the metoposaurid *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 laticopid amphibians, silesaurid dinosauriforms, and kannemeyeriiform 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

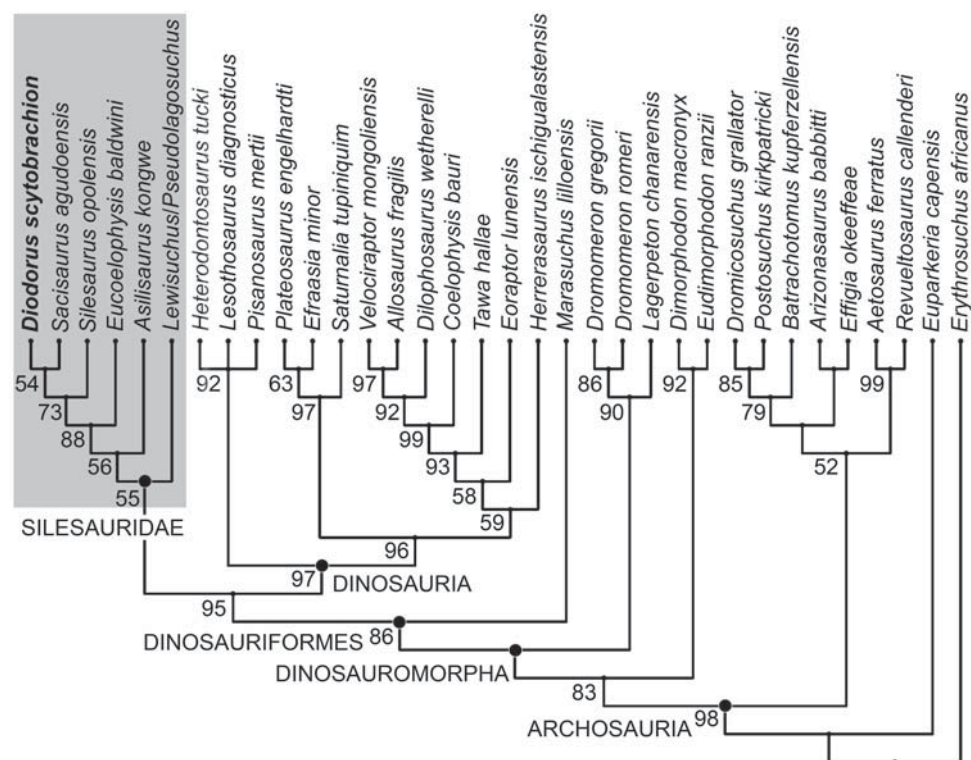


Fig. 4. Consensus tree from the phylogenetic analysis, illustrating the position of *Diodorus scytobrachion* gen. et sp. nov. (in bold) within silesaurids (boxed in grey). Numbers at nodes represent bootstrap values.

*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 dinosauriforms 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 dinosauriforms (and silesaurids in particular) in the Middle-to-Late Triassic. Rather than being a rare, geographically and temporally restricted grade, basal dinosauriforms 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 dinosauriforms compared to coeval pseudosuchians.

## Acknowledgements

We thank Bob Masek (University of Chicago, Chicago, Illinois, USA) for his skillful preparation of the extremely delicate holotype of *Diodorus scytobrachion* and Bill Amaral (Harvard University, Cambridge, Massachusetts, USA) and the late Will Downs for preparation of the appendicular elements. This research was supported by grants from the National Geographic Society and permission to work at the site was granted by the Moroccan Ministry of Energy and Mines, the town of Imi-n-Tanoute and the Berber village of Talaïnt. Fieldwork was performed by Bill Amaral, Ted Daeschler, Will Downs, Farish A. Jenkins Jr., Michael Shapiro, and Charles R. Schaff (all Harvard University, Cambridge, Massachusetts, USA). We thank Nour-Eddine Jalil (Faculté des Sciences Semlalia, Marrakech, Morocco) for providing accession data for these specimens in the Museum d'Histoire Naturelle de Marrakech. We thank Richard Butler (GeoBio-Center, Ludwig-Maximilians-Universität, Munich, Germany) and Max Langer (Universidade de São Paulo, São Paulo, Brazil) for their helpful reviews of the manuscript and Michael Benton (University of Bristol, Bristol, UK) for editing.

## References

- Abdala, F. and Smith, R.M.H. 2009. A Middle Triassic cynodont fauna from Namibia and its implications for the biogeography of Gondwana. *Journal of Vertebrate Paleontology* 29: 837–851.
- Angielczyk, K.D. and Kurkin, A.A. 2003. Has the utility of *Dicynodon* for Late Permian terrestrial biostratigraphy been overstated? *Geology* 31: 363–366.
- Arcucci, A. 1986. Nuevos materiales y reinterpretación de *Lagerpeton chanarensis* Romer (Thecodontia, Lagerpetonidae nov.) del Triásico medio de La Rioja, Argentina. *Ameghiniana* 23: 233–242.
- Arcucci, A. 1987. Un nuevo Lagosuchidae (Thecodontia–Pseudosuchia) de la fauna de los Chañares (Edad reptil Chañarensis, Triásico medio), La Rioja, Argentina. *Ameghiniana* 24: 89–94.
- Benton, M.J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society* 84: 97–164.
- Chatterjee, S. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London B* 267: 209–261.
- Cope, E.D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society, New Series* 14: 1–252.
- Dutuit, J.M. 1972. Découverte d'un dinosaure ornithischien dans le Trias supérieur de l'Atlas occidental marocain. *Comptes Rendus de l'Académie des Sciences, Paris* 275: 2841–2844.
- Dutuit, J.M. 1976. Introduction à l'étude paléontologique du Trias continental marocain. Description des premiers Stegocephales recueillis dans le couloir d'Argana (Atlas occidental). *Mémoires du Muséum National d'Histoire naturelle, Paris, Series C* 36: 1–253.
- Dzik, J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 23: 556–574.
- Ezcurra, M. 2006. A review of the systematic position of the dinosauriform archosaur *Eucoelophysis baldwini* Sullivan & Lucas, 1999 from the Upper Triassic of New Mexico, USA. *Geodiversitas* 28: 649–684.
- Ferigolo, J. and Langer, M.C. 2007. A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian predatory bone. *Historical Biology* 19: 23–33.
- Flynn, J.J., Nesbitt, S.J., Parrish, J.M., Ranivoharimanana, L., and Wyss, A.R. 2010. A new species of *Azendohsaurus* (Diapsida: Archosauromorpha) from the Triassic Isalo Group of southwest Madagascar: cranium and mandible. *Palaeontology* 53: 669–688.
- Flynn, J.J., Parrish, J.M., Rakotosamimanana, B., Simpson, W.F., Whatley, R.L., and Wyss, A.R. 1999. A Triassic fauna from Madagascar, including early dinosaurs. *Science* 286: 763–765.
- Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. *Memiors of the California Academy of Sciences* 8: 1–55.
- Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Hunt, A.P. 1993. Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from Western North America. *Museum of Northern Arizona Bulletin* 59: 67–97.
- Irmis, R.B. 2005. The vertebrate fauna of the Upper Triassic Chinle Formation in northern Arizona. *Mesa Southwest Museum, Bulletin* 9: 63–88.
- Irmis, R.B., Martz, J.W., Parker, W.G., and Nesbitt, S.J. 2010. Re-evaluating the correlation between Late Triassic terrestrial vertebrate biostratigraphy and the GSSP-defined marine stages. *Albertiana* 38: 40–52.
- Irmis, R.B., Nesbitt, S.J., Padian, K., Smith, N.D., Turner, A.H., Woody, D., and Downs, A. 2007a. A Late Triassic dinosauriform assemblage from New Mexico and the rise of dinosaurs. *Science* 317: 358–361.
- Irmis, R.B., Parker, W.G., Nesbitt, S.J., and Liu, J. 2007b. Early ornithischian dinosaurs: the Triassic record. *Historical Biology* 19: 3–22.
- Jalil, N.-E. 1999. Continental Permian and Triassic vertebrate localities from Algeria and Morocco and their stratigraphical correlations. *Journal of African Earth Sciences* 29: 219–226.
- Kammerer, C.F., Flynn, J.J., Ranivoharimanana, L., and Wyss, A.R. 2010. The first record of a probainognathian (Cynodontia: Chiniquodontidae) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* 30: 1889–1894.
- Klein, H., Voigt, S., Saber, H., Schneider, J.W., Hminna, A., Fischer, J., Lagnaoui, A., and Brosig, A. 2011. First occurrence of a Middle Triassic tetrapod ichnofauna from the Argana Basin (Western High Atlas, Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology* 307: 218–231.
- Langer, M.C. and Benton, M.J. 2006. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology* 4: 309–358.
- Langer, M.C., Ezcurra, M.D., Bittencourt, J.S., and Novas, F.E. 2010. The origin and early evolution of dinosaurs. *Biological Reviews* 85: 55–110.
- Long, R.A., and Murry, P.A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *Bulletin of the New Mexico Museum of Natural History and Science* 4: 1–254.
- Lucas, S.G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143: 347–384.
- Nesbitt, S.J., Irmis, R.B., Parker, W.G., Smith, N.D., Turner, A.H., and Rowe, T. 2009. Hindlimb osteology and distribution of basal dinosauriforms from the Late Triassic of North America. *Journal of Vertebrate Paleontology* 29: 498–516.
- Nesbitt, S.J., Sidor, C.A., Irmis, R.B., Angielczyk, K.D., Smith, R.M.H., and Tsuji, L.A. 2010. Ecologically distinct dinosaurian sister-group demonstrates early diversification of Ornithodira. *Nature* 464: 95–98.
- Novas, F.E. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology* 35: 51–62.
- Novas, F.E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology* 16: 723–741.
- Olshevsky, G. 1991. A revision of the Parainfraclass Archosauria Cope, 1869, excluding the advanced Crocodylia. *Mesozoic Meanderings* 2: 1–196.
- Parker, W.G. and Irmis, R.B. 2005. Advances in vertebrate paleontology based on new material from Petrified Forest National Park, Arizona. *New Mexico Museum of Natural History & Science Bulletin* 29: 45–58.
- Parker, W.G., Irmis, R.B., and Nesbitt, S.J. 2006. Review of the Late Triassic dinosaur record from Petrified Forest National Park, Arizona. *Museum of Northern Arizona Bulletin* 62: 160–161.
- Paul, G.S. 1988. *Predatory Dinosaurs of the World*. 464 pp. Simon and Schuster, New York.
- Raath, M.A. 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. In: K. Carpenter and P.J. Currie (eds.), *Dinosaur Systematics: Perspectives and Approaches*, 91–105. Cambridge University Press, Cambridge.
- Rayfield, E.J., Barrett, P.M., and Milner, A.R. 2009. Utility and validity of Middle and late Triassic “Land Vertebrate Faunachrons”. *Journal of Vertebrate Paleontology* 29: 80–87.
- Romer, A.S. 1971. The Chañares (Argentina) Triassic reptile fauna. X. Two new but incompletely known long-limbed pseudosuchians. *Breviora* 378: 1–10.
- Romer, A.S. 1972a. The Chañares (Argentina) Triassic reptile fauna. XIV. *Lewisuchus admixtus*, gen. et sp. nov., a further thecodont from the Chañares beds. *Breviora* 390: 1–13.
- Romer, A.S. 1972b. The Chañares (Argentina) Triassic reptile fauna. XV. Further remains of the thecodonts *Lagerpeton* and *Lagosuchus*. *Breviora* 394: 1–7.
- Sereno, P.C. and Arcucci, A.B. 1994a. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* 13: 385–399.
- Sereno, P.C. and Arcucci, A.B. 1994b. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *Journal of Vertebrate Paleontology* 14: 53–73.
- Stocker, M.R. 2010. A new taxon of phytosaurs (Archosauria: Pseudosuchia) from the Late Triassic (Norian) Sonsela Member (Chinle Formation) in Arizona, and a critical reevaluation of *Leptosuchus* Case, 1922. *Palaeontology* 53: 997–1022.
- Tourani, A., Lund, J.J., Benaouiss, N., and Gaupp, R. 2000. Stratigraphy of Triassic syn-rift deposition in Western Morocco. *Zentralblatt für Geologie und Paläontologie* 2000: 1193–1215.



## 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.

	11111	111111	2222222222222222222222222222	22	
88	99900000	444445	00000001111111111122222222	99	
56	78901234	567890	345678901234567890123456	12	
<i>Diodorus</i>	10	020?1010	0?0010	12111?01?10?0010010?1000	11

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).