C. R. Palevol 18 (2019) 747–763

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

The taxonomy, chronostratigraphy and paleobiogeography of glyptosaurine lizards (Glyptosaurinae, Anguidae)

Taxonomie, chronostratigraphie et paléobiogéographie des lézards glyptosaurins (Glyptosaurinae, Anguidae)

Robert M. Sullivan

New Mexico Museum of Natural History and Science, 1801 Mountain Rd. NW., 87104 Albuquerque, NM, USA

ARTICLE INFO

Article history:
Received 7 March 2019
Accepted after revision 23 May 2019
Available online 22 August 2019

Handled by Eric Buffetaut

Keywords:
Anguidae
Chronostratigraphy
Glyptosaurinae
Glyptosaurini
"Melanosaurini"
Paleobiogeography
Paleogene

ABSTRACT

Glyptosaurine lizards (Glyptosaurinae, Anguidae) are an extinct group of heavily armored lizards known from North America, Europe and Asia. Glyptosaurine lizards, taxa that possess fully developed tuberculated dermal armor, appear to have been established in North America by late early Puercan time (To3). "*Proxestops*," a taxon distinguished by a combination of vermiculate and tuberculated osteoderm sculpturing, is considered to be a non-glyptosaurine, a sister taxon of the Glyptosaurinae. Known from only fragmentary remains, its wide chronostratigraphic distribution suggests that "*Proxestops*" is a form genus that, in all probability, represents more than one taxon, that ranges from the middle Paleocene to the early Eocene of North America. Moreover, the taxa *Odaxosaurus piger*, *Parodaxosaurus sanjuanensis* and "*Proxestops*" are best considered "proto-glyptosaurines". "Melanosaurins" and glyptosaurins were well-established by the early Eocene, especially in North America, and are here documented by their type species and chronostratigraphic levels. Both tribes are present in Europe (MP7), too, but the record is not as estensive as that of North America. The North American taxon *Gaultia silvaticus* (Wa0) is transitional between a "melanosaurin" and glyptosaurin. Because it lacks the well-defined hexagonal osteoderms that characterize the Glyptosaurini, it is removed from that group and considered to be a "melanosaurin". The "melanosaurin" taxon "*Xestops*" *savagei* (Wa4–Wa6) cannot be referred to *Xestops* (Br2) based on non-corresponding elements and because superficial similarity does not justify assignment to this taxon. *Arpadosaurus sepulchralis* (Wa6?), whose holotype is a fragmentary right frontal, is considered a subjective junior synonym of *A. gazinorum*, based on minor differences in the epidermal scale pattern that probably represent individual variation. "*Glyptosaurus*" *agmodon* (Wa6?), based on a partial right maxilla, cannot be referred to *Glyptosaurus* (sensu stricto), and the material upon which this taxon is based bears strong resemblance to material identified as cf. "?*Paraglyptosaurus*" *yatkolai* (Wa5–Wa6). "*Glyptosaurus*" *rhodinos* (Wa5) is based on an incomplete parietal, and its reference to *Glyptosaurus* is considered problematic. *Eoglyptosaurus donohoei* (Wa7) is probably valid and is re-established here. *Glyptosaurus* (sensu stricto) is known solely from the middle Eocene (Br2) by *G. sylvestris*. *Dimetoposaurus wyomingensis* (Br3) is removed from *Xestops vagans* because its synonymy was based on superficial similarities. *Helodermoides tuberculatus*, the largest and last glyptosaurin (Ch3), is restricted to the Chadronian of North America. Only the "melanosaurin" *Peltosaurus granulosus* (Or2–Or3),

E-mail address: robertmsullivan@icloud.com

https://doi.org/10.1016/j.crpv.2019.05.006

which includes the species *P. abbotti*, seems to have crossed the Eocene-Oligocene boundary, and appears to be largely restricted to the Orellan, but extended into the Arikareean. European glyptosaurines are also represented by both glyptosaurins and "melanosaurins" early in the Eocene (MP7). *Placosauriops*-like "melanosaurins" are known from Dormaal (MP7), and the glyptosaurin taxon?*Placosaurus ragei* occurs at the same level. "*Placosauriops abderhaldeni*" has been identified from the Grube Messel (MP11), but this assignment remains dubious because the species has not been adequately diagnosed, and the holotype species is from the Geiseltal (MP13), which is some 4.5 million years younger. *Placosauriops weigelti* (MP13) is the only valid species of this genus. *Paraxestops stehlini* (MP14) is not referable to the North American taxon *Xestops*, and its relationship to *Placosauriops* has not been studied. The late Eocene glyptosaurins *Placosaurus estesi* (MP17) and *P. rugosus* (MP18) are the last glyptosaurines known from Europe and appear to have gone extinct at the Eocene-Oligocene boundary, casulties perhaps of the "Grande Coupure". Asian glyptosaurines are known solely from one species, *Stenoplacosaurus mongoliensis*, from the middle Eocene (Sharamurunian) of China. Glyptosaurines most likely originated in North America, diversified by late Paleocene time, and rapidly spread across the North Atlantic into Europe by the early Eocene. Both "melanosaurins" and glyptosaurins took a foothold in Europe by the early Neustrian, but the glyptosaurins, aside from one occurrence (Dormaal, MP7), were conspicuously absent for most of Neustrian through early Robiacian time. In North America, glyptosaurins diversified during the early and middle Eocene, while in Europe small "melanosaurins" were a prominent part of the paleoherpetofauna, and glyptosaurins are unknown for most of the Neustrian through the Geiseltalian, in both the fossilferous Lagerstätten of Messel and Geiseltal. *Stenoplacosaurus* is the only known glyptosaurin glyptosaurine from Asia, and its abrupt appearance during the late Eocene suggests the possiblity of a Beringian dispersal from North America into Asia.

RÉSUMÉ

Mots clés :
Anguidae
Chronostratigraphie
Glyptosaurinae
Glyptosaurini
« Melanosaurini »
Paléobiogéographie
Paléogène

Les lézards glyptosaurins (Glyptosaurinae, Anguidae) sont un groupe éteint de lézards à forte armure, connus en Amérique du Nord, en Europe et en Asie. Les lézards glyptosaurins, des taxons qui possèdent une armure dermique tuberculeuse fortement développée, semblent s'être établis en Amérique du Nord à la fin du Puercan inférieur (To3). « *Proxestops* », un taxon qui se distingue par une combinaison de sculptures d'ostéoderme verimiculées et tuberculées, est considéré comme un non-glyptosaurin, un taxon frère des Glyptosaurinae. Sa vaste distribution chronostratigraphique, connue à partir de restes fragmentaires, suggère que le « *Proxestops* » est un genre de forme qui, selon toute probabilité, représente plus d'un taxon, allant du Paléocène moyen à l'Éocène inférieur de l'Amérique du Nord. De plus, les taxons *Odaxosaurus piger*, *Parodaxosaurus sanjuanensis* et « *Proxestops* » sont plutôt considérés comme des « proto-glyptosaurins ». Les mélanosaurins et les glyptosaurins étaient bien établis au début de l'Éocène, en particulier en Amérique du Nord, et y sont documentés par leur espèce type et leurs niveaux chronostratigraphiques. Les deux tribus sont également présentes en Europe (MP7), mais le bilan n'est pas aussi bon que celui de l'Amérique du Nord. Le taxon nord-américain *Gaultia silvaticus* (Wa0) fait la transition entre un mélanosaurin et un glyptosaurin. Comme il ne possède pas les ostéodermes hexagonaux bien définis qui caractérisent les Glyptosaurini, il a été retiré de ce groupe et est considéré comme un mélanosaurin. Le taxon de mélanosaurin « *Xestops* » *savagei* (Wa4–Wa6) ne peut pas être rapporté à *Xestops* (Br2) sur la base d'éléments ne correspondant pas et à cause du fait que la similitude superficielle ne justifie pas l'attribution à ce taxon. *Arapadosaurus sepulchralis* (Wa6 ?), dont l'holotype est un frontal fragmentaire droit, est considéré comme un sujet junior synonyme d'*A. gazinorum*, basé sur des différences mineures dans le motif d'écailles épidermiques, qui représentent probablement une variation individuelle. « *Glyptosaurus* » *agmodon* (Wa6 ?), basé sur un maxillaire droit pariétal, ne peut pas être appelé *Glyptosaurus* (sensu stricto), et le matériel sur lequel ce taxon est basé ressemble fortement au matériel identifié comme «?*Paraglyptosaurus* » *yatkolai* (Wa5–Wa6). « *Glyptosaurus* » *rhodinos* (Wa5) est basé sur un pariétal incomplet et sa référence à *Glyptosaurus* est considérée comme problématique. *Eoglyptosaurus donohoei* (Wa7) est probablement valide et est rétabli ici. *Glyptosaurus* (sensu stricto) est connu uniquement à l'Éocène moyen (Br2) par *G. sylvestris*. *Dimetoposaurus* (sensu *wyomingensis*) (Br3) est retiré de *Xestops vagans* parce que sa synonymie était basée sur des similitudes superficielles. *Helodermoides tuberculatus*, le plus grand et dernier glyptosaurin (Ch3), est limité au Chadronien d'Amérique du Nord. Seul le mélanosaurin *Peltosaurus granulosus* (Or2–Or3), qui comprend l'espèce *P. abbotti*, semble avoir franchi la frontière Éocène–Oligocène et être en grande partie limité à l'Orellien, mais étendu dans l'Arikaréen. Les glyptosaurins européens sont également représentés à la fois par les glyptosaurins et les mélanosaurins au début de l'Éocène (MP7). Des mélanosaurins ressemblant

à *Placosauriops* sont connus de Dormaal (MP7), et le taxon de glyptosaurin – *Placosaurus ragei* – est présent au même niveau. « *Placosauriops abderhaldeni* » a été identifié dans la tranchée de Messel (MP11), mais cette assignation reste douteuse, car l'espèce n'a pas été correctement diagnostiquée et l'holotype appartient au Geiseltal (MP13), quelque 4,5 millions d'années plus jeune. *Placosauriops weigelti* (MP13) est la seule espèce valide de ce genre. *Paraxestops stehlini* (MP14) ne fait pas référence au taxon nord-américain *Xestops* et sa relation avec *Placosauriops* n'a pas été étudiée. Les glyptosaurins de l'Éocène tardif, *Placosaurus estesi* (MP17) et *P. rugosus* (MP18), sont les derniers connus en Europe et semblent s'être éteints à la frontière Éocène–Oligocène, victimes peut-être de la « Grande Coupure ». Les glyptosaurins asiatiques sont connus uniquement par une espèce, *Stenoplacosaurus mongoliensis*, de l'Éocène moyen (Sharamurunien) de Chine. Les glyptosaurins, très probablement originaires d'Amérique du Nord, se sont diversifiés à la fin du Paléocène et se sont rapidement propagés dans l'Atlantique nord jusqu'en Europe au début de l'Éocène. Les mélanosaurins et les glyptosaurins se sont imposés en Europe dès le début du Neustrien, mais les glyptosaurins, à l'exception d'un événement (Dormaal, Mp7), ont été remarquablement absents pendant la majeure partie de la période nuonienne jusqu'à la période du Robiacien. En Amérique du Nord, les glyptosaurins se sont diversifiés au début et au milieu de l'Éocène, tandis qu'en Europe, les petits « mélanosaurins » constituaient une part importante de la paléo-herpétofaune, et alors que les glyptosaurins sont inconnus dans la majeure partie du Neustrien au Geiseltalien, dans les deux Lagerstätten fossilifères de Messel et de Geiseltal. *Stenoplacosaurus* est le seul glyptosaurin d'Asie connu. Son apparition brutale à la fin de l'Éocène suggère la possibilité d'une dispersion béringienne d'Amérique du Nord vers l'Asie.

1. Introduction

Glyptosaurines lizards have been collectively known from North America, Europe and Asia for over 150 years, with the first record being the description of *Placosaurus rugosus* from the Eocene of France published by Gervais (1848–1852). A couple of decades later, O. C. Marsh published two short papers, the first naming the North American genus *Glyptosaurus* together with naming a few species (Marsh, 1871), and a second paper (Marsh, 1872) naming more species of *Glyptosaurus,* as well as erecting the extinct family Glyptosauridae for their reception. Many of Marsh's species were later synonymized (see Estes, 1983a; Gilmore, 1928; Smith, 2011a, b; Sullivan, 1979, 1986a, 1989). Camp (1923), in his classic work *Classification of the lizards*, later re-established Marsh's Glyptosauridae for the reception of these heavily armored fossil lizards. However, Gilmore (1928) recognized these fossil lizards to be members of the extant lizard family Anguidae. Years later, McDowell and Bogert (1954) established and placed the North American fossil anguids in the extinct subfamily Glyptosaurinae within the family Anguidae. The family Placosauridae (Kuhn, 1940), although having taxonomic priority, has been considered synonymous with Glyptosauridae, and thus the Glyptosaurinae (see Estes, 1983a; McDowell and Bogert, 1954).

Gilmore (1928) was the first to list the various species of *Glyptosaurus* in stratigraphic sequence and provided a taxonomic key to the species. However, this key did not provide an adequate means for discriminating the species of *Glyptosaurus*, a fact that, years later, prompted Sullivan (1979) to revise the genus. Sullivan (1979) established two tribes within the subfamily Glyptosaurinae: the Glyptosaurini and "Melanosaurini," and named two new genera, *Paraglyptosaurus* and *Eoglyptosaurus*, as well as resurrecting the genus *Helodermoides* Douglas (1903). Subsequent studies (Sullivan, 1986a, 1989) led to more synonymies and the establishing of another taxon, *Proglyptosaurus huerfanensis*.

Smith (2009) named the taxon *Gaultia silvaticus* based on a partial frontal that he believed was a transitional taxon between the tribes "Melanosaurini" and Glyptosaurini, and he assigned it to the latter tribe. In another paper, Smith (2011a) returned a couple of species to the genus *Glyptosaurus* because of Sullivan's (1989) synonymy of *Paraglyptosaurus princeps* with *Glyptosaurus sylvestris*. These included "*G.*" *hillsi* and, by default, "*G.*" *yatkolai*. Smith (2011a) also added to the diversity of this genus by naming *Glyptosaurus rhodinos* based on an incomplete parietal. In a more recent study, Smith and Gauthier (2013) named another species of *Glyptosaurus*, *G. agmodon*, based on an incomplete right maxilla, as well as naming two new "melanosaurins:" *Xestops savagei*, based on an incomplete parietal, and *Arpadosaurus sepulchralis*, based on an incomplete right frontal.

The purpose of this paper is to review and critique our current understanding of both the Old and New World glyptosaurine lizards, by scrutinizing their taxonomic validity, documenting their chronostratigraphic distribution through their type species, and providing a brief review of their paleobiogeography.

Institutional Abbreviations: AMNH FR (fossil reptiles), American Museum of Natural History, New York, New York, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; KU, Museum of Natural History, University of Kansas, Lawrence; MNHN, Museum national d'Histoire naturelle, Paris, France; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; SDNHM, San Diego Natural History Museum, San Diego, California, USA; UCMP, University of California, Museum of Paleontology, Berkeley, California, USA; UNM,

Department of Geology, University of New Mexico, Albuquerque; USNM, United State National Museum, Natural History, Washington, D.C., USA; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

2. Taxonomy

2.1. Background

Glyptosaurine lizards (Anguidae: Glyptosaurinae) are perhaps the most interesting and successful groups of lizards that lived during Paleogene time. Known for their distinctive tuberculate dermal armor (osteoderms covered their head and body), their origin has been traced back to the Late Cretaceous of North America (Estes, 1983a; Meszoely, 1970; Sullivan, 1979). Numerous specimens are known from both North America and Europe (Estes, 1983a; Meszoely et al., 1978; and others). Although there are differing opinions as to the definition of the Glyptosaurinae (Estes, 1983a; Gauthier, 1982; Smith, 2009), these opinions are based on technicalities that arguably a matter of one's perspective. Glyptosaurinae has been divided into two groups: the monophyletic Glyptosaurini, distinguished by hexagonal/polygonal osteoderms covering the skull; and the non-monophyletic "Melanosaurini," which are characterized by large dermal plates covering the top of the skull (Sullivan, 1979). A number of glyptosaurine genera and species have been named, some others no longer considered valid, and a few synonymies have been made (Gilmore, 1928; Meszoely et al., 1978; Smith, 2011a; Sullivan, 1979, 1986a, b, 1989). Generic and specific identity of glyptosaurine lizards is in a state of flux largely owing to recent synonymies, descriptions of new material and more theoretical aspects of classification. I largely follow the work of Sullivan (1979, 1986a, 1989) with recent modifications by Smith (2011a).

2.2. Terminology

The common terminology has changed over the years and has been somewhat inconsistent, in part, due to advances in the phylogenetic systematics of these lizards. The common terms "melanosaurinids" and "glyptosaurinids" were introduced by Sullivan (1979) for members belong to the "Melanosaurini" and Glyptosaurini, respectively. Because members of the "Melanosaurini" have not been united based on any known synapomorphies, this "tribe" is considered paraphyletic, and the group name has been offset by shutter quotes (i.e. "Melanosaurini") in subsequent studies. Sullivan (1989) later proposed to abandon the terms "glyptosaurinid" and "melanosaurinid," because of potential confusion with the traditional Linnaean familial rank. The terms "glyptosaur" for the monophyletic Glyptosaurini, and "melanosaur," for members of the paraphyletic "Melanosaurini" were adopted for a short time (Sullivan, 1989). However, these common terms have presented their own problems with respect to clarity, so the convention now is to commonly refer to these groups as glyptosaurins and "melanosaurins" to reflect these Linnaean ranks at the tribal level.

2.3. Genera and species

Any rigorous account of the paleobiogeographic distribution of the taxa within either the Glyptosaurini or "Melanosaurini" is dependent on the unambiguous taxonomic identification of taxa (at both the genus and species levels) as well as their precise biostratigraphic occurrences. From this, their respective chronostratigraphic ranges can be elucidated. Historically, a number of specimens have been assigned to taxa without rigorous scrutiny, and some have been misidentified, thus leading to erroneous biostratigraphic ranges. This is especially true for the "melanosaurin"-like forms known from the earliest Paleogene of both North America and Europe. Unfortunately, this is now true species for a number of species that have been recently returned to the genus *Glyptosaurus* by Smith (2011a), in large part due to synonymies by Sullivan (1986a, 1989).

2.4. Methods

In this present study, I regard *Glyptosaurus* as monotypic, known solely by its type species *G. sylvestris* Marsh, 1872, which is restricted to the Bridgerian (Br2) of North America. Other species that have been reassigned to "*Glyptosaurus*" are in need of revision and/or need a new generic name. The North American type species, together with their geographic locality and stratigraphic occurrence, recognized in this study are listed in Table 1. These taxa, together with the European and Asian glyptosaurines are reviewed below. I follow the definition of Sullivan (1979) by which the Glyptosaurinae is distinguished by the presence of fully developed tubercles as surface sculpturing on osteoderms. Those fossil anguids that have a combination of vermiculate sculpturing plus some tuberculate sculpturing (i.e. incipient development of tubercles) are viewed as being the sister taxa to the Glyptosaurinae (this includes all various examples of what I refer to as the "*Proxestops*" grade). The Late Cretaceous taxon *Odaxosaurus piger* (see Meszoely et al., 1978), considered to be a "melanosaurin" by Estes (1983b), and the enigmatic early Paleocene *Parodaxosaurus sanjuanensis* (Sullivan, 1986c) are sister taxa of ("*Proxestops*" + Glyptosaurinae). "*Proxestops*" is herein considered to include various primitive non-glyptosaurines (sensu stricto), distinguished by dermal armor bearing some degree of incipient tubercular sculpturing. These anguids span the early Paleocene through early Eocene (see below). Collectively, these structural precursors of glyptosaurines (sensu stricto, see Sullivan, 1979) can be informally referred to as "proto-glyptosaurines" and include *Odaxosaurus*, *Parodaxosaurus* and "*Proxestops*". I note here that a recent paper by Klembara et al. (2017), raised the possibility that *Odaxosaurus piger* may be a basal anguine. I strongly disagree with their conclusions and follow the interpretation of Estes (1983a: 147) who characterized *Odaxosaurus piger*, in part, to be "broadly ancestral to the glyptosaurs." The dentition alone (obtuse teeth, with striated, squared-off crowns, expanded tooth shafts) precludes affinities with the Anguinae and demonstrates affinities with the Glyptosaurinae.

Table 1
Stratigraphic position of type species and notable specimens of North American glyptosaurine and "proto-glyptosaurine" lizards (*Odaxosaurus*, *Parodaxosaurus* and "*Proxestops*"). "*Proxestops*" is considered to be a form genus (see text) and includes *Proxestops silberlingii* (and its synonymies, see Sullivan, 1991, p. 297). For purposes of this paper, *Proxestops jepseni* is a place holder, in this table and in Fig. 1, pending further study of these transitional forms.
Tableau 1
Position stratigraphique des espèces types et des spécimens remarquables de lézards nord-américains glyptosaurins et « protoglyptosaurins » (*Odaxosaurus, Parodaxosaurus* et « *Proxestops* »). « *Proxestops* » est considéré comme une forme de genre (voir texte) et inclut *Proxestops silberlingii* (et ses synonymes, voir Sullivan, 1991, p. 297). Pour les besoins de cet article, *Proxestops jepseni* occupe une place dans le Tableau 1 et sur la Fig. 1, dans l'attente d'une étude ultérieure de ces formes de transition.

Taxon	Formation/Mbr/beds	Horizon/Locality	Geographic place	Subzone
Peltosaurus granulosus	Cedar Creek	"C" or "D"	Cedar Creek, Logan Co., CO	Or2–Or3
Helodermoides tuberculatus	Pipestone Springs beds	"*Titantotherium* zone"	Pipestone Springs, MT	Ch3
SDNHM75932	Santiago	Member C	Rancho del Oro, San Diego Co., CA	Ui3
Dimetoposaurus wyomingensis	Bridger	upper	Tabernacle Buttes, WY	Br3
Glyptosaurus sylvestris	Bridger	"B"	Grizzly Buttes, WY	Br3
Xestops vagans	Bridger	"B"	Grizzly Buttes, WY	Br3
"Glyptosaurus" hillsi	Huerfano	Gardner Buttes	Muddy Fork of Huerfano River, near Gardner, CO	Br1a
Proglyptosaurus huefanensis	Huerfano	upper	Castillo Pocket, Gardner, CO	Br1a
Eoglyptosaurus donohoei	Wasatch	Lost Cabin	Boysen Reservoir, WY	Wa7
"Glyptosaurus" agmodon	Wasatch	UCMP loc. V74022	Washakie Basin, WY	Wa6?
"Arpadosaurus" sepulchralis	Wasatch	UCMP loc. V4022	Washakie Basin, WY	Wa6?
Arpadosaurus gazinorum	Wasatch	Knight Mbr.	La Barge-Big Piney regions, WY	Wa6–Wa7
"Glyptosaurus" yatkolai	San José	Regina Mbr.	Arroyo Blanco, NM	Wa5–Wa6
"Glyptosaurus" rhodinos	Willwood	UCMP loc. D2035Q	Bighorn Basin, WY	Wa5
"Xestops" savagei	Wasatch	UCMP loc. V70243	Washakie Basin, WY	Wa4–Wa6?
Melanosaurus maximus	Willwood (= Wasatch)	"above red-banned beds"	Clark's Fork Basin, Big Hom Co., WY	Wa2–Wa3
Gaultia silvaticus	Willwood	UCMP loc. V99019	Bighorn Basin, WY	Wa0
Proxestops jepseni	Fort Union	Princeton Quarry	Park Co WY	Ti5a
Parodaxosaurus sanjuanensis	Nacimiento	NMMNH loc. 312	Torreon Wash, San Juan Basin, NM	To3

The taxonomy of glyptosaurine lizards has changed over the years due, in part, to the discovery of new material and the reassessment of previously published specimens. One of the largest problems is taxa based on incomplete material or based on elements that cannot be compared to others because of the lack of corresponding material. Identifying taxa on primitive features, like the general epidermal scale impression patterns seen in the holotype coalesced frontals of *Xestops vagans*, for example, has led to the erroneous conclusion (see below) that the genus had a widespread paleogeographic (i.e. North America and Europe) distribution and also had a long stratigraphic range (49 Ma for *Xestops vagans* to 41.5 Ma for *Paraxestops* [*Xestops*] *stehlini*) (Estes, 1983b; Meszoely et al., 1978), and even longer (53 Ma–41.5 Ma) if one accepts the species *X. savagei* (Smith and Gauthier, 2013). The same problem exists for names given to incomplete specimens that bear some resemblance to other, better known taxa. Because the sample size of much of the material is so small, inter- and intraspecific variation cannot be addressed. Smith and Gauthier (2013) discussed some of the inherent problems dealing with assigning names to fossil material especially those based on single or limited elements. They advocated a population approach for the recognition of species. While in an ideal world such an approach has merit, difficulties still arise in assigning taxa to incomplete specimens with any degree of certainty. This is especially true for fossil lizard taxa that are too often represented by fragmentary skeletal elements. Whether they are from the same locality, or from ones that are separated both paleogeographically and/or chronostratigraphically, there is always some level of uncertainty in assigning incomplete specimens to a specific genus or species. Therefore, for the purposes of this contribution, I limit my discussion to the type species, based on their respective holotypes, not only for the characterization of the taxon but also for their biostratigraphic occurrence. I view extending the ranges of genera and species, based on fragmentary remains beyond their type locality, as problematic and challenge the reality of such extensions.

3. Chronostratigraphy and Paleobiogeography of glyptosaurine lizards

3.1. Chronostratigraphy

In a recent review of the Eocene amphibians and squamates of Europe, Rage (2012) presented a detailed account of taxa, their occurrences and ages. Here, I use this comprehensive study as a basis for discussing glyptosaurine paleobiogeography, focusing on their chronostratigraphic occurrences and paleogeographic distribution, not only in Europe, but expand it to include North America and Asia.

For North American taxa, I use the corresponding mammal zone or biochron in Woodburne (2004) for their respective type localities, except where noted. For the European taxa, the standard reference levels given by Rage (2012) are followed. The single Asian Sharamurunian correlation is based on the recent work of Wang et al. (2019) using polarity chrons. These, in turn, are correlated with the 2018 Geological Society of America Geologic Time Scale recently published by Walker et al. (2018). From this, a detailed correlation of glyptosaurine lizards for North America, Europe and Asia (Fig. 1

) is presented.

3.1.1. Paleocene of North America

"Proto-glyptosaurine" lizards are known from the early Paleocene (middle Puercan) of North America, represented

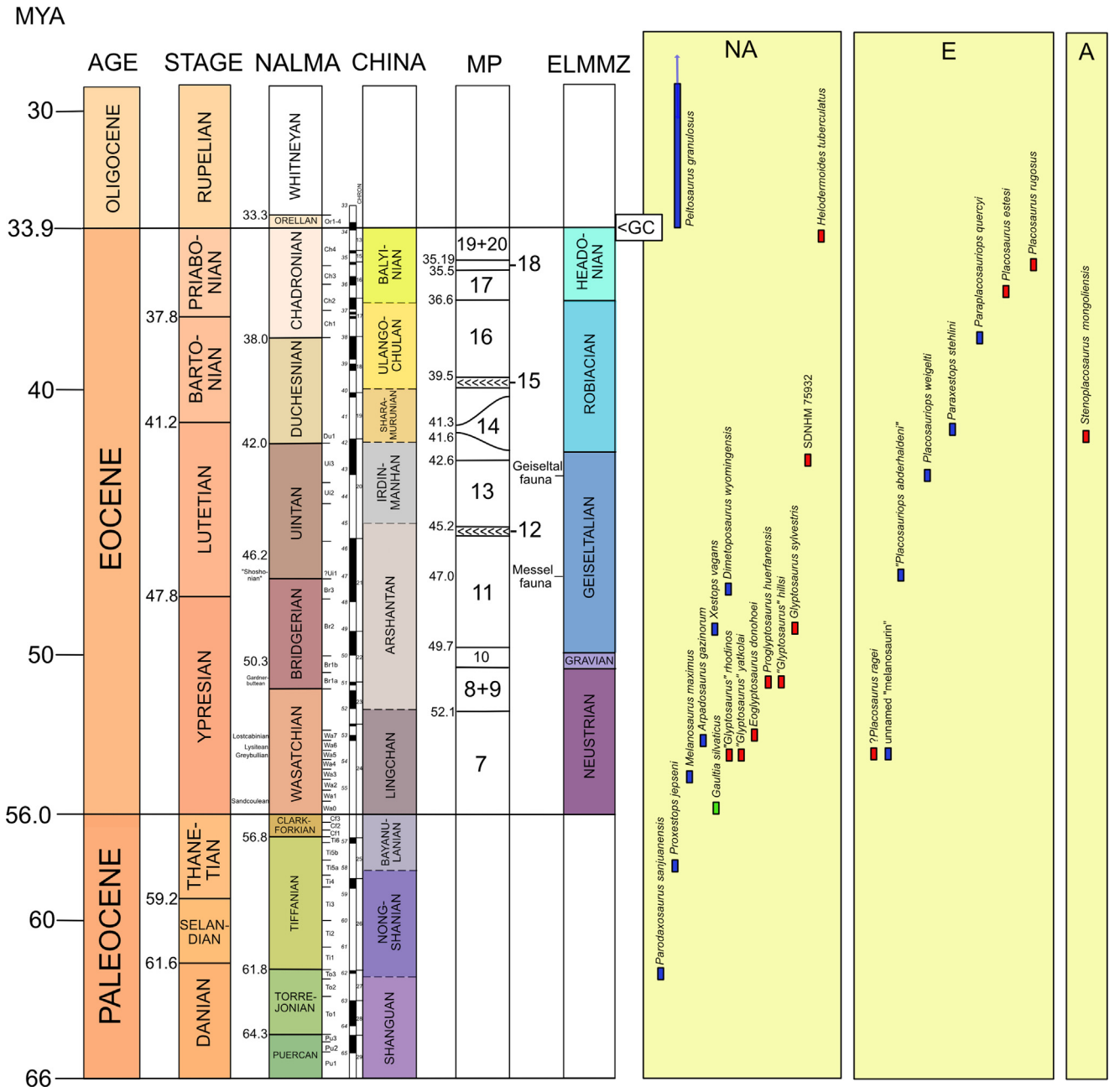

Fig. 1. Correlation and geographic distribution Glyptosaurine and "proto-glytosaurine" lizards (Paleocene–early Oligocene) recognized in this study, based on the occurrence of type species (text for discussion of ranges). Principle sources for correlation: Franzen (2005); Rage (2012); Walker et al. (2018); Wang et al. (2019) and Woodburne (2004). The Messel fauna includes "melanosaurin" *Placosauriops abderhaldeni* and the younger Geiseltal fauna includes *Placosauriops weigelti*; MP 12 and MP 15, indicated by ««< lack fossils (Rage, 2012); boundaries of the ELMMZ are based on those published by Franzen (2005). Dates for the upper boundaries of MP 8 + 9, 11 are not known, and MP 14 is only known to range between 41.3–41.6 mya. Numbers outside columns are all millions of years ago (mya). Dashed lines between the Chinese vertebrate ages are uncertain; there are no absolute dates known to anchor any of their boundaries. I regard the taxa "*Xestops*" *savagei* (Wa4–Wa6?) and "*Glyptosaurus*" *agmodon* (Wa6?) named by Smith and Gauthier (2013) as chimeras (see text) and *Arpadosaurus sepulchralis* (Wa6?) as a subjective junior synonym of *A. gazinorum* (see Appendix), so they are not included here. **Abbreviations**: GC = Grande Coupure; ELMMZ = European Land Mammal Mega Zone; MP = Mammalian Paleogene level; NALMA = North American Land Mammal age. Blue rectangle = "melanosaurin"; red rectangle = glyptosaurin; green = transitional "melanosaurin"/glyptosaurin, but more like the "melanosaurin" *Arpadosaurus* (see text).[[fr]]Corrélation et distribution géographique des lézards Glyptosaurins et « proto-glyptosaurin » (Paléocène–Oligocène inférieur), reconnus dans cette étude, sur la base de l'occurrence des espèces types (voir texte pour la discussion des rangs). Principales sources de corrélation : Franzen (2005), Rage (2012), Walker et al. (2018), Wang et al. (2019) et Woodburne (2004). La faune de Messel inclut le « mélanosaurin » *Placosauriops abderhaldeni* et la plus jeune faune de Geiseltal inclut *Placosauriops weigelti* ; MP 12 et MP15, indiqués par ««<, manquent de fossiles (Rage, 2012) ; les limites de l'ELMMZ sont basées sur celles publiées par Franzen (2005). Les données pour les limites supérieures de MP 8 + 9, 11 ne sont pas connues, et MP14 n'est connu que pour la période entre 41,3 et 41,6 mya. Les nombres en dehors des colonnes représentent tous des millions d'années (mya). Les lignes en tiretés entre les âges des vertébrés sont incertaines ; il n'y a aucune date absolue connue pour fixer une quelconque de leurs limites. Les taxa « *Xestops* » *savagei* (Wa4–Wa6 ?) et

mostly by isolated dentary, frontal and osteoderm material (Sullivan, 1981, 1986c; Sullivan and Lucas, 1986). A number of osteoderm specimens have been recovered from the Puercan by the author and reside in the collections of the Natural History Museum of Los Angeles County, California. Osteoderm, and other fragmentary skeletal remains, from both Puercan and Torrejonian age strata of New Mexico, are housed in the collections of the New Mexico Museum of Natural History and Science (pers. observation). Most of this material has yet to be studied in detail, but preliminary survey of the specimens suggests they are mostly referable to either *Odaxosaurus* sp. or "*Proxestops*"-grade taxa.

Sullivan (1981) reported on an incomplete frontal (KU 9734) from the Torrejonian (To2) of Kutz Canyon (KU locality 13), New Mexico, that displayed a combination of "pit-and-ridge" (vermiculate) sculpturing with some tuberculation, and an anterior part of a skull (KU 7897) with a frontal, largely encrusted and obscured by matrix, that appeared to be of the vermiculate ("pit-and-ridge") morphology. Both specimens were tentatively referred to "*Odaxosaurus* cf. *piger*." In a subsequent paper (Sullivan, 1986c), I reassigned KU 9734 to *Proxestops jepseni* and established a new taxon, *Parodaxosaurus sanjuanensis*, based on an anterior portion of a coalesced frontal (NMMNH P-12346, formerly UNM NP-1509) that retained vermiculate dermal sculpturing (seen in the Late Cretaceous taxon *Odaxosaurus piger*) from Torreon Wash, of New Mexico. *Parodaxosaurus* is Torrejonian (To3) age (late early Paleocene), equivalent to the "*Pantolambda* zone," as redefined by Lofgren et al. (2004), and may represent anguid lizards that were the last to retain this primitive sculpturing. A recently recovered specimen (NMMNH P-58618) from Torreon Wash, that has yet to be described, consists of a nearly complete coalesced frontal, that is slightly constricted between the orbits and bears near fully tuberculate dermal armor. This frontal suggests the presence of "melanosaurin" glyptosaurines by early Paleocene (To3) time in North America.

Bartels (1983) reported the Late Cretaceous taxon "cf. *Odaxosaurus piger*" from the *Plesiadapis cookei* Zone (FG-6), which presumably corresponds to the *Plesiadapis cookei* Lineage Zone (Cf2) of Lofgren et al. (2004). To my knowledge, no definitive Paleocene occurrence of *Odaxosaurus* has been established, let alone a late Paleocene (Clarkforkian) occurrence.

Suffice it to say, much of the North American Puercan and Torrejonian anguid lizard material may pertain to "*Proxestops*," a taxon named by Gauthier (1982), based on the type species *Peltosaurus jepseni* Gilmore (1942) from Princeton Quarry, Silver Coulee beds, Fort Union (formerly Polecat Bench) Formation (Tiffanian-Ti5a) of Wyoming (see Secord et al., 2006). These fossil anguid lizards display a transitional osteoderm morphology that falls between the vermiculate sculpturing characteristic of *Odaxosaurus-Parodaxosaurus* grade, to that of fully tuberculate sculpturing, characteristic of members of the Glyptosaurinae (sensu Sullivan, 1979), contra Estes (1983a) and Gauthier (1982), who considered both *Odaxosaurus* and *Proxestops* to be primitive glyptosaurines.

In a subsequent study, I (Sullivan, 1991, p. 297) established *Proxestops silberlingii*, a new taxonomic combination, synonymizing Gilmore's (1938) ?*Harpagosaurus silberlingii* (Gilmore, 1938), from the Paleocene Fort Union Formation Silberling Quarry (To2), along with *Peltosaurus jepseni* (Gilmore, 1942), *Pancelosaurus piger* (in part) (Meszoely, 1970), *Proxestops jepseni* (Gauthier, 1982),?*Paraprionosaurus silberlingii* (Estes, 1983) and the nomen nudum, *Proxestops gastrodon* (Bartels, 1988). *Proxestops silberlingii* has priority over *Proxestops jepseni* if the latter proves to be distinct from the former.

Smith (2009) assigned a number of specimens to "*Proxestops* sp." from the early Wasatchian (Wa0) Willwood Formation, Bighorn Basin, Wyoming, but he stated that these differed from the Tiffanian type material. He noted too, that *Proxestops* displays a number of characters that are primitive to both anguid and glyptosaurine lizards. As a consequence, the stratigraphic range of "*Proxestops,*" which, in part, includes the recently named "*Xestops*" *savagei* (Smith and Gauthier, 2013, see below) appears, to be quite long, possibility extending from the early Paleocene (Pu2) through the early Eocene (Wa0), approximately 10 million years (65–56 mya), an unusually long range for a lizard taxon. Given that the taxon's identification is based largely on the transitional sculpturing, and that a number of features of the taxon are pleisomorphic, it seems likely that "*Proxestops,*" as currently understood, represents a form genus, a name given to fragmentary material distinguished, in this case, by incipient tubercular sculpturing that probably occurred among a number of early Paleocene anguids. It is quite likely that there is more than one taxon that exhibits this primitive morphology. Clearly, more complete material is needed in order for "*Proxestops*" to be properly assessed and its validity confirmed. For the purposes of this study, *P. jepseni* is tentatively recognized for specimens assigned to *Proxestops* (including *P. silberlingii* and *P. gastrodon*).

Fully tuberculate osteoderms have been recently reported from the latest Paleocene of North Carolina (Cicimurri et al., 2016) that clearly establish that glyptosaurines were widespread across North America by that time. However, it is unknown whether this occurrence is a "melanosaurin" or glyptosaurin.

3.1.2. Eocene of North America

In North America, glyptosaurine lizards become a dominate part of the lizard fauna at the onset of the

« *Glyptosaurus* » *agmodon* (Wa6 ?), dénommés chimères (voir texte) par Smith et Gauthier (2013), et *Arpadosaurus sepulchralis* (Wa6 ?), qualifié de synonyme de sujet junior de *A. gazinorum* (voir Appendice), n'ont pas été inclus ici. **Abréviations :** GC = Grande Coupure; ELMMZ = mégazone de la terre européenne des mammifères ; MP = niveau paléogène des mammifères ; NALMA = âge des mammifères de la terre nord-américaine. Rectangle bleu = « mélanosaurin » ; rectangle rouge = glyptosaurin ; vert = transition « mélanosaurin »/glyptosaurin, mais qui est plus probablement le « mélanosaurin » *Arpadosaurus* (voir texte).

Eocene. "Melanosaurin"-like lizards, including those of the "*Proxestops*"-like grade, continued to flourish, with *Melanosaurus maximus* and the enigmatic *Arpadosaurus gazinorum* making their appearance in the early Eocene (Wasatchian). The taxon *Xestops vagans*, known from the middle Eocene (Bridgerian), appears to be one of the last of these early primitive "melanosaurin"-like taxa. But then there is an apparent, unexplainable dearth of "melanosaurins" until the early Oligocene, when *Peltosaurus* becomes the last representative of the Glyptosaurinae.

One of the earliest glyptosaurine lizards to appear in the Eocene of North America is *Gaultia silvaticus* from the Willwood Formation (Wa0), Bighorn Basin, Wyoming (Smith, 2009). This glyptosaurine lizard, while sporting the fully tuberculate dermal armor that defines this group, has dermal armor that is subdivided into heterogenous plates of different sizes. Its skull roof dermal armor is not divided into discrete, subequal hexagonal plates (osteoderms), which is characteristic of the clade Glyptosaurini as defined by Sullivan (1979). Instead, *Gaultia* is more reminiscent of *Arpadosaurus*, in which the frontal and parietal dermal armors are subdivided into larger units. Therefore, I do not consider *Gaultia* to be a member of the Glyptosaurini, but instead place it as the sister taxon to that group.

Smith and Gauthier (2013) added to the diversity of early Wasatchian glyptosaurines by naming three new taxa, "*Xestops*" *savagei* (Wa4–Wa6?), "*Arpadosaurus*" *sepulchralis* (Wa6?) and "*Glyptosaurus*" *agmodon* (Wa6?), as well as identifying two others, glyptosaurine sp. "A" and "B." Some of the material cited by Smith and Gauthier (2013) as pertaining to "*Xestops*" *savagei* had previously been assigned to the late Paleocene taxon *Proxestops jepseni* by Gauthier (1982), which underscores the problems in assigning these primitive glyptosaurines and protoglyptosaurines to specific genera and species. I note that the holotype of this species is based on a partial parietal (UCMP 146425), whereas the holotype of *Xestops vagans* (USNM 16532) is based on a pair of coalesced frontals and other skeletal elements that do not include a parietal (Gilmore, 1928; Meszoely, 1970; Meszoely et al., 1978; Sullivan, 1979). The partial right frontal UCMP 214628, while superficially resembling the frontals of the holotype of *Xestops vagans*, differs in that the anterior portion of the frontal is narrower and the posterolateral margins flare out compared to the holotype of *X. vagans*. These morphological differences, coupled with the fact that "*X.*" *savagei* is older (Wa4–Wa6?) than *X. vagans* (Br2), demonstrate that assignment to the genus *Xestops* is not defensible, so it is not accepted here. It must be pointed out that the two taxa have as their holotypes elements that do not overlap and therefore cannot be readily compared. *Arpadosaurus sepulchralis* from the Wasatch Formation of Wyoming was named by Smith and Gauthier (2013) based on a partial right frontal (UCMP 214431), which is questionably from the Wasatchian (Wa6?). The epidermal scalation pattern of *A. sepulchralis* is so similar to the holotype (USNM 25826) of *A. gazinorum* (Wa6–Wa7), that it must be considered to be within the realm of individual variation. The left dentary referred to this species (UCMP 214675) bears enlarged posterior teeth that are not unlike those seen in the type specimen described by Meszoely (1970). Because of the similarity to *A. gazinorum*, and fragmentary nature of *A. sepulchralis*, I consider it to be a subjective junior synonym of *A. gazinorum*. I note, too, that both species come from virtually the same stratigraphic level (see Appendix). Lastly, Smith and Gauthier (2013) named the taxon "*Glyptosaurus*" *agmodon* based on a partial right maxilla (UCMP 179384) from the Wasatch Formation (Wa6?) of Wyoming. The specimen is very similar to another specimen (UNM J-347, now NMMNH P-9982) published by Sullivan and Lucas (1988), in part, represented by a posterior part of a right maxilla bearing two bulbous crushing teeth, from the Regina Member, San José Formation (Wa5) of New Mexico. They are nearly the same size, and both have the same large, squared-off, obtuse teeth. The New Mexico specimen was one of many that was questionably referred to "*Paraglyptosaurus*" cf. "*P.*" *yatkolai* (see below).

Interestingly, the early Wasatchian is dominated by "melanosaurin" grade taxa, including *Melanosaurus maximus* (Wa2–Wa3) and the slightly younger *Arpadosaurus gazinorum* (Wa6–Wa7). There are a few specimens of the "melanosaurin"-grade that have been documented (Sullivan, 1979, 1981) but have remained largely unstudied. This pattern of occurrence seems to be repeated in Europe (see below) where small "melanosaurin"-like taxa are more common in the early and middle Eocene (see below).

In North America, early Eocene glyptosaurins are first represented by the enigmatic taxon "*Glyptosaurus*" ("*Paraglyptosaurus*") *yatkolai* (holotype AMNH 5181) and specimens referred to "cf. *P. yatkolai*" and "?*P.* cf. *P. yatkolai*" (Sullivan, 1979; Sullivan and Lucas, 1988). The holotype (AMNH 5181) and other AMNH referred specimens are from the Regina Member of the San José Formation, which mostly likely corresponds to Wa5, based on the correlations of Robinson et al. (2004). The referred UNM material (above), described by Sullivan and Lucas (1988), which now resides in the collections of the NMMNH, also comes from the Regina Member of the San José Formation. The NMMNH specimens are presently being re-evaluated by me.

Smith (2011a) named "*Glyptosaurus*" *rhodinos* based on a partial parietal (USNM 527814) and designated a partial right maxilla (USNM 527978) as the paratype. Both specimens are from the Willwood Formation (Wa5), Wyoming. They are of the same age as specimens referred to "*Glyptosaurus*" (*Paraglyptosaurus*) *yatkolai* noted above and may pertain to that taxon.

The species "*Glyptosaurus*" *donohoei* was established for an incomplete and somewhat crushed skull, partial left mandible, other incomplete postcranial material and osteoderms (USNM 18316), from the Boysen Reservoir region, of Fremont County, Wyoming (White, 1952). The specimen came from the Lost Cabin Member of the Wind River Formation (contra Sullivan, 1979; 1989) of the northern Wind River Basin, which spans Wa7–Br1a (Robinson et al., 2004). Sullivan (1979) established the genus *Eoglyptosaurus* for the holotype of "*G.*" *donohoei* and referred another more complete skull (AMNH 7431) to it. Later, Sullivan (1986a) described a new, more complete skull (UCMP 12600) of *Glyptosaurus sylvestris* and revised the taxon accordingly. As a consequence of this revision, Hirsch

et al. (1987), based on unpublished and unsubstantiated data, contended that *Eoglyptosaurus donohoei* could not be separated from *Glyptosaurus sylvestris* on the basis in differences in the pterygoid teeth and raised sub-conical osteoderms. This, in turn, prompted me (Sullivan, 1989) to synonymize *E. donohoei* with *Glyptosaurus sylvestris* and establish a new taxon, *Proglyptosaurus huerfanensis* for AMNH 7431, from the Huerfano Formation, of Colorado. However, it now seems that the late Wasatchian (Wa7) *Eoglyptosaurus donohoei* is distinct not only from the younger Bridgerian (Br2) *Glyptosaurus sylvestris*, but also from the Wasatchian (Br1a) *Proglyptosaurus huerfanensis* based on the features noted by me (Sullivan, 1979, 1986a, 1989). Smith (2011a) indicated the holotype of *Eoglytosaurus* ("*Glyptosaurus*") has yet to be properly described and that further study of the homodont dentition of *Proglyptosaurus huerfanensis* needs to be made. The taxon *Paraglyptosaurus* (*Glyptosaurus*) *princeps* was placed into synonymy with *G. sylvestris* (Sullivan, 1989).

"*Glyptosaurus*" (*Paraglyptosaurus*) *hillsi* and *Proglyptosaurus huerfanensis* are two very different glyptosaurins and are two of the few that actually co-occur, not only in the same geographic area, but nearly at the same stratigraphic level (Br1a). "*Glyptosaurus*" (*Paraglyptosaurus*) *hillsi* (holotype USNM 6004) is characterized, in part, by having a broad skull, with flat hexagonal osteoderms, heterodont dentition, and the posterior teeth expanded into a massive crushing dentition. Thus, it departs from *Proglyptosaurus huerfanensis* which has a relative narrow skull, more numerous inflated hexagonal osteoderms and homodont dentition. The Huerfano Formation material, that previously formed part of the hypodigm of "*Paraglyptosaurus*" *princeps* and was subsequently synonymized with *Glyptosaurus sylvestris* (Sullivan, 1989), probably pertains to either "*Glyptosaurus*" (*Paraglyptosaurus) hillsi* or *Proglyptosaurus huerfanensis* on the basis of their geographic and stratigraphic origin.

The enigmatic taxon *Xestops vagans* (holotype USNM 16532, formerly YPM 541, see Meszoely, 1970), which is considered a primitive "melanosaurin" glyptosaurine, is known from only one specimen from the Bridger "B" Formation, Grizzly Buttes, Wyoming. It is characterized by the definitive tuberculate dermal armor that is characteristic of all glyptosaurines, but it retains a primitive anguid epidermal scale pattern, features that are seen in a number of obscure and little known glyptosaurine lizards. This primitive morphology caused Meszoely et al. (1978) to refer a number of European "*Xestops*"-like taxa to this genus. However, it has since been demonstrated that limited and superficial resemblances cannot be used to define similar-looking glyptosaurine lizards, and that the European "melanosaurins," while similar in some respects to the North American taxon *Xestops*, have proven to be distinct (see Keller, 2009; Keller et al., 1991).

Hecht (1959) named *Dimetoposaurus wyomingensis*, based on a single complete left frontal (AMNH 3819) from the Tabernacle Butte area, upper Bridger Formation (Br3) of Wyoming, which he considered to be a primitive diploglossine and not a glyptosaurine. Although it is a glyptosaurine lizard, it differs from *Xestops vagans* in a number of respects, most notably having narrow frontals and a larger interparietal scute, contrary to the observations of Meszoely (1970). It was synonymized with *Xestops vagans* by Meszoely (1970) based largely on having a similar morphology and the same stratigraphic position. Estes (1983a), following Meszoely (1970), also considered it to be a synonym of *Xestops vagans*. However, *Dimetoposaurus wyomingensis* comes from slightly younger deposits (Br3, not Br2). Given the morphological differences, as well as the different stratigraphic level from which it came, I reject the synonymy of Meszoely (1970) and, accordingly, resurrect *Dimetoposaurus wyomingensis* as a valid melanosaurin glyptosaurine.

Glyptosaurins are more prominent in the middle Eocene (Bridgerian) and the latest Eocene (Chadronian) of North America. The holotype of *Glyptosaurus sylvestris* (UNSM 16523) is a single left frontal from the Bridger "B" Formation of Grizzly Buttes, Wyoming, which is Br2 level (Robinson et al., 2004). Numerous specimens from this interval have been assigned to the taxon (Sullivan, 1979) and subsequently, following the synonymy of *Paraglyptosaurus princeps* with *G. sylvestris* (Sullivan, 1989). This material was augmented by a complete skull from the (upper) Black's Fork Member, Bridger "B" Formation, Uinta County, Wyoming of the same level and age (Br2).

In contrast to middle Eocene taxa, late Eocene, Uintan-age glyptosaurine lizards from North America are poorly known. Schatzinger (1975) was the first to report dentary and osteoderm material from the Uintan of San Diego County, California (Friars and Mission Valley formations), but because of the fragmentary nature of the material, no generic and specific identifications could be made. More recently, Moscato (2013) described the most complete specimen recovered to date from the Santiago Formation (Ui3, see Robinson et al., 2004) of San Diego County, California. This specimen (SDNHM 75932) consists of the anterior portions of both frontals, a right prefrontal, posterior portion of the right maxilla, both jugals, greater posterior part of the left dentary, left humerus, and numerous body osteoderms, some of which remain articulated. It appears that this glyptosaurin is a sub-adult based on the incomplete fusion of cranial osteoderms on the frontals and absence of osteoderms on the jugals. Comparison of SDNHM 75932 to *Glyptosaurus sylvestris*, in particular to UCMP 12500 (see Sullivan, 1986a), led Moscato to conclude that it was referable to that species based on having: 1) flattened frontals; 2) broad cranial osteoderms; and 3) concentric rows of tubercles on the osteoderms. The frontals are extremely narrow, and the frontal/nasal articulation facet is clearly visible on both the left and right frontal. Two cranial, or cephalic, osteoderms are preserved along the right lateral side of the right frontal, representing the remnants of the right orbital row adjacent to the prefrontal. All the remaining cranial osteoderms were unfused and presumably detached from the frontals prior to burial, as is commonly reported for *Helodermoides* (Sullivan, 1979). The two frontals are in near contact, thus they indicate the anterior width of these two elements. The left lateral side of the right frontal suggests room for only a half of a single row of cephalic osteoderms, so there would be only three rostral-caudal rows across the width of the frontals at this location. This is even fewer than in *Stenoplacosaurus*

(i.e. four–two on each frontal). Considering the incomplete and sub-adult nature of the specimen, and given the stratigraphic and geographic occurrence, it seems probable that the San Diego specimen represents an unnamed glyptosaurin and thus it is not referable to the Bridgerian taxon *Glyptosaurus sylvestris*. The only other published accounts of glyptosaurine lizards from Uintan-age strata were by Westgate (1989), based on isolated glyptosaurine osteoderms from the Laredo Formation (also Ui3, see Robinson et al., 2004) of West Texas, and a glyptosaurin cephalic osteoderm from the Devil's Graveyard Formation (Ui3), also of West Texas (Stocker and Kirk, 2016).

The late Eocene (Chadronian) glyptosaurin *Helodermoides tuberculatus* is the best known of all the glyptosaurins and is represented by a number of specimens that span Ch-2 to Ch-4 (middle-late Chadronian). A few specimens, and some of the largest, purportedly came from the Orellan (Gilmore, 1938). However, both late Chadronian and early Orellan strata occur in the area where they were found, and the marker beds that divide these two ages in this part of eastern Wyoming were not recognized at the time they were collected (Prothero, pers. comm. to RMS, 2019). It seems more likely that the specimens originated from the latest Chadronian age strata of eastern Wyoming rather than early Orellan strata. Nevertheless, the Orellan represents a small amount of time, and it seems clear that *Helodermoides* became extinct at, or shortly after, the Grande Coupure event in Europe and the Eocene/Oligocene transition in North America.

The "melanosaurin" *Peltosaurus granulosus* (which here includes the species *P. abbotti* and *P. floridanus*, see Sullivan and Holman, 1996) is known from numerous specimens from the Orellan of North America, although there are unverified reports that a specimen is known from the Chadronian ("*Titantotherium* beds") by Gilmore (1928) and Estes (1983a). Smith (2011b) questionably referred a parietal fragment and other material (dentary and maxillary fragments) to cf. *Peltosaurus* sp. Because the parietal lacks any hint of tuberculation, I regard this assignment to *Peltosaurus* to be erroneous. *Peltosaurus* was briefly addressed by Meszoely (1970), but no comprehensive study of *Peltosaurus* has been completed. Suffice to say, a number of fossil lizards have been identified as "*Peltosaurus*," but these have subsequently been assigned to other taxa (see Estes, 1983a; Meszoely, 1970; Sullivan and Holman, 1996). A single early Arikareean (early late "middle" Oligocene) record of *Peltosaurus* has been reported (see Sullivan and Holman, 1996), but this specimen needs to be re-evaluated. Recently, Scarpetta (2019) documented *Peltosaurus granulosus* from the upper Sharps and Monroe Creek formations of Sharps Corner, South Dakota, extending its range into the early late Oligocene (Ar1 and Ar2 of the Arikareean, respectively; Tedford et al., 2004). Putative Miocene occurrences of *Peltosaurus* have been reported as well, but these latter specimens have been misidentified (Sullivan and Holman, 1996). Thus, with the exception of *P. granulosus*, it seems that nearly all glyptosaurine lizards became extinct shortly after the Grande Coupure event in Europe and the Eocene-Oligocene transition in North America.

3.1.3. Paleocene of Europe

European Paleocene herpetofaunas were recently summarized by Rage (2012) to include only caudates, anurans, lizards, amphisbaenians, scolecophidians and boids. With respect to the lizards, only scincids and necrosaurids are known. This lies in stark contrast to the Paleocene of North America, where Paleocene herpetofaunas are far more diverse (Estes, 1975, 1976; Gilmore, 1942; Sullivan, 1991). Moreover, anguids, represented primarily by the proto-glyptosaurines *Parodaxosaurus-Proxestops*-like taxa, dominate part of the herpetofauna in North America.

3.1.4. Eocene of Europe

In Europe, Glyptosaurine lizards, and as a consequence the family Anguidae, together with both tribes, the Glyptosaurini and "Melanosaurini," appeared abruptly in lowermost Eocene reference level MP7.

Hecht and Hoffstetter (1962) were the first to report on fossil amphibians and squamates from Dormaal (MP7), Belgium, but without figuring any of the material. Years later, additional glyptosaurine specimens from the Dormaal sands (Landen Formation) were the subject of a study by Sullivan et al. (2012), where they described a medial part of a right frontal pertaining to a "melanosaurin" (IRScNB R 266) with unusual epidermal scale impressions on the dorsal surface of the frontal. Since that study, one of the "melanosaurin" frontals described by Hecht and Hoffstetter (1962) resurfaced and was recently examined by one of us (RMS). This frontal (IRScNB R 392, Fig. 2), figured here for the first time, described by Hecht and Hoffstetter (1962), is nearly complete, is a little over 20 mm in length, the dorsal surface is covered with minute tubercles, and it has a sagittal suture that is clearly visible on the dorsal surface (Fig. 2a). The ventral surface (Fig. 2b) is completely fused, leaving no trace of the sagittal suture. This frontal departs from IRScNB R 266, figured by Sullivan et al. (2012, fig. 4), in that it lacks the anterior positioned epidermal scale impressions, but it bears the frontoparietal scale impression typically present in "melanosaurins". The interparietal portion of the coalesced frontals is missing, as is the right posterolateral side, so the corresponding interparietal and right frontoparietal scale impressions are not preserved. This frontal appears to be similar to that seen in both species of *Placosauriops*, but I refrain from assigning it to that taxon because of the limited amount of material upon which to base its identity.

Sullivan et al. (2012) also described a nearly complete left dentary (IRScNB R 263), which they questionably referred to *Placosaurus,* and established a new species for its reception, ?*P. ragei*. A nearly complete parietal table (IRScNB R264) was referred to the same species (cf.?*P. ragei*), as it originated from the same locality as the dentary. The dentary of?*Placosaurus ragei*, which is remarkably well-preserved, has a weakly developed heterodont dentition bearing space for only 19 teeth. The dentary had previously been referred to the stratigraphically younger cf. *Paraplacosauriops quercyi* (see Augé and Sullivan, 2006).

In 1940, Oskar Kuhn described a number of anguid lizards from the middle Eocene brown coals of Geiseltal, Germany (MP13), which is approximately 43.5 Ma. Among them were two "melanosaurins" that he named

Fig. 2. Indeterminate "melanosaurin" frontal from Dormaal (MP7) of Belgium IRScNB R 392. This specimen was briefly described by Hecht and Hoffstetter (1962) but never figured (see text for discussion). Bar scale = 1 cm.
Fig. 2. Frontal indéterminé de « mélanosaurin » de Dormaal (MP7) de Belgique, IRScNB R392. Ce spécimen a été brièvement décrit par Hecht et Hoffstetter (1962), mais n'a jamais été représenté (voir texte pour une discussion). Barre d'échelle = 1 cm.

Placosauriops abderhaldeni and *P. weigelti*. Their morphological similarity to the North American *Xestops vagans* caused Meszoely et al. (1978) to synonymize the Geiseltal species with the genus *Xestops*, together with *Paraxestops stehlini* (Hoffsetter, 1962). While these Eocene lizards superficially resemble the general pattern of cranial epidermal scutes seen in the North American *Xestops*, the shape and the size of the European taxa are readily distinguishable from *Xestops*. This fact led Keller et al. (1991) to suggest that they be returned to their respective genera and that the synonymy with their North American cousin *Xestops* be rejected. In their review of the European "melanosaurins," Augé and Sullivan (2006) reaffirmed the distinct nature of the European *Placosauriops* from the North American taxon *Xestops* based large on the morphology of the frontals, including the patterns of epidermal scale impressions, and noted that the characters used by Meszoely et al. (1978) to combine the two taxa were either inaccurate or misinterpreted. More importantly, Augé (2005) and Augé and Sullivan (2006) synonymized *Placosauriops abderhaldeni* with *P. weigelti*, because the differences between the taxa were viewed as trivial and because they came from the same deposit (Lagerstätte).

Keller (2009) was the first to describe, in great detail, the excellently preserved specimens from Messel (MP11), considered by Franzen (2005) to be 47 Ma, and he assigned all the material to "*Placosauriops abderhaldeni*". As pointed out by Keller (2009), Kuhn (1940) did not provide a diagnosis for either *Placosauriops abderhaldeni* or *P. weigelti*, and the diagnoses provided for these species by Meszoely et al. (1978) were based solely on comparisons to the North American taxon *Xestops vagans*. The type species "*P. abderhaldeni*" is distinguished by frontals with concave orbital borders and being slightly smaller than *P. weigelti*, which, in turn, is characterized by dorsal keeled osteoderms (Estes, 1983a; Keller, 2009; Meszoely et al., 1978). Keller (2009) not only suggested that "*P. abderhaldeni*" was not properly diagnosed, but that some of the features noted by Meszoely et al. (1978) should be removed from the diagnosis based on the Messel specimens. Although Keller (2009) suggested some features for discriminating *P. abderhaldeni*, primarily concerning the osteoderms of the orbital region of the frontal, number of presacral dorsal osteoderms transverse series, as well as the overall length and snout/vent lengths, he was unable to formally diagnose the species. Moreover, he did not offer any clarity as to why the Messel specimens should be referred to the species "*Placosauriops abderhaldeni*," let alone to the genus *Placosauriops*, despite the fact that there are approximately 4.5 Ma between the faunas of the Grube Messel and the younger Geiseltal Lagerstätte.

Hoffstetter (1962) named *Paraxestops stehlini* based on a nearly complete fused frontal and complete mandible from the upper Eocene (MP14) of Mormont-Saint-Loup, Switzerland. The species was synonymized with *Xestops* by Meszoely et al. (1978), largely because of its

superficial resemblance to the North American taxon. Augé and Sullivan (2006) again pointed out differences between the frontals of the two taxa and thus resurrected the genus *Paraxestops* for "*X.*" *stehlini*.

Augé and Sullivan (2006) established the genus *Paraplacosauriops* for material previously referred to "*Placosaurus*" *quercyi* from the Phosphorites du Quercy (MP16). *Paraplacosaurus quercyi* is the chronostratigraphically youngest and largest European "melanosaurin". It has a pronounced heterodont dentition and rectangular plate-like osteoderms fused to the lateral ascending portion of the maxilla. Other dentary material, some very fragmentary, was assigned to cf. *Paraplacosaurus quercyi*, and all are from the early Eocene (MP7, 8 + 9). However, the most complete specimen, a left dentary with heterodont dentition (IRScNB D 02) from Dormaal (MP7), is more gracile than the neotype (MNHH QU-16569), in which the dentary is not as deep or robust. The fragmentary dentary bearing heterodont teeth (MNHN CB 16445) from the early Eocene of Condé-en-Brie, France (MP 8 + 9) was considered too equivocal to be referred to *P. quercyi*. It seems that none of these European specimens are referable to *Paraplacosauriops quercyi*, rather they are incomplete remains most likely from some unknown taxa.

It should be abundantly clear, based on the conclusions presented by Augé and Sullivan (2006), and on the foregoing review of known "melanosaurin" taxa, that the European "melanosaurins" are in need of a thorough restudy and revision. This is similar to the situation with the North American genera "*Proxestops*" and "*Glyptosaurus*", where the assignment of fragmentary material to these genera from outside the type localities is problematic at best. It is doubtful that *Placosauriops* and/or *Paraplacosauriops* can be confidently assigned to the Dormaal material, nor can the Swiss taxon *Paraxestops stehlini* be referred to these taxa based on the known material. Even the nearly complete, beautifully preserved Messel specimens assigned to "*Placosaurus abderhaldeni*" by Keller (2009) must be viewed with skepticism.

It is noteworthy, if not perplexing, that aside from the occurrence of?*Placosaurus ragei* from Dormaal, glyptosaurins are largely absent for most of the early and middle Eocene of Europe. One exception is a specimen consisting of articulated osteoderms from the posterior border of the cranial region that Kuhn (1940) described and illustrated as "*Placotherium* (*Loricotherium*) *weigelti*." This specimen (Kuhn, 1940 Tafel VIII, figs. 1a, b) is of the dorsal neck region, based on the hexagonal osteoderms from the posterior portion of the parietal area and rectangular dorsal osteoderms from the anterior part of the shoulder area. Estes (1983a) reviewed the nature of the material, and the taxonomic history behind the interpretation of this unnumbered specimen. Other unnumbered isolated osteoderms, some hexagonal, were also figured in the same plate (see Kuhn, 1940, Tafel VIII, figs. 2–5), and were identified as belonging to "*Placosaurus waltheri.*" Estes (1983a) regarded this taxon as a nomen dubium. Whether this material can be referred to *Placosaurus* or to some other taxon, the importance of these specimens lies in the fact that they indicate the presence of glyptosaurins in the Lagerstätte of Geiseltal.

The holotype of the glyptosaurin *Placosaurus rugosus* (MNHN 1906-25) from the late Eocene of La Débruge (MP18) was redescribed and rediagnosed by Sullivan and Augé (2006) together with a new species, *P. estesi* (holotype MNHN QU-1773), from the new standard level of Fons 4, MP17 (Pierrère, Phosphorites du Quercyi). Aside from being slightly chronostratigraphically younger than *Placosaurus rugosus*, *P. estesi* differs from *P. rugosus* in being more robust, dorsally having many more hexagonal cephalic osteoderms along the posterior midline region of the coalesced frontals, and, ventrally, the cristae cranii frontalis are less divergent posteriorly.

In summary, the European glyptosaurines are represented by both glyptosaurins and "melanosaurins" early in the Eocene (MP7), but their generic and specific identities are far from certain due to the incomplete material upon which many taxa have been based. Comparisons of the somewhat complete Geiseltal (MP13) "melanosaurins" to excellently preserved "melanosaurins" of the older Messel Lagerstätte (MP11) are problematic based on our currently understanding of characters used to distinguish the species. In general, it seems that a number of small "melanosaurins" are known throughout the early and early late Eocene (Robiacian) of Europe (MP7–MP14). Glyptosaurins are known throughout the Eocene of Europe, but their record is spotty. They are conspicuously absent from the Messel Lagerstätte and represented by only isolated osteoderms and part of a dorsal neck region from the younger Geiseltal brown coals.

3.1.5. Paleocene and Eocene of Asia

The record of glyptosaurines in Asia is extremely poor. None have been recovered from the Paleocene deposits, in which only anguimorphs (Anguiodea indet.) have been documented (Ni et al., 2016; Van Itterbeeck et al., 2007) and Varaniformes (Dong et al., 2016). The Eocene record for Asia is only slightly better. The glyptosaurin *Stenoplacosaurus mongoliensis* is the only reported Asian glyptosaurine known (Sullivan and Dong, 2018). Up until recently only two specimens have been documented, the holotype AMNH FR 6669, first described by Gilmore (1943) and IVPP V898, described by Chow (1957) from the Shara Murun of Inner Mongolia China and the Heti Formation of Henan, respectively. New referred frontal material from near the type locality, which has yet to be described, further documents this taxon. However, these new specimens provide little additional knowledge regarding the morphology of these armored lizards.

3.2. Paleobiogeography

The holarctic distribution and paleobiogeography of lacertilian squamates, has been discussed by many workers, most notably Estes (1983b), Augé (2003; 2005), Augé and Smith (2009), Rage (2012), and Bolet and Evans (2013). Glyptosaurine distribution and paleobiogeography has been presented by Sullivan (1979, 1986a), Estes (1983a), Keller (2009), and Sullivan et al. (2012). Here, I

briefly review what is currently known based on the foregoing assessment of glyptosaurines from North America, Europe and Asia, together with previously published scenarios regarding the paleogeographic distribution of taxa.

3.2.1. Paleobiogeography of Paleocene "proto-glyptosaurine" and glyptosaurine lizards

The origin of glyptosaurine lizards probably occurred in North America based on the occurrence of the Late Cretaceous taxon *Odaxosaurus piger*, known mostly from deposits of Wyoming. Estes (1983a) considered *Odaxosaurus* to be "broadly ancestral" to the Glyptosaurinae. Paleocene proto-glyptosaurines, represented by the form genus "*Proxestops*," are known from the early Paleocene to the earliest Eocene of the North American Rocky Mountain region. These proto-glyptosaurines are considered transitional to the bona fide glyptosaurines and occur from the early Paleocene (Puercan) through early Eocene (Wasatchian). They probably represent a number of genera and species, but because of a poor fossil record and fragmentary remains, their taxonomic identities remain elusive. Interestingly, proto-glyptosaurines co-existed alongside the earliest glyptosaurines, suggesting an early and rather rapid diversification of species.

The earliest "melanosaurin" is now known from the early late Paleocene (To3) of New Mexico based on an undescribed nearly complete frontal (NMMNH P-58618) that displays prominent tuberculated dermal armor and retains the primitive pattern of epidermal scales and underlying osteoderms. The appearance of the "melanosaurins" this early is not surprising considering that similar taxa are known from the earliest Eocene (MP7) of Belgium. Dispersal of the early "melanosaurins" and glyptosaurins from North America to western Europe no doubt occurred prior to the Paleocene-Eocene thermal maximum and may have continued into the earliest Eocene.

3.2.2. Paleobiogeography of Eocene glyptosaurines North American Eocene glyptosaurines continued to diversify during Wasatchian time

Small "melanosaurins" represented by *Gaultia silvaticus* (Wa0), a species that seems transitional to glyptosaurins and considered to be the sister taxon to the glyptosaurins, is one of the earliest Eocene glyptosaurines. "Melanosaurins" continued to flourish throughout the Wasatchian of North America, represented by larger taxa such as *Melanosaurus maximus* (Wa2–Wa3) and *Arpadosaurus gazinorum* (Wa6–Wa7). The Wasatchian glyptosaurin taxa "*Glyptosaurus*" *rhodinos* (Wa5), "*Glyptosaurus*" ("*Paraglyptosaurus*') *yatkolai,* including material referred to cf. "*P. yatkolai*" (Wa5–Wa6), "*Glyptosaurus*" *agmodon* (Wa6?), and *Eoglyptosaurus donohoei* (Wa7) suggest a major radiation and diversification of glyptosaurin lizards before the Bridgerian. A single glyptosaurine caudal vertebra, reported by Estes and Hutchison (1980) from the late Wasatchian Margaret Formation (Eureka Sound Group) of Ellesmere Island, Canadian Arctic Archipelago (see Stidham and Eberle, 2016), suggests these lizards were thriving there in the peak of global warmth before they dispersed into western Europe.

In western Europe, "melanosaurins" and glyptosaurins were well established by the early Eocene (MP7), represented by a small unnamed "melanosaurin" and a medium-sized glyptosaurin, ?*Placosaurus ragei*. Due to the poor fossil record, little is known about glyptosaurine evolution during the early Eocene of western Europe. It's not until the middle Geiseltalian (equivalent to the earliest Uintan of North America, see Fig. 1) that "*Placosauriops abderhaleni*" from the Messel fauna (MP11) makes an appearance. The amount of interchange between North America and Europe during the early Eocene based on glyptosaurines cannot be adequately demonstrated. Bridgerian (late early Eocene) glyptosaurines continued to diversify in North America. The small "melanosaurins" *Xestops vagans* (Br2) and *Dimetoposaurus wyomingensis* (Br3) are known from limited material, and it seems that larger "melanosaurins" were already extinct by the outset of the Bridgerian. Glyptosaurins include the sympatric taxa *Proglyptosaurus huerfanensis* (Br1a) and "*Glyptosaurus*" *hillsi* (also Br1a) and suggest further diversity among the Glyptosaurini. Arguably, the best known North American glyptosaurin, *Glyptosaurus sylvestris*, occurs later in the Bridgerian (Br2). There is no evidence that these later glyptosaurins had any connection to Europe during Bridgerian time. Late early Eocene (Bridgerian equivalent) glyptosaurines are not known from this interval in Europe or Asia.

Isolated osteoderms from the Baca Formation of New Mexico were also considered to be glyptosaurin, cf. *Glyptosaurus* (Lucas, 1997; Lucas et al., 1983), but their identity is less certain. The age of the lower part of the Baca Formation (also referred to as the Hart Mine Formation) is considered to be Bridgerian (Lucas, 1997; pers. comm., 2019) and not Duchesnean age, as indicated by Robinson et al. (2004). The North American middle Eocene (Uintan) glyptosaurines are represented by few accounts. Isolated glyptosaurine osteoderms are known from Texas, (southern) California and North Carolina; all three of these records are known to be glyptosaurins (see above). One specimen, SDNHM 75932, from the late Uintan of San Diego, probably represents a new genus and species of glyptosaurin. European glyptosaurines of Uintan equivalent age, approximately middle to late Geiseltalian (MP11–MP13), are better known, but not adequately diagnosed or studied. These fossil lizards include a small "melanosaurin" taxon referred to "*Placosauriops abderhaldeni*," known from many exquisitely preserved specimens from the Grube Messel (MP11) (Keller, 2009) and from the younger *Placosauriops weigelti* (MP13) from the brown coals of Geiseltal. Only one undiagnostic glyptosaurin specimen is known from the Geisetalian interval, demonstrating how incomplete the fossil record is for these armored lizards. There are no Uintan, middle or late Geiseltalian age equivalent glyptosaurines known from Asia. Presumably the Geiseltalian "melanosaurins" evolved from the early "melanosaurins" that took a foothold early on at the beginning of the Eocene (MP7) in Europe. In Europe, the small enigmatic "melanosaurin" *Paraxestops stehlini* (MP14) from Mont-Saint-Loup, Switzerland, is roughly equivalent in age to the early Duchesnean of North America. Rage and Augé (2010) reported on a small herpetofauna from the middle Eocene

of Lissieu, France (MP14), that included the posterior portion of a left maxilla, which they identified as an indeterminate glyptosaurine. Based on their illustration (Rage and Augé, 2010, fig. 1.3, 1.4), the maxilla is clearly from a small "melanosaurin" glyptosaurine. It occurs at about the same level as the holotype of *Paraxestops stehlini* and may pertain to that species. The Asian glyptosaurin *Stenoplacosaurus mongoliensis* is known from the early Duchesnian time equivalent, approximately 41 Ma. Indeterminate glyptosaurine osteoderms were recently reported from the Brembridge Limestone (Bed 18) from the Hampshire Basin of England (MP20) by Klembara and Green (2010). They considered them to be Bartonian age, but they are now known to be younger (Priabonian) based on the correlation presented in Fig. 1. They are probably related to the late Eocene genus *Placosaurus* based on the known paleogeographic connection between what is now France and the United Kingdom.

The sudden appearance, and only glyptosaurine, *Stenoplacosaurus* from Asia (Inner Mongolia, China), poses an interesting question. Is this taxon more closely related to the North American taxa (i.e. *Helodermoides*, or the unnamed taxon represented by SDNMH 75932) or to the European *Placosaurus*? One can speculate that it is more closely related to the European taxa, a precursor to *Placosaurus*, or that it was derived from a western North America population of glyptosaurins, such as the unnamed San Diego specimen (SDNHM 75932), as the Beringian region provided a dispersal conduit for taxa from North America to Asia for much of the Paleogene (Beard and Dawson, 1999). In North America, the Chadronian record of glyptosaurin lizards is robust. Numerous specimens of *Helodermoides tuberculatus* are known (Sullivan, 1979), and the taxon is found through most of this land mammal age (Ch2–Ch4). It is arguably the most well-known and best documented glyptosaurine. Curiously, no North American "melanosaurins" have been reported for this time interval. In Europe, the "melanosaurin" *Paraplacosauriops quercyi* (MP16), and the glyptosaurins *Placosaurus estesi* (MP 17) and *P. rugosus* (MP18), are known from the North American Chadronian age equivalent. Finally, the "melanosaurin" *Peltosaurus granulosus* appears in the early Oligocene (Orellan) of North America, where it is known from hundreds of specimens. It apparently ranged through the middle Oligocene, and possibly later (Scarpetta, 2019), thus, it represents the youngest occurrence and the last of the glyptosaurine lizards.

In summary, it seems that glyptosaurines originated and dispersed from North America into northwestern Europe during the Paleocene/Eocene thermal maximum via the North Atlantic. Glyptosaurine populations in North America continued to diversify as endemic taxa throughout the early and middle Eocene. A notable decline in glyptosaurine species occurs during post-Bridgerian times in North America. Because of the brief intercontinental land bridge connection, no additional interchanges between North America and Europe occurred, and Europe was totally isolated by late Ypresian time (early Bridgerian in North America). The intermittent Beringia land corridor may have provided a dispersal route for late Eocene glyptosaurins into Asia, but a detailed study comparing *Stenoplacosaurus* to its North American cousins will need to be made in order to confirm this and will depend on acquiring more complete specimens.

3.3. Glyptosaurine extinction and the Grande Coupure

The Grande Coupure has long been considered a major extinction event in the faunal turnover of mammals, and, now, lower vertebrates in Europe (Rage, 2012). This event marks the extinction of the more "archaic" mammals, and to some extent lower vertebrates, distinct from the more advanced or modern taxa. The Grande Coupure also correlates with the Eocene–Oligocene North American faunal turnover or extinction event. The Glytosaurinae is mostly confined to the early and middle Paleogene (pre-Oligocene), thus provides an excellent example of the "archaic" forms among lower vertebrates.

Sullivan and Holman (1996) briefly summarized the North American squamate Eocene-Oligocene turnover in North America. A few additional late Eocene taxa are now known (Smith, 2011b, 2013) suggesting a more diverse herpetofauna prior to the Eocene-Oligocene transition. However, many of the new Chadronian taxa described by Smith (2011b; 2013) are woefully fragmentary and their identity is far from certain. With regards to the glyptosaurine lizards, *Helodermoides tuberuclatus* was the last of the North American glyptosaurins, and it appears to be extinct by the beginning of the Orellan time based on more recent correlations of the Chadronian-Orellan strata in eastern Wyoming. *Placosaurus rugosus* appears to be the last of the Old World glyptosaurins, becoming extinct prior to the Grande Coupure in Europe. To the extent that anything can be extrapolated from their fossil record, glyptosaurines diversified greatly in the early and middle Eocene in North America and became less diverse after Bridgerian time, with the glyptosaurins becoming extinct by Orellan time. "Melanosaurins" are absent from the fossil record in North America after the Bridgerian and "reappear" with only *Peltosaurus* during the Orellan and possibly extending into the Arikareean.

In Europe, the "melanosaurin" glyptosaurines are best known from the early and middle part of the Eocene (MP7–MP16), while glyptosaurin glyptosaurines are better known from the latest Eocene (MP17–MP20), suggesting that the "melanosaurins" died out before the Grande Coupure. *Placosaurus* (MP17–MP18), too, seems to have died out before the advent of the Grande Coupure, but again, the European fossil record of these lizards is lacking, so only generalizations can be made about their range and extinction.

Finally, the taxon *Stenoplacosaurus mongoliensis*, is the only glytosaurine known from Asia. Its origination and extinction, notwithstanding its relationship to both the North American and European cousins, are unknown. Clearly more specimens are needed from North America, Europe and Asia before relationships can be better established.

4. Conclusions

While glyptosaurines are arguably the best-known Paleogene lizards, known from hundreds of specimens,

mostly from North America, they continue to pose problems in identification at the genus and species levels because of their varying degrees of completeness. In general, glyptosaurines diversified early in Paleocene time in North America and spread into western Europe by the early Eocene. Numerous species evolved during the early Wasatchian and Bridgerian in North America, but their diversification in Europe is less understood due to their spotty fossil record. Species diversity in North America diminished significantly by late Eocene time, whereas they are slightly more diverse in Europe, a probable artifact of the fossil record. Glyptosaurines effectively became extinct at the Eocene–Oligocene boundary with the exception of the North American genus *Peltosaurus*, which survived until the middle, and possibl early late Oligocene. The stratigraphic ranges of a number of glyptosaurine genera (and species) are difficult to assess because of the fragmentary nature of most specimens. Names applied to such specimens from beyond their type localities should be viewed with skepticism. Therefore, drawing any conclusions about the stratigraphic range of any particular genus or species, based on isolated and fragmentary remains, cannot be supported. Paleobiogeography of glyptosaurines points to a North American origination and dispersal through the Canadian High Arctic by early Eocene time. Endemic populations in North America and Europe diversified during the early and middle Eocene, while the record is not all that robust for Europe. The Asian taxon *Stenoplacosaurus* maybe more closely related to the North American taxa than to its European counterparts, due to the physiographic isolation of the European continental land mass and the intermittent Beringian land corridor that existed between North America and Asia through much of the Paleogene.

Acknowledgments

I thank Kesler Randall (San Diego Natural History Museum, San Diego) for photos and additional information on SDNHM 75932; Liping Dong (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing) for letting me examine the newly discovered specimens of *Stenoplacosaurus*; Spencer G. Lucas (New Mexico Museum of Natural History & Science, Albuquerque) for discussions of Eocene biostratigraphy and for critiquing an early version of this contribution; Thomas E. Williamson (New Mexico Museum of Natural History & Science, Albuquerque) for discussions of Puercan and Torrejonian chronostratigraphy and for access to specimens under his care; Phil Gingerich (University of Michigan, Ann Arbor) for help in nailing down the precise interval for the holotype of *Melanosaurus maximus*; and Annelise Folei and Thierry Smith (Royal Belgium Institute of Natural Sciences) for access and permission to study IRScNB R 392.

I thank my two reviewers Liping Dong and Andrej Čerňanský (Comenius University, Bratislava) whose thoughtful critiques improved this paper.

Finally, I would be remiss if he did not thank the late Jean-Claude Rage for all his help over the years and especially during the early part of my career in the field of paleoherpetology. Jean-Claude was most gracious and very helpful in so many ways. I am especially grateful for the hospitality he afforded to me on my visits to the Museum national d'Histoire naturelle. Jean-Claude Rage was a true giant in the field of paleoherpetology and I am honored, and humbled, to have known him, and I consider him one of my most cherished colleagues.

Appendix A. Systematic paleontology

Squamata Oppel, 1811
Anguimorpha Fürbringer, 1900
Anguidae Gray, 1825
Glyptosaurinae Marsh, 1872
Glyptosaurini Sullivan, 1979

Apadosaurus gazinorum Meszoely, 1970, p. 136. *Apadosaurus sepulchralis* Smith and Gauthier, 2013, p. 187.

Holotype.— USNM 25826, disarticulated skull elements (frontals, parietal, dentary fragments, part of the right maxilla, incomplete left and right palatines, right articular and occipital condyle) vertebrae and osteoderms.

Type Horizon.— Wasatch Formation, Knight Member (Wa6–Wa7).

Diagnosis.— Meszoely (1970): A large anguid structurally intermediate between *Melanosaurus* and *Glyptosaurus* in scalation. *Arpadosaurus gazinorum* differs from the former in having an unusual epidermal scalation, as indicated by grooves on the frontal bone, and a less extensive patch of palatine teeth; from the latter it differs in that the head osteoscutes are not broken up into polygonal plates.

Comments on the species *A. sepulchralis*.— Smith and Gauthier (2013) diagnosed *Arpadosaurus sepulchralis* as follows: "Differs from *Arpadosaurus gazinorum* in the following features: frontals discrete at large size; interparietal scale restricted to the posteromedial corner of the bone; transverse groove more posteriorly located, coincident laterally with frontal-frontoparietal scale boundary; intramandibular lamella of dentary weak; and infoldings at tooth base absent." They based this diagnosis on the holotype (UCMP 214431), a fragmentary posterior portion of a right frontal, and on one of two paratypes (UCMP 214675), greater portion of a left dentary with teeth. A second paratype (UCMP?151761, presumably a questionable number), a partial?left?maxilla), was not considered in the diagnosis. The first two came from the same locality/quarry (V74022) while the third came from locality V74024. Although both UCMP 214431 (frontal fragment) and 214675 (dentary) are from the same locality, it is clear that they are not from the same individual, rather they are associated (hence the separate catalog numbers) by locality only. All three specimens, however, are from the same stratum (Wasatch Formation) of the Washakie Basin and are questionably from subzone Wa6 ("zone Wa6?") (Smith and Gauthier, 2013). Because there are no overlapping elements between the holotype and the paratypes, features of the dentary, one of the paratypes, cannot be included in the current diagnosis. Thus, the only available element for the diagnosis is the holotype. While the is a possibility that the dentary may pertain to this species it cannot be demonstrated and thus cannot figure into the diagnosis. Having said that, the differences between UCMP 214675 lack of infoldings at the tooth bases and weak intramandibular

lamella of the dentary, may be size related, features one would not necessarily expect to be observed in a much smaller individual. The holotype (UCMP 214431) frontal fragment differs only slightly from the holotype frontal of *A. gazinorum*. Because the patterns on the cranial dermal armor are often variable, it is difficult to determine whether these differences are taxonomic, or indicate individual variation within smaller, ontogenetically younger, individuals. Given that *Arpadosaurus* is known solely from the holotype of *A. gazinorum*, and that the material of *A. sepulchralis* is so fragmentary, couple with the fact that they are from the same geographic region and stratigraphic horizon (Wa6?-Wa7), I consider *A. sepulcharis* to be a subjective junior synonym of *A. gazinorum*.

References

Augé, M.L., 2003. Lacertilian faunal change across the Paleocene-Eocene boundary in Europe. In: Wing, S.L., Gingerich, P.D., Schmitz, B., Thomas, E. (Eds.), Causes and Consequences of globally warm climates in the early Paleogene. Geol. Soc. Am. Spec. Pap., 369, pp. 441–453.

Augé, M.L., 2005. Évolution des lézards du Paléogène en Europe. Mem. Mus. natl Hist. nat. 192, 369 p.

Augé, M.R., Smith, R.M., 2009. An assemblage of early Oligocene lizards (Squamata) from the locality of Boutersem (Belgium), with comments on the Eocene–Oligocene transition. Zool. J. Linn. Soc. 155, 148–170.

Augé, M., Sullivan, R.M., 2006. A new genus, *Paraplacosauriops* (Squamata, Anguidae, Glyptosaurinae) from the Eocene of France. J. Vert. Paleontol. 26, 133–137.

Bartels, W.S., 1983. A transitional Paleocene–Eocene reptile fauna from the Bighorn Basin, Wyoming. Herpetologica 39, 359–374.

Bartels, W.S., 1988. Fossil reptile assemblages and depositional environments of selected Tertiary vertebrate bone concentrations, Bighorn Basin, Wyoming. Dissert. Abstr. Int., B 48 (11), 3228 [Abstract].

Beard, K.C., Dawson, M.R., 1999. Intercontinental dispersal of Holarctic land mammals near the Paleocene/Eocene boundary: paleogeographic, paleoclimatic and biostratigraphic implications. Bull. Soc. geol. France 170, 697–706.

Bolet, A., Evans, S.E., 2013. Lizards and amphisbaenians (Reptilia, Squamata) from the late Eocene of Sossís (Catalonia, Spain). Palaeontol. Electron. 16 (1), 8A 23 p.

Camp, C.L., 1923. Classification of the lizards. Bull. Am. Mus. Nat. Hist. 48, 289–481.

Chow, M., 1957. Remarks on *Placosaurus* (or *Glyptosaurus*) of China. Vert. PalAsiatica 1, 155–157 (in English with Chinese summary).

Cicimurri, D.J., Knight, J.L., Self-Trail, J.M., Ebersole, S.M., 2016. Late Paleocene glyptosaur (Reptilia: Anguidae) osteoderms from South Carolina, USA. J. Paleontol. 90, 147–153.

Dong, L.-P., Evans, S., Wang, Y., 2016. Taxonomic revision of lizards from the Paleocene deposits of the Qianshan Basin, Anhui. China. Vert. PalAsiatica 54, 243–268.

Estes, R., 1975. Lower vertebrates from the Fort Union Formation, late Paleocene, Big Horn Basin, Wyoming. Herpetologica 31, 365–385.

Estes, R., 1976. Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana. J. Paleontol. 50, 500–520.

Estes, R., 1983a. Sauria terrestria, Amphisbaenia. Handbuch Paläoherpet. 10A, Gustav Fischer Verlag, 249 p.

Estes, R., 1983b. The fossil record and the early distribution of lizards. In: Rhodin, A., Miyata, K. (Eds.), Advances in Herpetology and Evolutionary Biology: Essays in honor of Ernest H. Williams. Mus. Comp. Zool. Harvard University, Cambridge, MA, USA, pp. 365–398.

Estes, R., Hutchison, J., 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeogr. Palaeoclimatol. Palaeoecol. 30, 325–347.

Franzen, J.L., 2005. The implications of the numerical dating of the Messel fossil pit deposit (Eocene, Germany) for mammalian biochronology. Ann. Paleontol. 91, 329–335.

Fürbringer, M., 1900. Zur vergleichenden Anatomie des Brustschulterapparates und der Schultermuskeln. Jenais. Zeitschr. Naturwiss. 34, 215–718.

Gauthier, J.A., 1982. Fossil xenosaurid and anguid lizards from the early Eocene Wasatch Formation, southeast Wyoming and a revision of the Anguioidea. Contr. Geol. Univ. Wyoming 21, 7–54.

Gervais, P., 1848–1852. Zoologie et Paléontologie françaises (Animaux vertébrés) : (3 volumes). Paris, 271 p.

Gilmore, C.W., 1928. Fossil lizards of North America. Mem. Natl. Acad. Sci. 22, 1–197.

Gilmore, C.W., 1938. Descriptions of new and little-known fossil lizards from North America. Proc. U.S. Nation. Mus. 86, 11–26.

Gilmore, C.W., 1942. Paleocene faunas of the polecat Bench Formation, Park County, Wyoming. Part II. Lizards. Proc. Am. Philos. Soc. 85, 159–167.

Gilmore, C.W., 1943. Fossil lizards of Mongolia: Bull. Am. Mus. Nat. Hist. 81, 361–385.

Gray, J.E., 1825. A synopsis of the genera of reptiles and amphibia, with a description of some new species. Thomson Ann. Phil., London 10, 193–217.

Hecht, M., 1959. Amphibians and reptiles In: McGrew, P., The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bull. Am. Mus. Nat. Hist. 117, 130–146.

Hecht, M.K., Hoffstetter, R., 1962. Note préliminaire sur les amphibiens et les squamates du Landien supérieur et du Tongrien de Belgique. Bull. Inst. Royal Sci. Nat. Belgique 39, 1–30.

Hirsch, K.F., Kristlaka, L., Stucky, R.K., 1987. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 8. First fossil lizard egg (?Gekkonidae) and a list of associated lizards. Ann. Carnegie Mus. 56, 223–230.

Hoffsetter, R., 1962. Additions á la faune reptilienne de l'Éocène supérieur de Mormont-Saint-Loup (Suisse). Bull. Soc. geol. France S7–IV, 109–117.

Keller, T., Sullivan, R.M., Haubold, H., 1991. Fossil anguid lizards from Geiseltal and Messel (middle Eocene) of Germany: A comparison and assessment. J. Vert. Paleontol. Supp. 3, Abstr. of Papers, 39A.

Keller, T., 2009. Beiträge zur Kenntnis von *Placosauriops abderhaldeni* Kuhn, 1940 (Anguidae, Glyptosaurinae Marsh, 1872) aus dem Mitteleozän der Grube Messel–Skelettanatomie. Taphonomie und Biomechanik. Kaupia 16, 3–145.

Klembara, J., Green, B., 2010. Anguimorph lizards (Squamata, Anguimorpha) from the middle and late Eocene of the Hampshire Basin of southern England. J. Syst. Paleontol. 8, 97–129.

Klembara, J., Miroslav, H., Čerňanský, A., 2017. The first record of anguine lizards (Anguimorpha, Anguidae) from the early Miocene locality Ulm — Westtangente in Germany. Hist. Biol., http://dx.doi.org/10.1080/08912963.2017.1416469.

Kuhn, O., 1940. Die Placosauriden und Anguiden aus dem mitteren Eozän des Geiseltales. Nova Acta Leopoldina (n. f.) 8, 461–486.

Lofgren, D.L., Lillegraven, J.A., Clemens, W.A., Gingerich, P.D., Williamson, T.E., 2004. Paleocene biochronology: The Puercan through Clarkforkian land mammal ages. In: Woodburne, M.O. (Ed.), Late Cretaceous Cenozoic Mammals of North America. Columbia Univ. Press, New York, pp. 43–105.

Lucas, S.G., Sullivan, R.M., Logan, T., 1983. Glyptosaurine lizard from Eocene Baca Formation, South-central New Mexico. New Mex. Geology, pp. 77–78.

Lucas, S.G., 1997. Middle Eocene (Bridgerian) mammals from the Hart Mine Formation, South-central New Mexico. New Mexico Mus. Nat Hist. Bull. 11, 65–72.

Marsh, O.C., 1871. Notice on some new fossil reptiles from the Cretaceous and Tertiary formations. Am. J. Sci. 1, 447–459.

Marsh, O.C., 1872. Preliminary description of new Tertiary reptiles. Parts I and II. Am. J. Sci. 4, 298–309.

McDowell, S.B., Bogert, C.M., 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Am. Mus. Nat. Hist. 105, 1–142.

Meszoely, C.A.M., 1970. North American fossil anguid lizards. Bull. Mus. Comp. Zool. Harvard 139, 87–149.

Meszoely, C.A.M., Estes, R., Haubold, H., 1978. Eocene anguid lizards from Europe and a revision of the genus *Xestops*. Herpetologica 34,156–166.

Moscato, D., 2013. A glyptosaurine lizard from the Eocene (late Uintan) of San Diego, California, and implications for glyptosaurine evolution and biogeography. East Tennessee State University, Electronic Theses and Dissertations. Paper 1176 http://dc.etsu.edu/etd/1176.

Ni, X., Li, Q., Stidham, T.A., Li, L., Lu, X., Meng, J., 2016. A late Paleocene probable metatherian (?deltatheroidan) survivor of the Cretaceous mass extinction. Sci. Repts. 6, 38547, http://dx.doi.org/10.1038/srep38547.

Oppel, M., 1811. Dei Ordnung, Familien und Gattungen der Reptilian als Prodrom einer Naturgeschichte derselben. Lindauer, München, 87 p.

Rage, J.-C., 2012. Amphibians and squamates in the Eocene of Europe: what do they tell us? Palaeobiodiv. Palaeoenviron. 92, 445–457.

Rage, J.-C., Augé, M., 2010. Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. Geobios 43, 253–268.

Robinson, P., Gunnell, G.F., Walsh, S.L., Clyde, W.C., Storer, J.E., Stucky, R.K., Froelich, D.J., Ferrusquia-Villafranca, I., McKenna, M.C., 2004. Wasatchian through Duchesnean biochronology. In: Woodburne, M.O. (Ed.), Late Cretaceous Cenozoic Mammals of North America. Columbia Univ. Press, New York, pp. 106–155.

Scarpetta, S.G., 2019. Peltosaurus granulosus (Squamata, Anguidae) from the middle Oligocene of Sharps Corner South Dakota, and the youngest known chronostratigraphic occurrence of the Glyptosaurinae. J Vert Paleo, e1622129 (9 pages).

Schatzinger, R., 1975. Later Eocene (Uintan) lizards from the greater San Diego area. M. Sci. thesis, San Diego State University, San Diego, CA, 212 p.

Secord, R., Gingerich, P.D., Smith, M.E., Clyde, W.C., Wilf, P., Singer, B.S., 2006. Geochronology and mammalian Biostratigraphy of middle and upper Paleocene continental strata, Bighorn Basin, Wyoming. Am. J. Sci. 306, 211–245.

Smith, K.T., 2009. A new lizard assemblage from the earliest Eocene (zone Wa0) of the Bighorn Basin, Wyoming, USA: biogeography during the warmest interval of the Cenozoic. J. Syst. Palaeontol. 7, 299–358.

Smith, K.T., 2011a. The long-term history of dispersal among lizards in the early Eocene: New evidence from a microvertebrate assemblage in the Bighorn Basin, Wyoming, USA. Palaeontol. 54, 1243–1270.

Smith, K.T., 2011b. The evolution of mid-latitude faunas during the Eocene: late Eocene lizards of the Medicine Pole Hill reconsidered. Bull. Peabody Mus. Nat. Hist. 52, 3–105.

Smith, K.T., 2013. A diverse new assemblage of late Eocene squamates (Reptilia) from the Chadron Formation of North Dakota. Palaeontol. Electron. 9 (5A), 44 p.

Smith, K.T., Gauthier, J., 2013. Early Eocene lizards of the Wasatch Formation near Bitter Creek, Wyoming: Diversity and Paleoenvironmental during an interval of global warming. Bull. Peabody Mus. Nat. Hist. 54, 135–230.

Stidham, T.A., Eberle, J.J., 2016. The palaeobiology of high latitude birds from the early Eocene greenhouse of Ellesmere Island, Arctic Canada. Sci. Repts. 6, 20912, http://dx.doi.org/10.1038/srep20912.

Stocker, M.R., Kirk, E.C., 2016. The first amphisbaenians from Texas, with notes on other squamates from the middle Eocene Purple Bench locality. J. Vert. Paleontol., E1094081 (15 pages).

Sullivan, R.M., 1979. Revision of the Paleogene genus *Glyptosaurus* Marsh. Bull. Am. Mus. Nat. Hist. 163, 1–72.

Sullivan, R.M., 1981. Fossil lizards from the San Juan Basin, New Mexico. In: Lucas, S.G., Rigby Jr., J.K., Kues, B.S. (Eds.), Advances in San Juan Basin paleontology. University of New Mexico Press, Albuquerque, NM, USA, pp. 76–88.

Sullivan, R.M., 1986a. The skull of *Glyptosaurus sylvestris* Marsh, 1871 (Lacertilia: Anguidae). J. Vert. Paleontol. 6, 28–37.

Sullivan, R.M., 1986b. *Glyptosaurus*? *obtusidens* is a nomen dubium. J. Herpetol. 20, 96–97.

Sullivan, R.M., 1986c. A new fossil anguid lizard *Parodaxosaurus sanjuanensis*, new genus, new species from the middle Paleocene (Torrejonian) Nacimiento Formation, San Juan Basin, New Mexico. J. Herpetol. 20, 109–111.

Sullivan, R.M., 1989. *Proglyptosaurus huerfanensis*, new genus, new species: Glyptosaurine lizard (Squamata: Anguidae) from the early Eocene of Colorado. Am. Mus. Novitates 2949, 8 p.

Sullivan, R.M., 1991. Paleocene Caudata and Squamata from Gidley and Silberling quarries, Montana. J. Vert. Paleontol. 11, 293–301.

Sullivan, R.M., Augé, M., 2006. Redescription of the holotype of *Placosaurus rugosus* Gervais, 1848-1852 (Squamata, Anguidae, Glyptosaurinae) from the Eocene of France and a revision of the genus. J. Vert. Paleontol. 26, 127–132.

Sullivan, R.M., Augé, M., Wille, E., Smith, R., 2012. A new glyptosaurine lizard from the earliest Eocene of Dormaal, Belgium. Bull. Soc. geol. France 183, 627–633 (in English with French summary).

Sullivan, R.M., Dong, L., 2018. *Stenoplacosaurus mongoliensis*, a new generic name for "*Placosaurus*" *mongoliensis* (Anguidae, Glyptosaurinae) from the Shara Murun Formation, Nei Mongol (Inner Mongolia) China. New Mex. Mus. Nat. Hist. & Sci. Bull. 80, 691–694.

Sullivan, R.M., Holman, J.A., 1996. Squamata. In: Prothero, D.R., Emry, R.J. (Eds.), The terrestrial Eocene-Oligocene transition in North America. Cambridge University Press, Cambridge, UK, pp. 354–372.

Sullivan, R.M., Lucas, S.G., 1986. Annotated list of lower vertebrates from the Paleocene Nacimiento Formation (Puercan-Torrejonian), San Juan Basin. New Mexico. J. Herpetol. 20, 202–209.

Sullivan, R.M., Lucas, S.G., 1988. Fossil Squamata from the San José Formation, early Eocene, San Juan Basin, New Mexico. J. Paleontol. 62, 631–639.

Tedford, R.H., Albright, L.B., Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt, R.M., Storer, J.E., Swisher, C.C., Voorhies, M.R., Webb, S.D., Whistler, D.P., 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). In: Woodburne, M.O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, pp. 169–231.

Van Itterbeeck, J., Missiaen, P., Folie, A., Markevich, V.S., Van Damme, D., Dian-Yong, G., Smith, T., 2007. Woodland in a fluvio-lacustrine environment on the dry Mongolian Plateau during the late Paleocene: Evidence from mammal bearing Subeng section (Inner Mongolia, P.R. China). Palaeogeogr. Palaeoclimatol. Palaeoecol. 243, 55–78.

Walker, J.D., Geissman, J.W., Bowring, S.A., Babcock, L.E., compilers, 2018. Geologic Time Scale v. 5.0. Geol. Soc. America., http://dx.doi.org/10.1130/2018.CTS005R3C.

Wang, Y., Li, Q., Bai, B., Jin, X., Mao, F., Meng, J., 2019. Paleogene integrative stratigraphy and time scale of China. Sci. China. Earth Sciences 62, 287–309.

Westgate, J., 1989. Lower vertebrates from an estuarine facies of the middle Eocene Laredo Formation (Claiborne Group), Webb County, Texas. J. Vert. Paleontol. 9, 282–294.

White, T.E., 1952. Preliminary analysis of the vertebrate fossil fauna of the Boysen Reservoir area. Proc. U.S. Natl. Mus. 102, 185–207.

Woodburne, M.O., 2004. Global events and the North American mammalian biochronology. In: Woodburne, M.O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, pp. 315–343.