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A New Species of *Globidens* from South Dakota,
and a Review of Globidentine Mosasaurs

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INTRODUCTION

The floors of the warm epicratonal seas of late Cretaceous time supported large populations of benthonic bivalves (Kauffman, 1972; 1973). Among the marine vertebrates which fed on them were a poorly known group of mosasaurs whose bulbous teeth have been collected on five continents. Smith Woodward (1891) was evidently the first to describe such a tooth, and suggested that it was derived from the posterior marginal dentition of a Cretaceous alligator. A very incomplete specimen, consisting of a fragmentary skull and a single vertebra, was described by Gilmore in 1912. He recognized the mosasaurian affinities of the creature, and named it *Globidens* in reference to its globular maxillary teeth. This remained the most complete specimen of the genus known until the present specimen (PR 846) was discovered by Priscilla F. Turnbull in 1967, for Field Museum of Natural History.

The specimen consists of a nearly complete skull and anteriormost 11 presacral vertebrae. The skull has been crushed, and the braincase and many of the finer cranial structures have been destroyed. Nevertheless, it is by far the finest specimen of *Globidens* known, and greatly augments our understanding of the morphology of the genus and of the group of mollusk-eating mosasaurs to which it belongs. The specimen was taken from the upper part of the dark, fissile shales of the Sharon Springs Member (Pierre Formation), on the southeastern flank of the Black Hills,

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South Dakota. Field Museum has made extensive collections of marine vertebrates from this horizon in this area (Zangerl, 1953; Russell, 1967; John Clark and W.D. Turnbull, 1974, *pers. comm.*). These include the remains of fishes, turtles (*Toxochelys browni*), mosasaurs (*Platecarpus* sp. undet; *Platecarpus* cf. *P. somenensis*), ?plesiosaurs, pterosaurs, and toothed birds (*Hesperornis* sp).

At the 1970 annual meeting of the Society of Vertebrate Paleontology in Toronto, Dr. Zangerl told me of the new *Globidens* specimen in Field Museum, and very generously made it available to me for study. The following summer Mr. Malcolm J. Heaton, of McGill University in Montreal, transported the specimen from Chicago to Ottawa. I am most grateful to Mr. Heaton for his assistance, and to Drs. John Clark and William D. Turnbull, both of Field Museum, for information relating to the stratigraphic occurrence of the mosasaur. It is a privilege to be able to present an outline of some of the attributes of this remarkable specimen in a volume honoring Dr. Zangerl's achievements in vertebrate paleontology.

Catalogue numbers given for specimens are preceded by the following abbreviations for different institutions:

PR – Field Museum of Natural History.

SDSM – Museum of the South Dakota School of Mines and Technology.

SMUSMP – Shuler Museum of Paleontology, Southern Methodist University.

USNM – United States National Museum.

YPM – Yale University, Peabody Museum of Natural History.

SYSTEMATICS

Order Sauria
Infraorder Platynota
Family Mosasauridae
Subfamily Mosasaurinae

Tribe Globidentini

Discussion. – Dollo (1924, p. 188) proposed the family-group name "Globidensidae" for mosasaurs with a crushing marginal dentition which presumably fed on hard-shelled marine invertebrates. *Globidens* and *Carinodens* (*Compressidens* Dollo) were

assigned to this group. Most subsequent authors have either retained the familial rank of the group (e.g., Arambourg, 1952), or considered it as a subfamily equal in rank to the Mosasaurinae, Plioplatecarpinae, and Tylosaurinae (e.g., Price, 1957; Telles Antunes, 1964). Noting *Clidastes*-like features in the fragmentary type material of *G. alabamaensis*, Russell (1967, pp. 144-145) placed the group within the Mosasaurinae as a distinct tribe. The morphology of the cranium and anterior presacral vertebrae of the type of *G. dakotensis* exhibits additional clidastoid characteristics (see below). Russell (1967, p. 147) referred *Compressidens* (=*Carinodens*) to the Mosasaurini because of the apparently less specialized nature of its very incompletely known skeletal morphology. In view of the probable derivation of both forms from clidastoid stock and the parallel development of a crushing marginal dentition in each, it is perhaps more useful to group them together within the Globidentini.

Genus **Carinodens** Thurmond, 1969, Jour. Paleontol., **43**, p. 1298.

Compressidens Dollo, 1924, p. 176 (preoccupied Pilsbry and Sharp, 1897).

Generic type. — *Carinodens fraasi* (Dollo 1913).

Diagnosis. — Small projection of dentary anterior to first dentary tooth. Median dentary teeth bilaterally compressed; subrectangular in lateral view and bearing one or more apical nubbins. Anterior dentary teeth sub-circular to circular in horizontal cross-section; triangular in lateral aspect, (?)becoming recurved near the anterior end of mandible.

Discussion. — Although Dollo (1924) separated the type dentary of *Carinodens fraasi* from *Globidens*, together with the type tooth of *C. belgicus*, others (Huene, 1935; Zdansky, 1935; Tzankov, 1939; Avnimelech, 1949; Arambourg, 1952; Price, 1957; Kruytzer 1961, 1964; Raab, 1963) have considered this material as indistinguishable from *Globidens*. Most recently, Telles Antunes (1964, p. 175-176, 247) has summarized the reasons for adopting the latter course, noting that material referred to these forms belongs to different skeletal parts and cannot be compared, and that the dentition of a single modern platynotan (*Varanus niloticus*) contains a range of tooth morphology analogous to that existing in fossil teeth placed by Dollo in two separate genera.

Carinodens is here regarded as probably distinct from *Globidens* because the dentary and teeth of *C. fraasi* appear too delicate to have withstood the stresses which may have been generated

within the skull of a living *Globidens*, and because the last tooth in a dentary referred to *Globidens* by Russell (1967, p. 145, SDSM 4612, see *G. dakotensis* below) is circular in cross-section, not compressed, and the posterior part of the dentary appears to be more powerfully constructed than in *C. fraasi*. Teeth possibly referrable to *Carinodens* have been discovered in Maestrichtian sediments in Bulgaria (Tzankov, 1939, pl. 5 figs. 1-2), Morocco (Arambourg, 1952, pl. 40 fig. 3), and Brazil (Price, 1957, pl. 1 figs. 6-9, pl. 2 figs. 1-5), as well as in Holland (Kruytzer, 1964) and Belgium (Dollo, 1924).

Genus **Globidens** Gilmore, 1912, Proc. U.S. Nat. Mus., **41**, p. 479.

Generic type. – *Globidens alabamaensis* Gilmore.

Revised diagnosis. – Skull short and broad, powerfully constructed. Premaxilla with small rostrum anterior to premaxillary teeth. Twelve (thirteen?) teeth in maxilla. Prefrontal forms small portion of posterolateral border of external nares, broad triangular ala projects laterally from supraorbital wing. Prefrontal and postorbitofrontal narrowly separated to broadly contacting above orbits. Lateral margin of frontal convex, median longitudinal crest present dorsally. Ventral process of postorbitofrontal to jugal confluent with or imperfectly separated from broadly exposed dorsal surface of postorbitofrontal. Ventroposterior tuberosities present on jugal. Parietal foramen small, located entirely within parietal. Median dorsal surface of parietal narrow. Squamosal sends broad wing medially to contact posterolateral ramus of parietal. Pterygoid dentition rudimentary or absent. Suprastapedial process of quadrate broadly fused distally to infrastapedial process; tympanic ala thick, particularly dorsolaterally. Stapedial pit elliptical in form. Marginal teeth inflated, becoming subspherical near center of jaws.

Articulating surfaces of cervical and anterior dorsal centra wider than deep, subcircular in outline. Synapophysis located near center of lateral surface of second and third cervical centra, occupies anterodorsal portion of lateral surface of posterior cervical and anterior dorsal centra. Ventral border of anteroventral extension of synapophysis well developed on cervicals and anterior dorsals, nearly reaching level of undersurface of centrum. Anterior zygopophysis of cervical and anterior dorsal vertebrae connected to synapophysis by rounded, posteriorly descending crest which becomes narrower near synapophysis. Zygosphene-zygantrum well

developed on anterior presacral vertebrae. Anterior base of atlas neural spine arises behind condylar facet; atlas synapophysis long and tubular. Hypapophyseal peduncle located posteriorly on ventral surface of cervical centra; articulation for hypapophysis flat and circular, inclined posteriorly on first two cervical vertebrae, faces directly ventrally on remaining cervical vertebrae. Five hypapophysis-bearing cervicals, one or two more with rudimentary peduncles. (Diagnosis based on type specimens of *G. dakotensis* and *G. alabamaensis*; compare with generic diagnoses in Russell, 1967, 1970).

Discussion. — Since the original description of *Globidens* in 1912 most of the material referred to the genus has consisted of the isolated, characteristically swollen teeth. Exceptions include the type dentary of *Carinodens fraasi* ("*Globidens fraasi*") and three very fragmentary specimens cited by Russell (1967, p. 145; 1970, p. 373). The teeth have been collected in Campanian and Maestrichtian marine (often phosphatic) sediments within a broad belt on either side of the course of the late Cretaceous equator. Although some of these have been named, they do not constitute an adequate morphological base to define species which can usefully be compared to other species of *Globidens* (Telles Antunes, 1964). The teeth can, however, be separated into several morphologic categories:

Type one. — Crowns subspherical with small, symmetrical apical nubbin; carinae and sulci at most faintly developed.

Gilmore, 1912, pls. 39-40 (type of *G. alabamaensis*, Campanian, Alabama, U.S.A.).
Dollo, 1924, pl. 5 figs. 1, 5 ("*G. alabamaensis*," ?*G. dakotensis* this paper, Campanian, Belgium).
This paper (type of *G. dakotensis*, Campanian, South Dakota, U.S.A.).

Type two. — Crowns subspherical with large, recurved apical nubbin, shallow vertical grooves present, crowns low in lateral profile.

Leonardi and Malaroda, 1946, pl. 1 figs. 1-3 ("*G.* cf. *alabamaensis*," Campanian fidé Raab, 1963, Egypt).
Avnimelech, 1949, fig. 2a, ?2b, 2c, ?2d, 2f ("*G. fraasi*," Campanian fidé Raab, 1963, Jordan).
Arambourg, 1952, pl. 40 figs. 4-6 ("*G. aegyptiacus*," Campanian fidé Raab, 1963, Egypt).
Price, 1957, pl. 1 figs. 1-5 ("*G.* cf. *fraasi*," Maestrichtian, Brazil).
Raab, 1963, pl. 4 figs. 5-6 ("*Globidens* ex gr. *G. fraasi* - *G. aegyptiacus*," Campanian, Israel).
Telles Antunes, 1964, pl. 26 fig. 13 (*Globidens* sp., Maestrichtian, Angola).

Type three. — Crowns conical, pointed in lateral profile and circular in horizontal cross-section, apical nubbins absent; some may occupy anterior position in jaws.

Huene, 1935, figs. 1-3 (types of ?*G. timorensis*, "höheren Obersenon," Timor, Indonesia).

Arambourg, 1952, pl. 40 fig. 1 ("*G. aegyptiacus*," Maestrichtian, Morocco).

Raab, 1963, pl. 4 figs. 1-4 ("*Globidens* ex gr. *G. fraasi* - *G. aegyptiacus*," Campanian, Israel).

Telles Antunes, 1964, pl. 26 figs. 12, 14 (*Globidens* sp., Maestrichtian, Angola).

Type four. — Crowns high and rounded in lateral profile, apical nubbin not well developed, anterior and posterior carinae present.

Zdansky, 1935, pl. 2 figs. 6-8 (*G. aegyptiacus*, nomen nudum fidé Telles Antunes, 1964, Campanian fidé Raab, 1963, Egypt).

Type five. — Crowns low and rounded in lateral profile with apical nubbins, irregular horizontal cross-section; some may occupy posterior position in jaws.

Avnimelech, 1949, fig. 2g ("*G. fraasi*," Campanian fidé Raab, 1963, Jordan).

Arambourg, 1952, pl. 40 fig. 2 ("*G. aegyptiacus*," Maestrichtian, Morocco).

It may some day be possible, through the description of new materials, to recognize the forms represented by the material referred to *G. timorensis* and "*G. aegyptiacus*." These teeth are quite unlike those in the type skulls of *G. alabamaensis* and *G. dakotensis*, and could belong to an unrecognized genus of durophagous mosasaur. Kuhn (1939, p. 77) designated a tooth, originally described as crocodilian by Stromer (1933, pl. 1 fig. 5) from the Bahariya Formation of the western desert of Egypt, to a new species of *Globidens*, ?*G. stromeri*. The crown of the tooth is not constricted where it meets the root, and the tooth probably does not belong to *Globidens*, or even to the Mosasauridae.

Globidens alabamaensis Gilmore, 1912, Proc. U.S. Nat. Mus., **41**, p. 479.

Globidens alabamaensis, Gilmore, 1927, p. 452; Russell, 1970, p. 373.

Type. — USNM 6527, left maxilla, frontal, both postorbitofrontals, basisphenoid, right splenial and first dorsal vertebra.

Distribution. — Selma Chalk, Alabama and Mississippi.

Revised diagnosis. — Height of crown less than greatest basal diameter of crown behind seventh maxillary tooth; length of crown exceeds width of crown on teeth anterior to tenth maxillary tooth. Maxilla long and frontal narrow relative to interarticular length of centrum of first dorsal vertebra (see table 5). Median longitudinal crest of frontal merges with dorsal surface of bone in interorbital region. Frontal narrowly enters dorsal margin of orbit.

Globidens dakotensis new species

Globidens alabamaensis, Dollo, 1924, pl. 5 figs. 1, 5; Russell, 1967, p. 144; Thurmond, 1969B, p. 71.

Type. – FMNH PR 846; skull lacking mandibles and ectopterygoids, cervical vertebrae one through seven, dorsal vertebrae one through four. Collected by W.D. and P.F. Turnbull.

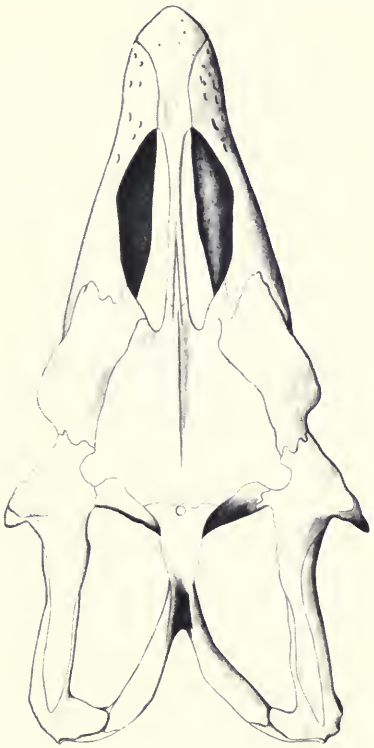

FIG. 1. *Globidens dakotensis*, reconstruction of skull in dorsal aspect, after PR 846.

Horizon and locality of type. – Upper part, Sharon Springs Member of Pierre Shale, Late Cretaceous. NW¼, SW¼, SW¼ section 29, T. 5S., R. 8E., 7½ miles south of Fairburn, Custer County, South Dakota.

Distribution. – Wolfe City or Lower Marl Members, Taylor Formation, Texas; ?Marlbrook Marl, Arkansas; lower Pierre Shale, South Dakota; Craie d'Obourg, Hainaut, Belgium.

Referred specimens. – SMUSMP 62102-62105, isolated teeth (Thurmond, 1969b); USNM 4993, coronoid, articular and axis

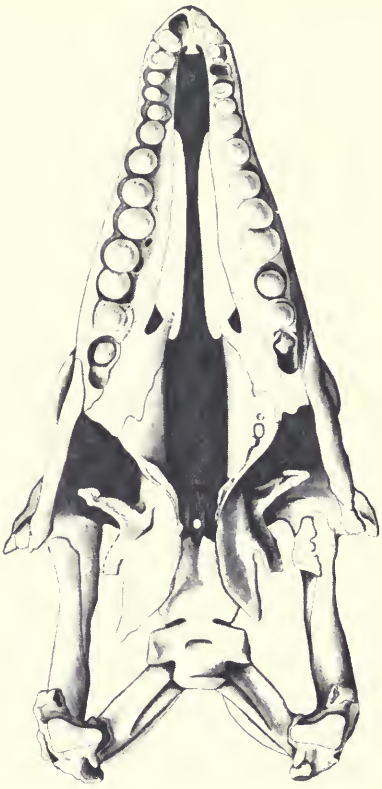

FIG. 2. *Globidens dakotensis*, reconstruction of skull in ventral aspect, after PR 846.

vertebra (Russell, 1967); SDSM 4612, splenial and posterior end of dentary (Russell, 1967); isolated tooth (Dollo, 1924).

Diagnosis. — Height of crown less than greatest basal diameter of crown behind fourth maxillary tooth; width of crown exceeds length of crown on teeth anterior to tenth maxillary tooth. Maxilla short and frontal broad relative to interarticular length of centrum of first dorsal vertebra. Median longitudinal crest of frontal merges with dorsal surface of bone behind interorbital region. Frontal broadly excluded from dorsal margin of orbit by prefrontal and postorbitofrontal.

Description. — The skull of PR 846 is of moderate length, but very broad and solidly built relative to conditions in other mosasaurs. The same robust construction is found in each of the

preserved cranial ossifications. It is also reflected in the development of a crushing marginal dentition and the probable strength of the temporal musculature (the ratio between the length of the supratemporal fenestra and the length of the skull in PR 846 is

FIG. 3. *Globidens dakotensis*, reconstruction of skull in lateral aspect, after PR 846.

0.27, but only 0.22 in *Prognathodon overtoni*, which also has a relatively powerfully constructed skull, see Russell, 1967, fig. 89). The external nares, occupying a position on the muzzle similar to that in most other mosasaurs, are of moderate length but unusual width. The internal nares are situated directly beneath them, on either side of a very wide interpterygoidal fissure. Beyond their unusually heavy proportions, the cranial elements of PR 846 are typically mosasaurian in morphology. Their general shape and position is readily apparent in Figures 1-3 and Plate 1.

Occupying the conical anterior end of the muzzle, the premaxilla is wedged between the maxillae like the keystone in an arch. Its dorsal surface is shallowly sulcate, in a longitudinal direction, and narrows posteriorly to form an internarial bar which is rather weak in comparison with the massive structure of the muzzle. The internarial portion of the premaxilla appears to be separated into two thin alae by a narrow, anteromedian projection of the frontal. The clefts between the two cranial bones appear to be continued onto the frontal portion of the internarial bar. Some of the fragments present may pertain to the nasals. It is unfortunate that the internarial bar is poorly preserved in PR 846, for the relationship between the component elements seems to differ from that in other mosasaurs. The anterior termination of the external nares lies above a point between the alveoli for the fifth and sixth maxillary teeth, as in *G. alabamaensis*. The contact between the maxilla and premaxilla is smooth and the keel formed by the intersection of this surface with the external surface of the

PLATE 1. PR 846, *Globidens dakotensis*, dorsal aspect of skull.

skull approximately parallels the longitudinal axis of the maxilla, as in other members of the Mosasaurinae.

The orbital region of the skull is broad and exceptionally short, although the orbits are of normal proportions. A triangular ala projects from the supraorbital ramus of the prefrontal, in typical mosasaurine fashion. Unlike in *G. alabamaensis*, the prefrontal and postorbitofrontal are broadly sutured to each other over the orbits. The latter element embraces a rounded, posterolaterally-directed lobe of the frontal, in a manner reminiscent of the relationship of these bones on the dorsal surface of the skull in *Clidastes*. The firmly knitted sutures of the cranial elements bordering the mesokinetic axis indicate that it was not functional. The jugal resembles that of *Clidastes* in that the suborbital ramus is broad

TABLE 1. Measurements of skull of *Globidens dakotensis*, PR 846.

	mm.
Length of skull, premaxilla to quadratic suspensoria	657
Length of skull, premaxilla to occipital condyle	591
Length of skull, premaxilla to posterior end parietal along cranial midline	562
Length of prepineal region of skull	452
Length of postpineal region of skull (to quadratic suspensoria)	209
Width of skull, across squamosals	277
Width of skull, across postorbitofrontals	315
Width of skull, across prefrontals	259
Maximum width of premaxilla	62
Length of supratemporal fenestra, left	173
Length of supratemporal fenestra, right	179
Length of orbit, left	140
Length of external naris, left	185
Length of external naris, right	180
Maximum width of frontal	180
Width of frontal, interorbital region	155
Width of maxilla, at nineth alveolus	58
Width of maxilla, at second alveolus	33
Length of alveoli for nine anterior maxillary teeth	195
Height of quadrate	102

and ventromedially inclined in cross-section. Most peculiarly, the suborbital ramus lies well below the alveolar border of the maxilla, and the quadratomaxillary ligament was evidently attached to ridged tuberosities on the lateral surface of the postorbital ramus.

The parietal is narrower than in *Clidastes*, and is deeply notched posteriorly to receive the median epaxial musculature from the neck. The temporal arcades are very powerfully constructed. A peculiar, oblong swelling is present on the anteroventral surface of the left postorbital (fig. 2). The supraorbital ala of this element is not smoothly convex, as in *Clidastes* and *G. alabamaensis*, but contains a shallow depression which is separated from the ramus descending to the jugal by semicircular crest of bone. The massively built squamosal resembles the element in *Clidastes* in that its posterior terminus is deflected ventrally, giving the bone a comma-shaped appearance in lateral profile. A broad tongue of the squamosal contacts the suspensorial ramus of the parietal medially, unlike in *Clidastes* but comparable to conditions in *Mosasaurus*, *Plotosaurus*, *Prognathodon*, and *Plesiotylosaurus* (cf. Camp, 1942; Russell, 1967; Welles and Gregg, 1971).

The anterior, lateral, and posterior extremities of the palate are incompletely preserved (pterygoids), or either unrecognizable or

PLATE 2. PR 846, *Globidens dakotensis*. **1,** left maxillary teeth five through eight, occlusal aspect. **2,** atlas-axis complex, lateral aspect.

absent (ectopterygoids, vomers). A sulcus in the anterior margin of the palatine, opposite the third alveolus from the posterior end of the maxillary tooth row, represents the posterior margin of the internal naris. The pterygoids are very broad and lack functional teeth, although a few rudimentary alveoli are present on the left pterygoid. No other mosasaur is known to lack a well-developed pterygoid dentition. The palatine ramus of the pterygoid in PR 846

PLATE 3. PR 846, *Globidens dakotensis*. **1,** right maxillary tooth ?three, lateral aspect. **2,** right quadrate, a- anterior aspect, b- posterior aspect. **3,** left maxillary tooth ten, occlusal aspect. **4,** left maxillary tooth twelve, occlusal aspect.

curves dorsomedially and then laterally into a longitudinal crest of bone from which the ectopterygoidal and quadratic rami diverge, much as in *Clidastes* (Russell, 1967, fig. 22B). The quadratic ramus is not completely preserved, but the posterior terminus is narrow and the structure may have been more slender than in other mosasaurs.

The quadrate (fig. 3; pl. 3, fig. 2) is unique among mosasaruines in that the supra- and infrastapedial processes are fused (the quadrate of the type specimen of *Halisaurus sternbergi* is pathologic, Russell, 1967, p. 127; 1970, p. 369), although this condition occurs in several plioplatecarpine genera (*Ectenosaurus, Prognathodon, Plesiotylosaurus*). The bone was probably derived from a quadrate similar to that of *Clidastes propython* (Williston, 1898, pl. 28 figs. 1-3). However, in its general shape, the massive construction of the dorsal part of the tympanic ala and the medially constricted suprastapedial process, it could easily be mistaken for the quadrate of an advanced species of *Prognathodon* (Russell, 1967, fig. 91; Welles and Gregg, 1971, fig. 34). A single, obvious difference lies in the fact that the glenoid articular surface is broad in the quadrate of *Prognathodon,* and narrow in that of *Globidens.*

The braincase of PR 846 has been crushed, and conduits for vascular, nerve, and otic structures are too imperfectly preserved to warrant description. The basioccipital resembles that of *Clidastes*, although the basal tubera are more powerfully constructed. As in other genera referred to the Mosasaurinae, the basipterygoidal processes of the basisphenoid project anterolaterally, and the terminal surfaces, which were capped with cartilage in life, also face in this direction. In the Plioplatecarpinae and Tylosaurinae these surfaces are more elongate and tend to more nearly parallel the

TABLE 2. Measurements of crowns of maxillary teeth of *Globidens dakotensis*, PR 846 in millimeters.

	Length		Width		Height*	
Tooth	Right	Left	Right	Left	Right	Left
1	—	—	—	—	—	—
2	12.6	—	13.5	—	—	—
3	?12.7	—	?14.6	—	?16.3	—
4	—	15.2	—	—	—	—
5	20.2	18.8	20.1	20.3	18.7	19.2
6	23.2	23.5	24.8	23.5	—	—
7	23.7	26.5	27.0	27.9	20.7	25.0
8	27.6	29.6	30.5	30.7	24.2	27.5
9	29.8	—	30.5	—	26.0	—
10	29.8	—	28.3	28.8	24.1	—
11	—	25.3	—	25.2	—	18.5
12	—	19.1	—	18.0	13.5	11.7
13	—	—	—	—	—	—

*Measured diagonally from edge to center of crown.

longitudinal axis of the skull posteriorly. Between the basipterygoidal processes and the dorsum sellae the basiphenoid of PR 846 appears identical to the basisphenoid fragment preserved in the type of *G. alabamaensis* (Russell, 1967, p. 32, 144).

Although very similar to those preserved with the type of *G. alabamaensis*, the crowns of the maxillary teeth of PR 846 are generally lower and broader (see pl. 2 and 3, and diagnoses of *G. alabamaensis* and *G. dakotensis*). In both species the enamel surface becomes more coarsely wrinkled toward the apex of the crown, which in unworn teeth ends in an apical nubbin (as on teeth occupying the ?third, fifth, sixth, seventh, tenth, and twelfth maxillary alveoli in PR 846). Gilmore (1912, p. 480) notes that faint carinae are present on maxillary teeth six, seven and nine of the type of *G. alabamaensis,* and these may also be seen in teeth occupying the fifth and sixth maxillary alveoli in the present specimen. Vertical sulci on the twelfth maxillary teeth of PR 846 lend them a subquadrangular outline in occlusal view. A shallow vertical groove is also present on the anteromedial surface of the left tenth maxillary tooth. Alveoli in the position of the thirteenth maxillary tooth, and a nubbin of hard, bony material in the anteromedial corner of the right alveolus, imply that a thirteenth tooth may have been present. No complete premaxillary teeth are preserved in PR 846, but the bases of the crowns suggest that they were short, inflated cones.

TABLE 3. Measurements of vertebrae of *Globidens dakotensis* PR 846 in millimeters.

Vertebra		Ventral length centrum, between articulations	Width across Synapophyses	Height of vertebra, posteriorly
cervical	1	—	68.4	89.4
	2	73.0	67.3*	99.6
	3	60.5	78.2*	—
	4	64.6	98.6	—
	5	62.7	100.8	—
	6	64.6	109.0	—
	7	71.9	113.4	—
dorsal	1	62.6	—	—
	2	61.5	105.3	—
	3	63.3	103.6	—
	4	—	—	—

*Laterally crushed.

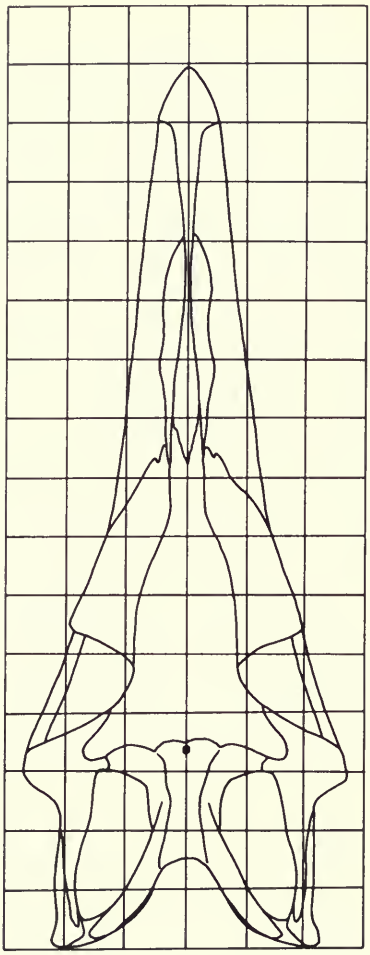

FIG. 4. *Clidastes liodontus,* dorsal aspect of skull after YPM 1335.

The anterior presacral vertebrae are robust, but otherwise rather similar to those of *Clidastes* in that zygosphene-zygantral articulations are strongly developed and the synapophyses occupy a position on the anterodorsal portion of the lateral surface of the centra. The synapophyseal process of the atlas arch is extremely massive and surmounted anteriorly by a heavy tuberosity for the attachment of cranio-cervical derivatives of the longissimus musculature (compare pl. 2; fig. 2 with Russell, 1967, fig. 39). The axis has been laterally crushed, but closely resembles the same bone in a specimen referred by Russell (1967, p. 145, USNM 4993) to

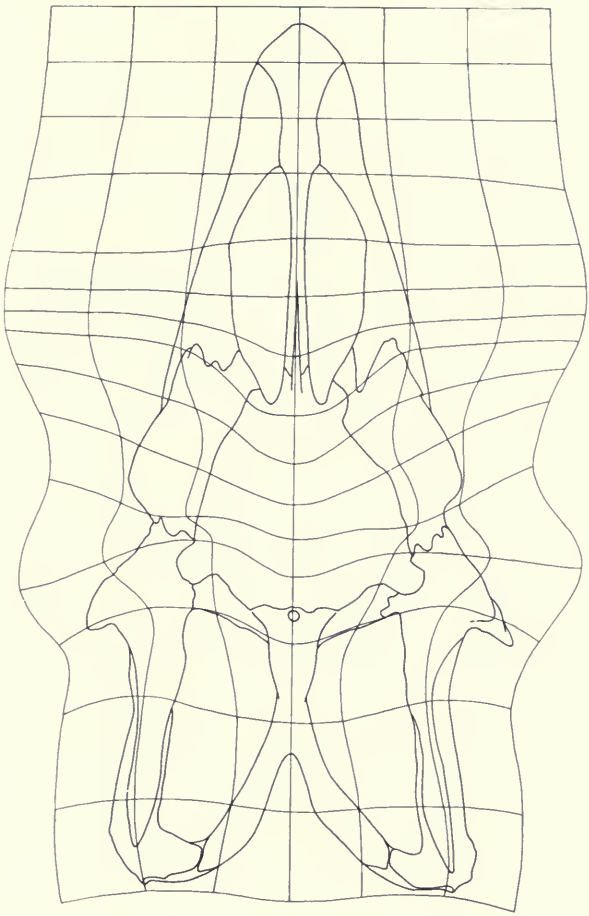

FIG. 5. *Globidens dakotensis*, dorsal aspect of skull. The grid has been drawn over the same cranial structures as in Figure 4 to highlight proportional differences between the two skulls.

Globidens. The outstanding feature of the latter element is its extreme breadth, for the width of the neural arch across the posterior zygapophyses equals the anteroposterior length of the blade of the neural spine. It is evident that the muscles linking the head with the neck were extremely powerfully developed in *Globidens*. Rudimentary zygantral articulations are present on the axis vertebra of PR 846, and the hypapophyseal articulation resembles that of *Clidastes*.

The remaining cervical vertebrae increase slightly in length behind the axis. Zygosphenes are small on the third cervical but are strongly developed on the fourth cervical through the fourth dorsal. The tips of the neural spines are expanded posteriorly on cervicals three through six and incipiently so on cervical seven. The hypapophyseal peduncle is large on this vertebra but lacks an articular surface of a hypapophysis. The peduncle is virtually absent on the succeeding first dorsal vertebra.

Discussion. — Specimens here referred to this species are done so on the basis of the generally greater breadth of the crowns of isolated teeth relative to their height, or because they occur in strata approximately equivalent to the Sharon Springs Member in age (Gill and Cobban, 1966; Stephenson et al., 1942), and younger than the Selma Chalk which has yielded material of *Globidens alabamaensis*. USNM 4993 is noteworthy for the circular profile of the articular in medial aspect, and the presence of a large, truncated tuberosity on the ventral margin of the bone behind the quadrato-mandibular articulation. The coronoid is very broad and depressed, and the axis vertebra, as noted above, is very powerfully constructed. In SDSM 4612 a narrow emargination separates the enlarged alveolar margin and posteriormost alveolus in the dentary from the posteroventral ala of the bone. The associated splenial bears an articulation for the angular as in *G. alabamaensis*.

Virtually every element preserved within the cranium and vertebral column of the type of *G. dakotensis* bears some attribute which is strongly reminiscent of the same element in *Clidastes*. Taken together, these characters imply that *Globidens* was derived from this genus. A comparison of the skull of a generalized species of *Clidastes* (*C. liodontus*, fig. 4) with that of *G. dakotensis* (fig. 5) suggests that the region of the skull anterior to the fronto-parietal suture in *Globidens* became shorter and broader during the phylogenetic development of the genus. Relative to the average length of the anterior presacral vertebrae (see table 4), the prepineal region of the skull is much shorter in *G. dakotensis*, while the supratemporal fenestra is larger, the quadrate is higher and the muzzle is broader than in *C. liodontus*. These proportional changes were evidently accompanied by an increase in the massiveness and rigidity of the cranial skeleton.

The morphology of skeletal elements preserved in the type specimen of *G. alabamaensis* indicates that this species differs less from *Clidastes* than does *G. dakotensis*. The supraorbital alae of

TABLE 4. Proportions of cranial structures in *Clidastes liodontus* and *Globidens dakotensis*, expressed as percentage of average length of presacral vertebrae.

	C. liodontus[1] (YPM 1335)	*G. dakotensis*[2] (PR 846)
Length of skull, pmx. to quad. suspen.	1380	1014
Length, prepineal region of skull	1060	698
Length, postpineal region of skull	303	323
Width of skull across squamosals	427	428
Width of skull across postorbitofrontals	482	487
Width of skull across prefrontals	358	400
Length of supratemporal fenestra	238	276
Height of quadrate	139	157

[1]Average interarticular length, cervical 7 through dorsal 3 . . . . .27.4 mm.
[2]Average interarticular length, cervical 6 through dorsal 3 . . . . . .64.8 mm.

the prefrontals and postorbitofrontals do not contact lateral to the frontal, and the relatively greater length of the alveolar margin of the maxilla (table 5) suggests a greater length for the muzzle in the more ancient form. Although it is difficult to distinguish isolated teeth of the two species, the crowns in *G. alabamaensis* are generally higher and more narrow. In the absence of evidence to the contrary, it may be assumed that *Globidens* separated from *Clidastes* in late pre-Campanian time, with the stabilization of a bulbous dentition and robust skull within a population of clidastoid mosasaurs which were feeding on benthonic mollusks. The number of marginal teeth may have been reduced at about this time. *Globidens alabamaensis* and *G. dakotensis* probably represent a more primitive and a more advanced stage, respectively, in the development of a single phylum of bivalve-eating marine lizards.

TABLE 5. Proportions of cranial structures in *Globidens alabamaensis* and *G. dakotensis*, expressed as percentage of length of first dorsal vertebra.

	G. alabamaensis[1] USNM 6527	*G. dakotensis*[2] PR 846
Length of alveoli for nine anterior maxillary teeth	398	311
Length of ninth maxillary tooth	48	48
Maximum width of frontal	303	288

[1]Interarticular length of first dorsal centrum 52.8 mm., other measurements after Gilmore, 1912.

[2]Interarticular length of first dorsal centrum 62.6 mm.

Globidens dakotensis may be considered as a rather specialized mosasaur. The extreme robustness and brevity of the skull, as well as the loss of a functional pterygoidal dentition, are in harmony with an advanced stage of specialization. However, this relatively specialized mosasaur, of apparent clidastoid derivation, resembles some species of the plioplatecarpine genus *Prognathodon* in several respects. Among these are the general massiveness of the skull, large size of the supratemporal fenestrae, morphology of the quadrate, slenderness of the parietal, presence of a broad tongue extending from the medial surface of the squamosal toward the suspensorial ramus of the parietal, and inflation of the marginal dentition (see Russell, 1967; Welles and Gregg, 1971). It is also possible that some species of *Prognathodon* subsisted largely on nektonic, shelled mollusks (Kauffman and Kesling, 1960; Russell, 1967, p. 68).

The similarities between certain structures within the skull of *Globidens dakotensis* and species belonging to another subfamily of mosasaurs are striking. The problem, then, of relating a *G. alabamaensis* - *G. dakotensis* line of descent to other, primarily dental, material referred to *Globidens* is aggravated not only by the incompleteness of this material, but also by the possibility of a parallel evolution of *Globidens*-like teeth in unrelated lineages of mosasaurs. It would not be surprising if teeth designated in this paper as types two through five were one day found to represent two or more phyla of mosasaurs, none of which could be assigned to *Globidens sensu stricto*, and not all of which were even closely allied to *Globidens*. However, in the present state of knowledge, it is probably most expedient to refer all of this material to the Globidentini.

SUMMARY

The type of *Globidens dakotensis*, consisting of a skull and anterior presacral vertebrae from the Sharon Springs Member of the Pierre Formation of South Dakota, is the most complete specimen of *Globidens* known. The species is more advanced than *G. alabamaensis* in that the cranial roof is more firmly knitted together, the muzzle is shorter, and the teeth are lower and broader. Although *Globidens* probably descended from *Clidastes*-like mosasaurs, many specializations in the type skull of *G. dakotensis* also occur in *Prognathodon*. The phyletic relationship of the North

American species of *Globidens* to material referred to this genus from other continents is difficult to assess because the latter material is essentially restricted to isolated teeth. At present two genera (*Globidens* and *Carinodens*) are referred to the Globidentini. Additional genera could be represented in the extra- North American material, some of which may even prove to belong to other, parallel-evolving groups of mosasaurs.

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