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GLOBAURA VENUSTA GEN. ET SP. N. AND *EOXANTA LACERTIFRONS* GEN. ET SP. N. — NON-TEIID LACERTOIDS FROM THE LATE CRETACEOUS OF MONGOLIA

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Two Late Cretaceous Mongolian lizards *Eoxanta lacertifrons* gen. et sp. n. (?middle Campanian) and *Globaura venusta* gen. et sp. n. (?late Santonian-?middle Campanian) are assigned to Lacertoidea (*sensu* Estes *et al.* 1988). *Eoxanta* is considered the sister group of the Xantusiidae, and, thus, the oldest known representative of the xantusiid line. *Globaura* is the sister group of the Lacertiformes (*sensu* Estes *et al.* 1988). The paper also considers the polarity of some scincomorphan characters. Formation of the anteroventral border of orbit by maxilla is considered synapomorphic for the Scincomorpha.

Key words: Cladistics, Reptilia, Sauria, Lacertoidea, Cretaceous, Mongolia.

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INTRODUCTION

Collected by the Polish-Mongolian Paleontological Expeditions to the Gobi Desert (1963—1971), the Late Cretaceous lizard material has been described in nine papers, five of them (Sulimski 1972, 1975, 1978, 1984 and Borsuk-Białynicka 1985, see also Borsuk-Białynicka 1987) concerning new scincomorphan taxa and/or problems of scincomorphan characters. All the scincomorphans that have been given a definite systematic affiliation in the above papers, are teiid relatives. The present paper describes two genera of non-teiid and non-teiioid lacertoids coming from the same localities. One of the new genera, *Globaura* gen. n. is considered the sister group of the monophyletic taxon Lacertiformes (*sensu* Estes *et al.* 1988). The second one, *Eoxanta* gen. n. is recognized as the sister group of the Xentusiidae, thus becoming the oldest known representative of this line of lizards.

The new genera share a great number of symplesiomorphies with each other and with *Slavoia* Sulimski, 1984, and some with the scincids and xantusiids as well. Most of these symplesiomorphies do not occur in the Lacertiformes, but they are substituted by novelties instead.

The material described here includes 22 more or less complete skulls, out of which 18 specimens are assigned to *Globaura venusta* and 4 specimens to *Eoxanta lacertifrons*. The *Globaura* material comes from the Bayn Dzak locality (the Djadochta Formation, ?upper Santonian and/or ?lower Campanian) and from the localities Khermeen Tsav and Khulsan (the red beds of Khermeen Tsav and Barun Goyot Formation respectively, both ?middle Campanian). One specimen is from the locality Nemegt (the strata underlying the Nemegt Formation, ?middle Campanian age). The above estimates of age are from Gradziński *et al.* (1968), Gradziński and Jerzykiewicz (1972) and Gradziński *et al.* (1977). The age of the Nemegt Formation has been considered slightly older by Karczewska and Ziembińska-Tworzydło (1983) on paleobotanical data, but the age differences between deposits, from the locality Bayn Dzak on one hand and those from Khermeen Tsav on the other are confirmed. The *Eoxanta* material comes from the Barun Goyot Formation from Khulsan and from the red beds of Khermeen Tsav.

Great variability in size and in some morphologic features characterizes the sample of *Globaura* skulls. This variability, considered with the fairly large stratigraphic span covered by the material, strongly suggests the presence of several species. However, difficulties in clearly segregating these characters (see p. 00) preclude any reasonable systematic division of this material. The small form common in Bayn Dzak may prove to be an earlier species of *Globaura*, and the larger form, prevalent in Khermeen Tsav and Khulsan a more recent species. However, more material is needed to solve this problem.

All the material is housed in the Institute of Palaeobiology Polish Academy of Sciences.

METHODS

The primary goal of this paper is an assignment of two new fossil lizards from the Late Cretaceous of Mongolia.

Any material to be assigned may or may not fit into a nested-set of relationships actually recognized. Fitting the new material to the cladogram tests the latter and sometimes leads to its falsification. In other cases not the cladogram proper but rather a morphocline polarity of inclusive characters is tested and may be falsified. As the fate of characters during the course of phylogeny is the main evolutionary content of taxonomic work, this type of testing is of great importance, and is a second goal of this paper.

Determination of polarity of character states in the present paper follows the method of Hennig (1966), as presented by Eldredge and Cracraft (1980) and precised by Maddison *et al.* (1984). The states distributed in the outgroups are considered more likely to be older (plesiomorphic) than those limited to the ingroup (apomorhic). Maddison *et al.* (1984) stress a seemingly trivial truth, that the common term "ancestral state" includes both the most recent ancestral state of the ingroup, and the more distant ancestral state (not obligatory identical with the state most common within the first outgroup). Maddison's *et al.* (1984) abbreviations, IN — corresponding precisely to the most recent ancestral state of the ingroup node of the cladogram, and ON — for the state of the first outgroup node (but not for the ingroup node of the first outgroup) are used in the present paper.

The rule of the global parsimony of Maddison *et al.* (1984) is applied here. The essence of this rule is, to me, a compromise between the issues from the ingroup and the outgroup analysis. According to these authors, the ancestral states (the ON states) should be considered "while the ingroup is being resolved, not merely added afterwards to root an unrooted network". I believe, that the reverse is equally important. The state of the ingroup node should be considered, while the ON is being determined. The ingroup is a descendent of the ON ancestor exactly equivalent to the outgroup, and thus, its ancestral state should as well be considered when the state of the ON (plesiomorphic for INs) is being deduced from those of the descendent groups.

Maddison *et al.* (1984) discuss a purely quantitative approach to the problem of parsimony. But, I believe, the choices between the alternative cladograms and between the alternative morphocline polarity hypotheses, are eventually based on the estimation of probability of independent development of character states (homoplasies) and reversals. The procedure is equal to testing cladograms, and the inclusive morphocline polarities, by contrasting them with hypotheses of some other kinds concerning the morphoclines. The existence of the latter is rejected by Gaffney (1979) because the polarity implicit in the morphocline concept is always deduced from the same distributional data pool on which the cladograms are based. In the present paper I show an example of a morphocline polarity hypothesis (fig. 7), which is something else than the cladogram itself and may be used for its testing. In spite of the fact that the extremities of the morphocline and its direction are based on the cladistic analysis, its total is organized according to minimum size of morphological distances between states, and, thus, basically differs from the cladogram.

Abbreviations:

Museal acronyms:

MCZ Museum of Comparative Zoology, Cambridge, Harvard University;
HUB Zoological Museum of Humboldt University;
ZPAL Institute of Palaeobiology, Polish Academy of Sciences.

Abbreviations used in cladograms:

A Agamidae, *An* Anguidae, *Am* Amphisbaenia, *C* Cordylidae, *G* Gymnophthalmidae, *Ge* Gekkota, *Ig* Iguania, *Igd* Iguanidae, *K* Kuehneosauridae, *L* Lacertidae, *Le* Lepidosauria, *nL* non-lepidosaurians, *LGT* Lacertiformes, *S* Scincidae, *Sph* Sphenodontidae, *Squ* Squamata, *T* Teiidae, *Xe* Xenosauridae, *X* Xantusiidae, *V* Varanoidea, Y Younginidae, *IN* in-group node, ON first out-group node, *R* reversal.

Ostelogical abbreviations:

ect ectopterygoid, *f* frontal, *j* jugal, *m* maxilla, *n* nasal, *pl* palatine, *prf* prefrontal, *pt* pterygoid, *v* vomer.

For explanations of the following abbreviations: *C/d* state, *D/c* state, *j* state, *mx* state, *f*-mx state, *n*-prf state, see p. 228.

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SYSTEMATIC PART

Infraorder **Scincomorpha** Camp, 1923
Superfamily **Lacertoidea** (*sensu* Estes *et al.* 1988)
Familia incerta
Genus *Globaura* nov.

Type species: *Globaura venusta* sp. n.

Etymology: Latin *globosus* — spherical, *auris* — ear. Because of the swollen otic region of the brain case.

Stratigraphic and geographic range. — Late Cretaceous Djadochta Formation (?late Santonian and/or ?early Campanian), Barun Goyot Formation and red beds of Khermeen Tsav (both ?middle Campanian); Gobi Desert, Mongolia.

Diagnosis. — Small non-teiioid lacertoid with paired premaxillae, and frontals fused and constricted. Ratio of minimum frontal width/sagittal length 0.16—0.19. Postfrontal posterior extension subject to variability. No osteoderms. Snout/skull length ratio 0.3—0.33. Ratio of length of tooth row underlying orbit/orbit length 0.18—0.27.

Globaura venusta sp. n.

(pl. 1: 1, pl. 2: 1, pls. 3 and 4, pl. 6: 2, pl. 7: 6)

Holotype: ZPAL MgR-III/40; pl. 3: 1.

Type horizon: Red beds of Khermeen Tsav (?middle Campanian).

Type locality: Khermeen Tsav. Gobi Desert, Mongolia.

Etymology: Latin *venustus*: beautiful, charming.

Diagnosis. — Skull length 14—25 mm. Modal skull length of 21.5 mm, as in holotype. Postfrontal rarely extends more posteriorly than half the length of the parietal table. Otic regions of the brain case globose.

Material. — A. Large specimens:

Khermeen Tsav:

ZPAL MgR-III/40. The holotype is a slightly damaged skull with both mandibles and some cervical vertebrae. Left jugal, right supratemporal arcade and right ectopterygoid missing.

ZPAL MgR-III/41. Slightly damaged skull with mandibles.

ZPAL MgR-III/43. Distorted skull with mandibles. Right jugal and supratemporal arcade missing.

Khulsan:

ZPAL MgR-I/45. Complete but poorly preserved skull with mandibles.

ZPAL MgR-I/46. Damaged skull; mainly brain case and snout.

ZPAL MgR-I/48. Parietal part of skull with brain case, posterior part of pterygoids and first cervical vertebrae.

ZPAL MgR-I/49. Damaged skull with mandibles.

ZPAL MgR-I/51. Fragmentary skull with anterior part of the palate perfectly preserved and two mandibles.

ZPAL MgR-I/55. Damaged skull with mandibles.

ZPAL MgR-I/118. Skull with mandibles; snout and left mandible damaged.

Nemegt:

ZPAL MgR-I/47. Skull with mandibles. Strongly damaged posterior and dorsal part.

Bayn Dzak:

ZPAL MgR-II/55. Posterior part of skull and mandibles.

B. Small specimens:

Khermeen Tsav:

ZPAL MgR-III/36. Skull with left mandible and a part of the right one. Right jugal and supratemporal arcade missing. The total of eight cervical and thoracic vertebrae and fragments of shoulder girdle and limb bones associated with the skull.

Khulsan:

ZPAL MgR-I/50. Fragment of skull (?juvenile).

ZPAL MgR-I/71. Skull with right side strongly damaged; right mandible missing.

Bayn Dzak:

ZPAL MgR-II/26. Damaged skull with mandibles.

ZPAL MgR-II/42. Damaged skull with mandibles.

ZPAL MgR-II/53. Damaged skull with mandibles (?juvenile).

Measurements. — See tables 1, 2.

Description. — Skull as a whole: Snout strongly tapers anteriorly. Elongated external nares face almost directly dorsal. Orbits large, jugal strongly arched. Supratemporal fenestra reduced by a laterally bent squamosal and, some-

Table 1

Dimensions of skull in *Globaura venusta* gen. et sp.n. and in *Eoxanta lacertifrons* gen. et sp. n.

Measurements in mm	*Globaura venusta*					*Eoxanta lacertifrons*		
	Holotype	Large form range	N	Small form range	N	Holotype	Range	N
Length (in projection) of:								
Skull (condylobasal)	21.5	20.5—25.0	10	14.0—18.0	6	18.0	18.0—19.0	2
Preorbital part	6.5	6.0—8.2	9	4.8—5.7	3	4.1	4.1—5.0	2
Orbit	8.0	8.0—9.0	8	4.3—6.2	4	5.5	5.0—5.5	2
Postorbital part	7.6	7.2—9.7	6	5.0—6.4	3	8.1	8.1—9.2	2
Nasal	3.6	3.2—3.6	2	3	1	e.2.5		1
Frontal	9.0	8.2—10.5	5	5.0—7.0	3	6.0		1
Parietal (in sagittal plane)	3.2	3.2—4.5	6	2.5—3.7	3	4.1		1
maximum	7.0	6.2—9.9	7	6.0—6.9	8	7.0		1
Basisphenoid + basioccipital (in sagittal plane)	7.0	5.0	3	4.2—5.2	4	5.1	5.1—6.0	2
Width of:								
Skull (maximum)	app. 12.5	11.2—16.0	6	8.2	1	e.9.5	e. 9.5	2
Frontal (anterior)	3.5	3.0—4.0	6	2.2—2.9	6	2.3		1
(posterior)	6.2	6.2—8.0		4.0—5.0	5	5.1		1
(minimum)	1.7	1.5—2.0	7	1.2—1.6	6	2.3		1
Parietal (anterior)	6.0	5.6—7.7	6	4.5—5.0	3	5.0	5.0—5.1	2
(minimum)	4.2	4.0—4.5	6	3.2—3.5	2	4.9	4.9—5.0	2
Lateral spread of supratemporal processes	e. 8.2	7.5—10.8	7	6.1	1	e.9.0	9.0—10.0	2
Proportions:								
Snout length to skull length	0.3	0.3—0.33	5	0.3—0.32	4	0.23	0.23—0.26	2
Minimum to maximum frontal width	0.27	0.23—0.27	5	0.26—0.33	4	0.45		1
Length to minimum width of parietal table	0.76	0.76—1.04	7	1.03	1	0.83		1
Length of tooth row underlying orbit to orbit length	0.2	0.19—0.27	7	0.18—0.25	3	0.02	0.01—0.02	2
Frontal minimum width to length	0.19	0.16—0.19	6	0.17	1	0.38		1

Table 1 continued

Measurements in mm	*Globaura venusta*					*Eoxanta lacertifrons*		
	Holotype	Large form range	N	Small form range	N	Holotype	Range	N
Basisphenoid + + basioccipital length to skull length	0.29	0.25—0.29	3	0.26—0.33	4	0.28	0.28—0.31	2
Tooth number (to base of premaxillary process)	12—13	12—15	8	13—14	4	9	9—10	4

e. estimated app. approximately

times by a postfrontal, which tends to extend posteriorly. Mandibular adductors attached on ventral surface of the parietal. Brain case has strongly swollen, globose otic parts.

Dermocranial roofing elements: The premaxillae are paired; the body of each premaxilla bears four teeth. The long nasal processes extend subhorizontally to overlap the nasals. The subtriangular nasals are joined by a fairly long internasal suture, but separated in their anteriormost and posteriormost parts. The triangular posterior parts of the nasals overlap the frontals and are split by longitudinal symmetrical fissures (pl. 1: 1a). The lateral process of the frontal is overlapped by the nasal process of the maxilla, which separates the prefrontal from the nasal. The frontals are fused and constricted at about their midlength. The frontoparietal suture interdigitates between the frontal tabs. Parietal tabs underlie the frontal laterally. The subolfactory processes are of medium size and do not meet beneath the subolfactory tract. They grow deeper at the contact with the prefrontals, but fail to separate the prefrontals from the boundary of the orbitonasal fenestra by contact with the palatines. The short parietal table is sharply enlarged just posterior of the frontoparietal suture and constricted at the midlength. The proportions of the parietal body vary (see p. 222 and table 1).

The supratemporal processes are not preserved in the type specimen, but were about one and a half as long as the parietal table, as evidenced by position of the posterior extremity of the squamosal. In some other specimens (ZPAL MgR-I/45, -I/118 and -III/41), the supratemporal processes are dorsally flattened and laterally enlarged to produce convex lateral borders (pl. 4: 1). Extensive surfaces for the nuchal musculature extend on the medial side of the supratemporal processes and face dorsally. Above the supraoccipital joint, they turn posterodorsally and are separated from each other by a medial angular extension from the dorsal surface of the parietal table. A circular parietal foramen pierces parietal table anterior to the midlength.

The lateral surface of the preorbital part of the skull turns gently into its dorsal surface, which is connected with the low profile of the snout. The nasal process of the maxilla overlaps the frontal. The premaxillary process of the maxilla is inflected into the naris to produce a triangular vomerine process, that extends between the premaxilla and the vomer almost to touch its mate. In ventral aspect it contributes to a narrow palatal shelf. A rounded foramen (?premaxillary) is present at the right side of the type specimen only, and is considered as an artifact. The posterior process of the maxilla underlies the anterior 1/3 of the orbit. At the contact with the jugal the posterior process bends laterally to contribute to the bending of the whole jugal arch. The jugal is less deep than the maxilla at this region, and leaves some space ventrally for a lateral process of the ectopterygoid. The jugal--maxilla suture is subvertical. A row of six labial foramina extends above the tooth row at the level of the ventral border of the naris.

The subtriangular dorsal surface of the prefrontal extends to about the level of the maximum anterior extent of the frontal. The posterior process extends to slightly less than half the length of the frontal. The orbital border is produced into an acute ridge situated slightly ventral to the main dorsal surface and is separated by a notch from the ventral orbital border.

The palatal process of the prefrontal contacts the suboflactory process of the frontal and the orbitonasal fenestra. Both the prefrontal and the tiny lacrimal contribute to the lacrimal foramen. Both lacrimal and jugal are entirely covered laterally by the maxilla. Posterior to the lacrimal, the jugal is separated from both the orbital border and the suborbital fenestra by the maxilla (holotype) and partly by the ectopterygoid (ZPAL MgR-I/47). The ascending ramus of the jugal is slender, and meets the postorbital in a sliding, anteroposteriorly-directed joint. Distally it has a short oblique contact with the squamosal. The postorbital overlaps the lateral part of the dorsal surface of the postfrontal but does not fuse to it. It contributes to the orbital border and has a long oblique suture with the squamosal. The postfrontal is a medially forked subquadrangular bone. The posterior extent of the parietal process and that of the whole postfrontal bone are unknown in the holotype owing to a damage. In some specimens, and particularly so in small ones the postfrontal reaches as far as the midlength of the parietal table.

The squamosal is a dorsally flattened bone closely adhering to the supratemporal process. It is laterally concave, and its proximal end is medially bevelled for the contact with the postorbital.

The posterior crest of the quadrate is strongly arched, the concavity facing posteroventrally. The tympanic crest is quite straight. Situated terminally on the tympanic crest, at the level of the dorsal condyle, a muscular tuber is present separated from the condyle by an incision that accomodates the posterior extremity of the squamosal. Both tympanic crest and anterior surface of the quadrate are flat.

The epipterygoid is a slender bone articulating with the columellar fossa of the pterygoid. It slopes anteroventrally, subparallel to the tympanic crest. Its dorsal tip is damaged in the holotype, but a preserved part almost reaches the parietal.

Palate: The vomers are sutured on the mid-line of the palate for their whole length. As demonstrated by ZPAL MgR-I/51, the posterior part of this suture is produced by finger-like processes of the posteromedial corners of the vomers. The ventral surface of the conjoined vomers is concave, as is the surface of the prolongation of the vomers anterior to the fenestrae vomerochoanales. The two concavities are separated from each other by a transverse ridge situated at the level of the lacrimal groove. A pair of vomerine foramina is situated at each side of this ridge. The main body of the vomer is bordered by a laterally convex acute ridge. Lateral to it is a flat flange of the vomer, which ascends into the nasal cavity. The fenestra exochoanalis is of a paleochoanate type. The vomeropalatine contact is mainly by means of the main body, which overlaps the palatine ventrally. The lateral flange is separated from the palatine by a narrow gap.

The vomerine process of the palatine extends only medially, its anterior border extending transversely at the posterior limit of the fenestra exochoanalis. Only the maxillary process of the palatine exceeds this line anteriorly. A longitudinal concavity of the ventral surface of the palatine extends from the anterior border, over most of the length of the bone. The palatines are widely separated except for anteriorly, where they touch each other in the midline. A very low ascending part of the palatine is pierced by the infraorbital foramen.

The palatine processes of the pterygoids are rather short. They overlap the palatines on the medial side, while being overlapped by them laterally; the resulting suture is zigzag-shaped. In some specimens (ZPAL MgR-I/47) the medial part of the palatine process bears two or three tiny teeth. In other specimens this part is damaged but provided with a protruding ridge separated from the ectopterygoid process by a shallow concavity. The angle between the axis of the quadrate process of the pterygoid and the medial border of the palatine process is approximately 140°. The medial knob makes up the anterior limitation of the basipterygoid joint. The quadrate ramus is delicate, and medially concave for the protractor pterygoidei muscle. It broadly overlaps the quadrate but the nature of the contact is obscure.

The ectopterygoid is a long, semilunar bone, posteriorly subdivided to overlap the ectopterygoid process of the pterygoid both dorsally and ventrally. The size of the process for the pterygoideus muscle is unknown. The anterior extent of the ectopterygoid is more than half the length of the suborbital fenestra, as demonstrated by ZPAL MgR-I/47. The remaining lateral border of the suborbital fenestra is formed by the maxilla (pl. 3: 1b).

Braincase: The sphenoccipital suture is an almost transverse, posteriorly--concave line. It is provided with a tiny incision, from which a sagittal ridge extends anterad over the body of the parasphenoid. The posterolateral extensions of the parasphenoid are short. Ventrolateral crests are distinct at the bases of the basipterygoid processes, but become attenuated posteriorly. With their slender stalks and much broadened articular parts, the basipterygoid processes extend ventrolaterally and slightly anteriorly. The articular surfaces converge anterad. The position of the posterior aperture of the vidian canal is unknown.

The lateral borders of the basioccipital, which are usually swollen to contribute to sphenoccipital tubercles, form only thin medial margins of the occipital recesses. The basioccipital is horizontal. Its sutures with the exoccipitals form the posterolateral limits of the braincase floor. The tuberal crest turns into a swelling that includes the posterior semicircular canal and extends dorsal to reach the much swollen posterior part of the exoccipital. The occipital recess is, thus, posteriorly open. Covering a strongly swollen lagenar part of the otic capsule, the opisthotic process of the exoccipital separates the occipital recess from the oval foramen. The jugular recess is very broad and subhorizontal. Bordering the jugular recesses of both sides, the prootic crests give a subpentagonal outline to the ventral aspect of the brain case. Each of the crests extends from the dorsal surface of the basipterygoid stalk to the ventral angle of the paroccipital process. The latter is just a small flange, triangular in posterior view, added to a spherical, balloon-shaped braincase. The horizontal semicircular canal remains separate and more dorsal from the prootic crest. Between the canal and the crest the lateral braincase wall is perpendicular.

The exoccipital, supraoccipital and the prootic regions of the braincase wall are strongly convex, so that the region including the crura communis and the processus ascendens of the supraoccipital as well as the dorsal border of the occipital foramen is situated in a deep longitudinal furrow.

Mandible: The long axis of the mandible is almost straight, with but a slight medial curving of the postcoronoid part (pl. 3: 1a). The adductor crest extends from the lateral corner of the articular condyle to about half the height of the shaft at the level of the coronoid (pl. 7: 6D). Dorsal to this crest, the surface of insertion of the adductor mandibulae muscle faces laterally but turns into the dorsal wall just anterior of the articular condyle. Directly behind the coronoid (pl. 4: 4b) there is no dorsal surface at all, but only a blunt ridge separating the labial surface of the mandible from the lingual one.

The adductor fossa (pls. 2: 1b, 7: 6a) is widely open dorsally and fairly broad, but is not inflated ventrally in transverse section. Its bottom is well exposed in the dorsal view of the mandible.

The dentary is laterally convex in transverse section and the line of bending is congruent with the adductor crest. Ventral to this line, the surface of the mandible faces ventrolaterally in the naturally articulated mandible. It becomes ventral only in the posterior half of the postcoronoid ramus, delimited by a faint pterygomandibular crest (pls. 2: 1a, 7: 6b). The latter is posteriorly convergent with the adductor crest. The surface for the pterygoideus muscle has a pulley-like extension that passes over the ventral side of the mandible to reach its lingual side. A subrhomboidal retroarticular process faces ventrolaterally in life position. Its medial border contributes to the ventrally and medially concave bending of the postcoronoid part of the mandible. The articular condyle faces posterodorsally. Separating two concavities of the condyle a blunt crest produces a small eminence at the anteromedial part of the condyle.

The dentary overlaps little of the lateral surface of the coronoid (pl. 3: 3).

The labial border of the subdental gutter is well above the lingual one. The gutter is shallow but wide. The subdental ridge descends to the ventral border of the mandible to touch it at about 1/4 the length of the dentary beginning with the top. Posteriorly the subdental ridge attenuates.

The splenial extends from the level of the posterior ramus of the coronoid to the level of the eight tooth position. Anterior to this point, the Mackelian fossa turns to the ventral side of the mandible. The splenial overlaps the ventral part of the anterior ramus of the coronoid. The medial surface of the coronoid is strongly concave, the posterior ramus being produced lingually perpendicular to the sagittal plane. Between the rami, the concavity has its lateral wall made of the supraangular and the bottom made of prearticular. The angular is very thin on the lingual surface, but is fairly large on the labial side. Nevertheless it is little exposed in the lateral view of the mandible owing to the medial bend of the mandibular ramus in this region. The pulley-like furrow for the pterygoideus muscle is produced mainly by the angular with a minor contribution of the prearticular.

The following foramina are recognized in the mandible: the anterior supraangular foramen is situated directly below the coronoid apex, on the labial surface of the supraangular and the posterior supraangular foramen opens below the posteriormost part of the adductor crest. Five mental foramina occur on the labial surface of the dentary. The dorsal border of the splenial is notched for the anterior inferior alveolar foramen at about the level of the 10th to 11th tooth position. Below it there is a small anterior mylohyoid foramen. The angular foramen pierces the angular at its contact with both the splenial and the supraangular.

Dentition: Each premaxilla bears 4 teeth, the maxilla 14 teeth and tooth positions and the dentary about 15 teeth and tooth positions. They are columnar in shape, straight, tapering distally with a tiny additional cusp anterior to the main cusp. The teeth are pleurodont with a directly successional type of growth, as shown by the resorptional pores preserved.

Systematic remarks. — The scincomorphan affiliation of *Globaura* is based on the following complex of character states (for discussion see p. 228): jugal excluded from the anteroventral border of the orbit; jugal-maxilla contact subvertical; presence of frontomaxilla contact; presence of dentary overlap on the lateral process of coronoid and ventral position of the adductor mandibulae muscles.

The following character states of *Globaura* dismiss the possibility of its teiid kinship (for discussion see p. 238): a snout dorso-ventrally flattened with a rounded outline in transverse section; palatines and pterygoids widely separated (except for the most anterior processes of palatines, which are fused in the midline); mandibular rami divergent; vomers short ventrally concave; a large, open suborbital fenestra partly bordered by the maxilla; squamosal arched to extend parallel to the supratemporal process instead of producing a dorsal process that contacts the parietal; paired premaxillae; mandibular fossa not inflated. Most of these character states are considered plesiomorphic within the Scincomorpha (see discussion p. 00 and table 3).

The braincase structure of *Globaura* recalls those of *Eoxanta* described herein (p. 223) and of the xantusiids (see pl. 6: 5). The similarities are as follows: a lagenar wall is strongly swollen at the opisthotic-prootic contact; ventrolateral crests are underdeveloped; sphenoccipital tubercles are small, surfaces for the rectus capitis anterior muscles face ventrally rather than posteriorly and are poorly marked. The same structure is probably shared by most scincids (except Acontinae according to Greer's 1970*b* figures), and, therefore, cannot be used as a case for the xantusiid affinity. It is more likely original for the Scincomorpha, but the polarity of the characters contributing to this structure remains obscure.

The lack of the xantusiid synapomorphies, such as a joint participation of postfrontal and postorbital in closing the supratemporal fossa, fusion of splenial and dentary, posterior extension of the parietal and a specialized configuration of the palate bones (huge ectopterygoid shifted forwards) do not support xantusiid relationships for *Globaura*. This genus displays primitive states of these characters instead (see table 3).

The posterior extension of the postfrontal to roof the supratemporal fossa tends to support the scincid affinity (but see discussion p. 239), but the lack of both osteodermal covering and any traces of a secondary palate (pls. 3: 1a, 6: 2) sets off this genus from the scincid evolutionary line.

From two mutually contradictory character states: the frontoparietal suture interdigitating between the parietal tabs, considered synapomorphic for the Lacertiformes by Estes *et al.* (1988), and the fused premaxillae shared by all the lacertoids known hitherto (?synapomorphic for them, see discussion p. 239), I have chosen the first one as indicative of a monophyletic relationship, because it seems more consistently distributed than the second one. On this basis *Globaura* is regarded as the sister genus of the Lacertiformes, the one retaining the complex of character states characteristic of the early scincomorphan grade (see p. 239) and shared with the scincids, xantusiids, *Eoxanta* (described herein) and *Slavoia* (Sulimski 1984).

Variability. — Eighteen specimens are assigned to *Globaura venusta*, but the number of measurements available for each character measured does not usually exceed 14, and is sometimes much less than this. Linear dimensions are highly variable (the difference between minimum and maximum value amounts to 50% of the maximum in the case of skull length). Most of them show bimodality (table 1), that suggests the presence of a small form and a large form. The observed ranges of variability for the two do not overlap, except in a few cases (parietal and ventral braincase length). On the other hand, the unimodal distribution of the overall skull proportions of the two forms, and the morphological similarity point, at least, to their congenerity.

The interpretation of the size bimodality as either specific or sex or ontogenetic differences largely depends on the existence of correlations between linear dimensions and other characters and/or stratigraphy.

Only few parts of skull reveal more variable proportions. They are: proportions of the parietal table (the length reaches from about 75% to more than 100% of the width), a relative length of the basisphenoid & basioccipital and a relative frontal constriction (see table 1). Among them only the latter seems to be correlated with skull dimensions. Some other characters, not measured but estimated because of state of preservation (width of the supratemporal arcade, i.e. of the squamosal and the postfrontal, and a posterior extension of the postfrontal) seem also to be size correlated.

The relatively less constricted frontals, the supratemporal fossa more closed, the squamosal and postfrontal more expanded seem to be characteristic of the small form, and the more constricted frontals, the more open supratemporal fossa and the relatively narrow squamosal of the larger form.

This segregation of characters suggests specific differences rather than sex dimorphism or ontogenetic variability. But much more material is needed to support this view. A clear stratigraphic separation of the two forms, if present, would support the specific differences. The large form and small form are considered conspecific for the time being.

Genus *Eoxanta* nov.

Type species: *Eoxanta lacertifrons* sp. n.

Etymology: Greek *eos* — dawn, *xanta* — shortening of the family name Xantusiidae.

Stratigraphic and geographic range. — Late Cretaceous Barun Goyot Formation and red beds of Khermeen Tsav (?middle Campanian), Gobi Desert, Mongolia.

Diagnosis. — Small xantusiid-like lacertoid with paired premaxillae; parietal not extended to cover dorsal aspect of the braincase; frontals fusing late in ontogeny, provided with ventral sagittal crest partly separating oflactory tracts. Ratio of minimum frontal width/sagittal length 0.38. Ectopterygoid massive, shifted anteriorly to parallel the palatine borders the slit-like suborbital fenestra. Postfrontal extending posteriorly to close the supratemporal fenestra. Postorbital and squamosal dorsoventrally flattened, band-like. Osteoderms present in some specimens. Snout/skull length ratio 0.23—0.26. Ratio of length of tooth row underlying orbit/orbit length almost 0.

Eoxanta lacertifrons sp. n.

(pl. 1: 2, pl. 2: 2, pl. 5: 1—3, pl. 6: 3, 4, pl. 7: 4, 5, pl. 8: 2)

Holotype: ZPAL MgR-III/37, pl. 5: 3.

Type horizon: Red beds of Khermeen Tsav (?middle Campanian).

Type locality: Khermeen Tsav, Gobi Desert, Mongolia.

Etymology: *lacertifrons* — Latin *frons* — forehead; scalation pattern of lacertid type on the frontals.

Diagnosis. — Skull length 18—19 mm. About 9 maxillary and 12 dentary teeth. Crown bases broadened in transversal plane.

Material. — **Khermeen Tsav**:

ZPAL MgR-III/37, the holotype is a slightly damaged skull with two associated mandibles, parietals and frontals preserved, premaxillae and jugals missing. Palate covered by the slightly displaced mandibles.

ZPAL MgR-III/38, skull with two mandibles associated. Skull roof missing, premaxillae partly preserved. Left mandible removed by preparation to show palate structure. Part of vertebral column with associated right shoulder girdle present but poorly preserved.

Khulsan:

ZPAL MgR-I/61, anterior part of skull. Parietal and brain case missing. Two mandibles preserved in association with the skull.

ZPAL MgR-I/74, damaged skull without the dorsal skull roof.

Measurements. — see tables 1, 2.

Table 2

Dimensions of mandible in *Globaura venusta* gen. et sp. n. and in *Eoxanta lacertifrons* gen. et sp. n.

Measurements in mm	*Globaura venusta*					*Eoxanta lacertifrons*		
	Holotype	Large form range	N	Small form range	N	Holotype	Range	N
Total length (in projection)	19.7	19.5—25.7	6	15.0—17.5	3	15.0	15.0—16.2	2
Length to mandibular articulation	17.0	17.0—21.5	6	12.0—14.5	3	13.0	13.0—14.2	2
Labial length of dentary	10.4	10.4—12.3	6	8.0—8.7	2	8.0	8.0—9.7	2
Length of tooth row	e 8.8	8.8—10	6	7.0—8.0	2	4.9	4.9—6.1	2
Length of postcoronoid part to mandibular articulation	5.0	4.8—6.7	6	3.2—4.7	2	4.4	4.4—5.3	3
Maximum precoronoid depth	3.7	3.7—5.2	6	2.5—2.8	3	2.9	2.9—3.0	2

e. estimated

Description. — Skull as a whole. Snout is short. External nares face anterodorsally. Orbits are large, jugal strongly arched. Postfrontal extends posteriorly to leave but a narrow slit of the supratemporal fossa. Mandibular adductors attached on ventral surface of the parietal. Ectopterygoid-maxilla contact is situated very close to the level of the vomeropalatine contact; pterygoid-ectopterygoid suture is almost in line with the pterygoid-palatine suture (pl. 1: 2b). Osteodermal thickening of skull roof bones with traces of scalation (lacertid type) left, present in some (ZPAL MgR-I/61).

Dermocranial roofing elements: Premaxillae are paired. The nasal processes are long and slender with a great amount of overlap on the premaxillary shelves of the nasals. Superficially they wedge in a deep incision between the nasals. Each lateral process of the frontal is overlapped by the nasal process of the maxilla, which separates the prefrontal from the nasal. The frontals are paired or fused, parallel-sided over 2/3 of their length and broadening at the fronto-parietal suture. As demonstrated by the holotype the suture is straight as a whole but finely interdigitating with a slight suggestion of frontal tabs. The suboflactory processes of medium size do not meet beneath the suboflactory tract. They grow deeper at the contact with the prefrontals but fail to reach the palatines to separate the prefrontals from the orbitonasal fenestra. The parietal is subquadrangular with almost no constriction. The supratemporal processes are triangular, dorsally flattened, separated by a concave sharp posterior border. A circular parietal foramen pierces the parietal table at about its midlength.

The dorsal part of the nasal process of the maxilla is medially bent to contribute to the dorsal surface of the skull roof. This part invades the dorsal surface of the prefrontal up to the level of the lacrimal incision. Its posteromedial angle overlaps the frontal. A short premaxillary process of the maxilla is sharply inflected into the naris to produce a triangular vomerine process that extends between the premaxilla and the vomer almost to touch its mate. A rounded incision of the anterior border of this process suggests a premaxillary foramen. The posterior process of the maxilla underlies the anterior third of the orbit, and produces the orbital border at this region. The last tooth of the tooth row is about the level of the anterior wall of the orbit. The suture between the jugal and maxilla is subvertical. The great amount of lateral bending of the posterior process implies a wide extent of the jugals. There are four lateral superior labial foramina.

The posterior process of the prefrontal extends over less than half the length of the frontal. The palatal process of the prefrontal contacts the orbitonasal fenestra. On the other side it contributes to the lacrimal foramen. The share of the lacrimal in the anterolateral wall of the orbit is unknown. In any case it is not exposed on the lateral surface of the skull. Extending from the lacrimal region, the jugal is less deep than the posterior process of the maxilla. It is separated from both the orbit and the suborbital fenestra by the maxilla and the ectopterygoid respectively. The ascending ramus is unknown.

The postfrontal is a bony blade extending far along the parietal border and covering the supratemporal fossa. Its exact posterior extent is unknown. Its anteromedial frontal process is slender and pointed. Narrower than the postfrontal but similar in dorsoventral flattening, the postorbital bone blade overlaps the anterior part of the postfrontal, then extends along its lateral border. The squamosal is also dorsoventrally flattened. It is bent posterolaterally and extends far posterior of the distal extremity of the supratemporal process of the parietal. It overhangs the dorsal condyle of the quadrate but its extreme distal end is unknown. The supratemporal is a semilunar, laterally-flattened bone situated at the contact between the squamosal and the paroccipital process of the braincase.

The posterior crest of the quadrate is strongly arched, the concavity facing posteroventrally. The tympanic crest is not preserved. The incision between the dorsal condyle and the tympanic crest is overhung by the squamosal. The details of this contact remain unknown. The epipterygoid is unknown.

Palate. The two vomers are sutured in the midline of the palate for their whole length. As demonstrated by ZPAL MgR-III/38 (pl. 6: 4) the ventral surface of the conjoined vomers is concave. The exact course of the vomero-palatine suture is unknown but the contact of the two bones was certainly broad.

The medial processes of the palatines fuse in the midline, thus producing a posterior prolongation of the sagittal suture within the palate. The more posterior 2/3 of the palatines are widely separated from each other. A longitudinal concavity of the ventral surface of the palatine extends from the anterior border over most of the length of the bone.

The palatine process of the pterygoid is very short. The pterygopalatine suture is interdigitating but almost transverse as a whole, and the pterygoectopterygoid suture is only slightly posterior to this line. Posterior to the maxilla, bordered by the palatine and the pterygoid medially and by the ectopterygoid laterally, the suborbital fenestra is a long and narrow slit. The ectopterygoid is a stout, longitudinally-oriented bone contacting the posterior angle of the maxillary process of the palatine, which does not produce any posterior extension to meet this bone. Laterally it is bordered by the jugal. The ectopterygoid process of the pterygoid is more anterior and less lateral than usually in squamates. A row of at least four pterygoid teeth extends along the medial border of the pterygoid, directly anterior to its bent at the basipterygoid joint.

Braincase. As far as it can be seen in ZPAL MgR-III/38, the sphenoccipital suture is of the angular type (*sensu* Borsuk-Białynicka 1984), with a short v-shaped incision in the middle. Consistent with the state of the cranial sutures (the frontoparietal suture and the interfrontal suture), that implies a young age of the holotype, the type specimen has the sphenoccipital region not entirely ossified.

The ventrolateral crests are distinct at the bases of the basipterygoid processes but they attenuate directly anterior of the occipital recesses. The basipterygoid processes extend ventrolaterally and anteriorly. The articular surface converge anteriorly. Preserved on the right side of ZPAL MgR-III/38 is a more or less bilaterally flattened sphenoccipital tubercle of the basioccipital with almost no indication of the sphenoccipital torus (*sensu* Borsuk-Białynicka 1984). Posterior to this region, the surface of the basioccipital faces ventrally. The posterior limitation of the occipital recess is rudimentary. The opisthotic process of the exoccipital covers the strongly swollen lagenar part of the otic capsule and separates the occipital recess from the oval foramen. The jugular recess is situated obliquely, aproximately 45° to the horizontal plane. The prootic crest extends from the dorsal surface of the basipterygoid stalk to the ventral angle of the paroccipital process. The latter is just a small flange, triangular in posterior view, added to the brain case. The horizontal semicircular canal is dorsal and well separated from the prootic crest.

Mandible: The long axis of the mandible is almost straight with but a slight medial curving of the postcoronoid part. The adductor crest extends from the lateral corner of the articular condyle towards the lower fourth of the shaft depth, at the level of the coronoid (pl. 2: 2a, 8: 2a). Dorsal to this crest and posterior of the posterior margin of the dentary, the surface of insertion of the adductor mandibulae muscle is deeply excavated. Destined for the medial part of the same muscle, the dorsal wall of the postcoronoid ramus is narrow and straight. It becomes slightly wider medially, just anterior of the articular condyle.

The adductor fossa (pl. 2: 2b, 8: 2b) is large oval, well delimited dorsally by a swollen dorsal part of the postcoronoid ramus. The bottom of the adductor fossa was only partly exposed dorsally in life position of the jaw.

The lateral surface of the dentary is evenly convex in transverse section with no definite line of bending. As suggested by the direction of the axis of the pulley-like furrow for the pterygoideus muscle, the insertion of this muscle was widely separated from the adductor crest in the anterior part, while converging with it posteriorly. The long and pointed retroarticular process has a large triangular angular process (*sensu* Oerlich 1956). The articular condyle faces posteriorly.

The dentary overlaps the anterior ramus of the coronoid by means of the stout process contributing to the lateral crest of the coronoid (pl. 2: 2a, 8: 2a). The dentary does not reach the level of the coronoid apex except near the ventral border of the mandible, as suggested by the trace left on the angular. The posterior border of the dentary is V-shaped, posteriorly open. There are five mental foramina. The labial border of the subdental gutter is well above the lingual one. The splenial extends to the level of the posterior ramus of the coronoid, and its anterior extent is unknown. It overlaps the ventral part of the anterior ramus of the coronoid. The angular is fairly large on both lingual and labial side, as well as on the thick ventral border of the mandible. The anterior supraangular foramen is situated at the level of the coronoid apex below the suture between the coronoid and supraangular. The posterior supraangular foramen is below the posterior part of the adductor crest. Five mental foramina occur on the labial surface of the dentary.

Dentition: The maxilla bears about nine teeth and tooth positions and the dentary about twelve. The teeth are columnar and pleurodont. The anterior five teeth are oblique to the long axis of the jaw, with their summits directed anteroventrally in the upper jaw and anterodorsally in the mandible. The crown bases are broadened transversely. A directly successional type of tooth replacement is presumed on the basis of the close spacing of teeth, but no resorptional pores may be ascertained.

Systematic remarks. — *Eoxanta* is included into the infraorder Scincomorpha by virtue of the following character states: the type of ventral bordering of the orbit (formed by maxilla), frontomaxilla contact present, dentary overlap on the lateral process of the coronoid and ventral position of the adductor mandibulae musculature on the parietal (for discussion see p. 228).

The shortness of the snout and the palate structure of *Eoxanta* strongly suggest the xantusiid relationship, which is supported by a persistent paired frontal condition, a probable share of the postorbital in the supratemporal roofing and deep excavation of the lateral surface of the mandible for the insertion of the external part of the adductor mandibulae muscle.

The xantusiid structure of the palate is characterized by (1) the anterior position of the ectopterygoid, its extremities being situated at about the same transverse lines (possible kinetic axes) as the extremities of the palatine and (2) the two-floor structure of the palatine connected with the development of a membranous secondary palate.

The shape and position of the ectopterygoid in *Eoxanta* seems to fall within the range of variability of the palate structure of the Xantusiidae (fig. 1).

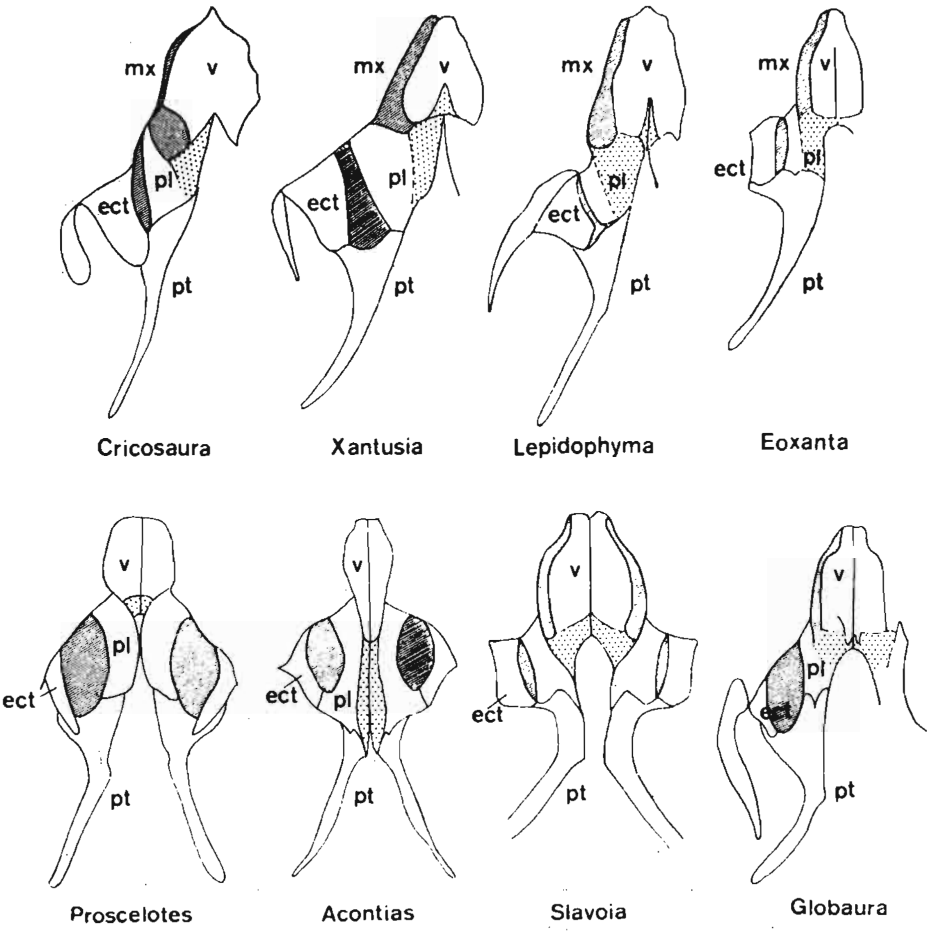
The two-floor structure of the palatine in the Xantusiidae consists in a more ventral position of the lateral part of the palatine (the one extending between the pterygoid and the maxilla) than that of the medial part (the one extending down to the vomer). The lateral part is horizontal. It protrudes medially to overhang (in ventral view) the oblique medial part and provides a place of attachment for the membranous secondary palate (pl. 6: 5, 6).

The Gymnophthalmidae display a similar type of membranous palate, which is, at least sometimes (*Echinosaura*) posteriorly extended by means of pterygoid shelves.

The bony secondary palate of the Scincidae is to be regarded as a more derived state of the same two-floor structure. The palate of *Slavoia* Sulimski, 1984 (pl. 6, 1) reveals also a two-floor structure, differing from that of the Xantusiidae in the palatine more rounded in transverse section and bearing no traces of the bony secondary palate. In may opinion, it may be interpreted as another state of a membranous secondary palate.

The different states of a secondary palate would, thus, occur in four separate taxa of the Scincomorpha: the Scincidae, Xantusiidae, Gymnophtalmidae and *Slavoia* (see p. 242). This would suggest that a tendency to develop this feature was primitive in this infraorder. I believe that the oblique position of the palatine of *Eoxanta* may be a rudimentary state of the same character. This, however, needs further investigation.

Other character states, primitive within the Scincomorpha, some of them alternative with respect to the xantusiid states, indicate a systematic position of *Eoxanta* outside rather than inside the family Xantusiidae. They are as follows: parietals with no posterior elongation, splenial not fused with the dentary, no perpendicular crest on the medial surface of the coronoid (compare pl. 8: 2b, 3a), and no



Cricosaura Xantusia Lepidophyma Eoxanta

Proscelotes Acontias Slavoia Globaura

Fig. 1. Palate structure in the new genera *Globaura* and *Eoxanta* as compared to those of the Xantusiidae (*Cricosaura*, *Xantusia* and *Lepidophyma*), Scincidae (*Proscelotes* and *Acontias*) and *Slavoia*. Out of scale. *Cricosaura* is from Savage (1963), *Proscelotes* from Greer (1970a), *Acontias* from Greer (1970b). Openings are shared; more dorsal and concave parts of palatines stippled.

distinct dental lappet on the coronoid lateral surface but the incipient overlap instead. The presence of the interpalatine contact just posterior to the vomers is shared by almost all the Scincomorpha known to me (table 3) and is probably primitive for this infraorder (characteristic of the scincomorphan IN). Among others, it occurs in *Xantusia* and *Lepidophyma* available to me, as well as in Rieppel's (1984*a*) specimens, and is probably consistent in the Xantusiidae in contrast to Savage's (1963) figures that show the palatines separate. Shared with *Globaura* (see p. 219), the xantusiids and some scincids (except for Acontinae, Greer 1970*b*) the braincase structure (a strongly swollen lagenar wall, underdeveloped ventrolateral crests, transverse course of the sphenoccipital suture and small sphenoccipital tubercles) is probably also plesiomorphic, and, thus, inconclusive.

In spite of an unknown significance of a paired state of the premaxillae within the Scincomorpha (see p. 239), this state, with the other non-xantusiid character states listed above, contributes to separating *Eoxanta* from either of both subfamilies quoted by Savage (1963), the Cricosaurinae and the Xantusiinae, and make me consider it as a sister taxon of the whole family.

If this hypothesis is correct, the traces of interdigitations of the frontoparietal suture between the parietal tabs, that occur in *Eoxanta*, will suggest that this character state is a synapomorphy of the whole lacertoid taxon, rather than of the Lacertiformes only, while having been reduced in the Xantusiidae proper.

The squamation pattern of the lacertoid type present on frontals of *Eoxanta*, with frontal scales apposited in the midline instead of being posteriorly separated by a reentrant (as it is usually the case in the xantusiids), is consequently regarded as a homoplasy with respect to the similar character state of the lacertids.

GENERAL PART

Infraordinal affiliation

Introductory remarks. — Character states discussed with respect to the problem of the infraordinal assignment of the two genera described herein, *Globaura* gen. n. and *Eoxanta* gen. n. are as follows:

1. Anteroventral border of the orbit formed by maxilla (referred to as mx state in this paper), with the jugal confined to the medial surface of the maxilla; no jugal-lacrimal contact. The jugal bordering referred to as j state, is alternative.
2. Lack of a nasal-prefrontal contact (of n-prf state); the alternative maxilla-frontal contact (f-mx state) present instead.
3. Lateral process of the coronoid overlapped by the dentary (D/c state). Dentary overlapped by the lateral process of the coronoid (C/d state) is alternative.
4. Adductor mandibulae musculature attached on the ventral surface of the parietal (Adm-V state). Lateral attachment is alternative.
5. Absence of ventral downgrowth of the parietal. Presence of the parietal descensus is alternative.

Characters 1-5 are suggestive of being synapomorphic for the Scincomorpha. Four of them (1-4) are shared by *Globaura* and *Eoxanta*, which is consistent with their assignement to this infraorder. However, they are not unique to the Scincomorpha and their specification as synapomorphic for this infraorder will be considered below.

Globaura and *Eoxanta* fail to share the presence of the parietal downgrowth (point 5), a character most unique of the above character complex and the one considered as a synapomorphy of the Scincomorpha by Estes *et al.* (1988). This lack does not falsify their assignment to the Scincomorpha as it does not in the case of the lacertids, some scincids and polyglyphanodontids.

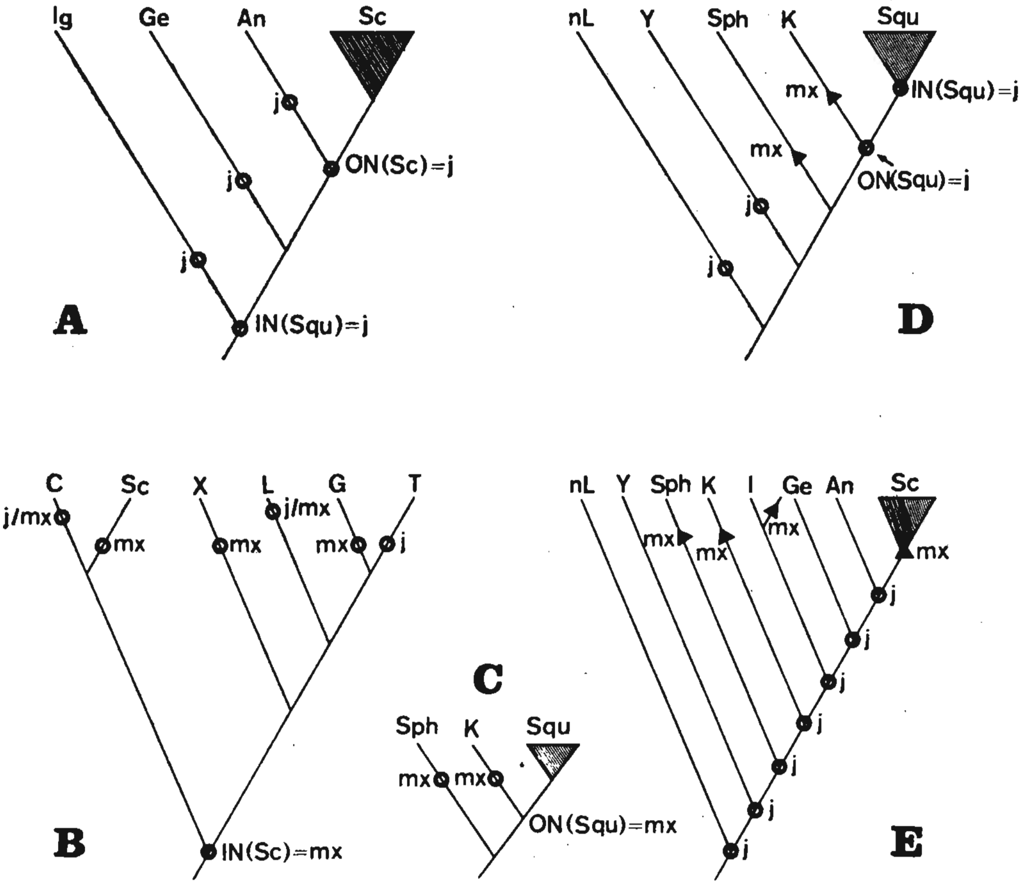


Fig. 2. Sequences of states of the orbital bordering in lepidosaurian phylogeny based on: *A*. Out-group analysis for the Scincomorpha, and in-group analysis for the Squamata. *B*. In-group analysis for the Scincomorpha. *C* and *D*. Out-group analysis for the Squamata, with conflicting results depending on number of included out--groups; in *D*, the IN state assessment of the Squamata has been considered while the out-group was being resolved (for theoretical background see p. 213). *E*. Sequence of character states in the phylogeny of Lepidosauria preferred herein and corresponding to a scenario on p. 230. Nested set of relationships from Estes *et al*. (1988).

Mx state synapomorphic for the Scincomorpha? — Two points critical for resolving this problem are: the state of the in-group node, given by the in-group analysis of the Scincomorpha (fig. 2B), and the state of the first out-group node of the Scincomorpha, i.e. that of the common ancestor of the Autarchoglossa (fig. 2A). The in-group analysis reveals a higher percent of genera displaying mx state than of those with j state within the Scincomorpha (fig. 2B). Although it is consistent only in three of the six scincomorphan groups: the Gymnophtalmidae, the Xantusiidae and the Scincidae, it also occurs in some late Jurassic cordyloids: the Paramacellodidae (as shown by Hoffstetter's 1967 figures 1F and 4D) and in some lacertids (according to Estes 1983) Its presence in the new described genera makes this percentage still higher. The mx-state is, thus, assumed to be inclusive within the ancestral morphotype of the Scincomorpha. I would also stress the consistency of this state in the stratigraphically old representatives of the infraorder, which I consider as another case for the IN state being mx. Whether it should be considered as synapomorphic or plesiomorphic for the IN may only be estimated on the out-group analysis. It is as follows: The j-state is consistent within the iguanids, some chamaeleontids (though the contribution of the jugal is minor), in the priscagamins (Borsuk-Białynicka and Moody 1984) and is present in most of the remaining agamids. It is, thus, assumed to be the IN state for the Iguania. It is the IN state for the Gekkota too, because, in this group, the jugal overlaps the maxilla (*Hemitheconyx* after Rieppel 1984, Gekko pers. observ.), if not atrophied. In the Anguimorpha, the state of the orbital bordering is consistently j (allowing for some minute shifts of the maxilla-jugal contact in *Ophisaurus*), while being equivocal in the Scincomorpha. The requirement of the first dublet rule (Maddison *et al.* 1984: 88) being satisfied, the state of the first out-group node of the Scincomorpha is considered j (fig. 2A).

The data given for the out-group analysis of the Scincomorpha may be used equally well for the in-group analysis of the *Squamata*. They show, that the same state (j) is the most parsimonious state assessment for the in-group node of the Squamata (fig. 2A). Two groups of the presquamatan lepidosauromorphs: the kuehneosaurs and the sphenodontids, display the mx state, which suggests this state being that of the squamatan ON (fig. 2C). But, the global parsimony rule of Maddison *et al.* (1984) indicates that the reverse is true. The coincidence (fig. 2D) between the most probable IN state of the Squamata (j) and the state of the presquamatan lepidosauromorphs (but two, above mentioned groups) and that of the earlier diapsids, makes the jugal bordering of the orbit (j state) the most likely ancestral state for all the lepidosaurians: the sphenodontids, kuehneosaurids and the squamatans. However, the choice between the alternative hypotheses (fig. 2C *versus* D) is based not only on the quantitative reasons but also on the estimation of the relative probability of homoplastic development of the mx states in the kuehneosaurids sphenodontids, agamids and in the scincomorphan ancestor *versus* that of reversals to the j state in the iguanids, gekkotans, anguimorphans and some scincomorphan groups. Eventually it is based on the estimation of the probability of the corresponding processes of skull transformation.

The scenario proposed for the sequence of character states demonstrated by the cladogram (fig. 2E) preferred here is as follows. Primitive lepidosaurians displayed the j state, as did their diapsid ancestors. The mx state has convergently developed in the kuehneosaurs sphenodontids and some agamids in connection with a posterior shift of the maxilla to underlie the orbit correlated with an increase of the maxilla depth associated with development of the heavy acrodont dentition. This scenario does not hold true in the case of the scincomorphan groups displaying the same state. I cannot imagine any simple factor, that could have made for an independent development of the mx state in so many branches of the scincomorphan line. So, I believe, that the transformation of the ancestral autarchoglossan j state into the mx state has occurred only once, in the common ancestor of the Scincomorpha, and is, thus, synapomorphic for this infraorder. See Estes *et al.* (1988) for a different approach.

F-mx state synapomorphic for the Scincomorpha? — The presence of the prefrontal-nasal contact is probably plesiomorphic for the lizards. In the early diapsids the maxilla has been separated from the central row of the skull roof bones, nasals and frontals, by the lacrimal, which tended to shrink in the phylogeny. As shown by the younginids, kuehneosaurids, sphenodontids, *Paliguana* and *Palaeagama*, used as the out-groups for the Squamata, the maxilla has not invaded the postfrontal-nasal contact until in some true lizards. The exact moment of this event remains to be indicated.

In view of the great amount of variability of this character within the Squamata, it seems advisable to analyze the processes leading from the nasal-prefrontal contact to the frontal-maxilla contact, to discriminate between homologic and homoplastic states. The main factor that may produce the frontal-maxilla contact is the above mentioned posterior invasion of the maxilla on the prefrontal (see types E, E′, F, fig. 3). However, a simultaneous increase of the posterior extent of the nasal may reduce or cancel the effect of extension of the maxilla (type C, fig. 3), whereas its shift in the opposite direction, equal to the anterior shift of the frontonasal suture, makes up a second factor, which may eventually produce the frontomaxilla contact (e.g. in *Cricosaura* — type F, fig. 3 or in *Diploglossus* according to Rieppel's 1980 fig. 1f). The third factor, that may interfere with the same effect, is a decrease in width of the nasals relative to the frontals (types E and E′, fig. 3)

Present in the out-group node of the Squamata the state (n-prf) of the sutures resulted from a very small overlap of the dorsal surface of the prefrontal by the maxilla, and the nasal reaching to the level of the anterior orbital border at least (as in type A, fig. 3). The maxillary overlap is usually more extensive than this, but very variable within the Squamata. It reaches the orbital border, or almost as far, in three groups of the lacertilians only: the modern agamids, most gekkotans and numerous scincomorphans. The overlap is moderate in the Late Cretaceous agamids — the priscagamines (Borsuk-Białynicka and Moody 1984); it is less than this in the chamaeleontids, and at most moderate in the iguanids, and, thus, should be assumed very small or moderate for the IN of the

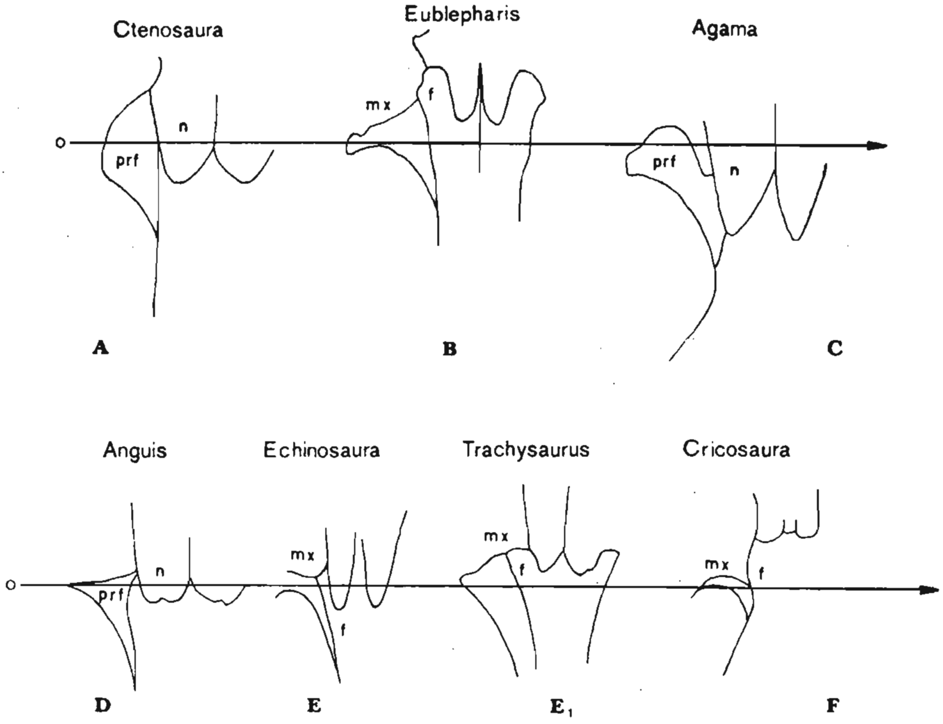


Fig. 3. Configuration of bones in the preorbital part of skull in Sauria: A. Nasal-prefrontal contact (plesiomorphic state); slight maxillary overlap on prefrontal; frontonasal contact posterior to or about the level of the orbital border; nasals broad (iguanids, some teiids, lacertids, some anguids, xenosaurids, most of varanoids, ?cordylids). *B*, *E*, *E*$_1$. Maxilla-frontal contact (derived states); extensive maxillary overlap on prefrontal; nasals tapering posteriorly (some gekkonids, some gymnophtalmids, some anguimorphans: *Gerrhonotus*, *Proplatynotia*, some scincids, and some gymnophtalmids). *C*. Nasal-prefrontal contact (derived state); both maxillary overlap on prefrontal and nasal overlap on prefrontal extensive (characteristic of agamids) *D*. Four-bone contact (derived state); extensive maxillary overlap on prefrontal. nasals broad (some anguids). *F*. Frontal-maxilla contact (derived state); extensive maxillary overlap on prefrontal; frontal-nasal contact shifted anterad (some scincids, some anguids, some teiids, some xantusiids). *Eublepharis* from Rieppel (1984a), *Cricosaura* from Savage (1963). All out of scale.

Iguania. In the modern Agamidae, the invasion of the maxilla upon the prefrontal is accompanied by the nasal extension upon the frontals and, very often, by a wide spread of the posterior ends of the nasals as well (Moody 1980), which tend to fix the primitive nasal-prefrontal contact (fig. 3C). The only exception known to me (f-mx state in *Calotes*) results from the narrowing of the nasals (a secondary modification of the same type C).

The frontomaxilla contact seems to be a modal condition within the Gekkonidae (but not in the Pygopodidae). The bone configuration in *Hemitheconyx* and *Eublepharis* (fig. 3B) suggests that the f-mx state of the Gekkonidae have developed mainly on account of the nasal position

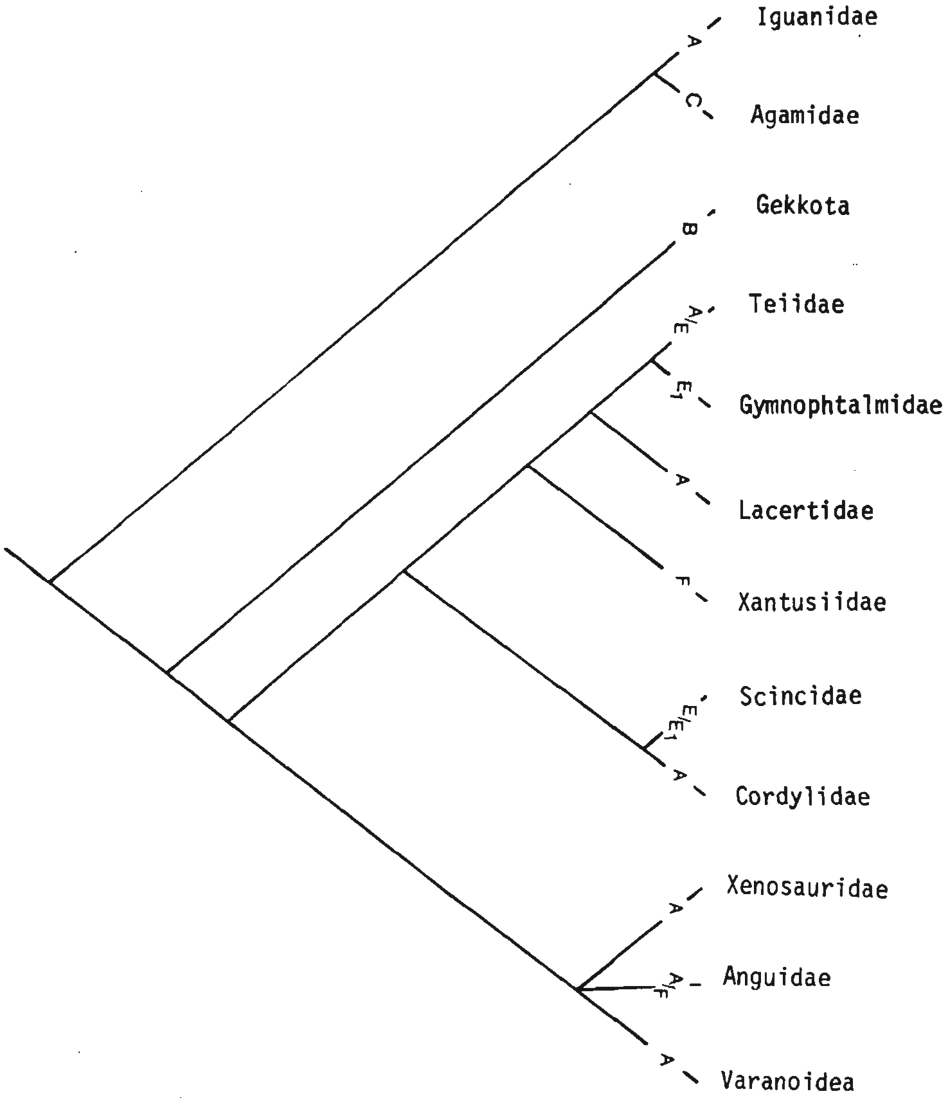


Fig. 4. Cladogram demonstrating distribution of types of bone configuration in preorbital region of skull roof (illustrated in fig. 3) in Sauria.

and shape. And conversely, in the Scincomorpha the f-mx state mainly results from the strong extension of the maxilla. However, the latter may not be considered synapomorphic for the infraorder as demonstrated by a scattered distribution of the different types of bone configuration among the subgroups of the Scincomorpha (fig. 4). I believe, that the f-mx state has developed in parallel in different subgroups, owing to a common tendency present in the scincomorphan ancestor, of which I do not know the reasons. The states of the nasals (their relative length and

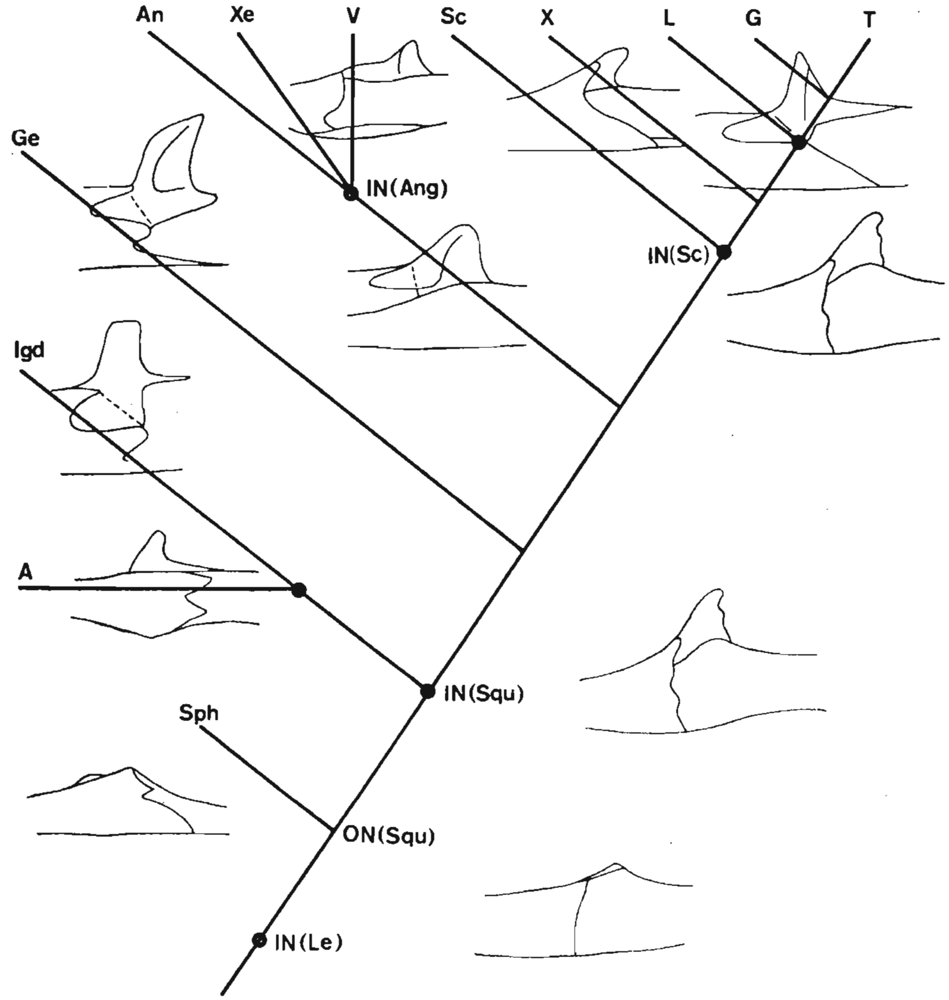


Fig. 5. One of the alternative hypotheses (p. 234) about sequence of states of dentary--coronoid contact in the phylogeny of Sauria. D/c state ancestral for the Scincomorpha. See also fig. 6. Cladogram from Estes *et al.* (1988).

position, see types E, E′ and F, fig. 3), still more randomly distributed, are considered convergences.

D/c versus C/d state synapomorphic for the Scincomorpha? — Figs 5 and 6 present two alternative hypotheses of state sequence of the coronoid-dentary contact, based on exactly the same nested-set of relationships, or cladogram (given by Estes *et al.* 1988). The outgroup analysis of the Lacertiformes (fig. 5), as well as stratigraphic premisses suggest that the dentary overlap on the coronoid (D/c) is most parsimonious state assessment for the IN of the Scincomorpha (fig. 5). The alternative hypothesis that the coronoid overlap on the dentary (C/d), characteristic of the

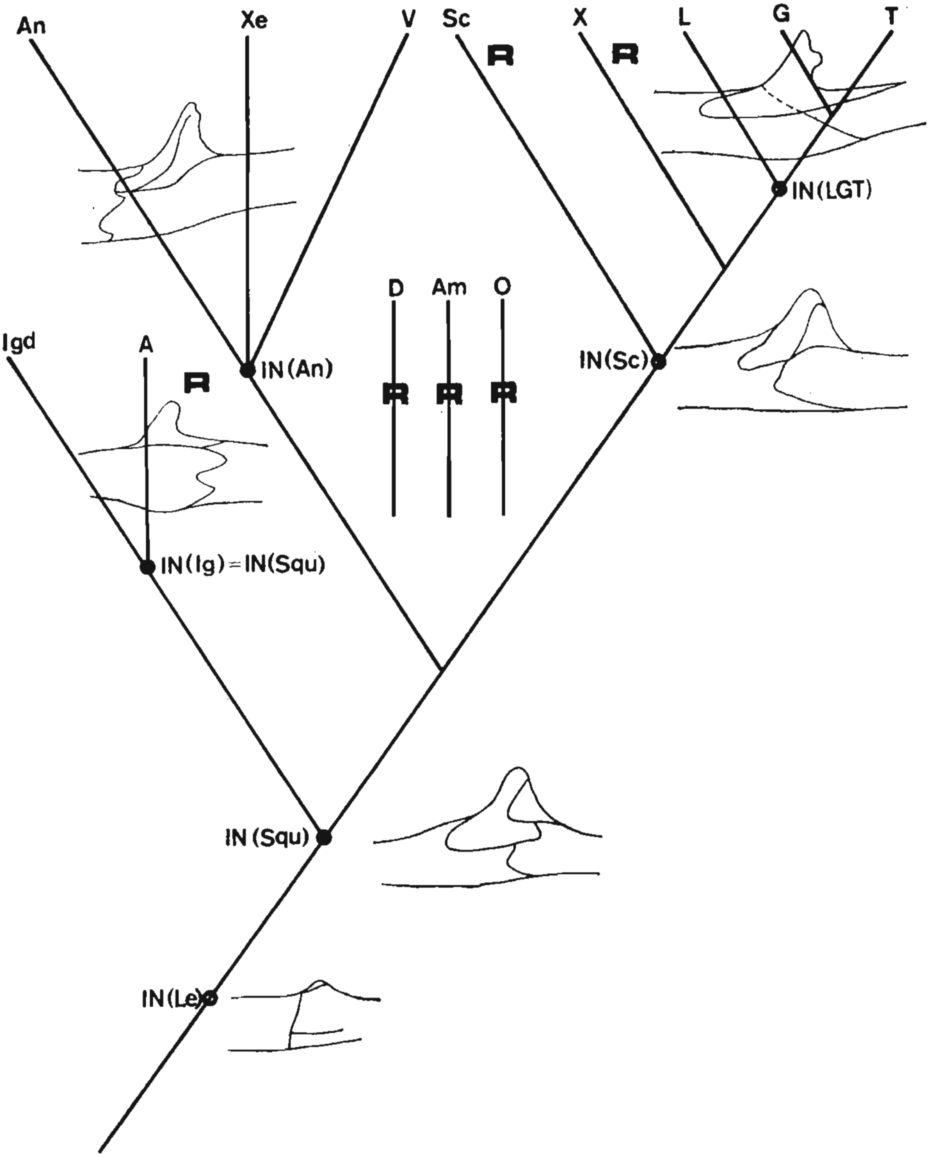


Fig. 6. One of the alternative hypotheses (p. 234) about sequence of states of dentary-coronoid contact in the phylogeny of Sauria. C/d state ancestral for the Scincomorpha. See also fig. 5. Cladogram from Estes *et al.* (1988).

gymnophthalmids, teiids and some lacertids, is an initial scincomorphan state (fig. 6) seems less probable at the first sight, but the in-group analysis of the Squamata makes it worth testing. This analysis reveals the commonality of the C/d states (though slightly different types) within the Squamata, which suggests that this type could have been original for the squamatan ancestor, then has been inherited by the scincomorphan ancestor and independently transformed into the D/c states in some scincomorphan groups and in the agamids. This is the hypothesis presented in fig. 6 alternative to the first one presented in the fig. 5.

Illustrated in fig. 7 a simple reasoning may be helpful in testing both of these hypotheses. It is equal to saying that the incipient D/c state (fig. 7B) present in all primitive scincomorphans (*Globaura* and *Eoxanta* included) is a type of coronoid-dentary contact most easily transformable into the different squamatan types and the one morphologically intermediate between them and the primitive lepidosaurian type (fig. 7A), given by the outgroup analysis of the *Squamata*. The transformation into the true C/d state requires still one link — the incipient C/d state of the anguid type (fig. 7F).

From the methodological point of view this reasoning is different from the basic cladistic analysis, because it is based on the size of morphological distances between different states rather than on the distributional data, and best corresponds to the morphocline concept of Maslin (1952), Schaeffer, Hecht and Eldredge (1972) (Eldredge and Cracraft 1980 define the morphocline as "the probable pathway, not direction, of change among character states"). No matter, that the polarity of the morphocline is based on the basic cladistic analysis, the morphocline itself is a kind of hypothesis different from the cladogram, which may be used for testing the latter.

Consistent with the hypothetic morphocline polarity the first hypothesis (fig. 5) is preferred here over the second one, that requires a significant number of reversals. The cladogram supported (fig. 5) implies a convergence or parallelism in the development of C/d states in the different squamatan lines (different iguanids, gekkotans and most of the representatives of the Lacertiformes). The probable selective agent behind this development is the advantage of an increased contact between the coronoid, to which the main muscle forces are imparted, and the dentary, which is the bone most loaded with food resistance. The same agent may be involved in the case of the D/c state of the agamids and sphenodontis (figs. 5A, Sph and 7E). We are, thus, dealing with two different solutions of the same mechanical problem.

The cladogram presented in fig. 5 also implies, that the incipient D/c state is the most probable scincomorphan IN assessment and the one probably plesiomorphic for the infraorder. From this state on, both types of the scincomorphan dentary-coronoid contact evolved, probably by several parallel lines.

The conclusion from this section is that neither C/d nor D/c state is synapomorphic for the Scincomorpha. Particular states of the character in question may be synapomorphic for some less inclusive groups.

Adm-V state synapomorphic for the Scincomorpha? — The in-group analysis of the Scincomorpha suggests that the ventral localization of the

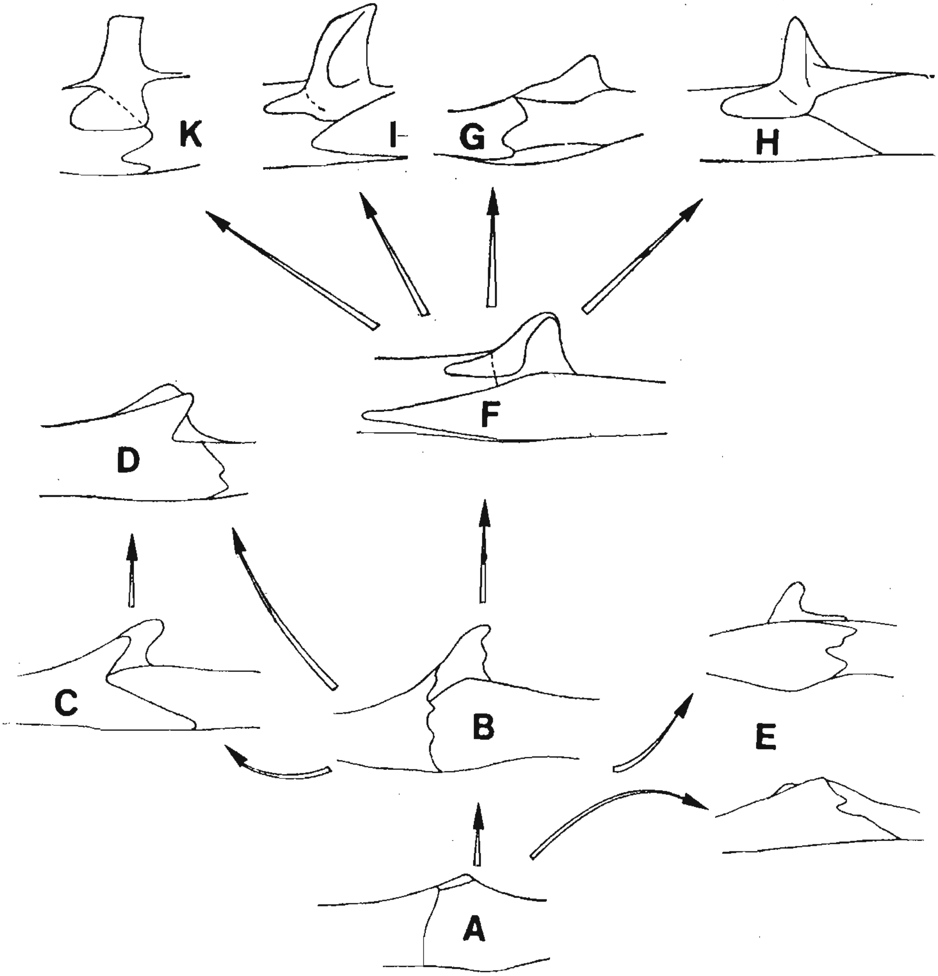


Fig. 7. Morphocline polarity of dentary-coronoid contact. *A*. State of lepidosaurian IN based on *Youngina* (from Evans 1980). Incipient D/c state characteristic of primitive scincomorphans. Differs from A only by size of coronoid. C and *D*. Two different D/c states readily derivable from *A* by invasion of dentary. Bottom figure based on *Gephyrosaurus* (from Evans 1980), top figure — agamid type based on *Physignathus*. *F*. Incipient C/d state readily derivable from *B*, based on *Anguis*. *G*. Varanoid type; no overlap because of posterior shortening of dentary. Based on *Heloderma*. *H*. C/d state based on *Echinosaura*. *I*. C/d state ?gekkonid type, based on *Gekko*. *K*. C/d state — iguanid type, based on *Ctenosaura*. All out of scale.

mandibular adductor was primitive for this group, i.e. characteristic of the scincomorphan IN. It is not excluded (although difficult to demonstrate, as the group is poorly resolved with respect to the anguimorphans) that it is synapomorhic for a more inclusive group: the Autarchoglossa, as Borsuk-Białynicka suggested in 1984, or even for the Scleroglossa, as suggested by Gauthier (1982) and Estes *et al.* (1988). Since the gekkotan affiliation of the genera is excluded, the safest conclusion from this character state is that we are dealing with the non-gekkotan scleroglossan and, thus, with the autarchoglossans.

SUBINFRAORDINAL AFFILIATION

Introductory remarks. — Two elements contribute to systematic assignment of *Globaura*: Considered synapomorphic for the Lacertiformes by Estes *et al.* (1988), the strong interdigitation of the frontoparietal suture between the parietal tabs, which points directly to the lacertiform kinship, and a set of characters alternative with those present in the latter taxon incongruent with this kinship, some of them probably plesiomorphic within the Scincomorpha. The same set of characters determines the systematic position of *Eoxanta* but the frontoparietal suture displays a less advanced state this time. Table 3 shows the distribution of character states relevant for the affiliation of *Globaura* and *Eoxanta* on the scincomorphan stem. They are discussed below.

Lacertiform features. — Best manifested in the Teiinae a tendency to snout narrowing (table 3: 1) is leading in the Lacertiformes. To put it another way, it consists in a lateral flattening of the snout which keeps the maxilla from extending onto the dorsal side of the snout, or diminishes its share in the dorsal wall, and produces a sharp bending between the lateral and dorsal sides. However, the degree of the lateral flattening was probably lower in the common ancestor of the three families than it is in the teiids and gymnophthalmids, as demonstrated by the intermediate state of the lacertid snout. Probably associated with the snout narrowing the medial apposition of the palatines and the pterygoids (table 3: 2, synapomorphy no 2 of Lacertiformes in Estes *et al.* 1988: 211) makes another teiioid character. This is, however, subject to a certain amount of variability (e.g. divergent pterygoids in *Teius*, MHU 379), which reduces its diagnostic value. I believe, there are some other character states associated with the snout narrowing and, probably subsequent to branching of this stem. Two of them, the narrowed and elongated vomers (table 3: 3) and the mandibular rami closely apposited to each other over much of the anterior length (table 3: 4; p. 7: 2) are shared by the teiids and the gymnophtalmids, and are probably synapomorphic to them. The vomers of this type are provided with long ventral crests continued onto palatines and closely apposited in the midline, in contrast to the vomers of *Globaura*, *Eoxanta* and *Slavoia*, some scincids (e.g. *Mabuya*) and some xantusiids (*Lepidophyma*, *Xantusia*) with the ventral crests bordering a central concavity.

The lacertids parallel the teiids and gymnophthalmids with respect to these character states, but they are less advanced, in fact intermediate, between them and the xantusiids, and display a certain amount of variability. *Globaura* and *Eoxanta* are shown (pp. 221, 226, table 3) not to share any of the teiid characters and not to be engaged into the lacertiform line of evolution. Still, the possibility of their direct lacertid affinity should be considered in detail, because of the outermost position of this family within the Lacertiformes. The only character state of the latter taxon absolutely consistent in the lacertids is the unpaired premaxilla. It is not shared by either *Globaura* or *Eoxanta*, which is a point critical for their affiliation outside the Lacertiformes rather than on the lacertid stem. This character is directly contradictory with the type of supratemporal roofing, which occurs by means of the postfrontal extension, according to a lacertid pattern, in *Globaura*, and mainly by this bone in *Eoxanta*. This situation requires discussion.

Paired versus fused premaxillae. — The polarity of the premaxilla states has been much discussed by Kluge (1967), Hecht (1976), Hecht and Edwards (1971), Moffat (1973) and Kluge (1988) but remains equivocal. According to Estes *et al.* (1988) the fusion has been synapomorphic for the Squamata and reversed in some scincids and some gekkotans. The mixed condition present within both these taxa indicates that homoplasy is involved. The paired states of *Globaura* and *Eoxanta* are provisionally considered reversals and homoplasy as well. However, the abundance of such reversals among the stratigraphically old scincomorphans (except for the Late Jurassic *Paramacellodus* Hoffstetter, 1967) needs some clarification in the future.

Supratemporal roofing. — The polarity of the type of supratemporal roof remains obscure as well. The distribution of states (predominance of prefrontal *versus* that of postorbital or both, table 3) runs absolutely across the best supported cladogram of this infraorder from Estes *et al.* (1988). This indicates that parallelism is involved. The closure of the supratemporal fenestra in all the scincomorphans but true teiids suggests it is primitive, probably synapomorphic, for this infraorder. I believe that the type of mandibular muscle attachment, for which the closure of the supratemporal fenestra is of some advantage, rather than the way in which the closure proceeds, is the true synapomorphy of the Scincomorpha. The facility of substitution of one bone by another to roof the supratemporal fenestra undermines the diagnostic value of these character states, to the extent that they cannot, alone, indicate the family affiliation.

Character complex of the early scincomorphan grade. — Alternative to the synapomorphic character states of the Lacertiformes, the presumedly plesiomorphic states (table 3): the snout rounded in transverse section (1), divergent pterygoids (3) and mandibular rami divergent with a short symphysis (5), vomers not elongated (sometimes ventrally concave) (6), are consistent in the Scincidae, Cordylidae, Xantusiidae,

Table 3

Distribution of character states among different scincomorphan taxa

	Taxa / Character states	Cordylidae	Scincidae	Xantusiidae	*Eoxanta*	*Globaura*	*Slavoia*	Lacertidae	Gymnophtalmidae	Teiidae	Specification of character states in cladistic terms	
											Infraordinal level (Sc)	Subinfraordinal level
1.	Anterior interpalatine contact	+ or –	+	+	+	+	+	+	+	+	+ synap.	
2.	Mx v. j state	j	mx	mx	mx	mx	mx	int.	mx	j	mx synap.	j? parallel within LGT
3.	D/c v. C/d state	D/c	D/c	D/c	D/c	inc D/c	D/c	usually C/d	C/d	usually C/d	inc. D/c synap.	C/d? parallel within LGT
4.	Snout narrow, angular (n) v. broad rounded (b)	b	b	b	b	b	b	int.	n	n	b IN state ples.	n synap. LGT
5.	Palatines and/or pterygoids divergent (d) v. apposed (app)	d	d	d	d	d	d	app	app	app	d IN state ples.	app synap. LGT
6.	Vomers long, crested (l) v. Short concave (sh)	int.	sh or int.	sh	sh	sh	sh	int.	l	l	sh IN state ples.	l synap. LGT
7.	Mandibular rami divergent (d) v. apposed (app)	d	d	d	d	d	d	int.	app	app	d IN state ples.	app? parallel within LGT
8.	Frontoparietal suture interdigitating or not	–	–	–	int	+	+	+	+	+ or –	– IN state ples.	+ synap. LGT or lacertoids

9.	Mandibular fossa inflated or not	–	–	?+	–	–	–	+	–	+	– IN state ples.	+ synap. lacertoids or LGT
10.	Premaxillae paired (p) v. fused (f)	f	p or f	f	p	p	p	f	f	f	f? IN state ples.	p? homopl. in some sincids, *Globaura*, *Eoxanta* and *Slavoia*
11.	Secondary palate membranaceous (m), bony (b), v. none	no	b	m	?m	no	?m	no	b	no	,,tendency" ? synap.	? parallel in scincids, xantusiids, gymnophtalmids, *Eoxanta* and *Slavoia*
12.	Supratemporal roofing by postfrontal (pf) v. postorbital (po) or postorbitofrontal (pof)	pof	pf or pof	po+ +pf	po+ +pf	pf	no	pf	po	no	,,tendency" ? synap.	not accomplished in teiids and *Slavoia*
13.	Posterior parietal extension	int.	–	+	–	–	–	+	–	–	– IN state ples.	+ homopl. in xantusiids and lacertids
14.	Splenial extending to symphysis (l) v. shortened (sh)	sh	sh	fused sh	sh	sh	sh	l	tiny	l	sh? IN state	l? homopl. in lacertids and teiids; reversal to presquamatan state

V versus; int. intermediate; inc. incipient; synap. synapomorphic; ples plesiomorphic; homopl. homoplastic; LGT Lacertiformes

Globaura, *Eoxanta* and *Slavoia*. Synapomorphic for the Scincomorpha (see p. 229) but plesiomorphic for the less inclusive groups, the maxillary bordering of the orbit (8) is almost consistent among these taxa. The transformation of the mx state into the j state, synapomorphic for the Lacertiformes or parallel in its different lines, occurs in the Cordylidae as well. It is homoplastic and probably size dependent. These five character states, along with some other that follow, define the early scincomorphan grade of evolution. They are: the lack of parietal extension to cover the brain case in dorsal view (14), alternative with the xantusiid and lacertid specializations; the interpalatine connection just posterior to the vomers (2), that is characteristic of the scincomorphan IN (on the in-group analysis), probably synapomorphic for the infraorder (on the comparison with the two immediate out-groups); the incipient D/c state of mandible (7), transformed into other states in all recent groups; unstable, very often paired, state of premaxilla (9); and no transverse inflation of mandibular fossa (11), alternative with a lacertiform (*sensu* Estes *et al.* 1988) condition, define the early scincomorphan grade of evolution.

This is a fairly stable complex of original scincomorphan character states (plesiomorphic or synapomorphic for the infraorder) that makes up the point of issue for the phylogenetic divergence including gradual closing of supratemporal fossa, gradual development of secondary palate, first in membranes, then in bone, various dermal skull covering and divergence in size. I believe that a tendency to close the supratemporal fossa and some inclination to the development of a secondary palate must have originally existed to result in a great amount of parallelism.

Among the Late Cretaceous Mongolian lizards, not only *Globaura* and *Eoxanta*, but also *Slavoia* (Sulimski 1984) represent this grade. The interdigitating frontoparietal suture of lacertiform type and the brain case structure different from the "xantusiid" type (see p. 221) along with the open supratemporal fossae, point to the teiid relationships, but the majority of the character states remain on the early scincomorphan level (table 3) suggesting a sister position with respect to the Lacertiformes. Which one of the two genera having this position, *Globaura* or *Slavoia*, is more closely related to this taxon may not be determined.

Suggested by the traces of the interdigitating frontoparietal suture, the relationships of *Eoxanta* with the Lacertiformes are much less obvious than those of *Globaura* and *Slavoia*. Neither its lacertoid nature is easy to demonstrate, except indirectly, by linking it with the Xantusiidae. The later relationship is suggested by the overall skull proportions, brain case and palate structure, but primitive character states of *Eoxanta* do not allow to include the genus into the family Xantusiidae, suggesting a sister relationship instead (see p. 226).

Conclusions. — The two new genera from the Late Cretaceous of Mongolia, *Globaura* and *Eoxanta*, described in the present paper, are assigned to the Lacertoidea (*sensu* Estes *et al.* 1988). *Globaura* is a sister genus of the Lacertiformes (*sensu* Estes *et al.* 1988) and *Eoxanta*, a sister genus of the Xantusiidae.

For the first time the existence of the lacertoids other than teiids, is demonstrated in the Late Cretaceous of Mongolia. *Eoxanta* is the oldest known representative of the xantusiid line *sensu lato*, which is suggestive of the Asiatic origin of this line, until new evidence comes.

The new genera, along with *Slavoia* Sulimski, 1984 and the extant families Scincidae and Xantusiidae, represent a uniform type of structure, which, nevertheless, gives no indications as to the interrelationships, but only determines the evolutionary grade — the early scincomorphan grade. The reason for that is, that the character states, which contribute to this type of structure are inherited from the common ancestor of the Scincomorpha. The complex of these characters, including both, plesiomorphies and novelties, is shown to have been very stable at the early stage of scincomorphan phylogeny. The Lacertiformes was the only line, which has been subject to more essential transformation of the ancestral morphotype. Apart from the latter line, the adaptive radiation included but various combinations and degree of development of parallel structures and size differentiation. The functional factors behind these events are not considered here.

Formation of the anteroventral bordering of the orbit by the maxilla is suggested to be synapomorphic for the Scincomorpha (for the opposite view see Estes *et al.* 1988).

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MAGDALENA BORSUK-BIAŁYNICKA

GLOBAURA VENUSTA GEN. ET SP. N. I *EOXANTA LACERTIFRONS* GEN. ET SP. N. — NIETEIIDOWE LACERTOIDY Z PÓŹNEJ KREDY MONGOLII

Streszczenie

Opracowany materiał pochodzi z kolekcji Polsko-Mongolskich Wypraw na Pustynię Gobi z lat 1963—1971. W pracy opisano dwa nowe rodzaje i gatunki jaszczurek: *Globaura venusta* gen. et sp. n. (pl. 1: 1; 2: 1; 3; 4; 6: 2; 7: 6, oraz tabele 1 i 2) z ?górnego santonu—?środkowego kampanu oraz *Eoxanta lacertifrons* gen. et sp. n. (pl. 1: 2; 2: 2; 5: 1—3; 6: 3, 4; 7: 4, 5; 8: 2 oraz tabele 1 i 2) ze ?środkowego kampanu i zaliczono je do Lacertoidea (*sensu* Estes i in. 1988). *Globaura* jest siostrzaną grupą taksonu obejmującego Lacertidae, Gymnophtalmidae i Teiidae, nazwanego Lacertiformes przez Estesa i in. (*l. c.*), *Eoxanta* siostrzaną grupą Xantusiidae.

Globaura i *Eoxanta* są to pierwsze nieteiidowe lacertoidy opisane z górnej kredy Mongolii, a *Eoxanta* jest najwcześniejszym przedstawicielem linii xantusiidowej jaszczurek i jedynym przedstawicielem tej linii znanym z Azji. *Globaura* dzieli z Lacertiformes swoisty szew czołowo-ciemieniowy lecz poza tym zachowuje cechy wspólnego przodka Scincomorpha, plezjomorficzne i synapomorficzne dla tego podrzędu, które ulegają unowocześnieniu u Lacertiformes. Są to cechy przedoczodołowej części czaszki i podniebienia. Cechy wspólnego przodka Scincomorpha zachowały się także u *Eoxanta* i *Slavoia* Sulimski, 1984, a także u rodzin Scincidae, Xantusiidae i Cordylidae żyjących i obecnie. Świadczą one o dużej stabilności morfotypu odziedziczonego po wspólnym przodku, który jedynie u Lacertiformes uległ zasadniczym zmianom (patrz tabela 3). Ten rys ewolucji Scincomorpha został podkreślony przez wprowadzenie nieformalnej jednostki — wczesnoscynkomorfowego gradu.

Pod względem metodologicznym praca opiera się na kladystyce (Henning 1966, Eldredge i Cracraft 1980). Dla uściślenia języka przyjęto terminologię i skróty za Maddisonem i in. (1984) rozróżniając wśród stanów wyjściowych (ancestralnych) danego taksonu stany jego wyłącznego przodka, odpowiadającego węzłowi grupy wewnętrznej (ingroup node IN) oraz stany przodka wspólnego z grupą zewnętrzną (outgroup node ON). Unika się w ten sposób dwuznaczności terminu ancestralny który obejmuje wszystkie stany wyjściowe, zarówno synapomorfie jak i plezjomorfie danego etapu filogenezy.

W pracy przedyskutowano rozmaite wersje sekwencji cech w filogenezie Squamata zawierające się w najbardziej aktualnym kladogramie tej grupy gadów zaczerpniętym z Estesa i in. (1988), posługując się zasadą globalnej oszczędności (Maddison'a i in. 1984) oraz prostymi hipotezami dotyczącymi sposobu transformacji cech. Te ostatnie hipotezy (patrz np. fig. 7), oparte na danych innych niż rozprzestrzenienie taksonomiczne i innych niż rozprzestrzenienie stratygraficzne, a głównie na bliskości morfologicznej stanów cech, odpowiadają najlepiej pierwotnej koncepcji morfokliny (Maslin 1952, Eldredge i Cracraft 1980: 54) jako sekwencje stanów cech nie osadzone w czasie geologicznym ani w filogenezie.

W wyniku przedyskutowania następujących cech: obrzeżenia oczodołu (fig. 2), kontaktów kości w części przedoczodołowej czaszki (fig. 3, 4), kontaktu kości żuchwy (fig. 5, 6, 7) oraz pewnych cech podniebienia (fig. 1), uznano szczękowe (zamiast jarzmowego) brzuszne obrzeżenie oczodołu za cechę synapomorficzną Scincomorpha. Wniosek ten nie jest zgodny z wnioskiem Estesa i in. (1988).

Praca została wykonana w ramach CPBP 04.03.

EXPLANATION OF PLATES 1—8

Plate 1

1. Reconstruction of skull of *Globaura venusta* gen. et sp. n.; *a* dorsal and *b* ventral views.
2. Reconstruction of skull of *Eoxanta lacertifrons* gen. et sp. n.; *a* dorsal and *b* ventral views.

Plate 2

1. Reconstruction of mandible of *Globaura venusta* gen. et sp. n.; *a* labial and *b* lingual views.
2. Reconstruction of mandible of *Eoxanta venusta* gen. et sp. n.; *a* labial and *b* lingual views.

Plate 3

Globaura venusta gen. et sp. n.

1. Skull with left mandible: ZPAL MgR-III/40, holotype, *a* ventral, *b* dorsal and *c* right side views, ×2.
2. Skull with mandibles: ZPAL MgR-I/45, dorsal view, ×2.
3. Right mandible: ZPAL MgR-III/43, labial view, ×2.

All stereophotographs

1 and 3: Khermeen Tsav, ?middle Campanian; 2: Khulsan, ?middle Campanian

Plate 4

Globaura venusta gen. et sp. n.

1. Skull with left mandible and fragmentary postcranial skeletons: ZPAL MgR-III/36, dorsal view, ×2.
2. Skull with both mandibles: ZPAL MgR-II/26, dorsal view, ×3.
3. Skull with right mandible: ZPAL MgR-I/118, dorsal view, ×2.
4. Right mandible: ZPAL MgR-III/43, *a* lingual and *b* occlusal views, ×2.

All stereophotographs

1 and 4: Khermeen Tsav, ?middle Campanian; 2: Bayn Dzak, ?upper Santonian and/or ?lower Campanian; 3: Khulsan, ?middle Campanian

Plate 5

Eoxanta lacertifrons gen. et sp. n.

1. Fragmentary skull with right mandible: ZPAL MgR-I/61, dorsal view, ×2.8.
2. Skull with right mandible: ZPAL MgR-III/38, dorsal view, ×2.5.
3. Skull with mandibles: ZPAL MgR-III/37, holotype, *a* dorsal view, ×2.5; *b* left side view, ×2.

Xantusia arisonae Klauber, 1931

4. Skull: MGZ 46156, *a* right side view, ×3.5; *b* dorsal view, ×4.

All stereophotographs

1: Khulsan, ?middle Campanian; 2 and 3: Khermeen Tsav, ?middle Campanian; 4: North America, Recent

Plate 6

1. Skull with mandibles of *Slavoia darevskii* Sulimski, 1984: ZPAL MgR-III/77, ventral view, ×2.5.
2. Fragmentary skull of *Globaura venusta* gen. et sp. n.: ZPAL MgR-I/51, ventral view, ×2.
3. Fragmentary skull of *Eoxanta lacertifrons* gen. et sp. n.: ZPAL MgR-I/61, ventral view, ×2.8.
4. Skull with right mandible of the same species: ZPAL MgR-III/38, ventral view, ×2.6.
5. Skull of *Xantusia arisonae* Klauber, 1931: MCZ 65156, ventral views, ×3.5.
6. Skull of *Lepidophyma? flavimaculatum* Duméril, 1851: MCZ 53800, ventral view, ×2.

All stereophotographs

1 and 4: Khermeen Tsav, ?middle Campanian; 2 and 3: Khulsan, ?middle Campanian; 5: North America, Recent; 6: South America, Recent

Plate 7

1. Mandible of *Lepidophyma? flavimaculatum* Duméril, 1851: MCZ 538 53800, occlusal view, stereophotographs, ×2.5.
2. Mandible of *Ameiva ameiva* (Linné, 1758): ZPAL R-I/10, ventral view, ×1.25.
3. Mandible of *Lacerta ocellata* Serres, 1822: HUB 27816, occlusal view, ×1.
4. Left mandible of *Eoxanta lacertifrons* gen. et sp. n.: ZPAL MgR-III/38, occlusal view, stereophotographs, ×3.
5. Skull with mandibles of the same species: ZPAL MgR-III/38, ventral view, stereophotographs, ×2.
6. Right mandible of *Globaura venusta* gen. et sp. n.: ZPAL MgR-I/51, *a* lingual and *b* labial views, stereophotographs, ×2.5.

1 and 2: South America, Recent; 3: provenience unknown, Recent; 4 and 5: Khermeen Tsav, ?middle Campanian; 6: Khulsan, ?middle Campanian

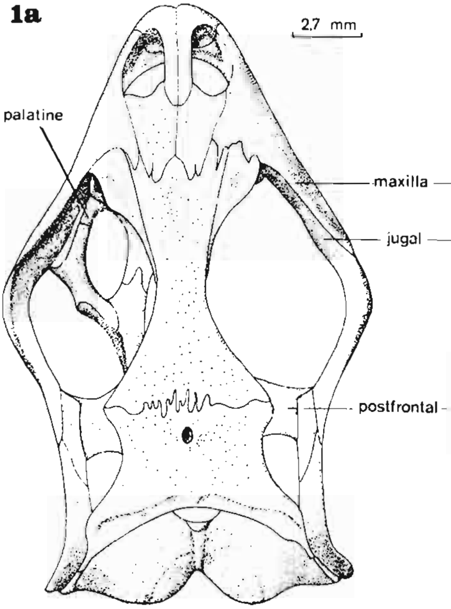
Plate 8

1. Left of mandible of *Xantusia arisonae* Klauber, 1931: MCZ 65156, *a* labial and *b* lingual views, ×3.
2. Left mandible of *Eoxanta lacertifrons* gen. et sp. n.: ZPAL MgR-III/38, *a* labial and *b* lingual views, ×3.
3. Right mandible of *Lepidophyma? flavimaculatum* Duméril, 1851: MCZ 53800, *a* lingual and *b* labial views, ×2.5.

All stereophotographs

1: North America, Recent; 2: Khermeen Tsav, ?middle Campanian; 3: South America, Recent

1a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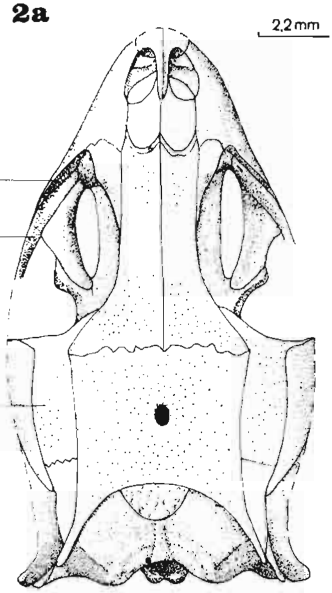
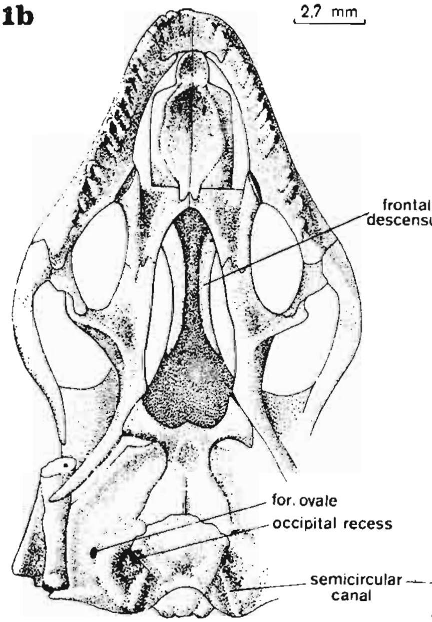
palatine
maxilla
jugal
postfrontal

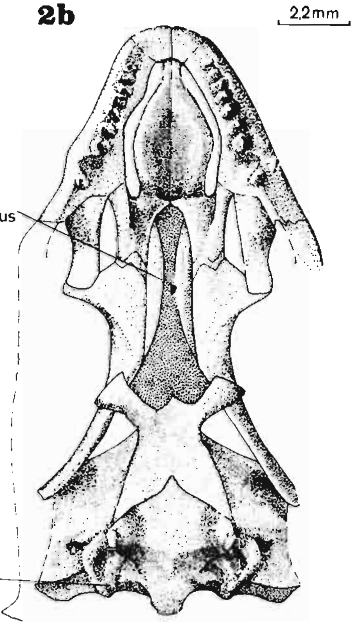
2a


2,2 mm

1b


2,7 mm
frontal descensus
for. ovale
occipital recess
semicircular canal

2b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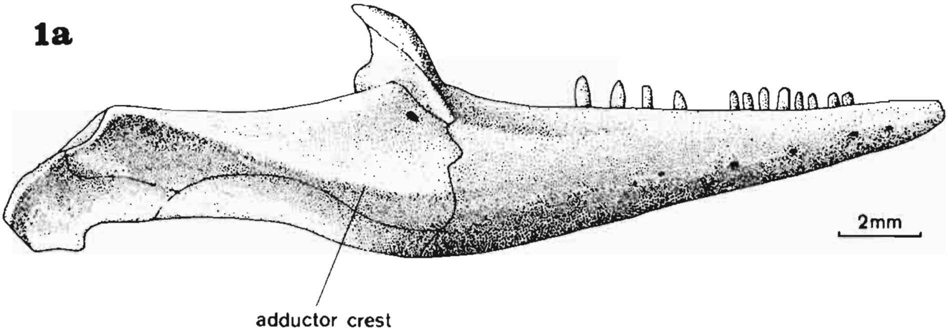
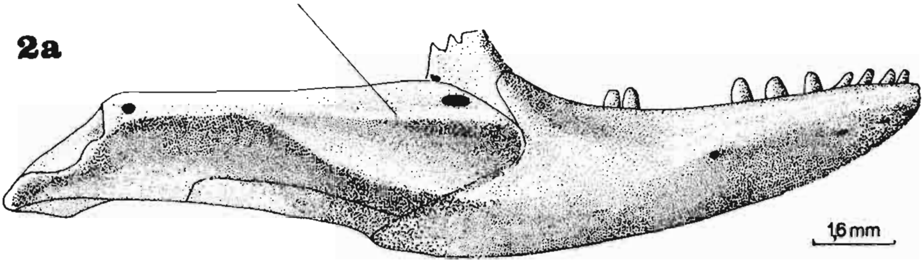
1a


2mm
adductor crest

2a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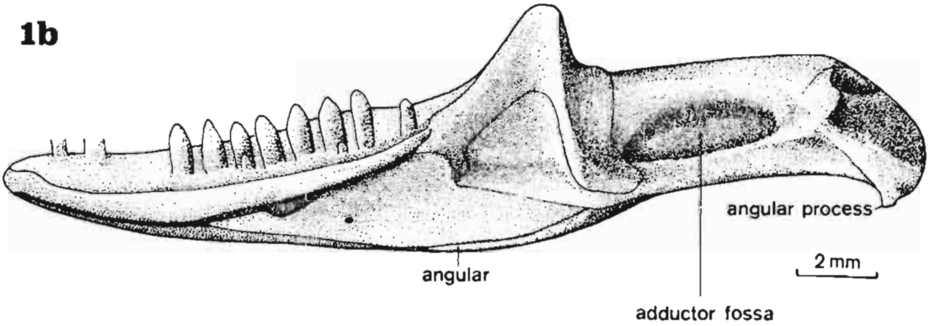
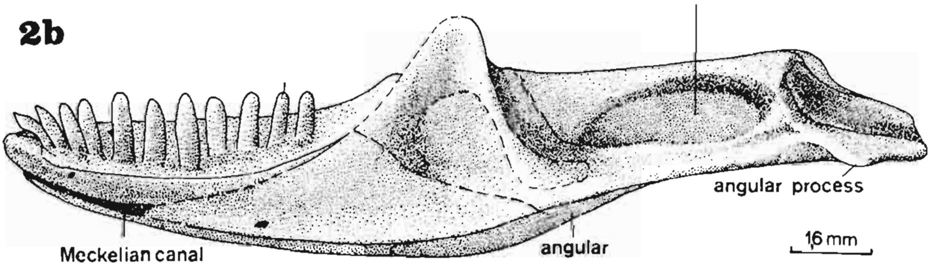
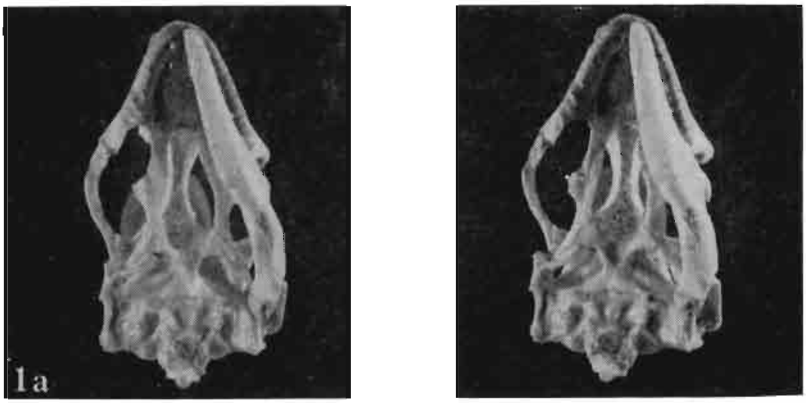
1b


angular process
2 mm
angular
adductor fossa

2b


angular process
Meckelian canal
angular
1,6 mm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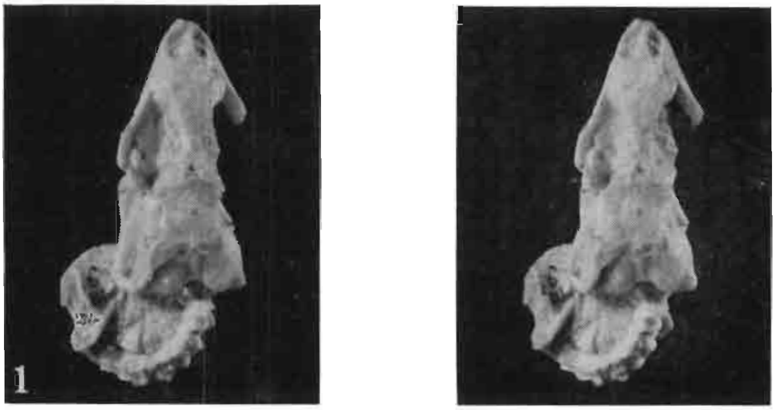
2


3


1b


1c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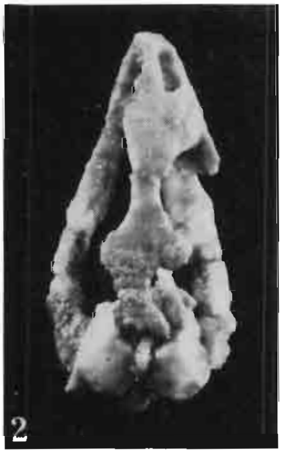
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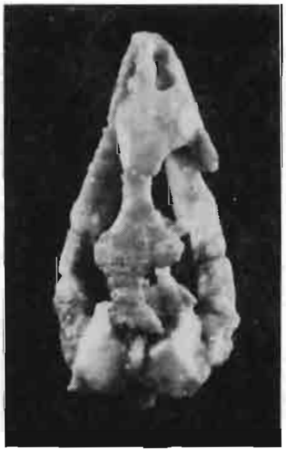
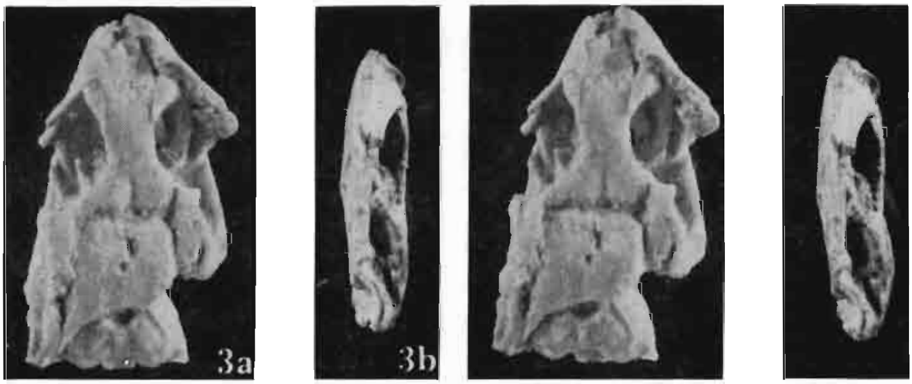



3


4b


1
2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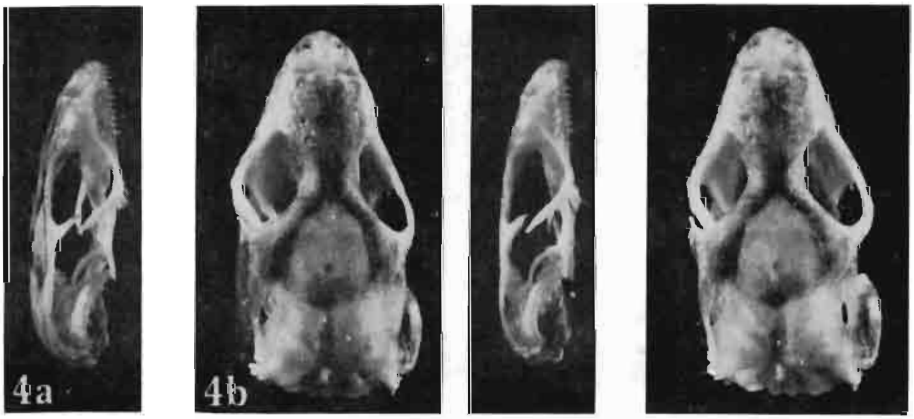
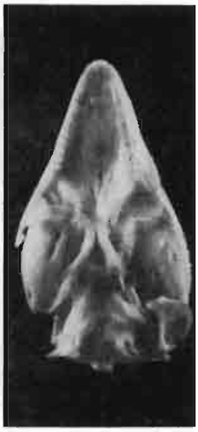
3b


4a
4b

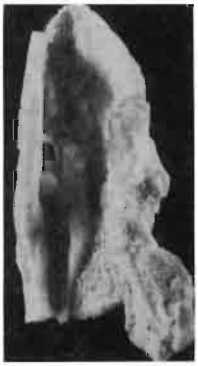

1


6




2


3




4


5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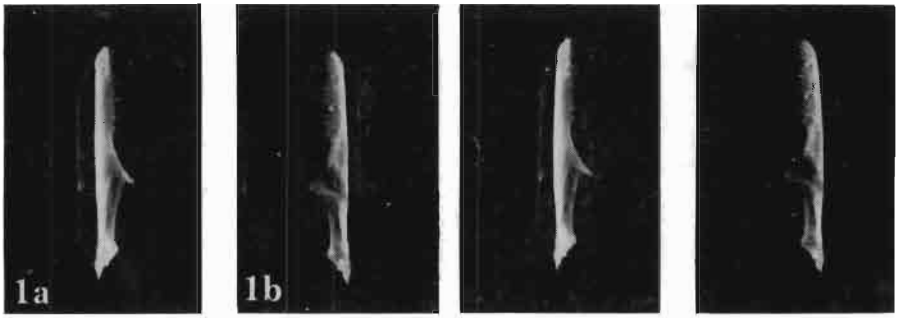
5


6a


6b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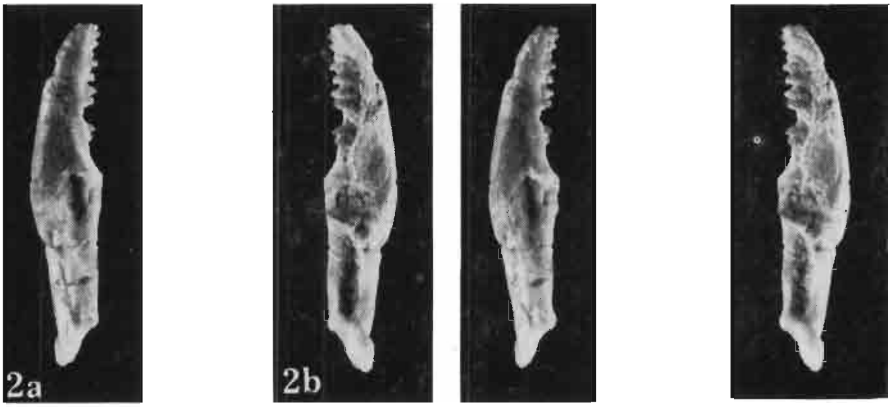
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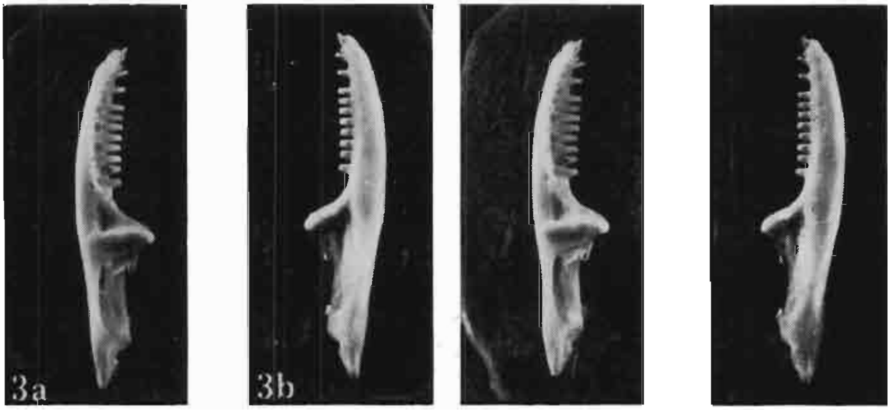
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